

Population growth and viability analyses of the clonal woodland herb, *Asarum canadense*

HANS DAMMAN* and MICHAEL L. CAIN†

*Department of Biology, Carleton University, Ottawa, Ontario K1S 5B6, Canada; and †Department of Biology, New Mexico State University, Las Cruces, NM 88003, USA

Summary

1 Long-term demographic field studies combined with simulation models that incorporated two types of stochasticity were used to investigate the relative impact of reproduction and survival on the persistence of populations of the North American woodland herb, *Asarum canadense*.

2 Field data were collected over 7 years in replicate plots located in early and late successional forest habitat. By following marked ramets from year to year it proved possible to investigate the demography both of ramets and of groups of genetically identical ramets (clones).

3 *A. canadense* exhibited considerable temporal and spatial variation in reproductive success, survivorship, and population growth rates. Populations of ramets and clones in late successional forest habitats held their own, while those in early successional forest habitats declined.

4 Sexual and clonal reproduction had less impact on population growth than did survival. Nonetheless, seedling recruitment was important, as indicated by the relatively high rates of genet turnover in *A. canadense* populations.

5 Results from simulations indicated that the vast majority of genets in both habitat types failed to reproduce. Over their lifetime, simulated genets produced a maximum of 44 and 77 seedlings in early and late successional forest habitat, respectively.

6 Although *A. canadense* genets are potentially immortal, the maximum life span for 2000 simulated genets was 104 years. Simulated genets lived a mean of 3.0 and 4.8 years in early and late successional forest habitat, respectively.

7 Simulated *A. canadense* populations only persisted in late successional forest habitat. Within simulated late successional forest populations, the number of ramets tended to decrease over time, while the number of genets tended to increase over time.

8 The minimum viable population size for *A. canadense* ramets in late successional forest was 25 individuals with environmental stochasticity only, and 1000 individuals with both environmental and demographic stochasticity; for genets in late successional forest, the corresponding numbers were 20 and 25, respectively.

9 Ramet and genet dynamics differed greatly in *A. canadense*, highlighting the importance of long-term demographic studies at each of these levels.

Keywords: clonal plants, demographic stochasticity, elasticity, environmental stochasticity, minimum viable population size, spatial and temporal variation, transition matrix

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Introduction

Understanding the selective pressures that shape plant life histories and developing effective approaches to the management of plant populations require a knowledge of the contribution of various components

of life history to population growth and persistence. These components can be difficult to estimate because survival, growth and reproduction in plants can vary significantly from site to site and year to year (Barkham 1980; Svensson & Callaghan 1988; Slade &

Hutchings 1989; Charron & Gagnon 1991; Menges 1991; Åberg 1992a,b; Nobel 1992; Piñero *et al.* 1994; Piñero *et al.* 1994; Oostermeijer *et al.* 1996). As a result, long-term studies may provide the only reliable way to uncover general patterns in plant demography and estimate long-term fates of plant populations.

Most demographic analyses depend on data from relatively few growing seasons or sites. For example, fewer than 25% of the 66 plant species surveyed by Silvertown *et al.* (1993) had data spanning more than one site or the necessary minimum of two growing seasons. Because of the great spatial and temporal variability in reproductive and survivorship values, however, data collected over many years or sites may prove essential in any effort to capture the general trends in the demography of plants (e.g. Menges 1991; Horvitz & Schemske 1995; Silvertown *et al.* 1996). In particular, when using demographic data to project future population growth, a failure to assess variation in reproductive and survivorship values forces acceptance of the implicit assumption that population parameters remain constant over time (Usher 1979). Population projections that assume deterministic growth may overestimate the rate of population growth relative to more realistic population models that allow for stochastic variation in population parameters, and this in turn may lead to inflated estimates of the chances that a population will persist (Boyce 1977; Tuljapurkar 1982; Menges 1992; Benton & Grant 1996).

Demographic studies on clonal plants can address the dynamics of ramets or genets, or both. Because of the difficulties involved in following the fates of genets, which often consist of many unconnected ramets, few studies have addressed genet demography (Hartnett & Bazzaz 1985; de Steven 1989; Falinska 1995). While ramet demography may provide an adequate perspective on the long-term persistence of a population, genet demography provides information essential for understanding the changes in the genetic structure of populations (Silander 1985). Eriksson (1993) suggests, moreover, that the dynamics of ramets and genets may differ dramatically within a given population.

This paper reports results from a 7-year-long study of the demography of wild ginger, *Asarum canadense* L., a common understorey herb in eastern North American forests. We first document fluctuations in the number of seedlings, ramets and clones over time. We then contrast the relative impact of survivorship, clonal growth, and seed-based reproduction on the population dynamics of *A. canadense*, taking into account both between-year and between-site variations. By keeping track of the often ephemeral connections between permanently marked ramets over a relatively long period of time, it became possible to develop and explore stochastic simulations of the long-term viability not only of ramet, but also of genet, populations.

Methods

SPECIES AND STUDY SITE

A. canadense grows in forest understories throughout north-eastern North America, from New Brunswick in the north-east to Missouri in the south-west. Figure 1 summarizes the life cycle of *A. canadense*. Seeds produced in June germinate the following summer. These seedlings typically bear only the two cotyledons, and produce their first true leaf as yearling plants in their second summer. During the first several years of their life, plants produce a single ramet bearing a single leaf. Typically, plants do not reproduce asexually by producing lateral shoots, or sexually by producing a flower until they have accumulated sufficient resources to produce two leaves. Only extremely rarely do ramets bear more than two leaves and never do they produce more than a single flower. The self-pollinated flowers (Peattie 1940; Wildman 1950) produce up to 31 seeds (Cain & Damman 1997), which show no dormancy and produce an epicotyl in the following spring (Baskin & Baskin 1996; Damman, personal observation). The rhizomatous connections between ramets rot after 1–10 years. Heithaus (1981), Baskin & Baskin (1996) and Cain & Damman (1997) provide more detailed accounts of the natural history of *A. canadense*.

We conducted our study at FrootLoops Farm, in the hamlet of Garretton, in eastern Ontario, Canada. This location included *A. canadense* growing in the understorey of a 3 ha forest of mature sugar maple (*Acer saccharum* Marsh.), as well as under an earlier successional trembling aspen (*Populus tremuloides* Michx.) canopy. The former areas were characterized by a relatively sparse understorey vegetation that received little insolation once the canopy closed. More light reached the understorey vegetation under the trembling aspen, but the density of competing understorey plants, particularly sensitive fern (*Onoclea sensibilis* L.), was much greater.

FIELD OBSERVATIONS

In the spring of 1989, we established four, permanent 2 × 3 m plots in sites harbouring relatively high densities of *A. canadense* (between 25 and 50 clones in each plot at the start of the study). Two of the four plots were situated under the mature sugar-maple canopy (called 'late successional forest' plots henceforth) and two were situated under the earlier successional trembling aspen canopy (called 'early successional forest' plots henceforth). The four plots were separated from one another by at least 20 m of *A. canadense*-poor habitat.

In our initial census in the spring of 1989 we recorded the position and status of all wild ginger ramets falling within each plot. Brushing away the loose litter layer allowed us to determine which ramets were

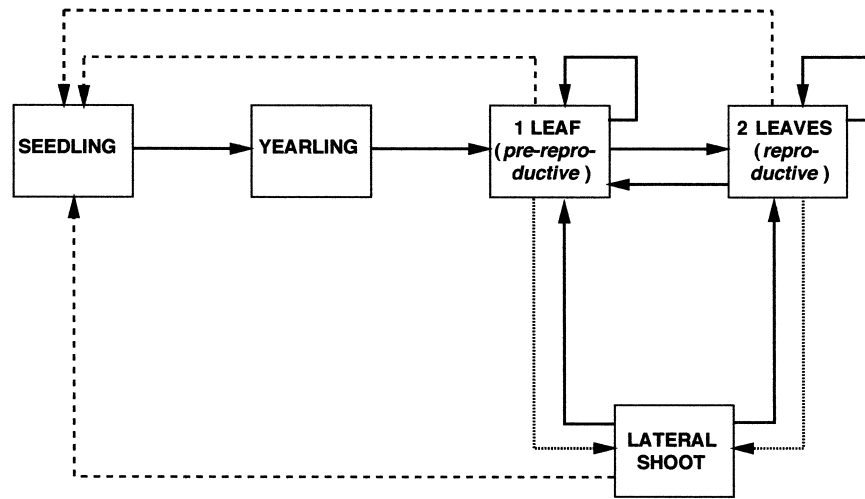


Fig. 1 The life cycle of *Asarum canadense* at the ramet level. The solid arrows indicate life-stage transitions involving survival and development of ramets, dashed arrows indicate transitions associated with sexual reproduction through seeds, and the stippled arrows indicate transitions associated with asexual production of potentially independent lateral branches.

attached to which other ramets, and thus formed a clonal fragment. If a clonal fragment included ramets lying outside the plot boundaries, we mapped these attached ramets as well. Each clonal fragment identified in 1989 was given a unique letter code, and each ramet within a clonal fragment was given a different number.

We conducted two censuses per year up to and including 1995. The spring census was done in May after the leaves had begun to expand and most of the flower buds had opened. At this time we recorded the position of each ramet, the presence of flowers, and whether the ramet had 1 or 2 leaves. Yearling plants were also identified at this time by their small, single leaf and by the presence of a twist in the stem just below the soil surface marking the position of the seed. Seedlings were only counted during the summer census of the last 2 years of the study. During the summer census, held in late July or August, we recorded the width of the widest leaf as an estimator of plant size (see Cain & Damman 1997) in all years except 1990, 1991 and, for late successional forest habitats, 1992.

Throughout the study we kept careful track of the connections between the ramets. Each spring, we distinguished between apical shoots arising from the apical bud of the previous year and lateral shoots arising from lateral buds of the previous year. We also determined if previously connected ramets retained their connections with other parts of the clonal fragment. Regardless of whether the connections between descendants of a clonal fragment persisted, however, they retained as part of their identifier the letter originally assigned to that clonal fragment. Yearling plants appearing in the plots were assigned letter combinations indicating a new genet. Groups of genetically identical ramets that descended either from a new seedling recruit or from one of the original clonal

fragments were denoted as members of the same 'clone.' The number of clones provided us with an upper bound on the number of genets within a plot; however, without additional genetical information, some of the original clonal fragments, and hence, some of the clones, almost certainly were members of the same genet.

TRANSITION MATRICES

The field data provided the raw material for constructing size-based transition matrices. These matrices are available on the *Journal of Ecology* archive on the World Wide Web. We used these matrices to describe the patterns of recruitment, growth, and death for the ramets and clones in each of the four plots. For the ramets we constructed two types of transition matrices: one based on developmental stage (seedling, yearling, lateral shoot, 1 and 2 leaves) and, where possible (1993→1994 and 1994→1995), another based on size as estimated by the width of the widest leaf (seedling, < 4 cm, 4–7 cm, 7–10 cm, > 10 cm). The choice of size classes based on leaf width reflected the most effective breakdown of size as determined by the technique described by Vandermeer (1978), modified to reflect reproductive size-thresholds. Later analyses indicated that both types of transition matrices gave essentially identical results; thus, we will limit our discussion to results obtained with the stage-classified matrices, which could be applied to all of the five year-to-year transitions for which we had sufficient data to construct such matrices.

We did not follow the fates of seeds in the field and thus had to arrive at the stage-specific fecundities (f_x) by a less direct route. The yearling plants that we recorded in the field censuses represented seeds that survived to the second growing season. To estimate

the number of seeds that germinated, the appropriate fecundity value in transition matrices (Caswell 1989), we used the following procedure. First, we had to back-calculate the number of seedlings from the observed number of yearlings; to do this, we assumed that half of all seedlings survived to the yearling stage ($p_{\text{seedling} \rightarrow \text{yearling}} = 0.5$). This value for the seedling to yearling survivorship lies within the range of values measured directly in 1994 and 1995; moreover, the choice of this value affects neither the finite rate of population growth nor the elasticities that we calculate from the data. Secondly, because *A. canadense* seeds lack seed dormancy, we estimated the reproductive contributions of the various size classes by dividing our estimate of the number of seedlings in a plot by the number of flowers produced in that plot during the previous year. We then weighted this value by the likelihood that an individual in a given stage produced its single flower in the previous year. This approach assumes that seeds produced by plants in different size classes were equally likely to produce yearling plants. In addition, because yearlings could have originated from seeds produced outside the plot, this approach assumes that the export of seeds out of a plot balances the import of seeds into the plot.

The matrices constructed for the clones were based on size as reflected by the number of active ramets known to be descended from an initially connected set of ramets. In transition matrices for the clones, growth, which meant an increase in the number of ramets from one year to the next, stemmed from clonal reproduction at the level of the ramet. Sexual reproduction was estimated as for the ramet-level matrices, taking into account that a clone could produce more than one flower in a given year.

Separate transition matrices were constructed for each of the four plots for each of the five possible transition intervals. Each matrix, \mathbf{A} , consisted of transition probabilities, a_{ij} , representing the number of individuals that an individual in class i at time t would contribute to class j at time $t + 1$. From these matrices we calculated the finite rate of population growth, λ (the dominant eigenvalue, where $\mathbf{A}_t \lambda = \mathbf{A}_{t+1}$), which estimates overall population performance. We also calculated the stable stage distribution, $\mathbf{w} = \{w_1, \dots, w_j\}$ (the right eigenvector), which describes the stage structure of the population, and the stage-specific reproductive values, $\mathbf{v} = \{v_1, \dots, v_j\}$ (the left eigenvector), which indicates the relative contribution of the different stages to future population growth. By standardizing the scalar product of the right and left eigenvectors to 1 it becomes possible to compare the elasticities, e_{ij} , of the different matrices (Caswell 1989). The elasticity reflects the relative contribution of each transition to λ , and thus provides an estimate of the impact of each transition on fitness (de Kroon *et al.* 1986; Caswell 1989; Silvertown *et al.* 1993). Because the e_{ij} values sum to 1, it is possible to add the e_{ij} for individual transitions that describe

similar processes (e.g. survival, sexual and asexual reproduction) to obtain an elasticity for that class of transition (Fig. 2; see also Silvertown *et al.* 1993).

LONG-TERM SIMULATIONS OF THE FATES OF GENETS AND POPULATIONS

We used the transition matrices developed from our field observations to incorporate environmental and demographic stochasticity into simulations of the long-term performance of *A. canadense* genets and populations. Environmental stochasticity involves chance variation in the environment caused by factors such as competition, herbivore loads, and the weather that directly affect the population-level probabilities of survivorship and reproduction (Shaffer 1981). Demographic stochasticity involves chance variation in survivorship and reproduction arising when the population-level probabilities of dying and flowering are translated into the death and flowering of individuals, both of which are all-or-nothing events (Shaffer 1981; Menges 1986).

Data from the four plots over five transition intervals generated 20 transition matrices, 10 from each of the early and late successional forest habitats. We used these matrices to provide snapshots of spatial and temporal variation in the performance of *A. canadense* under either the early or late successional canopy. Following the approach used by Bierzychudek (1982a), van Groenendael & Slim (1988), and Menges (1990), for each habitat type we simulated environmental stochasticity by randomly selecting a matrix from the pool of transition matrices observed in the field to provide the probabilities that ramets or clones would reproduce or survive from one year to the next. For the subsequent transition, a matrix would again be selected randomly from the pool of observed matrices. For some plot-transition combinations we could not determine $p_{i,j}$ because no individuals belonging to stage i were present at time t . To get around this problem, we substituted the $p_{i,j}$ calculated for the pooled observations for the two plots in that habitat (late or early successional forest) in that year. Estimates of the finite rate of population growth based on these modified matrices tended to be greater than those based on the original data.

We incorporated demographic stochasticity by using the randomly selected matrix as a guide to the probability that an individual of a given stage would reproduce or survive. For example, whether an individual alive at the start of a time interval flowered was determined by comparing a randomly selected number between 0 and 1 to the appropriate stage-specific probability of flowering. If the randomly chosen value fell at or below the measured probability, then the individual flowered. The production of a yearling plant required first flowering and seed production, and then survival of these seeds to germination. We randomized reproduction based on the

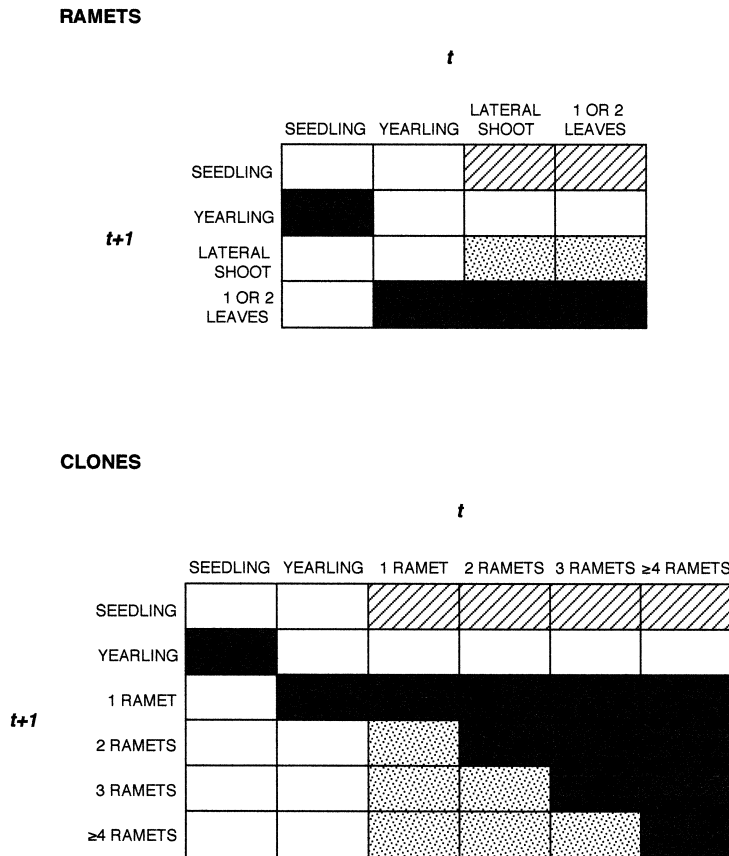


Fig. 2 Ramet- and clone-level transition matrices indicating the transitions (a_{ij}) associated with similar demographic events: survival (dark stippling), sexual reproduction (cross-hatching), and clonal reproduction by initiating lateral shoots (light stippling).

stage-specific flowering probability rather than the stage-specific reproductive rate because we could measure the former accurately while we could only estimate the latter. This approach also seemed to reflect most realistically the disproportionate contribution to reproduction of the relatively few individuals that flowered in any given year. The actual contribution of flowering individuals of a given stage to the yearling population at the start of the next time interval was estimated by multiplying the number of flowering individuals by the probability that a flowering individual would produce a yearling.

To simulate the long-term performance of individual genets, we first determined the probability that an individual would produce a seedling surviving to time $t + 1$, and then determined whether the genet itself would remain in its current size class, change in size, or die. These simulations used transition matrices based on data for clones. Genets entered the simulation as seedlings, and were followed until they died. We repeated the simulations for 1000 genets under both early and late successional forest conditions. We used the number of time intervals until the genet died and the lifetime production of seedlings as measures of genet performance.

We also used simulations to investigate the factors affecting the persistence of populations of *A. canadense*. In a first set of simulations investigating the influence of habitat and of environmental and demo-

graphic stochasticity on population performance, we followed the fate of a population of 100 ramets or genets equally distributed over the size classes. Simulation runs incorporated either environmental (plot-to-plot and time-to-time variability for early or late successional forest habitats) or environmental and demographic stochasticity as described above. The populations were allowed to grow for 100 time intervals, or 'years,' or until the populations went extinct. We replicated each simulation 1000 times, and used the proportion of runs resulting in extinction, the number of time intervals for which the population persisted, and the ratio of final to initial population size as indices of population viability. In a second set of simulations, we estimated the minimum population size required to establish viable populations of *A. canadense* ramets or genets under the late successional forest conditions that represent the core habitat of natural *A. canadense* populations. We varied initial population size from 5 to 1000 individuals, and measured performance as the proportion of populations that persisted for 100 time intervals.

DATA ANALYSIS

Data were analysed using parametric t -tests, analyses of variance (ANOVA), or linear regression; these data were checked for homogeneity of variances and independence of the mean and variance, but in no case

did we have to transform the data. To measure variability, we used coefficients of variation following the method of Sokal & Rohlf (1981), which incorporates a correction for small sample sizes. Simulation programs were written in the Pascal programming language.

Results

GENERAL PATTERNS IN THE DEMOGRAPHY OF *ASARUM CANADENSE*

Patterns of recruitment by seed and by clonal growth varied greatly from plot to plot and year to year. For example, the number of yearling plants, which represented both new ramets and new genets, that appeared in the four 6 m² plots was characterized by high coefficients of variation between plots and between years (Fig. 3a,b). There was no clear effect of either year or habitat on the density of yearling plants in the plots (Table 1). Recruitment of ramets by clonal growth also showed high coefficients of variation. Although habitat had no effect on lateral shoot production, year did produce a significant effect (Table 1).

Over the 7 years of the study the density of clones and of ramets tended to decline in the early successional forest plots, while remaining constant or increasing somewhat in the late successional forest plots. As proved true for yearling recruitment, habitat and year had no detectable effect on the total number of ramets and clones in the four plots. In contrast to the patterns for sexual and asexual recruitment, however, coefficients of variation for the number of ramets and clones were relatively low (Table 1, Fig. 3). Although the coefficients of variation for recruitment by seed and by clonal growth typically exceeded 80%, those for the total number of ramets and clones typically were below 50% and 40%, respectively. Also striking was the much lower between-year variation in the total number of ramets in the late successional forest as compared to the early successional forest plots.

The production of flowers by *A. canadense* correlated positively with clonal reproduction. Year-plot combinations in which a high proportion of ramets flowered were more likely to contain a high proportion of ramets that produced lateral shoots (linear regression: $F_{1,22} = 18.5$, $P = 0.003$, $R^2 = 0.46$). Thus,

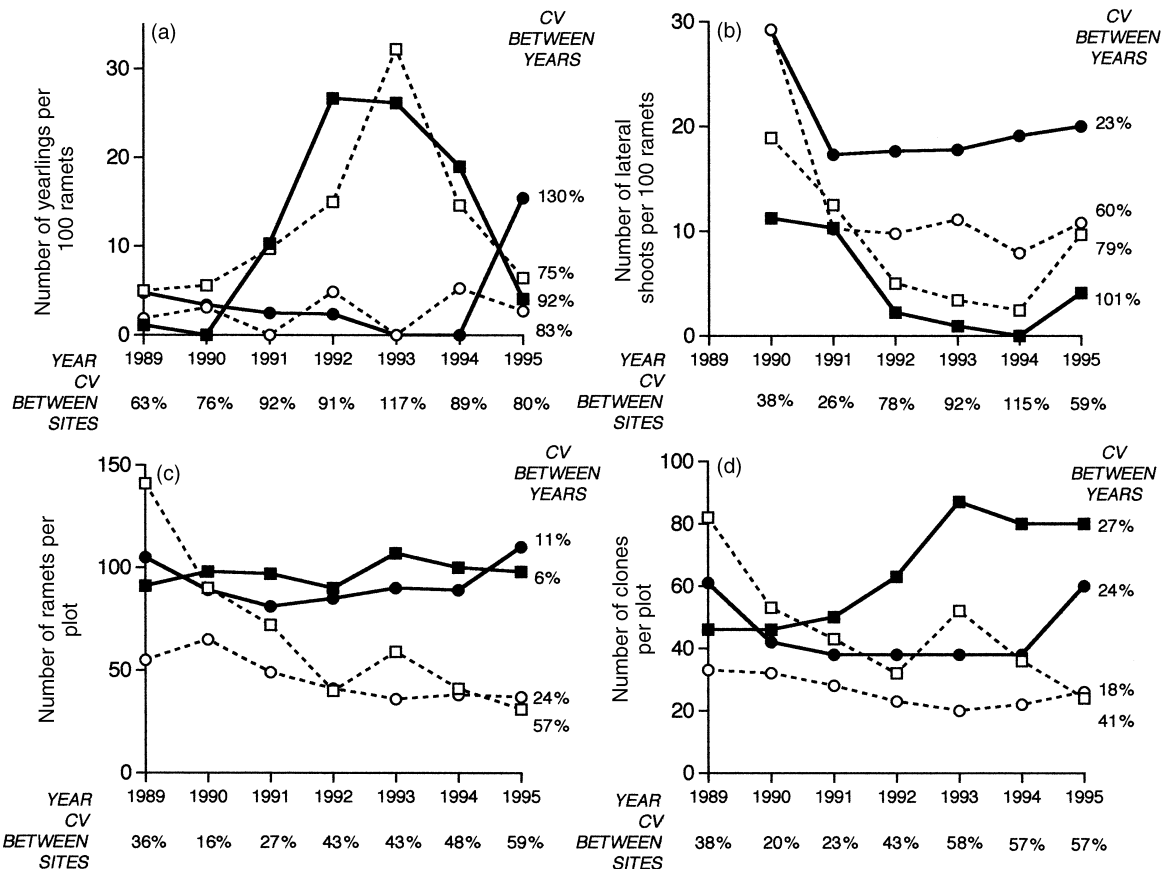


Fig. 3 Patterns in recruitment of *Asarum canadense* (a) from seeds and (b) from clonal growth, and in the overall abundance of (c) clones and (d) ramets over a seven-year-long period at four plots (late successional forest: filled symbols, solid line; early successional forest: open symbols, dashed lined; plot A: circle; plot B: square). Coefficients of variation for each plot over the seven years of the study are listed down the right-hand side of each panel, while the coefficients of variation for each year over the four plots are listed beneath each panel.

Table 1 Effect of habitat and year on the recruitment and population density of *Asarum canadense* in a repeated measures analysis of variance

Dependent variable	Independent variable*					
	Habitat			Year		
	d.f.†	<i>F</i>	<i>P</i>	d.f.†	<i>F</i>	<i>P</i> ‡
Yearlings per 100 ramets	1,2	0.011	0.93	6,12	0.955	0.35
Lateral shoots per 100 ramets	1,2	0.030	0.88	5,10	14.9	0.002
Clones per plot	1,2	1.81	0.31	6,12	0.706	0.65
Ramets per plot	1,2	11.7	0.07	6,12	2.04	0.14

*None of the interaction effects proved significant, $P > 0.15$.

†Degrees of freedom are listed as effect d.f., error d.f.

‡Corrected for non-independence of values from successive years using Huynh & Feldt's ϵ .

factors that affected sexual reproduction also seemed to affect asexual reproduction.

TRANSITION-MATRIX ANALYSES

Ramets

In most years, the finite rate of population increase (λ) for ramets fell below 1 in most of the plots, indicating that over the long run we should expect the number of ramets in the four plots to decrease (Table 2). Finite population-growth rates of ramets in the late successional forest were generally higher than those in the early successional forest habitats after removing the effect of temporal variation (overall two-way ANOVA with transition as a blocking factor: $F_{3,12} = 3.44$, $P = 0.051$; linear contrast of early vs. late successional forest plots: $F_{1,12} = 7.86$, $P = 0.016$). The early successional forest plots showed no evidence of having larger coefficients of variation for λ than the late successional forest plots (Table 2, $t = 0.926$, d.f. = 2, $P = 0.45$).

A comparison of the summed elasticity values for ramet transitions indicated that the stage-specific survivorship of established plants most strongly affected the finite rate of population growth in both early and

late successional forest habitats (Table 3; plot effect in an overall three-way ANOVA of plot \times transition type with year of transition as a blocking factor: $F_{3,44} < 0.0001$, $P \approx 1$; transition type effect in an overall three-way ANOVA of plot \times transition type with year of transition as a blocking factor: $F_{2,44} = 1468$, $P < 0.0001$; linear contrast of survival transition vs. sexual and clonal reproduction transitions: $F_{1,44} = 2931$, $P < 0.0001$). Both sexual and clonal reproduction contributed relatively little to the finite rate of growth of the ramet population, though clonal reproduction tended to have higher elasticities than sexual reproduction (linear contrast of sexual vs. clonal reproduction transitions: $F_{1,44} = 4.62$, $P < 0.037$). Compared to the elasticities for age-specific survivorship, however, the elasticities of both sexual and clonal reproduction varied greatly over time (Table 3). Thus, even though reproduction usually had only a small effect on the finite rate of population growth, the elasticity of both sexual and clonal reproduction reached values as high as 0.15. The patterns in elasticity proved similar for *A. canadense* growing in early and late successional forest plots.

Clones

The number of clones generally seemed to hold its own. For all four plots, the 95% confidence interval about the mean λ included 1 over all five transitions. Eight of the 20 calculated finite rates of population growth for the clone populations lay at or above 1 (Table 4). A comparison of the finite rates of clone population-growth among the four plots revealed no significant differences after removing the effects of temporal variation (two-way ANOVA with transition as a blocking factor: $F_{3,12} = 0.744$, $P = 0.55$). The coefficients of variation for the finite rates of growth of the clone populations were generally low, indicating little year-to-year variation, and did not differ consistently between early and late successional forest habitats (Table 4, $t = 1.51$, d. f. = 2, $P = 0.27$).

Although number of clones changed relatively little

Table 2 The finite rate of growth for the populations of *Asarum canadense* ramets in the early and late successional forest sites

Transition	λ			
	Late		Early	
	Plot A	Plot B	Plot A	Plot B
1990 \rightarrow 1991	0.882	0.886	0.841	0.797
1991 \rightarrow 1992	0.974	0.972	0.757	0.774
1992 \rightarrow 1993	1.108	1.013	0.879	0.823
1993 \rightarrow 1994	0.841	0.915	0.776	1.015
1994 \rightarrow 1995	0.875	1.014	0.662	0.963
CV	11.6%	6.04%	10.7%	12.3%

Table 3 Summed elasticities for sexual and clonal reproduction, and survival of *Asarum canadense* ramets in early and late successional forest sites

Site	Reproduction		
	Sexual	Clonal	Survival
Late successional A			
$\bar{x}_{\text{elasticity}} \pm \text{SE}$	0.074 ± 0.030	0.020 ± 0.015	0.91 ± 0.025
between-year CV	89.0%	170%	6.19%
Late successional B			
$\bar{x}_{\text{elasticity}} \pm \text{SE}$	0.00 ± 0.00	0.080 ± 0.021	0.92 ± 0.021
between-year CV	–	57.5%	4.99%
Early successional A			
$\bar{x}_{\text{elasticity}} \pm \text{SE}$	0.0051 ± 0.0051	0.15 ± 0.0070	0.85 ± 0.0056
between-year CV	224%	10.5%	1.48%
Early successional B			
$\bar{x}_{\text{elasticity}} \pm \text{SE}$	0.070 ± 0.043	0.053 ± 0.020	0.88 ± 0.044
between-year CV	138%	83.3%	11.3%

Table 4 The finite rate of growth for the populations of *Asarum canadense* clones in the early and late successional forest sites

Transition	λ			
	Late		Early	
	Plot A	Plot B	Plot A	Plot B
1990 → 1991	0.912	1.011	0.942	0.936
1991 → 1992	1.123	0.993	0.694	1.000
1992 → 1993	0.938	0.888	1.000	0.994
1993 → 1994	0.917	0.899	0.755	1.000
1994 → 1995	1.002	1.000	1.000	0.786
CV	9.05%	6.22%	16.4%	9.77%

from year to year, turnover proved substantial. Of the 222 clones identified in all plots in 1989, only 78 (35%) remained 6 years later, and these survivors made up a minority (46%) of the clones recorded in 1995. The percentage of clones recorded in 1995 that were also present in 1989 ranged from a low of 37% for late successional forest plot A to a high of 67% for early successional forest plot B, with no obvious early vs. late successional forest differences.

As we observed for the ramet-level matrix analyses, survivorship had the greatest impact on the finite rate of growth of clone populations (Table 5; transition-type effect in an overall three-way ANOVA of plot × transition type with year of transition as a blocking factor: $F_{2,38} = 238$, $P < 0.0001$; linear contrast of survival transition vs. sexual reproduction and clonal growth transitions: $F_{1,38} = 586$, $P < 0.0001$). Growth of the clones, which was equivalent to the production of lateral shoots at the ramet level, consistently had similar elasticity values, as did sexual reproduction

(linear contrast of sexual reproduction vs. clonal growth transitions: $F_{1,38} = 1.51$, $P = 0.23$). Elasticities for the growth of clones were more variable from one transition to the next than were elasticities for survival (Table 5); values of elasticity for sexual reproduction and clonal growth attained maxima of 0.098 and 0.12, respectively. Plants growing in the early and late successional forest habitats showed virtually identical patterns in the elasticities for sexual reproduction, clonal growth and survival (Table 5; plot effect in an overall three-way ANOVA of plot × transition type with year of transition as a blocking factor: $F_{3,38} < 0.0001$, $P \approx 1$).

SIMULATIONS

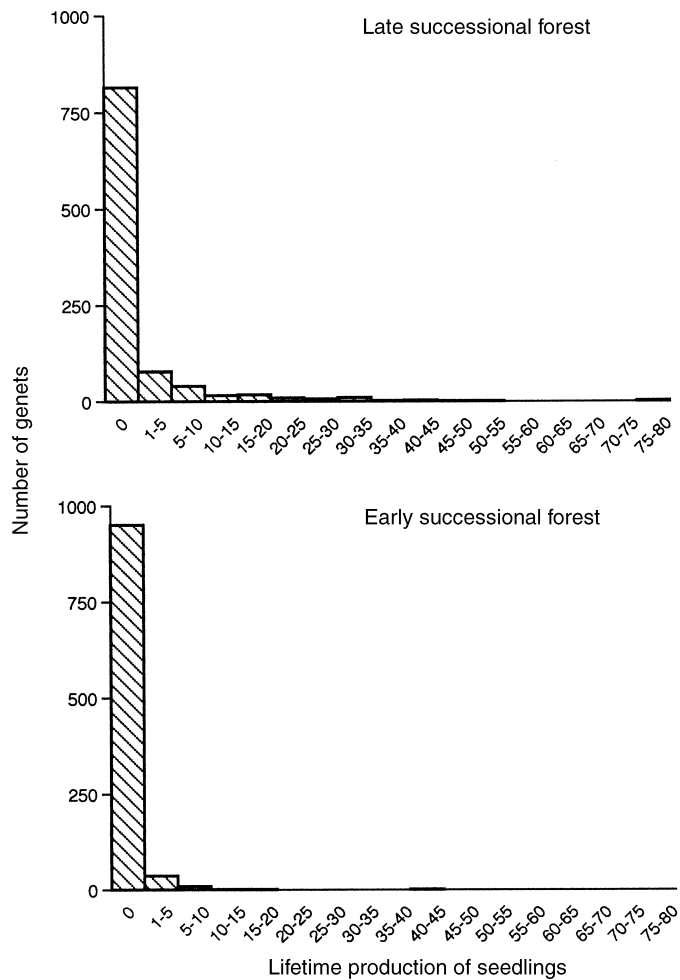
Genets

Using data gathered on clones to simulate the fates of genets suggested that the mean life spans of *A. canadense* genets should prove relatively brief and that a few individuals should produce the vast majority of offspring. Simulated genets in early and late successional forest habitats lived a mean of only 4.77 and 3.02 years, respectively. The highly skewed age distribution included relatively few long-lived individuals. Perhaps most surprisingly, even the longest-lived of the 2000 simulated genets lived only 104 years even though, in theory, the genets are immortal. The relatively short life span predicted by the simulation agrees well with the rapid turnover reported above for field populations (Transition matrix analyses: clones).

Lifetime reproductive output of genets, as estimated by the number of seedlings produced, suggested that few individuals would contribute to future generations (Fig. 4). In simulations based on data for late successional forest habitats, genets produced up

Table 5 Summed elasticities for sexual reproduction, growth and survival of *Asarum canadense* clones in early and late successional forest sites

Site	Reproduction		
	Sexual	Growth	Survival
Late successional A			
$\bar{x}_{\text{elasticity}} \pm \text{SE}$	0.098 \pm 0.044	0.11 \pm 0.081	0.79 \pm 0.072
between-year CV	99.9%	166%	20.4%
Late successional B			
$\bar{x}_{\text{elasticity}} \pm \text{SE}$	0.00 \pm 0.00	0.12 \pm 0.060	0.88 \pm 0.060
between-year CV	–	108%	15.2%
Early successional A			
$\bar{x}_{\text{elasticity}} \pm \text{SE}$	0.042 \pm 0.026	0.67 \pm 0.028	0.89 \pm 0.046
between-year CV	138%	93.4%	11.6%
Early successional B			
$\bar{x}_{\text{elasticity}} \pm \text{SE}$	0.00 \pm 0.00	0.033 \pm 0.033	0.97 \pm 0.033
between-year CV	–	173%	5.91%

**Fig. 4** Highly skewed frequency distributions of the lifetime reproductive output of individual genets simulated using early and late successional forest transition-matrices.

to 77 seedlings, while in those based on data for early successional forest habitats, the most productive individual produced 44 seedlings. The vast majority of genets in both habitats failed to reproduce sexually at all. As suggested by the consistently high elasticity

values for genet survivorship and growth presented above (Transition matrix analyses: clones), life span correlated strongly with lifetime reproductive output (linear regression for late successional forest simulations: $F_{1, 998} = 2486$, $P < 0.0001$, $R^2 = 0.71$; for

early successional forest conditions: $F_{1, 998} = 374$, $P < 0.0001$, $R^2 = 0.27$).

Populations

Two major predictions emerged from the projections of *A. canadense* population growth based on the ramet- and clone-level transition matrices: (i) only the late successional forest patches contained populations likely to persist indefinitely; and (ii) while the number of ramets in the late successional forest plots should decrease slowly over time, the number of genets should increase over time.

For early successional forest conditions, projections incorporating environmental and demographic stochasticity and environmental stochasticity agreed with the deterministic projections in predicting extinction of all replicate populations of 100 ramets and genets within 100 years (Table 6). The mean projected time to extinction for ramets (18–22 years) was less than that for genets (31–38 years, Table 6; effect of ramet vs. genet in a 2×2 ANOVA: $F_{1, 3996} = 2504$, $P < 0.0001$), and differed from that predicted by the deterministic model. Adding demographic stochasticity to environmental stochasticity increased the rate at which the populations went extinct (effect of stochasticity type in an individual type \times stochasticity type ANOVA: $F_{1, 3996} = 287$, $P < 0.0001$), but did not qualitatively affect the ability of the simulated populations to persist.

Under late successional forest conditions the projections incorporating stochasticity also agreed qualitatively with the deterministic projections in suggesting that both ramets and genets usually persisted

for the full 100 years. In fact, the only projections in which many populations went extinct were those for ramets subject to both environmental and demographic stochasticity (Table 6), in which case only 68.5% of the 1000 populations survived for 100 years. The simulations predicted very different patterns of persistence for ramets and genets: ramet populations tended to decline slowly over time ($N_{final}/N_0 < 1$ in Table 6), whereas genet populations increased over time. As was true of the simulations based on early successional forest data, adding demographic to environmental stochasticity reduced the time for which populations persisted (effect of stochasticity type in an individual type \times stochasticity type ANOVA: $F_{1, 3996} = 318$, $P < 0.0001$) and decreased the rate at which populations grew (effect of stochasticity type in an individual type \times stochasticity type ANOVA: $F_{1, 3678} = 6.84$, $P < 0.009$), but did not affect trends qualitatively. The change in size of populations in simulations incorporating stochasticity proved much greater than that in the deterministic model for the growing genet populations, but not for the declining ramet populations (Table 6).

By systematically varying the initial population size, it also proved possible to gain some insight into what represented a minimum population size needed to give *A. canadense* populations a reasonable chance of persisting. Using data from the late successional forest plots and a criterion of 95% survival of populations over 100 years for population viability, led to the conclusion that the minimum viable population size for *A. canadense* ramets was 25 individuals with environmental stochasticity only and 400 with demographic stochasticity added as well (Fig. 5). Using the

Table 6 Performance of simulated populations of 100 *Asarum canadense* ramets and genets based on demographic data collected in early and late successional forest sites. The 1000 simulations incorporated either environmental stochasticity alone or in combination with demographic stochasticity, and are compared to the outcomes of deterministic projections

Data source	Type of stochasticity	Performance measure		
		% surviving for 100 time intervals	Number of years persisted ($\bar{x} \pm SE$)	N_{final}/N_0^*
Early successional				
Ramet	None	0	26	–
	Environmental	0	21.8 ± 0.15	–
	Environmental + demographic	0	18.6 ± 0.18	–
Genet	None	0	70	–
	Environmental	0	37.3 ± 0.36	–
	Environmental + demographic	0	31.1 ± 0.35	–
Late successional				
Ramet	None	100	100	0.094
	Environmental	99.7	100.0 ± 0.01	0.380 ± 0.0087
	Environmental + demographic	68.5	90.6 ± 0.53	0.290 ± 0.0131
Genet	None	100	100	2.009
	Environmental	100	100 ± 0.01	37.3 ± 1.24
	Environmental + demographic	100	100 ± 0.01	32.0 ± 1.25

*Calculated based on only those simulations in which at least some individuals survived the full 100 time intervals.

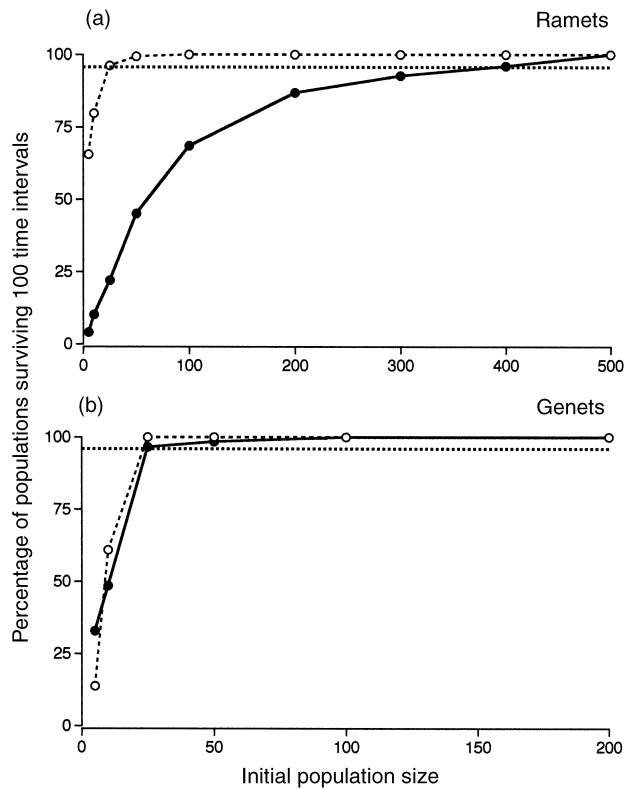


Fig. 5 The effect of initial population size on the proportion of *A. canadense* ramet and genet populations persisting for 100 years in population projections based on field data for late successional forest plots and incorporating either environmental stochasticity alone (open circles, dashed lines) or along with demographic stochasticity (closed circles, solid lines). The stippled, horizontal line represents persistence of 95% of the populations for 100 years.

same criteria, a minimum of 25 genets both with and without demographic stochasticity were needed to maintain late successional forest *A. canadense* populations for 100-time periods (Fig. 5). Even with environmental stochasticity only and initial population sizes as large as 30 000 ramets, no simulated populations under early successional forest conditions persisted for 100 years (mean time to extinction was 51 years).

Discussion

Relatively few demographic studies of clonal plants consider sufficiently long time spans and information from enough sites to provide an estimate of temporal and spatial variation (exceptions include Barkham 1980; De Steven 1989; Charron & Gagnon 1991; Nobel 1992; Falinska 1995). Even fewer studies of clonal plants use true genetical individuals as the basis of their demographic analyses (e.g. De Steven 1989; Eriksson & Bremer 1993). As a result, most studies must assume that demographic patterns vary relatively little from site to site or year to year and that the demography of genets may be inferred from that of ramets (Silvertown *et al.* 1993).

The data for *Asarum canadense* indicated that the performance of the sampled plants varied between plots and between years. The extensive spatial and temporal variation in demographic parameters shown by *A. canadense* matches that found in virtually every other study on the long-term demography of clonal

plants (e.g. Tamm 1956; Barkham 1980; De Steven 1989; Charron & Gagnon 1991; Nobel 1992; Falinska 1995). Collectively, these papers warn against the use of spatially or temporally limited studies as a path to understanding the demography of long-lived plants.

While the number of yearling plants and newly produced lateral shoots changed dramatically, the total number of ramets and clones changed relatively little over time or through space. Although relatively constant population sizes in the face of variable reproduction could be caused by density-dependent processes, our other work suggests that this is not the case: our observations provide little evidence for density dependence between *A. canadense* ramets, or between *A. canadense* and other plant species (Damman *et al.*, unpublished data).

Numbers of ramets and clones, and production of yearlings and ramets showed no consistent habitat effects, and only lateral shoot production showed a significant year effect. In a study that provided a greater focus on the performance of *A. canadense* ramets, Cain & Damman (1997) found that ramets in late successional forest habitat often survived better and flowered more often than ramets in early successional forest habitat. Our results are consistent with Cain & Damman's findings in that *A. canadense* performed better in the understorey of late successional forest. For example, ramet density showed greater temporal variability in early successional, as compared to the late successional, forest habitat, indicating that year-to-year variation in the physical

environment may be felt more severely in early successional habitats. The results of simulations showed similar patterns. Simulated populations based on data from the early successional forest plots invariably declined rapidly in size over time so that even ramet populations with initial sizes as great as 30 000 individuals went extinct within 100 years. Under early successional forest conditions the 95% confidence interval about the estimated value of λ usually was less than 1 for the ramet-level population projections. Late successional forest populations of both ramets and clones, in contrast, managed to hold their own; here the 95% confidence interval about the estimated value of λ usually included 1. Thus, although *A. canadense* grows commonly in the early successional forest habitat, these younger forests seem to represent a marginal environment.

In general, which life-history components most strongly affect population growth depends on the habitat in which the plants grow. Growth, which includes clonal reproduction, and survival most strongly influence the population growth rate of forest-understorey plants, while plants of other habitats rely more heavily on seed production (Bierzychudek 1982b; Silvertown *et al.* 1993; Silvertown *et al.* 1996). *A. canadense* fits this pattern: at the level of both the ramet and the clone, we found that clonal growth and, especially, survival most strongly influenced the finite population growth rates as determined by elasticity values. Sexual reproduction affected the finite rate of population growth very little, particularly at level of the ramet. At the same time, however, both sexual reproduction and clonal growth varied greatly spatially and temporally, as has been reported for other understorey herbs (Tamm 1956; Barkham 1980; Matlack 1987; Horvitz & Schemske 1995). As a consequence, seedling recruitment proved to be important in some years at some sites, leading to a substantial recruitment of new genets over the 7 years of our study.

Eriksson (1989, 1993) divided clonal plants into those that relied on sexual reproduction only during a brief, initial period of colonization and those that seeded into established populations repeatedly. Field observations and simulations suggest that *A. canadense* falls into the second of these categories. Eriksson (1993) predicted that the genetic structure of populations of the two types of plants should differ: plants that have initial seedling recruitment should show a steady attrition of genetic individuals over time, while plants that continually recruit seedlings should not show such a pattern. *A. canadense* populations appear to match this prediction: the total number of genetic individuals usually increased over time in our simulations. This result notwithstanding, three observations suggest that the genetic diversity of *A. canadense* populations may decrease over time: (i) simulations of the fate of genets suggest that a few individuals generate the vast majority of seedlings entering the populations (see also Meagher 1991); (ii)

all reports indicate that *A. canadense* relies entirely on self-fertilization (Peattie 1940; Wildman 1950); and (iii) although ant-dispersed, seeds of *A. canadense* move short distances even over long periods of time (Heithaus 1986; Matlack 1994; Cain *et al.* 1997). Overall, then, the few genotypes that reproduce abundantly will tend to surround themselves with genetically similar offspring, and over time, this should lead to a winnowing of genetic diversity in *A. canadense* populations. The extent to which this reduction in genetic diversity is counter-balanced by gene flow and new mutations is not known.

A. canadense genets, like those of all clonal plants, are potentially immortal. Our simulations, however, indicated that few genets live more than 100 years, even in the superior conditions provided by late successional forest habitat. Our simulations also indicated that the dynamics of ramets and genets can differ substantially: in early successional forest habitat populations of both ramets and genets declined over time, whereas in late successional forest habitat there was usually a decrease in the number of ramets and an increase in the number of genets over time. Clearly, populations of genets cannot persist if their constituent population of ramets declines over the long-term. The simultaneous decrease in ramet, and increase in genet, population-size suggests that our *A. canadense* populations were not in equilibrium. Over the course of this study mature clones consisting of several ramets tended to die off and were replaced by new genets consisting of a single ramet. Indeed, the field data showed that the death of established *A. canadense* genets and the recruitment of new seedlings occurred at surprisingly high rates. Age structure, and consequently the reproductive patterns of *A. canadense* populations, appear to be in constant flux in spite of the image of stability often associated with late successional forests. Overall, then, although there is a tendency to assume that late successional forests represent relatively stable environments, the evidence for *A. canadense* and other woodland herbs suggests that this habitat varies both spatially and temporally in ways that matter to plant performance (Tamm 1956; Barkham 1980; Matlack 1987; Horvitz & Schemske 1995).

Stochastic environmental and demographic variation strongly affected the performance of simulated populations. Theory predicts that relative to deterministic projections, matrix models that incorporate demographic and environmental stochasticity should decrease the rate at which populations grow and increase the rate at which populations decline (Tuljapurkar 1982; Metz *et al.* 1992; Benton & Grant 1996). Under early successional forest conditions, the inclusion of stochasticity in our models increased the extinction rate, as predicted by theory. In contrast, under late successional forest conditions, our results were the opposite of those predicted: the addition of stochasticity increased the rate of population growth

and decreased the rate of population decline. Tuljapurkar's (1982) model suggests that the late-successional forest outcome could result from a positive correlation between environmental conditions in successive time periods. This was not the case in our simulations, however, where transition matrices were selected randomly from the available pool to generate environmental stochasticity.

Demographic stochasticity should most strongly affect species with $\lambda^2 \geq 1$, because in these often small populations sampling effects should have the greatest impact on population growth (Lande 1988; Menges 1992). For simulations based on the late successional forest transitions, for which λ ranged between 0.84–1.11 (ramets) and 0.92–1.12 (clones), demographic stochasticity reduced the overall rate at which the populations increased in size and strongly influenced the effect of initial population size on population growth. Inclusion of demographic stochasticity in our simulations also caused minimum viable population sizes for ramets to be 16 times greater than those in simulations that only included environmental stochasticity. The general tendency for ramet populations to decline probably insured ramet population-sizes sufficiently small that demographic stochasticity could exert a strong influence. These findings suggest that demographic stochasticity may well play an important part in predicting the performance of forest-understorey herbs.

Because woodland herbs often cannot survive in habitats other than forest understorey (Helliwell 1975), the urban and agricultural habitats that disrupt once continuous forests may provide strong barriers to the exchange of seed and pollen between the remaining woodlots. Remnant woodlots may harbour such small populations of herbs that genetic diversity may decline or chance demographic events may lead to extinction. Woodland herbs include a disproportionate number of rare plant species, and typically share with *A. canadense* a poor dispersal ability (Primack & Miao 1992; Matlack 1994; Cain *et al.* 1997), a tendency to propagate both by seed and clonal growth (Bierzychudek 1982b; Eriksson 1989; Silvertown *et al.* 1993), and a value of λ close to one (e.g. Bierzychudek 1982a; Charron & Gagnon 1993). In our simulations, the minimum size needed to sustain demographically viable populations of *A. canadense* through 100 years were 25–1000 under late successional forest conditions and greater than 30 000 under early successional forest conditions. For late successional forest habitat, these values were safely below the size of our field populations: in the woodlot in which we conducted our study, we have estimated a total population of 30 000 ramets and 20 000 genets. Assuming similar demography, however, populations of rare species or isolated populations of common species could easily fall to sizes below our simulated minimum of 25 ramets or genets needed to maintain viable populations.

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