DEMOGRAPHY AND LIFE HISTORY OF ARABIS FECUNDA IN RAVALLI AND BEAVERHEAD COUNTIES, MONTANA

Prepared by:

Peter Lesica
929 Locust
Missoula, MT 59802

and

J. Stephen Shelly
Montana Natural Heritage Program
1515 E. 6th Ave.
Helena, MT 59620

Prepared for:

USDA Forest Service
Beaverhead National Forest
610 N. Montana
Dillon, MT 59725

January 1994

This report should be cited as follows:

Lesica, P. and J. S. Shelly. 1994l Demography and life history of Arabis fecunda in Ravalli and Beaverhead counties, Montana. Unpublished report to the Beaverhead National Forest. Montana Natural Heritage Program, Helena. 29 pp.

Summary

We monitored individuals of Arabis fecunda over four consecutive years at three sites in order to gain knowledge of this rare plant's life history. Arabis fecunda is a short-lived perennial with high fecundity. Recruitment is high as is mortality of juveniles. Plants flower by bolting or producing axillary inflorescences. Bolting plants produced 2.5 times as many seeds, matured earlier but had much higher mortality compared to axillary-flowering plants. Seeds germinate readily without stratification. Seed dormancy is induced by cold/dark conditions at some sites but not others.

Recruitment rate, survivorship, age at maturity and fecundity varied significantly among sites. Much of this difference in life history traits was due to differential bolting frequencies among the three sites. These results suggest that life history traits are locally adapted and that adaptive genetic differences may exist between populations.

Populations in the southern portion of A. fecunda's range appear to be stable and will be most sensitive to changes that cause a reduction in recruitment. On the other hand, populations in the north may be declining and should be most sensitive to declines in adult survivorship.

Introduction

Passage of the Federal Endangered Species Act of 1973 and subsequent recognition of the value of conserving biotic diversity (Wilson 1988) have resulted in many government agencies becoming active in species conservation. Surveys to determine the location and size of populations of rare species are being conducted on public lands throughout the west. These surveys are necessary in any species conservation program; however, knowing the location and size of populations at any one point in time is only the first step in a long-term protection strategy. (Sutter 1986). Extinction is a process requiring an understanding of population dynamics (Menges 1986). Periodic

inventories can detect trends but will do little to determine causality or help generate predictive hypotheses (Palmer 1987). Long-term conservation requires a knowledge of many life history parameters including fecundity, recruitment, survivorship, age structure, and population flux. Demographic monitoring techniques can provide information on factors regulating population density and persistence (Palmer 1987). This information, in turn, provides an essential basis for management decisions.

Arabis fecunda is a candidate for listing as a threatened or endangered species by the U.S. Fish and Wildlife Service (USDI-FWS 1993), is considered sensitive in Region One of the U.S. Forest Service, and is considered threatened in Montana (Lesica and Shelly 1991). Little is known about the life history and demography of Arabis fecunda populations. The purpose of this study is to determine demographic patterns and variability for this rare species and to use this knowledge to recommend appropriate management strategies for conservation.

METHODS

The Species

Arabis fecunda Rollins is a rosette-forming, perennial in the Mustard Family (Brassicaceae). This recently described species (Rollins 1984) is endemic to highly calcareous soils in the foothills of the Sapphire Range in Ravalli County and in the Pioneer Range in Beaverhead and Silver Bow counties in southwest Montana. Arabis fecunda plants flower in April and May, and fruits mature in June and July. Flowering occurs in one of two ways: (1) axillary flowering - 1 to many decumbent inflorescence stems develop from axillary buds among the tightly clustered leaves of the rosette or (2) bolting - a single inflorescence stem is produced from the terminal bud in the center of the rosette. Bolting inflorescences are generally larger and leafier than axillary inflorescences. An individual rosette may produce axillary inflorescences for numerous years, while bolting rosettes always die. Some

rosettes are iteroparous, producing axillary inflorescences for 1-many years before either dying or bolting and then dying. Others bolt once and are essentially semelparous. Individuals may branch at the root crown to form multi-rosette plants at any time during the life cycle. This is not vegetative reproduction as individual rosettes from multi-rosette plants never become independent plants. If only a portion of the rosettes in a multiple-rosette plant bolt, the whole plant may or may not die.

Study Sites

We conducted our study at Charleys Gulch in Ravalli County and Lime Gulch and Vipond Park in Beaverhead County, Montana. The Charleys Gulch site is on a moderate southwest-facing slope, at 1525 m. At Hamilton, ca. 8 km southwest and 300 m lower, mean temperatures for July and January are 19.4° and -3.8° C respectively, and mean annual precipitation is 32 cm. Vegetation surrounding the sites is foothills *Agropyron*-*Festuca* grasslands with scattered *Pinus ponderosa* Dougl. and *Pseudotsuga menziesii* (Mirb.) Franco. The Lime Gulch site occurs on moderate east- and west-facing slopes above a small drainage on the east side of the Pioneer Range at ca 1890 m. The Vipond Park site is on a moderate south-facing slope at 2195 m at the north end of the Pioneer Range. The two sites are separated from each other by ca. 32 km and from the Ravalli County site by ca. 130 km. For Divide, at 1675 m and north and east of the two sites, mean temperatures for July and January are 17.2° and -7.2° C respectively, and mean annual precipitation is 31 cm. Vipond Park is appreciably higher than the recording station, and thus likely experiences colder temperatures and greater precipitation. Vegetation around Lime Gulch is *Juniperus*/*Cercocarpus* woodland, while it is *Artemisia*-*Festuca*-*Agropyron* steppe at Vipond Park.

Soils at all sites are highly calcareous sandy loams derived from outcrops of metamorphosed calc-silicates or limestone. These soils have a tendency to slump on moderate to steep slopes. Vegetation at these sites is

sparse compared to surrounding grasslands and woodlands. Cryptogamic soil crusts are common at Charleys Gulch and Lime Gulch (Lesica and Shelly 1992a). Soils at Charleys Gulch have a lighter albedo than those at the Beaverhead County sites.

Field methods

In 1987 we established two permanent transects, one of 5 and one of 12 contiguous 1-m^2 plots at Charleys Gulch. In 1989 we established two permanent transects of 12 contiguous 1-m^2 plots each at both Lime Gulch and Vipond Park. Transects were located to be representative of the populations a whole. We censused *Arabis fecunda* in 1988-93 at all three sites. Sampling was conducted in late May at Charleys Gulch, mid-June at Lime Gulch and late June or early July at Vipond Park. We chose these times because *A. fecunda* fruits were mature or nearly so, but dispersal had not yet occurred. Plants smaller than 0.5 cm in diameter were not recorded because they could not be reliably distinguished from other species.

Individual *A. fecunda* plants were mapped and recorded following methods outlined in Lesica (1987) and using the following life history stage classification system:

Small (S) = single vegetative rosette < 2 cm in diameter
Juvenile (J) = single vegetative rosette $\geq$ 2 cm in diameter
Multiple-rosette (M) = multiple vegetative rosettes
Reproductive (R) = plants producing 1-many inflorescences

In addition, for each reproductive plant we recorded the number of inflorescences and the number of fruits matured. We recorded which plants bolted in 1990-93.

A plants's demographic properties are often more closely correlated with size and life-history stage rather than age (Werner and Caswell 1977, Caswell 1989), although both may be important in predicting an individual's fate (Young 1985). We chose these classes because they are correlated with age as well as size and because they also represent a reasonable compromise between having many categories with too few observations each and few categories with many observations (Vandermeer 1978).

In each year we collected one fruit from the middle of the inflorescence of each of 25 randomly chosen plants growing near the transects at each site. We counted the number of mature or nearly mature seeds in each fruit to obtain an estimate of seeds per fruit for each site.

In 1993 we collected one fruit each from 25 randomly selected axillary flowering plants and 25 bolting plants from each site. After counting the number of mature or developing seeds, those from Charleys Gulch and Vipond Park were used in germination tests. Seeds from Lime Gulch were not mature enough to be used. Seeds were stored dry at room temperature for 4 months prior to the tests. Two treatments were tested: (1) warm/light - constant 20°C with 14 hours of constant light per day and (2) cold/dark - constant 5°C in the dark. Seeds were placed on moist filter paper in petri dishes, 20 seeds from a single parent per dish with 6 bolting and 6 axillary flowering replicates from each site for each treatment. The warm/light and cold/dark treatments were given for 8 and 20 days respectively. Germinated seeds were recognized by the radicle emerging at least 1 mm from the seed coat.

We estimated canopy cover to the nearest 5% of all vascular plants as well as cover of rock, bare soil and basal vegetation in each plot (Daubenmire 1959).

Data analysis

Stage-structured transition matrix projection models summarize the way in which survival, growth and reproduction at various life-history stages interact to determine population growth (Caswell 1989, van Groenendael et al. 1988). Matrix projections assume fixed transition probabilities between stages in a population through time (Lefkovitch 1965, Menges 1990). They assume density-independent population growth and thus do not give an accurate projection of long-term population future. Nonetheless, they can be used to summarize short-term population dynamics or compare the dynamics of two populations (Caswell 1989). One-year transition probabilities were estimated as the number of plants in life-stage class i moving into class j over the course of one year divided by the number of plants in stage i at the beginning of the year. This method assumes that an individual's transition depends only on its life-stage class at the beginning of the period and is independent of its transition the previous year. The equilibrium growth rate (λ) is the dominant eigenvalue of the transition matrix (Caswell 1989, Lefkovitch 1965). $\lambda > 1.0$ indicates population increase, while $\lambda < 1.0$ indicates decrease. λ integrates the effects of survival, growth and fecundity of the different life-history stages into a single parameter. Details on the construction and use of matrix population models can be found in Caswell (1989) and Menges (1990).

Elasticity measures the relative change in the value of λ in response to changes in the value of a transition matrix element. Elasticity matrices allow comparison of relative importance to population growth and fitness among the various life history transitions (de Kroon et al. 1986). Elasticities sum to unity and regions of the matrix may be summed to compare the importance of growth and survival to recruitment (Caswell 1986).

When the majority of seeds pass directly from production to germination in less than one year, seeds should not appear as a separate stage in matrix

models (Caswell 1989, Silvertown et al. 1993). In most cases, the majority of seeds probably germinate without a dormant period (see Results), and we have used matrices with reproductive transition and recruitment columns combined to calculate λ. We calculated separate elasticities for reproductive transitions and recruitment by dividing the reproductive+recruitment elasticities proportionately between their two components.

We used the ratio of new recruits to survivors to compare annual recruitment rates among populations. Growth was measured as the ratio of plants in each population that grew into a larger size class to those that remained in the same class or became smaller. We examined differences in age at maturity by comparing ratios of plants that flowered during the first two years to those that flowered later. Differences in recruitment, growth, new recruit survival, survival of bolting plants, age at maturity and proportion of bolting plants were assessed with an overall chi-square goodness of fit test. If a 3 X 3 test showed a significant result, I used 2 X 2 tests to determine which pairs of sites were different. Probability values were not corrected for multiple tests.

We compared survivorship of the uneven-age sample population present in 1989 and the 1990 cohort among the sites using the nonparametric logrank test (Pyke and Thompson 1986, Hutchings et al. 1991). Survivorship curves were constructed following methods outlined in Hutchings et al. (1991). Probability values were not adjusted for multiple tests.

The effects of site (population), year and bolting on number of fruits per plant and number of seeds per fruit were analyzed using analysis of variance (ANOVA) followed by contrast tests. Dependent variables were log-transformed prior to analysis. The effects of treatment, site and bolting on the arcsine-transformed proportion of germinating seed were also analyzed by ANOVA.

Results

Vegetation

Mean canopy cover estimates for common vascular plant species are presented in Table 1. Total basal vegetation cover was lower at Charley's Gulch compared to Lime Gulch or Vipond Park (Table 1). Graminoids were common at Lime Gulch, but forbs were more common at the other two sites. Amounts of bare soil were highest at Charleys Gulch, intermediate at Lime Gulch, and lowest at Vipond Park, while rock was more abundant at Vipond Park (Table 1).

Population Growth

Density of *Arabis fecunda* varied among sites and years (Fig. 1). Population size was more variable at Lime Gulch and Vipond Park than at Charleys Gulch. The coefficient of variation for density for 1989-93 was 22% at Lime Gulch and Vipond Park but was 18% at Charleys Gulch.

Equilibrium population growth rate (λ) also varied among sites and years (Table 2). λ was lowest and least variable at Charleys Gulch. In 1989 there were no reproductive plants at Lime Gulch, but there were many in 1990. Thus, 1989-90 was a year of exceptional growth at Lime Gulch, but λ was nearly constant in the three ensuing year. λ showed the most consistent high variation at Vipond Park.

Recruitment

The ratio of new *Arabis fecunda* recruits to number of survivors was significantly greater at Vipond Park compared to Charleys Gulch for all four transition years (Fig. 2). In most years Vipond Park had higher recruitment than Lime Gulch, and Lime Gulch had higher recruitment than Charleys Gulch (Fig. 2). When all four years are pooled, the ratio of new recruits to number of survivors is 0.31 for Charleys Gulch, 0.65 for Lime Gulch, and 0.95 for Vipond Park, and these differences are significantly different between all possible pairs of sites ($P<0.001$).

Survivorship

Survivorship of the 1990 Arabis fecunda cohort over 1990-93 was significantly lower at Vipond Park than at either Lime Gulch (LR=9.22, $P<0.01$) or Charleys Gulch (LR=3.96, $P=0.05$; Fig. 3). Survivorship at Lime Gulch and Charley's Gulch was not different (LR=0.01, $P=0.91$; Fig. 3). Analysis of the depletion curve for the 1989 uneven-age populations gave similar results. Arabis fecunda populations at Charleys Gulch and Lime Gulch have type II survivorship curves where number of deaths is a constant with time, while the Vipond Park population's survivorship fits more closely a type III curve, where probability of death is a constant (Deevey 1947).

From 1991 through 1993, the proportion of new recruits that survived was 67% at Charleys Gulch, 74% at Lime Gulch and 57% at Vipond Park. The ratio of survivors to deaths of new recruits at Vipond Park was significantly lower than either Lime Gulch ($\chi^2=35.3$, $P<0.01$) or Charleys Gulch ($\chi^2=4.14$, $P=0.04$), while Lime Gulch and Charleys Gulch were not different ($\chi^2=1.90$, $P=0.17$).

Growth

In two out of four years, significantly more Arabis fecunda plants moved into larger size classes at Vipond Park compared to Charleys Gulch, and in three out of four years growth was significantly greater at Lime Gulch compared to Charleys Gulch (Fig. 4). When summed over all four years, there were significantly fewer plants moving into larger size classes at Charleys Gulch ($\chi^2=24.761$, df=2, $P<0.001$), but there was no difference between Lime Gulch and Vipond Park ($\chi^2=1.281$, $P=0.26$).

Fecundity

Over the course of the study the ratio of the number of Arabis fecunda plants that bloomed at an early age ($\leq$2 yr) to later (>2 yr) was 1.1 at Charleys Gulch, 1.75 at Lime Gulch and 4.0 at Vipond Park. Vipond park was significantly greater than both Lime Gulch ($\chi^2=17.05$, $P=0.001$) and Charleys

Gulch (χ^2=7.72, P=0.005), but the latter two sites were not different (χ^2=0.89, P=0.346). Thus, A. fecunda plants at Vipond Park matured earlier in life than those at the other two sites.

The number of fruits per reproductive plant varied significantly among sites and years (Table 3). Over the course of the study, the mean for Lime Gulch was 10.6, significantly lower than Charleys Gulch and Vipond Park which had means of 14.6 and 14.5 respectively (Table 3). The number of seeds per fruit also varied significantly among sites and years although differences were not large (Table 4). Over the course of the study, the means were 30.9, 32.4 and 34.0 for Charleys Gulch, Lime Gulch and Vipond Park respectively. Only Charleys Gulch and Vipond Park were significantly different (Table 4). For both number of seeds per fruit and fruits per plant, there was a significant interaction between the site and year effects, possibly due to different weather conditions at the sites.

Bolting plants

Over the period of 1990-93 the mean percentage of reproductive plants that produced a bolting inflorescence was 3%, 26% and 44% for Charleys Gulch, Lime Gulch and Vipond Park respectively (Fig. 6). These differences were statistically significant for all four years (χ^2>7.3, df=2, P<0.05).

Bolting plants had a mean of 19.9 fruits, while axillary-flowering plants had a mean of 9.8 fruits, and this difference was significant (Table 5). There were also significant effects of year, and site X year interaction, probably due to different weather conditions at the sites over the course of the study. There was also a strong interaction between bolting and year, suggesting that the number of fruits per plant is partially under environmental control. Bolting plants produced an average of 36.8 seeds per fruit, while axillary-flowering plants produced 29.8 seeds per fruit, and the difference was significant (ANOVA, F=26.4, P<0.001). Number of seeds per

fruit also varied among sites in the same manner as described above. On average, bolting plants produce 2.5 times as many seeds as axillary flowering plants.

During the period of 1991-93 at Lime Gulch, 63% of axillary flowering plants survived to the following year, while only 6% of bolting plants survived. Results for the Vipond Park population were similar, with 68% of axillary flowering and 16% of bolting plants surviving. Survivorship was significantly greater for axillary flowering plants at both sites for all three years (χ^2>17.3, df=2, P<0.001).

Germination requirements

Germination of _Arabis_ _fecunda_ seed occurred readily at room temperature in the light without stratification. Site (source of seed) had no effect on germination; 89% and 86% of seed from Charleys Gulch and Vipond Park respectively germinated within eight days (ANOVA F=0.048, df=24, P=0.828). 80% of seeds from Charleys Gulch germinated in the cold and dark after 14 days, but only 8% of seeds from Vipond Park germinated under the same conditions, and this difference was highly significant (F=129.59, df=24, P<0.001). Seeds from Vipond Park remained dormant after being placed in a warm light environment for eight days. The significant site*treatment interaction in the full ANOVA model (Table 6) indicates that seeds from the two sites are genetically different. Seeds from bolting plants germinated better than those from axillary flowering parents under warm-light conditions but germinated more poorly under cold, dark conditions. The significant bolting X treatment interaction term in the ANOVA model suggests that seeds from bolting and axillary flowering plants are genetically different (Table 6).

Elasticity analysis

Elasticities for the three sites for the four annual transitions are presented in Table 7. Growth and survival of plants in the non-reproductive stages accounted for ca. 50% of equilibrium population growth (λ) at all three sites. Growth and survival of reproductive plants was responsible for 36% of λ at Charleys Gulch but less than 20% at Lime Gulch and Vipond Park. On the other hand, recruitment from seed accounted for 34% and 36% of λ at these latter two sites but only 16% at Charleys Gulch (Table 7). Adult (reproductive) growth and survival was the most important transition at Charleys Gulch, while recruitment was predominant at Lime Gulch and Vipond Park.

Discussion

Life history

Arabis fecunda is a relatively short-lived perennial; only ca. half of the plants that establish live for more than two years, and only ca. one-third live for four years or more. Annual recruitment is generally high; the ratio of new recruits to survivors varied from 0.09 to 2.06 with means for 1989-93 between 0.31 and 0.95. Mortality of new recruits is also high; in 1991-93, it varied from ca. 20-50%. Fecundity is generally high; reproductive A. fecunda plants produced an average of 340-500 seeds per year. Plants that bolted produced ca. 2.5 times as many seeds per year as axillary flowering plants but had much higher mortality. Seeds become ripe in late spring or early summer and germinate readily without stratification. These results suggest that most seeds germinate in the fall of the same year that they are produced. Seeds from Charleys Gulch also show high germination in the cold and dark, suggesting that at this site only a transient type II seed bank is formed (sensu Thompson and Grime 1979). On the other hand, cold/dark conditions induce dormancy in seeds from Vipond Park; thus, A. fecunda probably does have a long-term seed bank at this site.

Variability in life histories

Life history theory predicts tradeoffs between traits that will maximize fitness for a particular environment. In particular, there is thought to be a negative relationship between reproduction and growth and survival. Some environments favor slower growth, greater age at first reproduction, smaller output per reproductive bout, and greater longevity. Other environments select for shorter lifespan, early maturity and larger reproductive output per bout. Early maturing, highly fecund populations have a higher intrinsic population growth rate. Early maturity is favored in environments where adult mortality is relatively high or highly variable (Stearns 1992). In plants, the extreme case is the annual habit.

There was great variation in life history traits among the three populations studied. In most cases, the Charleys Gulch and Vipond Park populations occupied the two extremes of life history trait continua with the Lime Gulch population intermediate. For the purpose of this discussion, we will compare the former two populations, bearing in mind that the Lime Gulch population was similar to Charleys Gulch for some traits but more similar to Vipond Park for most.

The *Arabis fecunda* population at Charleys Gulch had a lower recruitment rate but higher overall as well as new recruit survivorship. On average, plants grew more slowly, were older at first reproduction, and had lower annual fecundity as a result of producing fewer seeds per fruit. The Vipond Park population had higher recruitment, faster growth, and higher mortality. Annual fecundity was higher and plants became fecund at an earlier age. Population size was more stable at Charleys Gulch than at Vipond Park. The Vipond Park population demonstrated germination traits that make a long-term seed bank more likely than at Charleys Gulch.

The frequency of bolting was much higher at Vipond Park, and this is likely the source of much of the difference between Arabis fecunda life histories at the two sites. Bolting plants have higher annual fecundity and much higher mortality than axillary flowering plants. Axillary flowering plants are iteroparous (perennial or polycarpic), while bolting plants approach the semelparous (annual or monocarpic) life history.

Discussion of the environmental characters that cause these differences in Arabis fecunda life history can only be speculative. Charleys Gulch is warmer and likely has lower precipitation. Bare soil was more common and vegetation cover was lower. The bleached color of the mineral soil at Charleys Gulch may indicate a more extreme edaphic environment. These conditions may result in slower growth but lower density-dependent mortality which, in turn, should provide more stable population sizes and favor the iteroparous habit. The high elevation of the Vipond Park site may provide an more unstable habitat in which the semelparous habit and a long-term seed bank are favored (van Groenendael and Slim 1988).

The differences in life history traits exhibited among the populations studied could be the result of genetic differentiation, phenotypic plasticity (one genotype that produces different phenotypes under different conditions) or both. Quantitative genetics studies are required to determine the basis of the variation. Leeper et al. (in press) used starch gel electrophoresis to investigate apportionment of genetic variation in Arabis fecunda populations, including the three that we studied. Of 18 putative loci scored, 17 were invariant; however, the one polymorphic locus had different frequencies among the populations, suggesting a fair degree of differentiation. Results of the germination studies indicate that there is genetic differentiation between the Charleys Gulch and Vipond Park populations. Furthermore, they suggest that there is a genetic difference between plants that bolt and those that do not.

Together these results provide evidence that differences in life history traits between the two sites have a genetic basis.

Population growth and viability

Sample populations of *Arabis fecunda* at Lime Gulch and Vipond Park, the two study sites in the southern portion of the range became larger between 1989 and 1993. Equilibrium population growth rates (λ) at these sites were generally greater than or equal to one. Thus, our study provided no evidence that these populations are in decline. On the other hand, sample populations at Charleys Gulch and Birch Creek (Lesica and Shelly 1993) became smaller in number since 1987. Furthermore, λ at Charleys Gulch was appreciably less than one in two out of the four years that it was measured. Our study was designed to elucidate demographic and life history characters and may not provide a robust assessment of trend. Nonetheless, our results suggest that populations in Ravalli County may be declining. Populations of *A. fecunda* in Ravalli County have been invaded by the aggressive exotic, *Centaurea maculosa*, and Lesica and Shelly (manuscript submitted) provide evidence that the invader has a negative impact on population growth rates of *A. fecunda*. Furthermore, all Ravalli County sites are subject to livestock grazing (Lesica 1985, Schassberger 1988) which may have adverse effects on *A. fecunda* (Lesica and Shelly 1992). Taken together, these observations suggest that *A. fecunda* populations in the northern portion of its range may be in jeopardy.

Analysis of elasticity matrices indicates that Lime Gulch and Vipond Park populations of *Arabis fecunda* are heavily dependent on recruitment from seed to maintain population growth, while the Charleys Gulch population depends most on survivorship of mature individuals. This is consistent with the presence of germination responses promoting a long-term seed bank at Vipond Park but not at Charleys Gulch. Thus, populations at Lime Gulch and Vipond Park will be most sensitive to changes that reduce seedling establishment such as damping-off diseases or the introduction of aggressive

exotics. The Charleys Gulch population should be most affected by disturbances that destroy adults, such as trampling or herbicide application. The differences in life history traits are at least partly controlled by the frequency of bolting and axillary flowering, and the fact that both types of flowering occurred in all populations suggests that there is probably ample variation, genetic or plastic, to compensate for any changes that may occur if they are not too drastic and do not occur too quickly.

Management Considerations

Results of our studies suggest that Arabis fecunda populations at Lime Gulch and Vipond Park are stable or growing. Population growth at these sites depends heavily on recruitment from seed, a life history stage that is probably buffered by the presence of a long-term seed bank. Weed infestations could pose a serious problem as they can reduce recruitment of A. fecunda (Lesica and Shelly submitted). Furthermore, weed infestations are most frequent in the mesic grassland and xeric forest zones in western Montana (Forcella and Harvey 1983), the same habitats where A. fecunda is most common. At this time, there are no serious weed infestations near any known populations in Beaverhead or Silver Bow counties. Nonetheless, encroachment by exotics is a very real potential problem. Populations of A. fecunda should be regularly monitored for exotics, and roads and other disturbances that promote weed infestations should be minimized in these areas.

Populations of Arabis fecunda at Charleys Gulch and Birch Creek (Lesica and Shelly 1993) may be declining. Results of our studies indicate that the Charleys Gulch population will be most sensitive to declines in the survival of mature plants. Centaurea maculosa is present at all Ravalli County sites, and this aggressive exotic does have a negative effect on A. fecunda population growth (Lesica and Shelly, submitted). However, the main negative effect of C. maculosa on A. fecunda is to reduce recruitment, so the two species may be able to coexist (Lesica and Shelly, submitted). On the other

hand, livestock are also present at the Ravalli county *A. fecunda* sites, and trampling by livestock or large ungulates can have an adverse effect on adult survival (Lesica and Shelly 1992). Negative impacts resulting from heavy livestock trampling and *Centaurea maculosa* encroachment taken together may be enough to result in declines of *A. fecunda* populations.

Anthropogenic global climate change is considered a potential cause of species extinctions in the near future (Dobson et al. 1989, Peters 1988). Populations of *Arabis fecunda* occur throughout a wide range of elevations and habitats (Schassberger 1988), so it seems unlikely that climatic changes will have adverse effects.

Acknowledgements

Peter Achuff, Anne Garde, Bonnie Heidel, Lisa Roe and Jim Vanderhorst helped conduct field work. We are grateful to George Frost for allowing us to conduct our study on his ranch. This study was funded by Beaverhead National Forest, the U.S. Fish and Wildlife Service and The Nature Conservancy.

Literature Cited

Caswell, H. 1989. Matrix population models. Sinauer Associates, Sunderland, Massachusetts, USA.

Daubenmire, R. 1959. A canopy-coverage method of vegetational analysis. Northwest Science 33: 43-64.

Deevey, E. S. 1947. Life tables for natural populations of animals. Quarterly Review of Biology 22: 283-314.

Dobson, A., A. Jolly and D. Rubenstein. 1989. The greenhouse effect and biological diversity. Trends in Ecology and Evolution 4: 64-68.

de Kroon, H., A. Plaiser, J. M. van Groenendael and H. Caswell. 1986. Elasticity: the relative contribution of demographic parameters to population growth rate. Ecology 67: 1427-1431.

Forcella, F. and S. J. Harvey. 1983. Eurasian weed infestation in western Montana in relation to vegetation and disturbance. Madrono 30: 102-109.

Hutchings, M. J., K. D. Booth, and S. Waite. 1991. Comparison of survivorship by the logrank test: criticisms and alternatives. Ecology 72: 2290-2293.

Leeper, D., D. Pavek, R. Walsh and T. Mitchell-Olds. 1993. Preliminary report of combined demographic and genetic analyses for management of Arabis fecunda. In Plants and their environment in the Greater Yellowstone Ecosystem. National Park Service Transactions.

Lefkovitch, L. P. 1965. The study of population growth in organisms grouped by stage. Biometrics 21: 1-18.

Lesica, P. 1985. Report on the conservation status of Arabis fecunda, a potential candidate species. Report to the U.S. Fish and Wildlife Service, Office of Endangered Species, Denver, CO.

Lesica, P. 1987. A technique for monitoring nonrhizomatous perennial plant species in permanent belt transects. Natural Areas Journal 7: 65-68.

Lesica, P. 1992. Vascular and sensitive plant species inventory for the Highland Mountains, Deerlodge National Forest. Montana Natural Heritage Program, Helena.

Lesica, P. and J. S. Shelly. 1991. Endangered, threatened and sensitive vascular plants of Montana. Montana Natural Heritage Program, Occasional Publication No. 1, Helena, Montana, USA.

Lesica, P. and J. S. Shelly. 1992. The effects of cryptogamic soil crust on the population dynamics of Arabis fecunda (Brassicaceae). American Midland Naturalist 128: 53-60.

Lesica, P. and J. S. Shelly. 1993. Demographic monitoring of Arabis fecunda populations in the Sapphire and Beaverhead ranges, Montana. 1992 progress report. Unpublished report, Montana Natural Heritage Program, Helena.

Lesica, P. and J. S. Shelly. Submitted. Demographic analysis of competitive effects of Centaurea maculosa on Arabis fecunda. Journal of Ecology.

Menges, E. S. 1986. Predicting the future of rare plant populations: demographic monitoring and modeling. Natural Areas Journal 6: 13-25.

Menges, E. S. 1990. Population viability analysis for an endangered plant. Conservation Biology 4: 52-62.

Palmer, M. E. 1987. A critical look at rare plant monitoring in the United States. Biological Conservation 39: 113-127.

Peters, R. L. 1988. Effects of global warming on species and habitats: An overview. Endangered Species Update 5(7): 1-8.

Pyke, D. A. and J. N. Thompson. 1986. Statistical analysis of survival and removal experiments. Ecology 67: 240-245.

Rollins, R. C. 1984. Studies in the Cruciferae of western North America II. Contributions to the Gray Herbarium 214: 1-18.

Schassberger, L. A. 1988. An update of the report on the conservation status of Arabis fecunda, a candidate threatened species. Report to the U.S. Fish and Wildlife Service, Office of Endangered Species, Denver, CO.

Silvertown, J., M. Franco, I. Pisanty and A. Mendoza. 1993. Comparative plant demography - relative importance of life-cycle components to the finite rate of increase in woody and herbaceous perennials. Journal of Ecology 81: 465-476.

Stearns, S. C. 1992. The evolution of life histories. Oxford University Press, Oxford.

Sutter, R. D. 1986. Monitoring rare plant species and natural areas-ensuring the protection of our investment. Natural Areas Journal 6: 3-5.

Thompson, K. and J. P. Grime. 1979. Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. Journal of Ecology 67: 893-921.

USDI-Fish and Wildlife Service. 1993. Endangered and threatened wildlife and plants; review of plant taxa for listing as endangered or threatened species; notice of review. Federal Register 58: 51144-51190.

Vandermeer, J. 1978. Choosing category size in a stage projection matrix. Oecologia 32: 79-84.

van Groenendael, J, M. de Kroon and H. Caswell. 1988. Projection matrices in population biology. Trends in Ecology and Evolution 3: 264-269.

van Groenendael, J. M. and P. Slim. 1988. The contrasting dynamics of two populations of Plantago lanceolata classified by age and size. Journal of Ecology 76: 585-599.

Werner, P. A. and H. Caswell. 1977. Population growth rates and age versus stage-distribution models for teasel (Dipsacus sylvestris Huds.). Ecology 58: 1103-1111.

Wilson, E. O. 1988. Biodiversity. National Academy Press, Washington D.C.

Young, T. P. 1985. Lobelia telekii herbivory, mortality and size at reproduction: variation with growth rate. Ecology 66: 1879-1883.

Table 1. Mean ground cover and canopy cover of common vascular plant species in Arabis fecunda monitoring transects at three study sites.

	Charleys Gulch		Lime Gulch		Vipond Park	
	East	West	North	South	East	West
Rock	5	2	6	6	14	15
Soil	77	59	52	58	43	40
Basal vegetation	19	40	43	38	43	48
Agropyron spicatum	--	6	6	6	8	12
Aristida longiseta	--	--	--	3	--	--
Carex filifolia	--	--	--	5	--	2
Carex rossii	--	--	8	--	--	--
Oryzopsis hymenoides	--	<1	9	2	--	--
Poa secunda	3	1	--	--	--	--
Stipa comata	--	--	7	15	--	--
Artemisia frigida	2	--	2	2	10	9
Centaurea maculosa	--	30	--	--	--	--
Chrysopsis villosa	5	<1	--	--	--	--
Haplopappus acaulis	--	--	--	--	19	13
Oxytropis besseyi	--	--	--	--	<1	2
Phlox muscoides	--	--	--	--	8	11
Physaria geyeri	2	2	--	--	--	--
Sedum lanceolatum	--	--	--	--	3	2
Senecio canus	--	--	3	<1	--	--

Table 2. Stage-based transition matrices for Arabis fecunda at three sites in 1989-93. The reproductive and recruitment columns must be added together before solving for λ, the dominant eigenvalue (see Methods).

Charleys Gulch

1989-90 (From)

To	Sm	Ro	Mu	Rep	Rec
Small	0	0	0	0	.377
Rosette	.391	.375	.136	.076	.434
Multiple	.044	.025	.182	.057	.076
Repro	.087	.325	.409	.660	.094

λ=1.138

1991-92 (From)

To	Sm	Ros	Mul	Rep	Rec
Small	.455	.016	0	.036	.321
Rosette	.205	.492	0	.286	.071
Multiple	0	.064	.625	.179	0
Repro	0	.286	.250	.286	0

λ=0.898

1990-91 (From)

To	Sm	Ro	Mu	Rep	Rec
Small	.350	.056	.077	0	.321
Rosette	.150	.556	0	.286	.071
Multiple	0	.074	.539	.159	0
Repro	0	.148	.154	.286	0

λ=0.844

1992-93 (From)

To	Sm	Ros	Mul	Rep	Rec
Small	.091	0	0	0	.031
Rosette	.333	.306	0	.094	.156
Multiple	0	.020	.250	.031	.094
Repro	0	.204	.250	.653	.281

λ=1.050

Lime Gulch

1989-90 (From)

To	Sm	Ro	Mu	Rep	Rec
Small	.193	.022	.023	0	8.42
Rosette	.518	.248	.046	0	8.57
Multiple	.024	.071	.341	0	1.29
Repro	.036	.495	.364	.714	3.00

λ=4.909

1991-92 (From)

To	Sm	Ros	Mul	Rep	Rec
Small	.236	.009	0	0	.675
Rosette	.382	.307	.021	.065	.398
Multiple	.016	.031	.333	.008	.073
Repro	.033	.425	.396	.301	.114

λ=1.009

1990-91 (From)

To	Sm	Ro	Mu	Rep	Rec
Small	.161	.001	.023	.044	.635
Rosette	.543	.506	.046	.101	.522
Multiple	.049	.056	.250	.050	.082
Repro	.025	.269	.523	.327	.044

λ=1.068

1992-93 (From)

To	Sm	Ros	Mul	Rep	Rec
Small	.244	.017	.032	.012	1.11
Rosette	.435	.449	0	.089	.746
Multiple	.009	.017	.452	.012	.041
Repro	.009	.298	.323	.420	.036

λ=1.130

Vipond Park

1989-90 (From)

To	Sm	Ro	Mu	Rep	Rec
Small	.154	.036	.019	.049	.854
Rosette	.289	.255	0	.037	.976
Multiple	.039	.042	.245	.037	.439
Repro	.173	.442	.491	.598	.622

λ=1.815

1991-92 (From)

To	Sm	Ros	Mul	Rep	Rec
Small	.271	.031	.035	.010	1.75
Rosette	.157	.245	.035	.087	.505
Multiple	.186	.063	.368	.049	.272
Repro	.043	.453	.333	.447	.252

λ=1.357

1990-91 (From)

To	Sm	Ro	Mu	Rep	Rec
Small	.157	.037	.016	0	.246
Rosette	.326	.244	.079	.100	.322
Multiple	.079	.089	.413	.043	.147
Repro	.056	.296	.175	.194	.043

λ=0.783

1992-93 (From)

To	Sm	Ros	Mul	Rep	Rec
Small	.116	.025	.035	.006	.546
Rosette	.295	.280	.012	.081	.839
Multiple	.073	.059	.391	.040	.299
Repro	.024	.271	.138	.333	.052

λ=1.044

Table 3. Effect of site (population), year and their interaction on log-transformed number of fruits per reproductive *Arabis fecunda* plant in 1989-93 by ANOVA. Means (±SE) followed by different letters are significantly different (P<0.001) by contrast test after ANOVA.

Source of Variation	df	MS	F	P
Site	2	13.39	16.45	<0.001
Year	4	5.21	6.40	<0.001
Site*Year	8	4.61	5.66	<0.001
Error	1495	0.81		

Charleys Gulch	Lime Gulch	Vipond Park
14.6 ± 0.8^{a}	10.6 ± 0.4^{b}	14.5 ± 0.5^{a}

Table 4. Effect of site (population), year and their interaction on log-transformed number of seeds per fruit for *Arabis fecunda* in 1989-91 and 1993 by ANOVA. Means (±SE) followed by different letters are significantly different (P<0.05) by contrast test after ANOVA.

Source of Variation	df	MS	F	P
Site	2	234.1	4.15	0.017
Year	3	150.8	2.67	0.048
Site*Year	6	417.9	7.41	<0.001
Error	288	56.4		

Charleys Gulch	Lime Gulch	Vipond Park
30.9 ± 0.6^{a}	32.4 ± 0.7^{ab}	34.0 ± 1.0^{b}

Table 5. Effect of bolting, site (population), year and their interactions on log-transformed number of fruits per Arabis fecunda plant in 1990-93 by ANOVA.

Source of Variation	df	MS	F	P
Bolting	1	13.67	20.76	<0.001
Site	2	1.05	1.60	0.202
Year	3	6.08	9.24	<0.001
Bolting*Site	2	1.84	2.79	0.062
Bolting*Year	3	7.49	11.38	<0.001
Site*Year	6	3.03	4.60	<0.001
Error	1347	0.66		

	Charleys Gulch	Lime Gulch	Vipond Park
Bolting	17.3±3.9	18.3±0.9	20.9±0.8
Axillary flowering	14.3±0.9	8.1±0.3	9.8±0.5

Table 6. Effect of treatment, site (population), bolting and their interactions on arcsine-transformed proportion of Arabis fecunda seeds germinating by ANOVA.

Source of Variation	df	MS	F	P
Treatment	1	3.83	103.15	<0.001
Site	1	2.43	65.43	<0.001
Bolting	1	0.02	0.50	0.484
Treatment*Site	1	2.23	60.15	<0.001
Treatment*Bolting	1	0.18	4.90	0.033
Site*Bolting	1	0.01	0.28	0.602
Error	41	0.04		

	Warm-Light	Cold-Dark
Charleys Gulch		
Axillary flowering	0.87±0.04	0.86±0.05
Bolting	0.91±0.04	0.72±0.07
Vipond Park		
Axillary flowering	0.86±0.04	0.11±0.05
Bolting	0.87±0.07	0.05±0.02

Table 7. Mean elasticities for *Arabis fecunda* stage transition matrices at three sites for 1989-93. The left three columns represent non-reproductive growth and survival. The reproductive (Repro) column represents growth and survival of reproductives. The recruitment column represents recruitment from seed.

Charleys Gulch

	From				
To	Small	Rosette	Multiple	Repro	Recruit
Small	.0219	.0030	.0017	.0011	.0333
Rosette	.0340	.1481	.0015	.0518	.0467
Multiple	.0010	.0163	.0806	.0287	.0113
Repro	.0041	.1146	.0541	.2752	.0714
Total	.0610	.2820	.1379	.3568	.1627

Lime Gulch

	From				
To	Small	Rosette	Multiple	Repro	Recruit
Small	.0207	.0013	.0004	.0019	.0832
Rosette	.0740	.1156	.0012	.0136	.1242
Multiple	.0040	.0111	.0131	.0043	.0162
Repro	.0186	.2005	.0340	.1327	.1396
Total	.1171	.3285	.0487	.1525	.3632

Vipond Park

	From				
To	Small	Rosette	Multiple	Repro	Recruit
Small	.0173	.0055	.0026	.0012	.0836
Rosette	.0380	.0572	.0074	.0167	.1149
Multiple	.0160	.0135	.0483	.0073	.0428
Repro	.0389	.1580	.0695	.1651	.0965
Total	.1102	.2342	.1278	.1903	.3378

Figure 1. Number of <u>Arabis</u> <u>fecunda</u> plants at three study sites in 1989-93.

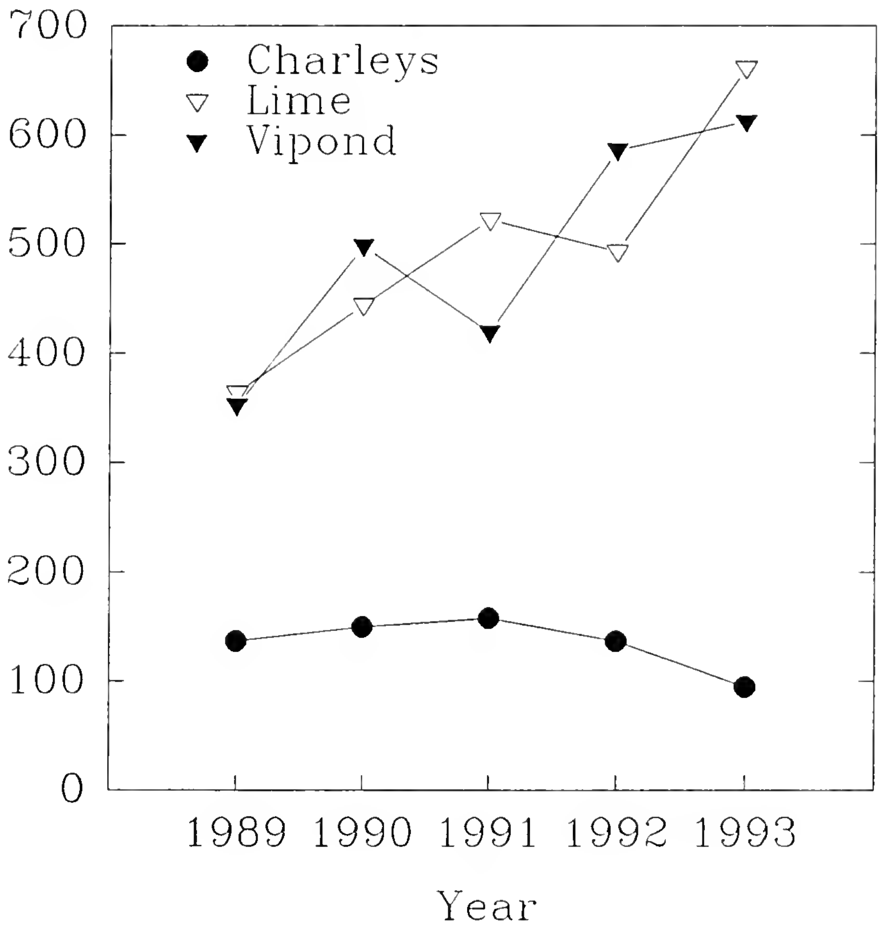

Figure 2. Annual recruitment in relationship to population size (survivors) of <u>Arabis fecunda</u> at three study sites in 1989-93. Sites with different letters had different recruitment rates (recruits/survivors) as determined by Chi-square tests (P<0.05).

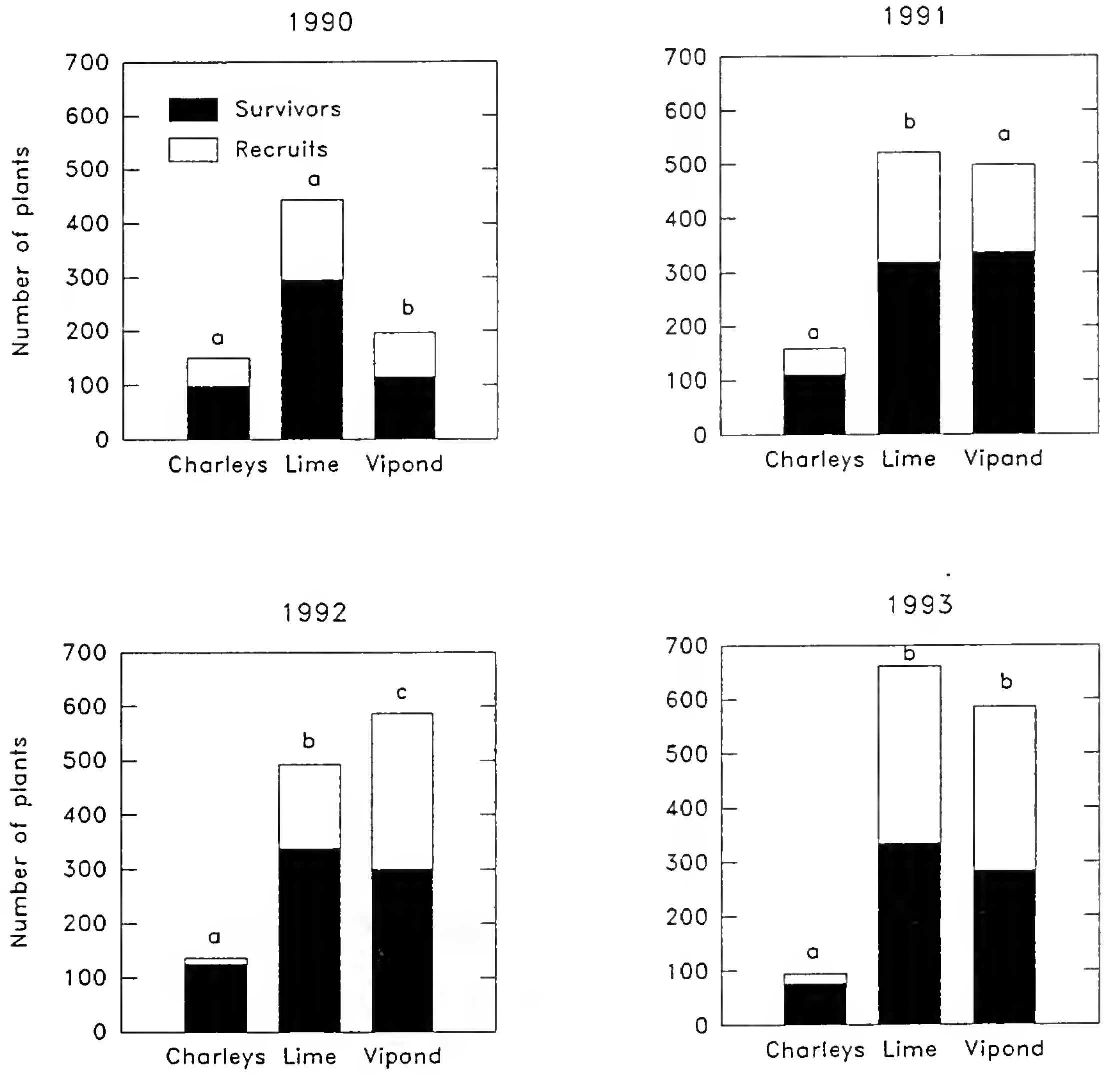

Figure 3. Survivorship curves for the 1990 _Arabis fecunda_ cohort at three study sites.

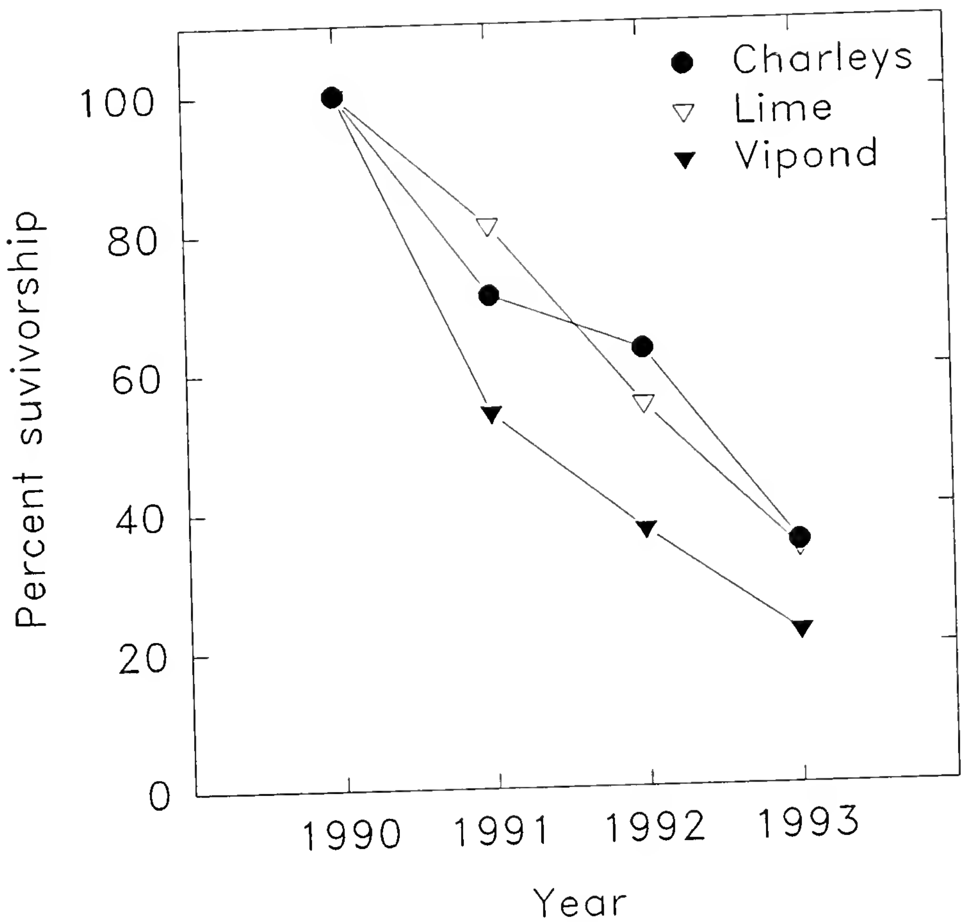

Figure 4. Arabis fecunda plants moving into a larger size class or moving into the same or a smaller class at three study sites in 1989-93. Sites with different letters had different growth rates (larger/smaller+same) as determined by Chi-square tests ($\underline{P}$<0.05).

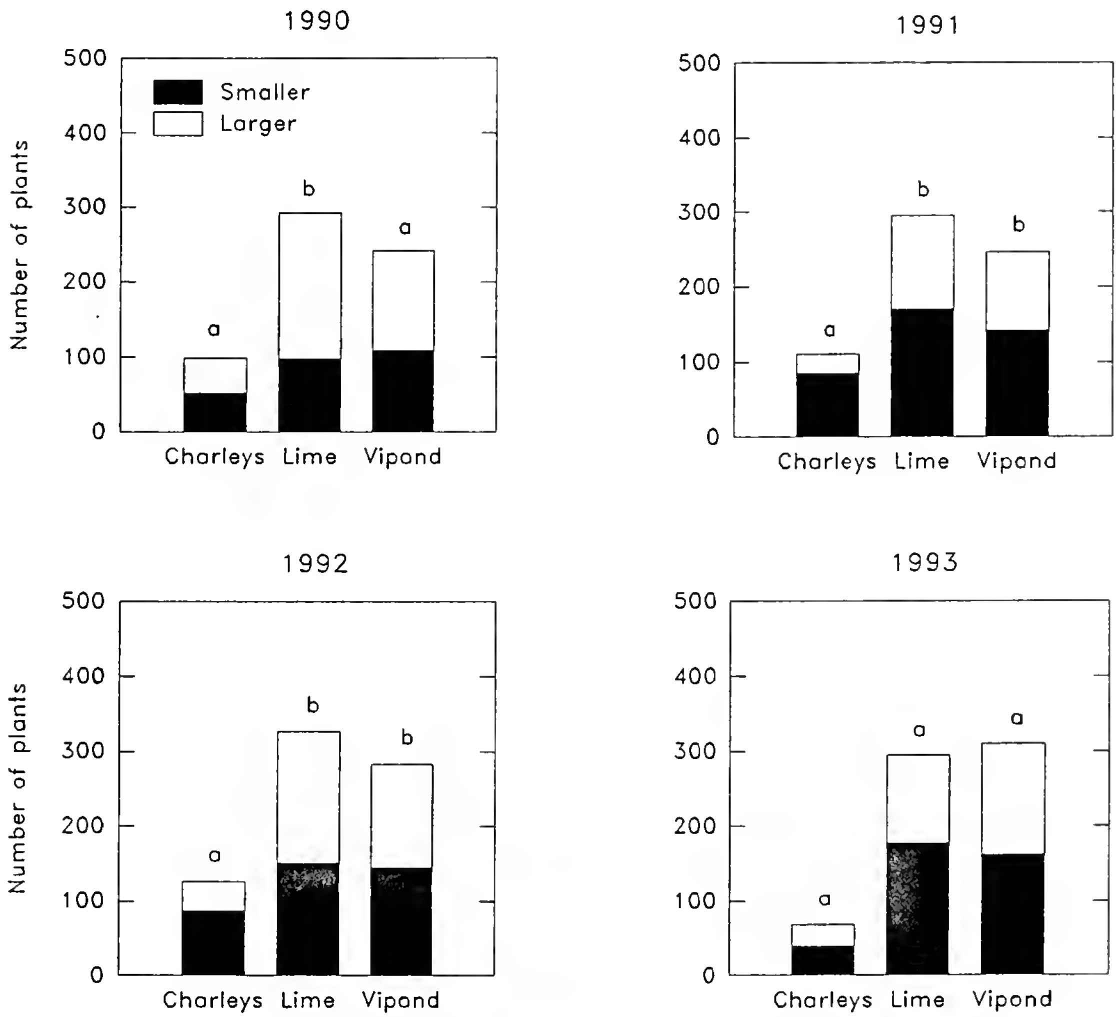

Figure 5. Number of bolting and axillary-flowering *Arabis fecunda* plants at three study sites in 1990-93. Sites with different letters had different proportions of bolting/axillary plants as determined by Chi-square tests (*P*<0.05).