THE EFFECT OF THE INTRODUCED WEED, CENTAUREA MACULOSA ON ARABIS FECUNDA, A THREATENED MONTANA ENDEMIC

Prepared for:

The Montana Natural Heritage Program
State Library
1515 East Sixth Avenue
Helena, Montana 59620

Prepared by:

Peter Lesica
P.O. Box 8944
Missoula, Montana 59807

and

J. Stephen Shelly
Montana Natural Heritage Program
State Library
1515 East Sixth Avenue
Helena, Montana 59620

January, 1991

THE EFFECT OF THE INTRODUCED WEED, CENTAUREA MACULOSA ON ARABIS FECUNDA, A THREATENED MONTANA ENDEMIC

Prepared for:

The Montana Natural Heritage Program
State Library
1515 East Sixth Avenue
Helena, Montana 59620

Prepared by:

Peter Lesica
P.O. Box 8944
Missoula, Montana 59807

and

J. Stephen Shelly
Montana Natural Heritage Program
State Library
1515 East Sixth Avenue
Helena, Montana 59620

January, 1991

Introduction

Competition is a difficult phenomenon to study effectively (Harper 1977, Keddy 1989). Much of the literature on competition is rife with circular reasoning and expositions of "the ghost of competition past" (Connell 1980). Experiments are often phenomenological and non-mechanistic, measuring what happens without examining how it happens (Tilman 1987). Tilman (1987, 1988) has urged a more mechanistic approach to the study of interspecific competition. He argues that such studies more often result in testable hypotheses, ultimately leading to more useful predictive generalizations.

Werner (1979) divided competitive interactions into two mechanistic categories: (1) preemptive i.e., competition for space and (2) interactive i.e., competition for water or nutrients. Similarly, Tilman (1988) divided resources into two broad groups: (1) space and light, and (2) nutrients and water. Many researchers have recognized the importance of regeneration in competitive interactions (Grubb 1977, Harper 1977, Grime 1979, Werner 1979). Nonetheless, most studies of plant interspecific interference have focused on competition for light, nutrients, and water during later life stages and have ignored the effects of competition for space on seedling establishment (Schoener 1983).

Another failing of many competition experiments is their short duration. Competition may be occurring, but relatively long periods of time may be necessary to observe it (MacArthur 1972). Furthermore, the effects of competition may change with time, thus a short-duration study can yield misleading results with regard to long-term community dynamics (Tilman 1988).

Arabis fecunda Rollins is a short-lived, rosette- and taproot-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 (Lesica 1985, Schassberger 1988). Plants bloom in early spring and disperse seed during early to mid-summer. The small seeds germinate readily without stratification (Lesica, unpublished data). Presumably most germination occurs following late summer and autumn rains, but a second bout of germination may occur in the spring. Mortality of seedlings and first year plants is high (Lesica and Shelly, unpublished data). Plants generally grow for at least one year before blooming and then produce one or more inflorescences with 3-many flowers. Individuals may branch at the root crown to form multi-rosette plants at any time during the life cycle. Rosettes are generally 1-4 cm in diameter.

Arabis fecunda is threatened by livestock trampling (Lesica and Shelly 1991a) and encroachment of habitat by the aggressive exotic Centaurea maculosa (spotted knapweed) at the Ravalli County sites. It also occurs in areas of historic mining activity in Beaverhead and Sliver Bow counties (Schassberger 1988). Arabis fecunda is a candidate for listing as a threatened or endangered species by the U.S. Fish and Wildlife Service (USDI-FWS 1990) and is considered threatened in Montana (Lesica and Shelly 1991b).

Centaurea maculosa Lam. (Asteraceae) is a native of Eurasia, widely introduced in North America, and has become a serious pest of semi-arid grasslands in the Pacific Northwest and intermountain valleys of the Northern Rocky Mountains (Watson and Renney 1974, French and Lacey 1983). Its ability to invade and replace native plants is well-documented (Morris and Bedunah 1984, Harris and Cranston 1979, Tyser and Key 1989). In addition, leachates of Centaurea maculosa inhibit germination of grass and conifer seedlings (Kelsey and Locken 1987); however, concentrations high enough to inhibit germination would seldom be found in natural environments (Kelsey and Bedunah 1989). Centaurea maculosa was introduced into western Montana in the 1920's and has since come to dominate large areas of rangeland (French and Lacey 1983). Like A. fecunda, it is a rosette-forming, taprooted perennial with an average life-span of 3-5 years (Watson and Renney 1974, Boggs and Story 1987).

Germination occurs in the fall or the following spring. Fall emerging plants overwinter as a rosette and may flower during their first summer. Spring-germinating plants generally bloom their second summer (Watson and Renney 1974).

In Ravalli County nearly all *Arabis fecunda* habitat has been invaded by *Centaurea maculosa*. Classical competition theory predicts that species with similar ecological requirements should compete most strongly (Hardin 1960). The morphological similarity between these two species suggests that *C. maculosa* may be interfering with *A. fecunda* at these sites. The purpose of our study was to examine the effects of *Centaurea maculosa* on populations of *Arabis fecunda* over a period of three years. We employed techniques of demographic monitoring (Menges 1986) in order to determine which life stages are being most affected and which mechanisms are most important.

Study Areas

We conducted our study at Birch Creek and Charley's Gulch, in Ravalli County. Both sites are on gentle southwest-facing slopes, the Birch Creek site at 1430 m and the Charley's Gulch site 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. Soils are sandy loams derived from calcareous parent material (Lesica

1985). Zonal vegetation surrounding the sites is foothills *Agropyron*-*Festuca* grasslands (Weaver 1980) with scattered *Pinus ponderosa* and *Pseudotsuga menziesii*. The effects of trampling and grazing by livestock are noticeable at both sites. At both sites *A. fecunda* occurs in communities with a relatively low density of vascular plants.

Methods

In 1987 we established a permanent belt transect consisting of 10 adjacent 1-m^2 plots at each of the study sites following methods outlined in Lesica (1987). Transects were placed in areas with moderate to high cover of *Centaurea maculosa* and *Arabis fecunda*. All *C. maculosa* plants were removed from five randomly selected plots in each transect in late May of each year by cutting the plants below the root crown using a sharp knife with a hooked blade. We were careful to disturb the soil as little as possible.

Individual *A. fecunda* plants were mapped and recorded using the following system:

S = plant with a single rosette < 2 cm diameter
R = plant with a single rosette > 2 cm diameter
S_x or R_x = a plant with x rosettes

In addition, for each reproductive plant we recorded the number of inflorescences and the number of fruits matured.

We classified plants into four life-stage classes:

Seedling = S_1
Single Rosette = R_1
Multiple Rosette = $S_{>1}$ or $R_{>1}$
Reproductive

A plants's demographic properties are often more closely correlated with life-stage (Werner and Caswell 1977, Caswell 1989), although both age and size may be important in predicting an individual's fate (Young 1985). We chose these classes because they correspond to age as well as size (Table 1; Lesica and Shelly, unpublished data). These categories also represent a reasonable compromise between having many categories with too few observations each and few categories with many observations (Vandermeer 1978).

We censused _Arabis fecunda_ in the permanent plots in late May, 1987-1990. We chose late May because _A. fecunda_ fruits are mature or nearly so, but dispersal has not yet occurred. Plants smaller than 0.5 cm in diameter were not recorded because they could not be reliably distinguished from other species. The experiment at Charley's Gulch had to be terminated after 1989 because plots were trampled by livestock.

We used stage-based transition matrix models to compare the performance of A. fecunda populations between the plots from which C. maculosa was removed (treatment) and the controls. Matrix projections assume fixed life-stage structures and simulate changes in a population through time (Lefkovitch 1965, Menges 1990). 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 one year depends only on its life-stage class at the beginning of the period, and is independent of its transition the previous year. Transition probabilities for the multi-year periods were made by summing the 1-year frequency tables for the period (Caswell 1989, p. 81). The "mean" matrix summarizes the behavior of the population over 2-3 years and integrates the effects of fluctuating environment during this period to give a more realistic estimate of the effect of the treatment on population growth. This method of constructing a mean matrix tends to minimize the effects of year-to-year differences in demographic patterns, but the bias is usually small (Huenneke and Marks 1987). The equilibrium growth rate (lambda) is the dominant eigenvalue of the transition probability matrix (Lefkovitch 1965, Caswell 1989). We estimated lambda and calculated confidence intervals using a bootstrap resampling procedure with a sample size of 1000 following methods outlined in Caswell (1989, p. 190). A lambda > 1.0 indicates population increase, while lambda < 1.0 indicates decrease.

We used 2 X 2 contingency table analysis to determine whether there were differences in performance of plants in particular life-stages between the treatment and control plots. At each site we compared the number of plants in a life-stage class that had moved to a smaller class (or died), with the number that had stayed in the same class or moved to a larger class between the treatment and control. Transitions from each of the three yearly intervals were pooled. All plants recorded during the study were either present at the beginning of the study or recruited during its course. The ratio of the latter to the former is a measure of recruitment over the three-year period, and the difference between treatment and control plots was also assessed in a 2 X 2 contingency table.

Simple population growth rate was calculated as the increase in number of individuals at the end of a time period divided by the number of individuals present at the beginning of the time period. A positive rate indicates that population size has increased. The effect of treatment on fecundity (fruits/reproductive plant) was analyzed using analysis of variance (ANOVA) on log-transformed data. Statistical calculations were performed on a microcomputer using SYSTAT (Wilkinson 1986). Eigenvalues and confidence intervals were obtained using GAUSS (Anon. 1988).

Results

Before the start of the experiment, cover of Centaurea maculosa was ca. 30% at Birch Creek and 25% at Charley's Gulch, and the difference between treatment and control plots was not significant (Table 2). After one year, C. maculosa cover was significantly reduced relative to controls at Charley's Gulch, but not at Birch Creek (Table 2). The resiliency of the C. maculosa population during the first year was due mainly to recruitment from the seed bank. In spite of this recruitment, removal of C. maculosa probably reduced competitive effects on A. fecunda. After two years, C. maculosa cover was significantly reduced at both sites (Table 2).

Summary demographic statistics for both sites are presented in Table 3. At Birch Creek there were fewer plants in the treatment plots compared to controls at the beginning of the experiment, but more than controls after one year. There were nearly equal numbers of fruiting plants in treatment and control plots during the first year of the experiment, but more in treatment plots in the last two years. Treatment plots had a higher recruitment rate during the first two years, but often also a higher mortality rate. Simple population growth was much higher in treatment plots the first year, but lower than controls the following two years. Nonetheless, simple population growth for the three years combined was greater for treatment plots (1.16) than controls (0.39).

At Charley's Gulch there were also fewer A. fecunda plants in the treatment plots compared to control plots at the beginning of the experiment, but more than in the control plots after one year. Treatment plots had more fruiting plants than controls at both the beginning and end of the experiment. Treatment plots had higher recruitment rates, and lower mortality, and higher simple population growth than controls. Over the two-year period, simple population growth for A. fecunda was greater for treatment plots (0.56) than controls (-0.03).

Fecundity, as measured by number of fruits per plant, was higher in treatment plots throughout the study period at both sites. Results of ANOVA indicate that treatment had a significant effect on the fecundity of Arabis fecunda (Table 4). However, a near-significant difference was present before the beginning of the experiment (ANOVA; N=135, F=3.16, p=0.078).

Recruitment rates at both sites were significantly higher in treatment plots than controls (Table 5). Otherwise, there were no significant differences between the performance of any life-stage classes between treatment and control plots at either site (Table 6). However, at Charley's Gulch, there was a trend for plants in both S_1 and R_1 classes to become larger in the treatment plots. Lack of a significant difference is probably due to the small sample size. If these two classes are combined, the difference between treatment and control is significant ($X^2=3.957$, $p<0.05$).

At both Birch Creek and Charley's Gulch, the equilibrium growth rate (lambda) of *Arabis fecunda* for the first two years of the study was significantly larger in plots with *Centaurea maculosa* removed compared to controls (Table 7). At Birch Creek the equilibrium growth rate is larger for the first three years as well, but the difference is not significant (Table 7). Over the study period, equilibrium growth rates of *A. fecunda* in control plots were not significantly different from 1.0 ($p<0.05$).

Discussion

The results of our study indicate that *Centaurea maculosa* is competing with *Arabis fecunda* and that this competition is being effected primarily by a reduction in recruitment (preemptive competition *sensu* Werner 1979) rather than interference at later stages. During the first two years following removal of *C. maculosa*, both equilibrium growth rate calculated from projection matrices and simple growth rate of *A. fecunda* populations were higher in treatment plots. Reproductive rates as measured by the number of new plants per reproductive individual were also higher in treatment plots at both sites for the first two years after removal of C. maculosa, and recruitment rate over the period of the study was significantly higher at both sites. With the exception of the slight tendency for small plants to survive better in treatment plots at Charley's Gulch, there is no evidence that plants in any life-stage class performed better in plots from which C. maculosa had been removed.

The presence of Centaurea maculosa could adversely affect Arabis fecunda recruitment by (1) reducing fecundity and/or (2) curtailing establishment of seedlings. We detected only a small increase in A. fecunda fecundity in the treatment plots during the first two years following removal of C. maculosa. Although this difference could be important, it is more likely that the observed increase in A. fecunda recruitment is due to enhanced seedling establishment. Establishment of A. fecunda seedlings could have been inhibited by competition with C. maculosa, but this seems unlikely since C. maculosa did not interfere with larger plants. Allelopathy could also explain our results, and extracts of cnicin from Centaurea maculosa do inhibit germination of grasses and conifers (Kelsey and Locken 1987). However, Kelsey and Bedunah (1989) concluded that concentrations of cnicin high enough to cause interference are rarely present in natural situations. Thus, it seems most likely that C. maculosa reduces

A. fecunda recruitment by usurping space and light from germinating seedlings. Gurevitch (1986) found that inhibition of seedling establishment was an important effect of interspecific competition on the grass, Stipa neomexicana, although she also found that competition limited the growth and flower production of mature plants.

At Birch Creek, removal of Centaurea maculosa resulted in increased recruitment and population growth for the first two years, but by the third year the difference between treatment and control plots had disappeared. This pattern suggests that A. fecunda underwent a two-year period of competitive release following removal of C. maculosa but was approaching a new, higher equilibrium after two years. Put simply, removal of Centaurea maculosa increased the carrying capacity of the habitat for Arabis fecunda.

The results of our study indicate that the main mechanism by which Centaurea maculosa interferes with Arabis fecunda is reduction of space available for seedling establishment. This hypothesis suggests that competitive displacement of A. fecunda will not occur if density of C. maculosa stays near current levels. The fact that equilibrium growth rates were near 1.0 for the study period lends support to this conclusion. If C. maculosa increases in these habitats, the size of A. fecunda populations will decrease and the risk of chance extinction events will become more likely (Goodman 1987).

Herbicide application is currently the most commonly employed method for controlling *Centaurea maculosa* infestations (Harris and Cranston 1979, McKone et al. 1989); however, little is known about specific effects on *Arabis fecunda*, and correct rates of application are difficult to determine for novel situations, such as the azonal *A. fecunda* sites (Peter Rice, pers. comm.). Removing *C. maculosa* by hand would result in serious damage to the fragile slope habitat. To date, biological control vectors have been unable to reduce infestations of *Centaurea maculosa*. Although introduced seed-head gall flies (*Urophora affinis* and *U. quadrifasciata*) can reduce seed production from 50-75% (Story 1989), they have been unable to reduce the density of *C. maculosa* (Muller and Schroeder 1989). However, with the recent introduction of a root-boring moth (*Agapeta zoegana*), control of *C. maculosa* should be possible (Story 1989, Muller and Schroeder 1989). Since biological control causes minimal disturbance and promises to have the ability to halt population growth of *C. maculosa*, it appears to be the best option for protecting populations of *Arabis fecunda* from extinction due to encroachment by *Centaurea maculosa*.

Acknowledgements

We are grateful to John Robbins and George Frost for permission to conduct this study on their land. Brian Steele and Dave Patterson helped with statistics. Keith Boggs and Peter Rice advised on the ecology of *Centaurea maculosa*.

Literature Cited

Anon. 1988. GAUSS. Aptech Systems Inc., Kent, Washington.

Boggs, K. W. and J. M. Story. 1987. The population age structure of spotted knapweed (Centaurea maculosa) in Montana. Weed Science 35: 194-198.

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

Connell, J. H. 1980. Diversity and the coevolution of competitors, or the ghost of competition past. Oikos 35: 131-138.

French, R. A. and J. R. Lacey. 1983. Knapweed, its cause, effect and spread in Montana. Montana State University, Cooperative Extension Service, Circular 307, Bozeman.

Goodman, D. 1987. The demography of chance extinction. In M. E. Soule (ed), Viable populations for conservation. Cambridge University Press, Cambridge.

Grime, J. P. 1979. Plant strategies and vegetation processes. John Wiley & Sons, Chichester.

Grubb, P. J. 1977. The maintenance of species richness in plant communities: the importance of the regeneration niche. Biological Reviews 52: 107-45.

Gurevitch, J. 1986. Competition and the local distribution of the grass, Stipa neomexicana. Ecology 67: 46-57.

Hardin, G. 1960. The competitive exclusion principle. Science 131: 1292-1297.

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

Harris, P. and R. Cranston. 1979. An economic evaluation of control methods for diffuse and spotted knapweed in western Canada. Canadian Journal of Plant Science 59: 375-382.

Huenneke, L. F. and P. L. Marks. 1987. Stem dynamics of the shrub Alnus incana ssp. rugosa: transition matrix models. Ecology 68: 1234-1242.

Keddy, P. A. 1989. Competition. Chapman and Hall, London.

Kelsey, R. G. and L. J. Locken. 1987. Phytotoxic properties of cnicin, a sesquiterpene lactone from Centaurea maculosa (spotted knapweed). Journal of Chemical Ecology 13: 19-33.

Kelsey, R. G. and D. Bedunah. 1989. Ecological significance of allelopathy for Centaurea species in the northwestern United States. Proceedings of the Knapweed Symposium. Montana State University, Cooperative Extension Service Bulletin No. 1315, Bozeman.

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. Unpublished report to the USDI Fish and Wildlife Service, Office of Endangered Species, Denver.

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

Lesica, P. and J. S. Shelly. 1991a. The effects of cryptogamic soil crust on the vascular plant, Arabis fecunda. Unpublished report to the Montana Natural Heritage Program, Helena.

Lesica, P. and J. S. Shelly. 1991b. Endangered, threatened and sensitive vascular plants of Montana. Montana State Library, Helena (in press).

MacArthur, R. H. 1972. Geographical ecology. Princeton University Press, Princeton, New Jersey.

McKone, M. B., C. A. Lacey and D. Bedunah. 1989. Evaluation of clopyralid rate and time of application on spotted knapweed (Centaurea maculosa Lam.). In P. K. Fay and J. R. Lacey (eds.) Proceedings of the 1989 Knapweed Symposium, Montana State University, Bozeman.

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.

Morris, M. S. and D. Bedunah. 1984. Some observations on the abundance of spotted knapweed (Centaurea maculosa) in western Montana. Proceedings of the Knapweed Symposium. Montana State University, Cooperative Extension Service Bulletin No. 1315, Bozeman.

Muller, H. and D. Schroeder. 1989. The biological control of diffuse and spotted knapweed in North America - What have we learned? In P. K. Fay and J. R. Lacey (eds.) Proceedings of the 1989 Knapweed Symposium, Montana State University, Bozeman.

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. Unpublished report to the USDI Fish and Wildlife Service, Office of Endangered Species, Denver.

Schoener, T. W. 1983. Field experiments on interspecific competition. American Naturalist 122: 240-285.

Story, J. M. 1989. The status of biological control of spotted and diffuse knapweed. _In_ P. K. Fay and J. R. Lacey (eds.) Proceedings of the 1989 Knapweed Symposium, Montana State University, Bozeman.

Tilman, D. 1987. The importance of the mechanisms of interspecific competition. American Naturalist 129: 769-774.

Tilman, D. 1988. Plant strategies and the dynamics and structure of plant communities. Princeton University Press, Princeton, New Jersey.

Tyser, R. W. and C. H. Key. 1988. Spotted knapweed in natural area fescue grasslands: An ecological assessment. Northwest Science 62: 151-159.

USDI-Fish and Wildlife Service. 1990. Endangered and threatened wildlife and plants; review of plant taxa for listing as endangered or threatened species; notice of review. Federal Register 55 (35): 6184-6229.

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

Watson, A. K. and A. J. Renney. 1974. The biology of Canadian weeds 6. _Centaurea diffusa_ and _C. maculosa_. Canadian Journal of Plant Science 54: 687-701.

Weaver, T. 1980. Climates of vegetation types of the Northern Rocky Mountains and adjacent plains. American Midland Naturalist 103: 392-398.

Werner, P. A. 1979. Competition and coexistence of similar species. _In_ O. T. Solbrig, S. Jain, G. G. Johnson and P. H. Raven, eds., Topics in plant population biology. Columbia University Press, New York.

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.

Wilkinson, L. 1986. SYSTAT: The system for statistics. SYSTAT Inc., Evanston, IL.

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

Table 1. Percent of *Arabis fecunda* plants in each life-stage class that are ≤1-year old at the two study sites. Numbers given are the mean of three years, 1988-1990.

	Birch Creek	Charley's Gulch
Seedling	98%	66%
Single Rosette	64%	32%
Multiple Rosette	44%	23%
Reproductive	18%	17%

Table 2. Mean canopy cover of *Centaurea maculosa* in *Centaurea maculosa* removal (treatment) and control plots at Birch Creek (1987-90) and Charley's Gulch (1987-89) and Mann-Whitney tests for significance. 1987 measurements were made before treatment began.

Birch Creek

Year	Control	Treatment	U	p
1987	31.8±4.5	28.2±5.6	16	0.46
1988	25.0±7.1	26.0±5.5	12	0.81
1989	25.2±9.5	10.0±5.0	24	0.02
1990	29.8±12.8	13.4±6.8	23	0.04

Charley's Gulch

Year	Control	Treatment	U	p
1987	22.6±2.5	25.2±4.0	8	0.28
1988	27.6±5.6	15.8±6.7	24	0.02
1989	29.2±3.0	5.8±3.2	25	0.01

Table 3. Demographic statistics for _Arabis fecunda_ in _Centaurea maculosa_ removal (treatment) and control plots at Birch Creek (1987-90) and Charley's Gulch (1987-89). Simple population growth is the increase in plants over the previous year divided by the number of plants present the previous year. Reproductive rate is the number of new plants divided by the number of reproductive plants present the previous year.

Birch Creek

	1987		1988		1989		1990	
	Control	Treatment	Control	Treatment	Control	Treatment	Control	Treatment
Total plants	106	76	120	165	95	121	147	164
Fruiting plants	40	42	7	6	28	42	32	46
New plants	--	--	68	128	40	55	87	106
Dead plants	--	--	54	39	74	98	26	63
Population growth	--	--	0.13	1.17	-0.21	-0.27	0.55	0.36
Reproductive rate	--	--	1.70	3.05	5.71	9.17	3.11	2.52

Charley's Gulch

	1987		1988		1989	
	Control	Treatment	Control	Treatment	Control	Treatment
Total plants	72	64	71	72	70	100
Fruiting plants/plot	24	29	2	2	28	32
New plants	--	--	15	21	14	38
Dead plants	--	--	16	13	15	10
Population growth	--	--	-0.01	0.13	-0.01	0.39
Reproductive rate	--	--	0.63	0.72	7.00	19.00

Table 4. Fecundity (fruits/plant) for *Arabis fecunda* at Birch Creek (1987-90) and Charley's Gulch (1987-89) and the effect of *Centaurea maculosa* removal (treatment), site, year and their interactions on *Arabis fecunda* fecundity during the first two years of the experiment by ANOVA. Fecundity was log-transformed before analysis. Sample sizes for individual sites and years can be found in the "Fruiting plants" rows in Table 3.

Birch Creek

	1987	1988	1989	1990
Control	4.9 (0.7)	5.7 (1.3)	26.0 (3.3)	18.0 (3.1)
Treatment	6.6 (0.7)	15.2 (3.2)	33.7 (3.2)	21.1 (2.5)

Charley's Gulch

	1987	1988	1989
Control	4.1 (0.9)	8.5 (5.5)	14.9 (2.6)
Treatment	4.6 (0.6)	11.5 (3.5)	16.5 (2.0)

Fruits/Plant (N=148)

Factor	df	Mean-Square	F	p
Treatment	1	4.999	5.780	**0.018**
Site	1	0.900	1.041	0.309
Year	1	5.609	6.485	**0.012**
Treatment*Site	1	0.010	0.012	0.915
Treatment*Year	1	0.923	1.067	0.303
Site*Year	1	2.811	3.250	0.074
Error	141	0.865		

Table 5. Recruitment rate (number new plants during study/number of plants at start of study) for Centaurea maculosa removal (treatment) and control plots at Birch Creek (1987-1990) and Charley's Gulch (1987-1989).

Birch Creek

Recruitment	New Plants	Original Plants	Total	
Control	195	106	301	1.84
Treatment	289	76	365	3.80

$X^2=17.21$, $p<0.001$

Charley's Gulch

Recruitment	New Plants	Original Plants	Total	
Control	29	72	101	1.84
Treatment	59	64	123	3.80

$X^2=8.620$, $p=0.003$

Table 6. Contingency tables for performance of individual *Arabis fecunda* life-stage classes at Birch Creek (1987-90) and Charley's Gulch (1987-1989). Plants either (1) reverted to a smaller class or died (smaller) or (2) moved to a larger class or stayed in the same class (larger).

Seedlings

Birch Creek

	Smaller	Larger	Total	
Control	18	7	25	$X^2=0.510$
Treatment	35	9	44	$p=0.475$

Charley's Gulch

	Smaller	Larger	Total	
Control	5	3	8	$X^2=1.650$
Treatment	4	8	12	$p=0.199$

Single Rosette Transitions

Birch Creek

	Smaller	Larger	Total	
Control	82	87	169	$X^2=1.198$
Treatment	100	84	184	$p=0.274$

Charley's Gulch

	Smaller	Larger	Total	
Control	23	56	79	$X^2=3.286$
Treatment	13	64	77	$p=0.070$

Multiple Rosette Transitions

Birch Creek

	Smaller	Larger	Total	
Control	22	22	44	$X^2=0.317$
Treatment	23	18	41	$p=0.573$

Charley's Gulch

	Smaller	Larger	Total	
Control	7	23	30	$X^2=0.060$
Treatment	4	11	15	$p=0.806$

Reproductive Transitions

Birch Creek

	Smaller	Larger	Total	
Control	64	11	75	$X^2=0.785$
Treatment	68	17	85	$p=0.376$

Charley's Gulch

	Smaller	Larger	Total	
Control	24	2	26	$X^2=0.033$
Treatment	29	2	31	$p=0.856$

Table 7. Equilibrium growth rate (lambda) for *Arabis fecunda* populations in *Centaurea maculosa* removal (treatment) and control plots at Birch Creek (1987-1990) and Charley's Gulch (1987-89). Values of lambda are best estimates from bootstrap resampling with a sample size of 1000 (see Methods).

Birch Creek 1987-1989

		From		
To	S_1	R_1	$S,R_{>1}$	$R_{F\geq0}$ + Rec.
S_1	.00	.00	.00	.00 + .53
R_1	.20	.23	.03	.30 + 1.36
$S,R>1$	.00	.07	.25	.06 + .28
$R_{F\geq0}$	.00	.14	.13	.13 + .10

Control: lambda=0.811

		From		
To	S_1	R_1	$S,R_{>1}$	$R_{F\geq0}$ + Rec.
S_1	.00	.01	.00	.00 + 1.00
R_1	.18	.25	.00	.30 + 2.42
$S,R>1$	.00	.05	.09	.14 + .46
$R_{F\geq0}$	.09	.13	.27	.14 + .35

Treatment: lambda=1.161

$t=3.395$, $p<0.001$

Birch Creek 1987-1990

		From		
To	S_1	R_1	$S,R_{>1}$	$R_{F\geq0}$ + Rec.
S_1	.04	.01	.00	.00 + .85
R_1	.16	.26	.02	.25 + 1.39
$S,R>1$	.04	.07	.25	.05 + .24
$R_{F\geq0}$	.04	.18	.25	.23 + .08

Control: lambda=0.977

		From		
To	S_1	R_1	$S,R_{>1}$	$R_{F\geq0}$ + Rec.
S_1	.00	.01	.00	.00 + 1.18
R_1	.14	.24	.05	.18 + 1.63
$S,R>1$	.00	.04	.10	.09 + .27
$R_{F\geq0}$	.07	.17	.34	.23 + .19

Treatment: lambda=1.070

$t=1.348$, $p=0.889$

Charley's Gulch 1987-89

		From		
To	S_1	R_1	$S,R_{>1}$	$R_{F\geq0}$ + Rec.
S_1	.25	.08	.03	.00 + .38
R_1	.13	.46	.07	.39 + .46
$S,R>1$	.00	.05	.43	.31 + .23
$R_{F\geq0}$	.00	.20	.33	.11 + .04

Control: lambda=0.962

		From		
To	S_1	R_1	$S,R_{>1}$	$R_{F\geq0}$ + Rec.
S_1	.00	.04	.07	.10 + .80
R_1	.58	.48	.07	.65 + .90
$S,R>1$	.00	.05	.40	.03 + .07
$R_{F\geq0}$	.08	.30	.33	.06 + .10

Treatment: lambda=1.199

$t=4.210$, $p<0.001$