Facilitation interference and demography in the rare mustard Lesquerella carinata var. languida.

John T. Greenlee
The University of Montana

Follow this and additional works at: https://scholarworks.umt.edu/etd

Let us know how access to this document benefits you.
Permission is granted by the author to reproduce this material in its entirety, provided that this material is used for scholarly purposes and is properly cited in published works and reports.

** Please check “Yes” or “No” and provide signature **

Yes, I grant permission

No, I do not grant permission

Author’s Signature

Date: 4/14/94

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.
FACILITATION, INTERFERENCE, AND DEMOGRAPHY IN THE RARE MUSTARD LESQUERELLA CARINATA var. LANGUIDA

by

John T. Greenlee

B.S. Indiana University, 1988

presented in partial fulfillment of the requirements for the degree of Master of Science

The University of Montana

1994

Approved by:

[Signature]
Chairperson

[Signature]
Dean, Graduate School

May 2, 1994
Date
Facilitation, Interference, and Demography in the Rare Mustard *Lesquerella carinata* var. *languida*

Director: Thomas Mitchell-Olds

Studies of rare species' ecology provide important information for conservation planning. I studied facilitation, interference, and competition in the rare mustard *Lesquerella carinata*, which is threatened by an invasive weed and by disturbance from cattle. I investigated potential facilitative effects of native bunchgrasses and potential interfering effects of the non-native *Centaurea maculosa* on the performance of *Lesquerella*. Natural seedling and adult *Lesquerella* were positively associated with bunchgrass canopies. To determine the importance of facilitation, *Lesquerella* seeds were planted in the field into four experimental treatments: under bunchgrasses, in the open, under clipped bunchgrass canopies, and under artificial shade. *Lesquerella* survivorship in the open treatment was significantly greater than under bunchgrasses, which suggests that bunchgrasses interfere with *Lesquerella*. Root and shoot biomass did not differ among the treatments. The effects of spotted knapweed interference were investigated with a removal experiment. *Centaurea* negatively affects *Lesquerella* seedling survivorship. Field experiments found no significant effects of bunchgrass facilitation of *Lesquerella*, but positive spatial associations between bunchgrasses and *Lesquerella* and *Centaurea* removal experiments indicate that both facilitation and interference may have important effects on the *Lesquerella*-bunchgrass system.

Matrix population models were used to investigate short term population dynamics and the importance of different life cycle stages to population growth for three natural populations of *Lesquerella*. Survival, growth, and recruitment were measured in all study populations, and these data were used to create a size/life history-based transition matrix having four stages: small, medium, large, and reproductive plants. Bootstrapping was applied to the data set to calculate 95% confidence intervals for the population growth rate, and an elasticity analysis was performed to determine which life cycle stage made the greatest contribution to population growth. All the populations were decreasing in 1991-1992 and increasing in 1992-1993. Survival of large and reproductive plants had the greatest contribution to population growth. Cattle trampling and environmental fluctuations have the potential to impact the most important stages of the *Lesquerella* life cycle. Biological control of *Centaurea* and fencing out of cattle are recommended to minimize the threats to the *Lesquerella* populations.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.
ACKNOWLEDGEMENTS

I would like to thank all my friends and colleagues who contributed to this research. I am grateful to Jeff Dole, Diane Krahe, Eric Zdilla, Charlene Hershner, Elaine Caton, Lynn Bacon, Matt Sanger, Christian Sarver, Chris Krumm, Kathy Rollins, and Kurt Menning for their diligent help in collecting the data. This project was greatly improved with the generous help of Dara Newman, Diana Pilson, Ray Callaway, and Peter Lesica. This project was supported by a National Science Foundation Graduate Research Fellowship, The Nature Conservancy, and National Science Foundation grant BSR-9100397 to Tom Mitchell-Olds.
# TABLE OF CONTENTS

<table>
<thead>
<tr>
<th>ABSTRACT</th>
<th>ii</th>
</tr>
</thead>
<tbody>
<tr>
<td>ACKNOWLEDGEMENTS</td>
<td>iii</td>
</tr>
<tr>
<td>TABLE OF CONTENTS</td>
<td>iv</td>
</tr>
<tr>
<td>LIST OF TABLES</td>
<td>vi</td>
</tr>
<tr>
<td>LIST OF FIGURES</td>
<td>vii</td>
</tr>
</tbody>
</table>

*Chapter 1:*

**BUCHGRASS FACILITATION, SPOTTED Knapweed INTERFERENCE, AND THEIR EFFECTS ON THE RARE PLANT **Lesquerella Carinata**

**INTRODUCTION**

**1**

**MATERIALS AND METHODS**

- Study sites
- Pattern analysis
- Facilitation experiment
- Interference experiment

**RESULTS**

- Association of *Lesquerella* with other species
- Mechanisms of facilitation of *Lesquerella* by bunchgrass
- Interference experiment

**DISCUSSION**

**10**

*Chapter 2:*

**DEMOGRAPHIC ANALYSIS OF THE RARE PLANT**

**Lesquerella Carinata**

**INTRODUCTION**

**19**

**MATERIALS AND METHODS**

- Species studied

**20**

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.
Study sites 21
Field methods 22
Data analysis 22

RESULTS 25
Population dynamics 25
Stable stage distribution and reproductive value 26
Elasticity analysis 27
Seed bank 28

DISCUSSION 29
Population persistance 31
Conservation implications 32

LITERATURE CITED 45 A

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.
LIST OF TABLES

Table 1. Analysis of spatial associations between bunchgrasses and *Lesquerella* 15

Table 2. Test statistics for measures of the response of *Lesquerella* to *Centaurea* removal 17


LIST OF FIGURES

Figure 1. Survivorship of Lesquerella seedlings planted in four experimental treatments. 18

Figure 2. The biomass of roots and shoots of Lesquerella planted in four experimental treatments. 18

Figure 3. Transition matrix and life cycle graph for Lesquerella. 39

Figure 4. Values of \( \lambda \) for three Lesquerella populations for 1991-1992 and 1992-1993. 41

Figure 5. The number of Lesquerella born into each life cycle stage at Bear, Mulkey, and Rattler Gulches in 1992 and 1993. 41

Figure 6. Mortality and mortality rate in the small, medium, large, and reproductive stages of Lesquerella in three populations for 1991-1992 and 1992-1993. 42

Figure 7. The proportion of Lesquerella in each stage in three populations for 1991-1992 and 1992-1993. 43

Figure 8. Life cycle graphs of Lesquerella showing elasticity values greater than 5%. 44

INTRODUCTION

Facilitative interactions, though historically thought to be an important structuring force in nature (Clements et al. 1928; Allee et al. 1949; Odum 1969), have received relatively little recent attention compared to competitive interactions. However, there is now a growing body of experimental evidence (Callaway 1992, 1994; Callaway et al. 1991; Bertness and Shumway 1993; Kellman and Kading 1992) to complement the numerous descriptive studies (e.g. Petranka and McPherson 1979; Werner and Harbeck 1982; McAuliffe 1988; Franco and Nobel 1989; Callaway and D'Antonio 1991; Valiente-Banuet et al. 1991a,b) which show facilitation to be an important interaction, especially in physically harsh environments (Bertness and Callaway, 1994). Plants may be facilitated by a number of potential mechanisms: subcanopy nutrient accumulation (Belsky et al. 1989; Callaway et al. 1991), higher subcanopy soil moisture (Joffre and Rambal 1988), shelter from herbivores (McAuliffe 1988; Callaway 1992), or lower subcanopy temperatures (Valiente-Banuet et al. 1991b; Franco and Nobel 1989).

Interference, on the other hand, has been studied extensively in many different plant and animal systems (reviewed by Connell 1983; Schoener 1983; Fowler 1986; Aarssen and Epp 1990; Goldberg and Barton 1992). Interference is thought to play an especially significant role in the invasion of natural communities by introduced species (Harris 1967; Bazzaz 1986; Caldwell et al. 1987).
In the northwestern United States, *Centaurea maculosa* Lam. (spotted knapweed) is one such invader. This invasive plant covers over 1.8 million hectares in Montana alone (Lacey et al. 1986) and has been found to reduce seed germination, seedling growth, and productivity of native grasses and forbs on economically important rangelands (Myers and Berube 1983; Fletcher and Renney 1963; Kelsey and Bedunah 1989) as well as in communities experiencing no livestock grazing (Tyser and Key 1988; Tyser and Worley 1992). The mechanism(s) by which spotted knapweed becomes the dominant species in invaded communities remains unclear. Lesica and Shelly (unpublished data) documented interference between spotted knapweed and the rare plant *Arabis fecunda* Rollins. Phytotoxic chemicals have been found in the leaves of spotted knapweed, but no studies have conclusively demonstrated allelopathic effects in the field (Kelsey and Bedunah 1989). Spotted knapweed competition via nutrient depletion has also been demonstrated, though not conclusively (Harvey and Nowierski 1989).

Both facilitation by bunchgrass and invasion by spotted knapweed appear to be important factors affecting the rare mustard *Lesquerella carinata* var. *languida* Rollins, which is a candidate for listing as threatened or endangered (USDI-FWS 1993). There is a positive association between *L. carinata* and native bunchgrasses (J. Greenlee, data presented below), and *Centaurea* is currently invading the *Lesquerella*-bunchgrass system. The interactions between *Lesquerella* and bunchgrasses and between *Lesquerella* and *Centaurea* are two potentially important factors influencing *Lesquerella* population dynamics. Here I have investigated the importance of bunchgrass facilitation to *Lesquerella*, the mechanisms of facilitation, and the importance of
interference to the Lesquerella-Centaurea interaction. By gaining an understanding of these aspects of Lesquerella ecology, improvements can be made in the conservation planning for this species.

MATERIALS AND METHODS

STUDY SITES

Lesquerella carinata var. languida Rollins (Brassicaceae) is a short-lived perennial herb that is only found in western Montana along the southern edge of the Garnet Range northwest of Drummond, Montana, and in the Sapphire Range approximately 32 km southwest of Philipsburg, Montana (Rollins 1993). The plants grow on easily disturbed, gravelly, calcareous soils on south to west facing slopes. These xeric, open sites are found in ecotonal areas between ponderosa pine/bitterbrush and bitterbrush/grassland habitat types, from 1,220 to 1,700 m in elevation (Schassberger 1991). The dominant herbaceous species in this community are bunchgrasses, primarily Pseudoregneria spicata (Pursh) Løve (blue-bunch wheatgrass).

I performed experiments at two sites. Rattler Gulch (elevation 1,646 m, 46° 44'N, 113° 15'W) is a dry south-facing site where I observed a positive association between bunchgrasses and Lesquerella. I performed the facilitation experiment at this site. Bear Gulch (elevation 1,311 m, 46° 45'N, 113° 21'W) is a moister, west-facing site located about 8 km west of Rattler Gulch. No bunchgrass-Lesquerella association was evident at Bear Gulch.

Both sites are being invaded by Centaurea maculosa Lam. (Asteraceae). This Eurasian native is a rosette-forming, tap-rooted perennial with an average lifespan of three to five years (Watson and Renney 1974; Boggs and Story...
1987). Much of the Bear Gulch Lesquerella population has been invaded by Centaurea, and very little of the Rattler Gulch population has been invaded. For this reason the interference experiment was performed at Bear Gulch.

**Pattern Analysis**

Associations between Lesquerella and all bunchgrasses were examined at Rattler and Bear Gulches with a spatial pattern analysis. In May, 1993, I determined vegetation cover in 60 randomly selected 0.25 m² plots in the absence of Centaurea along a 50 m transect at Rattler Gulch; 40 randomly selected plots were used at Bear Gulch, 20 of which were in Centaurea-invaded areas and 20 of which were not. In each plot at Rattler Gulch I measured presence/absence of open, bunchgrass, and forb canopy cover in 100 equally-sized squares formed by plastic line strung on a 0.5 m x 0.5 m plastic frame; at Bear Gulch litter and Centaurea cover classes were used as well. At Rattler Gulch I randomly located another 50 m transect and then randomly chose sampling points. At each sampling point I counted all seedling and adult Lesquerella within a 1 m radius of the point. I recorded the type of canopy cover each Lesquerella was associated with by standing directly overhead and determining whether the Lesquerella was under the canopy of the given cover type.

There are two errors in my sampling design. I recorded more than one Lesquerella per sampling point, so these measurements are not totally independent of one another. Because I did not record the number of sampling points I used, I cannot re-analyze the data properly. The results of my spatial pattern analysis may therefore be an artifact of my experimental design. Furthermore, I did not record the species of bunchgrass(es) that Lesquerella
was associated with; only bunchgrasses as a generic vegetation type were noted. This same sampling procedure was repeated at Bear Gulch for seedling and adult *Lesquerella* in the absence of *Centaurea* and for adult *Lesquerella* growing with *Centaurea*. Association with bunchgrass was recorded for 286 adult and 178 seedling *Lesquerella* at Rattler Gulch, for 110 adult and 119 seedling *Lesquerella* at Bear Gulch without *Centaurea*, and for 86 adult *Lesquerella* at Bear Gulch with *Centaurea*. A single classification G-test of goodness of fit was used to compare the observed distribution of adult or seedling *Lesquerella* for each site to the distribution expected if *Lesquerella* grew randomly in its environment.

**Facilitation Experiment**

I conducted a field experiment to study the positive association between *Lesquerella* and bunchgrasses (see Results) and to explore the potential facilitative mechanisms. *Lesquerella* seeds were planted in four treatments at Rattler Gulch. To determine if facilitation was an important interaction, *Lesquerella* seeds were planted under bunchgrass canopies and in the open. If the facilitation hypothesis is true, *Lesquerella* should perform better under the bunchgrass canopies. *Lesquerella* seeds were also planted under clipped bunchgrass canopies and under artificial shade to examine potential mechanisms of facilitation. The clipped bunchgrass treatment tests whether *Lesquerella* and bunchgrasses share common microsite requirements; if a shared microsite is the mechanism, plants in the clipped treatment should outperform plants in the shade treatment. Both treatments test whether shading is the facilitative mechanism; if this hypothetical mechanism holds, then plants
in the shade treatment should outperform plants in the clipped treatment. Artificial shade was provided by Hummert’s 47% shade cloth.

I planted 224 seeds into each of four randomly chosen 4m x 7m blocks. Each block consisted of 28 1 m² plots, and each plot contained two bunchgrass treatments, two open treatments, two clipped bunchgrass treatments, and two artificial shade treatments. All treatments were randomly located within each plot. Before planting, the seeds were scarified with sandpaper and stratified at 1 - 2°C in the dark for one month; this treatment enhances germination in the greenhouse (pers. obs.). Seeds were marked with a plastic toothpick. I planted seeds in mid-March, 1993, censused seedlings weekly until May 8, and then monitored seedlings approximately every ten days thereafter until September 19, 1993. At this time the seedlings were removed and dried at 50°C until repeated weighings showed no change in mass.

Seedling survivorship was analyzed in two ways. First, a loglinear model was used that included block, treatment, and survivorship as the variables. However, because several of the expected cell counts were less than one, the χ² approximation may not be valid. Therefore, I also carried out the analysis as a two-way G test (survival by treatment) in which I ignored the block effect, which did not have a significant effect on survival according to the first analysis. Both of the analyses showed a significant effect of treatment on survival (see Results), and I report the results of the second analysis.

Root and shoot biomass values were log transformed to normality and analyzed in two ways because there were missing cells in the ANOVA table. First, the incomplete block was dropped and a mixed model MANOVA (including the interaction term) was performed. Second, the incomplete block was kept, and a MANOVA without the interaction term was performed. Planned
contrasts were used to compare the canopy and open treatments. Neither analysis was significant (see Results), so the second analysis is reported.

INTERFERENCE EXPERIMENT

I tested for the effects of interference between Centaurea and Lesquerella by comparing the performance of Lesquerella growing with Centaurea to the performance of Lesquerella growing in quadrats from which I had removed Centaurea. In late March, 1993, I cut the taproot and removed all Centaurea in 13 randomly chosen 1m x 1m quadrats located in 9 existing belt transects at the Bear Creek Lesquerella site; the remaining 12 quadrats served as controls. 475 individual Lesquerella in these transects had been marked when the transects were established in 1992. In April, 1993, I marked all new Lesquerella seedlings. During the summer I monitored the removal quadrats for Centaurea germination and re-sprouting, removing it as it appeared.

In late September, 1993, I measured rosette diameter, leaf width, leaf length, leaf number, and survivorship for Lesquerella seedlings and adults. For adults that had flowered I also measured inflorescence number, inflorescence length, flower number, and fruit number. Flower number, fruit number, and leaf number were square root transformed to normality. All dependent variables but inflorescence number and seedling and adult survivorship were analyzed with MANOVA; follow-up ANOVAs were performed, though there is no accepted way to correct for multiple comparisons (Scheiner 1993). Because not all the transects (which were essentially blocks) received both treatments, there were missing cells in the ANOVA table. For this reason the ANOVAs were performed two ways. First, incomplete transects were dropped, and mixed model ANOVAs (with the transect*treatment interaction) were used. Second, incomplete blocks
were kept, but the interaction term was dropped and treatment and transect mean square were tested over the error mean square. I report the former analysis because it is more conservative.

Inflorescence number and adult and seedling survivorship could not be transformed to normality, so inflorescence number was analyzed with the Kruskal-Wallis one-way analysis of variance. Adult survivorship was analyzed in two ways. First, a loglinear model was used that included transect, treatment, and survivorship as the variables. However, because several of the expected cell counts were less than one, the $\chi^2$ approximation may not be valid. Therefore, I also carried out the analysis as a two-way G test (survival by treatment) in which I ignored the transect effect, which did not have a significant effect on survival according to the first analysis. Neither analysis showed a significant effect of treatment on survival (see Results), and I report the results of the second analysis. Seedling survivorship was analyzed with a loglinear model that included transect, treatment, and survivorship as the variables.

RESULTS

ASSOCIATION OF LESQUERELLA WITH OTHER SPECIES

At xeric Rattler Gulch, where Centaurea did not occur in the experimental transects, there was a significant positive association between Lesquerella adults and bunchgrasses (Table 1A). This pattern existed for seedling Lesquerella as well (Table 1B).

In contrast, a significant negative spatial relationship between adult Lesquerella and bunchgrasses was observed at more mesic Bear Gulch in transects without Centaurea; more adult Lesquerella were found growing in the
open than with bunchgrasses (Table 1C). No significant association of seedling *Lesquerella* with bunchgrasses was found at Bear Gulch in transects without *Centaurea* (Table 1D). At Bear Gulch in the presence of *Centaurea*, adult *Lesquerella* show no significant association with any other species (Table 1E).

**MECHANISMS OF FACILITATION OF *LESQUERELLA* BY BUNCHGRASS**

Only 76 out of 896 (8.5%) seeds germinated in all treatments combined, and there were no significant differences in germination between treatments. Although pattern analyses indicated a positive relationship between bunchgrasses and *Lesquerella*, I found that significantly fewer *Lesquerella* survived under bunchgrass canopies compared to the number that survived in the open (Figure 1). This result provides unexpected evidence that interference between bunchgrasses and *Lesquerella* is occurring.

No significant differences in root or shoot biomass were found between the open and bunchgrass treatments (Figure 2), which implies that facilitation was not occurring. Under the facilitation hypothesis, I expected roots and shoots to be bigger under bunchgrass canopies than in the open. However, roots in the open treatment tended to be larger than roots in the bunchgrass treatment, which is a pattern indicative of interference. No experimental evidence for facilitation or its potential mechanisms were found.

**INTERFERENCE EXPERIMENT**

Seedling *Lesquerella* survivorship was significantly greater with *Centaurea* removed (Table 2B). *Centaurea* removal did not have a significant effect on any other measures of *Lesquerella* performance (Wilks' lambda = 0.926, F=0.720, p=0.656; Table 2).
DISCUSSION

The positive associations between *Lesquerella* and bunchgrasses that were observed at Rattler Gulch suggest that facilitation may have been important in structuring this plant community in the past. Positive associations have been used as evidence of the importance of facilitation in other plant communities (e.g. Callaway 1992; Valiente-Banuet et al. 1991a, 1991b; McAuliffe 1988). However, the field experiment failed to support the facilitation hypothesis; in fact, the field experiment indicated that the bunchgrasses interfered with *Lesquerella*, contrary to my expectations. Just as there is temporal variation in competition (Connell 1983, Schoener 1983), it is probable that there is temporal variation in facilitation. Past competition is hypothesized to have structured Mojave Desert communities (Fonteyn and Mahall 1981); similarly, "the Ghost of Facilitation Past" (see Connell 1980) may have been important in establishing the pattern seen in the *Lesquerella*-bunchgrass system.

There are several possible reasons for the lack of evidence for bunchgrass facilitation. Facilitation may be important in some years and sites and not others because of temporal and spatial variation in the level of physical stress imposed by the environment. Grime (1984) considers stress, disturbance, and competition to be the three primary selective forces structuring plant communities. He hypothesizes that plants growing in high stress environments generally experience low levels of competition. A number of ecologists have argued that competition's role in stressful environments is further diminished by the importance of facilitative interactions. Positive or
facilitative interactions between species can potentially ameliorate physical stress and may be characteristic of stressful physical environments (Allee et al. 1949; Connell and Slayter 1977; Bertness 1989, 1993; Pennings and Callaway 1992; Bertness and Callaway in press).

Interactions between *Lesquerella* and bunchgrasses may vary in response to the physical characteristics of the growing season. In most years plants on the south-facing, well-drained slopes of Rattler Gulch experience very hot, dry conditions. In the summer of 1993, however, the lowest average July temperature since 1892 and the tenth wettest July since 1896 were recorded (average July 1993 precipitation = 51.3mm; average July 1993 temperature = 15.2°C) at the U.S. Weather Bureau station in Missoula, Montana (80 km west of the study area; elevation 975 m; NOAA 1993). No experimental evidence for facilitation was found during this time, despite the positive association between *Lesquerella* and bunchgrasses. Unexpectedly, the data suggested interference might be occurring. *Lesquerella* in the open had significantly higher survivorship (Figure 1) and bigger roots (though not significant; Figure 2) than *Lesquerella* under the bunchgrass canopy. These results are consistent with the idea that interference becomes more important during periods of low physical stress, while facilitation takes on greater importance during periods of high physical stress.

The pattern of association between *Lesquerella* and bunchgrasses at another site, Bear Gulch, provides correlative evidence for the physical stress hypothesis. I found a negative association between *Lesquerella* and bunchgrasses at Bear Gulch, which is just 5km west of Rattler Gulch. However, Bear Gulch seems to be a wetter microclimate than Rattler Gulch, so the plants may experience less physical stress at Bear Gulch. Consequently, the pattern
of association between bunchgrasses and *Lesquerella* is one that has been used to infer interference in many other studies (Anderson 1971; Yeaton and Cody 1976; Yeaton et al. 1977; Fonteyn and Mahall 1981; Phillips and MacMahon 1981; Fowler 1986).

Two alternative hypotheses may account for the lack of correspondence between the results of the pattern analysis and the facilitation experiment. I assumed that the critical time for the facilitation of *Lesquerella* by bunchgrasses was during the establishment of *Lesquerella* seedlings. However, facilitation may occur during another season and by other potential mechanisms. Another alternative concerns the identity of the grasses. When I gathered data for the pattern analysis, I did not record the identity of the grasses acting as facilitators; one to several species may have been important. I then randomly chose bunchgrass plants (i.e. multiple species were chosen as facilitators) while setting up the facilitation experiment. If one particular species of bunchgrass is important for facilitating *Lesquerella*, then I may have eliminated the possibility of seeing a treatment effect by randomly choosing bunchgrass plants. It is interesting to note that overall survivorship of seedlings in the facilitation experiment was 83%, which is extremely high for seedlings of open habitats (Werner and Caswell 1977; Fonteyn and Mahall 1981; Silander 1983; Moloney 1988); this would make distinguishing a treatment effect very difficult.

D'Antonio (1993) and others (Orians 1986; Crawley 1987) have demonstrated that invasion by an introduced species is a context-specific process; thus, the results of spotted knapweed invasion of the bunchgrass-*Lesquerella* system are difficult to predict. However, in a number of cases invading plants have been quite successful (e.g. *Myrica faya* in Hawaii [Walker and Vitousek 1991], kudzu vine in the southeastern United States [Carter and
Teramura 1988], cheatgrass in the Great Basin [Harris 1967], and Centaurea spp. in the northwestern United States [Lacey et al. 1986]). Except for decreases in seedling Lesquerella survivorship, I found very little experimental evidence that Centaurea interferes with Lesquerella. Interestingly, Lesica and Shelly (unpublished data) found that Centaurea reduces recruitment in another rare mustard, Arabis fecunda Rollins. The lack of Centaurea interference could have been due to poor experimental design; some transects lacked both treatments, and this prevented me from using the complete dataset in the analysis. The short duration of the experiment (one field season) could also have contributed to the lack of evidence for interference; Connell (1983) and Schoener (1983) cite several studies in which interference is important in some years but not others. Evidence for the negative impact of Centaurea on native plants abounds in the literature, and I still think that concern for Centaurea’s effects on Lesquerella is justified, in spite of my lack of experimental evidence for interference.

In Chapter Two I show that survivorship of seedling Lesquerella is one of the least sensitive parts of the Lesquerella life cycle. However, this does not necessarily mean that Centaurea is unlikely to have negative effects on the Lesquerella growth rate; large changes in demographically unimportant stages can have significant consequences for population growth (Schemske et al. 1994). A significant reduction in Lesquerella seedling survivorship over the long term would likely harm Lesquerella populations. Centaurea’s negative impacts on bunchgrasses (Myers and Berube 1983; Fletcher and Renney 1963; Kelsey and Bedunah 1989) may also harm Lesquerella populations by disturbing potential facilitory relationships between bunchgrasses and Lesquerella. Though I found little evidence for Centaurea interference, my data
are the result of only one field season of research; a conservative approach for the conservation of Lesquerella would be to make an effort to control Centaurea population growth. Manual removal and hand-spraying of Centaurea with herbicides would both disturb the delicate substrate on which Lesquerella grows. Biological controls are being employed against Centaurea, though without much success thus far. More Centaurea predators are being screened, however, and a root moth, Agapeta zoegana, looks especially promising (Story 1989). Biological controls hold the greatest promise for halting the spread of Centaurea (Story 1989, Muller and Schroeder 1989).

Despite my lack of experimental evidence for facilitation by bunchgrasses and my minor evidence for interference by Centaurea, I still think these interactions may be important factors affecting the Lesquerella-bunchgrass community; improved experimental design and several years of data would be needed to document these interactions. By understanding such ecological processes in communities where rare species occur, we can begin to improve conservation efforts for these species.
A. Rattler Gulch - No *Centaurea* - adult *Lesquerella*

<table>
<thead>
<tr>
<th>Cover type</th>
<th>Relative frequency</th>
<th>Observed</th>
<th>Expected</th>
</tr>
</thead>
<tbody>
<tr>
<td>Open</td>
<td>0.802</td>
<td>110</td>
<td>229</td>
</tr>
<tr>
<td>Bunchgrass</td>
<td>0.151</td>
<td>135</td>
<td>43</td>
</tr>
<tr>
<td>Forb</td>
<td>0.047</td>
<td>41</td>
<td>13</td>
</tr>
</tbody>
</table>

n=286 adults, G=241.8, df=2, p<0.001

B. Rattler Gulch - No *Centaurea* - seedling *Lesquerella*

<table>
<thead>
<tr>
<th>Cover type</th>
<th>Relative frequency</th>
<th>Observed</th>
<th>Expected</th>
</tr>
</thead>
<tbody>
<tr>
<td>Open</td>
<td>0.802</td>
<td>89</td>
<td>143</td>
</tr>
<tr>
<td>Bunchgrass</td>
<td>0.151</td>
<td>79</td>
<td>27</td>
</tr>
<tr>
<td>Forb</td>
<td>0.047</td>
<td>10</td>
<td>8.4</td>
</tr>
</tbody>
</table>

n=178 seedlings, G=88.7, df=2, p<0.001

C. Bear Gulch - No *Centaurea* - adult *Lesquerella*

<table>
<thead>
<tr>
<th>Cover type</th>
<th>Relative frequency</th>
<th>Observed</th>
<th>Expected</th>
</tr>
</thead>
<tbody>
<tr>
<td>Open</td>
<td>0.056</td>
<td>19</td>
<td>6</td>
</tr>
<tr>
<td>Bunchgrass</td>
<td>0.17</td>
<td>13</td>
<td>19</td>
</tr>
<tr>
<td>Litter</td>
<td>0.763</td>
<td>74</td>
<td>84</td>
</tr>
<tr>
<td>Forb</td>
<td>0.037</td>
<td>4</td>
<td>4</td>
</tr>
</tbody>
</table>

n=110 adults, G=14.4, df=3, p<0.005
### D. Bear Gulch - No *Centaurea* - seedling Lesquerella

<table>
<thead>
<tr>
<th>Cover type</th>
<th>Relative frequency</th>
<th>Observed</th>
<th>Expected</th>
</tr>
</thead>
<tbody>
<tr>
<td>Open</td>
<td>0.056</td>
<td>14</td>
<td>7</td>
</tr>
<tr>
<td>Bunchgrass</td>
<td>0.17</td>
<td>13</td>
<td>20</td>
</tr>
<tr>
<td>Litter</td>
<td>0.763</td>
<td>89</td>
<td>91</td>
</tr>
<tr>
<td>Forb</td>
<td>0.037</td>
<td>3</td>
<td>4</td>
</tr>
</tbody>
</table>

n=119 seedlings, $G=3.4$, df=3, n.s.

### E. Bear Gulch - *Centaurea* present - adult Lesquerella

<table>
<thead>
<tr>
<th>Cover type</th>
<th>Relative frequency</th>
<th>Observerved</th>
<th>Expected</th>
</tr>
</thead>
<tbody>
<tr>
<td>Open</td>
<td>0.048</td>
<td>7</td>
<td>4</td>
</tr>
<tr>
<td>Bunchgrass</td>
<td>0.118</td>
<td>8</td>
<td>10</td>
</tr>
<tr>
<td>Litter</td>
<td>0.841</td>
<td>63</td>
<td>72</td>
</tr>
<tr>
<td><em>Centaurea</em></td>
<td>0.06</td>
<td>2</td>
<td>5</td>
</tr>
<tr>
<td>Forb</td>
<td>0.055</td>
<td>6</td>
<td>5</td>
</tr>
</tbody>
</table>

n=86 adults, $G=-14.6$, df=4, n.s.

Table 1. Spatial pattern analysis of the association between bunchgrasses and seedling and adult *Lesquerella*.  

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.
A.

<table>
<thead>
<tr>
<th>Effects</th>
<th>Rosette Diameter</th>
<th>Leaf Width</th>
<th>Leaf Length</th>
<th>Leaf Number</th>
<th>Inflor. Length</th>
<th>Flower Number</th>
<th>Fruit Number</th>
</tr>
</thead>
<tbody>
<tr>
<td>Transect</td>
<td>7.26 (0)</td>
<td>4.30 (0)</td>
<td>5.95 (0)</td>
<td>9.30 (0)</td>
<td>2.73 (.04)</td>
<td>1.46 (.23)</td>
<td>3.33 (.02)</td>
</tr>
<tr>
<td>Treatment</td>
<td>1.34 (.31)</td>
<td>2.35 (.2)</td>
<td>1.46 (.29)</td>
<td>.18 (.70)</td>
<td>.09 (.78)</td>
<td>.06 (.83)</td>
<td>0 (1.00)</td>
</tr>
<tr>
<td>Trans.*Trt.</td>
<td>1.03 (.39)</td>
<td>69 (.60)</td>
<td>1.21 (.31)</td>
<td>1.72 (.15)</td>
<td>.37 (.83)</td>
<td>.98 (.42)</td>
<td>.98 (.42)</td>
</tr>
</tbody>
</table>

B.

<table>
<thead>
<tr>
<th>Effect</th>
<th>Inflorescence Number</th>
<th>Seedling Lesq. Survivorship</th>
<th>Adult Lesq. Survivorship</th>
</tr>
</thead>
<tbody>
<tr>
<td>Treatment</td>
<td>10,049 (.55)</td>
<td>4.96 (.026)</td>
<td>.02 (.88)</td>
</tr>
</tbody>
</table>

Table 2A. F values and (probabilities) for mixed model ANOVAs testing the effect of *Centaurea* removal on *Lesquerella* performance. Significant p values given in bold. 2B. Value of the Mann-Whitney U statistic (for inflorescence number), $G^2$ (for seedling and adult survivorship), and (probabilities) for determining the effect of *Centaurea* removal on *Lesquerella* performance.
Figure 1. Survivorship of *Lesquerella* seedlings planted in 4 experimental treatments. No treatment effects were detected ($G=9.61$, df=3, $p = .02$).

Figure 2. The biomass of roots and shoots of seedling *Lesquerella* planted in 4 experimental treatments: under a bunchgrass canopy, in the open, under a clipped bunchgrass canopy, and under shade cloth. No treatment effects were detected (Wilks' lambda=0.943, $F=1.664$, $p=0.199$ for planned comparison between the bunchgrass canopy and open treatments). Means ±1 s.e. are shown.
CHAPTER 2: DEMOGRAPHIC ANALYSIS OF POPULATIONS OF THE RARE PLANT LESQUERELLA CARINATA

INTRODUCTION

Studies of plant demography have contributed substantially to ecological theory (e.g. Harper 1977, Huenneke and Marks 1987, Moloney 1988, Åberg 1992a,b). More recently, demography has been recognized as an important consideration in the management of rare taxa (Lande 1988, Menges 1991). Matrix population modelling is an especially valuable tool that is gaining favor in the study of rare animals (Crouse et al. 1987, Wooton and Bell 1992) and plants (Meagher et al. 1978, Fiedler 1987, Pavlick and Barbour 1988, Hegazy 1990, Menges 1990, Charron and Gagnon 1991). Matrix models provide information about short term population dynamics and about the parts of a species' life cycle that are important contributors to the population growth rate (Caswell 1989); for these reasons, matrix models have useful applications in conservation planning (Crouse et al. 1987).

Lesquerella carinata var. languida Rollins (Brassicaceae) is a recently described variety known only to occur in western Montana (Rollins 1993). Since this variety is newly described, it is not yet listed by the United States Fish and Wildlife Service (USFWS); however, Lesquerella carinata (which includes all varieties) is a candidate for listing as threatened or endangered (C2) by the USFWS (USDI-FWS1993). In addition, the U.S. Department of Agriculture is currently domesticating Lesquerella fendleri because its seeds are of potential use as a source of oil for industrial and agricultural products (USDA 1991).
Preserving wild relatives of crop species is important to the long term viability and genetic diversity of domesticated species (Williams 1988).

Currently *Lesquerella carinata* var. *languida* Rollins (hereafter referred to as *Lesquerella*) is threatened by the invasive non-native plant *Centaurea maculosa* Lam. (spotted knapweed) and by cattle. *Centaurea* covers over 1.8 million hectares in Montana alone (Lacey et al. 1986) and has been found to reduce seed germination, seedling growth, and productivity of native grasses and forbs on economically important rangelands (Myers and Berube 1983; Fletcher and Renney 1963; Kelsey and Bedunah 1989) and in communities experiencing no livestock grazing (Tyser and Key 1988; Tyser and Worley 1992). In research on the related rare mustard *Arabis fecunda* Rollins, Lesica and Shelly (pers. comm.) found that spotted knapweed lowered recruitment and the population growth rate of *Arabis* in some years. Though a lesser threat, cattle have been known to trample *Lesquerella*, but grazing on *Lesquerella* has not been observed (Schassberger 1991). The objective of this research was to use matrix population models to investigate the short term population dynamics of *Lesquerella* and to determine the life cycle stages most critical to *Lesquerella* population growth in the face of *Centaurea* invasion and domestic cattle disturbance.

**MATERIALS AND METHODS**

**Species Studied**

*Lesquerella* is a short-lived, rosette- and taproot-forming perennial herb. It reproduces mainly by outcrossing, but in test crosses some selfing was detected (Greenlee, unpublished data). No vegetative reproduction was ever
observed. Pollinators include bees and flies (Greenlee, pers. obs.). The seeds require stratification to germinate, and scarification increases germination in the greenhouse (Greenlee, unpublished data). Germination occurs in early spring, and most flowering takes place in April and May. Fruits mature from May to July. Seeds have no known dispersal mechanism.

*Centaurea maculosa* Lam. (Asteraceae) is also a short-lived, rosette- and taproot-forming perennial herb. This Eurasian native germinates in the fall or in the spring following dispersal. Most flowering occurs in July and August.

**STUDY SITES**

*Lesquerella* is found only in western Montana along the southern edge of the Garnet Range northwest of Drummond, Montana, and in the Sapphire Range approximately 32 km southwest of Philipsburg, Montana (Rollins 1993). Plants grow on easily disturbed, gravelly, calcareous soils on south- to west-facing slopes. These xeric, open sites are found in ecotonal areas between ponderosa pine (*Pinus ponderosa* Dougl. ex Laws. & Laws.)/bitterbrush (*Purshia tridentata* Pursh D.C.) and bitterbrush/grassland habitat types, from 1,220 to 1,700 m in elevation (Schassberger 1991). The dominant herbaceous species in this community are bunchgrasses, primarily *Pseudoregneria spicata* (Pursh) Löve (blue-bunch wheatgrass).

Demographic monitoring was performed at Rattler Gulch (elevation 1,646 m, 46° 44'N, 113° 15'W), Mulkey Gulch (1,560 m, 46° 44'N, 113° 16'W), and Bear Gulch (elevation 1,311 m, 46° 45'N, 113° 21'W). All the sites are within 8 km of one another and are found on both Bureau of Land Management (BLM) and private property. Public grazing allotments cover all the BLM land, and livestock grazing also occurs on most of the private land. The Rattler Gulch and
Mulkey Gulch Lesquerella populations are on dry, south-facing slopes. Bear Gulch is west-facing and has a moister microclimate than the other two sites; more ponderosa pine and *Psuedotsuga menziesii* (Mirbel) Franco (Douglas fir) grow at Bear Gulch than at Mulkey or Rattler Gulches. All three sites are being invaded by *Centaurea*, whose populations are expanding upward from the slope bottom.

**FIELD METHODS**

In June, 1991, 2-5 permanent belt transects of variable length were established at each population in areas not yet invaded by *Centaurea*. Approximately 500 individuals in each population were counted and marked with plastic spoons. As *Lesquerella* density varies considerably at each site, the transects were not randomly located; rather, an attempt was made to place each transect in some of the denser parts of each population. Location and rosette diameter were recorded for each plant. Inflorescence number, maximum inflorescence length, flower number, and fruit number were measured on all flowering plants.

The populations were censused again in late-May to mid-June in 1992 and 1993. At each census, new plants were identified and surviving plants were recorded.

**DATA ANALYSIS**

Survival, growth, and reproduction were summarized in a stage/life history-structured transition matrix (Lefkovitch 1965, Caswell 1989; Figure 3A). The transition matrix contains the probabilities of an individual moving from one
stage to another and the fecundities of individuals in each stage. The linear, time-invariant population projection model takes the form:

\[ n_{t+1} = A \times n_t \]

where \( n_t \) is a column vector describing the size structure of the population at time \( t \), and \( A \) is the transition matrix (Caswell 1989). The transitions can also be depicted as a life cycle graph (Figure 3B). The projection interval for my model is one year. Six transition matrices were constructed (three populations \( \times \) two transitions [1991-1992 and 1992-1993]).

I attempted to use an algorithm (Moloney 1986) to determine the optimal size classes; this algorithm balances two common types of error that affect transition rates. However, it failed to distinguish individual size classes, so I decided upon three size categories and a reproductive stage. The size categories (small, medium, and large) were chosen by assigning approximately equal proportions of each population's 1991 rosette diameter distribution for non-reproductive plants to each stage. At Bear Gulch the size categories were 2-9 mm, 10-18 mm, and 19+ mm. At Mulkey Gulch the size categories were 2-10 mm, 11-18 mm, and 19+ mm. At Rattler Gulch the size categories were 2-11 mm, 12-17 mm, and 18+ mm.

Eigenvalues and eigenvectors were calculated for each matrix. The leading eigenvalue is the asymptotic population growth rate, \( \lambda \). The right eigenvector gives the stable stage distribution \( w \), which is the proportional representation of each stage once the population reaches the equilibrium growth rate (Caswell 1989). The reproductive value, \( v \), is described by the left...
eigenvector and represents what an individual is "worth" in terms of future reproduction. (Caswell 1989).

The matrix population model is deterministic; $\lambda$ describes population growth under the assumption that future conditions will be identical to present conditions. Because of these limitations, $\lambda$ is best used to describe short term population dynamics. $\lambda > 1$ indicates population increase, while $\lambda < 1$ indicates population decrease. I used a bootstrapping procedure (Lenski and Service 1982, Caswell 1989) to generate 95% confidence intervals for $\lambda$.

An elasticity analysis was also performed for each matrix. Elasticities ($e_{ij}$) are given by:

$$e_{ij} = (aij/\lambda) (\partial \lambda/\partial a_{ij})$$

where $aij$ represents the probability of an individual moving from stage $j$ to stage $i$ (Caswell 1989). Elasticities measure the proportional change in $\lambda$ resulting from a proportional change in $aij$. Transition matrix values with the largest associated elasticities have the greatest impact on population growth rate (de Kroon et al. 1986). Because elasticities sum to one, elasticity matrices from different years and different populations can be compared directly.

I also summed elasticities for transitions representing survival, reproduction, and growth to estimate the importance of these life history traits to Lesquerella population growth (Silvertown et al. 1993). Transitions representing survival are those in which plants stay in the same stage or move to smaller stages. Transitions characterizing reproduction are found only in stage four, the reproductive stage. The transition matrix elements for this stage are composed of two parts, one part deriving from the probability of moving from
one stage to another and the other part coming from the number of individuals a reproductive plant contributes to each stage (Figure 3A). Transitions representing growth are those in which plants move from a smaller stage to a larger stage.

RESULTS

POPULATION DYNAMICS

There was significant spatial and temporal variation in the population growth rate $\lambda$ for the *Lesquerella* populations at Bear, Mulkey, and Rattler Gulches in 1991-1992 and 1992-1993 (Table 3; Figure 4). In 1991-1992 $\lambda$ was significantly $<1$ in all the populations, indicating populations that were decreasing in size, while in 1992-1993 $\lambda$ was significantly $>1$, indicating growing populations of *Lesquerella* (Figure 4). Rattler and Mulkey Gulch *Lesquerella* populations had the most dramatic temporal fluctuations in $\lambda$; $\lambda$ increased almost 10-fold at Rattler Gulch and almost 4-fold at Mulkey Gulch from 1991-1992 to 1992-1993. In contrast, $\lambda$ was relatively stable at Bear Gulch. Within each year of measurement, $\lambda$ differed significantly between populations (Figure 4). The numbers of *Lesquerella* in 1991, 1992, and 1993, respectively, were 550, 612, and 950 at Bear Gulch; 492, 290, and 721 at Mulkey Gulch; and 504, 151, and 436 at Rattler Gulch.

Temporal variation in germination was dramatic. There were few births in 1992, especially in Mulkey and Rattler Gulches, while in 1993 many births occurred in all the populations (Figure 5). New individuals tended to enter the population in the small or medium stage, although there were occasional births.
into the large and reproductive stages (Figure 5). There was less variation in the number of births at Bear Gulch than at Mulkey or Rattler Gulch.

Mortality and mortality rate also varied temporally (Figure 6). Little temporal variation was observed at Bear Gulch, while mortality and mortality rate were both higher in 1991-1992 than 1992-1993 at Mulkey and Rattler Gulches (Figure 6A, 6B). Mortality seems to be highest among plants in the small and medium stages at Bear Gulch in both years of study. However, large vegetative plants and reproductive plants account for the most deaths at Mulkey and Rattler Gulches in 1991-1992 (Figure 6A).

**STABLE STAGE DISTRIBUTION AND REPRODUCTIVE VALUE**

The proportion of individuals in each stage stayed relatively constant at Bear Gulch (Figure 7A), while there was an increasing number of small *Lesquerella* and a decreasing number of reproductive *Lesquerella* at Mulkey and Rattler Gulches over time (Figure 7B, 7C). The actual proportions of individuals per stage (Figure 7) are in general fairly similar to the proportions predicted from the stable stage distribution (Table 4A); for example, the stable stage distribution for Rattler Gulch in 1992-1993 (Table 4A) does not differ much from the observed distribution for Rattler Gulch in 1993 (Figure 7C). Under the assumptions of matrix population models, a fixed proportion of the population will be found in each stage when the population reaches equilibrium. However, these assumptions include environmental constancy, which is clearly unrealistic; therefore, the similarity between the stable stage distribution and the observed stage distribution should not be interpreted as an indication that the populations are nearing equilibrium. This result is more likely due to chance.
In all *Lesquerella* populations the largest contribution to future reproduction comes from the reproductive stage (Table 4B). Reproductive values increased in all populations and times from the small stage to the reproductive stage. Bear Gulch in 1991-1992 and 1992-1993 showed the largest reproductive values (Table 4B).

**Elasticity Analysis**

The elasticity analysis reveals several important patterns. Survivorship of reproductive individuals contributes a great deal to $\lambda$ in all of the populations in all of the study years (Figure 8; Table 5); this transition has elasticity values of 0.34 and 0.23 at Bear Gulch and 0.54 and 0.24 at Rattler Gulch in 1991-1992 and 1992-1993, respectively (Figure 8; Table 5). These elasticity values indicate that a slight change in the survival probability of a reproductive adult would have large impact on $\lambda$. Similarly, the growth of an individual from the large to the reproductive stage makes a large contribution to population growth in all the populations in each year. This transition is one of the two most important transitions in Bear and Mulkey Gulches in 1991-1992 and in Bear and Rattler Gulches in 1992-1993 (Figure 8; Table 5). One caveat in interpreting the elasticity matrices is that they include no estimate of the variability of the elasticity values. This makes distinguishing significant differences between elasticities, and whether the elasticities differ from 0, impossible. Nevertheless, it is reassuring that patterns in the elasticities emerge.

A range of temporal variation in the pattern of elasticities exists at the three study sites. At Bear Gulch survivorship of reproductive individuals and growth of individuals from large to reproductive had the greatest impact on $\lambda$ in both 1991-1992 and 1992-1993 (Figure 8A, 8B). There was more temporal...
variation in elasticity at Mulkey Gulch; survivorship of reproductive individuals had the highest elasticities in both years, while growth from large to reproductive (second most important in 1991-1992) gave way to births of seedlings into the medium stage class as the transition with the second largest effect on $\lambda$ in 1992-1993 (Figure 8C, 8D). Rattler Gulch had the most variation in the pattern of elasticities. In 1991-1992 survival of medium and large individuals were the transitions with the greatest elasticities, and in 1992-1993 growth of plants from large to reproductive and births of small seedlings had the largest impact on $\lambda$ (Figure 8E, 8F).

When elasticities for transitions representing growth, survival, and reproduction are summed for each year and for each population, the importance of survival to *Lesquerella* in all three populations in 1991-1992 becomes evident (Figure 9). In 1992-1993 growth and reproduction all take on greater importance in all the populations (Figure 9).

**Seed bank**

I found evidence for a seed bank for *Lesquerella* at Rattler Gulch in 1993. There were 26 fruiting plants in all three transects at Rattler Gulch in 1992, with a total of 68 fruits. I used a 1991 fecundity estimate (1.53-2.13 seeds/fruit [95% confidence limits]) to calculate 1992 seed production. The three transects at Rattler Gulch produced an estimated 104-145 seeds in 1992. There were 323 *Lesquerella* seedlings in the transects at Rattler Gulch in 1993. These extra seedlings could have resulted from seeds dispersed by insects the previous summer, though I have never observed insects dispersing *Lesquerella* seeds. Because *Lesquerella* have no other known dispersal mechanism, it is likely that the extra seedlings originated from a seed bank.
DISCUSSION

Elasticity analysis of single year transition matrices of three Lesquerella populations indicates that survival of reproductive individuals is the most important part of the Lesquerella life cycle at Bear and Mulkey Gulches in all three study years and a relatively important part of the life cycle at Rattler Gulch in each study year (Figure 8). Any threats to the Lesquerella populations which impact this particular part of the life cycle will have a considerable effect on the population growth rate, \( \lambda \), and hence population viability. Threats to population viability can be considered as either systematic or stochastic forces (Shaffer 1981). Three such pressures affecting Lesquerella populations are Centaurea, cattle, and environmental fluctuations.

Centaurea represents the primary systematic threat to populations of Lesquerella. In Chapter One, I found that seedling Lesquerella had significantly lower survivorship in quadrats in which Lesquerella grew with Centaurea compared to Lesquerella survivorship in quadrats from which Centaurea had been experimentally removed. The elasticities of small and medium Lesquerella, which are the stages most typical of seedlings, are generally small (Figure 8), indicating that small changes in seedling survivorship will not have much of an impact on Lesquerella population growth. However, a long term decrease in Lesquerella seedling survivorship would be likely to have a negative impact on the Lesquerella population growth rate, and large changes in demographically unimportant stages can have significant consequences for population growth (Schemske et al. 1994).

Disturbance by cattle is another systematic threat to Lesquerella populations. Because of high elasticity values for survivorship, cattle trampling...
and killing of *Lesquerella* could have strong negative impacts on *Lesquerella* population growth. In addition to trampling plants, cattle can create a soil disturbance that opens the way to *Centaurea* invasion. *Centaurea* is a ruderal species that shows a positive response to disturbance (Muller et al. 1989).

Environmental fluctuations caused by climate create stochastic perturbations for *Lesquerella* populations. Spring, 1992, was very warm and dry, and summer, 1993, was quite cool and wet (see below). Births and deaths in the *Lesquerella* populations seemed to track these changes; high mortality and few births occurred at Rattler and Mulkey Gulches in 1992, and lower mortality and numerous births occurred at these two sites in 1993. Because of high survivorship elasticities and high recruitment elasticities at Mulkey and Rattler Gulches (in 1992-1993), stochastic fluctuations in climate had a large impact on population growth rate (Figure 4). It is interesting to note that the Bear Gulch *Lesquerella* populations varied the least of all three populations with respect to $\lambda$, number of births, number of deaths, elasticity patterns, population stage structure, and census number of plants (see Results). The Bear Gulch population tends to experience a wetter microclimate because it sits in a narrow valley on a west facing slope with greater tree canopy cover (hence greater shade) than the populations at Mulkey and Rattler Gulches.

I have found evidence that *Lesquerella* does have a seed bank. Though I did not include the seed bank as an explicit stage in my demographic analysis, it probably does play an important role in some years. For example, at Rattler Gulch in 1993 germination of seeds from the seed bank contributed greatly to the number of births in the population. The importance attributed to a seed bank probably depends greatly on the years in which demographic studies are carried out. Silvertown, et al. (1993), found that a seed bank existed in 13/45
herb populations that they reviewed. In only two cases did the seed bank contribute over 10% to changes in $\lambda$. Kalisz and McPeek (1992) measured demography of *Collinsia verna* in three growing seasons, and found that the seed bank made a significant contribution to $\lambda$ in one of the years. Though the seed bank is a potentially important life cycle stage in annual and perennial herbs, it is a difficult stage to investigate in rare plants such as *Lesquerella*.

**Population Persistence**

Predictions of long term population performance based on standard matrix models are difficult to make with any accuracy because the assumption of environmental constancy rarely, if ever, holds. Some have used stochastic theory (Cohen 1987, Tuljapurkar 1989, Caswell 1989) to perform stochastic matrix projections for natural populations of plants (Bierzychudek 1982, Åberg 1992b) and animals (Cohen et al. 1983, Heyde and Cohen 1985), though the theory of time-varying matrix models is relatively new (Caswell 1989) and there is still no way to ascertain the accuracy of such projections. Because of these difficulties, $\lambda$ can best be used as a short term measure of population growth.

The *Lesquerella* population growth rate paralleled annual climatic fluctuations. Data from the U.S. Weather Bureau station in Missoula, Montana (80 km west of the study area; elevation 975 m) show that the spring of 1992 was long, warm, and dry (NOAA 1992). Mean February precipitation was 4.6 mm, compared to a record low set in 1973 of 4.3 mm, and the daily mean February temperature was 2.4°F, close to the record high of 2.6°F. The three study populations had an average $\lambda$ of .52 during these warm, dry conditions. In contrast, the summer of 1993 was unusually wet and cool, and $\lambda$ in the three populations averaged 1.80. The lowest average July temperature since 1892
and the tenth wettest July since 1896 were recorded (average July 1993 precipitation = 51.3mm; average July 1993 temperature = 15.2°C). Such dramatic variation in \( \lambda \) is typical for herbs of open habitats (Werner and Caswell 1977, Fetcher and Shaver 1983, Eriksson 1988, Moloney 1988, Menges 1990, Kalisz and McPeek 1992, Silvertown et al. 1993), while minor variation in \( \lambda \) is more common for perennial herbs of forest habitats (Bierzychudek 1982, Meagher 1982, Kinoshita 1987, Charron and Gagnon 1991, Silvertown et al. 1993). Although two transitions is a small sample size, it does appear that Lesquerella populations track the weather fairly closely, at least in these rather extreme years.

Climatic variation alone does not pose a great threat to Lesquerella population persistence. If global warming is occurring, however, then a succession of warm, dry years could have negative consequences for Lesquerella populations. Of more immediate concern are the threats of Centaurea invasion and cattle trampling. Given the results of my elasticity analysis, these threats do have the potential to cause a long term decline in population growth and hence population viability.

**Conservation Implications**

Conservation plans for Lesquerella should revolve around mitigating the effects of Centaurea invasion and cattle grazing. As noted earlier, Centaurea decreases seedling Lesquerella survival. These results, as well as the extensive literature on the negative effects of Centaurea on native plants, suggest that control of Centaurea is likely to be important to the survival of the Lesquerella populations. Limited hand-spraying of herbicides or manual removal might be effective against small patches of Centaurea; however, this
plant is generally too widespread at the study areas, and both of these methods would disturb the delicate substrate. Biological controls are being employed against *Centaurea*, though without much success thus far. More *Centaurea* predators are being screened, however, and a root moth, *Agapeta zoegana*, looks especially promising (Story 1989). Biological controls hold the greatest promise for halting the spread of *Centaurea* (Story 1989, Muller and Schroeder 1989).

Cattle grazing presents a lesser threat to the *Lesquerella* population at Rattler Gulch. A fence built at the bottom of the slope on which *Lesquerella* grow would prevent cattle from trampling *Lesquerella* and would minimize soil disturbance and further Centaurea invasion.

The success of conservation efforts depends on the availability of accurate ecological and genetic data for species of concern (Kesseli 1992). Demographic studies of rare species (e.g. Crouse et al. 1987, Charron and Gagnon 1991) can provide an understanding of key life history elements. For example, I have found that $\lambda$, and by extension population persistance, is most sensitive to changes in survival of reproductive adult plants. These data indicate that management efforts should be concentrated on identifying threats that impact this sensitive stage. Incorporating such knowledge in management plans is an important step towards achieving viable populations of threatened and endangered species.
A. Bear Gulch

1991-1992

<table>
<thead>
<tr>
<th>To</th>
<th>S</th>
<th>M</th>
<th>L</th>
<th>R</th>
<th>Recruit</th>
</tr>
</thead>
<tbody>
<tr>
<td>S</td>
<td>.25</td>
<td>.14</td>
<td>.05</td>
<td>.01</td>
<td>.72</td>
</tr>
<tr>
<td>M</td>
<td>.12</td>
<td>.27</td>
<td>.17</td>
<td>.05</td>
<td>.76</td>
</tr>
<tr>
<td>L</td>
<td>.03</td>
<td>.15</td>
<td>.34</td>
<td>.18</td>
<td>.09</td>
</tr>
<tr>
<td>R</td>
<td>.01</td>
<td>.01</td>
<td>.17</td>
<td>.55</td>
<td>.05</td>
</tr>
</tbody>
</table>

1992-1993

<table>
<thead>
<tr>
<th>To</th>
<th>S</th>
<th>M</th>
<th>L</th>
<th>R</th>
<th>Recruit</th>
</tr>
</thead>
<tbody>
<tr>
<td>S</td>
<td>.18</td>
<td>.05</td>
<td>.0</td>
<td>.0</td>
<td>1.20</td>
</tr>
<tr>
<td>M</td>
<td>.23</td>
<td>.22</td>
<td>.03</td>
<td>.02</td>
<td>2.43</td>
</tr>
<tr>
<td>L</td>
<td>.04</td>
<td>.31</td>
<td>.47</td>
<td>.20</td>
<td>.56</td>
</tr>
<tr>
<td>R</td>
<td>.02</td>
<td>.04</td>
<td>.35</td>
<td>.64</td>
<td>.02</td>
</tr>
</tbody>
</table>

B. Mulkey Gulch

1991-1992

<table>
<thead>
<tr>
<th>To</th>
<th>S</th>
<th>M</th>
<th>L</th>
<th>R</th>
<th>Recruit</th>
</tr>
</thead>
<tbody>
<tr>
<td>S</td>
<td>.18</td>
<td>.14</td>
<td>.17</td>
<td>.04</td>
<td>.02</td>
</tr>
<tr>
<td>M</td>
<td>0</td>
<td>.19</td>
<td>.13</td>
<td>.08</td>
<td>.03</td>
</tr>
<tr>
<td>L</td>
<td>.05</td>
<td>0</td>
<td>.11</td>
<td>.12</td>
<td>.01</td>
</tr>
<tr>
<td>R</td>
<td>0</td>
<td>.07</td>
<td>.19</td>
<td>.40</td>
<td>0</td>
</tr>
</tbody>
</table>

1992-1993

<table>
<thead>
<tr>
<th>To</th>
<th>S</th>
<th>M</th>
<th>L</th>
<th>R</th>
<th>Recruit</th>
</tr>
</thead>
<tbody>
<tr>
<td>S</td>
<td>.07</td>
<td>.04</td>
<td>.02</td>
<td>0</td>
<td>1.65</td>
</tr>
<tr>
<td>M</td>
<td>.17</td>
<td>.11</td>
<td>.02</td>
<td>.01</td>
<td>1.36</td>
</tr>
<tr>
<td>L</td>
<td>.32</td>
<td>.30</td>
<td>.33</td>
<td>.05</td>
<td>.45</td>
</tr>
<tr>
<td>R</td>
<td>.15</td>
<td>.37</td>
<td>.51</td>
<td>.79</td>
<td>.08</td>
</tr>
</tbody>
</table>
Table 3. Transition matrices for three *Lesquerella* populations for 1991-1992 and 1992-1993. Values in matrix cells represent probabilities of transition from one stage to another or the number of births into a given stage. S=small, M=medium, and L=large vegetative rosette, R=reproductive individual, Recruit=births per reproductive adult. The transition values of stage four (reproductive adult) are shown as the sum of the last two columns, R and Recruit, to emphasize the differing contributions of survival (R) and reproduction (Recruit) to this stage.

### 1991-1992

<table>
<thead>
<tr>
<th>From</th>
<th>S</th>
<th>M</th>
<th>L</th>
<th>R</th>
<th>Recruit</th>
</tr>
</thead>
<tbody>
<tr>
<td>S</td>
<td>.06</td>
<td>.07</td>
<td>.08</td>
<td>.06</td>
<td>.02</td>
</tr>
<tr>
<td>M</td>
<td>0</td>
<td>.10</td>
<td>.06</td>
<td>.09</td>
<td>.01</td>
</tr>
<tr>
<td>L</td>
<td>0</td>
<td>.02</td>
<td>.14</td>
<td>.07</td>
<td>.01</td>
</tr>
<tr>
<td>R</td>
<td>.02</td>
<td>.02</td>
<td>.02</td>
<td>.06</td>
<td>0</td>
</tr>
</tbody>
</table>

### 1992-1993

<table>
<thead>
<tr>
<th>From</th>
<th>S</th>
<th>M</th>
<th>L</th>
<th>R</th>
<th>Recruit</th>
</tr>
</thead>
<tbody>
<tr>
<td>S</td>
<td>.05</td>
<td>.05</td>
<td>0</td>
<td>.04</td>
<td>7.74</td>
</tr>
<tr>
<td>M</td>
<td>.08</td>
<td>.07</td>
<td>0</td>
<td>0</td>
<td>2.67</td>
</tr>
<tr>
<td>L</td>
<td>.30</td>
<td>.23</td>
<td>.33</td>
<td>.04</td>
<td>1.56</td>
</tr>
<tr>
<td>R</td>
<td>.10</td>
<td>.42</td>
<td>.55</td>
<td>.52</td>
<td>0</td>
</tr>
</tbody>
</table>

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.
A. Bear Gulch

### 1991-1992

<table>
<thead>
<tr>
<th>To</th>
<th>S</th>
<th>M</th>
<th>L</th>
<th>R</th>
<th>Recruit</th>
</tr>
</thead>
<tbody>
<tr>
<td>S</td>
<td>.02</td>
<td>.01</td>
<td>.00</td>
<td>.00</td>
<td>.03</td>
</tr>
<tr>
<td>M</td>
<td>.02</td>
<td>.05</td>
<td>.02</td>
<td>.00</td>
<td>.06</td>
</tr>
<tr>
<td>L</td>
<td>.01</td>
<td>.08</td>
<td>.10</td>
<td>.04</td>
<td>.02</td>
</tr>
<tr>
<td>R</td>
<td>.01</td>
<td>.02</td>
<td>.13</td>
<td>.34</td>
<td>.03</td>
</tr>
</tbody>
</table>

### 1992-1993

<table>
<thead>
<tr>
<th>To</th>
<th>S</th>
<th>M</th>
<th>L</th>
<th>R</th>
<th>Recruit</th>
</tr>
</thead>
<tbody>
<tr>
<td>S</td>
<td>.00</td>
<td>.00</td>
<td>.00</td>
<td>.00</td>
<td>.02</td>
</tr>
<tr>
<td>M</td>
<td>.01</td>
<td>.03</td>
<td>.00</td>
<td>.00</td>
<td>.12</td>
</tr>
<tr>
<td>L</td>
<td>.01</td>
<td>.10</td>
<td>.11</td>
<td>.03</td>
<td>.08</td>
</tr>
<tr>
<td>R</td>
<td>.01</td>
<td>.03</td>
<td>.21</td>
<td>.23</td>
<td>.01</td>
</tr>
</tbody>
</table>

B. Mulkey Gulch

### 1991-1992

<table>
<thead>
<tr>
<th>To</th>
<th>S</th>
<th>M</th>
<th>L</th>
<th>R</th>
<th>Recruit</th>
</tr>
</thead>
<tbody>
<tr>
<td>S</td>
<td>.02</td>
<td>.01</td>
<td>.01</td>
<td>.01</td>
<td>.00</td>
</tr>
<tr>
<td>M</td>
<td>.00</td>
<td>.03</td>
<td>.02</td>
<td>.03</td>
<td>.01</td>
</tr>
<tr>
<td>L</td>
<td>.03</td>
<td>.00</td>
<td>.04</td>
<td>.10</td>
<td>.01</td>
</tr>
<tr>
<td>R</td>
<td>.00</td>
<td>.05</td>
<td>.11</td>
<td>.54</td>
<td>.00</td>
</tr>
</tbody>
</table>

### 1992-1993

<table>
<thead>
<tr>
<th>To</th>
<th>S</th>
<th>M</th>
<th>L</th>
<th>R</th>
<th>Recruit</th>
</tr>
</thead>
<tbody>
<tr>
<td>S</td>
<td>.00</td>
<td>.00</td>
<td>.00</td>
<td>.00</td>
<td>.10</td>
</tr>
<tr>
<td>M</td>
<td>.02</td>
<td>.01</td>
<td>.00</td>
<td>.00</td>
<td>.14</td>
</tr>
<tr>
<td>L</td>
<td>.04</td>
<td>.04</td>
<td>.03</td>
<td>.01</td>
<td>.05</td>
</tr>
<tr>
<td>R</td>
<td>.05</td>
<td>.12</td>
<td>.13</td>
<td>.24</td>
<td>.02</td>
</tr>
</tbody>
</table>
C. Rattler Gulch

1991-1992

<table>
<thead>
<tr>
<th>To</th>
<th>S</th>
<th>M</th>
<th>L</th>
<th>R</th>
<th>Recruit</th>
</tr>
</thead>
<tbody>
<tr>
<td>S</td>
<td>.02</td>
<td>.02</td>
<td>.02</td>
<td>.01</td>
<td>+ .00</td>
</tr>
<tr>
<td>M</td>
<td>.00</td>
<td>.12</td>
<td>.07</td>
<td>.06</td>
<td>+ .01</td>
</tr>
<tr>
<td>L</td>
<td>.00</td>
<td>.05</td>
<td>.29</td>
<td>.08</td>
<td>+ .01</td>
</tr>
<tr>
<td>R</td>
<td>.06</td>
<td>.06</td>
<td>.05</td>
<td>.07</td>
<td>+ .00</td>
</tr>
</tbody>
</table>

1992-1993

<table>
<thead>
<tr>
<th>To</th>
<th>S</th>
<th>M</th>
<th>L</th>
<th>R</th>
<th>Recruit</th>
</tr>
</thead>
<tbody>
<tr>
<td>S</td>
<td>.00</td>
<td>.00</td>
<td>.00</td>
<td>.00</td>
<td>+ .15</td>
</tr>
<tr>
<td>M</td>
<td>.01</td>
<td>.00</td>
<td>.00</td>
<td>.00</td>
<td>+ .13</td>
</tr>
<tr>
<td>L</td>
<td>.06</td>
<td>.02</td>
<td>.03</td>
<td>.00</td>
<td>+ .09</td>
</tr>
<tr>
<td>R</td>
<td>.08</td>
<td>.12</td>
<td>.18</td>
<td>.11</td>
<td>+ .00</td>
</tr>
</tbody>
</table>

Table 5. Elasticity matrices for three *Lesquerella* populations for 1991-1992 and 1992-1993. Values in matrix cells represent elasticities for given transitions. S=small, M=medium, and L=large vegetative rosette, R=reproductive individual, Recruit=elasticities for recruitment. Stage four is shown as the sum of the last two columns, R and Recruit, to emphasize the differing contributions of survival (R) and reproduction (Recruit) in this stage.
FROM

<table>
<thead>
<tr>
<th>To</th>
<th>Small</th>
<th>Medium</th>
<th>Large</th>
<th>Surv.</th>
<th>Recruit</th>
</tr>
</thead>
<tbody>
<tr>
<td>S</td>
<td>a11</td>
<td>a12</td>
<td>a13</td>
<td>a14</td>
<td>= s14 + f1</td>
</tr>
<tr>
<td>M</td>
<td>a21</td>
<td>a22</td>
<td>a23</td>
<td>a24</td>
<td>= s24 + f2</td>
</tr>
<tr>
<td>L</td>
<td>a31</td>
<td>a32</td>
<td>a33</td>
<td>a34</td>
<td>= s34 + f3</td>
</tr>
<tr>
<td>R</td>
<td>a41</td>
<td>a42</td>
<td>a43</td>
<td>a44</td>
<td>= s44 + f4</td>
</tr>
</tbody>
</table>

Figure 3A. Transition matrix for *Lesquerella*. Small, medium, and large represent vegetative stages. The fourth stage, reproductive adults, is the sum of two components, survival (Surv.) and reproduction (Recruit). $a_{ij}$ represents the probability of passing from stage $j$ to stage $i$. $s_{i4}$ is the probability of passing from the reproductive stage to stage $i$. $f_i$ is the number of individuals born into each stage per reproductive adult. B. Life cycle graph for *Lesquerella*. Arrows connecting two circles (and the letters adjacent to them) indicate the transition probabilities. The time scale for the transition between stages is one year.
Figure 4. Values of $\lambda$, the population growth rate, for three *Lesquerella* populations in 1991-1992 and 1992-1993. Means ± 95% c.i. are shown.

Figure 5. The number of *Lesquerella* born into each life cycle stage at Bear, Mulkey, and Rattler Gulches in 1992 and 1993.
Figure 7. The proportion of individuals in each stage in 1991, 1992, and 1993 at A. Bear Gulch, B. Mulkey Gulch, and C. Rattler Gulch.
Figure 8A-F. Life cycle graphs showing elasticity values >5%. Bold arrows indicate the two transitions that have the greatest impact on population growth rate. (S) indicates transitions in which survival is most important, and (R) indicates transitions in which recruitment is most important.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.


Harris, G. 1967. Some competitive relationships between *Agropyron spicatum* and *Bromus tectorum*. Ecological Monographs 37: 89-111.


