AN ABSTRACT OF THE DISSERTATION OF

Elizabeth F. Martin for the degree of Doctor of Philosophy in Botany and Plant
Pathology, presented on August 17, 2010.

Title: Reproduction, Demography, and Habitat Characterization of *Astragalus peckii*
(Fabaceae), a Rare Central Oregon Endemic

Abstract approved:

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Robert J. Meinke

   With little previous research on *Astragalus peckii* (Fabaceae), a state-listed
Threatened species in Oregon, I investigated three facets of its biology which are
integral to the conservation and management of the species. First, a four-year
demographic study of two large populations revealed increasing population growth at
one site (Chiloquin) and stable to declining population growth at another (Bull Flat).
Both sites had varying levels of herbivory from a microlepidopteran larva,
Sparganothis tunicana. Herbivore damage, regardless of when it occurred during the
plant growing season, was correlated with increased plant mortality at Bull Flat but
not Chiloquin. At Chiloquin, greater moth damage was correlated with decreased
reproduction, particularly when the moth was active earlier in the growing season.
These reductions in plant vital rates did not appear to contribute to negative population
growth at either site. Rather, below-average precipitation levels during the growing
season could be correlated with periods of population decline.

   From a series of experiments on the reproductive biology of *A. peckii*, fruit and
seed set were generally not limited by the quantity of pollen delivered by pollinators.
Instead, high levels of seed abortion prevented most ovules from fully developing to
seed. Quality of pollen (self- versus cross-pollen) also did not limit reproduction
under natural pollination levels, but self-pollen reduced seed set, and to a lesser degree
fruit set, during one of two years of hand-pollination experiments. Possible

explanations for the treatment effect, including procedural causes, are discussed. Significant inbreeding depression was evident in the growth of greenhouse-grown seedlings but no statistical differences were found for seed germination or seedling survival. In order to minimize inbreeding depression in the field, adequate sizes of plant and pollinator populations need to be maintained.

Finally, using vegetation, habitat, climate, and soil data in a habitat model, greater *A. peckii* abundance was correlated with patches of low litter and soil crust cover within sites. Supporting these model results, greenhouse-grown seedlings with 1 cm of juniper litter on the soil surface had lower survival than those grown with less or no litter. There were no strong vegetation associations for *A. peckii*, though, indicating that within its restricted geographical range, *A. peckii* can be found in a diversity of plant habitats that have low litter cover.

Reproduction, Demography, and Habitat Characterization of *Astragalus peckii*
(Fabaceae), a Rare Central Oregon Endemic

by
Elizabeth F. Martin

A DISSERTATION

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APPROVED:

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Chair of the Department of Botany and Plant Pathology

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Dean of the Graduate School

I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

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Elizabeth F. Martin, Author

ACKNOWLEDGEMENTS

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Chapter 1

INTRODUCTION

Many plant populations are at risk from habitat loss, fragmentation, and other factors; consequently, conservation protection is needed. Considering the limited resources available to address many conservation concerns, land managers and conservation biologists are faced with making decisions using limited information. But without sufficient biological knowledge of a species and its expected response to management actions, the success of conservation and restoration efforts will be bleak.

In this dissertation, I will investigate three aspects of the biology and ecology of *Astragalus peckii* (Fabaceae), a state-listed Threatened species in Oregon, with the aim of providing information on which management decisions can be based. Broadly, the three foci of this dissertation are demography, reproductive biology, and delineation of habitat associations of *A. peckii*. Considering little research has previously been conducted on *A. peckii*, results presented in these three chapters will provide valuable information from which I will assess the current status of this species and potential threats to long-term persistence. Additionally, it is my hope that information in this dissertation will be used as a baseline for any future work on *A. peckii*. In this introduction, I will first provide an overview of the study species, including descriptions of the associated geology, climate, and vegetation, and conclude with a synopsis of the goals and rationale for each chapter.

ASTRAGALUS PECKII

Astragalus peckii is one of over 1,700 members of the extremely species-rich genus *Astragalus* (Mabberley 1997). Despite a world-wide distribution, many of the species, including *A. peckii*, are localized soil endemics in arid regions (Barneby 1964). The distribution of *A. peckii* is limited to a two-county region in Central

Oregon on sites with sandy, pumice-influenced soils. These soils are volcanic in nature, originating from the eruptions of Mt. Mazama (present day Crater Lake) approximately 7500 years ago and a series of eruptions from Newberry Volcano occurring as recently as 1500 years ago. Characteristics of pumice soils include high water-holding capacity and high temperature extremes when dry. Nutrient levels, after accounting for the low bulk density of soil particles, are typically low in nitrogen, sulfur, and phosphorus (Youngberg and Dyrness 1964; Carlson 1979).

Due to its limited distribution, *A. peckii* is listed as Threatened by the state of Oregon and as a Species of Concern by the United States Fish and Wildlife Service. All known populations of *A. peckii* are located in Deschutes and Klamath Counties, Oregon, on sites with little to no slope immediately east of the Cascade Mountains. The distributional range spans approximately 200 km from north to south and only about 50 km from east to west. Within this region there are several distinct population clusters. The main population center, where an estimated 25 populations are currently located (ORNHIC 2003), is in the northern extent of the range. In this region, populations are on a mix of public and private land with the majority of public land sites administered by the Prineville District of the Bureau of Land Management. South of the population center are three disjunct areas with between 1 and 3 recorded populations each (ORNHIC 2003); each cluster is separated by between 40 and 75 km. Many of these sites are on public land administered by the Fremont-Winema National Forest.

Climate in this region is characterized by hot, dry summers and cold winters. Average annual precipitation over the past century ranges from 354 mm in the north to 505 mm in the south of the range (PRISM 2010). Almost no precipitation falls during summer months and much of the winter precipitation falls as snow. During the four years of this research (2006-2009), annual precipitation in the north was between 182 and 352 mm and annual precipitation in the south was between 485 and 608 mm (PRISM 2010).

Astragalus peckii typically grows in open habitats with low vegetation cover. The northern end of the range is characterized by sagebrush-steppe and juniper woodland communities whereas lodgepole and ponderosa pine forests dominate throughout the rest of the range; *A. peckii* is found within canopy gaps and open meadows in the forested regions (Amsberry and Meinke 2003). Vegetation at *A. peckii* sites is predominately shrubs and bunchgrasses. Common shrubs are *Artemisia tridentata* (sagebrush) and *Purshia tridentata* (antelope bitterbrush). Common grasses are *Festuca idahoensis* (Idaho fescue), *Poa secunda* (Sandberg bluegrass), *Achnatherum occidentale* (western needle grass) and *Elymus elymoides* (squirreltail).

Astragalus peckii plants are low-growing, prostrate, perennial legumes. Compared to other North American *Astragalus* species, *A. peckii* is unique in the presence of stiff petioles that persist from year to year (Barneby 1964). Plants produce numerous axillary inflorescences of 5-9 papilionaceous flowers; flowers are small (6-7 mm in length), hermaphroditic, and contain 7-9 ovules each (Piper 1924; Barneby 1964). Lacking clonal growth, reproduction is solely by seed. Previous studies on the reproductive biology report flowers are not autogamous, and average seed production is between 1.0 and 1.5 seeds/fruit (Gisler and Meinke 2001; Amsberry and Meinke 2003). Seeds are small (1.5 mm), black, and lack an obvious dispersal mechanism (Barneby 1964).

GOALS AND RATIONALE

I investigated three aspects of the biology and ecology of *A. peckii*: demography, reproduction, and habitat delineations. Within each of these study areas, my general goal was to describe the basic biology or habitat preferences of *A. peckii* and then use the results to assess the current status of this species and potential threats to its survival. More specific goals within individual chapters are given below.

I begin with a comparative demographic study of two large populations in Chapter 2. These two populations are located at opposite ends of the distributional range, with one in the northern population center and the other from a disjunct locale.

Stage-based transition matrix models will be used to analyze the demographic data because these models provide an estimate of current population growth rate (λ) and the relative contribution of each size class or life history stage (elasticity) to population growth (de Kroon et al. 1986; Caswell 2001). Results from this section will provide important baseline data for future work along with the first estimates of population growth for this species.

Continuing in Chapter 2, the impact of herbivory on population vital rates (survival, growth, and fecundity) will be made. Herbivores can have large negative impacts on different stages of a plant life cycle and have been cited as a contributor to plant rarity in certain instances (Bevill et al. 1999). Previous work on *A. peckii* identified a larval, microlepidopteran herbivore as potentially affecting survival (Amsberry and Meinke 2003), and I focus on this species (*Sparganothis tunicana* [Tortricidae]) as the primary herbivore in my work. No other single herbivore species was observed to have as great an impact on *A. peckii* at these sites.

In Chapter 3, I take a closer look at the reproductive biology of *A. peckii*. With no clonal growth, successful seed set is critical for population survival. However, many reproductive traits, particularly those associated with the breeding system and self-compatibility, are hypothesized to contribute to rarity through decreasing reproductive output (Gaston and Kunin 1997). In this study, I will focus on how pollen quantity, pollen quality (whether pollen is from the same or different individual) and pollinator abundance affect fruit and seed set in *A. peckii*. Because the effects of reproduction can carry into the next generation through inbreeding depression and because inbreeding depression is a major conservation concern in many rare plants, I also will compare seed germination, seedling survival, and seedling growth among progeny of different pollination treatments.

Using a broader perspective in Chapter 4, I examine characteristics of the habitat that potentially explain the distribution of *A. peckii* across the landscape. Because endemic species tend to be found more frequently than expected on less productive sites with sparse vegetation cover (Lavergne et al. 2004; Stohlgren et al.

2005), environmental and habitat characteristics may be important in explaining distributional limitations. Using multivariate statistical methods, I examined relationships between *A. peckii* abundance, vegetation cover, soils, and climate at two spatial scales, a broad site-level scale and a local 1 m^2 plot-level scale. Further investigation was made specifically on the effect of litter on seedling establishment and survival because many of the open habitats *A. peckii* are associated with could potentially be lost to canopy closure or woody plant encroachment.

REFERENCES

Amsberry, K., and R. J. Meinke. 2003. Life history and conservation status of *Astragalus peckii* Piper (Fabaceae). Native plant conservation program, Oregon Department of Agriculture.

Barneby, R. C. 1964. Atlas of North American *Astragalus*. Memoirs of the New York Botanical Garden 13: 1–1188.

Bevill, R. L., S. M. Louda, and L. M. Stanforth. 1999. Protection from Natural Enemies in Managing Rare Plant Species. *Conservation Biology* 13: 1323-1331.

Carlson, G.T. 1979. Soil resource inventory. Report for the Winema National Forest, US Forest Service.

Caswell, H. 2001. Matrix Population Models: Construction, Analysis, and Interpretation. *Sunderland, Massachusetts: Sinauer*.

Gaston, K.J., and W.E. Kunin. 1997. Rare-common differences: an overview. In *The biology of rarity*. Springer.

Gisler, S., and R. Meinke. 2001. Reproductive ecology, seed banking, and cultivation of five at-risk legume species in Oregon. Oregon Department of Agriculture Plant conservation biology program.

de Kroon, H., A. Plaisier, J. van Groenendael, and H. Caswell. 1986. Elasticity: The Relative Contribution of Demographic Parameters to Population Growth Rate. *Ecology* 67: 1427-1431.

Lavergne, S., J.D. Thompson, E. Garnier, and M. Debussche. 2004. The biology and ecology of narrow endemic and widespread plants: a comparative study of trait variation in 20 congeneric pairs. *Oikos* 107: 505-518.

Mabberley, D.J. 1997. *The Plant-Book, A Portable Dictionary of the Vascular Plants, 2nd edition.* Cambridge: Cambridge University Press.

ORNHIC (Oregon Natural Heritage Information Center). 2003. Oregon Natural Heritage Information Center Database. Oregon Natural Heritage Information Center, Portland, Oregon.

Piper, C. V. 1924. New flowering plants of the Pacific coast. *Proceedings of the Biological Society of Washington* 37: 91-96.

PRISM Climate Group. *Oregon State University*. http://www.prismclimate.org.

Stohlgren, T.J., D.A. Guenther, P.H. Evangelista, and N. Alley. 2005. Patterns of plant species richness, rarity, endemism, and uniqueness in an arid landscape. *Ecological Applications* 15: 715-725.

Youngberg, C.T., and C.T. Dyrness. 1964. Some physical and chemical properties of pumice soils in Oregon. *Soil Science* 97: 391-399.

Chapter 2

SPATIOTEMPORAL VARIATION IN THE DEMOGRAPHICS OF A RARE
CENTRAL OREGON ENDEMIC, *ASTRAGALUS PECKII* (FABACEAE), WITH
FLUCTUATING LEVELS OF HERBIVORY

Elizabeth F. Martin and Robert Meinke

Prepared for submission to Population Ecology

ABSTRACT

Plant vital rates (survival, growth, and reproduction) and population demographic parameters respond to environmental, climatic, and biotic variation throughout the range of a species. Understanding these responses in rare plant taxa facilitates effective management of populations for long-term persistence. This study evaluated two populations of the rare plant *Astragalus peckii* (Fabaceae), a state-listed Threatened plant in Oregon, USA. The two study sites differed in their proximity to neighboring populations; one was located in the main population center (Bull Flat) and the other in an isolated cluster of three widely separated populations (Chiloquin). Additionally, we assessed the impact an associated microlepidopteran herbivore, *Sparganothis tunicana*, had on vital rates in each population. Data on plant size, reproductive state, and herbivore damage were recorded from permanent field plots for four years, 2006-2009. Spatial and temporal variability in population growth rate (λ) and elasticity were evaluated with stage-based transition matrix models, and herbivory effects on plant vital rates were analyzed with regression analyses. Population growth at Bull Flat, in the main population center, was estimated at stable to slightly declining (λ=0.96, 95% CI 0.91-1.00) whereas Chiloquin, the isolated population, had increasing population growth (λ=1.20, 95% CI 1.15-1.24). Several factors, including precipitation levels and plant longevity, were identified as potential contributors to spatial and temporal variation in vital rates and demographic parameters between these two sites. Microlepidopteran herbivory affected different vital rates at each population. At Bull Flat, survival was lower with greater herbivory. At Chiloquin, reproduction was reduced in plants with more herbivore damage during the 2007-08 study period, with greater negative effects on *A. peckii* later in the growing season. Despite these effects on plant vital rates, there was no strong evidence that herbivory impacted long-term population growth under current conditions.

INTRODUCTION

In order to effectively manage rare and endemic plant populations for long-term persistence, land managers need to understand how plant vital rates and population growth fluctuate with respect to the inevitably variable abiotic and biotic conditions throughout a species' range. Different patterns in vital rates (e.g., survival and fecundity) emerge against changing resource and biotic backgrounds, even for species with extremely restricted distributions and relatively little habitat heterogeneity (Freville et al. 2004). If strong enough, this variability could complicate range-wide prescribed management plans when a management strategy appropriate for populations in one region is not best for populations in a different region.

The abiotic environment is never static. A suite of factors including climate fluctuation (Maschinski et al. 2006), microhabitat variability (Kephart and Paladino 1997; Volis et al. 2004), and disturbance history (Maschinski et al. 1997; Lesica 1999; Evans et al. 2008) affect both individual plant vital rates and long-term population abundance, with contributing factors often intertwined as disturbance events and climatic variation shape the environment (Menges and Kimmich 1996; Endels et al. 2005; Yates et al. 2007). Underlying environmental gradients also influence population dynamics across a species' range because plant growth and abundance change in relation to variables such as elevation, soil nutrients, and precipitation (Angert 2006; Dahlgren and Ehrlen 2009; Miller et al. 2009).

In addition to abiotic conditions, proximity to neighboring populations can affect demographic processes through changes in gene flow, which in turn affect reproduction, genetic diversity, and ultimately the resilience of a population to stochastic events (Shaffer 1981; Menges 1991). Demographic studies of naturally isolated populations (in contrast to newly isolated populations from recent habitat fragmentation) have found reduced population growth rates in the more isolated or disjunct populations (Menges and Dolan 1998; Groom 2001). However, isolation can sometimes have beneficial impacts as Groom (2001) found when isolated populations were protected from herbivores.

Herbivory and seed predation of plants by their native predators also affect plant abundance through short-term changes in growth, reproduction, and survival (Louda 1982; Crawley 1989; Doak 1992). This can have a relatively large and detrimental impact on rare plant populations that are small in size or few in number (Bevill and Louda 1999). However, the relationship with long-term population growth is less defined because the direct impact of predators on vital rates does not necessarily correspond to an impact on population growth (Halpern and Underwood 2006). For example, if herbivory strongly reduces plant survival but a reduction in plant survival has little effect on λ, as in the case with annual plants, then the overall impact of herbivory on population growth will be minimal.

Furthermore, negative impacts of seed predation on perennial plants have traditionally been thought to be mitigated with seedbanks, density-dependent regulation of seedling survival, and safe-site limitation in the environment (Crawley 1992; Louda and Potvin 1995). With one or more of these traits, plant populations can overcome high mortality or reproductive loss through compensation in another stage of the life cycle. Some recent studies, however, have shown that under certain environmental and habitat conditions, negative impacts of seed loss still manifest at the population level regardless of these regulating mechanisms (Maron and Gardner 2000; Kauffman and Maron 2006). Overall, studies to date which have looked at demographic effects of native herbivores on plant demography have found populations with herbivory to have lower population growth than those where herbivory is absent or excluded, but the effect of herbivores is not strong enough to cause population decline (Ehrlen 1995; Kauffman and Maron 2006; Leimu and Lehtilä 2006; Weppler and Stöcklin 2006; Dahlgren and Ehrlen 2009).

This study uses stage-based transition matrix models to describe the population dynamics of *Astragalus peckii* (Fabaceae), a state-listed Threatened species in Oregon, USA, over three transition periods (2006-2009). *A. peckii* has a disjunct distribution within a two-county area in central Oregon, and despite the restricted range, dominant vegetation, precipitation, and associated insect fauna all vary among the isolated

populations. Using two populations, one from the main population center and the other from a disjunct locale, population growth rate (λ) and elasticity, the proportional contribution each life cycle transition has on λ, are estimated using transition matrix models (de Kroon et al. 1986; Caswell 2001). Elasticity is a particularly useful calculation because between-population and between-year comparisons can be made using these scaled values, and elasticities can be summed by contribution to each vital rate to assess the impact of change in these on λ (Silvertown et al. 1993).

We further assess differences between these two populations with respect to a prominent herbivore, the microlepidopteran *Sparganothis tunicana* (Tortricidae), which is found throughout the range of *A. peckii*. Damage from the larval stage of this moth is in two main forms: direct consumption of plants through herbivory and indirect effects from obscuring portions of plants with webbing for pupation. The effect of *S. tunicana* on individual vital rates has not been studied but likely impacts include reduced reproduction, decreased growth, and increased mortality of individual plants. The effect of *S. tunicana* on population growth rate will then depend on how heavily the individual vital rates contribute to λ.

The specific research questions for this study are: 1) How do population structure and vital rates of *A. peckii* differ between a population in the primary population center and a disjunct population from a smaller population grouping?; 2) How do demographic parameters (population growth rate and elasticity) differ between populations and years?; and 3) What is the effect of *S. tunicana* on *A. peckii* vital rates and population growth, and does the effect depend on the timing of damage during the growing season?

METHODS

Study species and range

Astragalus peckii is a low-growing, prostrate, perennial legume with stiff petioles that persist from year to year (Barneby 1964). There is no clonal growth in *A. peckii*, but it does reproduce by seed and maintains a persistent seed bank; seed

longevity within the seed bank is not known. *A. peckii* is thought to be a relatively short-lived perennial, but information on longevity is lacking. First-year seedling plants are never reproductive, and older, non-seedling plants can become reproductive anytime from the second year on (E. Martin, personal observation).

Found solely in Deschutes and Klamath Counties, Oregon, USA, all known populations are immediately east of the Cascade Mountains in areas with sandy, pumice-influenced soils. The distributional range spans approximately 200 km from north to south, and within this range there are several distinct population clusters (Figure 2.1). The majority of known populations are located in the northern extent of the range, where habitat is typically sagebrush-steppe or juniper woodland. South of this main population center are three disjunct population clusters; these populations differ from those in the north in that they are found within canopy openings of coniferous forest ecosystems. Due to its limited distribution, *A. peckii* is listed as Threatened by the state of Oregon and as a Species of Concern by the United States Fish and Wildlife Service.

Study sites

Two study sites, one in the northern population center (Bull Flat) and one in the southernmost cluster of populations (Chiloquin), were selected because they had large populations (over 1000 flowering plants/site) and were easily accessed on public lands (Figure 2.1). The Bull Flat site (44º 09′ 40.35″N, 121º 26′ 05.54″W, 1062-m elevation) is located northwest of Bend, Oregon, on Bureau of Land Management (BLM) land and is approximately 0.4 km^2. There are approximately 25 *A. peckii* populations in this region, most likely once comprising a larger meta-population before population growth and agricultural development in this region led to habitat fragmentation. Bull Flat is a large sagebrush-steppe flat, dominated by *Artemisia tridentata* (big sagebrush) and *Festuca idahoensis* (Idaho fescue). The nearest neighboring *A. peckii* population is about 0.75 km away.

Figure 2.1. Distribution of *A. peckii* in central Oregon and demographic study sites. Mapped locations include all current (●) and presumed extirpated populations (**X**).

The Chiloquin site (42º 32′ 36.45″ N, 121º 44′ 10.01″ W, 1358-m elevation) is located northeast of Klamath Falls, Oregon, on United States Forest Service (USFS) land. This site is located between a wet meadow and ponderosa pine-dominated forest and is approximately 0.1 km^2. There are only three known populations in this region, the nearest one 5 km away. The closest population outside of the southern population cluster is approximately 60 km away. Like Bull Flat, dominant vegetation in the immediate vicinity of *A. peckii* is *Artemisia tridentata* and *Festuca idahoensis*, but unlike Bull Flat, this site supports greater vegetation density and a higher diversity of plant species, and it is adjacent to different habitat types.

Field sampling

Five 4×8 m plots were established at each site, for a total sampling area of 160 m^2/site. Plots were selectively located to ensure the presence of *A. peckii* within each plot and data were collected during three sampling trips each year to maximize the number of plants recorded. The three sampling trips were early-, mid-, and late-growing season and roughly correlate with May, June, and July. Although *A. peckii* does not have clonal growth, below-ground branching or partial burial by sand occasionally makes identification of individuals difficult. An individual was therefore defined as a stem at least 2 cm away from the nearest neighboring stem, unless plants were previously known to have arisen from multiple seedlings. First-year seedlings were identified by the presence of cotyledons and/or the lack of persistent petioles that older plants retain (Barneby 1964).

Data were recorded on the location, size, reproductive output, and moth damage of *A. peckii* plants for four years, 2006-2009. The location of each individual was mapped using an x-y grid within each 1 m^2 and non-seedling plants were staked for identification later in the season and in subsequent years. Size measurements for each non-seedling plant were taken by measuring plant width (to the nearest 0.1 cm) at the widest diameter and the diameter perpendicular to this. Because *A. peckii* has a prostrate growth form, no height measurement was recorded, and the 2-dimensional area of each plant was calculated using the formula for area of an ellipse. The number

of fruits/plant was either directly counted for small reproductive plants or extrapolated using a count from a portion of the plant for large individuals. Size measurements were made during the mid-season trip and fruit counts were made both mid- and late-season; the larger of the two counts was used in analyses. Moth larval damage can be of two types, coverage with webbing and tissue damage via herbivory. Both were measured as a percent of the plant affected mid- and late-season in 2007 and 2008 only.

Matrix construction

Life cycle stages – First-year plants were classified as seedlings and included as their own stage. In order to delimit non-seedling plants into different stage categories, variables which significantly affect plant survival, growth, and reproduction were first identified with regression analyses and then used to group plants into stages (Morris and Doak 2002). Three potential predictor variables were included in each regression: plant size (cm^2, log-transformed), reproductive state (+/-), and fruit set (# fruits/plant, log-transformed). Three regressions were run for each site and transition-year combination. Each of the three regressions had a different response variable: survival (+/-), growth ($log[size_{t+1}] – log[size_t]$), or fruit set in the following year (log-transformed). Logistic regression was used for plant survival and normal linear regression was used for growth and fruit set. AIC model selection was used to identify variables that best explained the response and assessment of significance for each variable was made from the final model. These and all other analyses were made using R v2.9.2 (R Development Core Team 2009).

Plant size was significantly correlated with survival, growth, and reproduction more often than either reproductive state or fruit set (Table 2.1). Using size measurements, all non-seedling plants were then delimited into three stage classes with approximately equal number of plants in each class. Because the distribution of plant sizes differed between sites, different class boundaries were used at Bull Flat and Chiloquin. At Bull Flat, the size classes were 0-15 cm^2, 15-75 cm^2, and >75 cm^2, while at Chiloquin the size classes were 0-12 cm^2, 12-150 cm^2, and >150 cm^2. The

final life cycle model for *A. peckii* thus contains five stages: seed bank, seedling, small, medium, and large plants (Figure 2.2).

Table 2.1. Variable selection for demographic stage classes. Explanatory variables were chosen with AIC model selection using either logistic (survival) or linear (growth and fruit set) regression. Explanatory variables included in each model were size (cm^2), fruit set (# fruits/plant) and repro (+/- flowering). Sample size for each model is in parentheses. Asterisks represent significance levels of variables in the final model (*p<0.05, **p<0.01, ***p<0.001).

Site	Response variable	Explanatory variables selected with AIC		
		2006-2007	2007-2008	2008-2009
Bull Flat	Survival	Size ** Fruit set ** (n=316)	Size ** (n=199)	Repro (n=138)
	Growth	Size *** (n=169)	Size *** (n=72)	Size *** (n=91)
	Fruit set/plant	Size *** Repro * (n=169)	Size *** (n=72)	Size *** (n=91)
Chiloquin	Survival	Fruit set * Repro * (n=198)	Size** (n=195)	Size *** Fruit set ** (n=228)
	Growth	Size * Fruit set * (n=130)	Size *** Fruit set * Repro * (n=150)	Size *** (n=174)
	Fruit set/plant	Fruit set ** Repro *** (n=130)	Size *** Repro (n=150)	Size Fruit set ** (n=174)

Seed production/plant – Average seed production/plant was estimated each year at both sites for use in fecundity calculations. Seed production was calculated for each *A. peckii* individual as the product of fruit set and average seed set. Average seed set data for each site and year was from a separate study where fully formed seeds were counted in fruits from 30 randomly selected plants (see Chapter 3 for complete

methods). These plants were located outside the demographic plots. Average seed set values used in our calculations each year from 2006-2008 were 1.04, 1.13, and 1.39 seeds/fruit at Bull Flat and 0.73, 0.79, and 1.03 seeds/fruit at Chiloquin, respectively. Since our estimates of fruit set were from one day of field observation, this number likely underestimates actual seed production.

Fecundity (seed bank) – Buried seed bags were used to estimate seed survival in the soil for two years using seed collected at each site in August, 2006. Twenty bags, each filled with 10 *A. peckii* seeds and soil from a region of the site lacking *A. peckii*, were buried in November, 2006, at each site. Ten bags per site were retrieved in August, 2007, and the remaining 10 were retrieved in August, 2008. After retrieval, seeds were sieved out of the soil, scarified with sandpaper, and germinated on moistened filter paper in an Oregon State University greenhouse to assess viability (Gisler and Meinke 2001).

Seed bank fecundity values for each plant were calculated as the percent of viable seeds remaining in the soil at year one multiplied by seed production/plant. Averages were then computed for each stage class to add to the matrices. Survival of seeds from year one to year two, calculated as the percent of year one viable seeds that were still viable after a second year, was used to estimate stasis in the seed bank. Seed bags were buried only once in 2006 and the estimates of viability from each site were applied to all transition-years.
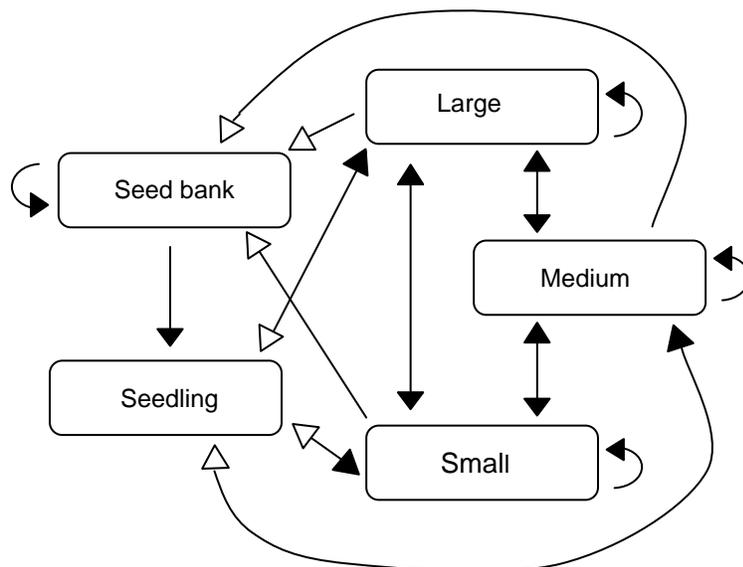
Figure 2.2. Life cycle diagram for *Astragalus peckii*. Filled arrowheads represent stage transitions of growth, stasis, or retrogression, open arrowheads represent fecundity via recruitment into the seed bank or seedling establishment, and transitions without arrowheads do not occur.

Fecundity (seedling establishment) – Two approaches for estimating fecundity were used – one for recruitment from the persistent seed bank and one for recruitment directly from reproductive plants. To estimate seedling recruitment from the persistent seed bank, 16 0.2×0.2 m seed plots were established at each site in November 2006. Plots were paired (8 pairs/site) and within each pair one plot was randomly assigned as a seed addition plot and the other as a control. Each plot was filled with soil from a region of the site that did not have *A. peckii* to minimize the pre-existing seed bank. Fifty seeds, collected during the summer of 2006, were added to each seed addition plot and covered with a thin layer of soil; control plots were left unseeded. Seedling establishment was recorded during the summer of 2007 and 2008. Recruitment from the seed bank was estimated as the number of newly established seedlings during the second year ($seedlings_{2008}$) per number of seeds remaining in the seed bank at the beginning of the growing season with the following formula:

$$Fecundity = \frac{seedlings_{2008}}{\# seeds_{original} \times seedbank_{2007} - seedlings_{2007}}$$

The number of seeds remaining in the seed bank was estimated as the proportion of seeds originally added to each plot (# seeds$_{original}$) that survived one year in the seedbank (seedbank$_{2007}$) minus the number of seeds that established in the first growing season (seedlings$_{2007}$). Seedling establishment numbers were corrected if any recruitment was observed in the control plots.

Because seedling recruitment between years was highly variable at our sites (see results) and our estimate of first-year recruitment in the seed plots (seedlings$_{2007}$) was from only one of these years, fecundity for reproductive plants was calculated differently. For this, we used the number of seedlings present at time$_{t+1}$ and weighted recruitment from each size class in the previous year by average seed production at time$_t$. Although this overestimates total fecundity because additional recruitment will be from the persistent seed bank, it more accurately represents observations of seedling numbers than using estimated recruitment rates from seed plots explained above.

Statistical Analyses

Spatiotemporal variation of demographic parameters – Eight matrices were compiled: three individual transition year matrices plus one pooled matrix for each site. Population growth rate (λ) was calculated for each site-by-year combination and overall for each site using the pooled data. Plant lifespan for each site was also estimated using the pooled matrices. Lifespan was estimated using the average time till death once reaching the medium stage class plus the average amount of time spent in both the seedling and small stage classes before this. All matrix calculations were made using the popbio package in R (Stubben and Milligan 2007).

Elasticity was computed for each element in all eight matrices. Individual elasticities were then summed by starting stage class to create five grouped elasticity values for each site-by-year combination. Within the seed bank, small, medium, and large stage classes, elasticities were further divided into those that contribute to reproduction (fecundity transitions to seed bank or seedling stage classes) and those that contribute to survival or growth. Ninety-five percent confidence intervals were

computed for λ and each elasticity estimate using 2000 runs of bootstrapped data (Caswell 2001).

Comparisons of λ were made both between transition years within each site and between sites (using pooled data) with nonparametric randomization tests where individuals were randomly permuted among pairs of years (or sites) while keeping the sample size for each year or site fixed (Caswell 2001). One thousand permuted data sets were used for each comparison and a two-tailed test was run to assess differences. Since three sets of comparisons were made between transition years at each site, a Bonferroni corrected α-level was set at 0.017 (0.05/3).

Moth effects on survival, growth, and reproduction – The effect of year, site, and timing of moth damage (mid- or late-season) was made for each type of damage (% webbing and % herbivory, both log-transformed) with a 3-way ANOVA. Regression analyses were then used to test the hypothesis that plants with greater moth damage had lower survival, decreased growth in the following year, and lower fruit set in the current year. Only non-seedling plants were used in these analyses because seedlings were never reproductive and had much lower survival than non-seedlings (see results). Regressions were run independently for each site and year with four predictor variables: mid- and late-season webbing and mid- and late-season herbivory. If the full model was significantly different than the null model ($\alpha=0.05$), then the full model was compared to one with only mid-season webbing and herbivory to assess the influence of season.

Logistic regression was used for survival data and normal linear regression for growth and fruit set data. Both growth and fruit set were log-transformed in order to meet the assumption of normal distribution of the residuals; growth was the log of the area in the second year of measurement minus the log of the area in the first year of measurement. Moth herbivory was not recorded for plants in 2006; therefore, only data from 2007-2009 were used.

RESULTS

Site variation in population structure and vital rates

Population structure and survival differed between the two populations. Bull Flat consistently had fewer plants present, lower seedling recruitment, higher percent seedling survival, and lower percent survival of non-seedling plants compared to Chiloquin (Table 2.2; Figure 2.3). A total of 1543 plants were surveyed at Bull Flat over the four years and annual plant densities were between 2.2 and 3.8 plants/m^2 (Table 2.2). Chiloquin had over twice as many plants present in the same size area during this time; a total of 3211 plants were surveyed and annual densities were between 5.3-8.9 plants/m^2 (Table 2.2). While the population size remained fairly stable at Chiloquin, with the exception of 2008 when there was a large pulse of seedling recruitment, population numbers declined steadily from 2007-2009 at Bull Flat (Figure 2.3).

Table 2.2. Summary statistics from *A. peckii* demographic plots at two sites, Bull Flat (BF) and Chiloquin (CQ), from 2006-2009. Numbers are from pooled data each year at each site. Survival percentages indicate how many plants in each category survived to the following year.

Variable	Site	2006	2007	2008	2009
Plant density (plants/m^2)	BF	3.7	3.8	3.2	2.2
	CQ	5.5	5.3	8.9	5.5
Seedling survival (% of plants)	BF	15.7	19.4	18.2	--
	CQ	12.4	12.6	11.5	--
Non-seedling survival (% of plants)	BF	53.6	34.0	63.8	--
	CQ	60.4	72.5	75.2	--
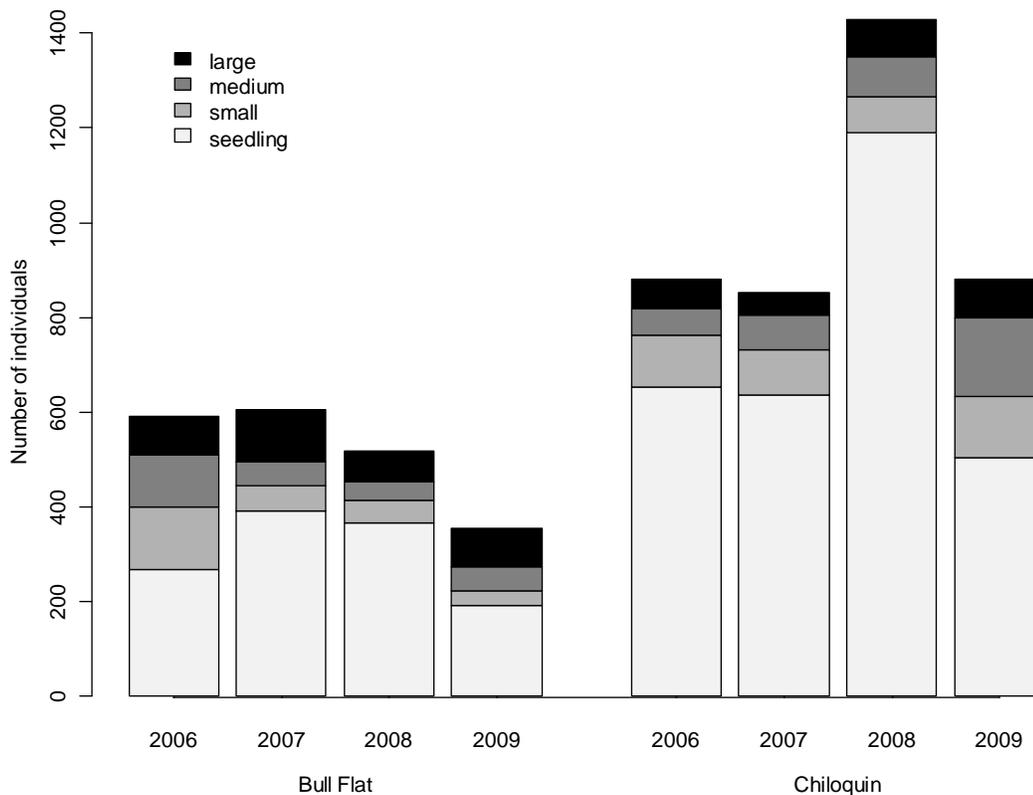
Figure 2.3. Number of *A. peckii* plants by demographic stage class recorded from permanent plots at two study sites (Bull Flat and Chiloquin). Total plot area at each site is 160 m^2.

Both sites had high annual seedling recruitment coupled with low seedling survival (Table 2.2, Figure 2.3). Each year, between 190 and 400 seedlings established at Bull Flat and between 500 and 1200 established at Chiloquin (Figure 2.3). Despite differences in the magnitude of seedling recruitment between years, seedling survival was relatively stable with 15.7-19.4% survival at Bull Flat and 11.5-12.6% survival at Chiloquin. In comparison, survival of non-seedling plants fluctuated over time, ranging from 34.0-63.8% at Bull Flat and from 60.3-75.2% at Chiloquin (Table 2.2). Given higher percent survival at Chiloquin, plant lifespan was also higher at this site. It took about 2.3 years to reach the medium size class, and once a plant reached this class, lifespan was estimated at 4.7±13.5 years. In

comparison, at Bull Flat it took about 2.1 years to reach the medium size class, and estimated lifespan for medium plants was 2.0±1.6 years.

Plant size was correlated with reproductive output (R^2=0.74 for 2008 data, other years were similar); larger plants, on average, had higher seed production per plant because they were both more likely to be reproductive and when reproductive, they had a greater number of flowers and fruits than plants in smaller size classes. When comparing reproductive output between sites, both small and medium plants at Bull Flat produced, on average, more seed per individual than those at Chiloquin (Table 2.3). This was mainly due to more plants within these categories being reproductive at Bull Flat (Table 2.3). Overall, though, the majority of seed produced at both sites was from large plants and reproductive output within this stage class was variable over the years. At Bull Flat, seed production from large plants in 2008 was more than twice as much as either 2006 or 2007, and at Chiloquin, seed production in both 2006 and 2008 was approximately 3x higher than in 2007 (Table 2.3).

Seed survival in the seed bank was lower at Bull Flat than Chiloquin. After one year at Bull Flat, 36.4% of the original buried seeds were viable, and after two years, only 16.0% of the original seeds were viable. After one year at Chiloquin, 60.1% of seeds were viable, which was two-thirds more than at Bull Flat. After two years, 34.2% were viable, twice as many as Bull Flat. Stasis in the seed bank from year one to two was 44.0% at Bull Flat and 53.2% at Chiloquin.

Table 2.3. Average seed production/plant/stage class (± 1 SD) for *A. peckii* at two sites over a three-year period. Sample size for each site and year given in parentheses.

Site	Year	Number of seeds/plant ± 1 SD		
		Small	Medium	Large
Bull Flat	2006	0.7±4.0 (n=133)	15.1± 33.6 (n=109)	93.7±108.23 (n=81)
	2007	0.1±0.9 (n=55)	32.1±50.8 (n=51)	124.7±90.5 (n=109)
	2008	0.4±1.5 (n=47)	32.6±31.7 (n=39)	321.7±237.1 (n=63)
Chiloquin	2006	0.1±0.5 (n=110)	6.5±14.8 (n=55)	206.1±190.7 (n=62)
	2007	0.0±0.0 (n=97)	9.4±35.6 (n=72)	70.9±72.6 (n=49)
	2008	0.0±0.0 (n=78)	11.7±30.9 (n=83)	238.3±233.9 (n=77)

Recruitment in the seed plots averaged 1.1 seedlings/plot at Bull Flat and 1.4 seedlings/plot at Chiloquin. One pair of the seed plots was dislodged at the Chiloquin site – most likely from elk disturbance – lowering the sample size at this site. The percentage of seeds which established after one winter was between 2-3% at both sites. In the second year, only one seedling established in the plots at Chiloquin and three established at Bull Flat. After accounting for seed attrition in the seed bank, recruitment of seedlings from two-year-old seeds in the seed bank was 2.2% at Bull Flat and 0.6% at Chiloquin.

Spatiotemporal variation in demographic parameters

Population growth rate (λ) using pooled data from 2006-2009 was significantly lower (p=0.002) at Bull Flat where growth was stable to slightly declining (λ=0.96, 95% CI 0.91-1.00) compared to Chiloquin where growth was increasing (λ=1.20, 95% CI 1.15-1.24; Figure 2.4; matrices included in Appendix 2.1). Within each site, λ also differed between transition years (Figure 2.4). At Bull Flat, population growth was just below stable during the first transition-year, declined during second, and increased during the third. The third transition-year, from 2008-09, had significantly greater growth than the two previous transition periods (p<0.01 for both comparisons), but 2006-07 and 2007-08 did not differ from one another (p=0.36). At Chiloquin, λ was stable or increasing for all three transition-years. The 2006-07 transition-year had a significantly lower λ than the 2007-08 transition period (p<0.01) and a marginally lower λ than the 2008-09 transition-year (p=0.03) when significance level was Bonferroni corrected for multiple comparisons. The 2007-08 and 2008-09 transition years did not statistically differ (p=0.86).

When elasticity values were summed by stage class, large plants contributed most to λ at Bull Flat, with values ranging from 28.2% during 2007-08 to 39.3% during 2008-2009 (Figure 2.5; Appendix 2.2). Large plants also had the greatest contribution to fecundity (19-20%) with recruitment from the seed bank as a secondary contributor (6-11%; Figure 2.5; Appendix 2.2). Seedling survival contributed between 20.0% and 23.6% to population growth, and survival and growth

of seedlings often ranked among the highest elasticity values each year at Bull Flat
(Figure 2.5; Appendix 2.2).

At Chiloquin, large plants had a similar influence on λ, with elasticities
ranging from 34.5% during 2006-07 to 41.0% during 2007-08. Unlike Bull Flat,
though, medium plants had an almost equal contribution to λ with elasticities ranging
from 27.0% during 2007-08 to 32.0% during 2008-09 (Figure 2.5; Appendix 2.2).
Fecundity contributions were again mostly from large plants (14-17%) but there was
less recruitment from the seed bank at this site (0-5%; Figure 2.5). Elasticity for
seedling survival was slightly lower at Chiloquin, but still contributed between 14.7-
19.6% of λ (Figure 2.5). Stasis in the seed bank (0-3%) was much lower than at Bull
Flat (Figure 2.5).
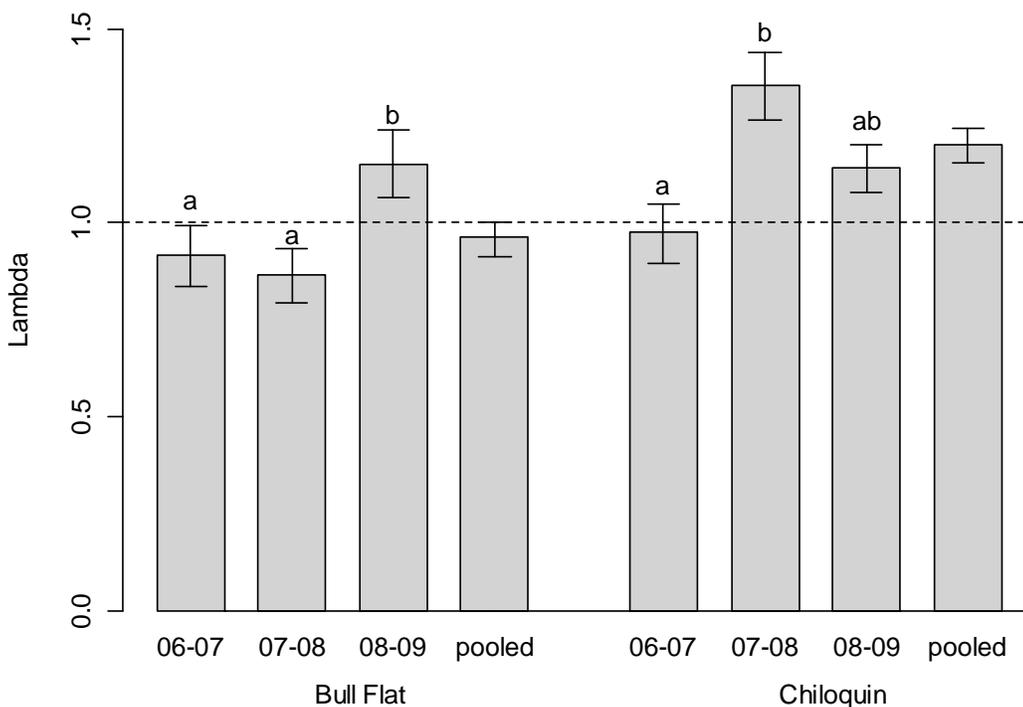
Figure 2.4. Population growth rates (λ) and 95% CI (computed using 2000 runs of
bootstrapped data) for two *A. peckii* sites, Bull flat and Chiloquin. The dashed line at
$\lambda=1$ represents stable population growth. Letters represent significant differences in λ
between years within each site. A between site comparison was made with pooled
data only and was significantly different (p=0.002)
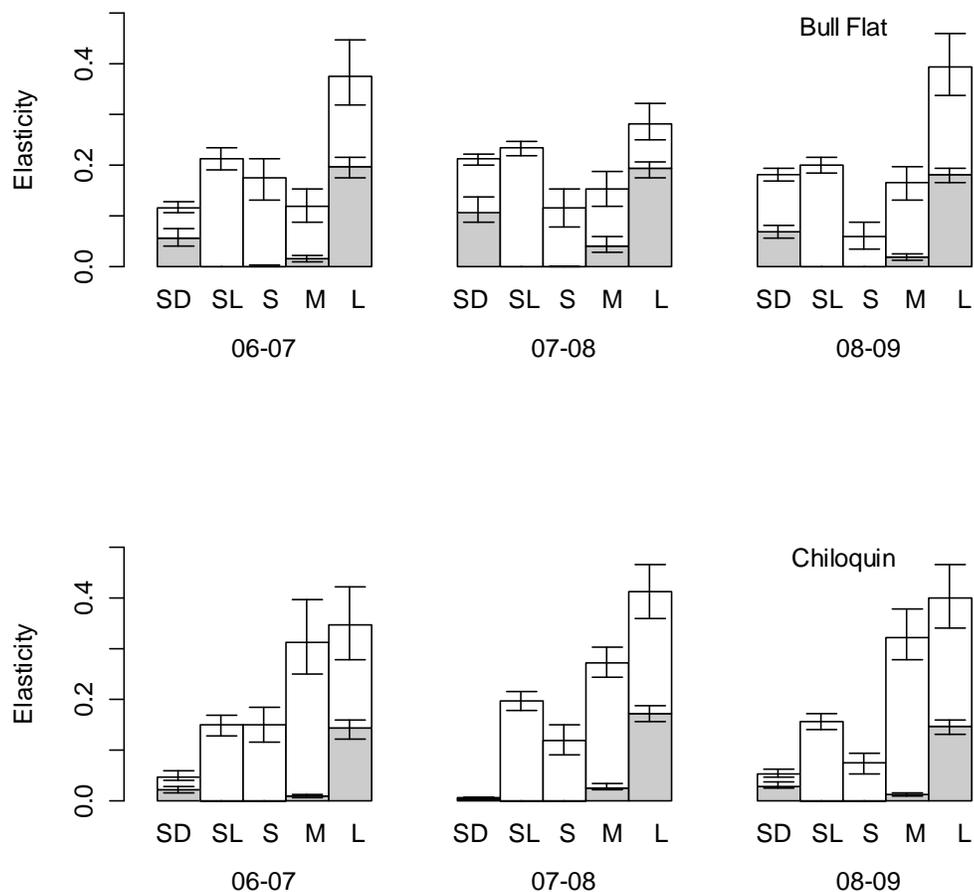
Figure 2.5. Elasticities for *A. peckii* summed by stage class for each transition-year at two sites (Bull Flat and Chiloquin). Within each stage class, elasticities are partitioned into survival elasticities representing both stasis and growth of individuals (white bars) and fecundity elasticities (grey bars). Error bars represent 95% CI (computed using 2000 runs of bootstrapped data) of the summed elasticities. Stage classes are seed bank (SD), seedling (SL), small (S), medium (M), and large plants (L).

Moth effects on survival, growth, and reproduction

  Sparganothis tunicana was present at both sites each year of study, but the amount of webbing or herbivory depended on the year, site, and time during the growing season that it was measured (herbivory: all 2-way interactions significant at $p<0.001$; webbing: three-way interaction, $F_{1,1481}=43.2$, $p<0.001$). At Bull Flat, there was minimal damage by *S. tunicana* to plants mid-season when *A. peckii* was in flower (Table 2.4). Late-season when *A. peckii* was in fruit, 20-54% of plants had signs of either webbing or herbivory; for those plants with damage, 8-26% of the plant was affected (Table 2.4). A similar pattern was evident at Chiloquin in 2008, but in 2007, *S. tunicana* was active much earlier in the season. In June, when plants were in flower, 66-80% of plants had either webbing or tissue loss from herbivory, and on each plant, this damage covered 20-47% of the plant (Table 2.4).

  At Bull Flat, damage by *S. tunicana*, but not the timing of damage during the season, was correlated with *A. peckii* survival (Table 2.5). Plants that survived to the next year had, on average, half or less than half the damage as those that died before the next year. Conversely, moth damage did not significantly affect survival at the southern site where *S. tunicana* was more prevalent (Table 2.4; Table 2.5). Instead, both the presence of *S. tunicana* and the season of damage affected growth and fruit set at Chiloquin from 2007-08; no significant effects were found at this site from 2008-2009 (Table 2.5). During 2007-2008, the moth variables explained more of the variation in reproduction at Chiloquin (Adjusted $R^2=0.19$) than in growth (Adjusted $R^2=0.06$). Plants without herbivore damage had higher seed production than undamaged plants both mid- and late-season. Mid-season, plants without herbivore damage had 2x greater seed production than damaged plants. Late-season, plants without herbivore damage had 3x greater seed production than damaged plants.

Table 2.4. Damage by *S. tunicana* on *A. peckii* at two sites in 2007 and 2008. The two sites were Bull Flat (BF) and Chiloquin (CQ). Two types of moth damage, webbing and herbivory, were recorded. Both the percentage of plants at each site with damage (population-level data) and the percentage of each individual plant that was damaged (individual-level data) were recorded. Damage was recorded twice during the growing season, mid- and late-season.

| Site | Year | Time of growing season | Webbing | | Herbivory | | n |
			Population (mean % of plants)	Individual (mean % for each plant)	Population (mean % of plants)	Individual (mean % for each plant)	
BF	2007	Mid	2.0	3.8	3.0	8.8	198
		Late	39.6	14.0	19.8	8.1	192
	2008	Mid	6.7	3.8	6.0	1.8	134
		Late	54.0	25.8	50.4	13.8	137
CQ	2007	Mid	80.5	30.4	70.8	35.2	195
		Late	66.3	20.9	78.6	46.7	187
	2008	Mid	31.1	13.9	13.6	24.7	228
		Late	75.7	30.9	62.8	27.0	218

Table 2.5. Effect of moth damage, including both herbivory and webbing, and timing of damage (mid- or late-season) on *A. peckii* survival, growth, and fruit set. Comparison of the full and null model was used to assess the moth effect. Timing of damage was assessed only if there was a significant moth effect. Logistic regression was used for the survival data and significance was evaluated with χ^2 statistics. Linear regressions were used for growth and fruit set data and significance was evaluated with F-statistics. Significant differences are indicated by an asterisk (*).

	Moth		Timing	
	test-statistic (df)	p-value	test-statistic (df)	p-value
Survival				
Bull Flat 07-08	10.35 (4)	0.035 *	2.84 (2)	0.24
Bull Flat 08-09	9.55 (4)	0.049 *	2.26 (2)	0.33
Chiloquin 07-08	5.56 (4)	0.235		
Chiloquin 08-09	6.02 (4)	0.198		
Growth				
Bull Flat 07-08	0.70 (3,65)	0.558		
Bull Flat 08-09	0.98 (4,82)	0.425		
Chiloquin 07-08	3.14 (4,142)	0.016 *	5.41 (2,144)	0.005 *
Chiloquin 08-09	0.78 (4,167)	0.541		
Fruit set (current year)				
Bull Flat 07-08	0.74 (3,65)	0.535		
Bull Flat 08-09	1.50 (4,83)	0.211		
Chiloquin 07-08	9.60 (4,145)	<0.001 *	5.76 (2,147)	0.004 *
Chiloquin 08-09	0.60 (4,83)	0.665		

DISCUSSION

Because disjunct or isolated populations can have reduced population growth compared to non-disjunct populations within the same species (Menges and Dolan 1998; Groom 2001), we predicted reduced vital rates and/or population growth at the Chiloquin site when compared to Bull Flat. However, survival of non-seedling plants, average plant lifespan, and plant density are all higher at Chiloquin, culminating in a higher population growth rate at this site. Greater population growth also occurred despite higher herbivore levels from the moth, *S. tunicana*, which primarily affected reproduction when active earlier in the growing season. Possible explanations for the observed site differences and temporal variation within each site include regional climatic variation and the interplay of climate with plant survival and seed bank dynamics.

Spatial and temporal variation in population structure and vital rates

Water is very limiting in the semi-arid region that *A. peckii* inhabits and small differences in precipitation between sites, and even among years within a site, could affect populations. Average annual precipitation is 505 mm at Chiloquin and 354 mm at Bull Flat (PRISM Climate Group 2009). With more precipitation, plants will be less stressed, and although it was not tested, this could explain higher plant density, lower mortality of non-seedling plants, and higher λ at Chiloquin in comparison to Bull Flat.

Within sites, growing season precipitation (April-July) could also contribute to the temporal variation in λ. For instance, population growth was lower at Bull Flat during the first two transition years, which were both marked by below-average precipitation during the succeeding growing season (April-July 2007 had 53% of average precipitation, April-July 2008 had 45%; PRISM Climate Group 2009). In contrast, the 2009 growing season had above average precipitation (154%; PRISM Climate Group 2009) and population growth increased during the 2008-09 period. It is important to note that even though absolute population size continued to decline from 2008-09 due to lower seedling recruitment (Figure 2.3), λ increased because of

greater survival and growth of medium and large plants. A similar association between growing-season precipitation and λ was not seen at Chiloquin, but unlike Bull Flat, precipitation was at or above average for all years of our study at this site.

Plant longevity is intertwined with several demographic parameters. For example, λ is influenced more by survival in long-lived plants and fecundity in short-lived plants (Silvertown et al. 1993; Garcia et al. 2008). Although this correlation is often exemplified with species of widely varying longevities, it could also be tested on a finer scale within species. Between our two sites, lifespan was approximately 4 years at Bull Flat and 7 years at Chiloquin. Bull Flat also had comparably lower elasticities for survival and higher elasticities for fecundity (Appendix 2.2, Figure 2.5), which means reproduction and seedling establishment are comparatively more important to long-term population persistence at this site. These differences will be important if they lead to different management actions for different populations, such as maintaining conditions for establishment at one site versus plant survival at another. Further investigation into this possible relationship is needed, though. Our estimates of seedling recruitment from the seed bank, which were the basis for part of the fecundity term, were based on very little recorded recruitment in our seed plots from only one time period. Considering the impact of the seed bank on population growth and elasticity depends in part on current environmental conditions (Kalisz and McPeek 1993), more studies of seed longevity and seedling establishment under different environmental conditions should be conducted.

The 2008 growing season at Chiloquin was unique in our study because there was a large pulse of seedling recruitment; almost twice as many seedlings established this year compared to other years. This increased establishment, in turn, contributed to high λ. Pulse recruitment in semi-arid plants is often linked to favorable growing conditions (West et al. 1979), and the pulse of *A. peckii* establishment could have been triggered by high precipitation and cold winter temperatures inducing seed scarification. From October 2007 to March 2008, there was above-average winter precipitation (125% of average) coupled with low winter temperatures (average low of

-5.4ºC; PRISM Climate Group 2009). The benefits of this pulse seedling recruitment event on population growth continued into the next growing season as percent survival of seedlings was comparable to other years. Because there were twice as many seedlings present the previous year, the number of seedlings that survived was also twice as many as other years.

Moth effects on survival, growth, and reproduction

Consumers will negatively impact long-term plant population persistence if there is a decline in vital rates which is correlated with a decrease in λ. But, if lower vital rates are not coupled with population decline, then herbivores are not predicted to have a long-term effect on the plant population (Halpern and Underwood 2006). Several results point to this second statement for *A. peckii* and its primary herbivore, *S. tunicana*. First, at Bull Flat, lower plant survival was correlated with higher levels of *S. tunicana* during both time periods data were recorded. Even though population growth declined during the first of these periods (2007-08), it increased substantially during the second (2008-09). Second, at Chiloquin, reproduction of *A. peckii* decreased with increasing moth levels in 2007, but the time period from 2007-08 had a higher λ than any other time frame of the study. Therefore, because reductions in vital rates were not consistently correlated with reductions in λ, effects of *S. tunicana* on population growth are not thought to be strong enough to cause population decline under current conditions. This result is similar to several other studies which have assessed herbivore effects on plant populations (Ehrlen 1995; Kauffman and Maron 2006; Leimu and Lehtilä 2006; Weppler and Stöcklin 2006; Dahlgren and Ehrlen 2009).

One reason for the disconnect between herbivore effects on plant vital rates and population growth is that survival, growth, and reproduction weight differently on λ. Because of this, several studies have found stable or increasing λ despite high predation levels (Lesica 1995; Kolb et al. 2007). For example, Kolb et al. (2007) found populations with high seed predation to be less sensitive to demographic changes in fecundity than populations with low seed predation levels, resulting in a

comparably small effect of herbivory on λ when predation levels were high. In our study, herbivory at Chiloquin affected reproduction more than growth or survival. But since fecundity at this site contributed less to λ than either growth or survival, reductions in reproduction will have a comparably smaller effect on λ. At Bull Flat, on the other hand, herbivory significantly affected survival, and survival (including growth and stasis) at this site contributed more to λ than fecundity (Appendix 2). Therefore, herbivory could potentially be associated with negative population growth at Bull Flat. Currently, though, moth abundance is relatively low at this site and the number of plants with any evidence of the moth – even a very minimal amount – was low at all sample periods except late-season in 2008.

In addition to the relationship between moth herbivory, vital rates, and λ, several additional observations were made that are important to note. First, survival was negatively affected at Bull Flat, where herbivory levels were lower, but not at Chiloquin. Because plant lifespan was shorter at Bull Flat, with an average of about 4 years, *S. tunicana* may have exasperated mortality in plants that were already at the end of their lives. This relationship also appeared heightened during periods of low rainfall such as 2007-08, when precipitation was well below average and adult plant survival was only 34% (Table 2.2).

Second, the only instance of reduced reproduction in *A. peckii* in relation to the moth larva, *S. tunicana*, was at Chiloquin in 2007 when *S. tunicana* was active earlier in the growing season. Seed production in large plants this year was one-third the amount of other years (Table 2.3). Because *S. tunicana* is a leaf-rolling species, earlier activity means more of the plant is covered with webbing during peak flowering. This could indirectly affect seed production by obscuring flowers and preventing pollinator visitation. Alternatively, *S. tunicana* could directly reduce seed production through consumption of flowers and immature fruits when active during this time. Regardless of the mechanism, timing of herbivory may be important in long-term dynamics of *A. peckii* as it is in other legume species (Evans et al. 1989).

On the other hand, reduced fecundity in perennial plants will not have a strong effect on λ if density-dependent seedling mortality, safe-site limitation, the presence of a seed bank, or any combination of these factors compensates for seed loss due to herbivory (Crawley 1992; Louda and Potvin 1995; but see Kauffman and Maron 2006; Maron and Gardner 2000). At our sites, density-dependent seedling mortality does not appear to be currently regulating plant numbers as seedling survival percentages remained constant among years despite a nearly two-fold difference in seedling density. There is a persistent seed bank, though, which could buffer *A. peckii* against temporary reductions in seed production or plant loss from increased mortality. However, as Maron and Gardner (2000) have shown, the seed bank is not a fail-safe means to compensate for seed loss. Because the seed bank is also a "memory" of past reproduction, cumulative reductions in seed production over several years may result in lower seedling establishment for as long as the seed remains viable in the soil.

Implications for conservation

Astragalus peckii is listed as Threatened in the state of Oregon due to its limited distribution in Klamath and Deschutes Counties. Increasing population pressure, particularly in the northern part of the range, will likely lead to increased recreational use, habitat fragmentation, and potential habitat loss for *A. peckii*. Within the limited range of *A. peckii*, several large populations remain, such as the two in this study. Although large population size is a hopeful sign for long-term persistence, results from this study remind us that all populations will experience periods of population decline.

Like most perennial plants, survival of adult plants should be a priority in management plans for *A. peckii* because survival of these plants has a larger effect on population growth than reproduction or survival of other stage classes. In addition to protection of adult plants, protection of habitat for seedling establishment may be needed at sites where plants have a shorter lifespan and fecundity plays a relatively larger role in population growth. This is important because recreational activities at these sites, which vary in type and intensity, may have different impacts on

populations. Horseback riding, off-road vehicle (ORV) use, hiking, and hunting are among the more common uses at these sites. *A. peckii* sites with shorter plant longevity may be more vulnerable to a wider range of uses whereas sites with longer longevity may only be vulnerable to high-intensity uses, such as heavy ORV activity, which are more likely to damage adult plants. Based on studies of other *Astragalus* species, negative impacts of high use are reversible. For example, Maschinski et al. (1997) found heavy foot traffic at Grand Canyon National Park, particularly when coupled with bad weather years, led to population decline in another rare species of *Astragalus*. Once the population was protected, plant survival increased and probability of extinction decreased.

Extended periods of low precipitation may also lead to declines in *A. peckii*. At Bull Flat, years of negative population growth were also years of below average precipitation. Although we did not experimentally test for a causative relationship, many studies have shown climate to have a large effect on population growth (Maschinski et al. 2006; Miller et al. 2009). Additionally, *S. tunicana* could have a negative synergistic effect on *A. peckii* survival when coupled with low precipitation. Under conditions encountered during this study, though, *S. tunicana* does not appear to negatively affect λ despite continued persistence over time and negative correlation with certain vital rates.

Future directions

This is the first study to assess demographics and population stability of *A. peckii* anywhere within its range and will provide a baseline for future work. This study focused on two, large populations to assess population dynamics. From here, comparisons of sites with smaller populations or varying degrees of isolation will give insight into effects of habitat fragmentation and population size on population stability. Incorporation of measures of genetic diversity from populations will also help explain differences in growth, herbivore resistance, and/or reproductive success between populations. Finally, a better understanding of the role of the seed bank in *A. peckii's* life cycle and factors that affect germination and establishment will strengthen

future demographic models. Currently, it is not known how long seed persists in the seed bank, the rate of seedling establishment from the seed bank versus newly dispersed seed, or factors that promote pulse recruitment and seedling survival.

REFERENCES

Amsberry, K., and R. J. Meinke. 2003. Life history and conservation status of *Astragalus peckii* Piper (Fabaceae). Native plant conservation program, Oregon Department of Agriculture.

Angert, A. L. 2006. Demography of central and marginal populations of monkeyflowers (*Mimulus cardinalis* and *M. lewisii*). Ecology 87: 2014-25.

Barneby, R. C. 1964. Atlas of North American *Astragalus*. Memoirs of the New York Botanical Garden 13: 1–1188.

Bevill, R. L., and S. M. Louda. 1999. Comparisons of Related Rare and Common Species in the Study of Plant Rarity. Conservation Biology 13: 493-498.

Carlson, G.T. 1979. Soil resource inventory. Report for the Winema National Forest, US Forest Service.

Caswell, H. 2001. Matrix Population Models: Construction, Analysis, and Interpretation. Sinauer, Sunderland, MA.

Crawley, M. J. 1992. Seed predators and plant population dynamics. In Seeds: the ecology of regeneration in plant communities, 167-182. C.A.B. International, Oxon, UK.

Crawley, M.J. 1989. Insect herbivores and plant population dynamics. Annual Review of Entomology 34: 531-562.

Dahlgren, J. P., and J. Ehrlen. 2009. Linking environmental variation to population dynamics of a forest herb. Journal of Ecology 97: 666-674.

Doak, D. F. 1992. Lifetime impacts of herbivory for a perennial plant. Ecology 73: 2086–2099.

Ehrlen, J. 1995. Demography of the perennial herb *Lathyrus vernus*. II. Herbivory and population dynamics. Journal of Ecology 83: 297-308.

Endels, P., H. Jacquemyn, R. Brys, and M. Hermy. 2005. Rapid response to habitat restoration by the perennial *Primula veris* as revealed by demographic monitoring. Plant Ecology 176: 143-156.

Evans, E. W., C. C. Smith, and R. P. Gendron. 1989. Timing of reproduction in a prairie legume: seasonal impacts of insects consuming flowers and seeds. Oecologia 78: 220-230.

Evans, M., K. Holsinger, and E. Menges. 2008. Modeling the effect of fire on the demography of *Dicerandra frutescens ssp. frutescens* (Lamiaceae), an endangered plant endemic to Florida scrub. Population Ecology 50: 53-62.

Freville, H., B. Colas, M. Riba, H. Caswell, A. Mignot, E. Imbert, and I. Olivieri. 2004. Spatial and temporal demographic variability in the endemic plant species *Centaurea corymbosa* (Asteraceae). Ecology 85: 694-703.

Garcia, M. B., F. X. Pico, and J. Ehrlen. 2008. Life span correlates with population dynamics in perennial herbaceous plants. American Journal of Botany 95: 258-262.

Gisler, S., and R. Meinke. 2001. Reproductive ecology, seed banking, and cultivation of five at-risk legume species in Oregon. Oregon Department of Agriculture Plant conservation biology program.

Groom, M. J. 2001. Consequences of subpopulation isolation for pollination, herbivory, and population growth in *Clarkia concinna concinna* (Onagraceae). Biological Conservation 100: 55-63.

Halpern, S. L, and N. Underwood. 2006. Approaches for testing herbivore effects on plant population dynamics. Journal of Applied Ecology 43: 922–929.

Kalisz, S., and M. A. McPeek. 1993. Extinction dynamics, population growth and seed banks. Oecologia 95: 314-320.

Kauffman, M.J., and J.L. Maron. 2006. Consumers limit the abundance and dynamics of a perennial shrub with a seed bank. The American naturalist 168: 454-470.

Kephart, S.R., and C. Paladino. 1997. Demographic change and microhabitat variability in a grassland endemic, *Silene douglasii var. oraria* (Caryophyllaceae). American Journal of Botany 84: 179-189.

Kolb, A., R. Leimu, and J. Ehrlén. 2007. Environmental context influences the outcome of a plant-seed predator interaction. Oikos 116: 864-872.

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

Leimu, R., and K. Lehtilä. 2006. Effects of two types of herbivores on the population dynamics of a perennial herb. Basic and Applied Ecology 7: 224-235.

Lesica, P. 1995. Demography of *Astragalus scaphoides* and effects of herbivory on population growth. Great Basin Naturalist 55: 142-150.

---. 1999. Effects of fire on the demography of the endangered, geophytic herb *Silene spaldingii* (Caryophyllaceae). American Journal of Botany 86: 996-1002.

Louda, S. M. 1982. Distribution ecology: Variation in plant recruitment over a gradient in relation to insect seed predation. Ecological Monographs 52: 25-41.

Louda, S. M., and M. A. Potvin. 1995. Effect of inflorescence-feeding insects on the demography and lifetime of a native plant. Ecology 76: 229-245.

Maron, J. L., and S. N. Gardner. 2000. Consumer pressure, seed versus safe-site limitation, and plant population dynamics. Oecologia 124: 260-269.

Maschinski, J., J.E. Baggs, P.F. Quintana-Ascencio, and E.S. Menges. 2006. Using population viability analysis to predict the effects of climate change on the extinction risk of an endangered limestone endemic shrub, Arizona cliffrose. Conservation Biology 20: 218-228.

Maschinski, J., R. Frye, and S. Rutman. 1997. Demography and population viability of an endangered plant species before and after protection from trampling. Conservation Biology 11: 990-999.

Menges, E. S. 1991. The application of minimum viable population theory to plants. In Genetics and conservation of rare plants, 45–61. Oxford University Press, Inc., Oxford.

Menges, E. S., and R. W. Dolan. 1998. Demographic viability of populations of *Silene regia* in midwestern prairies: Relationships with fire management, genetic variation, geographic location, population size and isolation. The Journal of Ecology 86: 63-78.

Menges, E. S., and J. Kimmich. 1996. Microhabitat and time-since-fire: Effects on demography of *Eryngium cuneifolium* (Apiaceae), a Florida scrub endemic plant. American Journal of Botany 83: 185-191.

Miller, T.E.X., S.M. Louda, K.A. Rose, and J.O. Eckberg. 2009. Impacts of insect herbivory on cactus population dynamics: experimental demography across an environmental gradient. Ecological Monographs 79: 155-172.

Morris, W.F., and D.F. Doak. 2002. Quantitative Conservation Biology: Theory and practice of population viability analysis. Sinauer Associates Inc., Sunderland, MA.

PRISM Climate Group. Oregon State University. http://www.prismclimate.org.

R Development Core Team. 2009. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org.

Shaffer, M. L. 1981. Minimum population sizes for species conservation. BioScience 31: 131-134.

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

Stubben, C., and B. Milligan. 2007. Estimating and analyzing demographic models using the popbio package in R. Journal of Statistical Software 22: 1-23.

Volis, S., S. Mendlinger, and D.S. Bigger. 2004. Demography and role of the seed bank in Mediterranean and desert populations of wild barley. Basic and Applied Ecology 5: 53-64.

Weppler, T., and J. Stöcklin. 2006. Does pre-dispersal seed predation limit reproduction and population growth in the alpine clonal plant *Geum reptans*? Plant Ecology 187: 277-287.

West, N. E., K. H. Rea, and R. O. Harniss. 1979. Plant demographic studies in sagebrush-grass communities of southeastern Idaho. Ecology 60: 376-388.

Yates, C. J., P. G. Ladd, D. J. Coates, and S. McArthur. 2007. Hierarchies of cause: Understanding rarity in an endemic shrub *Verticordia staminosa* (Myrtaceae) with a highly restricted distribution. Australian Journal of Botany 55: 194-205.

Youngberg, C.T., and C.T. Dyrness. 1964. Some physical and chemical properties of pumice soils in Oregon. Soil Science 97: 391-399.

Chapter 3

POLLEN EFFECTS ON REPRODUCTION IN *ASTRAGALUS PECKII*, A RARE
CENTRAL OREGON ENDEMIC

Elizabeth F. Martin and Robert Meinke

ABSTRACT

We studied the effects of pollen supplementation, self- versus cross-pollen, and inbreeding depression on the reproductive output and progeny vigor for *Astragalus peckii* (Fabaceae), a rare plant endemic to sagebrush habitats in south-central Oregon. Results from these studies were interpreted in light of pollinator observations on abundance and behavior to assess natural levels of pollen quantity and quality limitation. During the course of our study, fruit set was variable (7-61%) and seed set was low (1.3-2.0 seeds/fruit). Pollen quantity supplementation did not have a strong effect on reproduction, and pollinator visitation rates were typically high enough for most flowers to be visited. Together, these findings indicate that *A. peckii* was not limited by pollen quantity. There was a significant effect of pollen quality (self-versus cross-pollen) on seed set, and to a lesser degree on fruit set, during one of the two study years. This could indicate elevated inbreeding depression during a low precipitation year or procedural differences in how we self-pollinated flowers; further investigation should be made as to causation. Inbreeding depression was evident in seedling growth but not in seed germination or seedling survival in greenhouse grown plants. However, naturally pollinated plants from this site did not show similar signs of inbreeding depression in offspring performance, indicating that inbreeding depression, although possible, was not evident in the field. This was despite evidence of geitonogamous pollination by the most predominant pollinator during this time period. Although current reproduction did not tend to be limited by pollen quantity or quality, reduction in either plant or pollinator population size is predicted to have a negative impact on *A. peckii* reproduction.

INTRODUCTION

Plants produce a finite number of ovules. For insect-pollinated plants, the fraction of these that develop to seed depends on pollinator abundance and efficiency along with inherent reproductive traits that govern mating success. For rare and endangered plants, understanding mechanisms of reproduction and constraints on

reproductive output can facilitate conservation and management decisions regarding population maintenance (Kruckeberg and Rabinowitz 1985; Dudash and Murren 2008). This is especially important for short-lived and non-clonal species which lack life-history adaptations to compensate for multiple years of poor reproduction (Bond 1994; Schemske et al. 1994).

Pollen limitation, the reduction in fruit or seed set resulting from inadequate pollen receipt, is common in plants and often quite severe (Burd 1995; Ashman et al. 2004; Knight et al. 2006). Several factors correlated with increased pollen limitation include small population size (Agren 1996; Ward and Johnson 2005), low flowering density (Crone and Lesica 2006), and population isolation (Groom 2001). Considering rare and endangered plant populations often share some or all of these properties, pollen limitation is a realistic threat to reproduction that has been documented on numerous occasions (Kearns et al. 1998).

Pollen limitation is categorized into quantity limitation (not enough pollen) and quality limitation (incompatible/inferior pollen). These two types of limitation differ in underlying causes and population level effects, and uncertainty remains on which is more prevalent in plant populations (Aizen and Harder 2007). Quantity limitation is a function of pollinator abundance and efficiency. When pollinator numbers decline or pollinator species composition shifts to less effective pollinators, reproduction declines as a result of decreased pollen delivery (Sih and Baltus 1987; Liu and Koptur 2003; Franzén and Larsson 2009). Small populations, particularly those below a minimum threshold size, can also experience greater magnitudes of pollen limitation than large populations because pollinator attraction decreases when fewer flowering plants are present (Waites and Agren 2004; Bernhardt et al. 2008).

Pollen quality limitation is a function of both the genetic make-up of the plant population and pollinator behavior and efficiency. In plant populations with low genetic diversity, the likelihood of receipt of self or closely related pollen increases (Ellstrand and Elam 1993). Pollinators can also contribute to deposition of low quality pollen through geitonogamous pollination (Harder and Barrett 1995; Karron et al.

2009) or low species specificity (Bell et al. 2005). For self-incompatible species, this results in reduced reproductive output. For other species, particularly those with mixed-mating systems, inbreeding depression can occur. Inbreeding depression manifests at various life cycle stages, from fertilization to reproduction in the offspring, with population level consequences dependent on the severity of the inbreeding (Keller and Waller 2002).

This multiyear study integrates various aspects of the reproductive biology for the rare plant, *Astragalus peckii* (Fabaceae). Because *A. peckii* is a non-clonal, short-lived perennial, successful reproduction is essential for population persistence. Early descriptions of this species report seeds as seldom seen (Barneby 1964) and more recent surveys confirm low seed number/fruit (Amsberry and Meinke 2003). Our goal is to identify factors which limit reproductive output in *A. peckii*. Of particular interest are how variation in pollen receipt affects fruit and seed set, how pollinators mediate this relationship, and whether inbreeding depression occurs in subsequent seed and seedling growth stages. Specific questions that will be addressed are: 1) Does adding supplemental pollen increase fruit and/or seed set?; 2) Does the effect of supplemental pollen differ depending on population size?; 3) What is the effect of self-versus cross-pollen on fruit and seed set?; and 4) Does *A. peckii* experience inbreeding depression in seed and seedling growth stages?

METHODS

Study species and range

Astragalus peckii is a small, prostrate, perennial legume endemic to a two-county region immediately east of the Cascade Mountains in central Oregon (Figure 3.1). This is a semi-arid region with most precipitation occurring during winter months. *A. peckii* typically grows in sandy, open habitats dominated by sagebrush *(Artemisia tridentata)* and Idaho fescue *(Festuca idahoensis)*. Plants produce numerous axillary inflorescences of 5-9 papilionaceous flowers; flowers are small (6-7 mm in length), hermaphroditic, and contain 7-9 ovules each (Piper 1924, Barneby

1964). Reproduction is solely by seed, flowers are not autogamous, and average seed production is between 1.0 and 1.5 seeds/fruit (Gisler and Meinke 2001, Amsberry and Meinke 2003). Flowering occurs from late May through early July with some variation dependent on elevation. Due to its limited distribution, *A. peckii* is listed as Threatened by the state of Oregon and as a Species of Concern by the United States Fish and Wildlife Service.

Study sites

Three main study sites, Bull Flat, Chemult, and Chiloquin, were used each year of this study from 2007-09. Each of these sites has a large, reproductive population with over 1000 flowering plants (ORNHIC 2003) and they are located in the northern, middle, and southern regions of *A. peckii's* range, respectively (Figure 3.1). Relative to other *A. peckii* populations, these three sites are considered large-sized sites. Five additional smaller sites were used in 2008 to test for the effect of population size on pollen limitation. Three of these sites, Gerking Market Road, Innes Market Road, and Chiloquin Powerline (Figure 3.1), have between 100–1000 flowering plants (ORNHIC 2003) and are considered medium-sized in our study. The other two sites, Snow Creek and 8827 (Figure 3.1), have fewer than 100 flowering plants (ORNHIC 2003) and are categorized as small.
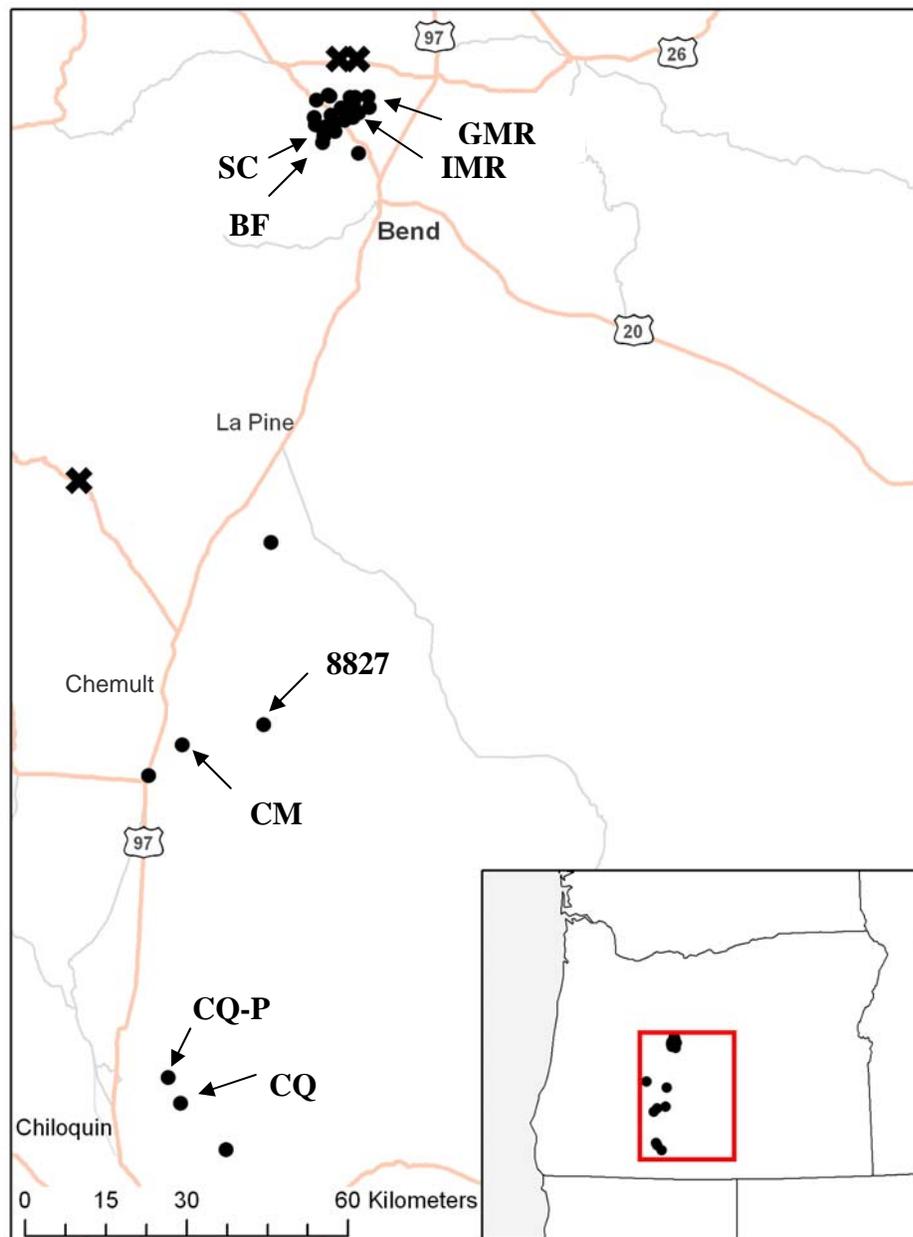
Figure 3.1. Distribution of *A. peckii* in south-central Oregon and study site locations. Site codes are in Table 3.1.

General experimental design (field)

Fruit and seed set were recorded from plants for three years, 2007-2009, after application of different pollination treatments. Because different protocols were employed each year to address the various research questions, we will first describe the field set up by year, followed by a summary of how each protocol relates to the research questions.

In 2007 and 2008, 30 plants were randomly selected at each field site (3 sites in 2007 and 8 in 2008) and separate branches on each plant were haphazardly assigned to different treatments. In 2007, the treatments were open-pollination (control), pollen supplementation, manual self-pollination, and manual cross-pollination. One additional treatment, autogamy, was also included on the plants but not reported on here. In 2008, only open-pollination and pollen supplementation treatments were used. Because the open-pollination and supplemental pollen treatments were never bagged, two branches were used for each in order to compensate for potential flower loss from herbivory. In this design, each plant was a replicate and treatments were nested within plant.

In 2009, 80 plants were selected at the three large field sites and each plant was randomly assigned to one of four different treatments or treatment combinations, with 20 plants in each group. The treatments were open-pollination, manual self-pollination, manual cross-pollination, and a paired open-pollination and pollen supplementation treatment. For the paired treatment, open-pollinated and pollen-supplemented flowers were located on different branches of the same plant, similar to previous years.

To address the first research question concerning pollen quantity and reproduction, the paired open-pollination and supplemental pollen treatments were compared at the three large sites (Table 3.1). These same treatments were also compared using all sites in 2008 to address the second question relating population size and pollen quantity limitation (Table 3.1). The effect of pollen quality on reproduction (question 3) was made by comparing the self- and cross-pollination

treatments in 2007 and 2009, the only years when these treatments were administered (Table 3.1). In addition, the open-pollination treatment was also included for comparison to natural pollination levels. Effects of inbreeding depression on the next generation (question 4) were assessed with seed collected from the Bull Flat site in 2009 (Table 3.1).

Table 3.1. Sites used and years of experimental study for each research question. Sites are listed by their geographical location, from north to south. Populations sizes are small (S, <100 flowering plants), medium (M, 100-1000 flowering plants), and large (L, >1000 flowering plants). Questions are as follows:
A. Does supplemental pollen increase fruit and/or seed set?
B. Does the effect of supplemental pollen differ based on population size?
C. Does pollen quality (self and cross) affect fruit and seed set?
D. Does *A. peckii* experience inbreeding depression in seed and seedling growth stages?

| Site | Site code | Size | Research questions addressed | | |
			2007	2008	2009
Innes Market Road	IMR	M		B	
Gerking Market Road	GMR	M		B	
Snow Creek	SC	S		B	
Bull Flat	BF	L	A,C	A,B	A,C,D
8827	8827	S		B	
Chemult	CM	L	A,C	A,B	A,C
Chiloquin powerline	CQ-P	M		B	
Chiloquin	CQ	L	A,C	A,B	A,C

Treatment application

Before anthesis, branches in the self- and cross-pollination treatments were bagged with fine mesh bags to exclude pollinators in 2009, but in 2007 they were not bagged until after treatments were applied. The open-pollination and pollen supplementation treatments were never bagged. All manual pollinations were conducted once during the flowering season when plants were in full flower. Pollen-supplementation and cross-pollination were administered by brushing dehisced anthers of a donor flower against the stigma of a recipient flower three times. Donor flowers for these treatments were collected within site and at least 5 m away from the recipient

flower. Self-pollinations were conducted differently in 2007 and 2009. In 2007, tweezers were used to depress the keel and release pollen into the flower. In 2009, donor flowers were used to brush dehisced anthers against the stigma; donor flowers were always from the same plant resulting in geitonogamous pollination. Flowers were not emasculated prior to pollination in any treatment because of damage emasculation caused in greenhouse trials. Without emasculation, some self pollen could have been transferred during cross-pollination although care was taken to minimize this.

After pollination, treated flowers were marked for identification later in the season and the self- and cross-pollination treatments were bagged to further exclude pollinators. All open flowers in the open-pollination treatment were likewise marked at this time to control for temporal variation in fruit and seed set but were otherwise not manipulated. Even though each treatment had a sample size of 30 plants in 2007 and 2008 and 20 plants in 2009, animal disturbance and other natural causes reduced this number each year.

Calculating fruit and seed set

Developing fruits were collected approximately three weeks after application of pollination treatments for all treatments except the self- and cross-pollination treatments at Bull Flat in 2009. For these two treatments, only two fruits were collected per plant and the rest were left to fully mature (see "Inbreeding depression" below). Although fruits were not completely mature at this point, they were collected to prevent seed loss from dehiscence. Each collected fruit was examined under a dissecting microscope to count the number of filled seeds/fruit. Filled seeds were dark in color, opaque when backlit, and not shriveled in appearance. In 2008 and 2009, aborted, unfertilized, and total ovules/fruit were also counted for all treatments. Unfertilized ovules were defined as less than 0.5 mm in diameter, thin, and membranous. Aborted ovules were greater than 0.5 mm in diameter, often darker in color, and either shriveled in appearance or contained no embryo when backlit.

Fruit set was defined as the proportion of fruits with at least one filled seed/number of marked flowers for each treatment and plant combination, and seed set was defined as the mean number of filled seeds/fruit for each treatment and plant combination. Occasionally there were fruits present with evidence of seed predation and these were included in calculations of fruit set but made up less than 1% of the total number of fruits. Because of damage inside predated fruits, ovules could not be counted and these fruits were not included in seed set calculations.

Inbreeding depression

Fruits from the self- and cross-pollinated plants at Bull Flat in 2009 were allowed to fully mature before being collected to test for inbreeding effects on later life-history stages. Seeds from these plants were also compared to seed from naturally pollinated plants to assess naturally occurring levels of inbreeding. For this, 50 additional seeds were collected from ten randomly selected plants (5 seeds per plant) that had been open-pollinated. These ten plants were not otherwise used in this study.

All seeds were scarified with sandpaper, placed on moistened filter paper in petri dishes, and germinated in the greenhouse. Seeds began to germinate within a few days, and after three weeks, germinants were planted in 10-inch deep tree seedling pots filled with a 3:1 mixture of potting soil and native soil from the Bull Flat site. After an additional three weeks, for a total of 6 weeks, total germination was recorded in order to include late germinants; these late germinants were not planted out. Seedlings were grown for 15 weeks after planting with 8 hours of artificial light/day and water when needed. At this time, survival and stem height were recorded and above-ground biomass was collected, dried for 2.5 days at 33ºC, and weighed.

Pollinators

From 2007 to 2009, pollinator observations were conducted at the Bull Flat, Chemult, and Chiloquin sites throughout the flowering season from mid-May to early July, depending on the year and site. For each observation period, one or a few closely clustered plants were observed for 15 minutes wherein each visiting species was recorded along with the number of flowers/plant visited during each foraging

bout. When species could not be visually identified, they were collected after the observation period from the site. Pollinators were distinguished from floral visitors based on whether they entered the flower by pulling down the keel and exposing the reproductive parts.

Data analysis

Fruit and seed set (control) **–** To test for spatial and temporal variation in reproductive output, fruit and seed set from the open-pollination (control) treatments were analyzed for site and year differences. Fruit set (proportion data) was analyzed with a generalized linear model (GLM) with binomial error structure corrected for overdispersion. Seed set (log-transformed) was analyzed with ANOVA and significant effects were then compared with Tukey post-hoc tests. For the 2008 and 2009 data only, the mean proportion of fertilized ovules ([filled + aborted]/total) and aborted ovules (aborted/total) were analyzed for site and year differences using the same GLM structure as used with the fruit set data. In 2009 there were open-pollination treatments on plants both with and without a paired pollen supplementation treatment. These two open-pollination treatments did not differ in fruit set (p=0.73) or seed set (p=0.33) and were combined for the above analyses. These and all other analyses were made using Rv2.9.2 (R Development Core Team 2009).

Pollen quantity **–** To test whether reproduction in *A. peckii* was limited by the quantity of pollen received, the open-pollination and pollen supplementation treatments were compared for the three, large sites from 2007-2009 using both fruit set and seed set as response variables. Fruit set was analyzed with a GLM (quasibinomial family) which included treatment, site, year, all interactions between these three variables, and maternal plant nested within site-by-year. Seed set (log-transformed) was analyzed with ANOVA using the same explanatory variables as the fruit set model.

Pollen quantity and population size – To determine if population size affects pollen limitation, fruit and seed set from open-pollination and pollen supplementation treatments in small, medium, and large populations were compared using only 2008

data. Fruit set was again analyzed with a GLM and seed set with ANOVA; response variables in both models were site nested within population size, treatment, interactions of site, size, and treatment, and maternal plant nested within site. A significant population size-by-treatment interaction would indicate population size has an effect of pollen limitation.

Pollen quality – To determine if pollen quality affects reproduction in *A. peckii*, fruit and seed set from self- and cross-pollinated flowers were compared. Because of design differences (treatments were paired in 2007 and independent in 2009) and different methodologies in treatment application, the two years were analyzed separately. Fruit set was analyzed with a GLM including treatment, site, and treatment-by-site interaction. In 2007, maternal plant nested within site was also included in the model. Seed set (log-transformed) was analyzed with ANOVA including the same effects for each year as fruit set

Inbreeding depression –To assess inbreeding at different life history stages, the effect of pollen source (treatment) on seed germination, seedling survival, seedling height, and seedling biomass was analyzed. For seed germination and seedling survival, the proportion of germinants (or surviving plants, depending on analysis) for each maternal plant was the response variable in a binomial family GLM. Seedling height and biomass were averaged by maternal plant, log-transformed, and analyzed with ANOVA. Tukey post-hoc tests were used to compare the different pollination treatments when there was a significant effect of pollen source.

Pollinators – The number of visitors/plant/hour was calculated by multiplying the number of visitors/number of plants for each 15-minute observation period by 4; this will be referred to as visitation rate throughout this paper. To determine if visitation rates were correlated with either fruit or seed set, the average visitation rate (log-transformed) for each site and year was compared to average fruit set and average seed set using Pearson's product-moment correlations. In addition, the average number of flowers/plant visited per foraging bout (number of geitonogamous visitations) was computed for the most common floral visitor(s) at each site.

RESULTS

Fruit and seed set (control)

Fruit set for open-pollinated flowers ranged from 7-61% (Table 3.2), with variation between years dependant on the site (site×year $F_{4,263}$=8.2, p<0.001). Two sites stand out as having either exceptionally high or exceptionally low values. Chemult, in 2008, had 61% of marked flowers develop into fruits, which was over 2-times greater than other years at this site (Table 3.2). Chiloquin, on the other hand, only had 7% of flowers develop into fruit in 2009, which was half as much as other years (Table 3.2).

Seed set in open-pollinated flowers was generally low with 1.3-2.0 filled seeds per fruit (Table 3.2). Seed set differed between sites ($F_{2,131}$=5.0, p=0.008) but not years ($F_{2,131}$=1.0, p=0.36). However, there was only a difference of 0.6 (95% CI from 0.4 to 0.9) seeds/fruit between Bull Flat, the site with greatest seed set, and Chemult, the site with the lowest seed set.

Table 3.2. Fruit and seed set for *A. peckii* in the open-pollination controls. Fruit set (# fruits/# flowers) and seed set (# filled seeds/fruit) were recorded at three, large, reproductive sites from 2007-2009. Sites are Bull Flat (BF), Chemult (CM), and Chiloquin (CQ). Values represented are the mean ± 1 SD with sample size in parentheses.

Year	Site	Fruit set	Seed set
2007	BF	0.18±0.30 (25)	1.7±0.9 (7)
	CM	0.16±0.26 (20)	1.6±0.8 (6)
	CQ	0.15±0.24 (26)	1.4±0.7 (10)
2008	BF	0.36±0.27 (30)	1.6±0.6 (25)
	CM	0.61±0.25 (27)	1.3±0.4 (26)
	CQ	0.39±0.32 (29)	1.6±0.5 (13)
2009	BF	0.31±0.23 (39)	2.0±0.8 (27)
	CM	0.26±0.29 (36)	1.6±0.6 (19)
	CQ	0.07±0.19 (40)	1.4±0.8 (7)

Within fruits, most ovules were fertilized but subsequently aborted. Between 78-87% of all ovules were fertilized with fewer ovules fertilized at Bull Flat than either Chemult or Chiloquin ($F_{2,111}$=3.17, p=0.05). Over half the ovules in each fruit aborted, though, with the proportion of aborted ovules ranging from 0.54 at Bull Flat to 0.64 at Chemult ($F_{2,299}$=7.0, p=0.001). There were no between year differences.

Pollen quantity

The effect of pollen addition on fruit set depended on the site and year (Table 3.3, significant 3-way interaction). Flowers given supplemental pollen had 1.9-times higher fruit set than open-pollinated flowers at Chemult in 2007 and 1.4-times higher fruit set at Bull Flat in 2008. In contrast, flowers had 1.9-times lower fruit set after supplemental pollination at Chiloquin in 2008. All other sites and years had similar fruit set between treatments.

For seed set, there was a marginally significant three-way interaction of supplemental pollen, site, and year, and a significant two-way interaction of supplemental pollen and site (Table 3.3). However, because the individual effects of site and year were strongly significant and treatment was not, these significant interactions were driven primarily by spatial and temporal variation and not by pollen supplementation. For both fruit and seed set there was also a strong effect of maternal plant (Table 3.3).

Pollen quantity and population size

Comparison of pollen limitation in small, medium, and large sites was limited by high herbivory levels at the two small sites. Early season herbivory and overall poor site conditions at the 8613 site left only a few plants with flowers by the time plants should have been in full flower. Deer herbivory at the Snow Creek site occurred between when we pollinated plants and when we returned to collect fruit. Therefore, our assessment of the effect of population size on pollen limitation only included medium- and large-sized populations. A significant treatment-by-size effect would indicate that supplemental pollen had a differential effect in populations of varying sizes. This interaction was non-significant for fruit set and marginally

significant for seed set (Table 3.4). Counter to our prediction that smaller sites would have more pollen limitation, the large sites had an increase in seed set after pollen addition while the medium sites had a decrease.

Table 3.3. Effect of supplemental pollen (treatment) on fruit and seed set in *A. peckii* at three, large sites (Bull Flat, Chemult, and Chiloquin) from 2007-2009. Fruit set was analyzed with a GLM (quasibinomial family) and effects were approximated with F-tests. Seed set (log-transformed) was analyzed with ANOVA. Significant relationships are bolded.

Source	Fruit set			Seed set		
	Df	F	p	df	F	P
Treatment	1	2.9	0.09	1	0.03	0.86
Site	2	59.0	**<0.001**	2	26.9	**<0.001**
Year	2	61.7	**<0.001**	2	14.3	**<0.001**
Treatment x site	2	7.4	**<0.001**	2	1.7	0.20
Treatment x year	2	0.9	0.43	2	4.1	**0.02**
Site x year	4	7.6	**<0.001**	4	0.9	0.47
Treatment x site x year	4	3.2	**0.01**	4	2.4	0.06
Maternal plant (site x year)	209	2.2	**<0.001**	136	2.7	**<0.001**
Error df	188			72		

Table 3.4. Effect of population size and supplemental pollen (treatment) on fruit and seed set in *A. peckii*. Data were collected from three large and three medium sites in 2008. Fruit set was analyzed with a GLM (quasibinomial family) and effects were approximated with F-tests. Seed set (log-transformed) was analyzed with ANOVA. Significant relationships are bolded.

Source	Fruit set			Seed set		
	df	F	p	Df	F	P
Treatment	1	1.7	0.19	1	1.0	0.32
Population size	1	47.5	**<0.001**	1	3.8	0.06
Site (population size)	4	11.2	**<0.001**	4	5.9	**<0.001**
Treatment x population size	1	1.4	0.24	1	3.1	0.08
Treatment x site (population size)	4	7.0	**<0.001**	4	1.8	0.13
Maternal plant (site x year)	150	2.2	**<0.001**	115	3.2	**<0.001**
Error df	139			72		

Pollen quality

There was higher seed set ($F_{1,35}$=25.5, p<0.001), and to a lesser degree higher fruit set ($F_{1,63}$=3.9, p=0.05), after cross-pollination in 2007 but no difference between the two treatments in 2009 (Figure 3.2). Flowers that were cross-pollinated in 2007 had 0.5 more seeds than self-pollinated flowers (95% CI 0.4-0.6) and 14% more flowers develop into fruit. There was no treatment effect in 2009 although fruit set at Chemult was lower in self-pollinated plants (Figure 3.2B). Overall low fruit set in this year also drastically reduced sample sizes for seed set.

Inbreeding depression

Sample sizes in the self-pollination treatment were low because some flowers were used as pollen donors, thereby reducing the number of recipient flowers. This, coupled with low fruit and seed set, resulted in only 16 seeds from five plants in this treatment. In comparison, there were 48 seeds from 10 plants in the cross-pollination treatment and 50 seeds from 10 plants in the open-pollination treatment.

Effects of inbreeding were more detrimental to seedling growth than either seed germination or seedling survival. Seed germination was nearly 100% for all treatments with no effect of pollen source on germination (Figure 3.3A; p=0.30). Survival after 15-weeks of growth was slightly lower for progeny from self-pollinated flowers but not statistically different from the open- and cross-pollinated progeny (Figure 3.3B; p=0.15). Both seedling height and biomass differed between the treatments (height: p=0.007, biomass: p=0.005) with self-pollinated progeny being shorter and smaller than open- and cross-pollinated progeny (Figure 3.3C, 3.3D). There was no difference between the open- and cross-pollinated treatments for any of the seed or seedling variables measured (Figure 3.3).
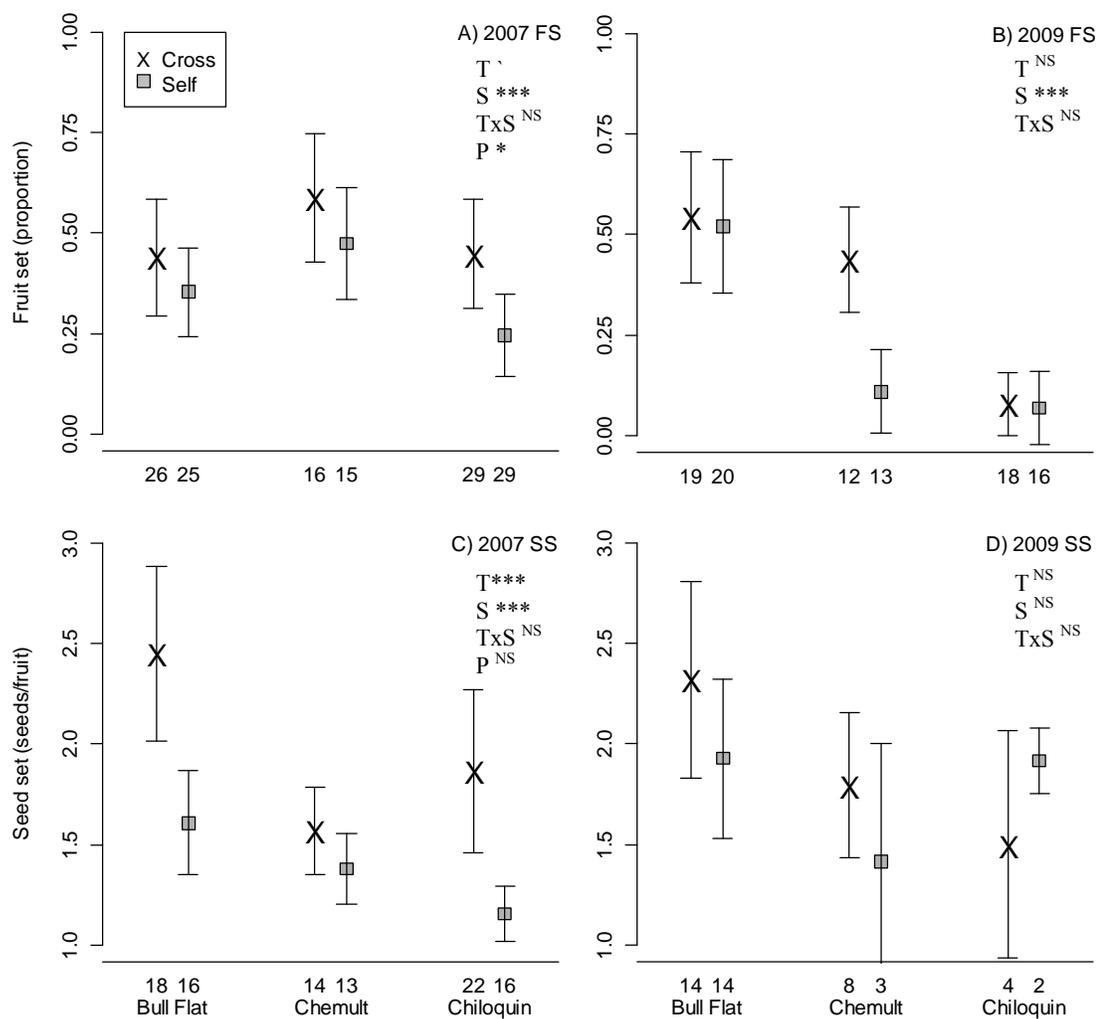
Figure 3.2. Fruit and seed set in *A. peckii* after manual self- and cross-pollination treatments. Pollinations were conducted at three field sites (Bull Flat, Chemult, and Chiloquin) during two field seasons (2007 and 2009). Graph panels are as follows: A) 2007 fruit set data; B) 2009 fruit set data; C) 2007 seed set data; and D) 2009 seed set data. In each panel mean values are shown with 95% CI, and sample sizes for each treatment are listed below the x-axis. GLM (fruit set) and ANOVA (seed set) results are summarized for treatment (T), site (S), treatment-by-site (TxS), and maternal plant (P) effects in the upper right corner of each panel (see methods for model details). Significance levels are $p < 0.001$ ***, $p < 0.01$ **, $p < 0.05$ *, $p < 0.1$ `, and $p > 0.1$ [NS].
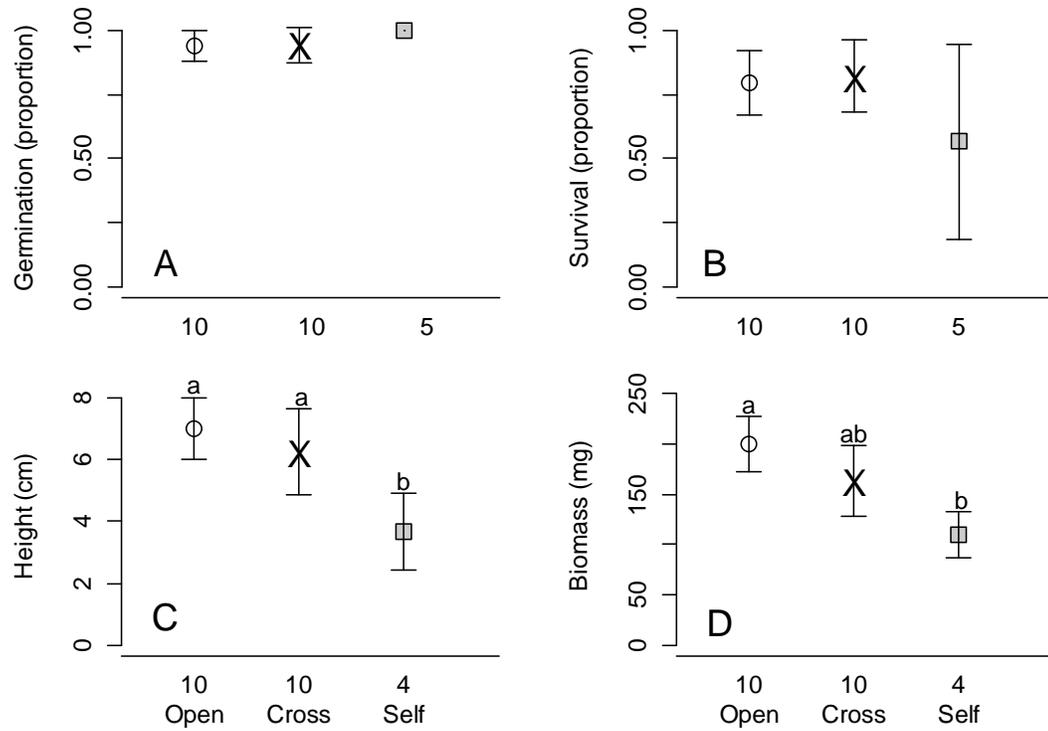
Figure 3.3. Effect of open-, cross-, and self-pollination on four measures of offspring fitness: A) seed germination; B) seedling survival to 15-weeks; C) seedling height at 15-weeks; and D) seedling biomass at 15-weeks. Mean values are shown with 95% CI and sample sizes are listed below the x-axis. Significant differences, when present, are indicated by different letters above the error bars.

Pollinators

Cumulatively, 49.5 hours of observation trials were conducted with 12 hours in 2007, 17 hours in 2008, and 20.5 hours in 2009. From these, 173 insect visitors were recorded representing 5 orders: Hymenoptera, Diptera, Lepidoptera, Hemiptera, and Orthoptera. The most frequent visitors were solitary bees in the genera *Osmia*, *Ashmeadiella*, and *Anthidum* (Table 3.5). These three genera accounted for 67.1% of all recorded visits to *A. peckii*, and because they carried the characteristic orange pollen of *A. peckii*, they were considered pollinators.

Average visitation rates ranged from 1.0-14.0 visitors/plant/hour, with most rates between 1.0-5.2 visitors/plant/hour (Table 3.5). Floral visitors tended to be less abundant in 2008, particularly at Bull Flat which had only 1.0 visitor/plant/hour. There was a slightly negative but non-significant correlation between visitation rate and fruit set ($r=$ -0.60, $p=0.09$) and no correlation between visitation rate and seed set ($r=$ -0.01, $p=0.99$). Some geitonogamous visitation occurred; bees visited an average of 2.0-6.7 flowers per individual plant before leaving to forage on another individual (Table 3.5).

Table 3.5. Floral visitation rates and common pollinators for *A. peckii* at three sites from 2007-2009. The number of open flowers/plant and number of flowers/plant visited during a single foraging bout by the most common pollinator at each site are given as reference numbers to evaluate pollinator abundance and amount of geitonogamous pollen transfer. Sites are Bull Flat (BF), Chemult (CM), and Chiloquin (CQ).

Year	Site	Visitation rate (visitors/plant/ hour)	# open flowers/ plant	Most frequent pollinator (genus level identification)	Flowers visited/ plant/foraging bout
2007	BF	5.1 ± 5.4 (n=16)	32.6	*Osmia*	5.0 (n=14)
	CM	14.0 ±15.9 (n=15)	20.3	*Ashmeadiellla*	2.3 (n=41)
	CQ	2.9 ± 3.6 (n=17)	70.1	*Anthidum, Osmia*	3.8 (n=4), 5.5 (n=4)
2008	BF	1.0 ± 1.4 (n=23)	96.1	*Osmia*	2.0 (n=3)
	CM	2.1 ± 2.5 (n=22)	34.4	*Ashmeadiellla*	2.3 (n=23)
	CQ	2.8 ± 2.4 (n=23)	60.2	*Osmia*	4.4 (n=17)
2009	BF	2.4 ± 4.5 (n=32)	40.0	*Osmia*	3.8 (n=25)
	CM	3.9 ± 3.9 (n=21)	14.9	*Ashmeadiellla*	2.3 (n=22)
	CQ	5.2 ± 8.0 (n=29)	79.9	*Osmia*	6.7 (n=45)

DISCUSSION

Fruit and seed set (control)

Consistent with previous findings (Gisler and Meinke 2001; Amsberry and Meinke 2003), fruit set in *A. peckii* widely fluctuated between sites and years whereas seed set remained relatively stable. Within each fruit, most ovules were fertilized but later aborted, which is common in plants that either produce excess floral resources for pollinator attraction or have high levels of selective abortion in low resource environments (Stephenson 1981; Lee and Bazzaz 1986). Unlike many other species of *Astragalus* (e.g. Green and Bohart 1975; Kaye 1999), predispersal seed predation was not a primary cause of seed loss in *A. peckii.* Less than 1% of fruits had exit holes or larva present. Causes of fruit set variability will be discussed below as they are related to different pollination treatments.

Pollen quantity

Seed set was not pollen limited but fruit set differed between open-pollinated and pollen-supplemented flowers in certain sites and years. The seed set results were consistent with the high abortion rates recorded from the control flowers, which suggest resources rather than pollen limit reproduction. Fruit set, however, appeared to be affected by different factors which fluctuated spatiotemporally. Several potential explanations for this will be discussed below. First, though, it should be noted that treatment effects did not always indicate pollen limitation. Sometimes, fruit set was lower after pollen supplementation, such as at Chiloquin in 2008. The exact reason for this is not known, but possible explanations as suggested by Young and Young (1992) include damage to the stigma during hand pollination, excess pollen grains clogging the stigma, and low pollen diversity compared to natural deposition levels.

Pollen limitation in *A. peckii* fruit set was uncommon, but when it did occur, up to twice as many fruits developed from flowers given supplemental pollen. For populations with more than 1000 flowering plants, this extrapolates to a considerable increase in fruit number at the site level. Stochastic fluctuations in both pollinator abundance and flowering density can lead to pollen limitation (Kunin 1997). During

our study, we had a 10-fold difference in visitation rates, ranging from 1-14 visitors/plant/hour, and a 5-fold difference in the average number of flowers/plant (Table 3.5). Low visitation rates coupled with copious flowering could explain pollen limitation at Bull Flat in 2008 but not at Chemult in 2007. Mechanisms behind pollen limitation at this site are unknown.

In addition to occasional pollen limitation, floral herbivory may have an even stronger impact on fruit set at our sites. Although we did not set out to quantify floral herbivory in our study, drastic differences in fruit set between the pollen-supplementation treatments and the bagged, cross-pollinated treatments indicated its presence. These two treatments had identical methodology except that the cross-pollinated flowers were bagged; fruit set was 1.6-3.6 times higher when protected with the bag. Floral herbivores are known to greatly reduce reproductive output in plants (Breedlove and Ehrlich 1968; Evans et al. 1989; Krupnick et al. 1999). The presence of several floral herbivores at our sites, including larva from lycaenid butterflies, the tortricid larva *Sparganothis tunicana*, and grasshoppers (E. Martin, personal observation), led us to believe florivores were an important contributor to the observed bagging effect. To bring this back to pollen limitation, if high levels of floral herbivory reduced fruit set in both the open-pollinated and pollen-supplemented treatments in our studies, then pollen limitation, if present, would be obscured and therefore not detected.

Pollen quantity and population size

Even though we found no difference in pollen limitation with respect to population size, small sites (those with less than 100 flowering individuals) failed to reproduce and were not included in the analysis. If pollen limitation only increases in the smallest of sites, then we do not have the resolution needed to detect a size effect. Bernhardt et al. (2008) found this in populations of *Lupinus perennis* where pollen limitation dramatically increased once population size dropped below a threshold level of about 215 plants, which is smaller than any of the medium-sized sites we used. However, with the reproductive failure that we witnessed, these populations may be

more at risk of decline from stochastic events (Menges 1991; Matthies et al. 2004). In general, small populations of *A. peckii* were difficult to locate for this study. Possible reasons for this are that they were never present in the landscape or that once created, through fragmentation or other processes, they fail to remain in existence. Determining why small populations are rare would be a useful avenue of future research in order to more effectively manage this species.

Pollen quality

Self-pollinated flowers had lower reproductive output than cross-pollinated flowers in 2007 but not in 2009 (Figure 3.2). Because inbreeding depression increases in severity under harsher growing conditions (Dudash 1990), differences could reflect temporal variation in the resource environment between years. At both Bull Flat and Chiloquin, the two sites with the strongest reduction in seed set in 2007, June rainfall (the month when the pollinations were conducted) was almost 3-times lower in 2007 than 2009. At Chemult, pollinations were conducted in July because of later phenology, and average rainfall was much higher in 2007 than 2009. Therefore, the stronger inbreeding effects could be associated with periods of low precipitation although further exploration into this relationship is needed.

Another possible explanation for a treatment effect only in 2007 is procedural differences between years. In 2007, tweezers were used to trip the floral mechanism. Although much pollen was visibly released into flowers, this method did not ensure direct contact with the stigma. In contrast, flowers were pollinated by rubbing dehisced anthers against the stigma in 2009. Many species of legumes have a cuticle over the stigma that prevents pollen germination until physical agitation, such as contact with a pollinator, ruptures the cuticle (Heslop-Harrison and Heslop-Harrison 1983; Nair et al. 2004; Galloni et al. 2007). If hand pollinations in 2007 were less disruptive to the cuticle, then procedure – and not pollen quality – would account for the observed treatment difference.

Inbreeding depression

Inbreeding depression was evident at the Bull Flat site in seedling growth but not seed germination or seedling survival. Possible repercussions of smaller seedling size are lower competitive ability for resources and decreased survival into the next year as a result of lower nutrient uptake (Donovan et al. 1993). Because progeny from open-pollinated plants were similar in size to cross-pollinated plants, inbreeding depression was not evident at Bull Flat under natural pollination levels. Although these are encouraging results for this site, Bull Flat is a large population with lower likelihood of low genetic diversity or restricted pollinator movement. Finally, because our study was conducted in the greenhouse, the magnitude of inbreeding depression may be underestimated compared to harsher conditions experienced in the field (Dudash 1990).

Pollinators

With little to no autogamous reproduction (Gisler and Meinke 2001), pollinators control the quantity and quality of pollen delivered to *A. peckii* flowers. Despite a range of recorded floral visitation rates and differences in pollinator composition between sites (Table 3.5), pollen quantity limitation was not evident in *A. peckii* with the possible exception of Bull Flat in 2008. In fact, assuming 10 hours of pollinator activity/day, the visitation rates we recorded were typically high enough that most open flowers/day would receive at least one visit, assuming equal visitation to all flowers (Table 3.5). Similar high rates of pollinator activity have recently been used to explain the lack of pollen limitation in other studies as well (Hegland and Totland 2008; Elliott and Irwin 2009).

Changes in pollinator efficiency and behavior affect the quality of pollen received by a flower. At Bull Flat in 2009, inbreeding depression was not found in open-pollinated plants. During that year, *Osmia gaudiosa* (identification by T. Griswald and M. Gee, Utah Bee Lab), the most common pollinator, visited an average of 3.8 flowers per plant before moving to the next individual (Table 3.5). Since this is the only site and year with an estimate of inbreeding depression, we cannot compare

other years and sites with different levels of geitonogamous pollinator movement. However, Karron et al. (2009) found 2-5 geitonogamous visits by *Bombus* to *Mimulus ringens* flowers was sufficient for self pollination and inbreeding depression.

Conclusions

Astragalus peckii has prolific flowering; however, the majority of flowers do not produce fruit and the majority of ovules within each fruit do not reach full maturity. In this study, we addressed how pollen quantity and quality contribute to reproductive success and how pollinators mediate this relationship, with the hope of identifying factors that directly limit reproduction in *A. peckii*. Overall, we found that pollinator abundance was typically high enough under current site conditions to avoid a shortage in the amount of pollen delivered to flowers. Also, despite observed geitonogamous pollinator visitations at Bull Flat in 2009, there was no significant inbreeding depression detected in open-pollinated plants. Therefore, neither pollen quantity nor quality directly limited reproduction at our sites under natural pollination levels. However, we did identify other avenues of potential reproductive limitation, such as floral herbivory and resource limitation, which deserve future study. Also, because *A. peckii* is self-compatible and inbreeding depression does occur with self pollination, assessment of current inbreeding depression at more than just the one, large site used here should be made.

Conservation implications

Because bees are integral to successful reproduction in *A. peckii*, conservation efforts should not only aim to protect plant populations but also bee populations. The majority of pollinators for *A. peckii* are ground- or twig-nesting solitary bees. In order to maintain adequate habitat for these species, ground disturbances such as heavy vehicle traffic that result in soil compaction and destruction of vegetation cover should be minimized. Also, pesticide and insecticide use, which increases bee mortality, should be restricted in areas where populations need to be maintained.

Plant population size should also be an important consideration in managing *A. peckii* populations. With the current high rates of human population growth in the

northern part of *A. peckii's* range, where most of these populations are found, habitat fragmentation is a growing concern. In this study we illustrated that inbreeding depression can occur in *A. peckii*. Although not evident in the field with current pollination levels at Bull Flat, reduction in plant population size could lead to increased inbreeding depression through a loss of genetic diversity in the population. Furthermore, considering the short pollinator flight distances of solitary bees, movement between populations is not likely, further exacerbating the effects of habitat fragmentation and population isolation.

REFERENCES

Agren, J. 1996. Population size, pollinator limitation, and seed set in the self-incompatible herb *Lythrum salicaria*. Ecology 77: 1779-1790.

Aizen, M. A., and L. D. Harder. 2007. Expanding the limits of the pollen-limitation concept: Effects of pollen quantity and quality. Ecology 88: 271-281.

Amsberry, K., and R. J. Meinke. 2003. Life history and conservation status of *Astragalus peckii* Piper (Fabaceae). Native plant conservation program, Oregon Department of Agriculture.

Ashman, T. L., T. M. Knight, J. A. Steets, P. Amarasekare, M. Burd, D. R. Campbell, M. R. Dudash, M. O. Johnston, S. J. Mazer, and R. J. Mitchell. 2004. Pollen limitation of plant reproduction: Ecological and evolutionary causes and consequences. Ecology 85: 2408-2421.

Barneby, R. C. 1964. Atlas of North American *Astragalus*. Memoirs of the New York Botanical Garden 13: 1–1188.

Bell, J.M., J.D. Karron, and R.J. Mitchell. 2005. Interspecific competition for pollination lowers seed production and outcrossing in *Mimulus ringens*. Ecology 86: 762-771.

Bernhardt, C. E., R. J. Mitchell, and H. J. Michaels. 2008. Effects of population size and density on pollinator visitation, pollinator behavior, and pollen tube abundance in *Lupinus perennis*. International Journal of Plant Sciences 169: 944-953.

Bond, W. J. 1994. Do mutualisms matter? Assessing the impact of pollinator and disperser disruption on plant extinction. Philosophical Transactions of the Royal Society B: Biological Sciences 344: 83-90.

Breedlove, D. E., and P. R. Ehrlich. 1968. Plant-herbivore coevolution: Lupines and Lycaenids. Science 162: 671-672.

Burd, M. 1995. Ovule packaging in stochastic pollination and fertilization environments. Evolution 49: 100-109.

Crone, E. E., and P. Lesica. 2006. Pollen and water limitation in *Astragalus scaphoides*, a plant that flowers in alternate years. Oecologia 150: 40-49.

Donovan, L.A., J. Mausberg, and J.R. Ehleringer. 1993. Seedling size and survival for *Chrysothamnus nauseosus*. Great Basin Naturalist 53: 237-245.

Dudash, M. R. 1990. Relative fitness of selfed and outcrossed progeny in a self-compatible, protandrous species, *Sabatia angularis* L. (Gentianaceae): A comparison in three environments. Evolution 44: 1129-1139.

Dudash, M. R., and C. J. Murren. 2008. The influence of breeding systems and mating systems on conservation genetics and conservation decisions. In Conservation biology: evolution in action.

Elliott, S. E., and R. E. Irwin. 2009. Effects of flowering plant density on pollinator visitation, pollen receipt, and seed production in *Delphinium barbeyi* (Ranunculaceae). American Journal of Botany 96: 912-919.

Ellstrand, N.C., and D.R. Elam. 1993. Population genetic consequences of small population size: Implications for plant conservation. Annual Review of Ecology Evolution and Systematics 24: 217-242.

Evans, E. W., C. C. Smith, and R. P. Gendron. 1989. Timing of reproduction in a prairie legume: seasonal impacts of insects consuming flowers and seeds. Oecologia 78: 220-230.

Franzén, M., and M. Larsson. 2009. Seed set differs in relation to pollen and nectar foraging flower visitors in an insect-pollinated herb. Nordic Journal of Botany 27: 274-283.

Galloni, M., L. Podda, D. Vivarelli, and G. Cristofolini. 2007. Pollen presentation, pollen-ovule ratios, and other reproductive traits in Mediterranean Legumes (Fam. Fabaceae - Subfam. Faboideae). Plant Systematics and Evolution 266: 147-164.

Gisler, S., and R. Meinke. 2001. Reproductive ecology, seed banking, and cultivation of five at-risk legume species in Oregon. Oregon Department of Agriculture Plant conservation biology program.

Green, T.W., and G.E. Bohart. 1975. The Pollination Ecology of *Astragalus cibarius* and *Astragalus utahensis* (Leguminosae). American Journal of Botany 62: 379-386.

Groom, M. J. 2001. Consequences of subpopulation isolation for pollination, herbivory, and population growth in *Clarkia concinna concinna* (Onagraceae). Biological Conservation 100: 55-63.

Harder, L. D., and S. C. H. Barrett. 1995. Mating cost of large floral displays in hermaphrodite plants. Nature 373: 512-515.

Hegland, J., and O. Totland. 2008. Is the magnitude of pollen limitation in a plant community affected by pollinator visitation and plant species specialisation levels? Oikos 117: 883–891.

Heslop-Harrison, J., and Y. Heslop-Harrison. 1983. Pollen-stigma interaction in the Leguminosae: The organization of the stigma in *Trifolium pratense* L. Annals of Botany 51: 571-583.

Karron, J. D., K. G. Holmquist, R. J. Flanagan, and R. J. Mitchell. 2009. Pollinator visitation patterns strongly influence among-flower variation in selfing rate. Annals of Botany 103: 1379-1383.

Kaye, T. 1999. From flowering to dispersal: reproductive ecology of an endemic plant, *Astragalus australis var. olympicus* (Fabaceae). American Journal of Botany 86: 1248-1256.

Kearns, C. A., D. W. Inouye, and N. M. Waser. 1998. Endangered mutualisms : The conservation of plant-pollinator interactions. Annual Review of Ecology and Systematics 29: 83-112.

Keller, L.F., and D.M. Waller. 2002. Inbreeding effects in wild populations. Trends in Ecology & Evolution 17: 230-241.

Knight, T. M., J. A. Steets, and T. L. Ashman. 2006. A quantitative synthesis of pollen supplementation experiments highlights the contribution of resource reallocation to estimates of pollen limitation. American Journal of Botany 93: 271-277.

Kruckeberg, A.R., and D. Rabinowitz. 1985. Biological aspects of endemism in higher plants. Annual Review of Ecology and Systematics 16: 447-479.

Krupnick, G. A., A. E. Weis, and D. R. Campbell. 1999. The consequences of floral herbivory for pollinator service to *Isomeris arborea*. Ecology 80: 125–134.

Kunin, W. E. 1997. Population size and density effects in pollination: Pollinator foraging and plant reproductive success in experimental arrays of *Brassica kaber*. The Journal of Ecology 85: 225-234.

Lee, T. D., and F. A. Bazzaz. 1986. Maternal regulation of fecundity: non-random ovule abortion in *Cassia fasciculata* Michx. Oecologia 68: 459-465.

Liu, H., and S. Koptur. 2003. Breeding system and pollination of a narrowly endemic herb of the Lower Florida Keys: impacts of the urban-wildland interface. American Journal of Botany 90: 1180-1187.

Matthies, D., I. Bräuer, W. Maibom, and T. Tscharntke. 2004. Population size and the risk of local extinction: empirical evidence from rare plants. Oikos 105: 481-488.

Menges, E. S. 1991. The application of minimum viable population theory to plants. In Genetics and conservation of rare plants, 45–61. Oxford: Oxford University Press, Inc.

Nair, R. M., I. S. Dundas, M. Wallwork, D. C. Verlin, L. Waterhouse, and K. Dowling. 2004. Breeding system in a population of *Trigonella balansae* (Leguminosae). Annals of Botany 94: 883-888.

ORNHIC (Oregon Natural Heritage Information Center). 2003. Oregon Natural Heritage Information Center Database. Oregon Natural Heritage Information Center, Portland, Oregon.

R Development Core Team. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. http://www.R-project.org.

Schemske, D. W., B. C. Husband, M. H. Ruckelshaus, C. Goodwillie, I. M. Parker, and J. G.Bishop. 1994. Evaluating approaches to the conservation of rare and endangered plants. Ecology 75: 584-606.

Sih, A., and M. Baltus. 1987. Patch size, pollinator behavior, and pollinator limitation in Catnip. Ecology 68: 1679-1690.

Stephenson, A. G. 1981. Flower and fruit abortion: proximate causes and ultimate functions. Annual Review of Ecology and Systematics 12: 253-279.

Waites, A. R., and J. Agren. 2004. Pollinator visitation, stigmatic pollen loads and among-population variation in seed set in *Lythrum salicaria*. Journal of Ecology 92: 512-526.

Ward, M., and S. D. Johnson. 2005. Pollen limitation and demographic structure in small fragmented populations of *Brunsvigia radulosa* (Amaryllidaceae). Oikos 108: 253-262.

Young, H. J., and T. P. Young. 1992. Alternative outcomes of natural and experimental high pollen loads. Ecology 73: 639-647.

Chapter 4

HABITAT CHARACTERIZATION OF *ASTRAGALUS PECKII*, A RARE
CENTRAL OREGON ENDEMIC

Elizabeth F. Martin and Robert Meinke

ABSTRACT

Astragalus peckii (Fabaceae) is a rare, edaphic endemic with a restricted range in south-central Oregon. Our goal in this paper is to describe habitat preferences for *A. peckii* within this range in order to better delineate preferred, suitable habitat for conservation. We used two multivariate statistical methods, nonparametric multiplicative regression (NPMR) and nonmetric multidimensional scaling (NMS), to model habitat preferences and identify correlations with vegetation, soil, climate, and habitat variables. Additionally, we took a closer look at one of the habitat variables, litter, to assess the effect of different litter depths on seedling survival and growth in *A. peckii*. For this, we used litter collected from beneath a *Juniperus occidentalis* (Western juniper) canopy. Results from the habitat model showed greater *A. peckii* abundance (measured as a combination of percent cover and density) when litter cover was less than 16% and bryophyte and lichen cover, which mainly comprised soil crust species, was nearly absent. Because litter had a higher sensitivity value and was therefore a stronger predictor in our model, we predict litter to have a greater influence on the spatial distribution of *A. peckii* than bryophyte and lichen cover. For greenhouse-grown plants, seedlings grown under 1 cm of juniper litter had lower survival than those grown under 0.5 cm of litter or no litter; no difference in seedling height was found. There were no significant associations with the vascular plant community or any of the generalized plant variables, such as total percent forb or shrub cover, with abundance of *A. peckii*. In conclusion, despite a restricted geographic range *A. peckii* does not have strict habitat requirements within this range as long as litter cover is low. This is hopeful for conservation of the species because it is able to grow in multiple habitats.

INTRODUCTION

Predictive models of habitat and species associations have numerous conservation and restoration applications. First, considering many conservation decisions are made with time constraints and limited available data, habitat models are

a means to predict where rare and endangered species are or are not likely to be found. Focused searches for new populations can then be conducted using predicted occurrences across the landscape (Raxworthy et al. 2003; Engler et al. 2004). Sites with high potential for future colonization, restoration, or reintroduction can be also identified. Additionally, impacts of disturbance, including land cover alterations and climate change, can be assessed using current knowledge about species distributional requirements (Thomas et al. 2004).

Given these benefits, we aim to delineate habitat and species associations for *Astragalus peckii* (Fabaceae), a state-listed Threatened species in Oregon. Like many species of *Astragalus*, *A. peckii* is a localized soil endemic (Barneby 1964). The geographic range is limited to two counties in south-central Oregon, just east of the Cascade Mountains. Soils in this area are pumice-influenced from the eruption of Mt. Mazama (present day Crater Lake) approximately 7500 years ago and numerous eruptions from Newberry Volcano occurring as recently as 1500 years ago. These pumice soils are characterized by a high water-holding capacity and high temperature extremes when dry. Nutrient levels, after accounting for the low bulk density of soil particles, are typically low in nitrogen, sulfur, and phosphorus (Youngberg and Dyrness 1964; Carlson 1979).

Habitat for *A. peckii* includes open shrub-steppe and canopy openings in lodgepole and ponderosa pine forests. On a regional scale, *A. peckii* is very patchily distributed. The majority of known populations are at the northern end of the range, which is characterized by sagebrush-steppe and juniper woodland communities (Amsberry and Meinke 2003). Several other disjunct population clusters are located up to 200 kilometers south of this region in areas dominated by lodgepole and ponderosa pine forests (Amsberry and Meinke 2003). Given the disjunct distribution of *A. peckii* among different plant community types within a limited geographic range, we are interested in identifying unifying characteristics of all *A. peckii* sites.

Increased tree establishment of Western juniper (*Juniperus occidentalis*) over the past century in central and eastern Oregon (Rose and Miller 1995; Knapp and

Soulé 1998; Miller and Rose 1999) has lead to a shift in vegetation cover for several plant community types (Miller et al. 2000). This is a concern for *A. peckii* because many of the northern populations are in or adjacent to juniper woodlands. With a denser juniper canopy, litter accumulation at the soil surface will also increase. Plant litter alters both the abiotic and biotic environment for seeds (Facelli and Pickett 1991) and potential impacts of this on *A. peckii* include reduced seed germination, seedling establishment, and plant growth.

The primary objective of this study is to determine the relationship between *A. peckii* abundance and vegetation, soil, and climate variables across the range of the focal species. Because *A. peckii* appears to have limited seed dispersal, this question will be examined both on the site level, where broad-scale differences in soil, climate, and vegetation could potentially influence spatial distribution patterns, and at the plot level, where local species composition and habitat structure could play a greater role. A second objective is to assess the effect of plant litter from overstory juniper trees on seedling survival and growth with the prediction that litter will inhibit both survival and growth.

METHODS

Objective 1: Describe the relationship between A. peckii abundance and vegetation, soil, and climate variables.

Study Design

Data on plant species composition, soil, climate, and general habitat characteristics were recorded at seven *A. peckii* sites (Table 4.1). Sites were selected to span the entire geographic range and elevation gradient of *A. peckii* and were sampled during the summer growing season of either 2007 or 2008 (Table 4.1). Vegetation and habitat data were collected from $1m^2$ plots located at 5m intervals along randomly placed transects. Depending on the size and heterogeneity of the site, between 30 and 50 plots were sampled at each site. In each plot, the percent cover for every vascular plant species was recorded. If *A. peckii* was present in the plot, the total density, density of seedlings, and density of reproductive individuals were

recorded along with percent cover. On the one rare occasion where *A. peckii*
contributed to percent cover but was not rooted in the plot, density was recorded as
zero. For each vegetation growth form (graminoid, forb, shrub, tree, and
bryophyte/lichen) and six other habitat variables, total percent cover was recorded;
together, these eleven variables will be referred to as habitat variables (Table 4.2).

Soil and climate data were also collected for each of the seven sites. Soil
samples were collected at the end of three transects within each site. Samples were
taken between 5 and 15 cm in depth and combined for one representative sample per
site. Northwest Agricultural Consultants, Inc. in Kennewick, Washington, analyzed
our samples for eight different soil variables (Table 4.2). Climate data for each site
were downloaded from Oregon State University's PRISM group to calculate four
different precipitation and temperature variables (Table 4.2, PRISM 2009).

Table 4.1. Site location, elevation, and sampling date for seven *A. peckii* study sites.

| Site | Code | UTM coordinates (zone 10) | | Elevation (m) | Date sampled |
		Northing	Easting		
Bull Flat	BF	625397	4890479	1062	7/18/07
Innes Market Rd	IMR	628587	4895092	991	7/12/07
Chemult 8603	CM	602489	4777578	1430	7/10/07
Chemult 8603T	CM-T	602311	4777033	1428	7/22/08
Chemult 8613	CM-S	617277	4781662	1526	7/18/08
Chiloquin	CQ	603781	4710886	1358	7/20/07
Chiloquin-P	CQ-P	601512	4715211	1322	7/15/08

Table 4.2. Habitat, soil, climate, and elevation variables used in environmental
matrices and the code used for each variable throughout this paper. At the plot level,
only habitat variables were used in the environmental matrix. At the site level, all
variables were used.

Variable code	Description (measurement units)
Habitat	
B/L	All bryophyte and lichen species (% cover)
BG	Bareground (% cover)
Wood	Standing dead shrubs + detached wood with dbh> 1cm (% cover)
Gram	All graminoid (grass, sedge, and rush) species (% cover)
Forb	All non-graminoid, herbaceous species (% cover)
Shrub	Multi-stemmed, woody plants (% cover)
Over	Overstory, woody plants, dbh>10cm (% cover)
Litter	Dead, detached plant material (% cover)
Gravel	Rock pieces 2-64 mm in diameter (% cover)
Cobble	Rock pieces 64-256 mm in diameter (% cover)
Boulder	Rock greater than 256 mm in diameter (% cover)
Soil	
Salts	Soluble salts (mmhos/cm)
OM	Organic matter (%)
NO3	NO3-N (lbs/acre)
NH4	NH4-N (lbs/acre)
Sulfur	Sulfur (ppm)
pH	pH
P	P (bic) (ppm)
K	K (bic) (ppm)
Climate	
Avg prp	Average long-term precipitation 1895-2007 (mm)
Ann prp	Total annual precipitation (July-June) year before sampling (mm)
Tmax	Growing season average maximum temperature (Apr-June) of sampling year (ºC)
Tmin	Growing season average minimum temperature (Apr-June) of sampling year (ºC)
Elev	Site elevation (m)

Analysis

Data matrices – The relationship between the abundance of *A. peckii* and
recorded species and habitat data was analyzed at two spatial scales, plot and site. For
each scale of analysis, three matrices were constructed. First, a species matrix
contained percent cover values for all species encountered except *A. peckii*. This
matrix was 310 sample units (rows) by 85 species (columns) at the plot level and 7
sample units by 85 species at the site level (see Appendix 4.1 for species list). Second,
a demographic matrix contained the four *A. peckii* abundance metrics; dimensions
were 310 sample units by 4 variables at the plot level and 7 sample units by 4

variables at the site level. Third, an environmental matrix contained habitat, soil, climate, and elevation data. At the plot level, where only habitat data were measured, the matrix contained 310 sample units and 11 habitat variables. At the site level, the matrix contained 7 sample units and 24 habitat variables (Appendix 4.2).

Astragalus **performance variable** – A composite performance variable for *A. peckii* was first created from the four demographic variables with principal components analysis (PCA) in PCORD, version 6 (McCune and Mefford 2009a). Combining different abundance metrics that have different levels of correlation with one another, allows for a single – and potentially stronger – relationship to emerge in the analyses explained below. Before running the PCA, total *A. peckii* density, density of seedlings, and density of reproductives were log-transformed after the addition of one, and the percent cover of *A. peckii* was arcsine square root transformed to improve heteroscedascity and linear relationships among the variables.

A PCA was run using a correlation cross-products matrix and the first eigenvector, which captured 78.5% of the variance, was used to assign performance scores for each plot. All subsequent axes had lower eigenvalues than those expected by chance and were therefore not used. Eigenvector coefficients, scaled to their standard deviation, for the first axis are: density (-0.98), number of seedlings (-0.69), number of reproductives (-0.89), and percent cover (-0.95). Since these coefficients, or V vectors, are scaled to their standard deviation, they can be interpreted as correlation coefficients (McCune and Mefford 2009a). The solution was rotated 180º so the composite demographic values would be greater for those plots with more *A. peckii*. This newly created variable will be referred to as *Astragalus* performance throughout the paper and was added to the matrices containing environmental variables. For the site level analysis, *Astragalus* performance was computed by averaging the individual plot values for each site.

Ordination – Nonmetric multidimensional scaling (NMS) was used to assess trends in species and habitat characteristics in relation to *Astragalus* performance (Kruskal 1964; Mather 1976). Species data were transformed by first deleting species

that occurred in less than 2% of the plots or at only one site, leaving 44 species at the plot level and 40 at the site level. Percent cover values were then square-root transformed to reduce skewness and the coefficient of variation for row and column totals.

NMS analysis was run using the medium thoroughness autopilot settings with Sorenson distance measures in PCORD. Fifty runs were made with the real data, using random starting configurations. The dimensionality of the final solution was assigned by PCORD and verified with scree plots. Final solutions were rotated to align the *Astragalus* performance variable on axis one and joint plots were used to overlay habitat variables.

Habitat model – Non-parametric multiplicative regression (NPMR) was then used assess the relationship between habitat variables and *Astragalus* performance at the plot level. NPMR was chosen over other multiple regression techniques because of several key features. One, it automatically includes multiplicative interactions between all model variables (McCune 2006). Second, it does not assume a global response across the dataset; instead, localized means are computed throughout the dataset using smoothing kernels (McCune 2006). The combination of these two characteristics results in a final response surface that reflects complex changes in plant abundance across environmental gradients.

Model fit in NPMR is evaluated with a cross-validated R^2 (xR^2) for quantitative response variables. This is a more conservative estimate of model fit than traditional R^2 because the leave-one-out cross validation procedure reduces overfitting in the model (McCune 2006). There are no regression coefficients with this technique, and the relative importance of predictors can be assessed in several ways including sensitivity values. Sensitivity is defined as the average estimated absolute standardized change in the response per the same magnitude change in the predictor. Therefore, if an average change in litter cover of 10% results in an average change in *Astragalus* performance of 10%, then sensitivity of the variable litter is 1. If this same change in litter results in a 5% change in *Astragalus* performance, the sensitivity

would be 0.5. Sensitivities can thus be used to assess the relative importance of predictors within a model.

Our NPMR model was run with *Astragalus* performance as the response variable and the 11 habitat variables (Table 4.2) as predictors. Forb cover was adjusted by removing *A. peckii* cover from the total amount because *A. peckii* cover is also a component of the response variable. All habitat variables were square root transformed as described above. A free search using local means and Gaussian weights was used to screen potential predictors in HyperNiche v2.07 (McCune and Mefford 2009b). The model with the highest xR^2 was chosen as the best model and was subsequently "fine tuned". Fine tuning involves small adjustments to the tolerance values (which are related to sensitivity values) of each chosen predictor to attain the best possible fit. Sensitivity values for all selected predictors were computed for the final model and a Monte Carlo randomization test with 200 runs of random data was used to assess significance.

Objective 2: Describe the effect of juniper litter on seedling growth and survival.
Study design

Seedlings of *A. peckii* were grown in the greenhouse under one of three litter treatments: no litter added, 0.5 cm of litter added to the soil surface, and 1 cm of litter added. Seeds for this study were collected at the Bull Flat site during the summer of 2009 and stored at room temperature until use. In January, 2010, seeds were scarified with sandpaper, placed on moistened filter paper in petri dishes, and germinated in the greenhouse. Approximately three weeks after scarification, 63 seedlings were planted in 10-inch deep tree seedling pots with a 3:1 mixture of potting soil to native soil from the Bull Flat site. Litter treatments were randomly applied to the pots at the time of planting with 21 seedlings per treatment. Litter was collected from beneath a juniper canopy within the range of *A. peckii* just prior to use in January, 2010. Seedlings were grown in the greenhouse for seven weeks with 8 hours of artificial light/day and water when needed. After this time, survival and height of seedlings were recorded for each individual.

Analysis

To determine the effect of litter addition on seedling survival, a logistic regression was run using a generalized linear model with binomial error distribution and logit link function in Rv2.9.2 (R Development Core Team 2009). The effect of litter addition on seedling growth was analyzed with ANOVA using seedling height (log-transformed) as the response variable.

RESULTS

Objective 1: Describe the relationship between A. peckii abundance and vegetation, soil, and climate variables.

Ordination – At the plot-level scale, the NMS ordination of sample plots in species space had a 3-dimensional solution (final stress=19.0, final instability<0.00001, 164 iterations). This solution was rotated to align *Astragalus* performance with axis one. This first axis explained 12.2% of the variance in distance and was weakly correlated with *Astragalus* performance (r=0.07). This weak correlation can also be seen in the ordination by the presence of plots with *A. peckii* scattered throughout the entire ordination space (Figure 4.1). The second and third axes explained more of the variation, with 30.6% and 23.1% each, respectively. Of the 11 habitat variables, only two had a moderate level of correlation with the axes and none were strongly correlated. Graminoid cover was positively associated with the first axis (r=0.59), and the amount of gravel present was negatively associated with the second axis (r= -0.45; Figure 4.1).

At the site-level scale, the NMS ordination of sample sites in species space had a 2-dimensional solution (final stress=1.65, final instability<0.00001, number of iterations=69). After rotation to align the first axis with *Astragalus* performance, the first axis explained 7.8% of the variance in distance between sites and the second axis explained 74.6% of the variance. *Astragalus* performance was weakly correlated with axis 1 (r=0.30). Rather, axis 1 was positively correlated with shrub cover (r=0.86) and negatively correlated with cover of the larger size classes of rock (r= -0.81 for cobble and r= -0.88 for boulders). Axis 2, which explained most of the variance in the

ordination, was correlated with numerous climate, soil, and habitat variables (Figure 4.2). The strongest relationships were with climate variables; average long-term precipitation is negatively correlated with this axis (r= -0.94) and temperature is positively correlated (r=0.93 for maximum temperature and r=0.96 for minimum temperature; Figure 4.2).

Figure 4.1. NMS ordination of plots in species space. The solution was rotated to align the *Astragalus* performance variable with axis 1. Plots are depicted with triangles and lines represent joint plot vectors of habitat variables with an $r^2 > 0.20$. Axis 1 vs. axis 2 (A) and axis 1 vs. axis 3 (B) are depicted.
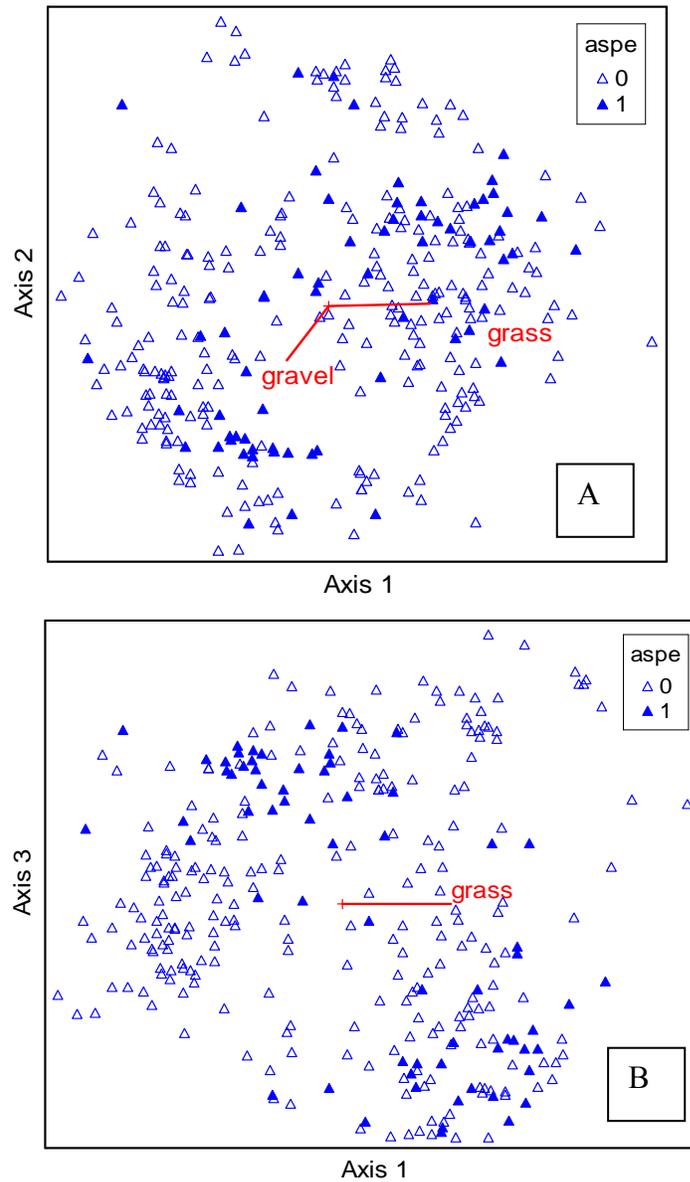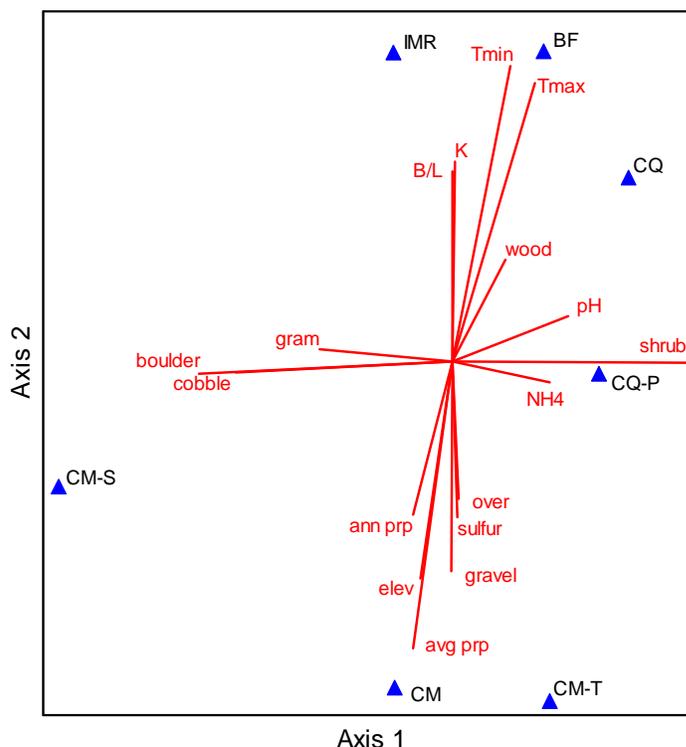
Figure 4.2. NMS ordination of sites in species space. The solution was rotated to align the *Astragalus* performance variable with axis 1. Plots are depicted with triangles and lines represent joint plot vectors of habitat variables with an $r^2 > 0.30$. Site codes are given in Table 4.1 and habitat variable codes and descriptions are in Table 4.2.

Habitat model – The model that best described *Astragalus* performance included litter and bryophyte/lichen cover as predictor variables (Table 4.3). The xR^2 after fine-tuning was 0.16 and this model was significantly better than the naïve model (p=0.005) in explaining abundance patterns for *A. peckii*. *Astragalus* performance was more sensitive to litter than bryophyte/lichen cover; therefore, changes in litter cover had a larger effect on *A. peckii* than changes in bryophyte/lichen cover (Table 4.3). In our sample plots, litter cover was 3-times lower in plots with *A. peckii* ($13.3 \pm 2.3\%$, mean±SE) compared to those with no *A. peckii* present ($38.6 \pm 2.2\%$). Bryophyte/ lichen cover, however, was within one percentage point between plots with and without *A. peckii* (overall mean of $2.9 \pm 0.3\%$). The results from the habitat model

should not be used to interpret single variable relationships, though, because of the interactions incorporated into the model. Therefore, *Astragalus* performance was greatest when both litter cover was less than 16% and bryophyte/lichen cover was less than 1% (Figure 4.3). There were two other minor peaks in performance, each occurring when one of these variables was at the upper end of its range and the other was at the lower end (Figure 4.3).

Table 4.3. NPMR model results for *Astragalus* performance. Model was run with 11 different habitat variables as possible predictors using local means and Gaussian weights.

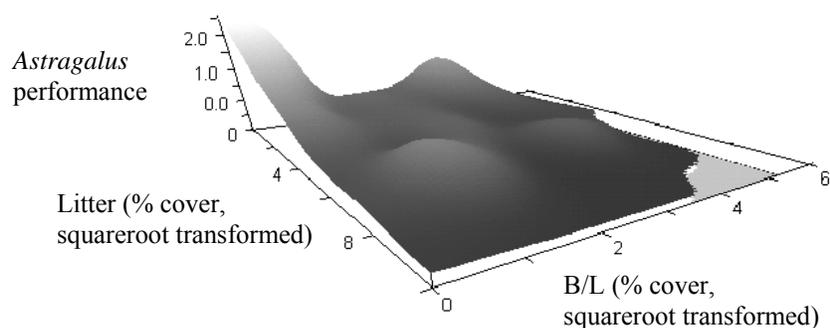| Response variable	xR^2	Avg. neighb. Size	Predictor variables (sensitivity)	
Astragalus performance	0.16	28.0	Litter (0.78)	B/L (0.33)

Figure 4.3. Three-dimensional habitat model from NPMR. *Astragalus* performance (the response) is a composite demographic variable created with PCA (see text for details). Lighter shades represent greater *Astragalus* performance. When *Astragalus* performance is greater than 0, *A. peckii* is present.

Objective 2: Describe the effect of juniper litter on seedling growth and survival.

There was a significant effect of litter treatment on survival of *A. peckii* seedlings (χ^2=23.2, df=2, p<0.001). Survival was 100% when grown without litter and 86% when grown under 0.5 cm of litter. Under 1 cm of litter, though, survival dropped to 43%. Height of surviving seedlings after 7 weeks did not vary between the three treatment groups ($F_{2,45}$=0.95, p=0.39).

DISCUSSION

Within the seven *A. peckii* sites used in our habitat model, we found *A. peckii* to be locally most abundant where litter cover was sparse (<16%) and bryophyte/lichen cover was nearly absent (<1%). Because the bryophyte and lichen species at our sites were mostly soil crust components, both of the variables selected in our model are hypothesized to influence the spatial distribution of *A. peckii* through soil level processes, such as seed germination and establishment. There was no significant correlation, however, between *Astragalus* performance and any of the variables representing the vascular plant community in the habitat model. This was also supported by the ordination results which found a low correlation between *Astragalus* performance and the ordination axes at both the plot and site level. It should be noted that all but one of the sites used in these analyses were, like most *A. peckii* sites, sagebrush or rabbitbrush communities with relatively few non-native or invasive species (Appendix 4.1). The one non-shrub site was dominated by graminoid species and also had few non-native species.

From the habitat model, litter had a stronger effect on the spatial distribution of *A. peckii* than bryophyte/lichen cover (Table 4.3). Litter can influence spatial distribution through numerous effects on seed germination and seedling establishment. First, litter can form a physical barrier between the seed and the soil, which prevents some seeds from reaching the soil surface (Hamrick and Lee 1987; Facelli and Pickett 1991). Because *A. peckii* seeds need physical scarification in order to germinate, retention in the litter rather than the soil may be detrimental if this precludes

scarification. Conversely, seeds buried beneath litter need additional energy reserves to penetrate through the litter, which some small-seeded species may not be able to endure (Facelli and Pickett 1991). With seeds only 1.5 mm in length (Barneby 1964), *A. peckii* seeds may not be able to withstand deep burial. Litter also alters light and water availability at the soil surface and chemical composition of the soil; these changes in the abiotic environment can thus affect seed germination and establishment (Facelli and Pickett 1991; Xiong and Nilsson 1999). For example, in a structurally similar semi-arid shrub habitat in Spain, Navarro-Cano et al. (2010) found pine litter inhibited seed germination and establishment of several native forb species through a combination of allelopathic and physical mechanisms associated with burial.

Supporting results from the habitat model, litter also reduced seedling survival in our greenhouse study. Unlike the litter variable used in the above model, though, litter for the greenhouse study was specifically collected from beneath a juniper canopy. Several different juniper species are known to inhibit seed germination and seedling growth through allelopathy (Ramsey 1990; Young and Bush 2009) and alteration of the abiotic environment (Yager and Smeins 1999). However, if allelopathy were to have an effect in our study, then we would expect reduced seedling survival along with reduced seedling growth. Because growth was similar when grown with and without litter addition, allelopathy of Western juniper does not appear to be inhibiting *A. peckii*. Also working with Western juniper in Oregon, Bates et al. (1998) found reduced perennial forb cover in juniper duff areas compared to adjacent interspaces whereas individual plant growth was comparable or greater in the juniper duff. This, again, suggests physical rather than allelopathic effects of Western juniper litter on seed germination and establishment.

Bryophyte and lichen cover, the other explanatory variable from our model, primarily comprises a biological soil crust layer in our plots. Beneficial effects of soil crusts on vascular plant establishment include soil stabilization and increased nutrient and water availability (Belnap 2003; Hawkes 2004) whereas negative effects include increased competition for water and nutrients and the presence of a barrier between

seed and soil (Belnap 2003; Deines et al. 2007). The lack of consensus among researchers concerning an overall effect of crusts on seeds likely reflects the diversity of soil crusts and seed morphologies studied (Serpe et al. 2006; Escudero et al. 2007).

In our study, *Astragalus* performance was highest when soil crusts were nearly absent. Although this could represent an inhibitory effect, several other factors indicate bryophyte and lichen cover is not a strong predictor in our model. First, the sensitivity value for this variable is much lower than that for litter (Table 4.3), indicating it has a comparably weaker effect on *A. peckii* abundance. In line with this, average bryophyte/lichen cover is nearly equal (approximately 3%) between plots with and without *A. peckii*. Furthermore, with such a low presence in the environment, it is not likely that this variable has a strong influence on *A. peckii* spatial patterns.

To summarize the model results, litter and bryophyte/lichen cover best explained the spatial distribution of *A. peckii* within our sites. However, for reasons explained above, litter cover is a much stronger predictor than bryophyte/lichen cover. Also, it should be emphasized that *A. peckii* cover is highest when there is a combination of low litter and no bryophyte/lichen cover. Even though we discussed each of these terms separately, the model incorporated interactions between them. Finally, there are many other variables which were not addressed here which likely contribute to the spatial distribution of *A. peckii* including seed dispersal distances, herbivore levels, and disturbance. With only 16% of the variation in *A. peckii* abundance explained with the current habitat model, these untested factors are likely to increase the explanatory power.

No significant relationships between individual vascular plant species or vascular plant growth forms emerged in our analyses. This was unexpected considering the variation in *A. peckii* abundance observed both between and within sites. One potential explanation for this is the loss of resolution that occurred when multiple demographic metrics were collapsed into a single performance variable. For example, the two sites with the highest *Astragalus* performance scores, Chemult and Chiloquin, had different demographic variables influencing the scores. At Chemult,

plant density was high but percent cover was low due to the small stature of plants at this site. At Chiloquin, fewer, large plants resulted in high cover values but low plant density. These two sites also fall at opposite ends of the ordination axis that best describes patterns in plant composition among sites (Figure 4.3). With two vegetatively different sites having the highest demographic scores for *A. peckii*, it makes sense that no overall trends are discernable in the ordinations and why no vascular plant growth forms emerged in the habitat model as explanatory variables.

Another potential explanation is that *A. peckii* does not have strict habitat requirements within its geographical range. This is less informative when the objective is to delineate habitat characteristics for identification of current or future high quality habitat sites. On the other hand, it is encouraging for conservation if a broad range of habitats can support *A. peckii* populations. Although several studies have found endemic species to be restricted to harsh or less productive habitats (Lavergne et al. 2004; Stohlgren et al. 2005), Lesica et al. (2006) found endemic species to be more abundant than widespread species at a local scale in a the western United States. Recent speciation events and lack of time to disperse to new habitats were hypothesized to contribute to the high local abundances of these geographically restricted species (Lesica et al. 2006). Likewise, *A. peckii* could represent a recent speciation event after volcanic eruptions of the last 7500 years produced the pumice-based soils it is associated with. The restricted range would therefore be a function of limited dispersal into new areas rather than ecological restrictions.

Conservation implications

The lack of significant plant associations for *A. peckii* indicates this species can grow in a diversity of habitats throughout its range. Given its restricted geographical range, a broader habitat range makes *A. peckii* less at risk of extirpation (Rabinowitz 1981). However, changes in plant community composition that result in increased litter deposition are predicted to have a negative impact on *A. peckii*. In the field, litter is densest beneath the tree canopy, reaching depths of several centimeters (E. Martin, personal observation). In the northern part of *A. peckii*'s range, which is where the

majority of known populations are located, Western juniper is the most common tree species. Encroachment of this species beyond its historical range is a growing concern in Oregon (Rose and Miller 1995), and one impact on *A. peckii* will be reduced seedling survival. In other parts of *A. peckii*'s range, populations are found within canopy gaps of vast lodgepole and ponderosa pine forests; closure of these gaps will likewise detrimentally impact populations if pine litter has a similar negative effect on seedlings. Therefore, selected tree removal may be a future management need in order to maintain habitat for *A. peckii*.

REFERENCES

Amsberry, K., and R. J. Meinke. 2003. Life history and conservation status of *Astragalus peckii* Piper (Fabaceae). Native plant conservation program, Oregon Department of Agriculture.

Barneby, R. C. 1964. Atlas of North American *Astragalus*. Memoirs of the New York Botanical Garden 13: 1–1188.

Bates, J.D., R.F. Miller, and T. Svejcar. 1998. Understory patterns in cut western juniper (*Juniperus occidentalis spp. occidentalis* Hook.) woodlands. Great Basin Naturalist 58: 363-374.

Belnap, J. 2003. The world at your feet: Desert biological soil crusts. Frontiers in Ecology and the Environment 1: 181-189.

Carlson, G.T. 1979. Soil resource inventory. Report for the Winema National Forest, US Forest Service.

Deines, L., R. Rosentreter, D.J. Eldridge, and M.D. Serpe. 2007. Germination and seedling establishment of two annual grasses on lichen-dominated biological soil crusts. Plant & Soil 295: 23-35.

Engler, R., A. Guisan, and L. Rechsteiner. 2004. An improved approach for predicting the distribution of rare and endangered species from occurrence and pseudo-absence data. Journal of Applied Ecology 41: 263-274.

Escudero, A., I. Martínez, A. de la Cruz, M.A.G. Otálora, and F.T. Maestre. 2007. Soil lichens have species-specific effects on the seedling emergence of three gypsophile plant species. Journal of Arid Environments 70: 18-28.

Facelli, J.M., and S.T. Pickett. 1991. Plant litter: its dynamics and effects on plant community structure. The Botanical Review 57: 1-32.

Hamrick, J. L., and J.M. Lee. 1987. Effect of soil surface topography and litter cover on the germination, survival, and growth of Musk Thistle (*Carduus nutans*). American Journal of Botany 74: 451-457.

Hawkes, C.V. 2004. Effects of biological soil crusts on seed germination of four endangered herbs in a xeric Florida shrubland during drought. Plant Ecology 170: 121-134.

Knapp, P.A., and P.T. Soulé. 1998. Recent *Juniperus occidentalis* (Western Juniper) expansion on a protected site in central Oregon. Global Change Biology 4: 347-357.

Kruskal, J.B. 1964. Nonmetric multidimensional scaling: A numerical method. Psychometrika 29: 115-129.

Lavergne, S., J.D. Thompson, E. Garnier, and M. Debussche. 2004. The biology and ecology of narrow endemic and widespread plants: a comparative study of trait variation in 20 congeneric pairs. Oikos 107: 505-518.

Lesica, P., R. Yurkewycz, and E.E. Crone. 2006. Rare plants are common where you find them. American Journal of Botany 93: 454-459.

Mather, P.M. 1976. Computational methods of multivariate analysis in physical geography. J. Wiley & Sons, London.

McCune, B. 2006. Non-parametric habitat models with automatic interactions. Journal of Vegetation Science 17: 819-830.

McCune, B., and M.J. Mefford. 2009a. PC-ORD, Multivariate analysis of ecological data, version 6.91 beta. MjM Software, Gleneden Beah, Oregon, USA.

---. 2009b. HyperNiche, Nonparametric multiplicative habitat modeling, Version 2.07. MjM Software, Gleneden Beah, Oregon, USA.

Miller, R.F., and J.A. Rose. 1999. Fire history and Western juniper encroachment in sagebrush steppe. Journal of Range Management 52: 550-559.

Miller, R.F., T.J. Svejcar, and J.A. Rose. 2000. Impacts of Western juniper on plant community composition and structure. Journal of Range Management 53: 574-585.

Navarro-Cano, J.A., G.G. Barberá, and V.M. Castillo. 2010. Pine litter from afforestations hinders the establishment of endemic plants in semiarid scrubby habitats of Natura 2000 Network. Restoration Ecology 18: 165-169.

PRISM Climate Group. Oregon State University. http://www.prismclimate.org, accessed February 11, 2009.

R Development Core Team. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. http://www.R-project.org.

Rabinowitz, D. 1981. Seven forms of rarity. pp 205-217. In The biology aspects of rare plant conservation. H. Synge, ed. Wiley, Chichester, United Kingdom.

Ramsey, K.J. 1990. Influence of leachates from western juniper slash on three native grasses. Thesis/Dissertation, Oregon State University. http://ir.library.oregonstate.edu/jspui/handle/1957/11881.

Raxworthy, C.J., E. Martinez-Meyer, N. Horning, R.A. Nussbaum, G.E. Schneider, M.A. Ortega-Huerta, and A. Townsend Peterson. 2003. Predicting distributions of known and unknown reptile species in Madagascar. Nature 426: 837-841.

Rose, J., and R. Miller. 1995. Historic expansion of *Juniperus occidentalis* (Western juniper) in southeastern Oregon. Great basin naturalist 55: 37-45.

Serpe, M., J. Orm, T. Barkes, and R. Rosentreter. 2006. Germination and seed water status of four grasses on moss-dominated biological soil crusts from arid lands. Plant Ecology 185: 163-178.

Stohlgren, T.J., D.A. Guenther, P.H. Evangelista, and N. Alley. 2005. Patterns of plant species richness, rarity, endemism, and uniqueness in an arid landscape. Ecological Applications 15: 715-725.

Thomas, C.D., A. Cameron, R.E. Green, M. Bakkenes, L.J. Beaumont, Y.C. Collingham, B.F.N. Erasmus, et al. 2004. Extinction risk from climate change. Nature 427: 145-148.

Xiong, S., and C. Nilsson. 1999. The effects of plant litter on vegetation: a meta-analysis. Journal of Ecology 87: 984-994.

Yager, L.Y., and F.E. Smeins. 1999. Ashe juniper (*Juniperus ashei*: Cupressaceae) canopy and litter effects on understory vegetation in a juniper-oak savanna. The Southwestern Naturalist 44: 6-16.

Young, G., and J. Bush. 2009. Assessment of the allelopathic potential of *Juniperus ashei* on germination and growth of *Bouteloua curtipendula*. Journal of Chemical Ecology 35: 74-80.

Youngberg, C.T., and C.T. Dyrness. 1964. Some physical and chemical properties of pumice soils in Oregon. Soil Science 97: 391-399.

Chapter 5

CONCLUSIONS

Prior to this research, the bulk of information on *Astragalus peckii* consisted of site localities and preliminary studies on the reproductive ecology and life history of the species. My goal with this work was to expand on this base by investigating three aspects of this species. Broadly outlined, these three aspects are demography, reproduction, and delineation of preferred habitat. Results from these studies are intended to provide more information on the basic biology and habitat for *A. peckii* and be used to make better informed decisions on conservation and management for long-term persistence.

In Chapter 2, I began with a comparative demographic study of two large populations, one located in the northern population center and the other from a disjunct locale. Contrary to our prediction, the disjunct Chiloquin population had a higher population growth rate while the Bull Flat population, located in the population center, had a population growth rate ranging from stable to declining. During the timeframe of this research, the Bull Flat population also experienced several years of below average precipitation which could have contributed to the lower population growth rate. Future comparison with years of greater rain and/or snowfall will elucidate whether or not population growth rate will remain low once growing conditions improve. One important point to take away from this portion of the research is that even large populations are susceptible to periods of declining population growth.

Continuing in Chapter 2, I focused on the effect of the microlepidopteran herbivore, *Sparganothis tunicana*, on survival, growth, and fecundity of *A. peckii* plants. Depending on the site and year, different vital rates were negatively impacted. However, none of the effects on vital rates appear large enough to cause negative

population growth. During most of the study, the webbing and leaf tissue damage caused by *S. tunicana* was highest later in the growing season for *A. peckii*, after plants had finished flowering. The temporal separation of plant reproduction and moth damage may minimize the overall impact of the moth on the plant. However, during the first year I measured herbivore damage, moth activity was earlier in the season at Chiloquin. If overlap in activity of these two species becomes more frequent in the future, herbivore effects on plant survival, growth, and reproduction should be reevaluated under the changed conditions.

In Chapter 3, I investigated several aspects of the reproductive biology of *A. peckii* with the goal of identifying factors that limit reproduction. I specifically addressed how pollen quantity and quality contributed to reproductive success and how pollinators mediated this relationship. Overall, I found fruit and seed set was generally not limited by the quantity of pollen delivered by pollinators. Supporting this were pollinator visitation levels high enough to visit the majority of flowers per plant during most years at my sites. Also, pollen quality was not limited under natural pollination levels despite observed geitonogamous pollinator visits. However, when flowers were manually self-pollinated, seed set, and to a lesser degree fruit set, were lower compared to a cross-pollination treatment. In the next generation, inbreeding depression was also found in seedling growth traits. These results indicate that maintaining both plant and pollinator populations are critical to ensure reproductive success in *A. peckii*. Furthermore, reduction in plant population size that occurs with habitat loss and fragmentation will likely lead to increased inbreeding depression in *A. peckii*.

In the final chapter, I examined characteristics of the habitat that potentially explain the distribution of *A. peckii* across the landscape. Using vegetation, habitat, climate, and soil data, *A. peckii* abundance was correlated with areas of low litter and soil crust cover. Supporting these results, seedlings grown under 1 cm of juniper litter in the greenhouse had lower survival than those grown with less or no litter. Overall, though, there were no strong vegetation associations for *A. peckii* indicating that

despite its restricted geographical range it does not have a restricted habitat range. This is a hopeful sign for future management since strict vegetation associations do not need to be maintained. However, with increased canopy cover from juniper encroachment or the closure of canopy gaps in the lodgepole and ponderosa pine forests, litter levels will increase, and *A. peckii* abundance is likely to decline.

REFERENCES

Agren, J. 1996. Population size, pollinator limitation, and seed set in the self-incompatible herb Lythrum salicaria. *Ecology* 77: 1779-1790.

Aizen, M. A., and L. D. Harder. 2007. Expanding the Limits of the Pollen-Limitation Concept: Effects of Pollen Quantity and Quality. *Ecology* 88: 271.

Amsberry, K., and R. J. Meinke. 2003. Life history and conservation status of *Astragalus peckii* Piper (Fabaceae). Native plant conservation program, Oregon Department of Agriculture.

Angert, A. L. 2006. Demography of central and marginal populations of monkeyflowers (Mimulus cardinalis and M. lewisii). *Ecology* 87: 2014-25.

Ashman, T. L., T. M. Knight, J. A. Steets, P. Amarasekare, M. Burd, D. R. Campbell, M. R. Dudash, M. O. Johnston, S. J. Mazer, and R. J. Mitchell. 2004. Pollen limitation of plant reproduction: Ecological and evolutionary causes and consequences. *Ecology* 85: 2408-2421.

Barneby, R. C. 1964. Atlas of North American *Astragalus*. Memoirs of the New York Botanical Garden 13: 1–1188.

Bates, J.D., R.F. Miller, and T. Svejcar. 1998. Understory patterns in cut western juniper (Juniperus occidentalis spp. occidentalis Hook.) woodlands. *Great Basin Naturalist* 58: 363-374.

Bell, J.M., J.D. Karron, and R.J. Mitchell. 2005. Interspecific competition for pollination lowers seed production and outcrossing in Mimulus ringens. *Ecology* 86: 762-771.

Belnap, J. 2003. The World at Your Feet: Desert Biological Soil Crusts. *Frontiers in Ecology and the Environment* 1: 181-189.

Bernhardt, C. E., R. J. Mitchell, and H. J. Michaels. 2008. Effects of Population Size and Density on Pollinator Visitation, Pollinator Behavior, and Pollen Tube Abundance in Lupinus perennis. *International Journal of Plant Sciences* 169: 944-953.

Bevill, R. L., and S. M. Louda. 1999. Comparisons of Related Rare and Common Species in the Study of Plant Rarity. *Conservation Biology* 13: 493-498.

Bevill, R. L., S. M. Louda, and L. M. Stanforth. 1999. Protection from Natural Enemies in Managing Rare Plant Species. *Conservation Biology* 13: 1323-1331.

Bond, W. J. 1994. Do Mutualisms Matter? Assessing the Impact of Pollinator and Disperser Disruption on Plant Extinction. *Philosophical Transactions of the Royal Society B: Biological Sciences* 344: 83-90.

Breedlove, D. E., and P. R. Ehrlich. 1968. Plant-Herbivore Coevolution: Lupines and Lycaenids. *Science* 162: 671-672.

Burd, M. 1995. Ovule packaging in stochastic pollination and fertilization environments. *Evolution* 49: 100-109.

Carlson, G.T. 1979. Soil resource inventory. Report for the Winema National Forest, US Forest Service.

Caswell, H. 2001. Matrix Population Models: Construction, Analysis, and Interpretation. *Sunderland, Massachusetts: Sinauer*.

Crawley, M. J. 1992. Seed predators and plant population dynamics. In *Seeds: the ecology of regeneration in plant communities*, 167-182. Oxon, UK: C.A.B. International.

Crawley, M.J. 1989. Insect herbivores and plant population dynamics. *Annual Review of Entomology* 34: 531-562.

Crone, E. E., and P. Lesica. 2006. Pollen and water limitation in *Astragalus* scaphoides, a plant that flowers in alternate years. *Oecologia* 150: 40-49.

Dahlgren, J. P., and J. Ehrlen. 2009. Linking environmental variation to population dynamics of a forest herb. *Journal of Ecology* 97: 666-674.

Deines, L., R. Rosentreter, D.J. Eldridge, and M.D. Serpe. 2007. Germination and seedling establishment of two annual grasses on lichen-dominated biological soil crusts. *Plant & Soil* 295: 23-35.

Doak, D. F. 1992. Lifetime impacts of herbivory for a perennial plant. *Ecology* 73: 2086–2099.

Donovan, L.A., J. Mausberg, and J.R. Ehleringer. 1993. Seedling size and survival for Chrysothamnus nauseosus. *Great Basin Naturalist* 53: 237-245.

Dudash, M. R. 1990. Relative Fitness of Selfed and Outcrossed Progeny in a Self-Compatible, Protandrous Species, Sabatia angularis L. (Gentianaceae): A Comparison in Three Environments. *Evolution* 44: 1129-1139.

Dudash, M. R., and C. J. Murren. 2008. The influence of breeding systems and mating systems on conservation genetics and conservation decisions. In *Conservation biology: evolution in action*.

Ehrlen, J. 1995. Demography of the perennial herb Lathyrus vernus. II. Herbivory and population dynamics. *Journal of Ecology* 83: 297-308.

Elliott, S. E., and R. E. Irwin. 2009. Effects of flowering plant density on pollinator visitation, pollen receipt, and seed production in Delphinium barbeyi (Ranunculaceae). *American Journal of Botany* 96: 912-919.

Ellstrand, N.C., and D.R. Elam. 1993. Population Genetic Consequences of Small Population Size: Implications for Plant Conservation. *Annual Review of Ecology Evolution and Systematics* 24: 217-242.

Endels, P., H. Jacquemyn, R. Brys, and M. Hermy. 2005. Rapid response to habitat restoration by the perennial Primula veris as revealed by demographic monitoring. *Plant Ecology* 176: 143-156.

Engler, R., A. Guisan, and L. Rechsteiner. 2004. An improved approach for predicting the distribution of rare and endangered species from occurrence and pseudo-absence data. *Journal of Applied Ecology* 41: 263-274.

Escudero, A., I. Martínez, A. de la Cruz, M.A.G. Otálora, and F.T. Maestre. 2007. Soil lichens have species-specific effects on the seedling emergence of three gypsophile plant species. *Journal of Arid Environments* 70: 18-28.

Evans, E. W., C. C. Smith, and R. P. Gendron. 1989. Timing of reproduction in a prairie legume: seasonal impacts of insects consuming flowers and seeds. *Oecologia* 78: 220-230.

Evans, M., K. Holsinger, and E. Menges. 2008. Modeling the effect of fire on the demography of Dicerandra frutescens ssp. frutescens (Lamiaceae), an endangered plant endemic to Florida scrub. *Population Ecology* 50: 53-62.

Facelli, J.M., and S.T. Pickett. 1991. Plant litter: its dynamics and effects on plant community structure. *The Botanical Review* 57: 1-32.

Franzén, M., and M. Larsson. 2009. Seed set differs in relation to pollen and nectar foraging flower visitors in an insect-pollinated herb. *Nordic Journal of Botany* 27: 274-283.

Freville, H., B. Colas, M. Riba, H. Caswell, A. Mignot, E. Imbert, and I. Olivieri. 2004. Spatial and Temporal Demographic Variability in the Endemic Plant Species Centaurea corymbosa (Asteraceae). *Ecology* 85: 694-703.

Galloni, M., L. Podda, D. Vivarelli, and G. Cristofolini. 2007. Pollen presentation, pollen-ovule ratios, and other reproductive traits in Mediterranean Legumes (Fam. Fabaceae - Subfam. Faboideae). *Plant Systematics and Evolution* 266: 147-164.

Garcia, M. B., F. X. Pico, and J. Ehrlen. 2008. Life span correlates with population dynamics in perennial herbaceous plants. *American Journal of Botany* 95: 258-262.

Gaston, K.J., and W.E. Kunin. 1997. Rare-common differences: an overview. In *The biology of rarity*. Springer.

Gisler, S., and R. Meinke. 2001. Reproductive ecology, seed banking, and cultivation of five at-risk legume species in Oregon. Oregon Department of Agriculture Plant conservation biology program.

Green, T.W., and G.E. Bohart. 1975. The Pollination Ecology of *Astragalus* cibarius and *Astragalus* utahensis (Leguminosae). *American Journal of Botany* 62: 379-386.

Groom, M. J. . 2001. Consequences of subpopulation isolation for pollination, herbivory, and population growth in Clarkia concinna concinna (Onagraceae). *Biological Conservation* 100: 55-63.

Halpern, S. L, and N. Underwood. 2006. Approaches for testing herbivore effects on plant population dynamics. *Journal of Applied Ecology* 43: 922–929.

Hamrick, J. L., and J.M. Lee. 1987. Effect of Soil Surface Topography and Litter Cover on the Germination, Survival, and Growth of Musk Thistle (Carduus nutans). *American Journal of Botany* 74: 451-457.

Harder, L. D., and S. C. H. Barrett. 1995. Mating cost of large floral displays in hermaphrodite plants. *Nature* 373: 512-515.

Hawkes, C.V. 2004. Effects of biological soil crusts on seed germination of four endangered herbs in a xeric Florida shrubland during drought. *Plant Ecology* 170: 121-134.

Hegland, J., and O. Totland. 2008. Is the magnitude of pollen limitation in a plant community affected by pollinator visitation and plant species specialisation levels? *Oikos* 117: 883–891.

Heslop-Harrison, J., and Y. Heslop-Harrison. 1983. Pollen-Stigma Interaction in the Leguminosae: the Organization of the Stigma in Trifolium pratense L. *Annals of Botany* 51: 571-583.

Kalisz, S., and M. A. McPeek. 1993. Extinction dynamics, population growth and seed banks. *Oecologia* 95: 314-320.

Karron, J. D., K. G. Holmquist, R. J. Flanagan, and R. J. Mitchell. 2009. Pollinator visitation patterns strongly influence among-flower variation in selfing rate. *Annals of Botany* 103: 1379-1383.

Kauffman, M.J., and J.L. Maron. 2006. Consumers limit the abundance and dynamics of a perennial shrub with a seed bank. *The American naturalist* 168: 454-470.

Kaye, T. 1999. From flowering to dispersal: reproductive ecology of an endemic plant, *Astragalus* australis var. olympicus (Fabaceae). *American Journal of Botany* 86: 1248-1256.

Kearns, C. A., D. W. Inouye, and N. M. Waser. 1998. Endangered mutualisms : The conservation of plant-pollinator interactions. *Annual Review of Ecology and Systematics* 29: 83-112.

Keller, L.F., and D.M. Waller. 2002. Inbreeding effects in wild populations. *Trends in Ecology & Evolution* 17: 230-241.

Kephart, S.R., and C. Paladino. 1997. Demographic change and microhabitat variability in a grassland endemic, Silene douglasii var. oraria (Caryophyllaceae). *American Journal of Botany* 84: 179-189.

Knapp, P.A., and P.T. Soulé. 1998. Recent Juniperus occidentalis (Western Juniper) expansion on a protected site in central Oregon. *Global Change Biology* 4: 347-357.

Knight, T. M., J. A. Steets, and T. L. Ashman. 2006. A quantitative synthesis of pollen supplementation experiments highlights the contribution of resource reallocation to estimates of pollen limitation. *American Journal of Botany* 93: 271-277.

Kolb, A., R. Leimu, and J. Ehrlén. 2007. Environmental context influences the outcome of a plant-seed predator interaction. *Oikos* 116: 864-872.

de Kroon, H., A. Plaisier, J. van Groenendael, and H. Caswell. 1986. Elasticity: The Relative Contribution of Demographic Parameters to Population Growth Rate. *Ecology* 67: 1427-1431.

Kruckeberg, A.R., and D. Rabinowitz. 1985. Biological Aspects of Endemism in Higher Plants. *Annual Review of Ecology and Systematics* 16: 447-479.

Krupnick, G. A., A. E. Weis, and D. R. Campbell. 1999. The consequences of floral herbivory for pollinator service to Isomeris arborea. *Ecology* 80: 125–134.

Kruskal, J.B. 1964. Nonmetric multidimensional scaling: a numerical method. *Psychometrika* 29: 115-129.

Kunin, W. E. 1997. Population Size and Density Effects in Pollination: Pollinator Foraging and Plant Reproductive Success in Experimental Arrays of Brassica Kaber. *The Journal of Ecology* 85: 225-234.

Lavergne, S., J.D. Thompson, E. Garnier, and M. Debussche. 2004. The biology and ecology of narrow endemic and widespread plants: a comparative study of trait variation in 20 congeneric pairs. *Oikos* 107: 505-518.

Lee, T. D., and F. A. Bazzaz. 1986. Maternal regulation of fecundity: non-random ovule abortion in Cassia fasciculata Michx. *Oecologia* 68: 459-465.

Leimu, R., and K. Lehtilä. 2006. Effects of two types of herbivores on the population dynamics of a perennial herb. *Basic and Applied Ecology* 7: 224-235.

Lesica, P. 1995. Demography of *Astragalus* scaphoides and effects of herbivory on population growth. *Great Basin Naturalist* 55: 142-150.

---. 1999. Effects of fire on the demography of the endangered, geophytic herb Silene spaldingii (Caryophyllaceae). *American Journal of Botany* 86: 996-1002.

Lesica, P., R. Yurkewycz, and E.E. Crone. 2006. Rare plants are common where you find them. *American Journal of Botany* 93: 454-459.

Liu, H., and S. Koptur. 2003. Breeding system and pollination of a narrowly endemic herb of the Lower Florida Keys: impacts of the urban-wildland interface. *American Journal of Botany* 90: 1180-1187.

Louda, S. M. 1982. Distribution ecology: Variation in plant recruitment over a gradient in relation to insect seed predation. *Ecological Monographs* 52: 25-41.

Louda, S. M., and M. A. Potvin. 1995. Effect of Inflorescence-Feeding Insects on the Demography and Lifetime of a Native Plant. *Ecology* 76: 229-245.

Mabberley, D.J. 1997. *The Plant-Book, A Portable Dictionary of the Vascular Plants, 2nd edition.* Cambridge: Cambridge University Press.

Maron, J. L., and S. N. Gardner. 2000. Consumer Pressure, Seed versus Safe-Site Limitation, and Plant Population Dynamics. *Oecologia* 124: 260-269.

Maschinski, J., J.E. Baggs, P.F. Quintana-Ascencio, and E.S. Menges. 2006. Using Population Viability Analysis to Predict the Effects of Climate Change on the Extinction Risk of an Endangered Limestone Endemic Shrub, Arizona Cliffrose. *Conservation Biology* 20: 218-228.

Maschinski, J., R. Frye, and S. Rutman. 1997. Demography and Population Viability of an Endangered Plant Species before and after Protection from Trampling. *Conservation Biology* 11: 990-999.

Mather, P.M. 1976. *Computational methods of multivariate analysis in physical geography.* J. Wiley & Sons, London.

Matthies, D., I. Bräuer, W. Maibom, and T. Tscharntke. 2004. Population size and the risk of local extinction: empirical evidence from rare plants. *Oikos* 105: 481-488.

McCune, B. 2006. Non-parametric habitat models with automatic interactions. *Journal of Vegetation Science* 17: 819-830.

McCune, B., and M.J. Mefford. 2009a. PC-ORD, Multivariate analysis of ecological data, version 6.91 beta. *MjM Software, Gleneden Beah, Oregon, USA*.

---. 2009b. HyperNiche, Nonparametric multiplicative habitat modeling, Version 2.07. *MjM Software, Gleneden Beah, Oregon, USA*.

Menges, E. S. 1991. The application of minimum viable population theory to plants. In *Genetics and conservation of rare plants*, 45–61. Oxford: Oxford University Press, Inc.

Menges, E. S., and R. W. Dolan. 1998. Demographic Viability of Populations of Silene regia in Midwestern Prairies: Relationships with Fire Management, Genetic Variation, Geographic Location, Population Size and Isolation. *The Journal of Ecology* 86: 63-78.

Menges, E. S., and J. Kimmich. 1996. Microhabitat and Time-Since-Fire: Effects on Demography of Eryngium cuneifolium (Apiaceae), A Florida Scrub Endemic Plant. *American Journal of Botany* 83: 185-191.

Miller, R.F., and J.A. Rose. 1999. Fire History and Western Juniper Encroachment in Sagebrush Steppe. *Journal of Range Management* 52: 550-559.

Miller, R.F., T.J. Svejcar, and J.A. Rose. 2000. Impacts of Western Juniper on Plant Community Composition and Structure. *Journal of Range Management* 53: 574-585.

Miller, T.E.X., S.M. Louda, K.A. Rose, and J.O. Eckberg. 2009. Impacts of insect herbivory on cactus population dynamics: experimental demography across an environmental gradient. *Ecological Monographs* 79: 155-172.

Morris, W.F., and D.F. Doak. 2002. *Quantitative Conservation Biology: Theory and practice of population viability analysis*. Sunderland, MA: Sinauer Associates Inc.

Nair, R. M., I. S. Dundas, M. Wallwork, D. C. Verlin, L. Waterhouse, and K. Dowling. 2004. Breeding System in a Population of Trigonella balansae (Leguminosae). *Annals of Botany* 94: 883-888.

Navarro-Cano, J.A., G.G. Barberá, and V.M. Castillo. 2010. Pine Litter from Afforestations Hinders the Establishment of Endemic Plants in Semiarid Scrubby Habitats of Natura 2000 Network. *Restoration Ecology* 18: 165-169.

ORNHIC (Oregon Natural Heritage Information Center). 2003. Oregon Natural Heritage Information Center Database. Oregon Natural Heritage Information Center, Portland, Oregon.

Piper, C. V. 1924. New flowering plants of the Pacific coast. *Proceedings of the Biological Society of Washington* 37: 91-96.

PRISM Climate Group. *Oregon State University*. http://www.prismclimate.org, accessed February 11, 2009.

R Development Core Team. *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. http://www.R-project.org.

Rabinowitz, D. 1981. Seven forms of rarity. pp 205-217. In *The biology aspects of rare plant conservation. H. Synge, ed*. Wiley, Chichester, United Kingdom.

Ramsey, K.J. 1990. Influence of leachates from western juniper slash on three native grasses. Thesis/Dissertation, Oregon State University. http://ir.library.oregonstate.edu/jspui/handle/1957/11881.

Raxworthy, C.J., E. Martinez-Meyer, N. Horning, R.A. Nussbaum, G.E. Schneider, M.A. Ortega-Huerta, and A. Townsend Peterson. 2003. Predicting distributions of known and unknown reptile species in Madagascar. *Nature* 426: 837-841.

Rose, J., and R. Miller. 1995. Historic expansion of Juniperus occidentalis (Western juniper) in southeastern Oregon. *Great basin naturalist* 55: 37-45.

Schemske, D. W., B. C. Husband, M. H. Ruckelshaus, C. Goodwillie, I. M. Parker, and J. G.Bishop. 1994. Evaluating Approaches to the Conservation of Rare and Endangered Plants. *Ecology* 75: 584-606.

Serpe, M., J. Orm, T. Barkes, and R. Rosentreter. 2006. Germination and seed water status of four grasses on moss-dominated biological soil crusts from arid lands. *Plant Ecology* 185: 163-178.

Shaffer, M. L. 1981. Minimum Population Sizes for Species Conservation. *BioScience* 31: 131-134.

Sih, A., and M. Baltus. 1987. Patch Size, Pollinator Behavior, and Pollinator Limitation in Catnip. *Ecology* 68: 1679-1690.

Silvertown, J., M. Franco, I. Pisanty, and A. Mendoza. 1993. Comparative Plant Demography--Relative Importance of Life-Cycle Components to the Finite Rate of Increase in Woody and Herbaceous Perennials. *Journal of Ecology* 81: 465-476.

Stephenson, A. G. 1981. Flower and fruit abortion: proximate causes and ultimate functions. *Annual Review of Ecology and Systematics* 12: 253-279.

Stohlgren, T.J., D.A. Guenther, P.H. Evangelista, and N. Alley. 2005. Patterns of plant species richness, rarity, endemism, and uniqueness in an arid landscape. *Ecological Applications* 15: 715-725.

Stubben, C., and B. Milligan. 2007. Estimating and analyzing demographic models using the popbio package in R. *Journal of Statistical Software* 22: 1-23.

Thomas, C.D., A. Cameron, R.E. Green, M. Bakkenes, L.J. Beaumont, Y.C. Collingham, B.F.N. Erasmus, et al. 2004. Extinction risk from climate change. *Nature* 427: 145-148.

Volis, S., S. Mendlinger, and D.S. Bigger. 2004. Demography and role of the seed bank in Mediterranean and desert populations of wild barley. *Basic and Applied Ecology* 5: 53-64.

Waites, A. R., and J. Agren. 2004. Pollinator visitation, stigmatic pollen loads and among-population variation in seed set in Lythrum salicaria. *Journal of Ecology* 92: 512-526.

Ward, M., and S. D. Johnson. 2005. Pollen limitation and demographic structure in small fragmented populations of *Brunsvigia radulosa* (Amaryllidaceae). *Oikos* 108: 253-262.

Weppler, T., and J. Stöcklin. 2006. Does pre-dispersal seed predation limit reproduction and population growth in the alpine clonal plant Geum reptans? *Plant Ecology* 187: 277-287.

West, N. E., K. H. Rea, and R. O. Harniss. 1979. Plant Demographic Studies in Sagebrush-Grass Communities of Southeastern Idaho. *Ecology* 60: 376-388.

Xiong, S., and C. Nilsson. 1999. The effects of plant litter on vegetation: a meta-analysis. *Journal of Ecology* 87: 984-994.

Yager, L.Y., and F.E. Smeins. 1999. Ashe Juniper (Juniperus ashei: Cupressaceae) Canopy and Litter Effects on Understory Vegetation in a Juniper-Oak Savanna. *The Southwestern Naturalist* 44: 6-16.

Yates, C. J., P. G. Ladd, D. J. Coates, and S. McArthur. 2007. Hierarchies of cause: understanding rarity in an endemic shrub Verticordia staminosa (Myrtaceae) with a highly restricted distribution. *Australian Journal of Botany* 55: 194-205.

Young, G., and J. Bush. 2009. Assessment of the Allelopathic Potential of Juniperus ashei on Germination and Growth of Bouteloua curtipendula. *Journal of Chemical Ecology* 35: 74-80.

Young, H. J., and T. P. Young. 1992. Alternative Outcomes of Natural and Experimental High Pollen Loads. *Ecology* 73: 639-647.

Youngberg, C.T., and C.T. Dyrness. 1964. Some physical and chemical properties of pumice soils in Oregon. *Soil Science* 97: 391-399.

APPENDICES

Appendix 2.1. Matrix transitions for *Astragalus peckii* at two sites from 2006-2009. The top two rows of each matrix are fecundity transitions to the seed bank (row 1) and seedling establishment (row 2). The bottom three rows are growth, stasis, or retrogression transitions. Stages are abbreviated as follows: seed bank (SD), seedling (SL), small (S), medium (M), and large (L) plants.

Bull Flat

2006-2007

	SD	SL	S	M	L		SD	SL	S	M	L
SD	0.44	0	0.25	5.51	34.12	SD	0.53	0	0.04	3.89	123.86
SL	0.02	0	0.03	0.65	3.93	SL	0.03	0	0.00	0.31	9.96
S	0	0.12	0.13	0.04	0.01	S	0	0.11	0.21	0.02	0.02
M	0	0.02	0.22	0.15	0	M	0	0.01	0.28	0.47	0.10
L	0	0.01	0.20	0.40	0.43	L	0	0	0.02	0.27	0.52

Chiloquin

2007-2008

	SD	SL	S	M	L		SD	SL	S	M	L
SD	0.44	0	0.05	11.68	45.39	SD	0.53	0	0	15.72	48.58
SL	0.02	0	0.01	0.77	2.96	SL	0.03	0	0	2.66	20.00
S	0	0.12	0.04	0	0	S	0	0.10	0.16	0.01	0.02
M	0	0.08	0.11	0.02	0.01	M	0	0.03	0.39	0.31	0.08
L	0	0	0.26	0.39	0.27	L	0	0	0.01	0.56	0.74

2008-2009

	SD	SL	S	M	L		SD	SL	S	M	L
SD	0.44	0	0.16	11.86	117.11	SD	0.53	0	0	7.05	143.22
SL	0.02	0	0.01	0.60	2.63	SL	0.03	0	0	0.31	6.23
S	0	0.07	0.09	0	0.02	S	0	0.09	0.21	0.04	0.03
M	0	0.10	0.19	0.13	0.02	M	0	0.07	0.40	0.54	0.05
L	0	0.01	0.26	0.56	0.60	L	0	0.00	0	0.30	0.69

Pooled

	SD	SL	S	M	L		SD	SL	S	M	L
SD	0.44	0	0.19	8.33	59.64	SD	0.53	0	0.02	7.37	114.27
SL	0.02	0	0.00	0.67	3.17	SL	0.03	0	0.00	1.09	12.06
S	0	0.10	0.10	0.02	0.01	S	0	0.10	0.19	0.02	0.02
M	0	0.07	0.19	0.11	0.01	M	0	0.05	0.35	0.44	0.07
L	0	0.01	0.23	0.43	0.40	L	0	0.00	0.01	0.38	0.64

Appendix 2.2. Elasticities for *Astragalus peckii* at two sites from 2006-2009. The top two rows of each matrix are fecundity transitions to the seed bank (row 1) and seedling establishment (row 2). The bottom three rows are growth, stasis, or retrogression transitions. Stage are abbreviated as follows: seed bank (SD), seedling (SL), small (S), medium (M), and large (L) plants.

Bull Flat

2006-2007

	SD	SL	S	M	L
SD	0.06	0	0.00	0.00	0.06
SL	0.06	0	0.00	0.01	0.14
S	0	0.15	0.02	0.00	0.00
M	0	0.04	0.06	0.02	0
L	0	0.03	0.09	0.08	0.18

2007-2008

	SD	SL	S	M	L
SD	0.11	0	0.00	0.02	0.09
SL	0.10	0	0.00	0.02	0.11
S	0	0.11	0.00	0	0
M	0	0.13	0.02	0.00	0.00
L	0	0	0.09	0.11	0.09

2008-2009

	SD	SL	S	M	L
SD	0.07	0	0.00	0.01	0.11
SL	0.11	0	0.00	0.01	0.08
S	0	0.05	0.00	0	0.00
M	0	0.13	0.02	0.02	0.00
L	0	0.02	0.04	0.13	0.21

Pooled

	SD	SL	S	M	L
SD	0.07	0	0.00	0.01	0.08
SL	0.09	0	0.00	0.01	0.12
S	0	0.10	0.01	0.00	0.00
M	0	0.11	0.03	0.02	0.00
L	0	0.02	0.07	0.12	0.14

Chiloquin

2006-2007

	SD	SL	S	M	L
SD	0.03	0.00	0.00	0.00	0.02
SL	0.02	0.00	0.00	0.01	0.12
S	0.00	0.11	0.03	0.00	0.00
M	0.00	0.03	0.11	0.15	0.02
L	0.00	0.00	0.01	0.15	0.18

2007-2008

	SD	SL	S	M	L
SD	0.00	0.00	0.00	0.00	0.00
SL	0.00	0.00	0.00	0.02	0.17
S	0.00	0.10	0.01	0.00	0.00
M	0.00	0.09	0.10	0.06	0.01
L	0.00	0.00	0.00	0.18	0.22

2008-2009

	SD	SL	S	M	L
SD	0.02	0.00	0.00	0.00	0.03
SL	0.03	0.00	0.00	0.01	0.12
S	0.00	0.05	0.01	0.00	0.00
M	0.00	0.10	0.06	0.15	0.01
L	0.00	0.00	0.00	0.15	0.24

Pooled

	SD	SL	S	M	L
SD	0.01	0	0.00	0.00	0.01
SL	0.01	0	0.00	0.02	0.15
S	0	0.08	0.02	0.00	0.00
M	0	0.10	0.08	0.11	0.01
L	0	0.00	0.00	0.17	0.21

Appendix 4.1. Percent cover, averaged by site, for each species found in community data plots. In total, 86 species were recorded. Eighty-five were assembled into data matrices for use in analyses (*A. peckii* was removed as a predictor). Rare species (defined as occurring in less than 2% of the plots or at only one site) were deleted from the data matrices prior to analysis, leaving 40 species for the site-level analysis and 44 for the plot-level analysis. Nomenclature follows the USDA PLANTS Database.

Species	Site (number of 1 m^2 plots sample)						
	BF (50)	IMR (50)	CM-T (50)	CM (50)	CM-S (30)	CQ (50)	CQ-P (50)
Asteraceae							
Achillea millefolium	0.25	-	-	-	-	0.36	0.04
Antennaria dimorpha	0.02	-	-	-	-	0.10	-
Antennaria microphylla	0.05	-	-	0.01	0.88	0.12	-
Artemisia tridentata	10.69	4.68	-	-	-	13.19	-
Aster sp.	-	-	-	-	-	-	0.13
Blepharipappus scaber	-	0.16	-	-	-	0.15	-
Chaenactis douglasii	-	0.05	-	-	-	-	-
Chrysothamnus Viscidiflorus	8.55	1.91	-	-	-	0.76	3.87
Cirsium scariosum	-	-	-	-	0.27	0.01	-
Ericameria bloomeri	-	-	5.06	5.45	-	-	-
Ericameria nauseosa	0.01	-	-	-	-	-	-
Eriophyllum lanatum	0.02	0.35	-	-	-	0.05	6.11
Hemizonella minima	-	0.02	-	-	0.06	0.21	1.28
Machaeranthera Canescens	-	-	0.02	0.18	-	-	0.03
Packera cana	0.1	-	-	-	-	-	-
Senecio hydrophiloides	-	-	-	-	0.40	-	-
Taraxacum officinale	-	-	-	-	0.17	-	-
Townsendia florifer	0.08	-	-	-	-	-	-
Tragopogon dubius	-	-	-	-	-	0.01	-
unknown Asteraceae	-	-	-	-	-	-	0.17
Boraginaceae							
Cryptantha simulans	-	-	-	-	0.07	-	0.28
Cryptantha torreyana	-	-	-	-	-	<0.01	-
Brassicaceae							
Alyssum desertorum	-	0.34	-	-	-	-	-
Arabis holboellii	-	-	-	-	-	0.02	<0.01
Erysimum capitatum	0.07	-	-	-	-	-	-

Appendix 4.1 (Continued)

Species	Site (number of 1 m² plots)						
	BF (50)	IMR (50)	CM-T (50)	CM (50)	CM-S (30)	CQ (50)	CQ-P (50)
Caryophyllaceae							
Arenaria congesta	-	-	-	-	-	0.02	-
Cupressaceae							
Juniperus occidentalis	0.12	12.76	-	-	-	1.30	-
Cyperaceae							
Carex rossii	0.4	-	2.17	0.34	-	0.95	1.60
Carex sp.	-	-	-	-	35.53	-	-
Equistaceae							
Equisetum sp.	-	-	-	-	-	0.06	-
Fabaceae							
Astragalus peckii	0.26	0.17	0.02	1.01	-	1.19	0.23
Astragalus purshii	0.05	-	-	-	-	-	-
Lotus sp.	-	-	-	-	0.01	-	-
Lupinus lepidus	0.35	<0.01	-	0.02	-	0.35	-
Trifolium eriocephalum	-	-	-	-	0.01	-	-
Hydrophyllaceae							
Phacelia hastata	-	-	-	-	0.03	-	-
Juncaceae							
Juncus sp.	-	-	-	-	11.79	-	-
Liliaceae							
Leucocrinum montanum	-	-	-	-	-	0.22	-
Linaceae							
Linum perenne	0.23	-	-	-	-	0.16	0.28
Malvaceae							
Sidalcea oregana	-	-	-	-	0.45	-	0.21
Onagraceae							
Epilobium brachycarpum	-	0.01	-	-	-	1.28	0.59
Gayophytum diffusum	-	-	-	-	-	0.02	-
Gayophytum ramosissimum	0.2	0.01	0.01	-	0.02	0.34	0.02
Orobanchaceae							
Orobanche corymbosa	-	-	-	-	-	0.01	-
Pinaceae							
Pinus contorta	-	-	28.10	18.84	2.00	-	-
Pinus ponderosa	-	-	-	-	-	3.75	4.18

Appendix 4.1 (Continued)

	Site (number of 1 m^2 plots)						
Species	BF (50)	IMR (50)	CM-T (50)	CM (50)	CM-S (30)	CQ (50)	CQ-P (50)
Poaceae							
Achnatherum hymenoides	-	0.1	-	-	-	-	-
Achnatherum occidentale	1.27	1.25	0.90	1.81	5.90	0.80	1.54
Agrostis scabra	-	-	-	-	0.02	-	-
Aira sp.	-	0.06	-	-	-	-	-
Bromus sp.	-	-	-	-	0.50	-	-
Bromus tectorum	-	5.48	-	-	-	-	0.43
Elymus elymoides	0.72	1.31	0.35	0.50	1.23	0.31	1.73
Festuca idahoensis	23.12	1.08	0.36	-	-	19.30	0.60
Muhlenbergia sp.	-	-	-	-	-	-	0.01
Muhlenbergia filiformis	-	-	-	-	0.15	-	-
Poa sp.	-	-	-	-	2.07	-	3.14
Poa secunda	-	0.65	-	-	2.29	1.07	-
Thinopyrum intermedium	-	0.04	-	-	-	6.15	-
Vulpia microstachys	-	0.01	-	-	-	-	-
Vulpia myuros	-	0.29	-	-	-	-	-
unknown Poaceae 1	-	-	-	-	0.20	-	-
unknown Poaceae 2	-	-	-	-	-	0.03	-
unknown Poaceae 3	-	-	-	-	0.23	-	-
unknown Poaceae 4	-	-	-	-	-	-	0.12
Polemoniaceae							
Collomia grandiflora	-	-	-	-	-	0.33	0.14
Eriastrum sparsiflorum	-	0.04	-	-	-	-	-
Leptosiphon harknessii	-	-	-	-	0.41	-	0.03
Leptosiphon sepentrionalis	-	<0.01	-	-	-	-	-
Linanthus sp.	-	-	-	-	-	-	1.42
Linanthus pungens	1.22	0.59	-	-	-	0.24	-
Microsteris gracilis	-	0.32	-	-	<0.01	2.18	-
Navarretia capillaris	-	-	-	-	-	-	0.07
Polygonaceae							
Eriogonum umbellatum	1.36	0.02	-	0.37	-	0.58	3.12
Eriogonum vimineum	-	0.12	-	-	0.03	-	-
Polygonum sp.	-	-	-	-	-	<0.01	-
Portulaceae							
Cistanthe umbellata	0.01	-	-	0.12	-	0.01	-

Appendix 4.1 (Continued)

Species	Site (number of 1 m^2 plots)						
	BF (50)	IMR (50)	CM-T (50)	CM (50)	CM-S (30)	CQ (50)	CQ-P (50)
Rosaceae							
Fragaria sp.	-	-	-	-	-	-	0.02
Horkelia fusca	-	-	-	-	-	0.22	0.03
Purshia tridentata	-	-	24.64	5.12	-	5.12	26.06
Scrophulariaceae							
Castilleja pilosa	-	-	-	-	-	1.15	-
Collinsia parviflora	0.02	0.03	-	-	-	0.39	-
Penstemmon sp.	-	-	0.02	-	-	-	-
Violaceae							
Viola purpurea	-	-	0.03	0.06	0.23	-	0.01
Unknown							
unknown sp. 1	-	-	-	-	0.44	-	-
unknown sp. 2	0.01	-	-	-	-	-	-
Total number of species	25	27	12	13	27	39	31

Appendix 4.2. Habitat, climate, soil, and elevation data used in the NMS ordinations. Habitat data were recorded in the community data plots and are averaged by site. Climate data were downloaded from the PRISM website and soil data were from analysis of three, combined soil samples per site. See Table 4.2 for variable codes and descriptions

Variable (unit)	Site						
	CM-S	CQ-P	CM-T	BF	IMR	CQ	CM
Habitat (% cover)							
Gravel	6.48	5.71	25.26	7.05	4.05	0.00	36.70
Cobble	0.27	0.00	0.00	0.04	0.00	0.08	0.07
Boulder	1.13	0.00	0.00	0.00	0.00	0.00	0.00
Gram	59.86	8.92	3.81	24.79	10.27	28.78	2.63
Forb	2.94	11.76	0.14	3.07	1.52	9.40	1.75
Shrub	0.00	32.47	28.43	21.30	7.19	19.23	10.22
Over	2.00	4.17	29.32	0.00	12.76	5.00	18.80
BG	19.00	32.80	11.40	32.18	57.62	27.02	38.92
Litter	64.83	45.78	57.54	8.82	25.42	31.20	16.74
B/L	3.18	0.00	0.54	8.56	3.86	3.28	0.00
Wood	0.03	0.40	3.48	8.22	3.34	2.50	0.60
Climate							
Avg prp (mm)	631.0	445.8	654.1	356.5	311.21	477.3	654.1
Ann prp (mm)	778.2	500.1	643.5	243.1	227.21	612.6	523.3
Tmax (ºC)	16.1	17.5	16.5	19.1	19.3	19.6	15.6
Tmin (ºC)	-0.9	0.7	-1.1	2.0	2.1	1.4	-0.5
Soil							
Salts (mmhos/cm)	0.1	0.14	0.06	0.1	0.1	0.1	0.1
OM (%)	1.43	2.14	3.41	1.38	1.3	2.24	0.89
NO3 (lbs/acre)	7	4	7	6	4	1	2
NH4 (lbs/acre)	2	6	10	4	4	4	2
Sulfur (ppm)	2	2	7	3	3	2	6
pH	5.6	6.9	6.3	6.4	6.4	5.9	5.6
P (ppm)	19	28	12	18	11	29	10
K (ppm)	294	348	68	310	285	364	71
Elev (m)	1526	1322	1428	1062	991	1358	1430