

Invasive competitor and native seed predators contribute to rarity of the narrow endemic *Astragalus sinuatus* Piper

JULIE K. COMBS,^{1,5} SARAH H. REICHARD,¹ MARTHA J. GROOM,² DAVID L. WILDERMAN,³ AND PAMELA A. CAMP⁴

¹School of Forest Resources, University of Washington, Seattle, Washington 98195 USA

²Interdisciplinary Arts and Sciences, University of Washington, Bothell, Washington 98011 USA and Department of Biology, University of Washington, Seattle, Washington 98195 USA

³Washington Department of Natural Resources, Natural Areas Program, P.O. Box 47014, Olympia, Washington 98504 USA

⁴U.S. Bureau of Land Management, 915 Walla Walla Avenue, Wenatchee, Washington 98801 USA

Abstract. The conservation of rare plant species hinges on our ability to identify the underlying mechanisms that limit rare plant populations. Theory on rarity suggests that both predispersal seed predation and competition can be important mechanisms influencing abundance and/or distribution of rare plant populations. Yet few studies have tested these interactions, and those that have evaluated each mechanism independently. *Astragalus sinuatus* Piper (Whited's milkvetch) is a narrow endemic plant species restricted to eight populations within a 10-km² area in eastern Washington. We used experimental and observational methods to test the effects of native insect predispersal seed predators and an invasive grass (*Bromus tectorum* L. [cheatgrass]) on seed set and population density of *A. sinuatus*. We quantified per capita seed production and pod predation rates across four sites and among four years. Seed predation rates were high across four sites (66–82%) and all years (65–82%). Experimental reduction of predispersal seed predators significantly increased per capita seed set of *A. sinuatus* (164–345%) at two experimental sites. Concurrently, two seed addition experiments demonstrated the effect of seed loss and presence of *B. tectorum* on seedling recruitment and establishment of *A. sinuatus* over four growing seasons. In the first seed addition experiment, we found no difference in recruitment and establishment between low (40) and high (120) seed addition levels. In the second addition experiment (one level of addition; 40 seeds), we found that recruitment and survivorship increased 200% in plots where *B. tectorum* was removed compared to plots where *B. tectorum* was present. Thus, seed addition had no impact in the presence of *B. tectorum*; conversely, in the absence of *B. tectorum*, seed addition was highly effective at increasing population numbers. Results suggest that, in areas where *B. tectorum* is present, recruitment is site limited, and it is seed limited when *B. tectorum* is absent. We recommend that managers reduce *B. tectorum* in an effort to increase population growth of *A. sinuatus*; in areas where *B. tectorum* is absent, short-term reduction of insect predators should be considered as a strategy to increase population growth of this rare species.

Key words: *Astragalus sinuatus* Piper; *Bromus tectorum* L.; bruchid beetle (*Bruchidae*); *Grapholita imitativa* Heinrich (*Tortricidae*); invasive species; plant competition; predispersal seed predation; rare plant conservation; rare plant management; seed addition; seed weevil (*Curculionidae*); Wenatchee Mountains, Washington, USA.

INTRODUCTION

The conservation of rare plant species hinges on our ability to identify the underlying mechanisms that limit their populations (Kruckeberg and Rabinowitz 1985, Kunin and Gaston 1997). Theory on rarity suggests that both predispersal seed predation and competition are important mechanisms influencing abundance and/or distribution of rare plant populations (Griggs 1940, Drury 1980, Rosenzweig and Lomolino 1997). Yet few studies have tested these hypotheses; and to the best of

our knowledge, no study has reported simultaneous examination of multiple mechanisms in the limitation of a rare plant population. This is surprising considering that researchers (Stebbins 1980, Kruckeberg and Rabinowitz 1985, Fiedler 1986) have suggested that plant rarity is a result of multiple, interacting factors.

In general, seed predation and plant competitive interactions have been widely studied and implicated as major forces structuring plant communities (Whittaker 1965, Harper 1981, Louda et al. 1990, Crawley 1997, Tilman 1997). Much research has been devoted to understanding how predispersal seed predators affect individual plant performance (Wilson and Janzen 1972, Louda 1982a, b, Miller 1996, Ohashi and Yahara 2000, Leimu et al. 2002, Honek and Martinkova

Manuscript received 8 December 2010; accepted 18 March 2011; final version received 27 April 2011. Corresponding Editor: J. Belnap.

⁵ E-mail: jkcombs@u.washington.edu

2005, Vanhoenacker et al. 2009, Kolb and Ehrlén 2010) and population-level performance of common plant species (Louda 1982a, b, Louda and Potvin 1995, Kelly and Dyer 2002, Maron et al. 2002, Lau and Strauss 2005, Rose et al. 2005, Maron and Crone 2006, Kolb et al. 2007). Similarly, much attention has focused on competitive interactions among introduced species and common native plant species (Louda et al. 1990, D'Antonio and Mahall 1991, D'Antonio et al. 1998, Fargione et al. 2003, Humphrey and Schupp 2004, Garcia-Serrano et al. 2007, D'Antonio et al. 2009). Despite the considerable work done in these areas, relatively few studies examine how these interactions impact rare plant populations; thus we have very little predictive power to evaluate the importance of predispersal seed predation and plant competition as contributing factors of plant rarity.

Prior research provides some evidence demonstrating that predispersal seed predators cause significant declines in individual-level rare plant fitness (Hegazy and Eesa 1991, Gisler and Meinke 1997, Kaye 1999, Zimmerman and Reichard 2005). For example, Hegazy and Eesa (1991) documented that predispersal seed predators consumed nearly 95% of seeds from the rare species *Ebenus armitagei*. Similarly, predispersal seed predators damaged >80% of developed ovules in *Astragalus cottonii*, a narrow endemic of the Olympic Mountains (Kaye 1999). While these studies reveal severe seed destruction by seed predators, the next step of asking how high rates of seed loss affect population-level dynamics of rare plant species is seldom taken.

However, there are two studies that we are aware of (Münzbergova 2005, Dangremond et al. 2010) that showed seed predators impact rare plants negatively. For example, Dangremond et al. (2010), using stage-structured, stochastic population models, showed that two out of three study populations of the rare species *Lupinus tidestromii* declined toward extinction under ambient levels of seed consumption. Because studies such as these are sparse, it remains difficult to evaluate the degree to which seed predators limit rare plant populations. In addition, seed predation rates are known to vary in time and space (reviewed in Kolb et al. 2007, Vanhoenacker et al. 2009). If possible, it is important for researchers to examine multiple populations across multiple years to assess the overall degree to which seed predators impact target populations.

Rare species may also be limited due to poor competitive abilities (Griggs 1940, Drury 1980). Alternatively, rare species may have evolved the ability to persist in low density and as a result are, in fact, good competitors (Rabinowitz et al. 1984). More recently, some researchers have experimentally tested the importance of competition for rare plant growth and reproduction (reviewed in Brigham [2003] and Thomson [2005]). Out of the 14 studies reviewed, eight field studies concluded that competition reduced rare-plant fitness, while six showed no effect (Brigham 2003).

Interestingly, Dangremond et al. (2010) showed that apparent competition was an important factor in limiting the population growth rate of *L. tidestromii*. They found that predispersal seed predation by the deer mouse *Peromyscus maniculatus* (also a postdispersal seed predator; see Maron and Simms 2001, Maron et al. 2010), was higher when in close proximity to the invasive grass, *Ammophila arenaria*. Currently, it seems that competition is an important limiting factor for some rare species, but more studies are needed to examine general patterns.

We examined the joint effects of predispersal seed predation by native insects and competition by an invader, *Bromus tectorum* L. (cheatgrass), on the individual and population-level fitness of a narrowly distributed rare species, *Astragalus sinuatus* Piper (Whited's milkvetch). We used both observational and experimental data to ask three questions. (1) Does predispersal seed predation significantly decrease per capita seed production, leading to seed limitation in *A. sinuatus*? (2) Does *B. tectorum* decrease seedling-juvenile recruitment and establishment of *A. sinuatus*? (3) Do seed predation rates and seed set vary across sites and years? Since *A. sinuatus* is a rare species, we examined population-level effects of seed predation and cheatgrass competition using seed augmentation (Harper 1981, Turnbull et al. 2000) and recorded subsequent recruitment and survival over four growing seasons. We quantified plant community composition to determine the dominance of *B. tectorum* in relation to other community members. Overall, the study simultaneously tested competing theories on the importance of herbivory and competition by an introduced species on rare plant performance and survival. The study outcomes have applications for rare species conservation and management.

METHODS

Study sites

All sites were located in the *Artemisia tridentata*-*Pseudoroegneria* shrubsteppe zone in the foothills of the Wenatchee Mountains, Chelan County, Washington, USA. The data were collected at four sites over five growing seasons (2003–2007). Primary study sites included Colockum Creek (CC) and Upper Dry Gulch (UDG); secondary sites were Lone Fir Draw (LFD) and Mid-fork Dry Gulch (MDG). Colockum Creek is managed by the U.S. Bureau of Land Management, and it was designated as an Area of Critical Environmental Concern in 1985 to protect the large population of *Astragalus sinuatus* Piper. Upper Dry Gulch is managed by the Department of Natural Resources (DNR), and it was designated as a Natural Area Preserve in 1989 to conserve the largest known population of *A. sinuatus*, containing >50% of all individuals. Grazing has not been allowed at the CC and UDG sites since 1985 and 1990, respectively. In contrast, the MDG population, which occurs on private and DNR

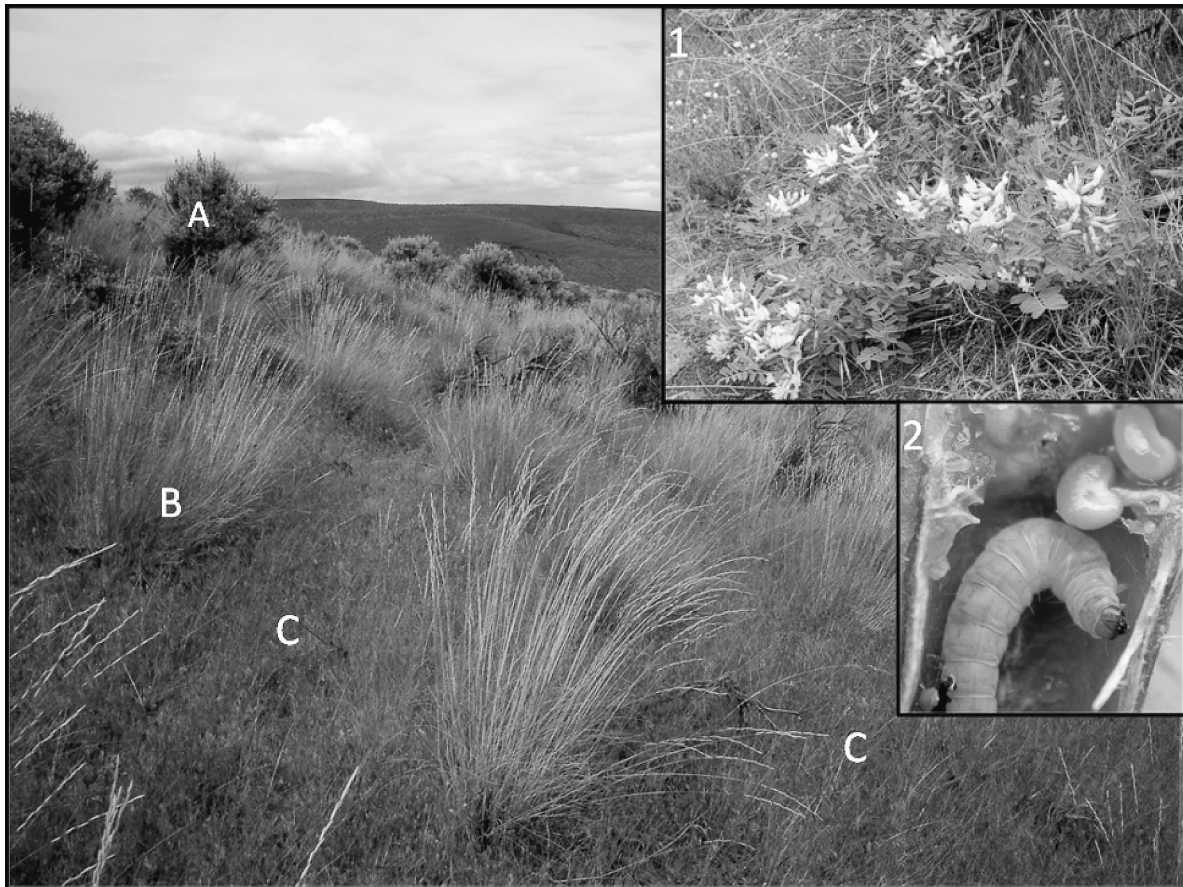


FIG. 1. Sagebrush steppe community where populations of White's milkvetch, *Astragalus sinuatus* Piper (inset 1) occur at Upper Dry Gulch in the foothills of the Wenatchee Mountains, Chelan County, Washington, USA. Dominant shrub and grasses are (A) tall sagebrush (*Artemisia tridentata* Nutt.), (B) blue-crested wheatgrass (*Pseudoroegneria spicata* Pursh), and (C) cheatgrass (*Bromus tectorum* L.). *B. tectorum* heavily invades the area between and under shrubs at Upper Dry Gulch. Inset 2 shows a predispersal seed predator, *Grapholita imitativa* Heinrich (Tortricidae) consuming developing seeds inside an *A. sinuatus* pod. Photo credits: J. K. Combs.

land, and the LFD population, which occurs on DNR property, are currently grazed by cattle at low intensities.

Study species

A. sinuatus (Fig. 1; Inset 1) is narrowly restricted to 10 km² in the Wenatchee foothills and is listed in the Federal Register as a Species of Concern (58 FR 51 144 51 190). The eight known populations range in density from five to an estimated 10000 individuals (J. K. Combs, D. L. Wilderman, and P. A. Camp, *unpublished data*). Population densities at our research sites ranged from ~1200 to 10 000 individuals. *A. sinuatus* is an iteroparous, herbaceous perennial with a woody taproot. It mainly occurs on southwest- and southeast-facing slopes, and it is a relatively long-lived species, documented to live up to 10 years (D. Wilderman, *unpublished data*). Leaf emergence of *A. sinuatus* occurs in early to mid-March, and buds appear in early April. Peak anthesis occurs in late April through May. The fruits (legumes) form in mid-April. They are referred to as pods hereafter. Mature pods develop in June to early

July, and plants begin to senesce in mid-to-late July (J. K. Combs, *personal observation*). Each *A. sinuatus* produces on average 8–16 flowers per raceme and 24–30 ovules per pod (Barneby 1964; J. K. Combs, *unpublished data*). *A. sinuatus* is a source of nectar and pollen for >25 bee species in the genera *Bombus*, *Andrena*, *Anthophora*, *Habropoda*, *Apis*, *Eucera*, *Osmia*, *Melecta*, and *Lasioglossum* (J. K. Combs, *unpublished data*).

There are three primary and various secondary predispersal seed predators of *A. sinuatus* (see Combs 2005). Of the primary species, two are native seed-feeding specialists, the seed weevil *Tychnius semisquamosus* LeConte (Curculionidae), and the seed beetle *Acanthoscelides fraterculus* Horn (Bruchidae). Both are widely distributed across North America and feed exclusively on members of the legume family (Center and Johnson 1974, Clark 1977, Kingsolver 2004). *T. semisquamosus* is a narrower specialist, with all known hosts being *Astragalus* spp. (Clark 1977). The third primary seed predator was identified as a micro moth species, *Grapholita imitativa* Heinrich (Tortricidae; Fig.

1; J. Brown, *personal communication*); all known hosts have been genera in the Legume family (*Astragalus* and *Lupinus*). Secondary seed predators include generalists such as *Chlorochroa uhleri* Stal. (Pentatomidae), *Thyanta custator* Fabricius. (Pentatomidae), and unidentified hymenopteran larvae.

Bromus tectorum L. (cheatgrass or downy brome; Fig. 1) is of Eurasian origin and is the most abundant invasive grass species in western North America, occupying millions of hectares (Mack 1981, 1989, Upadhyaya et al. 1986). Cheatgrass is a winter annual that can germinate in fall, winter, or spring, depending on moisture conditions. Seedlings can either lie dormant or grow continuously through the winter if warm, wet conditions occur. It is a highly self-fertile, cleistogamous species. Cheatgrass is proficient at extracting available moisture from the rooting depth profile, allowing it to outcompete many native species (Upadhyaya et al. 1986).

Insect reduction experiment

To test the hypothesis that predispersal seed predators significantly lower per capita seed production in *A. sinuatus*, we arbitrarily marked 50 *A. sinuatus* plants, separated by 2–3 m from one another, at CC and UDG on 10 April 2003. In each site, 25 plants were randomly assigned to one of two treatments, insect reduction or control. For the reduction treatment, we initially sprayed individuals with a nonsystemic insecticide, Thiodan (active ingredient Endosulfan; concentration = 0.75 mL/L; Southern Agricultural Insecticides, Palmetto, Florida, USA), at two 10–12 day intervals. After the first two spray treatments, we shifted to manual removal of insects using an aspirator every eight to 12 days throughout the flowering period (April–May), because we found some evidence suggesting insecticide phytotoxicity. The insecticide was applied early in the morning when pollinator activity was minimal and under low wind conditions to avoid insecticidal drift. After the second application, leaf tissue on five individuals of *A. sinuatus* began to turn yellow, likely a phytotoxic reaction to the insecticide; we then removed these individuals from the study and ended the insecticide treatment. To maintain an equal sample size among control and treatment groups, we randomly removed five control plants (final $n = 20$ plants per treatment). For the remainder of the study (April–May), an aspirator was used to remove insects manually from reduction treatment plants (every 8–12 days). In addition, tortricid moth larvae were reduced by applying *Bacillus thuringiensis* (Bt) once on reduction treatment plants on 7 June 2003 when moth damage was first noticed.

When pods were mature (mid-June), 15 pods per plant were collected at random from control and treatment plants at CC and UDG. Seed damage and pod damage were quantified using a dissecting microscope. For each pod, we recorded the number of viable seeds (i.e., filled,

undamaged) and scored the level of pod damage observed (1, <50%; 2, 50–90%; 3, >90%), based on the estimated percentage of seeds consumed within a pod. A previous seed viability study (Combs 2005) showed very high seed viability for filled, undamaged seeds at CC and UDG (98–99%, respectively). Thus, filled, undamaged seeds were assumed viable. Insects found within pods were identified. Total seed production per plant was estimated by multiplying average seeds produced per pod for the sampled pods by the total number of pods counted on each plant at the end of the growing season.

Analyses.—To examine the effects of predispersal seed predation on seed loss and pod damage in *A. sinuatus*, we used a GLM MANOVA. In the model, we assigned site (CC, UDG) and treatment (insects reduced vs. control) as fixed factors, and per capita seed production and proportion of pod damaged as dependent variables. Per capita seed production was log-transformed, and proportional pod damage was angular-transformed prior to analysis to meet assumptions of normality and reduce variance heterogeneity. All statistical tests were performed using SPSS 12.0 (SPSS 2001).

Seed addition and Bromus removal experiments

We conducted two concurrent seed addition experiments to test indirectly the effects of seed predators and test directly the effects of *B. tectorum* on seedling recruitment and establishment rates of *A. sinuatus* over four growing seasons (2004–2007) at one site (UDG). Both experiments were set up on 4 November 2003. In the first experiment, we examined whether *A. sinuatus* is seed limited by adding seeds at two different densities and then following recruitment and survival. In this experiment, we set up two permanent 36-m transects at UDG. Along each transect, we marked 18 plots (1 × 1 m, with 1-m buffer between plots; $n = 36$ total). Of these, 12 plots were seeded at a low-addition level (40 seeds added), 12 plots were seeded at a high-addition level (120 seeds added), and 12 plots were kept as controls (zero seeds added). The two levels of seed addition represent natural per capita seed production rates in plants exposed to seed predators (40 seeds) vs. plants in which seed predators were reduced (120 seeds) in 2003 (Table 1). Seed addition treatments were assigned randomly, and seed was added in the first year only. The seeds were distributed across each plot to reduce potential density-dependent, self-thinning effects. *Bromus* cover in plots ranged from 10–50% (J. K. Combs, *unpublished data*). Prior to seeding, a subset of seeds was tested for viability and showed high viability (98–99%; see Combs 2005). Monitoring took place from March to June every seven to 14 days in 2004, every 12 to 20 days in 2005, and once at the end of the season in 2006 and 2007. Based on results from 2004 and 2005, monitoring at the end of the season was sufficient to obtain an accurate estimate of cumulative establishment over a growing season.

We tested whether the presence of *B. tectorum* inhibits germination and establishment of *A. sinuatus* through a combined *Bromus* removal and seed addition experiment at UDG. A 30-m transect was established in an area of high *B. tectorum* cover (>50% average cover) within the primary *A. sinuatus* population at UDG. Along this transect, 14 plots (1 × 1 m) were permanently marked. Of these, seven plots were randomly designated as *Bromus* removal, and seven plots were assigned controls. All *Bromus* plants and loose seeds were cleared from the removal plots by hand prior to seeding. Removal was maintained throughout the experiment and carefully done so as not to introduce significant disturbance. One level of addition, 40 *A. sinuatus* seeds, was added to each treatment plot ($n = 7$) and each control plot ($n = 7$); seed addition density was based on per capita seed production from plants in this population (Combs 2005). Unfortunately, we did not have enough seeds to initiate a second-level (120) addition because seed set was low due to seed predation during the previous seed collection year. We monitored seedling recruitment and survival over the same intervals reported in this section. All seedlings were marked to track seedling fate over time.

Analyses.—To examine whether seedling and juvenile establishment differed between low-addition (40 seeds) and high-addition (120 seeds) levels, we used a repeated-measures ANOVA. Data were log-transformed prior to analyses to meet assumptions of the test. Census data were based on the total numbers of seedlings, juveniles, and mature adults alive in plots at each census. There were 22 census periods over the four years (2004–2007). Control plots, where zero seeds were added, were excluded from all analyses because no germination occurred within those plots, indicating minimal to no seed bank effects in the treatment and control plots. We also tested for differences in seedling and juvenile establishment in the *Bromus* removal vs. control plots using the same monitoring protocol and the same statistical approach as the seed density addition study.

Fecundity and predation rate across populations and years

We quantified pod production and pod predation rates (i.e., proportion of pod damage) and per capita seed production at four of the eight known sites in 2003 (CC, UDG, LFD, and MDG) and at the two main sites in 2004 (CC, UDG). Parameter estimates were based on 20 individuals sampled at each of the four sites. We used data from the control plants in the insect reduction experiment conducted at the two main sites to minimize the number of plants disturbed. In 2004, we sampled additional plants at CC and UDG ($n = 46$, $n = 30$, respectively).

Analyses.—We compared pod production, pod predation rate (level 2 or more), and per capita seed production among populations and among years. We also asked if plant productivity (i.e., average pod production per plant) and seed predation rate were correlated. For 2003, ANOVA was used to detect

potential differences in fecundity and herbivory rates among site populations. For 2004, a *t* test was used to test for differences between CC and UDG sites. To examine if plant productivity (i.e., mean pods produced) and the proportion of damaged pods were correlated, we used Pearson correlation tests in both 2003 and 2004. Data were log-transformed prior to analyses to meet assumptions of the test.

Percent cover of Bromus tectorum and associated species

We documented plant abundance, especially *B. tectorum*, and plant composition in proximity to *A. sinuatus* at CC and UDG in 2003. We estimated species composition and percent cover (ocular estimates of percent cover within a 1 × 1 m square) of all vascular plant species, bare ground, and rock within 1-m² quadrats centered around experimental plants and control plants in the insect reduction experiment at CC and UDG. In addition, we added 60 arbitrarily placed 1-m² quadrats at each site ($n = 100$ per site).

RESULTS

Insect reduction experiment

Reduction of seed-feeding insects by using insecticide for two weeks followed by hand-removal increased mean per capita production of viable seed by 164% at CC and by 345% at UDG. The control plants at Colockum Creek (CC) averaged 132 ± 58 viable seeds, while the reduction plants averaged 349 ± 94 viable seeds; at Upper Dry Gulch (UDG), control plants averaged 44 ± 11 viable seeds, while the reduction plants averaged 196 ± 65 viable seeds (Fig. 2). Values are reported as mean \pm SE. Further, the site differences came close to being significant, with a larger response at CC, the site with higher control plant seed production (ANOVA $F_{1,79} = 3.39$, $P = 0.07$). Thus, the reduction treatment was highly effective, and the results demonstrate significant insect herbivore effect on the number of viable seeds per plant.

Underlying part of this response, we found proportionally fewer pods damaged on reduction treatment plants than on control plants (CC, 36% vs. 82%, respectively; UDG, 33% vs. 78%, respectively). The treatment effect on the proportion of pods damaged was significant at both sites (MANOVA $F_{2,75} = 0.4147$, $P < 0.001$; Appendix), and site differences were not significant (ANOVA $F_{1,79} = 0.92$, $P = 0.345$). Thus, a significantly higher proportion of pods was damaged when insects were allowed access to inflorescences.

Reduction of insects did not significantly increase the average number of pods per plant. At CC, reduction plants produced on average 102 ± 20 pods, while control plants averaged 119 ± 21 pods ($F_{1,38} = 0.61$, $P = 0.44$); at UDG, reduction plants averaged 65 ± 2 pods, while control plants averaged 68 ± 13 pods ($F_{1,38} = 0.76$, $P = 0.38$). However, there was a significant difference in pod production per plant between sites. At CC, the reduction and control plants combined produced $110 \pm$

14 pods, while at UDG, the average was only 67 ± 12 pods per plant ($F_{1,78} = 11.6$, $P = 0.001$). In sum, the two sites differed in the number of pods produced per plant, and reducing insect access to inflorescences did not increase the number pods filled but did decrease the proportion of pods damaged, thus leading to a highly significant increase in the number of viable seeds produced per plant under field growing conditions. It is likely that the CC population produced more pods per plant as a result of higher soil moisture at this site (see Combs 2005).

Seed addition experiments

In the seed density experiment (low vs. high seed addition), we found no difference between treatments in establishment rate of seedlings and subsequent juveniles over four growing seasons (Fig. 3; repeated-measures ANOVA, $F_{1,22} = 2.37$, $P = 0.138$); thus, establishment of *A. sinuatus* was not seed limited. The ability to detect a difference in the seed density experiment was due to several factors (see *Discussion*).

In contrast, in the *Bromus* removal/seed addition experiment, seedling recruitment and juvenile establishment differed significantly between treatments over the four growing seasons (repeated-measures ANOVA, $F_{1,12} = 5.134$, $P = 0.043$). The establishment of *A. sinuatus* was limited by the presence of *B. tectorum* cover (Fig. 3). Thus, recruitment was limited by competitive interaction with an exotic grass, rather than by absolute seed availability per se.

Fecundity and predation rates across populations and years

In 2003, seed production, pod production, and pod damage per plant did not differ significantly among all four sites (seed production, $F_{3,79} = 1.729$, $P = 0.168$; pod production, $F_{3,79} = 2.223$, $P = 0.092$; proportion of pods damaged, $F_{3,79} = 0.204$, $P = 0.115$). Unexpectedly, seed production did not differ significantly even though a fourfold difference occurred between the least productive site (UDG) and the most productive site (Lone Fir Draw [LFD]; Table 1). This outcome most likely reflects the large standard errors on the estimates from two sites (Table 1).

In 2004, seed production and pod production per plant were significantly higher at CC than at UDG (Table 1; seeds *t* test, $t = -2.766$, $df = 74$, $P = 0.007$; pods *t* test, $t = -5.115$, $df = 74$, $P < 0.001$). While seed production per plant varied threefold between CC and UDG, the proportion of pods damaged only trended toward difference between sites (*t* test, $t = 1.823$, $df = 74$, $P = 0.072$). Overall, pod damage was consistently high in all sites in both years, while seed production per plant and pods produced per plant varied among populations (Table 1).

In 2003, the number of pods produced per plant was not related to the proportion of pods damaged at two sites and only marginally at a third site (Pearson values

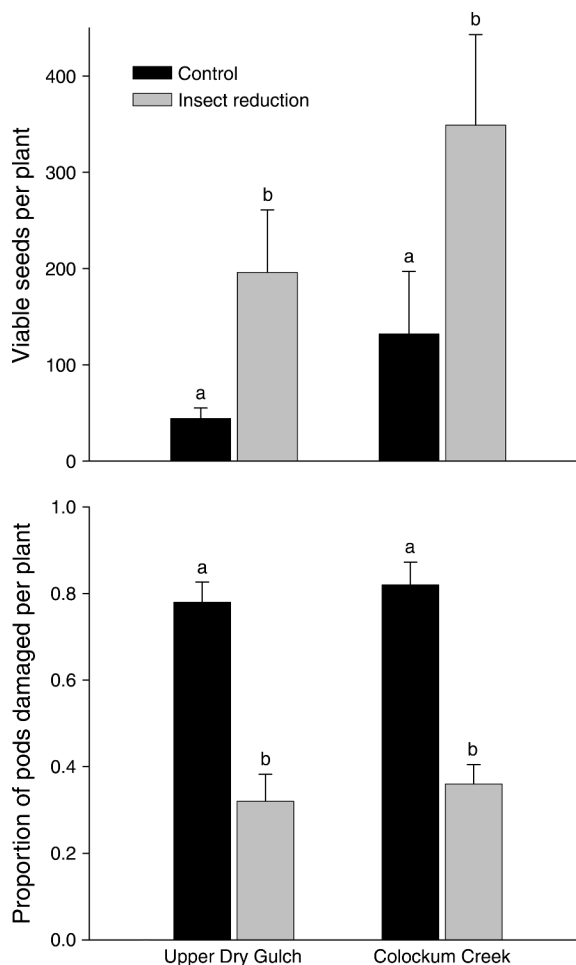


FIG. 2. Mean viable seed production (upper panel), and proportion of damaged pods per plant (lower panel) in the insect reduction and control treatments for *A. sinuatus* in 2003 at two sites. Bars represent untransformed means (+SE); different letters signify statistical difference at $P < 0.001$.

per site: MDG, -0.093 , $P = 0.696$; UDG, -0.178 , $P = 0.453$; CC, -0.434 , $P = 0.056$). Only at LFD was the number of pods produced per plant correlated negatively with the proportion of pods damaged (Pearson value -4.94 , $P < 0.05$). In 2004, per capita pod production was not correlated with predation rates at either UDG (Pearson value 0.030 , $P = 0.875$) or CC (Pearson value -0.042 , $P = 0.875$). Overall, across sites and between years, we found little evidence that predispersal predation rates correlated significantly with per capita pod production, suggesting that the number of pods per plant did not influence seed predation rates.

Percent cover of *Bromus tectorum* and associated plant species

At each site, *B. tectorum* (cheatgrass) was the most dominant species (CC, 15.4%; UDG, 17.95%; Fig. 4) in plots where *A. sinuatus* was the focal species. Bare ground was more prevalent at UDG (32%) than CC

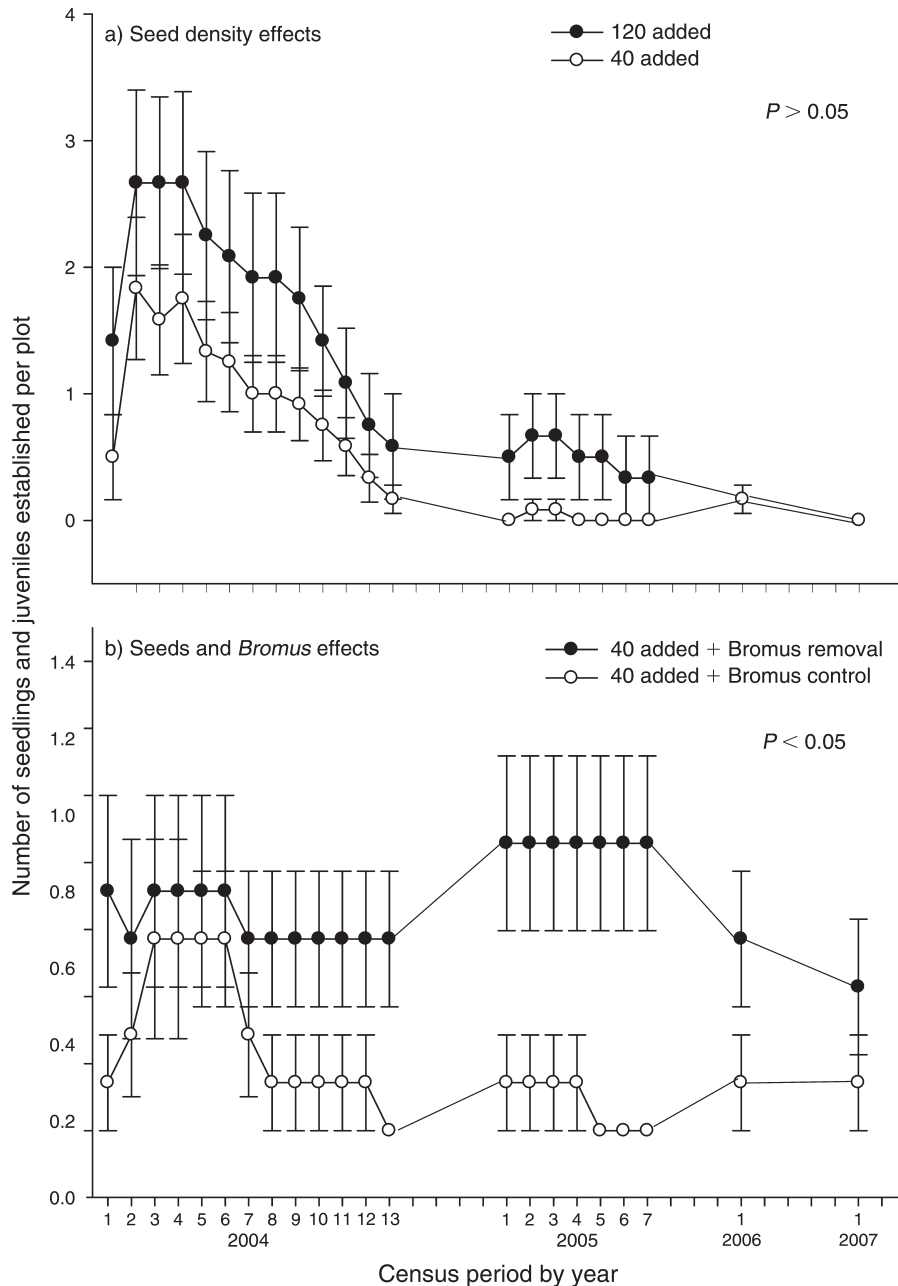


FIG. 3. Seedling and juvenile plants of *A. sinuatus* recruited and established at Upper Dry Gulch in two seed addition experiments: (a) seed density effects (40 vs. 120 seeds added per plot), and (b) seed addition and *Bromus* effects (control vs. removal) over four growing seasons (2004–2007). Plots were 1 m². Census period refers to the number of times plots were monitored in each year (see *Methods: Seed addition and Bromus removal experiments* for discrepancy in monitoring periods across years). Means and standard errors are presented as untransformed data.

(15%). Rock (metamorphic basalt) cover was higher at CC (22.15%) than UDG (6.09%).

DISCUSSION

Both predispersal seed loss to insect herbivores and competition with an invasive grass competitor acted as important mechanisms limiting both individual fitness and population density for the narrow endemic plant

Astragalus sinuatus. Predispersal seed predators had the strongest effect on individual fitness, reducing the number of seeds produced per plant. Further, competitive interactions with *Bromus tectorum* resulted in significant declines in seedling and subsequent juvenile establishment over four seasons. The combined results from seed addition and removal experiments suggest that seed loss to seed predators may play an important

TABLE 1. Parameters of fecundity and rate of predispersal pod predation (mean \pm SE) observed in *Astragalus sinuatus* (Whited's milkvetch) at four sites over two years in foothills of the Wenatchee Mountains, Chelan County, Washington, USA.

Year \times site	~Population estimate	No. pods per plant	No. viable seeds per plant	Proportion of pods damaged per plant	No. plants (<i>n</i>)
2003					
Colockum Creek, CC	~1200	119 \pm 21	132 \pm 58	0.82 \pm 0.05	20
Lone Fir Draw	~3000	77 \pm 14	191 \pm 64	0.66 \pm 0.07	20
Mid-fork Dry Gulch	~3500	70 \pm 12	57 \pm 17	0.67 \pm 0.05	20
Upper Dry Gulch, UDG	~10 000	68 \pm 13	44 \pm 11	0.78 \pm 0.05	20
2004					
Colockum Creek, CC	~1200	56 \pm 5	56 \pm 11	0.65 \pm 0.03	46
Upper Dry Gulch, UDG	~10 000	24 \pm 6***	17 \pm 13**	0.73 \pm 0.04	30

Notes: In 2004, there was a significant difference in pods per plant and number of viable seeds per plant between plants at UDG and CC. In 2003, there were no significant differences in the three parameters among sites.

** $P < 0.01$; *** $P < 0.001$.

role in recruitment under certain circumstances (i.e., when *B. tectorum* is absent or at very low abundance) in patches and perhaps under preinvasion conditions. Both antagonistic interactions acted to appreciably limit the reproduction and recruitment of *A. sinuatus*.

Native predispersal seed predators had a large impact on individual fitness (Fig. 2; Appendix). Reduction of seed predators increased seed production per plant by 164–345% in populations at the main sites (Colockum Creek [CC], Upper Dry Gulch [UDG], respectively; Fig. 2). Furthermore, we documented consistently high rates of pod damage, leading to low rates of seed production, among all four populations in 2003 and at the main sites in 2004 (Table 1). In contrast, other studies have generally shown greater variability in predation rates across sites and years (reviewed in Kolb et al. 2007, Vanhoenacker et al. 2009). Yet, although predation rates in *A. sinuatus* were consistently high among populations and years, fecundity parameters (mean per capita pod production, seed production) varied considerably among populations and years (Table 1).

Spatiotemporal differences in fecundity patterns could be driven by a number of intrinsic or extrinsic factors. For example, other studies found that seed predation rate is often positively correlated with flower or fruit production (Hainsworth et al. 1984, Ohashi and Yahara 2000). However, in this study we did not detect a correlation between pod production and predation rate at three of our four study populations, indicating that the number of pods produced is not an important underlying mechanism driving predation rate; i.e., insects are not selecting plants with more pods. There is some evidence to support the idea that extrinsic factors such as soil moisture may explain why pod and seed production was highest at CC. For example, a soil moisture study conducted in 2003 showed significantly higher gravimetric soil moisture at CC compared to UDG, indicating that soil moisture may play a role in increased plant fecundity at CC (Combs 2005). This result is not surprising considering that plant performance in semiarid environments, such as the sagebrush

steppe, is often limited by water availability. Combs (2005) also investigated the possibility that the presence of *B. tectorum* may influence fecundity and predation rates in *A. sinuatus*. However, there was no difference in mean pod production or seed loss due to seed predators in *A. sinuatus* in experimental removal plots with and without *B. tectorum*.

Even though seed predation rates were very high for all populations measured in both years, seed loss did not translate directly into demographic declines, based on the results of the first seed addition experiment. Unexpectedly, seedling recruitment and juvenile establishment of *A. sinuatus* did not differ statistically at the end of the four growing seasons between our high (120) or low (40) seed addition levels (Fig. 3). The inference is that *A. sinuatus* populations were not seed limited at the densities tested. This conclusion differs from other studies that found seed predators to be a primary cause of population-level declines in common plant species (Louda and Potvin 1995, Maron et al. 2002, Rose et al. 2005). However, the methods used to assess the demographic effect of seed loss to predators also differed between this study and these previous studies; we used experimental seeding in our experiment, whereas the other studies used predator exclusion with natural seeding in their experiments. Although it has been argued that predator exclusion is a preferable technique to test predator effects (e.g., Louda and Potvin 1995, Maron et al. 2002), the seed addition technique has also been widely used (Turnbull et al. 2000). However, Turnbull et al. (2000) recommend that an addition of at least 10 times the natural seed output be used to achieve unequivocal results. Unfortunately, seed predation rates were so high in *A. sinuatus* that it was not possible to collect enough undamaged seeds for such a high addition level. Instead, our two experimental levels (addition at 40 seeds [low] and 120 seeds [high]) were based on average seed production under natural field conditions (see 2003 CC and UDG sites in Table 1). We suspect that we may have seen a seed limitation effect if we had a third treatment that included a much

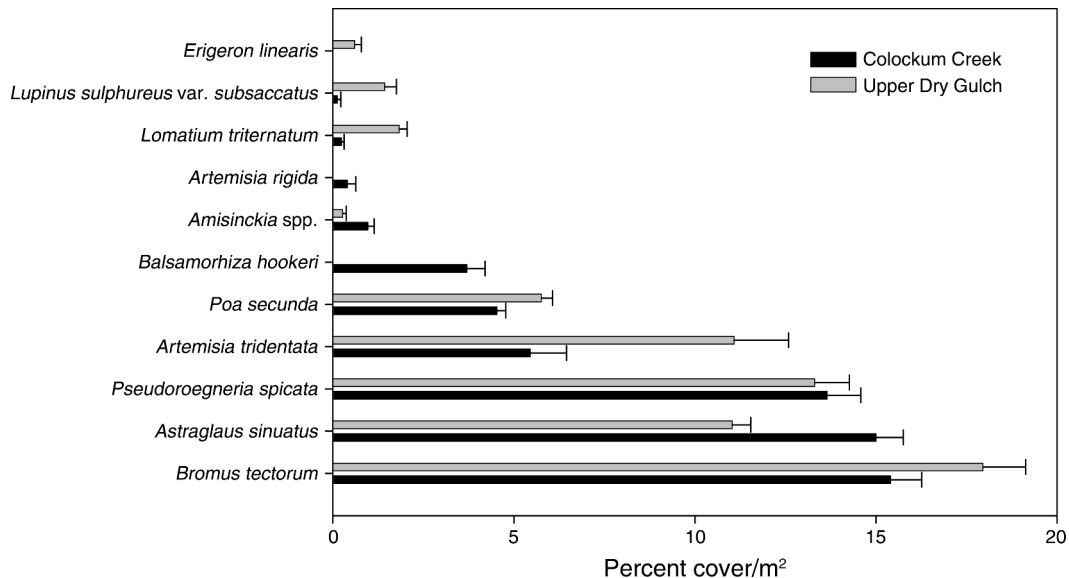


FIG. 4. Percent cover (mean + SE) of *B. tectorum* and associated species surrounding *A. sinuatus* at Colockum Creek ($n = 100$ 1-m² plots) and Upper Dry Gulch ($n = 100$) in 2003. *A. sinuatus* was the focal species within each 1-m² plot. *B. tectorum* represents the highest cover at both sites. Species with minimal cover values (<0.05%) are not shown.

higher level of addition. Lastly, our seed addition experiment was conducted in areas of relatively high cheatgrass cover (>50%), whereas *A. sinuatus* may be more limited by seed in areas where cheatgrass is sparse, i.e., where microsite conditions are favorable for recruitment. In any case, in this experiment initial seed density could not explain density of recruits after four years.

In contrast, in the *Bromus* removal plus low seed addition experiment, we found that establishment remained significantly higher in plots where *B. tectorum* had been removed (Fig. 3); so, dense stands of *B. tectorum* significantly lowered the population-level fitness of *A. sinuatus*. These results complement the handful of other studies that show competitive interactions with introduced species have negative demographic consequences for rare plant species (Huenneke and Thomson 1995, Lesica and Shelly 1996, Walck et al. 1999, Thomson 2005). While this experiment was done at only one site (UDG), the seven other sites where *A. sinuatus* occurred supported relatively high abundances of *B. tectorum* (J. K. Combs and D. L. Wilderman, *personal observation*). Thus, we predict that the mechanistic patterns documented at UDG may be generalized to these other sites where *B. tectorum* was abundant. Moreover, since >50% of all individuals of *A. sinuatus* occurred at UDG, and it was one of only two sites where active management was possible, the results here are significant to the conservation of this species. An additional concern that managers should consider is that the presence of *B. tectorum* will likely lead to increases in fire frequency, which may, in turn, lead to greater abundance of *B. tectorum* and lower abundance of *A. sinuatus*. Casual observations suggest that a fire

event at one site where *A. sinuatus* occurred resulted in increased *B. tectorum* cover and reduced *A. sinuatus* seedling growth (P. A. Camp, *personal observation*). Many studies have documented the ability of *B. tectorum* to increase fire frequencies and act as a superior competitor in postfire environments (Leopold 1941, Klemmedson and Smith 1964, Upadhyaya et al. 1986, Yensen et al. 1992). Indeed, it was Leopold (1941) who said, "The more you burn cheat the thicker it grows the next year, for the seeds shatter early and harbor in cracks in the ground." Thus competition with *B. tectorum* will most likely be greatest following fire events.

To the best of our knowledge, this study is the first to document population-level declines in a rare plant species in competition with *B. tectorum*, one of the most prolific plant invaders in western North America (Mack 1981). Similar individual- and population-level declines have been observed in common plant species as a result of competition with *B. tectorum* (Stewart and Hull 1949, Harris 1967, Melgoza et al. 1990, Humphrey and Schupp 2004). For example, Stewart and Hull (1949) found that bunchgrass seedlings, *Agropyron cristatum*, died rapidly as a result of soil moisture depletion by *B. tectorum*, although adult individuals persisted in the presence of *B. tectorum*. We hypothesize that *A. sinuatus* now may be limited in a similar manner, as we often observed plants in the adult stage persisting with *B. tectorum*, including very robust reproductive individuals. Since *A. sinuatus* has a woody taproot system (Barneby 1964), it seems likely that adult plants (with rooting depths greater than *B. tectorum*) are able to escape competition with *B. tectorum*. Thus, *A. sinuatus*

in the seedling and juvenile stages may be most vulnerable to competition with *B. tectorum*.

While the data here suggest that competition with *B. tectorum* is currently an important factor contributing to the rarity of *A. sinuatus*, seed predators likely reduce population growth when *B. tectorum* is absent or in very low abundance. All *A. sinuatus* sites are heavily invaded by *B. tectorum*, but disturbances (e.g., gopher activity) occur, allowing recruitment and establishment of *A. sinuatus* seedlings in areas with low *B. tectorum* abundance (J. K. Combs, *personal observation*). Also, the *B. tectorum* removal plus seed addition experiment showed higher recruitment in plots without *B. tectorum* even at the low (40 seed) addition level. Thus in areas where *B. tectorum* is sparse, recruitment of *A. sinuatus* may be seed limited rather than site limited.

Because conservation action is often limited by time and resources, it is important to identify which mechanisms limit species and under what circumstances. Based on our results we recommend small-scale reductions of *B. tectorum*, either by hand-pulling or using grass-specific herbicides around the perimeter of mature *A. sinuatus* individuals. Since *A. sinuatus* disperses seed close to the parent plant, short-term suppression of *B. tectorum* may enable seedlings to recruit and survive to a stage where they can coexist with *B. tectorum*.

In addition, in populations where *B. tectorum* density is low (currently no known populations meet this criterion), short-term reduction of predispersal insect seed predators also may be an effective management approach. Manual removal of insects or short-term targeted uses of insecticides are two methods of insect reduction. There has been some disagreement in the literature concerning the use of insecticides to conserve rare plant populations (Bevill et al. 1999, Lesica and Atthowe 2000, Louda and Bevill 2000). However, it should be noted that researchers on both sides of this debate agree that under certain circumstances, insecticides may be an appropriate management tool for threatened and endangered species, if care is taken to avoid nontarget effects on pollinators and other community members.

This study supports theory on rarity that suggests competition and predispersal seed predation are important mechanisms influencing both reproductive and population-level fitness of a rare plant species. We demonstrated that a reduction both in competition from the invasive grass *B. tectorum* and in seed loss to native predispersal seed predators should be considered in management and restoration of *A. sinuatus*, and perhaps other rare plants that are similarly affected by seed predators and/or plant invaders. We encourage managers to consider how climate changes may create feedbacks that could intensify predation and competition factors. For example, it is predicted that the Columbia Basin will experience milder, wetter winters and dryer spring–summer seasons (Ferguson 1997, E. A. Parson, P. W. Mote, A. Hamlet, et al., *unpublished*

manuscript). Since *B. tectorum* is a winter annual, it will most likely have a competitive edge compared to many species, such as *A. sinuatus*, that germinate or emerge later in the season. Additionally, the combination of drier spring–summer seasons and the presence of *B. tectorum* will likely increase fire events that can further stimulate *B. tectorum* invasion. Similarly, milder winters may lead to an increase in the survivorship of overwintering predispersal insects, which in turn may lead to higher rates of predation. Thus, conservation managers developing adaptive management and research plans should consider how factors such as competition and predation may change in a climate-altered future.

ACKNOWLEDGMENTS

We thank A. M. Lambert, S. M. Louda, C. A. Brigham, and one anonymous reviewer for comments that greatly improved our manuscript. We are grateful for the entomological expertise of C. O'Brien, J. Kingsolver, J. Brown, and D. Thomas for identification of seed predators. We also thank those who assisted in the lab and field: J. Chan, S. Collman, A. M. Lambert, B. Williams, and especially K. Craig. Finally, we thank J. L. Maron and S. M. Louda, who contributed to early discussions in our project design phase. Partial funding was provided by Washington Department of Natural Resources and the U.S. Bureau of Land Management.

LITERATURE CITED

- Barneby, R. C. 1964. Atlas of North American *Astragalus*. Part I. The phacoid and homaloboid. The New York Botanical Garden 13:1–596.
- 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.
- Brigham, C. A. 2003. Factors affecting persistence in formerly common and historically rare plants. Pages 59–97 in C. A. Brigham and M. W. Schwartz, editors. *Population viability in plants: conservation, management and modeling of rare plants*. Springer-Verlag, Berlin, Germany.
- Center, T. D., and C. D. Johnson. 1974. Coevolution of some seed beetles (Coleoptera: Bruchidae) and their hosts *Ecology* 55:1096–1103.
- Clark, W. E. 1977. North American *Tychius*: new synonymy and observations on the phylogeny and zoogeography (Coleoptera: Curculionidae). *Entomologica Scandinavica* 8:287–300.
- Combs, J. K. 2005. *Astragalus sinuatus* (Piper), a Washington State endangered plant species: pre-dispersal seed predation, seedling-recruitment and interactions with *Bromus tectorum* L. Thesis. University of Washington, Seattle, Washington, USA.
- Crawley, M. J. 1997. Plant–herbivore dynamics. Pages 401–474 in M. J. Crawley, editor. *Plant ecology*. Blackwell Science, Oxford, UK.
- Dangremond, E. M., E. A. Pardini, and T. M. Knight. 2010. Apparent competition with an invasive plant hastens the extinction of an endangered lupine. *Ecology* 91:2261–2271.
- D'Antonio, C. M., J. C. Chambers, R. Loh, and J. T. Tunison. 2009. Applying ecological concepts to the management of widespread grass invasions. Pages 123–149 in R. L. Inderjit, editor. *Management of invasive weeds*. Springer, Dordrecht, The Netherlands.
- D'Antonio, C. M., R. F. Hughes, M. Mack, D. Hitchcock, and P. M. Vitousek. 1998. The response of native species to removal of invasive exotic grasses in a seasonally dry

- Hawaiian woodland. *Journal of Vegetation Science* 9:699–712.
- D'Antonio, C. M., and B. E. Mahall. 1991. Root profiles and competition between the invasive, exotic perennial, *Carpobrotus edulis*, and two native shrub species in California coastal scrub. *American Journal of Botany* 78:885–894.
- Drury, W. H. 1980. Rare species of plants. *Rhodora* 82:3–48.
- Fargione, J., C. S. Brown, and D. Tilman. 2003. Community assembly and invasion: an experimental test of neutral versus niche processes. *Proceedings of the National Academy of Sciences USA* 100:8916–8920.
- Ferguson, S. A. 1997. A climate-change scenario for the Columbia River Basin. Research Paper PNW-RP-499. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.
- Fiedler, P. L. 1986. Concepts of rarity in vascular plant species, with special reference to the genus *Calochortus* Pursh (Liliaceae). *Taxon* 35:502–518.
- García-Serrano, H., F. X. Sans, and J. Escarré. 2007. Interspecific competition between alien and native congeneric species. *Acta Oecologia* 31:69–78.
- Gisler, S. D., and R. J. Meinke. 1997. Reproductive attrition by pre-dispersal seed predation in *Sidalcea nelsoniana* (Malvaceae): implications for the recovery of a threatened species. Pages 56–61 in T. N. Kaye et al., editors. Conservation and management of native plants and fungi. Native Plant Society of Oregon, Corvallis, Oregon, USA.
- Griggs, R. F. 1940. The ecology of rare plants. *Bulletin of the Torrey Botanical Club* 67:575–594.
- Hainsworth, F. R., L. L. Wolf, and T. Mercier. 1984. Pollination and pre-dispersal seed predation: net effects on reproduction and inflorescence characteristics in *Ipomopsis aggregata*. *Oecologia* 63:405–409.
- Harper, J. L. 1981. Population biology of plants. Academic Press, New York, New York, USA.
- Harris, G. A. 1967. Some competitive relationships between *Agropyron spicatum* and *Bromus tectorum*. *Ecological Monographs* 37:89–111.
- Hegazy, A. K., and N. M. Eesa. 1991. On the ecology, insect seed-predation, and conservation of a rare endemic plant species, *Ebenus armitagei* (Leguminosae). *Conservation Biology* 5:317–324.
- Honek, A., and Z. Martinkova. 2005. Pre-dispersal predation of *Taraxacum officinale* (dandelion) seed. *Journal of Ecology* 93:335–344.
- Huenneke, L. F., and J. K. Thomson. 1995. Potential interference between a threatened endemic thistle and an invasive non-native plant. *Conservation Biology* 9:416–425.
- Humphrey, L. D., and E. W. Schupp. 2004. Competition as a barrier to establishment of a native perennial grass (*Elymus elymoides*) in alien annual grass (*Bromus tectorum*) communities. *Journal of Arid Environments* 58:405–422.
- Kaye, T. N. 1999. From flowering to dispersal: reproductive ecology of an endemic plant, *Astragalus australis* var. *olympicus* (Fabaceae). *American Journal of Botany* 86:1248–1256.
- Kelly, C. A., and R. J. Dyer. 2002. Demographic consequences of inflorescence-feeding insects for *Liatrix cylindracea*, an iteroparous perennial. *Oecologia* 132:350–360.
- Kingsolver, J. M. 2004. Handbook of Bruchidae of the United States and Canada (Insecta, Coleoptera). U.S. Department of Agriculture, Technical Bulletin 1912.
- Klemmedson, J. O., and J. G. Smith. 1964. Cheatgrass (*Bromus tectorum* L.). *Botanical Review* 30:226–262.
- Kolb, A., and J. Ehrlén. 2010. Environmental context drives seed predator-mediated selection on a floral display trait. *Evolutionary Ecology* 24:433–445.
- Kolb, A., J. Ehrlén, and O. Eriksson. 2007. Ecological and evolutionary consequences of spatial and temporal variation in pre-dispersal seed predation. *Perspectives in Plant Ecology, Evolution and Systematics* 9:79–100.
- Kruckeberg, A. R., and D. Rabinowitz. 1985. Biological aspects of endemism in higher plants. *Annual Review of Ecology and Systematics* 16:447–479.
- Kunin, W. E., and K. J. Gaston. 1997. The biology of rarity. Chapman and Hall, London, UK.
- Lau, J. A., and S. Y. Strauss. 2005. Insect herbivores drive important indirect effects of exotic plants on native communities *Ecology* 86:2990–2997.
- Leimu, R., K. Syrjänen, J. Ehrlén, and K. Lehtilä. 2002. Pre-dispersal seed predation in *Primula veris*: among-population variation in damage intensity and selection on flower number. *Oecologia* 133:510–516.
- Leopold, A. 1941. Cheat takes over. *The Land* 1:310–313.
- Lesica, P., and H. E. Atthowe. 2000. Should we use pesticides to conserve rare plants? *Conservation Biology* 14:1549–1550.
- Lesica, P., and J. S. Shelly. 1996. Competitive effects of *Centaurea maculosa* on the population dynamics of *Arabidopsis fecunda*. *Bulletin of the Torrey Botanical Club* 123:111–121.
- Louda, S. M. 1982a. Distribution ecology: variation in plant recruitment over a gradient in relation to insect seed predation. *Ecological Monographs* 52:25–41.
- Louda, S. M. 1982b. Limitation of the recruitment of the shrub *Haplopappus squarrosus* (Asteraceae) by flower-feeding and seed-feeding insects. *Journal of Ecology* 70:43–53.
- Louda, S. M., and R. L. Beville. 2000. Exclusion of natural enemies as a tool in managing rare plant species. *Conservation Biology* 14:1551–1552.
- Louda, S. M., K. H. Keeler, and R. D. Holt. 1990. Herbivore influences on plant performance and competitive interactions. Pages 413–444 in J. M. Grace and D. Tilman, editors. Perspectives on plant competition. Academic Press, New York, New York, USA.
- 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.
- Mack, R. N. 1981. Invasion of *Bromus tectorum* L. into western North America: an ecological chronicle. *Agro-Ecosystems* 7:145–165.
- Mack, R. N. 1989. Temperate grasslands vulnerable to plant invasions: characteristics and consequences. Pages 155–179 in J. A. Drake, editor. Biological invasions: a global perspective. John Wiley, London, UK.
- Maron, J. L., J. K. Combs, and S. M. Louda. 2002. Convergent demographic effects of insect attack on related thistles in coastal vs. continental dunes. *Ecology* 83:3382–3392.
- Maron, J. L., and E. Crone. 2006. Herbivory: effects on plant abundance, distribution and population growth. *Proceedings of the Royal Society B* 273:2575–2584.
- Maron, J. L., D. E. Pearson, and R. J. Fletcher. 2010. Counterintuitive effects of large-scale predator removal on a midlatitude rodent community. *Ecology* 91:3719–3728.
- Maron, J. L., and E. L. Simms. 2001. Rodent-limited establishment of bush lupine: field experiments on the cumulative effect of granivory. *Journal of Ecology* 89:578–588.
- Melgoza, G., R. S. Nowak, and R. J. Tausch. 1990. Soil water exploitation after fire competition between *Bromus tectorum* (cheatgrass) and two native species. *Oecologia* 83:7–13.
- Miller, M. F. 1996. *Acacia* seed predation by bruchids in an African savanna ecosystem. *Journal of Applied Ecology* 33:1137–1144.
- Münzbergova, Z. 2005. Determinants of species rarity: population growth rates of species sharing the same habitat. *American Journal of Botany* 92:1987–1994.
- Ohashi, K., and T. Yahara. 2000. Effects of flower production and pre-dispersal seed predation on reproduction in *Cirsium purpuratum*. *Canadian Journal of Botany* 78:230–236.

- Rabinowitz, D., J. K. Rapp, and P. M. Dixon. 1984. Competitive abilities of sparse grass species: means of persistence or cause of abundance. *Ecology* 65:1144–1154.
- Rose, K. E., S. M. Louda, and M. Rees. 2005. Demographic and evolutionary impacts of native and invasive insect herbivores on *Cirsium canescens*. *Ecology* 86:453–465.
- Rosenzweig, M. L., and M. V. Lomolino. 1997. Who gets the short bits of the broken stick? Pages 64–90 in W. E. Kunin and K. J. Gaston, editors. *The biology of rarity*. Chapman and Hall, London, UK.
- SPSS. 2001. SPSS for Windows: statistics. Version 12.0. SPSS, Chicago, Illinois, USA.
- Stebbins, G. L. 1980. Rarity of plant species: a synthetic viewpoint. *Rhodora* 82:77–86.
- Stewart, G., and A. C. Hull. 1949. Cheatgrass (*Bromus tectorum* L.)—an ecologic intruder in southern Idaho. *Ecology* 30:58–74.
- Thomson, D. 2005. Measuring the effects of invasive species on the demography of a rare endemic plant. *Biological Invasions* 7:615–624.
- Tilman, D. 1997. Mechanisms of plant competition. Pages 238–261 in M. J. Crawley, editor. *Plant ecology*. Blackwell, Oxford, UK.
- Turnbull, L. A., M. J. Crawley, and M. Rees. 2000. Are plant populations seed-limited? A review of seed sowing experiments. *Oikos* 88:225–238.
- Upadhyaya, M. K., R. Turkington, and D. McIlvride. 1986. The biology of Canadian weeds. *Bromus tectorum*. *Canadian Journal of Plant Science* 66:689–710.
- Vanhoenacker, D., J. Agren, and J. Ehrlén. 2009. Spatial variability in seed predation in *Primula farinosa*: local population legacy versus patch selection. *Oecologia* 160:77–86.
- Walck, J. L., J. M. Baskin, and C. C. Baskin. 1999. Effects of competition from introduced plants on establishment, survival, growth and reproduction of the rare plant *Solidago shortii* (Asteraceae). *Biological Conservation* 88:213–219.
- Whittaker, R. H. 1965. Dominance and diversity in land plant communities. *Science* 147:250–260.
- Wilson, D. E., and D. H. Janzen. 1972. Predation on scheelea palm seeds by bruchid beetles: seed density and distance from the parent palm. *Ecology* 53:954–959.
- Yensen, E., D. L. Quinney, K. Johnson, K. Timmerman, and K. Steenhof. 1992. Fire, vegetation changes, and population fluctuations of Townsend's ground squirrels. *American Midland Naturalist* 128:299–312.
- Zimmerman, T. G., and S. H. Reichard. 2005. Factors affecting persistence of Wenatchee Mountains checker-mallow: an exploratory look at a rare endemic. *Northwest Science* 79:172–178.

APPENDIX

MANOVA results showing the effect of insect reduction on per capita seed production and pod damage at Colockum Creek and Upper Dry Gulch in 2003 in the foothills of the Wenatchee Mountains, Washington, USA. (*Ecological Archives* A021-111-A1).