Reproductive Success and Soil Seed Bank Characteristics of
*Astragalus ampullarioides* and *A. holmgreniorum* (Fabaceae):
Two Rare Endemics of Southwestern Utah

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Reproductive Success and Soil Seed Bank Characteristics of *Astragalus ampullarioides* and *A. holmgreniorum* (Fabaceae),
Two Rare Endemics of Southwestern Utah

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A Thesis submitted to the faculty of
Brigham Young University
in partial fulfillment of the requirements for the degree of

Master of Science

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ABSTRACT

Reproductive Success and Soil Seed Bank Characteristics of *Astragalus ampullarioides* and *A. holmgreniorum* (Fabaceae), Two Rare Endemics of Southwestern Utah

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*Astragalus ampullarioides* and *A. holmgreniorum* are two rare endemics of southwestern Utah. Over two consecutive field seasons (2009-2010) we examined pre-emergent reproductive success, based on F/F and S/O ratios, from populations of both *Astragalus ampullarioides* and *A. holmgreniorum*, estimated the density of the soil seed bank of *A. holmgreniorum* as a measure of potential post-emergent reproductive success, and estimated seed persistence within the soil seed bank. Fruit/flower (F/F) ratios and seed/ovule (S/O) ratios varied significantly between populations and among years in both species, and showed low reproductive output in both taxa. In *Astragalus ampullarioides* F/F and S/O were 0.06±0.01 and 0.16±0.02, respectively (2009), and 0.14±0.01 and 0.41±0.02, respectively (2010). For *Astragalus holmgreniorum* F/F and S/O ratios were 0.11±0.01 and 0.38±0.02, respectively (2009), and 0.23±0.01 and 0.66±0.02, respectively (2010). Although *Astragalus holmgreniorum* exhibited a low soil seed bank density (4.3 seeds m\(^{-2}\)), seed persistence data showed low a low percentage of seeds germinated during the first year in the soil seed bank. Seeds remaining in the seed bank maintained high percent viability. Soil seed persistence of *Astragalus ampullarioides* differed from *A. holmgreniorum* in that a high percentage of seeds germinated during the first year in the soil seed bank. A high percentage of viability in ungerminated seeds was also maintained in *A. ampullarioides*. Although these species differ in life histories and dependence on soil seed banks, an understanding of the strategies unique to each species will prove useful in management plans.

Key words: Fruit/flower ratio, seed/ovule ratio, *Astragalus*, endangered species, seed bank, seed persistence, milkvetch
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Introduction

Reproductive capacity is frequently at the heart of any study in evolutionary biology because it directly affects fitness (Harper 1977, Wiens et al. 2002). Reproductive success in rare species is often low in small, isolated populations, where genetic variability may be reduced (Allphin et al. 2005, Allphin et al. 2002, Wiens et al. 2002). Reproductive ecology, as well as aspects of seed biology play important roles in sustaining rare plant populations (Pavone and Reader 1982, Cabin and Marshall 2000). Small population sizes, usually exhibited by rare species, are more susceptible to environmental variation and human impacts (Barrett and Kohn 1991, McCue and Holtsford 1998). Populations that maintain reproductive capacity, as well as a soil seed bank, may be more likely to exhibit long-term persistence across varying environmental conditions. Increasing our understanding of the reproductive strategies of rare species is crucial, not only for conservation purposes, but to gain a better understanding of the factors contributing to rarity.

Reproductive strategies and soil seed bank characteristics vary greatly among taxa (Henderson et. al 1988, Lyons et al. 1989, O’Neil and Parker 2005), breeding systems and life histories (Wiens 1984, Tonsor et. al 1993), and under varying environmental conditions (Lechowicz and Blais 1988). Two rare endemic species of Astragalus from southwestern Utah show differences in life history strategies and their dependence on soil seed banks for survival (Van Buren and Harper 2003a). Astragalus holmgreniorum Barneby (Holmgren’s milkvetch) is a short-lived perennial. Demographic studies have shown fluctuations in population structure with environmental variation, and researchers have documented zero emergences of vegetative or reproductive individuals during years (2002 and 2007) of extreme drought (Van Buren and Harper 2003b, Van Buren 2008).
Growing seasons following such events show recolonization of *A. holmgreniorum* by seeds, suggesting it is dependent upon the soil seed bank for survival (Van Buren and Harper 2004b, Searle and Yates 2009).

*Astragalus ampullarioides* (Welsh)Welsh (Shivwits milkvetch) does not exhibit the same dependence on soil seed banks as *A. holmgreniorum*. Although this species relies on the soil seed bank for seedling recruitment, demographic studies have shown that, while plants may not emerge during extreme drought conditions, mature adults have the ability to re-emerge the following growing season (Van Buren and Harper 2004a, Searle and Yates 2009). Therefore, to better understand these alternative strategies, we must understand the reproductive biology and soil seed bank dynamics.

As a species completes its reproductive cycle, seeds develop, mature, and enter the soil seed bank. Wiens et al. (1987) describe two types of reproductive success: pre-emergent and post-emergent. Pre-emergent reproductive success is the proportion of mature, viable seeds that are produced by a reproductive parent plant. Post-emergent reproductive success is the percentage of those seeds that germinate, establish, mature, and reproduce.

Pre-emergent reproductive success of a plant is the product of the fruit to flower ratio (F/F ratio) and the seed to ovule ratio (S/O ratio) (Wiens et al. 1987). Wiens (1984) found that in general perennial out-crossing individuals have low S/O ratios, while perennial, in-breeding species show higher S/O ratios. This hypothesis has been supported in other studies (Eriksen 1996, Wiens et al. 2002, Allphin et al. 2002, Allphin et al. 2005). Variation in S/O ratios has been attributed to various conditions such as resource availability (Herrera 1991, Vaughton 1991, Griffin and Barrett 2002), insufficient

Post-emergent reproductive success is the proportion of pre-emergent seeds that germinate and mature to reproductive individuals. In species that maintain a persistent seed bank, many post-emergent individuals survive as dormant seeds in the soil seed bank, until conditions are optimal for germination. In highly variable environments seeds may have the ability to lay dormant in the soil for several years before germination (Priestly 1986, Kemp 1989), and at times these seeds may be the only viable form of the species (Cabin et al. 2000). Thus, soil seed banks play an important role in the long-term survival of many plant species (Adams et al. 2005, Meyer et al. 2005, Coteff and Van Auken 2006).

The ability of seeds to remain dormant in the soil is crucial in years when conditions are less favorable (Fischer and Matthies 1998). Desert ecosystems are one such habitat that exhibits fluctuations in environmental conditions. Seed germination events, in plant populations occupying these habitats, often fluctuate with the environmental fluctuations (Venable and Brown 1988, Pake and Venable 1996). During years of unfavorable growing conditions, a soil seed bank can act as a buffer (Venable and Brown 1988, Stocklin and Fischer 1999, Adams et al. 2005). Populations of rare species may be the most susceptible to environmental variation, since densities of these populations are likely to be low. However, species that maintain a persistent seed bank can reverse a decline in the population, if management is taken in these habitats to reduce harmful disturbances (Thompson et al. 1993, Allphin et al. 1998, Meyer et al. 2005).
For this study, we focused on the reproductive biology and soil seed bank characteristics of two rare species of *Astragalus* endemic to Washington, County, Utah, *A. ampullarioides* (Welsh) Welsh and *A. holmgreniorum* Barneby. The genus *Astragalus* is the largest within the family Fabaceae, with approximately 1500-2000 species worldwide (Isely 1998). The evolution of this genus is relatively recent, having had much success adapting to new habitats in arid environments (Barneby 1989).

*Astragalus ampullarioides* (Shivwits milkvetch) occurs in small, isolated populations (spanning a distance of 45 miles), on outcrops of soil derived from the Triassic Petrified Forest Member of the Chinle Shale Formation (Miller et al. 2007). The Shivwits milkvetch is a perennial species, flowering mid-spring and producing small, unilocular inflated pods (Welsh 1998). Seeds, at maturity, are approximately 2-3mm in length (Figure 2). In contrast with most species belonging to this genus, *A. ampullarioides* is highly palatable and is often grazed by deer, livestock (Welsh et al. 2003), and rabbits (Miller et al. 2007).

*Astragalus holmgreniorum* Barneby (Holmgren’s milkvetch) is a short-lived perennial, flowering in mid-spring and developing bilocular legume fruits. Seeds, at maturity, are approximately 2-3mm in length (Figure 2). This species is limited to warm desert shrub communities found within the Virgin River Valley washes on Virgin limestone (Moenkopi Formation). This species is restricted to the area of ecological convergence of the Mojave Desert, Great Basin, and Colorado Plateau, and has specific ecological requirements for survival (Stubben 1997). Populations of this taxon are restricted to areas not more than 10 miles outside the city of St. George, Utah (US Fish and Wildlife 2006), one of the most rapidly growing urban areas in Utah (Utah State Office of Planning and Budget 2009).
Over the last two decades increases in disturbances such as off-road vehicle (ORV) use, urban development, grazing, and displacement by invasive plant species have resulted in decreased population sizes for both species. Therefore, in 1996, both taxa were designated as potential candidates for federal listing, and in 2001 listed as endangered under the Endangered Species Act (US Fish and Wildlife 2001). Critical habitat was proposed and finalized in 2006, which included 2,421 acres for *A. ampullarioides* and 6,475 acres for *A. holmgreniorum* (US Fish and Wildlife 2006).

Low reproductive success has been documented in other rare species (Fischer and Matthies 1997, Kaye 1999, Luijten et al. 2000, Schmidt and Jensen 2000, Alphin et al. 2002, Brys et al. 2004, Alphin et al. 2005) and may ultimately have confounding effects on the long-term survivability of any population. Therefore, an understanding of reproductive capacity is crucial in the conservation of *Astragalus ampullarioides* and *A. holmgreniorum*.

The objectives of this study were to 1) examine pre-emergent reproductive success, based on F/F and S/O ratios, from populations of both *Astragalus ampullarioides* and *A. holmgreniorum*, 2) estimate the density of the soil seed bank of *A. holmgreniorum*, as a measure of potential post-emergent reproductive success, and 3) estimate seed persistence within the soil seed bank. An understanding of the reproductive biology of both rare species will prove critical for land managers making decisions regarding potential recovery.

Materials and Methods

*Study sites*

The six populations of *Astragalus ampullarioides* sampled in this study are small, and widely spaced (Figure 1), spanning a distance of 45 miles (Miller et al. 2007). Two
populations, Shivwits and Pahcoon Springs Wash, are located west of St. George, Utah on the Shivwits Reservation and BLM land adjacent to the reservation. Three populations, Coral Canyon, Harrisburg, and Silver Reef, are located to the north of St. George. The Coral Canyon population is located on the edge of a golf course and residential development. The Harrisburg population is west of Quail Creek Reservoir near Interstate 15, extending into the median. The Silver Reef population, named for the old mining town, is just west of Leeds, Utah. The most disjunct population (Zion) is located within the Petrified Forest region of Zion National Park (Figure 1). Most populations of this species have been fenced to minimize disturbances, however urban sprawl, recreational activities, grazing, and competition with exotic species still pose threats, and further fragment these populations.

Currently, there are six remaining populations of *Astragalus holmgreniorum* (Figure 1). All populations are found within a 10-mile radius of the city of St. George. Three populations, State Line, Central Valley, and Gardner Well, are located approximately seven miles south of St. George, found within an area that extends from the Virgin River on the west to White Dome on the East, and south into Mojave County, Arizona. Two populations, Stucki Springs, and South Hills, are located approximately five miles northwest of St. George, just south of the city of Santa Clara, Utah. The smallest population, Purgatory, is located in Purgatory Flat, approximately nine miles northeast of the city of St. George, Utah. Three of the six *Astragalus holmgreniorum* populations occur on federal lands (South Hills, State Line, and Stucki Spring), two are on state lands (Central Valley and Gardner Well), and one population is located on private land. The habitats in which these populations occur have been severely degraded and fragmented over the past several decades by urban
sprawl, ORV use, grazing, and displacement by exotic species. Currently the greatest threat to this species is habitat loss (US Fish and Wildlife 2006).

Reproductive success

To determine pre-emergent reproductive success, fruit to flower (F/F) ratios and seed/ovule (S/O) ratios were examined at each population for both taxa. At each population, a 50-meter transect line was placed and 50 individuals were selected by tagging the nearest individual to each 2-meter point on the line, and tagging its nearest neighbor (Cottam and Curtis 1956). Point-to-plant and plant-to-plant distances were recorded to determine local plant density at each population. At populations with less than 50 individuals, all individuals within the population were tagged. For each tagged individual, the number of flowers and the diameter of the basal rosette were recorded. Sites were revisited during fruit development and the number of fruits per individual was recorded. Due to the rarity of these species, only 1-2 fruits were collected, prior to dehiscence, from each tagged individual and taken to the laboratory where S/O ratios and percent fruit parasitism were determined.

Percent ovule abortions and percent fruit parasitism were analyzed from fruits collected at each population. Abortion rates were determined for each fruit by whether or not ovules produced filled seed (Figures 4 and 5). Ovule abortions were also categorized by the degree of ovule development (no development, early abortion, partial abortion, and late abortion). These categories were determined based on size, color, and overall appearance of the ovule.
Temperature and precipitation data were collected from the National Climatic Data Center (NCDC) weather stations located near populations of *Astragalus ampullarioides*. Data for the Pahcoo Wash population was collected from the Gunlock weather station, while data for Harrisburg, Coral Canyon, and Silver Reef populations were collected from the St. George station, and data for the Zion population was collected from the Zion weather station.

The percent of fruit parasitism was also determined from collected fruits brought back to the laboratory. This was determined by opening and examining fruits for insect larvae (Figure 4) and determining percentage of all fruits examined that contained parasites.

**Data Analysis**

Fruit/flower ratios were calculated for individuals tagged in each population by dividing the number of developed fruits by the number of flowers produced, then these were averaged for a population mean. Fruits collected in the field were analyzed for S/O ratios by dividing the number of seeds that reached maturity (filled viable seed) by the number of total ovules in the fruit (filled seed plus aborted seeds). Differences in F/F and S/O ratios between populations and years were tested using analysis of variance (ANOVA) and Tukey multiple means comparisons. All data were visually inspected for normality and a Levene’s Test used to test the homogeneity of variance. An arcsine transformation was applied to F/F and S/O data to meet the assumptions of the test. Linear regressions were used to determine relationships between rosette diameter and flower and fruit set, and
relationships between population size and fruit set. Statistical significance was defined as \( \alpha \leq 0.05 \). All statistical analyses were conducted using R (R Development Core Team, 2009).

**Soil seed persistence**

A seed retrieval study was conducted to estimate seed persistence in the soil seed bank. To accurately assess seed persistence in natural habitats, experiments were conducted in the field within each species habitat. We modified methods outlined by Meyer et al. (2005) for this experiment. Seeds used in this experiment were those collected from fruits used to determine S/O ratios, therefore seeds were of known age. Due to herbivory of all inflorescences of *Astragalus ampullarioides* at the Shivwits and Zion populations, and minimal seed set at the Silver Reef and Coral Canyon populations in 2009, these populations were not added to this study. Thus only the Harrisburg and Pahcoon Wash populations were included in persistence analysis. From each population there was a total of 400 seeds, which were divided into 20 groups of 20 seeds.

Due to limited seed set at the Gardner Well, Purgatory Flat, and South Hills populations of *A. holmgreniorum*, no seeds from these populations were added to this study. Thus only seed from the Central Valley, State Line, and Stucki Spring populations were used. We collected 600 seeds from both the Central Valley and State Line populations, and 570 from Stucki Spring. These seeds were divided into 30 groups with 20 seeds/group (Central Valley and State Line) and 19 seeds/group (Stucki Spring).

Each group was placed in a 4 cm\(^2\) nylon mesh bag. Bags were buried in sets (1 bag from each population) approximately 2 cm below the soil surface approximately 1 m apart, at 2 populations for *A. ampullarioides*, and 3 populations for *A. holmgreniorum*, with 2
replications per population. The location of each buried set was marked for later retrieval. To avoid predation of the bags, wire mesh was secured over the soil where bags were buried.

Seed viability was tested on a sample of recently harvested seeds from each population, and on seed samples retrieved from the soil after one year. Viability was determined by seed germinability and by using a standard tetrazolium test (TZ) (International Seed Testing Association 1985). Methods for testing viability were consistent between years. Samples were retrieved from the soil at each burial location after one year. Since we did not observe any obvious predation or other damage (i.e. fungus) to bags, we assumed that if the number of seeds within each bag summed to less than the original number, then the number of seeds missing had germinated.

Seeds that had not germinated and remained in each bag were taken to the laboratory and tested for germinability. Seeds were scarified using fine-grained sandpaper and placed on moist blotter paper in petri dishes (Bench 2004). Dishes were placed in an environmental growth chamber (Biotronette Mark III Environmental Chamber, Lab-Line Instruments, Melrose Park, IL) at 30°C for one week, after which seeds were checked for germination.

Seeds that did not germinate were tested for viability using a standard tetrazolium test, which detects dehydrogenase enzyme activity in live tissues. Seeds that had imbibed water were sectioned longitudinally to expose the embryo. Three drops of 1% Tetrazolium solution was added to each seed, and allowed to sit for 1 h. Embryos that stained red for enzyme activity were deemed viable and counted. Overall viability was computed by
summing the number of lab germinated seeds with the number positively stained embryos and dividing by total seeds tested.

**In situ seed bank**

An estimate of the *in situ* seed bank was determined for *Astragalus holmgreniorum*. At each of the six extant populations of *A. holmgreniorum* a 100-meter transect line was established across an area where plants were found. Soil samples were collected systematically along the transect line by obtaining 300 random numbers between 1 and 100 from a random number generator. For each random number a second random number was generated between -5 and 5. The first number corresponded to the location on the transect line, and the second number to a distance, in meters, right or left (positive or negative, respectively) of the line, zero corresponded to the sample being collected on the line. Soil samples were collected by pressing a small tin can (6.5 cm diameter, 4.6 cm height) into the ground, then using a masonry trowel to hold the soil in the can, the can was pulled up with the soil. The soil was placed in labeled small paper bags, and brought back to the laboratory for analysis.

In the laboratory, individual soil samples were passed through a series of standard wire-mesh sieves (#5-5mm, #10-3mm, and #35-0.5mm) to separate soil particles. Seeds were extracted from soil particles remaining in the #35 sieve by careful examination of each sample by naked eye. The number of seeds found in each sample was recorded. Another species, *Astragalus nuttallianus* A. de Candolle, commonly grows at all populations of *A. holmgreniorum*. We identified seeds of this species and extracted their seeds from the soil samples for comparison. To estimate density of the soil seed bank, the number of seeds found per population was divided by the total area of soil sampled per population. Since
two other studies previously reported the *in situ* seed bank of *A. ampullarioides* and reported densities of 49.4 seeds m\(^{-2}\) (Bench 2004) and 45.7 seeds m\(^{-2}\) (Miller et al. 2009) we refer to their results for this analysis (Figure 11).

Seed viability was tested on seeds extracted from the soil samples. Viability tests follow those outlined previously in the soil seed persistence study.

Results

Reproductive Success

*Astragalus ampullarioides*: For the two-year duration of our study, the reproductive success of *Astragalus ampullarioides*, exhibited by F/F and S/O ratios, showed variation across populations and among years (Table 1; Table 2). In 2009, the overall mean F/F ratio was 0.04, and overall mean S/O ratio of 0.17 (Table 1). Means for ovule and seed number were 20.3 and 3.4, respectively. In 2010, the mean F/F ratio was 0.06, and mean S/O ratio of 0.41 (Table 1).

The mean number of flowers and fruits of *Astragalus ampullarioides* differed between years (Figure 3). Data show mean flower and fruit numbers in 2009 were 227.1 and 11.2, respectively, while 2010 data show mean flower and fruit of 366.2 and 41.5, respectively (Figure 3). The mean number of ovules and seeds per fruit however did not differ significantly between years. In 2009 means for ovule and seed numbers were 20.3 and 3.4, respectively, and 2010 means of 20.5 and 8.4, respectively (Figure 3).

Data were used to calculate seed rain per plant. This was done by multiplying the mean seed output per plant by the number of plants. At all populations of *Astragalus ampullarioides*, except Harrisburg, average seed rain was higher in 2010, than in 2009.
Several factors likely contributed to this outcome such as precipitation, temperature, herbivory, insect predation, and pollination.

Overall percent ovule abortions over the two years of study in *Astragalus ampullarioides*, were high, with a mean of 79.0 in 2009 and 50.6 in 2010, and differed among populations and between years (Table 3). Ovule abortion percentages based on the degree of ovule development in 2009 were 4.5 (no development), 31.7 (early abortions), 27.5 (partial abortions), and 15.7 (late abortions) (Table 3; Figure 5). Percent abortions in 2010 were 2.1 (no development), 19.1 (early abortions), 27.2 (partial abortions), and 2.3 (late abortions).

During both years of study we found a significant positive correlation between plant diameter and flower number ($R^2=0.237, P<0.001; R^2=0.304, P<0.000$), and between flower number and fruit set ($R^2=0.159, P<0.000; R^2=0.436, P<0.000$) in *Astragalus ampullarioides*. Our data showed that individuals with larger diameters produced greater numbers of flowers, and individuals with greater numbers of flowers tended to produce more fruits. Population density was not significantly correlated with fruit set in either field season (2009: $R^2=0.170, P=0.588$; 2010: $R^2=0.371, P=0.275$). We also found no significant correlation between population size and fruit set (2009: $R^2=0.087, P=0.706$; 2010: $R^2=0.149, P=0.520$).

Temperature and precipitation variables were considered in relationships with early embryo abortion. We found a significant positive correlation between mean May temperatures and the percent early embryo abortions ($R^2=0.601, P=0.014$), however, no significant relationships were found between precipitation and early embryo abortion ($R^2=0.052, P=0.555$).
Two insects, a parasitic wasp and weevil, were found in fruit of *Astragalus ampullarioides* collected at 5 of the 6 sampled populations (Figure 4). Reproductive adult weevils lay eggs inside fruits, and larvae feed on the developing seeds. Reproductive parasitic wasps also lay eggs inside the fruits of this species, however, the developing larvae feed on the weevil. In 2009, all parasitized fruits developed no viable seed, however, in 2010 some viable seeds were found in fruits with evidence of insect larvae. In 2009, percent insect fruit predation ranged from 0% (Coral Canyon) to 68.4% (Silver Reef) (Table 5). Percent insect predation ranged, in 2010, from 0% (Coral Canyon) to 74.6% (Silver Reef) (Table 5).

Herbivory was observed at all populations of *Astragalus ampullarioides*, with herbivores typically eating only the inflorescences (personal observation). Herbivory in 2009 was only recorded as a field observation at each population; however, in 2010 we recorded this parameter for each individual (Figure 6). Herbivory in 2009 had significantly devastating effects at the Shivwits and Zion populations, with 100% herbivory of all flowering stems. In 2010, the Shivwits population again exhibited 100% herbivory of flowering stems.

*Astragalus holmgreniorum*: Reproductive success measured in *Astragalus holmgreniorum* also varied among populations and years as indicated by both F/F and S/O ratios (Table 1; Table 2). In 2009, the mean overall F/F ratio was 0.11, with an overall S/O ratio mean of 0.38. In 2010, the overall mean F/F ratio was 0.23, and mean overall S/O ratio was 0.66 (Table 1).

Mean flower and fruit numbers produced, in populations of *Astragalus holmgreniorum*, also differed between years (Figure 3). In 2009 mean flowers and fruits
produced were 26.9 and 3.4, respectively, while mean flower and fruits measured in 2010 were 41.4 and 10.0, respectively (Figure 3). Ovule number did not differ between years; however, differences in seed number were recorded between years, and show a mean of 13.3 in 2009, and 22.8 in 2010 (Figure 3). Seed rain per plant was also calculated for *Astragalus holmgreniorum*. Similar to *Astragalus ampullarioides*, the seed rain for *A. holmgreniorum* during the 2010 field season was higher, than seed rain data for 2009 (Table 6).

Percent ovule abortion data for *Astragalus holmgreniorum* showed lower abortion percentages than observed in *A. ampullarioides*. The percent of ovule abortions in 2009 was 61.4 and 34.0 in 2010 (Table 4). Ovule abortion percentages also differed significantly among populations and between years (Table 4). The percent of ovule abortions based on degree of development (Figure 5) during the 2009 field season were 4.3 with no development, 17.1 early abortions, 29.1 partial abortions, and 10.9 late abortions. In 2010, ovule abortion percentages were 2.7 (no development), 15.3 (early abortions), 14.0 (partial abortions), and 2.0 (late abortions) (Table 4).

Our data showed, for *Astragalus holmgreniorum*, a significant positive correlated between flower number and plant diameter (2009: $R^2=0.526$, $P<0.001$; 2010: $R^2=0.306$, $P<0.001$). Although there was no correlation between flowers per plant and fruits produced in 2009 ($R^2=0.01$, $P=0.190$), there was a significant positive relationship ($R^2=0.375$, $P<0.001$) in 2010. For *A. holmgrenirom* we found no correlation between population density and fruit set (2009: $R^2=0.057$, $P=0.650$; 2010: $R^2=0.355$, $P=0.212$) as in *A. ampullarioides*. We did, however, find a positive correlation between population size and fruit set (2009: $r^2=0.874$, $P=0.006$; 2010: $r^2=0.661$, $P<0.05$) in this taxon.
Insect predation of fruit of *Astragalus holmgreniorum* was observed only during the 2009 field season. Only 1 fruit at the Gardner Well population was affected, in which no viable seed was produced. Unfortunately, severe degradation of the insect did not allow for identification. Herbivory was observed during both years of study at populations of *A. holmgreniorum*. Data, however, were only collected during the 2010 field season (Figure 7). The Purgatory Flat population showed the highest degree of herbivory. Only 1 fruit was found on 1 plant in the entire population, with herbivory of the flowering stems observed on all other individuals.

*Soil seed persistence*

Germination percentages of seeds of *Astragalus ampullarioides* in the field retrieval bags showed 51.4-64.6% of seeds germinated during the first growing season (Figure 8). Viability was tested on the ungerminated seeds remaining in the retrieved bags. Data showed 32.9-37.8% germinated under laboratory conditions, while another 1.4% were deemed viable by positive tetrazolium staining. Low percentages of seeds lost viability before germinating (<10%) (Figure 8).

*Astragalus holmgreniorum* seed germination percentages were lower than those observed in *A. ampullarioides*. Data showed <11% of seed germinated during the first growing season (Figure 9). This species also showed high percentages of seeds germinate under laboratory conditions (71.6-77.5%), while 10.8-13.3% showed a positive result for the tetrazolium stain (Figure 9). Less than 7% of seeds within the retrieval bags had lost viability prior to germination.
In situ seed bank

The number of seeds extracted from population soil samples of *Astragalus holmgreniorum* ranged from 1 (Purgatory) to 57 (South Hills). Density was estimated for each population (Table 7; Figures 10) and ranged from 1.02 seeds m\(^{-2}\) (Purgatory) to 58.04 seeds m\(^{-2}\) (South Hills). The South Hills population is an outlier, showing a significantly higher density than all other populations (Figure 10). This is likely a result of the surrounding landscape. Soil at South Hills was collected near the bottom of a wash, and seeds extracted from the soil had obvious signs of scouring suggesting that seeds had been washed down the drainage. Excluding this population, the soil seed bank density for this species was 4.3±1.19 seeds m\(^{-2}\).

Seeds of *Astragalus nuttallianus*, a species commonly associated with *A. holmgreniorum* were also extracted from samples at all populations (Table 7). Seed densities of this species ranged from 2.01 seeds m\(^{-2}\) at Stucki Spring to 538.41 seeds m\(^{-2}\) at Purgatory. The seed bank density observed at the Stucki Spring population is an outlier, with all other populations averaging a density of 290.99 seeds m\(^{-2}\). Although we do not have frequency data for *A. nuttallianus*, we observed very few individuals at the Stucki Spring population, thus the low density is expected.

Seeds of both *Astragalus holmgreniorum* and *A. nuttallianus* extracted from the soil samples were tested for viability (Table 8). Between 20-100% of seeds of *A. holmgreniorum* germinated under laboratory conditions, while another 0-29% showed a positive tetrazolium stain. Total percent viability of this species ranged from 20% (Gardner Well) to 100% (Purgatory).
Percent viability of seeds of *Astragalus nuttallianus* extracted from soil samples showed 100% viability at all populations. All seeds tested germinated under laboratory conditions.

Discussion

Over the past several decades, changes to the landscape surrounding populations of these endangered species have resulted in degradation and fragmentation of habitat. As pressures on populations increase, shifts in population density or population size are often the result (Mustajarvi et al. 2001). Small populations have increased risks of extinction due to loss of genetic diversity, which increases the likelihood of genetic drift (Barrett and Kohn 1991), and inbreeding or inbreeding depression (Ellstrand 1992).

Rare species may be more prone to extinction due to limited geographic range, number of populations, and population size (Primack 2008), and thus need special considerations when determining conservation management plans. Conservationists must take into account demographic parameters, reproductive success, and soil seed biology in management plans, if rare species are to persist long-term.

Demographic studies of *Astragalus ampullarioides*, conducted by Van Buren and Harper (2003a and 2004a) at the Pahcoo Wash population, show a stable population structure with an average life span of approximately 5-8 years. Mean seedling emergence, over a 10-year period, was estimated at 37.2 seedlings per year (Van Buren and Harper 2004a, Searle 2010), with a mean seedling mortality of 44.1% (Van Buren and Harper 2004a, Searle 2010).
Van Buren and Harper (2003a) also reported an average life span for *A. holmgreniorum* of approximately 2-3 years. Mean seedling emergence over a 10-year period was 54.5 (Van Buren and Harper 2004b, Searle 2010), with a mean seedling mortality of 67.2% (Van Buren 2008, Searle 2010). However, 84-100% seedling mortality has been documented in this species in years of unfavorable conditions (Van Buren and Harper 2004b and Van Buren 2008). Population age-class structure in *A. holmgreniorum* is highly variable due its short life span, dependence on seedling emergence and survivorship.

In this study, the reproductive success of both rare taxa varied between populations and years. The between year differences we observed in both F/F and S/O ratios suggest that the maternal investment in reproduction is not fixed (Lloyd 1980) in either species we studied. Furthermore, we found no significant correlation among the F/F and S/O ratios suggesting that fruit and seed set are likely independent processes (Herrera 1990, Obeso 1993).

Reproductive success reported for these rare taxa in 2009 are consistent with those of other rare species (Fischer and Matthies 1997, Sipes and Wolf 1997, Luijten et al. 2000, Schmidt and Jensen 2000, Allphin et al. 2002, Wiens et al. 2002, Brys et al. 2004, Allphin et al. 2005). Other rare taxa of *Astragalus* also exhibit low reproductive success similar to our 2009 data. *Astragalus cremnophylax* var. *cremnophylax* and *A. humillimus*, from the Grand Canyon and northwestern New Mexico, had S/O ratios near 0.30 (Allphin et al. 2005), and *Astragalus australis* var. *olympicus*, endemic to the Olympic Mountains in Washington, showed only 3.8% seed-set (Kaye 1999). However, reproductive data collected in 2010 are consistent with results reported by Wiens (1984) for perennial out-breeding species. Thus,
it appears that certain requirements must be met to maintain higher levels of reproductive success.

We considered environmental variables (precipitation and temperature) as factors to explain differences in S/O ratios among years. Precipitation was not correlated with S/O ratios in either species. Wiens (1984) suggested that resource availability may have a larger effect on flower production than on S/O ratios, and several studies have shown a correlation between precipitation and flower production and seed production (Lalonde and Roitberg 1989, 1994, Herrera 1991, Allphin et al. 2002, Wiens et al. 2002). Our results are similar to those of other rare species of *Astragalus*, indicating no relationship between precipitation and S/O ratios (Lalonde and Roitberg 1989, Wiens et al. 2002, Allphin et al. 2005).

Temperatures in May, however, were significantly positively correlated with early ovule abortions in *Astragalus ampullarioides*. Fruit development in this species typically occurs early to mid May. In 2009 temperatures were, on average, 10 degrees warmer than temperatures during the same period in 2010 (U.S. Department of Commerce 2009, 2010). Recent studies have documented adverse affects of temperature on reproductive success, where increased temperatures decreases S/O ratios due to an increased number of early aborted embryos, in a variety of species (Owens et al. 2001, Zinn et al. 2010). This phenomenon has also been documented in crop species exhibiting similar effects of decreased S/O ratios with increased temperatures (Hanft et. al 1990, Prasad et. al 2002, Prasad et. al 2008).

Variation in fruit set between years, observed in both species, may be a result of pollination failure due to environmental variability during the pollination period (Wilcock
and Neiland 2002). This failure has been documented to vary between populations and years, among and within species (Burd 1994). During the flowering and fruiting season of 2009, we observed lower S/O ratios at all populations of both *Astragalus ampullarioides* and *A. holmgreniorum*, than those observed in 2010. The proportion of ovules with no development varied between years and may be attributed to lack of pollination (Tables 2 and 3).

Environmental conditions, such as temperature, may have been a factor limiting pollinator activity (Arroyo et al. 1985). Temperature has also been reported to have adverse effects on pollen tube development (Lewis 1942), and early degeneration of stigmas (Burgos et al. 1991). In species that rely on a limited diversity of pollinators, Wilcock and Neiland (2002) suggest an intermediate risk of pollen failure, due to environmental change or disturbance. Tepedino (2005) reported that primary pollinators of both *Astragalus* species are native, solitary bees in the genus *Anthophora*, and suggests that pollinators must be protected for long-term survival of these rare *Astragal*.

Pollinators are particularly important for maintenance of species that rely on them for cross-pollination. Tepedino (2005) showed that both F/F and S/O ratios were significantly reduced in *Astragalus holmgreniorum*, and S/O ratios were significantly reduced in *A. ampullarioides* under pollinator exclosures or selfing had occurred. Kaye (1999) also reported decreased fruit set in *Astragalus australis* var. *olympicus* in plants under pollinator exclosures. Wiens (1984) and Wiens et al. (1987) have suggested that S/O ratios are a function of breeding system, where inbreeders typically have S/O ratios higher than out-crossing species. Although these reports appear contradictory, an outcrossing species such as *Astragalus* has not undergone selection for efficient inbreeding strategies.
The reduced F/F and S/O ratios observed by Tepe dino (2005) for self-pollinated flowers might be the result of partial self-incompatibility, or a mechanical barrier interfering with self-pollination (Juncosa and Webster 1989, Kaye 1999).

For both Astragalus ampullarioides and A. holmgreniorum, maximum reproductive success is dependent upon cross-pollination. Higher density of plants did not appear to attract pollinators to populations of either Astragalus species, however, we did find that population size was positively correlated to the F/F ratio, both years, in A. holmgreniorum. During the 2009 field season, we observed fewer individuals at most populations. For example, at the Gardner Well population we recorded 20 individuals, with 17.9 flowers/plant in 2009 and 50+ individuals, with 38.5 flowers/plant in 2010. The between year differences in F/F ratios might be attributed to the likelihood that significantly more flowers selfed in 2009, due to fewer numbers of individuals in the population and fewer number of flowers per plant, which may have decreased the potential for pollinator visits.

Population size and density are factors that attract potential pollinators to a population (Agren 1996, Groom 1998, Steffan-Dewenter and Tscharntke 1999). Wilcock and Neiland (2002) suggest that if population size or density decreases it will impact pollinator interactions, where pollinators may no longer be attracted to a population or site. Although we found no significant correlation between population size or density in fruit set of Astragalus ampullarioides, this species typically grows in very small geographical areas exhibiting high plant densities and individuals producing numerous flowers.

For populations of Astragalus holmgreniorum we found a significant positive relationship between population size and fruit set, suggesting that pollinators are attracted to populations with larger numbers of individuals. Increased disturbances such as
development, ORV use, and grazing to populations of this species may ultimately cause declines in population size leading to disruptions in plant-pollinator interactions. Population fragmentation will result in fewer pollinators servicing an area (Rathcke and Jules 1993, Kearns 1998). With a loss of pollinators to these species, reproductive success is likely to decline due to an increase in self-pollination, and ultimately resulting in decreased genetic diversity within populations.

Populations of *Astragalus ampullarioides* were found to be fragmented into genetically differentiated populations (Breinholt et al. 2009). The lack of gene flow between populations, suggested by Breinholt et al. (2009), may be due to the short distance foraging nature of the primary pollinators and the large distances between populations. Several studies have attributed low S/O ratios to increased embryo abortions due to inbreeding in small, isolated populations of typically outcrossing species (Ledig 1986, Charlesworth and Charlesworth 1987, Levin 1991, James 2000, Allphin et al. 2002, Wiens et al. 2002, Allphin et al. 2005). The low S/O ratios observed in *A. ampullarioides* may be a result of inbreeding due to lack of gene flow between populations.

Studies have shown a link between genetic diversity and reproductive success (Wiens 1984, Karron et al. 1988, Karron 1989, Allphin et al. 2002, Allphin et al. 2005). Genetic diversity within a species increases its evolutionary fitness. However, as genetic diversity decreases, S/O ratios may also be reduced (Wiens 1984), especially in inbreeding populations of outcrossing species, where inbreeding depression may be taking place (Levin 1991). Wiens (1984) and Wiens et al. (1987) argued that genetics, rather than resource availability, largely determines S/O ratios within a species. Our data show, for *Astragalus ampullarioides*, the Pahcoo Wash population with the highest S/O ratio (Table
1) over both years of study, under different environmental conditions. Breinholt et al. (2009) also reported this population with the highest genetic diversity. Thus, it may be likely, for this species, that reproductive success is higher with increased genetic diversity of a population, or less inbreeding.

Herbivory and fruit parasitism also had strong influences on the reproductive success of *Astragalus ampullarioides*. Many species of *Astragalus* are known to be toxic, concentrating high levels of selenium, nitrotoxins, or locoine (alkaloidal substance) (Barneby 1989, Braun et al. 2003, Ralphs et al. 2008). Secondary compounds are used as defense mechanisms against predators, and may have evolved due to the selective pressures from predators (Janzen 1969). However the presence or effectiveness of any toxin produced by these rare *Astragalus* species has not been analyzed to date.

All populations of *Astragalus ampullarioides* exhibited some degree of herbivory, however at some populations we observed zero reproductive success (Shivwits and Zion populations in 2009 and Shivwits population in 2010), due to 100% herbivory of the inflorescences. The primary herbivores are likely rabbits and other small rodents (Miller et al. 2007). Herbivory has been reported yearly at the Pahcoon Wash and Harrisburg populations (Van Buren and Harper 2000, Searle 2010) and authors have suggested reductions in reproductive success due to these disturbances (Van Buren and Harper 2000).

Although only qualitative data on herbivory were collected in this study, herbivory decreased F/F ratios simply by removal of inflorescences. Beyond herbivory of the inflorescence, Obeso (1993) showed defoliation of vegetation had negative effects on F/F and S/O ratios, which may be a result of limited resource acquisition. This follows the
theory of induced defense (Rhoades and Cates 1976). When resources are limiting, such as water, less recourses are available for plant defense (Coley et al. 1985, Gershenzon 1987).

Herbivory was observed at populations of *A. holmgreniorum*. However, the effect was minor at all populations both years, except at the Purgatory Flat population. In 2010, prior to fruit collection, we observed that all fruiting stems showed significant signs of herbivory and only one fruit on one plant remained. Unfortunately, we did not collect data to measure the result of herbivory on overall reproductive output.

Fruit parasitism, by a parasitic wasp and weevil, reduced S/O ratios at all populations of *Astragalus ampullarioides*, except Coral Canyon where no evidence of insect predators were found. In both years of study, the Silver Reef population showed the highest percent of fruit parasitism, and in 2009 no viable seed were found in any parasitized fruit, ultimately contributing to the low S/O ratio observed. We did not observe fruit parasitism at any of the populations of *A. holmgreniorum*, thus these parasitic insects may prefer similar habitat characteristics as *A. ampullarioides*, or have a preference for this species (Lavergne et al. 2005). To determine insect preference for *A. ampullarioides* additional work should be done on fruit parasitism for other pant species found within these populations.

To maximize reproductive success, it is crucial for desert species to maintain a soil seed bank. For seedling recruitment, short-lived species, in particular, are dependent upon soil seed banks. Soil seed bank estimates for these rare species show that both maintain seed banks at higher densities than estimates of seedling emergence densities. Searle (2010) estimated mean seedling emergence densities for *Astragalus ampullarioides* in 2010 at 0.24±0.04 seedlings m\(^{-2}\) and *A. holmgreniorum* 0.07±0.03 seedlings m\(^{-2}\). These species
were also found to have higher seed bank densities than densities reported for above ground individuals (*A. ampullarioides* 0.92 plants m\(^{-2}\), *A. holmgreniorum* 0.13±0.04) (Searle 2010). These data are supporting evidence that these rare taxa maintain dormant viable soil seed banks. Although *A. ampullarioides* was estimated to have a higher seed bank density than *A. holmgreniorum* (Figure 13), this is likely a result of the higher density of reproductive individuals due to its specific soil requirement.

*Astragalus nuttallianus*, commonly associated with *A. holmgreniorum*, showed a significantly higher soil seed bank density. Although these species share common habitats, their reproductive and life history strategies are very different. *Astragalus nuttallianus* is an annual species that flowers in early spring, sets fruit, and finishes its life cycle by early summer (personal observations). This species is also consistently found at higher frequencies than *A. holmgreniorum* (Searle 2010), and due to its life-history strategy, likely exhibits higher reproductive output (Wiens 1984).

Long-term viability of seeds in the soil seed bank helps maintain levels of genetic diversity within a population (Morris et al. 2002), as well as maintain or increase the density of the seed bank. High levels of genetic diversity in the soil seed bank can be attributed to the contribution of seeds from different individuals, over generations (Templeton and Levin 1979), and can increase above ground diversity if seed emergence varies among genotypes (Hedrick 1995, Allphin et al. 1998).

Van Buren and Harper (2004b) and Van Buren (2008) report years when no emergence of any individuals of *Astragalus holmgreniorum* occurred due to extreme drought conditions. The next growing season following such events proved devastating for populations of *A. holmgreniorum*, where Van Buren and Harper (2004b) report no
surviving adults. Continuance of these populations relied on seedling emergence from the soil seed bank. Thus, maintenance of a soil seed bank is critical in the persistence of this species. Our results show little change in soil seed bank viability over a 1-year period, and are consistent with other studies showing high viability in soil seed bank seeds for several years in the soil (Pavone and Reader 1982, Ralphs and Cronin 1987, Fischer and Matthies 1998, Adams et al. 2005, Meyer et al. 2005, Arroyo et al. 2006).

Conclusions

For the conservation of these two rare species of *Astragalus*, conservation management plans must focus on sustaining viable populations. Population structure, reproductive success, and a soil seed bank all contribute to sustainable populations. The habitats that support populations of these species have been fragmented primarily by urban sprawl. ORV use, grazing, and competition with exotic species have further degraded habitats. Population fragmentation and degradation often results in reductions in population size and population isolation, leading to decreased genetic variability, and inbreeding (Jennersten 1988, Young et al. 1996). Therefore, an understanding of the effects of small population size, population structure, reproductive success, and soil seed bank dynamics are essential for the conservation of these rare species.

Increased understanding on limitations to reproductive success will be a vital next step in improving the seed set for these rare species. There are very few studies that report the reproductive process from reproductive individuals through seed germination events (Kaye 1999). For the conservation of these rare species it is important to understand what stages are limiting reproductive success. We have shown that both
species exhibit low pre-emergent reproductive success, while other studies on demographic parameters have shown high mortality in post-emergent reproductive success. Future studies should focus on possible limiting factors, such as the extent to which herbivory and fruit/seed predation decrease success, particularly in Astragalus ampullarioides, resource limitations, fertilization limitations, pollen source effects, selective embryo abortion, and effects of genetic diversity (inbreeding).

Reduced reproductive success has been documented in fragmented habitats, and Jennersten (1988) suggested that most seed in fragmented populations of Dianthus deltoids is the result of self-pollination. Tepedino (2005) has shown that reproductive success in both Astragalus ampullarioides and A. holmgreniorum is limited by self-pollination. Additionally, self-pollination over time will reduce genetic diversity, and may ultimately decrease the evolutionary adaptability of these species. Breinholt et al. (2009) has shown that populations of A. ampullarioides are genetically distinct, and suggests augmentation should be a serious consideration, especially in genetically depauperate populations. Increasing the genetic diversity via augmentation may increase the reproductive success of individuals within populations. However, where possible, pollinators and corridors between populations should also be protected.

Post-emergent reproductive success is also low in these species. Seedling mortality in both rare species is high, with few reaching reproductive maturity (Renee Van Buren, Dept of Biology, Utah Valley University, Orem, UT, personal communication). High seedling mortality is likely a result of resource availability, however a portion may be attributed to competition by exotic species, and human disturbances. Simpson (2003) has shown that seedling mortality in Astragalus holmgreniorum is significantly higher when a competitor is
rooted within 3 cm of the seedling. Although seedling mortality did not differ between native and introduced competitor species, Simpson (2003) showed that 5 exotic species contributed 65-76.7% of the competitors, while 15 native species contributed only 35% of the competition.

With populations of these rare species located near the urban center of St. George, Utah, and with intense recreational use of surrounding landscapes, management plans must focus on minimizing disturbances to these habitats, while sustaining reproductive output and soil seed banks in order to maintain viable populations.
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Tables and Figures

Table 1. Means and standard errors of F/F ratios, S/O ratios examined at all six populations of *Astragalus ampullarioides* and six populations of *A. holmgreniorum*. F statistics and P values testing for significant differences among populations were calculated using one-way ANOVA and Tukey multiple means comparison. Differing letters represent values that differed significantly at p≤0.05.

<table>
<thead>
<tr>
<th></th>
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<tbody>
<tr>
<td><em>A. ampullarioides</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Coral Canyon</td>
<td>0.02±0.01b</td>
<td>0.09±0.02b,c</td>
<td>0.28±0.07a</td>
<td>0.51±0.06a,b</td>
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<td>0.12±0.02a</td>
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<td>0.17±0.02a</td>
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<td>0.23±0.06a</td>
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<td>Silver Reef</td>
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<td>0.24±0.02a</td>
<td>0.02±0.01b</td>
<td>0.32±0.03c</td>
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<td>0.0</td>
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<td>19.05</td>
<td>6.73</td>
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<td><em>A. holmgreniorum</em></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Central Valley</td>
<td>0.15±0.02a</td>
<td>0.33±0.03a</td>
<td>0.31±0.04b</td>
<td>0.67±0.03</td>
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<td>Gardner Well</td>
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<td>0.33±0.03a</td>
<td>0.05±0.03c</td>
<td>0.67±0.03</td>
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<tr>
<td>Purgatory Flat</td>
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<td>0.005±0.005c</td>
<td>0.17±0.06b</td>
<td>0.0</td>
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<td>South Hills</td>
<td>0.04±0.02b</td>
<td>0.08±0.02c</td>
<td>0.60±0.17a</td>
<td>0.73±0.05</td>
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<td>State Line</td>
<td>0.10±0.02a</td>
<td>0.27±0.04a,b</td>
<td>0.49±0.05a</td>
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<td>Stucki Spring</td>
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<td>0.48±0.05a</td>
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Table 2. Significant between year differences of Fruit/Flower ratios and Seed/Ovule ratios at populations of *Astragalus ampullarioides* and *A. holmgreniorum*. Statistically significant differences set at $p \leq 0.05$.

<table>
<thead>
<tr>
<th>Population</th>
<th>F/F ratios</th>
<th>S/O ratios</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>A. ampullarioides</em></td>
<td></td>
<td></td>
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<tr>
<td>Coral Canyon</td>
<td>0.0153</td>
<td>0.0970</td>
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<tr>
<td>Harrisburg</td>
<td>0.9999</td>
<td>0.0122</td>
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<td>Pahcoom Wash</td>
<td>0.5284</td>
<td>&lt;0.000</td>
</tr>
<tr>
<td>Silver Reef</td>
<td>&lt;0.000</td>
<td>&lt;0.000</td>
</tr>
<tr>
<td><em>A. holmgreniorum</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Central Valley</td>
<td>0.0001</td>
<td>&lt;0.000</td>
</tr>
<tr>
<td>Gardner Well</td>
<td>&lt;0.000</td>
<td>&lt;0.000</td>
</tr>
<tr>
<td>Purgatory</td>
<td>0.9995</td>
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<td>South Hills</td>
<td>0.9999</td>
<td>0.9982</td>
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<td>State Line</td>
<td>0.0002</td>
<td>0.6575</td>
</tr>
<tr>
<td>Stucki Spring</td>
<td>0.6992</td>
<td>0.0822</td>
</tr>
</tbody>
</table>

*n/a – no fruit were collected at the Purgatory population during the 2010 field season.*
Table 3. Percent ovule abortions in fruits collected at populations of *Astragalus ampullarioides*.

Differing letters represent values that differed significantly at p≤0.05.

<table>
<thead>
<tr>
<th>Population</th>
<th>2009 (N)</th>
<th>ND*</th>
<th>Early</th>
<th>Partial</th>
<th>Late</th>
<th>Total Mean Abortions</th>
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<tbody>
<tr>
<td>Coral Canyon</td>
<td>13</td>
<td>3.2±0.02a,b</td>
<td>36.2±0.09a,b</td>
<td>30.2±0.07a</td>
<td>2.9±0.02a</td>
<td>72.5±0.07a,b</td>
</tr>
<tr>
<td>Harrisburg</td>
<td>31</td>
<td>3.1±0.01a</td>
<td>31.1±0.03a,b</td>
<td>23.9±0.02a</td>
<td>24.8±0.03b</td>
<td>82.9±0.02a,c</td>
</tr>
<tr>
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<td>3.4±0.03a,b</td>
<td>40.1±0.05a</td>
<td>10.2±0.02b</td>
<td>12.4±0.03a</td>
<td>66.0±0.06b</td>
</tr>
<tr>
<td>Silver Reef</td>
<td>19</td>
<td>10.3±0.03b</td>
<td>19.8±0.03b</td>
<td>51.4±0.05c</td>
<td>11.0±0.03a</td>
<td>92.5±0.04c</td>
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<tr>
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<td></td>
</tr>
<tr>
<td>Mean</td>
<td></td>
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<td>27.5±0.02</td>
<td>15.7±0.02</td>
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<td>2.67</td>
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<td>6.05</td>
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<th>Population</th>
<th>2010 (N)</th>
<th>ND*</th>
<th>Early</th>
<th>Partial</th>
<th>Late</th>
<th>Total Mean Abortions</th>
</tr>
</thead>
<tbody>
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<td>Coral Canyon</td>
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<td>28.9±0.07a,b</td>
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<tr>
<td>Harrisburg</td>
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<td>27.0±0.05a,b</td>
<td>4.0±0.03</td>
<td>57.0±0.05a</td>
</tr>
<tr>
<td>Pahcoon Wash</td>
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<td>0.9±0.004</td>
<td>22.2±0.03</td>
<td>15.8±0.03a</td>
<td>1.1±0.01</td>
<td>39.9±0.04b</td>
</tr>
<tr>
<td>Silver Reef</td>
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<td>34.00.03b</td>
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<td>55.5±0.03a</td>
</tr>
<tr>
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<td>49.8±0.03a,b</td>
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</table>

*No development of ovule
n/a – no fruit collected at population.
Table 4. Percent ovule abortions in fruits collected at populations of *Astragalus holmgreniorum*.

Differing letters represent values that differed significantly at \( p \leq 0.05 \).

<table>
<thead>
<tr>
<th>Population</th>
<th>2009 (N)</th>
<th>ND*</th>
<th>Early</th>
<th>Partial</th>
<th>Late</th>
<th>Total Mean Abortions</th>
</tr>
</thead>
<tbody>
<tr>
<td>Central Valley</td>
<td>36</td>
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<td>12.7±0.01</td>
<td>33.7±0.02a</td>
<td>18.0±0.03a</td>
<td>70.3±0.03a</td>
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<tr>
<td>Gardner Well</td>
<td>5</td>
<td>5.2±0.03</td>
<td>23.9±0.08</td>
<td>25.3±0.07a,c</td>
<td>40.2±0.07b</td>
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<tr>
<td>Purgatory Flat</td>
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<td>54.8±0.07b</td>
<td>9.5±0.05a</td>
<td>82.9±0.06b</td>
</tr>
<tr>
<td>South Hills</td>
<td>3</td>
<td>3.7±0.02</td>
<td>11.8±0.07</td>
<td>21.4±0.11a,c</td>
<td>1.1±0.01a,c</td>
<td>38.1±0.16a,c</td>
</tr>
<tr>
<td>State Line</td>
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<td>3.2±0.01</td>
<td>16.1±0.03</td>
<td>29.0±0.04a,c</td>
<td>3.2±0.01c</td>
<td>51.4±0.04c</td>
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<tr>
<td>Stucki Spring</td>
<td>23</td>
<td>4.0±0.01</td>
<td>23.4±0.05</td>
<td>19.2±0.03c</td>
<td>5.4±0.02c</td>
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</tr>
<tr>
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<td>10.9±0.02</td>
<td>61.4±0.02</td>
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<table>
<thead>
<tr>
<th>Population</th>
<th>2010 (N)</th>
<th>ND*</th>
<th>Early</th>
<th>Partial</th>
<th>Late</th>
<th>Total Mean Abortions</th>
</tr>
</thead>
<tbody>
<tr>
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<td>16.6±0.02</td>
<td>12.6±0.02a,b</td>
<td>0.6±0.004</td>
<td>33.1±0.03</td>
</tr>
<tr>
<td>Gardner Well</td>
<td>42</td>
<td>2.3±0.01</td>
<td>11.9±0.02</td>
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<td>2.0±0.01</td>
<td>32.9±0.03</td>
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<tr>
<td>Purgatory Flat</td>
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<td>n/a</td>
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<td>n/a</td>
</tr>
<tr>
<td>South Hills</td>
<td>12</td>
<td>2.4±0.02</td>
<td>13.6±0.03</td>
<td>9.7±0.02a,b</td>
<td>1.0±0.01</td>
<td>26.7±0.05</td>
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<td>16.0±0.03</td>
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<td>1.4±0.01</td>
<td>38.9±0.04</td>
</tr>
<tr>
<td>Stucki Spring</td>
<td>36</td>
<td>2.8±0.01</td>
<td>18.6±0.03</td>
<td>9.4±0.01b</td>
<td>4.0±0.02</td>
<td>34.8±0.04</td>
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<tr>
<td>Mean</td>
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<td>0.004</td>
<td>0.175</td>
<td>0.391</td>
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</table>

*No development of ovule
n/a – no fruit collected at population.
Table 5. Sample size and percent fruit parasitism at populations of *Astragalus ampullarioides*.

<table>
<thead>
<tr>
<th>Population</th>
<th>2009 (N)</th>
<th>% Parasitism</th>
<th>2010 (N)</th>
<th>% Parasitism</th>
</tr>
</thead>
<tbody>
<tr>
<td>Coral Canyon</td>
<td>13</td>
<td>0</td>
<td>11</td>
<td>0</td>
</tr>
<tr>
<td>Harrisburg</td>
<td>31</td>
<td>3.0</td>
<td>19</td>
<td>26.3</td>
</tr>
<tr>
<td>Pahcoo Wash</td>
<td>23</td>
<td>43.0</td>
<td>32</td>
<td>15.6</td>
</tr>
<tr>
<td>Silver Reef</td>
<td>19</td>
<td>68.4</td>
<td>57</td>
<td>74.6</td>
</tr>
<tr>
<td>Zion</td>
<td>na</td>
<td>na</td>
<td>48</td>
<td>70.8</td>
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Table 6. Estimated seed rain for populations of *Astragalus ampullarioides* and *A. holmgreniorum*.

<table>
<thead>
<tr>
<th></th>
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</tr>
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<tbody>
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<td><em>A. ampullarioides</em></td>
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<td></td>
</tr>
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<td>566</td>
<td>3,154</td>
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<tr>
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</tr>
<tr>
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<td><em>A. holmgreniorum</em></td>
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</tr>
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<td>9,215</td>
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</table>
Table 7. Soil seed bank density and percent viability of *Astragalus holmgreniorum* and *A. nuttallianus*. Density reported as seeds m$^{-2}$.

<table>
<thead>
<tr>
<th>Population</th>
<th>Density <em>A. holmgreniorum</em></th>
<th>Viability (%)</th>
<th>Density <em>A. nuttallianus</em></th>
<th>Viability (%)</th>
</tr>
</thead>
<tbody>
<tr>
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<td>83.3</td>
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<td>100.0</td>
<td>538.4</td>
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<td>58.04</td>
<td>86.5</td>
<td>131.4</td>
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<td>95.5</td>
<td>338.5</td>
<td>100.0</td>
</tr>
<tr>
<td>Stucki Spring</td>
<td>6.03</td>
<td>20.0</td>
<td>2.0</td>
<td>100.0</td>
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</table>
Table 8. Percent viability of seeds of *Astragalus holmgreniorum* and *A. nuttallianus* extracted from soil seed bank samples.

<table>
<thead>
<tr>
<th>Population</th>
<th>Lab Germinated (%)</th>
<th>Positive TZ* (%)</th>
<th>Dead (%)</th>
<th>Total Viability (%)</th>
</tr>
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<td></td>
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<td>33.0</td>
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<td>83.3</td>
</tr>
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<td>50.0</td>
<td>50.0</td>
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<td>Purgatory</td>
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<td>0</td>
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<td>Gardner Well</td>
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<td>0</td>
<td>0</td>
<td>100.0</td>
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<tr>
<td>Purgatory</td>
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<td>100.0</td>
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<tr>
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<td>0</td>
<td>0</td>
<td>100.0</td>
</tr>
</tbody>
</table>

*TZ – Tetrazolium test (International Seed Testing Association 1985)*
Figure 1. Map of population distribution for *A. ampullarioides* and *A. holmgreniorum* in Washington, County, Utah, and Mojave County, Arizona.
Figure 2. Mature seeds of *Astragalus ampullarioides* (left) and *A. holmgreniorum* (right).
Figure 3. Mean overall species values and standard errors for flowers, fruits, ovules, and seeds of *Astragalus ampullarioides* and *A. holmgreniorum*.
Figure 4. Insect parasitism of *Astragalus ampullarioides* fruit and seed. Left: parasitic wasp (above) and weevil (below), middle: parasitized fruit, and right: parasitized seed.
Figure 5. Seeds and aborted ovules in fruits of *Astragalus ampullarioides* and *A. holmgreniorum*.  
Top left: early aborted ovules of *A. ampullarioides*. Top right: *A. holmgreniorum* fruit with partial aborted ovules. Below: filled seeds of *A. holmgreniorum*. 
Figure 6. Percent herbivory at populations of *Astragalus ampullarioides* in 2010.
Figure 7. Percent herbivory at populations of *Astragalus holmgreniorum* in 2010.
Figure 8. Seed Persistence – graph shows the proportion of buried seeds of *Astragalus ampullarioides* that 1) germinated under field conditions, 2) germinated under lab conditions, 3) tested viable in tetrazolium test, and 4) were dead.
Figure 9. Seed Persistence – graph shows the proportion of buried seeds of *Astragalus holmgreniorum* that 1) germinated under field conditions, 2) germinated under lab conditions, 3) tested viable in tetrazolium test, and 4) were dead.
Figure 10. Soil seed bank densities at populations of *Astragalus holmgreniorum*. 
Figure 11. Comparison of soil seed bank densities studies for *Astragalus ampullarioides* and *A. holmgreniorum*.