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14. ABSTRACT The Lane Mountain milkvetch, <i>Astragalus jaegerianus</i> , is an endangered species that exists in fragmented populations in the Mojave Desert. UCLA monitored populations have declined by 76% since 1999 due to drought. Reintroduction experiments support this idea: supplemental water increased seedling survivorship. Phenological studies suggest that between-year differences in <i>A. jaegerianus</i> phenology are pronounced, and controlled by annual differences in precipitation. Seed production per plant is highly variable. Study plants had significant					
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Report Title

Community Dynamics and Soil Seed Bank Ecology of Lane Mountain Milkvetch (*Astragalus jaegerianus* Munz)

ABSTRACT

The Lane Mountain milkvetch, *Astragalus jaegerianus*, is an endangered species that exists in fragmented populations in the Mojave Desert. UCLA monitored populations have declined by 76% since 1999 due to drought. Reintroduction experiments support this idea: supplemental water increased seedling survivorship. Phenological studies suggest that between-year differences in *A. jaegerianus* phenology are pronounced, and controlled by annual differences in precipitation. Seed production per plant is highly variable. Study plants had significant reproductive potential that was unrealized in 2011 and 2012. High precipitation in 2011 is a likely explanation for increases in seed production in some plants, but the strong negative effect of herbivory on other plants appears to have overwhelmed the positive effect of precipitation on seed production. The soil seed bank may be categorized as low, persistent, and largely restricted to the area beneath host shrubs with active *A. jaegerianus*. Seed dispersal is low. The post-dispersal seed bank, significantly declined in 2011 despite increases in precipitation. Decreases in soil seed density are attributable to two factors: (1) a decrease in seed production due to increases in herbivory, and (2) an increase in seed predation due to high seed predator populations and an extended fruit dehiscing period.

Enter List of papers submitted or published that acknowledge ARO support from the start of the project to the date of this printing. List the papers, including journal references, in the following categories:

(a) Papers published in peer-reviewed journals (N/A for none)

<u>Received</u>	<u>Paper</u>
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TOTAL:

Number of Papers published in peer-reviewed journals:

(b) Papers published in non-peer-reviewed journals (N/A for none)

<u>Received</u>	<u>Paper</u>
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TOTAL:

Number of Papers published in non peer-reviewed journals:

(c) Presentations

1. Huggins, T. R., B. A. Prigge, M. R. Sharifi, and P. W. Rundel. 2012. Ecological factors contributing to the rarity and decline of the Lane Mountain milkvetch, *Astragalus jaegerianus* Munz. California Native Plant Society Conference 2012 Conservation Conference: Conserving and restoring the roots of California's richness. San Diego, CA.
2. Huggins, T. R., B. A. Prigge, M. R. Sharifi, and P. W. Rundel. 2011. The effects of substrate on adjacent shrub communities, and the distribution of the California endemic, *Astragalus jaegerianus* Munz. Medecos XII: linking science to resource management. The International Mediterranean Ecosystems Conference. University of California, Los Angeles.

Number of Presentations: 2.00

Non Peer-Reviewed Conference Proceeding publications (other than abstracts):

Received Paper

TOTAL:

Number of Non Peer-Reviewed Conference Proceeding publications (other than abstracts):

Peer-Reviewed Conference Proceeding publications (other than abstracts):

Received Paper

TOTAL:

Number of Peer-Reviewed Conference Proceeding publications (other than abstracts):

(d) Manuscripts

Received Paper

01/28/2010 1.00 T. Huggins, B. Prigge, M. Sharifi, P. Rundel. THE EFFECTS OF LONG-TERM DROUGHT ON HOST PLANT CANOPY CONDITION AND SURVIVAL OF THE ENDANGERED ASTRAGALUS JAEGERIANUS (FABACEAE), (01 2010)

09/12/2011 2.00 Barry A. Prigge, Thomas R. Huggins,, M. R. Sharifi, Philip W. Rundel. Bottom-up effects of substrate on two adjacent shrub communities and the distribution of a rare and endangered plant species, Astragalus jaegerianus Munz, Conference Proceeding of the Wildland Shurb Simposium XVI (09 2011)

TOTAL: 2

Number of Manuscripts:

Books

Received Paper

TOTAL:

Patents Submitted

Patents Awarded

Awards

Graduate Students

<u>NAME</u>	<u>PERCENT SUPPORTED</u>
FTE Equivalent:	
Total Number:	

Names of Post Doctorates

<u>NAME</u>	<u>PERCENT SUPPORTED</u>
Thomas R. Huggins	1.00
FTE Equivalent:	1.00
Total Number:	1

Names of Faculty Supported

<u>NAME</u>	<u>PERCENT SUPPORTED</u>	National Academy Member
Philip Rundel	0.10	
FTE Equivalent:	0.10	
Total Number:	1	

Names of Under Graduate students supported

<u>NAME</u>	<u>PERCENT SUPPORTED</u>	Discipline
Suh Young Woo	0.25	
Uyen Thuc Nguyen	0.25	
FTE Equivalent:	0.50	
Total Number:	2	

Student Metrics

This section only applies to graduating undergraduates supported by this agreement in this reporting period

- The number of undergraduates funded by this agreement who graduated during this period: 2.00
- The number of undergraduates funded by this agreement who graduated during this period with a degree in science, mathematics, engineering, or technology fields:..... 2.00
- The number of undergraduates funded by your agreement who graduated during this period and will continue to pursue a graduate or Ph.D. degree in science, mathematics, engineering, or technology fields:..... 1.00
- Number of graduating undergraduates who achieved a 3.5 GPA to 4.0 (4.0 max scale):..... 2.00
- Number of graduating undergraduates funded by a DoD funded Center of Excellence grant for Education, Research and Engineering:..... 0.00
- The number of undergraduates funded by your agreement who graduated during this period and intend to work for the Department of Defense 0.00
- The number of undergraduates funded by your agreement who graduated during this period and will receive scholarships or fellowships for further studies in science, mathematics, engineering or technology fields: 0.00

Names of Personnel receiving masters degrees

<u>NAME</u>
Total Number:

Names of personnel receiving PHDs

<u>NAME</u>
Total Number:

Names of other research staff

<u>NAME</u>	<u>PERCENT SUPPORTED</u>
M. Rasoul Sharifi	0.30
Barry A. Prigge	0.05
FTE Equivalent:	0.35
Total Number:	2

Sub Contractors (DD882)

Inventions (DD882)

Scientific Progress

The endangered Lane Mountain milkvetch, *Astragalus jaegerianus* Munz, is a narrowly endemic plant that exists in small fragmented populations restricted to shallow, granitic soils in the central Mojave Desert. A climbing, herbaceous perennial, *Astragalus jaegerianus* belongs to a relatively unstudied group of desert plant species whose life histories occur largely within the canopies of desert shrubs (thamnophytes). *Astragalus jaegerianus* grows in a variety of co-occurring desert shrubs but appears to be incompatible with the regional dominant *Larrea tridentata*. This incompatibility seems to restrict *A. jaegerianus* to patchy habitats of shallow-soil where the density of *Larrea* is reduced, and the density of compatible host shrubs is high. Thus, *A. jaegerianus* could be a novel example of a second-order edaphic endemic whose distribution is indirectly controlled by edaphics through the effect of edaphics on its community of host shrubs.

Population dynamics. Since the listing of *A. jaegerianus* as an endangered species in the late 1990's, this historically rare plant has undergone significant population contractions, and in 2009 monitored populations were only 16% of their size in 1999, leaving some monitored populations at critically low levels, and in danger of local extinction. The results of this 13-year study demonstrate that *A. jaegerianus* population dynamics from 1999-2012 were controlled by growing-season precipitation, and as a result, drought conditions since 1999 in the Mojave Desert have led to major population declines in UCLA monitored populations (-76% in 2011). The population dynamics of *A. jaegerianus* study plants differed from the "boom or bust" dynamics of the other xeric *Astragalus* species. *Astragalus jaegerianus* recruitment has been relatively modest, even during an extraordinary wet season such as 2005 (352 mm), and mortality, though higher in drought years such as 2007 (19 mm), has been more or less gradual. As a result, the frequency and amplitude of population cycles should be lower in *A. jaegerianus*, and in phase with wet and dry climate-periods in the Mojave Desert (the climate-period hypothesis). While *A. jaegerianus* recruitment is an unambiguous function of seasonal precipitation, mortality as a function of precipitation is complicated by host shrub effects, including time-lags in mortality due to drought-damage to host shrubs, and "drought-selection" in which *A. jaegerianus* populations become increasingly drought tolerant as plants and host shrubs less capable of withstanding drought are removed through drought mortality. Dormancy was a relatively uncommon phenomenon during the study period, and did not exceed 3 plants per year except the drought year of 2007 when 19 out of 20 study plants went dormant. Episodes of dormancy (1 season or 2 consecutive seasons) were observed 25 times in 22 different *A. jaegerianus* study plants between 1999 and 2011.

Phenology. The results of this study support our previous suggestion that between-year differences in *A. jaegerianus* phenology might be pronounced, and controlled by annual differences in precipitation (Rundel et al. 2010). The initiation of resprouting in 2011, which began 1 to 2 weeks after the first winter storm of the season, suggests that a precipitation event of as little as 20.6 mm is sufficient to trigger resprouting. Differences between plants in their sensitivity to precipitation could explain differences in the timing of resprouting between plants, and could explain why some plants resprout during years of low rainfall, and others remain dormant. A precipitation cue to resprouting could cause plant and pollinator mismatch if *A. jaegerianus* precipitation cues and insect temperature cues are not synchronized. The results of this study demonstrate that the quantity and timing of seasonal precipitation can have a strong effect on *A. jaegerianus* phenology. Precipitation during the 2011 reproductive season (high rainfall, relatively early) resulted in appreciable phenological shifts in the duration and timing of *A. jaegerianus* phenology relative to 2010, a year of average precipitation. Phenological shifts of the magnitude observed in 2011 could have substantial negative effects on *A. jaegerianus* reproduction. Precipitation during the 2012 reproductive season (low rainfall, relatively late) resulted in substantial dormancy and reproductive failure. Long-term, multi-year studies of the effects of interannual variation in precipitation on *A. jaegerianus* phenology will help wildlife managers anticipate the possible effects of climate change on *A. jaegerianus* phenology and reproductive success.

Seed production. Seed production per plant in *A. jaegerianus* was highly variable in 2010 and 2011, and significant reproductive potential went unrealized in both years. The greatest loss in reproductive potential was flower abortion (81.0%), but of the 19.0% of flowers that matured into fruit, 59% of ovules were lost because of lack of fertilization and aborted seed. The similarity between basic reproductive metrics in 2010 and 2011 suggests that these intrinsic features of *A. jaegerianus* reproduction may be more or less invariant in wet years like 2010 and 2011, but more study is needed in dry years. While seed production in 2011 cumulatively decreased among *A. jaegerianus* study plants, individual plants increased or decreased seed production independently suggesting that countervailing forces may have been acting on plants simultaneously. High precipitation in 2011 is a likely explanation for increases in seed production in some plants, but the strong negative effect of herbivory on other plants appears to have overwhelmed the positive effect of precipitation on seed production. Early precipitation may also have contributed to decreases in seed production by advancing *A. jaegerianus* phenology, and leading to some degree of plant-pollinator asynchrony.

Re-introduction experiment. In this study, we presented the results of our pilot reintroduction study in which we document the effect of supplemental watering, herbivore exclusion, and competition with annuals on the seedling establishment of *A. jaegerianus*. Our results demonstrate that for the purposes of *A. jaegerianus* reintroduction, the combination of supplemental water, herbivore exclusion, and the removal of annuals, provided the best conditions for growth and survival of *A. jaegerianus* seedlings. Using these methods, wildlife managers can expect 85% seedling survival the first year. The results of this study suggest that host shrubs only weakly protect *A. jaegerianus* seedlings from herbivory; herbivory was high in uncaged treatments and herbivores were small and likely to be insects and possibly lizards. We have previously hypothesized that *A. jaegerianus* recruitment failure was a consequence of long-term drought (Huggins et al. 2010), and these results support this idea: without water supplementation, seedlings had low growth and high mortality from wilting even in a year of above average precipitation such as 2010.

Soil seed bank. Soil seed bank sampling in 2011 confirmed sampling in 2009 and 2010 that suggests that *Astragalus*

jaegerianus has a low density, long-term persistent seed bank of approximately 140 seeds•m⁻², and a transient seed bank which fluctuates between a pre- and post-dispersal density of approximately zero and 700 seeds•m⁻². While our results indicate that seed may persist in the soil seed bank after active *A. jaegerianus* have died, recruitment of new plants to shrubs with once active *A. jaegerianus* has been observed only twice in 14 years of field surveys. The dispersal of seed beyond host shrubs with actively growing *A. jaegerianus* is rare and restricted to shrubs in the immediate vicinity of host shrubs with actively growing *A. jaegerianus*. Long distance dispersal of seed to shrubs 10 m from host shrubs with actively growing *A. jaegerianus* was not detected in this study. An analysis of inter-seasonal decreases in seed density, suggested that seed predation occurs primarily during the summer, and that rates of seed consumption decline during the fall and winter, as the transient seed bank is depleted. Pre-dispersal seed densities in 2011 remained nearly identical to 2009 and 2010, but post-dispersal densities in 2010 increased, possibly because of increased precipitation. Our prediction that years with high precipitation should produce higher density transient seed banks than years with low precipitation was not supported by our results in 2011: the post-dispersal transient seed bank, significantly declined in 2011 by 53% despite substantial increases in precipitation. These decreases in soil seed density are attributable to two factors: (1) a decrease in seed production due to increases in herbivory, and (2) a putative increase in seed predation due to high seed predator populations and an extended seed dispersal period. Rough estimates suggest that post-dispersal seed predation is high (≈98%), and as a result, granivores exclusion is likely to be the most effective method of maintaining and reintroducing *A. jaegerianus* populations that are now at very low levels.

Technology Transfer

Community dynamics and Soil Seed Bank Ecology of the Lane Mountain milkvetch (*Astragalus jaegerianus* Munz)

Final Report
Research Period: October 2008-October 2012
(ARO Contract Num. 55166-EV)

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SUMMARY

The endangered Lane Mountain milkvetch, *Astragalus jaegerianus* Munz, is a narrowly endemic plant that exists in small fragmented populations restricted to shallow, granitic soils in the central Mojave Desert. A climbing, herbaceous perennial, *Astragalus jaegerianus* belongs to a relatively unstudied group of desert plant species whose life histories occur largely within the canopies of desert shrubs (thamnophytes). *Astragalus jaegerianus* grows in a variety of co-occurring desert shrubs but appears to be incompatible with the regional dominant *Larrea tridentata*. This incompatibility seems to restrict *A. jaegerianus* to patchy habitats of shallow-soil where the density of *Larrea* is reduced, and the density of compatible host shrubs is high. Thus, *A. jaegerianus* could be a novel example of a second-order edaphic endemic whose distribution is indirectly controlled by edaphics through the effect of edaphics on its community of host shrubs.

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Soil seed bank. Soil seed bank sampling in 2011 confirmed sampling in 2009 and 2010 that suggests that *Astragalus jaegerianus* has a low density, long-term persistent seed bank of approximately 140 seeds·m⁻², and a transient seed bank which fluctuates between a pre- and post-dispersal density of approximately zero and 700 seeds·m⁻². While our results indicate that seed may persist in the soil seed bank after active *A. jaegerianus* have died, recruitment of new plants to shrubs with once active *A.*

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SECTION 1

POPULATION DYNAMICS, 2011

INTRODUCTION

The genus *Astragalus* (Fabaceae) is currently the world's largest genus of flowering plants with 3210 known species (Frodin 2004). *Astragalus* has a primarily circumboreal distribution in semiarid, arid, and cool temperate regions of the northern hemisphere, with a lesser presence in South America, equatorial Africa, and subtropical India (Mabberley 2008, Welsh et al. 2007, Rundel 2012). There are two major centers of diversification: western North America, and Asia from the eastern Mediterranean Basin to the western Himalayan Plateau (Rundel 2012). There are approximately 390 to 450 species in North America commonly known as milkvetch or locoweed (Welsh et al. 2007, Barneby 1964). *Astragalus* species exhibit an extraordinary capacity for edaphic specialization, often leading to highly restricted geographic ranges of distribution and rarity (Rundel 2012). Consequently, the genus *Astragalus* has the highest number of protected species in the continental United States; 13 species and 7 varieties of are currently listed as threatened or endangered species, with an additional 5 candidate taxa (Rundel 2012).

One of these endangered *Astragali* is the Lane Mountain milkvetch, *Astragalus jaegerianus* Munz, a narrowly endemic plant that exists in small fragmented populations restricted to shallow, granitic soils in the central Mojave Desert. Two-thirds of all known

A. jaegerianus occur within the boundaries of the U.S. Army's National Training Center at Fort Irwin, approximately 50 km NE of Barstow, CA (Charis Professional Services, 2002). The distribution of the species is concentrated in four geographic areas (Coolgardie Mesa, Paradise Valley, Brinkman Wash-Montana Mine, and the Gemini Conservation Area; Fig. 1) that total approximately 8,000 ha (Charis Professional Services 2002). Surveys of these areas in 2001 found 5,723 mature *A. jaegerianus* plants, though the total population size of the species was likely to be higher depending on the observability of plants, and the density of plants in un-surveyed areas within the plant's range (Charis Professional Services 2002). Because of its limited distribution and potential threat from military training, the U.S. Fish and Wildlife Service (USFWS 1998) listed *A. jaegerianus* as a federally endangered species in 1998.

Astragalus jaegerianus is a climbing, herbaceous perennial that belongs to a relatively unstudied group of desert plant species whose life histories occur largely within the canopies of desert shrubs (thamnophytes). *Astragalus jaegerianus* grows in a variety of co-occurring desert shrubs commonly including *Thamnosma montana*, *Ambrosia dumosa*, and *Eriogonum fasciculatum*. In a 2001 survey, less than 0.1% of *A. jaegerianus* were found outside of host shrubs, suggesting that in all but the most rare circumstances, *A. jaegerianus* requires a host shrub to survive (Charis Professional Services 2002). Our previous studies demonstrate that *A. jaegerianus* has no preference in its selection of host shrub species, except in its antipathy for *Larrea tridentata*, in which it rarely occurs and appears to be incompatible (Prigge et al. 2011). This incompatibility with the regionally dominant *Larrea* appears to restrict *A. jaegerianus* to patches of shallow-soiled habitat where the density of *Larrea* is reduced, and the density

of compatible host shrubs is high (Prigge et al. 2011). Thus, *A. jaegerianus* appears to be a novel example of a second-order edaphic endemic whose distribution is indirectly controlled by edaphics through the effect of edaphics on its community of host shrubs (Prigge et al. 2011).

Despite the close relationship between *A. jaegerianus* and its host shrubs, the nature of the interaction is not entirely clear, and is likely to be complicated because positive and negative effects of host plants on protégé occur simultaneously (Holmgren et al. 1997), and may change with host or protégé life-stage (Shumway 2000, Miriti 2007, Reisman-Berman 2007). Positive host shrub effects on *A. jaegerianus* include the use of host shrub canopies as structural support (Gibson et al. 1998), and as protection from large herbivores such as jackrabbits (Rundel et al. 2011). Host shrub canopies also produce a modified microclimate that is conducive to *A. jaegerianus* growth and seedling recruitment (Huggins et al. 2010). Because of their proximity, *A. jaegerianus* and its host shrubs may share water resources, but the degree to which they may compete for water resources is unknown. Although the relationship between *A. jaegerianus* and its host plants could to be antagonistic in some respects (e.g. competition for water or nutrients), in other respects host plants may benefit from the increased soil nitrogen associated with *A. jaegerianus* nitrogen fixation (Gibson et al. 1998).

Astragalus jaegerianus is capable of dormancy within and between years. Typically, *A. jaegerianus* germinates or resprouts with winter rains, and then climbs through its host shrub until it emerges from its host shrub canopy to set flower and fruit in late spring. Soon after primary seed dispersal in early summer, plants enter summer dormancy until winter rains in the following season trigger resprouting. If insufficient

precipitation occurs to trigger resprouting, plants may remain dormant through years of extreme drought.

Since the listing of *A. jaegerianus* as an endangered species in the late 1990's, this historically rare plant has undergone significant population contractions, and in 2009 monitored populations were only 16% of their size in 1999, leaving some monitored populations at critically low levels, and in danger of local extinction (Rundel et al. 2009). These population declines have occurred simultaneously with recent drought conditions in the Mojave Desert (Hamerlynck and McAuliffe 2008). Dry and wet climate periods in the Mojave cycle every 20-30 years, and so recent drought conditions may represent the onset of a new dry climate period (Hereford et al. 2006). Alternately, drought conditions since 1999 may represent the evolution of a novel climate in the Mojave Desert as the result of global climate change processes (Hoerling and Kumar 2003). If so, dry conditions in the Mojave Desert could continue for an indefinite period as projected by global climate change-type drought (Cook et al. 2004, Breshears et al. 2005, Seager et al 2007).

The following study describes the results of a 13-year population study (1999 to 2011), and analyses the role of seasonal precipitation in *A. jaegerianus* population dynamics including its recent declines.

METHODS

Population Demography (Field surveys)

The *A. jaegerianus* populations monitored in this study are located in two neighboring geographic areas, the Goldstone and Brinkman Wash, previously established

as discrete areas of *A. jaegerianus* distribution (Fig. 1; Prigge et al. 2000, Charis Professional Services 2002, Walker & Metcalf 2008). The UCLA monitored populations within Goldstone are located in a protected zone that is off-limits to Army training called the Gemini Conservation Area. Each geographic area contains two study populations. These monitored sites were initially chosen because of their high density of *A. jaegerianus* compared to adjacent areas, and therefore represent areas of unusually high densities within the GCA and Brinkman Wash. The soils at these sites are composed of shallow granitic colluvium and granite outcrops, within the transition zone between Mojavean creosote bush scrub and Joshua tree woodland communities between 3000 and 4000 ft. of elevation (see Barbour 1988 for description of communities).

Each *A. jaegerianus* study population is located on a permanent plot that was first established in 1999 (Brinkman Wash) and 2003 (GCA). Each season from 1999 to 2012, several site visits were conducted to each of these permanent survey plots, with the exception of 2000-2002 in which no surveys were conducted, and 2005-2008 in which no surveys were conducted at Brinkman 3 (Table 1). During these visits, old, previously tagged plants and their host shrubs were located and searches were conducted for new *A. jaegerianus* plants under previously tagged and adjacent host shrubs. Tagged *A. jaegerianus* plants were assessed to determine if they had resprouted (active) or not (inactive), and their size and reproductive condition was noted. Inactive plants were either dead or dormant, but were assumed dead if inactive in years with above average precipitation (e.g. 2005 or 2010). Seedlings found during surveys were marked with small, coded stakes, and measured for height and number of leaves. Seedlings were revisited on subsequent surveys to monitor their development and survival. For all *A.*

jaegerianus plants found, UTM coordinates were recorded and readings from previous years were updated for accuracy.

While surveys were focused on previously tagged plants, new plants were discovered through unstructured, meandering searches of the study plots between visits to previously recorded plants. In addition to these unstructured searches, every shrub in the permanent plots was inspected for *A. jaegerianus* through high intensity sweeps in 2011 and 2012. High intensity sweeps consisted of edge-to-edge walking transects with observers 4 m apart, and at a speed sufficient to allow each observer to inspect each shrub within their transect. This survey method is capable of detecting mature plants that have emerged from their host shrub canopy; sub-emergent seedlings, even large seedling as long as 20 cm, are virtually undetectable within their host shrubs (see *Recruitment* below).

Recruitment

The period from the germination of an *A. jaegerianus* seed to its first flowering, referred to here as the seedling stage, is obscure and not well understood, because seedlings are inconspicuous and easily missed within the dense interior vegetation of their host shrub. The best information we have about this life history stage comes from seedling growth experiments conducted in 2010 within a monitored study population at the Gemini Conservation Area (Section 4). In the experiment, seedlings in the cotyledon stage were transplanted under typical *A. jaegerianus* host shrubs, and watered to an extent equivalent to years of high precipitation at the Gemini Conservation Area (GCA). Despite average natural precipitation and supplemental watering, first-year seedling did not flower and most did not emerge from the canopy of their host shrubs. The next year

(2011), despite well above-average precipitation and supplemental watering, many resprouting second-year seedlings did not flower. Because sterile, non-emergent *A. jaegerianus* seedlings are highly cryptic, this study suggests that under conditions of natural precipitation, seedlings may be active but remain unobserved within nurse shrub canopies for at least two years prior to emergence and flowering. Therefore, previously unobserved reproductive plants are likely to be the product of 2 or more years of above-average precipitation and cryptic growth within nurse shrub canopies. As a result, we use the term recruitment to mean the year of first flowering and not germination, which is likely to have occurred 1 or 2 years previously.

Precipitation data

Analyses used October through May precipitation because it includes winter and spring rainfall that affects *A. jaegerianus* growth, reproduction and germination, and excludes summer precipitation that occurs during *A. jaegerianus*' dormant period. Precipitation data (October-May) from 1999 to 2011 was assembled from a set of weather stations within and adjacent to *A. jaegerianus* population areas. The weather station closest to our monitored *A. jaegerianus* study sites (6 km) is the Goldstone Echo #2 weather station (35°17' N, 116°47' W; elevation 950 m). Available precipitation data from the Goldstone Echo #2 weather station ended in 2006. Precipitation data for 2003, and from 2007 through 2009 were generated by the remote automated weather station (RAWS) at Opal Mountain CA (35°09'N; 117°10'W; 980 m.). This weather station is approximately 30 km SW of UCLA's milkvetch study sites. Opal Mountain and Goldstone monthly precipitation from 1992 through 2006 was compared using linear

regression, and the slope (0.96) was used to convert Opal Mountain precipitation into an estimated chronosequence of Goldstone precipitation from 2007 through 2009 ($y = 0.96x + 0.390$, $r^2 = 0.83$, $p < 0.0001$, $n = 112$ months). From 2010 through 2012, precipitation data were collected from a UCLA weather station (Hobo Weather Station, H21-001, Onset Computer Corporation) located within *A. jaegerianus* study population at the GCA (35°14' N, 116°47' W; elevation 1,100 m); these data were unadjusted because of its proximity to the Goldstone Echo #2 weather station (6 km).

Statistical analyses

Precipitation and population data were analyzed using the open-source statistical computing program R (R Development Core Team, 2011). Linear regression analysis was used in two contexts: to compare and adjust monthly precipitation data between weather stations, and to examine the relationship between the population change, recruitment, and seasonal precipitation. Population change (P_c) was defined as the relative change between years:

$$P_c = (P_{x+1} - P_x)/P_x,$$

where P_x equals population size in year x , and P_{x+1} equals population size the following year. The exception to this procedure was 2003; because population surveys were not conducted from 2000 to 2002, population change was determined relative to 1999, and compared to the average seasonal precipitation between 1999 and 2003. Additionally, correlation analysis was used to determine the effect of the previous years precipitation on recruitment.

RESULTS

Precipitation

Mean growing season precipitation during the study period ($112 \text{ mm} \cdot \text{season}^{-1}$) was 16 mm below the mean precipitation of the previous wet period from 1978 to 1998 ($128 \text{ mm} \cdot \text{season}^{-1}$, Fig. 2). The study period contained two multi-year droughts with mean precipitation of $63 \text{ mm} \cdot \text{season}^{-1}$ (1999-2002) and $60 \text{ mm} \cdot \text{season}^{-1}$ (2006-2009, Fig. 2). Precipitation variation during the study period was high ($SD = 91 \text{ mm}$), with three years falling at or beyond 1 standard deviation of the mean: 2002 (21 mm), 2005 (352 mm) and 2007 (21 mm).

Population dynamics

Monitored *A. jaegerianus* populations decreased through the 13-year study-period from a high of 124 plants in 1999, to 30 plants in 2011, a decline of 76% (Fig. 2, Table 2). Within the overall population declines, there were modest increases associated with years of high precipitation in 2005 and 2011 (Fig. 2, Table 2); populations increased by 47% and 36% respectively. The greatest observed decrease in annual population size (-63%) was associated with severe drought in 2007 (Fig. 2, Table 2). Since 2007, populations have remained stable but low, increasing modestly in 2010 and 2011 (Fig. 2, Table 2). There was a strong positive relationship between proportion population change and seasonal precipitation (Fig. 3a, $r^2 = 0.72$, $P = 0.004$), which is strong evidence that the observed population fluctuations are controlled by inter-annual variation in precipitation.

The long-term survival of plants first surveyed in 1999 and 2003 was low: 14% at Brinkman Wash sites, and 9% at GCA sites (Fig. 4, Table 3). The initial Brinkman Wash

populations surveyed in 1999 suffered substantial mortality (61%) between 1999 and 2003, a period that included moderate drought in 1999 and 2000, and severe drought in 2002, the driest year since 1949 (Fig. 4a). Mortality within these initial Brinkman Wash populations slowed and then stopped after 2007, a severe drought year with 40% mortality (Fig. 4a). Population dynamics within the initial 2003 GCA populations occur in three distinct periods: (i) moderate decline from 2003 to 2006, (ii) high mortality (79%) in 2007, and (iii) stasis from 2007 to 2011 (Fig. 4b). Though less obvious, similar patterns in population dynamics are discernable within the decline of the 1999 Brinkman Wash populations illustrated in Figure 4a. Six plants initially surveyed in 1999 survived to 2011, demonstrating that the life span of *A. jaegerianus* is at least 13 years, and is likely to be longer given that plants appear to require at least two seasons of growth to flower and become visible (Huggins et al. 2012). Moreover, a single plant in population MM3 tagged by Connie Rutherford of the US Fish and Wildlife in 1993 has survived to 2011, which suggests that the life span of *A. jaegerianus* may exceed 18 years (pers. comm. Connie Rutherford USFWS).

Recruitment

The recruitment of reproductive plants into study populations was observed 43 times between 2003 and 2011 (Table 4). Of these 43 recruits, 20 (47%) survived to 2011. Consequently, the total population of 30 live study plants in 2011 consisted of 10 plants from the initial surveys of 1999 and 2003, and 20 plants recruited between 2003 and 2011. There was a strong positive relationship between precipitation and recruitment (Fig. 3b, $r^2 = 0.89$, $P < 0.001$). The highest recruitment years, 2005 and 2011, also had the highest

precipitation (352 and 215 mm respectively, Table 4). Both of these high recruitment years were preceded by years of modest recruitment and precipitation around the wet period average (Fig. 2). While there was a strong correlation between interannual precipitation and recruitment (0.952), there was no correlation between recruitment and the preceding year's precipitation (0.182).

As part of our annual surveys, the fate of seedlings found growing beneath *A. jaegerianus* host shrubs was monitored between 1999 and 2011. During this period, 202 seedlings were marked and revisited. Of these 202 seedlings marked in winter, only 85 survived into spring (Fig. 5). Of the 85 first-year seedlings that survived into spring, 17 resprouted in the following winter, and 9 of these second-year seedlings survived into spring (Fig. 5). Of these 9 second-year seedlings, none resprouted the following winter (Fig. 5).

Dormancy

Dormancy was a relatively uncommon phenomenon during the study period, and did not exceed 3 plants per year except in the drought year of 2007 when 19 out of 20 study plants went dormant (Table 5). Of the 19 plants that went dormant in 2007, 17 survived to the end of the study period in 2011. The single plant that resprouted in 2007 died the following year. Episodes of dormancy (1 season or 2 consecutive seasons) were observed 25 times in 22 different *A. jaegerianus* study plants between 1999 and 2011. Most episodes of dormancy (23) lasted a single season; 2 study plants had dormancies that lasted two consecutive seasons. Most study plants that experienced dormancy had a

single episode of dormancy during the study period; 3 study plants had 2 single-year episodes of dormancy; both of these plants survived to 2011.

2012

Seasonal precipitation in 2012 was low (65 mm). This low precipitation contributed to a further drop in mean precipitation during the recent climate period (1999–2012) to $108 \text{ mm}\cdot\text{season}^{-1}$, or 20 mm below the previous wet period from 1978 to 1998 ($128 \text{ mm}\cdot\text{season}^{-1}$). Resprouting was also low in 2012; only 55% of UCLA study plants alive in 2011 resprouted in 2012. Inactive plants in 2012, were either dormant or dead, but the proportion of dead to dormant plants can not be determined until one or more years of sufficient precipitation triggers resprouting of dormant plants. UCLA study plants that resprouted in 2012 failed to produce flowers, and so seed production among study plants was zero. Reproductive failure attributed to low precipitation has been reported in other endangered desert *Astragalus* (Buren and Harper 2003).

Total precipitation in 2012 was similar to 2009, but *A. jaegerianus* populations behaved very differently; all study plants resprouted in 2009, and all but one produced seeds. These differences in population behavior may be due to differences in the distribution of precipitation in 2009 and 2012 (Table 6). Both years had similar total precipitation (66.7 mm vs. 65.4 mm), but in 2009, precipitation occurred primarily in the winter (96%), and in 2012, precipitation occurred primarily in the spring (51%; Table 6). These differences suggests that when total seasonal precipitation is low, winter rains in excess of 30 mm are necessary to break summer dormancy for complete population resprouting. Furthermore, differences in seed production between 2009 and 2012 suggest

that, at least during dry years, the proportion of winter versus spring precipitation can have important effects on reproductive output of *A. jaegerianus*.

DISCUSSION

Population dynamics and precipitation

The results of this 13-year study demonstrate that *A. jaegerianus* population dynamics from 1999–2011 were controlled by growing season precipitation (Fig. 3a), and as a result, drought conditions since 1999 in the Mojave Desert have led to major population declines in UCLA monitored populations (-76%, Fig. 2).

The association between precipitation and population density of arid and semi-arid *Astragalus* is well known to North American range-managers because of the toxic effects of several *Astragalus* species on livestock (i.e. locoweed poisoning; e.g. Marsh 1909). Most reports of correlations between precipitation and *Astragalus* density are anecdotal or non-statistical (e.g. Ralphs and Bagley 1988, Purvines and Graham 1999). Statistical tests of relationship between precipitation and density appear to be restricted to two species, *Astragalus holmgreniorum*, in which seedling density was correlated with seasonal precipitation (Buren and Harper 2003), and *Oxytropis sericea*, a closely related genus to *Astragalus*, in which mortality was negatively correlated with total water-year precipitation in a fenced population from 1995–1999 (Ralphs et al. 2002). In the Mojave Desert, Beatley (1970) found a positive, though non-statistical correlation between percentage survival of seedlings across an elevation-precipitation gradient in *Astragalus lentiginosus* var. *fremontii*.

Astragalus jaegerianus mortality

One way to look at the population dynamics of our *A. jaegerianus* study plants (Fig. 2, Table 2) is as the composite dynamics of two populations: the initial population of plants surveyed in 1999 and 2003 (Fig. 4, Table 3), and new plants recruited in the years between 1999 and 2011 (Table 4). The recruitment of *A. jaegerianus* plants into study populations has been more or less unambiguously related to seasonal precipitation (Fig. 3b), but the effect of precipitation on patterns of mortality within initial populations is more complex and requires careful examination.

The dynamics of the initial populations are composed of two phases: an early period of population declines, followed by a period of population stasis in which declines in both areas ceased, and populations settled at low but stable densities (Fig. 4, Table 3). Within the declining phase, the highest *A. jaegerianus* mortality occurred during the first drought period at Brinkman Wash (1999–2002), and in both areas in 2007. Mortality during these periods (61 and 68 percent respectively) was clearly related to drought during the extraordinary dry years of 2002 and 2007 (Fig. 2). However, populations continued to decline despite increases in precipitation in 2003, 2004, and 2005, an extraordinary wet season in the Mojave Desert (Fig. 4).

We have previously argued that these moderate declines after 2002 might represent time lags in mortality due to the accumulated damage to slow-growing host shrub canopies caused by severe drought from 1999 to 2002 (Huggins et al. 2010). Sometimes referred to as the 21st Century Drought, this early drought period led to unusually high shrub mortality and canopy dieback in the Mojave Desert and other parts of the arid southwest US, including *A. jaegerianus* population areas where canopy

deterioration and host shrub mortality were high (Bowers 2005, Hereford et al. 2006, Miriti et al. 2007, Hamerlynck and McAuliffe 2008, Hamerlynck and Huxman 2009, Huggins et al. 2010, Prigge et al. 2011). The deterioration of host shrub canopies due to drought should negatively affect protégé plants such as *A. jaegerianus*, because shrub canopies provide shade, which affects the microclimate and water availability within and below shrubs (Valiente-Banuet et al. 1991, Nolasco et al. 1997, Shumway 2000, Flores et al. 2004, Barchuk et al. 2005, Huggins et al. 2010). This idea is supported by our previous study showing a significant decrease in survival of *A. jaegerianus* among host shrubs with canopies reduced by drought (Huggins et al. 2010). However, the negative effects of host shrub canopy dieback may not be immediately lethal to *A. jaegerianus*, resulting in a time lag in mortality after severe droughts.

Just as early declines of initial populations were more or less unaffected by increases in precipitation in 2003-2005, initial populations after 2007 remained virtually static (Fig. 4), despite two concurrent drought years in 2008 and 2009 (Fig. 2). These low, but drought-resistant *A. jaegerianus* populations may have developed through a process of drought selection, in which the proportion of drought tolerant plants increased as plants and host shrubs less capable of withstanding drought were removed through drought mortality. Because the capacity of an *A. jaegerianus* individual to withstand drought depends to a large extent on the condition of its host shrub (Huggins et al. 2010), drought selection is likely to have acted both directly on *A. jaegerianus* and indirectly through its host shrubs, which suffered as much as 48 percent mortality from 2000-2009 (Huggins et al. 2010). This process of drought selection appears to have been initially rapid at Brinkman Wash; 61 percent of *A. jaegerianus* died from 1999 to 2002, a period

of severe drought that included the lowest seasonal precipitation since 1949 (2002, 18 mm, Fig. 2). The transition from high, drought sensitive populations to low, drought-resistant populations appears to have been complete in 2007, after severe drought that year removed 68 percent of the remaining *A. jaegerianus* plants in initial populations.

Population cycling

In an attempt to explain the low recruitment we observed during the early drought and dry conditions from 1999–2004, we hypothesized that pulses in high annual precipitation, such as those associated with ENSO events, drive *A. jaegerianus* recruitment through mass germination and seedling establishment (Rundel et al. 2004, Sharifi et al 2011). This type of episodic recruitment has been reported in a number of arid and semi-arid species of perennial *Astragalus* including *A. amphioxys*, *A. crassicaarpus*, *A. lentiginosus*, *A. mollissimus*, and *A. pubentissimus* (Marsh 1909, James et al. 1968, Beatley 1970, Ralphs and Bagley 1988, Welsh 1989, Pomerinke et al. 1995, Purvines and Graham 1999, Ralphs et al. 2002, Ralphs and Jensen 2007). Typically, these *Astragalus* species occur at low population densities, until high seasonal precipitation triggers mass germination. Seedlings are then recruited in dense concentrations many times higher than typical densities. Though capable of perennation, seedling recruits of these mass-germinating *Astragalus* species commonly behave like functional annuals and biennials, flowering and fruiting their first or second year, and then suffering mass mortality their second or third year, completely disappearing or leaving small populations as continuity between years of high precipitation, mass germination, and high recruitment (Beatley 1974). A consequence of this type of

episodic recruitment is extreme population cycling (Ralphs and Jensen 2007), in which the production of seed is restricted to peaks in the cycle that occur at 5 to 8 year intervals.

The population dynamics of our *A. jaegerianus* study plants differ from the “boom or bust” dynamics of the xeric *Astragali* described above: *A. jaegerianus* recruitment has been relatively modest, even during an extraordinary wet season such as 2005 (352 mm), and mortality, though higher in drought years such as 2007 (19 mm), has been more or less gradual. As a result, the frequency of population cycles should be lower in *A. jaegerianus*, and in phase with wet and dry climate-periods in the Mojave Desert (Huggins et al. 2010). This dampening of population cycles in *A. jaegerianus* could be a consequence of its more or less obligate association with host shrubs which (1) restricts the distribution of seed and recruitment sites, thus inhibiting rapid population growth, and (2) reduces drought-induced mortality through canopy facilitation including shading (Huggins et al. 2010), thus reducing the mass mortality seen in other arid *Astragali* such as *A. lentiginosus* var. *fremontii* (Beatley 1970).

SUMMARY

The results of this 13-year study demonstrate that *A. jaegerianus* population dynamics from 1999-2011 were controlled by growing-season precipitation, and as a result, drought conditions since 1999 in the Mojave Desert have led to major population declines in UCLA monitored populations (-76%). The population dynamics of *A. jaegerianus* study plants differed from the “boom or bust” dynamics of the other xeric *Astragalus* species. *Astragalus jaegerianus* recruitment has been relatively modest, even during an extraordinary wet season such as 2005 (352 mm), and mortality, though higher in drought

years such as 2007 (19 mm), has been more or less gradual. As a result, the frequency of population cycles should be lower in *A. jaegerianus*, and in phase with wet and dry climate-periods in the Mojave Desert (the climate-period hypothesis). While *A. jaegerianus* recruitment is an unambiguous function of seasonal precipitation, mortality as a function of precipitation is complicated by host shrub effects, including time-lags in mortality due to drought damage to host shrubs, and “drought-selection” in which *A. jaegerianus* populations acquire drought tolerance as plants and host shrubs less capable of withstanding drought are removed through drought mortality. Dormancy was a relatively uncommon phenomenon during the study period, and did not exceed 3 plants per year except the drought year of 2007 when 19 out of 20 study plants went dormant. Episodes of dormancy (1 season or 2 consecutive seasons) were observed 25 times in 22 different *A. jaegerianus* study plants between 1999 and 2011.

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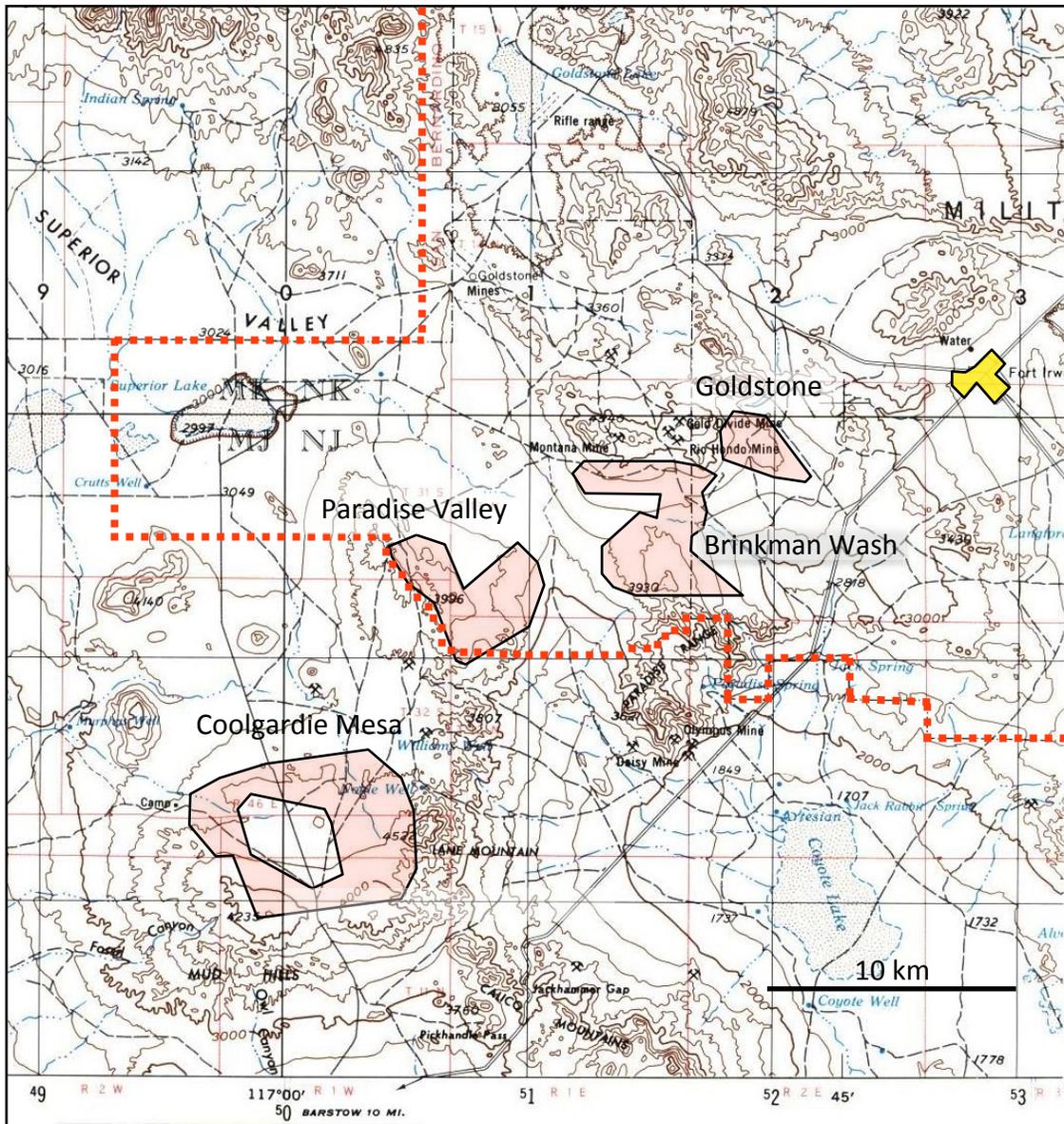


Figure 1. Map of *Astragalus jaegerianus* population areas identified by extensive surveys in 2001 (Charis Professional Services Corporation 2001). Populations within the four population areas are small and highly fragmented.

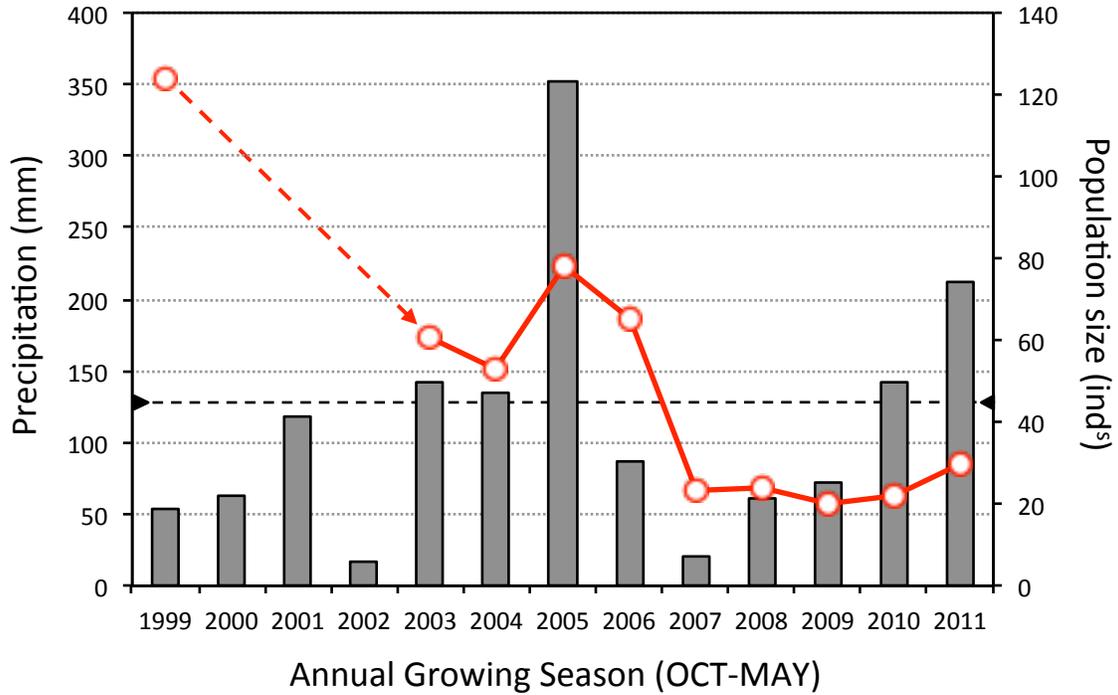


Figure 2. *Astragalus jaegerianus* growing season precipitation (OCT-MAY) and population dynamics from 1999 to 2011. Years refer to the season (Spring) in which *A. jaegerianus* is reproductive. Yearly population numbers are live plants, and so include dormant plants that resprouted the following year. Population data were not collected for the three year period from 2000 to 2002. Population size in 1999 is based on observed and extrapolated data (see Table 4). Precipitation data is a composite of data collected from within the Gemini Conservation Area, and the nearby Goldstone Echo #2 weather station, as well as adjusted data collected from Daggett CA, Barstow CA, and the RAWS weather station at Opal Mountain. The dashed line is mean growing season precipitation (OCT-MAY) during the wet period from 1978-1998 (128 mm·season⁻¹). Mean precipitation during the recent period (1999-2011) was 112 mm·season⁻¹.

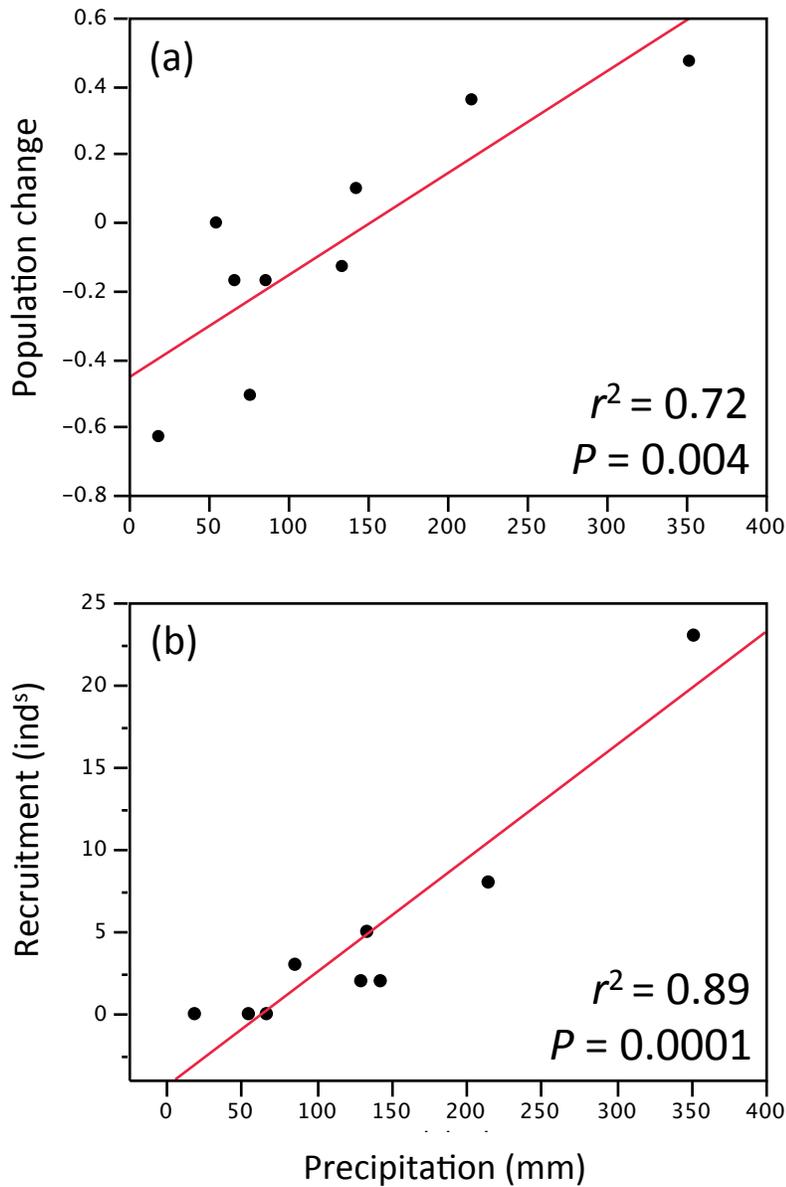


Figure 3. The effect of seasonal precipitation (OCT-MAY) on the population dynamics of *A. jaegerianus*. (A) Precipitation versus population change; population change is the proportional change in interannual population size and direction. The precipitation datum that corresponds to the population change from 1999-2003 is the mean precipitation from 1999-2003 (77 mm). (B) Precipitation versus *A. jaegerianus* recruitment.

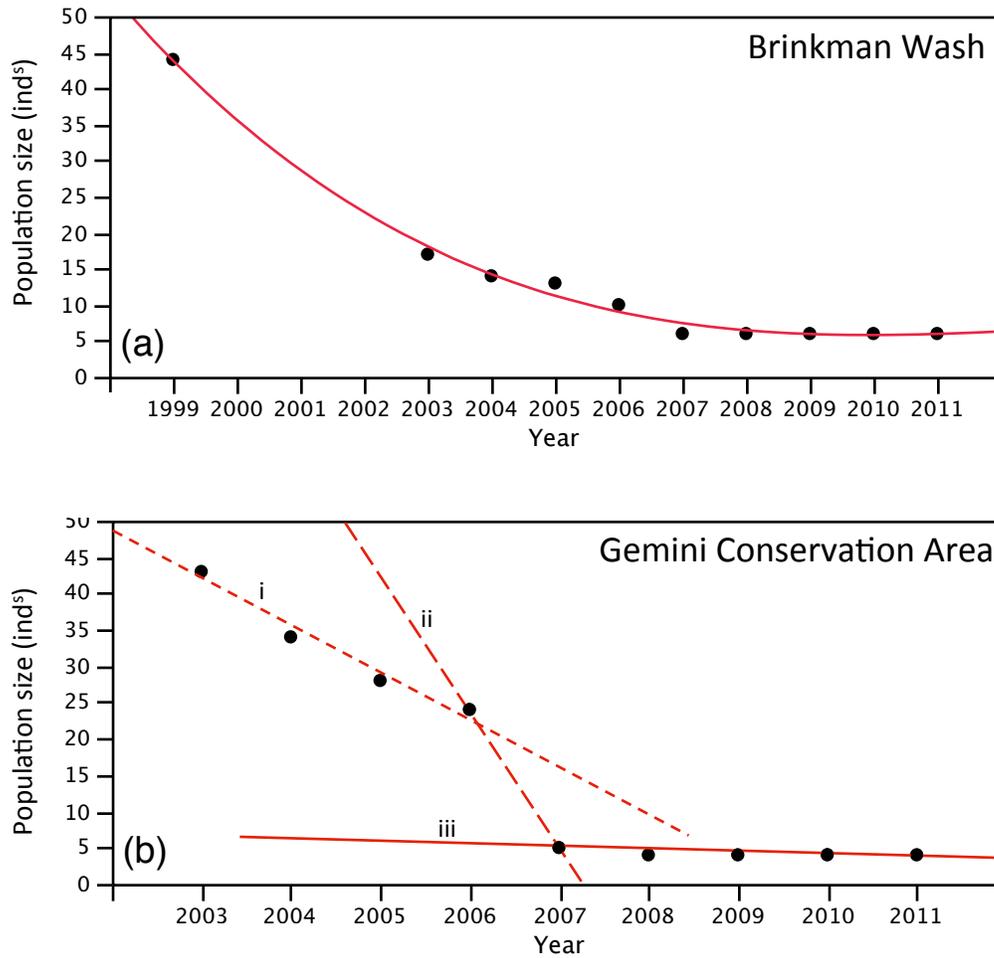


Figure 4. Survival of initial populations of *A. jaegerianus* plants first surveyed in 1999 at (A) Brinkman Wash, and 2003 at (B) the Gemini Conservation Area. Yearly population numbers are live plants, and so include dormant plants that resprouted the following year. Because the recruitment of new plants into populations is not included, population numbers only reflect the long-term survival of plants surveyed in 1999 and 2003, and not total population size. Population dynamics within the initial 2003 GCA populations occur in three distinct periods: (i) moderate decline from 2003 to 2006, (ii) high mortality (79%) in 2007, and (iii) relative stasis from 2007 to 2011. Similar patterns in population dynamics are discernable within the overall decline of the 1999 Brinkman Wash populations (A).

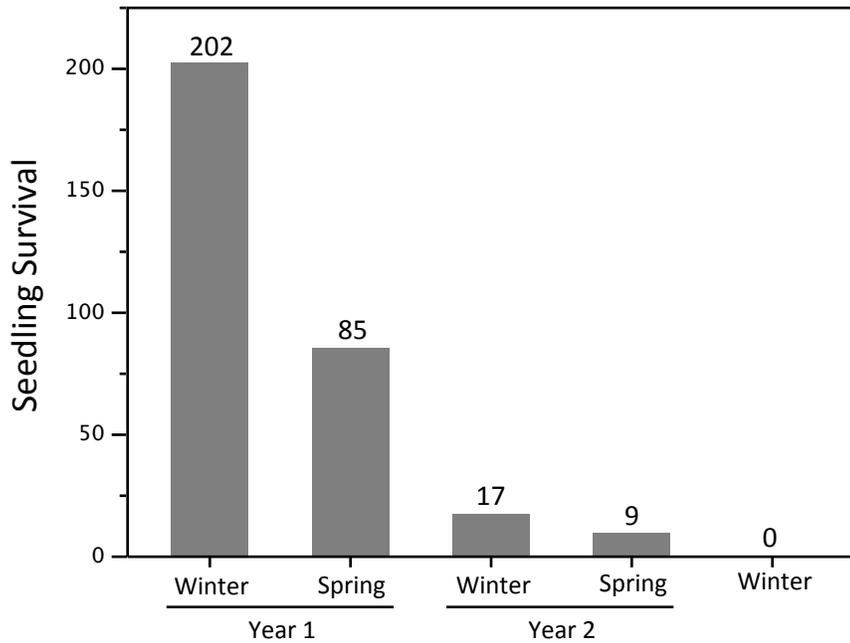


Figure 5. Survival of 202 marked *Astragalus jaegerianus* seedlings through time. Data are lumped over several years of observation and over several sites. Seeds germinate in the winter (winter, year 1) and some fraction of those seedlings survive until spring (spring, year 1). Some fraction of the seedling from the previous spring resprout the next winter (winter, year 2), and some fraction of these survive until spring (spring, year 2). None of the monitored seedling resprouted the third year.

TABLE 1. Schedules of seasonal surveys of *Astragalus jaegerinus* from 1999 to 2011 at the population areas known as Brinkman Wash and the Gemini Conservation Area. Shaded years were not surveyed. Years refer to spring seasons in which *A. jaegerinus* is reproductive.

Study Site Population Area	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011
MM 1 Brinkman	SURVEY				SURVEY								
MM 2 Brinkman	SURVEY				SURVEY								
MM 3 Brinkman	SURVEY				SURVEY								
BW3 Brinkman	SURVEY				SURVEY	SURVEY					SURVEY	SURVEY	SURVEY
GCA 1 Goldstone					SURVEY								
GCA 2 Goldstone					SURVEY								

TABLE 2. Total *Astragalus jaegerianus* population size from 1999 to 2011. Red numbers are population estimates for years in which populations were not surveyed; estimates for Gemini Conservation Area in 1999 are based on population changes observed in Brinkman Wash populations MM1, MM2, MM3, and BW3 between 1999 and 2003 (mean change -46%); estimates for BW3 from 2005-2008 are based on the mean annual population change of the other 5 study populations; these factors were 1.74 (2005), 0.82 (2006), 0.43 (2007), and 0.92 (2008). Total population decline from 1999 to 2011 was 76%.

Study Site Population	UTM East	UTM North	1999	2003	2004	2005	2006	2007	2008	2009	2010	2011
			MM 1	512540	3897460	20	6	7	15	12	6	8
MM 2	512640	3897540	2	2	2	3	3	1	1	1	1	1
MM 3	512810	3897550	5	2	3	7	4	3	3	3	3	5
BW3	514290	3897590	17	8	4	7	6	3	3	2	3	3
GCA 1	519610	3899890	37	20	14	26	23	8	8	6	6	9
GCA 2	519080	3899520	43	23	23	20	17	2	1	1	2	5
Totals			124	61	53	78	65	23	24	20	22	30

TABLE 3. Survival of initial populations of *A. jaegerianus* plants first surveyed in 1999 (**Brinkman Wash** sites MM 1, MM 2, MM 3, and BW 3) and 2003 (**Gemini Conservation Area** sites GCA 1 and GCA 2). Survival to 2011 was 14% at Brinkman Wash and 9% at the Gemini Conservation Area. Yearly population numbers are live plants, and so include dormant plants that resprouted in subsequent years (maximum dormancy 2 years). Because the recruitment of new plants into populations is not included, population numbers only reflect the long-term survival of plants surveyed in 1999 and 2003, and not total population size. Red numbers are population estimates for years in which populations were not surveyed; estimates for BW3 from 2005-2008 are based on the mean of the proportional annual population change of the 3 Montana Mine study populations; these factors were 0.94 (2005), 0.77 (2006), 0.58 (2007), and 1.00 (2008).

Study Site Population	1999	2003	2004	2005	2006	2007	2008	2009	2010	2011
MM 1	20	6	6	5	4	3	3	3	3	3
MM 2	2	2	2	2	2	0	0	0	0	0
MM 3	5	2	2	2	1	1	1	1	1	1
BW3	17	7	4	4	3	2	2	2	2	2
Totals	44	17	14	13	10	6	6	6	6	6
GCA 1	-	20	14	12	10	3	3	3	3	3
GCA 2	-	23	20	16	14	2	1	1	1	1
Totals	-	43	34	28	24	5	4	4	4	4

TABLE 4. Recruitment of *Astragalus jaegerianus* plants in 6 study populations at Brinkman Wash (MM and BW) and the Gemini Conservation area (GCA) from 2003 to 2011.

Study Site Population	2003	2004	2005	2006	2007	2008	2009	2010	2011	Recruitment Total
MM 1	0	1	4	1	0	0	0	0	0	6
MM 2	1	1	1	0	0	0	0	0	0	3
MM 3	0	0	4	0	0	0	0	0	2	6
BW3	1	0	-	-	-	-	0	1	0	2
GCA 1	-	0	13	0	0	0	0	0	3	16
GCA 2	-	3	1	2	0	0	0	1	3	10
Totals and Means	2	5	23	3	0	0	0	2	8	43

TABLE 5. Dormant *Astragalus jaegerianus* plants in 6 study populations from 2003 to 2011. Plants were considered dormant (1) if they resprouted after 1 or more years of inactivity, and (2) if observed to be mature from the diameter and woodiness of their caudex.

Study Site Population	2003	2004	2005	2006	2007	2008	2009	2010	2011	Totals
MM 1	3	1	1	0	6	0	0	0	0	11
MM 2	0	0	0	0	1	0	0	0	0	1
MM 3	0	1	0	0	3	0	0	0	0	4
BW3	0	0	-	-	-	-	0	0	0	0
GCA 1	-	0	0	0	8	1	0	0	0	9
GCA 2	-	0	1	0	1	0	0	0	0	2
Totals	3	2	2	0	19	1	0	0	0	27
Percent										
Dormancy	5%	4%	3%	0%	95%	5%	0%	0%	0%	0%

TABLE 6. The distribution of seasonal precipitation (mm) in 2009 and 2012. Both years had similar total precipitation (66.7 mm vs. 65.4 mm), but in 2009 its distribution occurred primarily in the winter (96%), and in 2012 its distribution occurred primarily in the spring (51%). Years refer to the season (spring) in which *Astragalus jaegerianus* is reproductive.

Precipitation	
2009	2012
0.0	OCT 12.2
15.6	NOV 9.5
15.6	DEC 5.4
0.8	JAN 4.4
32.2	FEB 0.8
2.2	MAR 10.9
0.0	APR 22.2
0.3	MAY 0.0
66.7	65.4
96%	49%
4%	51%

SECTION 2

PHENOLOGY

INTRODUCTION

Despite its endangered conservation status, this study represents the first quantitative study of *Astragalus jaegerianus* phenological stages and transitions. Understanding the periodic events in the life cycle of *A. jaegerianus*, is important because changes in the onset of resprouting, flowering, and fruiting may have a strong effect on flower pollination, seed production, and ultimately population growth or decline. Furthermore, by studying the effects of interannual variation in precipitation on phenology, we can better predict the effects of climate change on *A. jaegerianus*. Annual phenological monitoring of our long-term study populations will help answer questions concerning the effects of climate variation on *A. jaegerianus* reproduction.

METHODS

Weekly phenological observations on twenty *A. jaegerianus* study plants began on 14 December 2009, and 11 October 2010 and continued until all seedpods had opened in June 2010 and 2011. Phenological observations included initiation of resprouting, stem elongation (longest stem), initiation and duration of flowering, fruiting, seedpod dehiscence and seed drop. In 2012, the schedule of observations was reduced to four phenological assessments on 24 January, 29 March, 21 April and 25 May 2012.

The twenty study plants were located in two adjacent geographic areas, the Gemini Conservation Area (GCA) and Brinkman Wash, previously established as discrete areas of *A. jaegerianus* distribution (Prigge et al. 2000, Charis Professional Services 2002, Walker & Metcalf 2008, Huggins et al. 2010; the GCA was previously referred to as Goldstone). These study plants are part of a long-term monitoring study, and have been surveyed more or less regularly since 1999 at Brinkman Wash, and since 2003 at the Gemini Conservation Area. As part of this long-term study, monitored plants are tagged and their location established using GPS (see Methods, Section 1). Each area contains two study populations. All 20 study plants were active and reproductive in Spring 2009.

Precipitation data were generated by the remote automated weather station (RAWS) at Opal Mountain CA (35°09'N; 117°10'W; 980 m.). This weather station is approximately 30 km SW of UCLA's milkvetch study sites. Data was adjusted to better approximate precipitation at *A. jaegerianus* study sites (see Methods, Section 1). Analyses used October through May precipitation because it includes winter and spring rainfall that affects *A. jaegerianus* growth, reproduction and germination, and excludes summer precipitation that occurs during *A. jaegerianus*' dormant period.

RESULTS

Precipitation

October to May precipitation at *A. jaegerianus* study sites during the three years of phenological observation was variable. Precipitation in the 2009-2010 was 27 mm above average for the recent period (108 mm, 1999-2012), and the first rain event over 20

mm did not occur until January 2010 (Table 1). Precipitation in 2010-2011 was 125 mm above the average, and began early with over 20 mm of precipitation between 17 and 20 October 2010 (Table 1). Precipitation in 2011-2012 was 43 mm below average, with the majority of precipitation occurring in March and April, and no storm greater than 17 mm occurring until 13 April 2012 (Table 1).

Caudex and PGS

For several weeks after the initiation of observations in 2010, plants remained dormant. During this period, deciduous host shrubs were leafless, allowing relatively clear observation of dormant *A. jaegerianus* stems. *Astragalus jaegerianus* plants die back to a caudex each year after seed-pod dehiscence. The caudex is a knotty root-crown composed of stem-bases, which give rise to new herbaceous growth each year. The location of the caudex in *A. jaegerianus* has been described by Barneby (1964) as buried or subterranean, 1 to 4 cm deep. Similarly, Gibson et al. (1998) described *A. jaegerianus* as a hemicryptophyte (i.e. a plant with perennial buds situated at or just below the soil surface (Blackmore and Tootill 1984)). In this study, 13 study plants had caudices at or below the soil surface, and 7 plants had aerial caudices (sensu. Barneby 1964, pp. 9), 2 cm to 10 cm above the soil surface, a caudex location previously unreported in *A. jaegerianus*. The portion of the stem between the soil surface and the aerial caudices was conspicuously woody and up to 1.1 cm in diameter (plant 7), suggesting a relatively old age for the stem (at least 11 years since it was first surveyed). In one case (study plant 458), the woody stem was branched into three stems each supporting an aerial caudex. While most or all of the stems produced the previous season die back to the caudex,

every study plant had at least one, but as many as 5 stems that remained partially green from the previous season. These persistent green stems (PGSs) were as long as 38 cm. The presence of PGSs on dormant *A. jaegerianus* has been previously noted by Bagley (1998).

Resprouting and Stem Elongation

Resprouting of the first study plants began the week of 25 January 2010, and all plants had resprouted two weeks later on 8 February 2010 (Fig. 1, Fig. 2). Study plants produced new shoots from both caudices and PGSs. The production of shoots from PGSs and caudices was staggered, with all initial resprouting occurred from PGSs simultaneously from several nodes along the same stems; by the week of 8 February when all 20 study plants were resprouting from PGSs, only 6 plants had begun to resprout from caudices. Three weeks later, during the week of 1 March, 18 study plants were producing shoots from caudices. Resprouting from PGS was somewhat more common than resprouting from caudices: 20 study plants produced shoots from the nodes of PGS, and 18 plants produced shoots directly from caudices. Stem elongation proceeded more or less regularly for 10 weeks.

The following reproductive season (2011), the storm that occurred between 17 and 20 October 2010 triggered the resprouting of dormant plants the week of 1 November 2010 (Fig. 1, Fig. 3), and all but three plants had resprouted the week of 22 November 2010. These three late resprouters remained dormant through a relatively dry November, but resprouted the week of 22 and 27 December 2010 after heavy rains that month (Table 1). All study plants had resprouted by the week of 3 January 2011, 10 weeks after the

first plants resprouted, and growth continued into March, for a total growth period of approximately 21 weeks (Fig. 1, Fig. 3, Table 2). This growth period lasted only 10 weeks in 2010 (Table 2) and began the week of 25 January 2010 (Figure 1), a difference of 12 weeks between the date of initial resprouting in 2010 and 2011 (Table 3).

The reproductive season 2012 was a low precipitation year with a reduce number of observations (4), and a high degree of dormancy/death. Four study plants were observed resprouting in 24 January 2012. The number of resprouted study plants increased to 17 by 29 March 2012, but did not increase further despite significant rainfall in March and April. Only 55% of UCLA study plants alive in 2011 resprouted in 2012. Inactive plants in 2012, were either dormant or dead, but the proportion of dead to dormant plants can not be determined until one or more years of sufficient precipitation triggers resprouting of dormant plants.

Flowering and Fruiting

In 2010, *A. jaegerianus* reproductive activity occurred during a 15-week period beginning with the initiation of flower bud production the week of 1 March (Fig. 1). The week of 15 March, three weeks after the initiation of flower bud production, the first study plants began to flower (Fig. 2). Two weeks after the initiation of flowering, the first study plants began to form seedpods (Fig. 2). The week of May 17, six weeks after the initiation of seedpod production, the first seedpods opened. Seedpods dehisced for a period of 4 weeks from the week of May 17 to June 17 (Fig. 2).

The following reproductive season (2011) *A. jaegerianus* reproductive activity (flower budding to seed-pod dehiscence) occurred during a 21-week period beginning

with the initiation of flower bud production the week of 17 January 2011 (Fig. 3). In comparison, in 2010, this reproductive period lasted 15 weeks and began the week of 1 March 2010 (Fig. 3). This early production of flower buds led to loss of racemes through frost damage during the weeks of 24 and 31 January 2010; leaves and stems were not damaged. In 2011, three weeks after the initiation of flower bud production, the first study plants began to flower (Fig. 2), suggesting that flower buds require 3 weeks of development before anthesis (flower opening). Five weeks after the initiation of flowering, the first study plants began to form seedpods. The week of May 17, eight weeks after the initiation of seedpod production, the first seedpods opened, and began to drop their seed. Seedpods dehisced for a period of 5 weeks from the week of May 9 to June 6 (Fig. 3).

No reproductive activity, including residual structures such as dry racemes, was observed during three phenological surveys in March, April, and May. On 25 May 2012, only 6 study plants were still active, and 11 of the 17 resprouts had entered summer dormancy.

Phenological Differences Between 2010, 2011, and 2012

The timing of phenological stages was significantly affected by interannual differences in the amount and timing of precipitation. Low precipitation in 2011-2012 led to the disruption of phenological stages, a high degree of dormancy/death, and reproductive failure among study plants that manager to resprout. Furthermore, active study plants were unable to produce reproductive structures despite significant

precipitation in late March and early April, suggesting that the timing of precipitation has important phenological effects and reproductive consequences.

The timing of phenological stages was significantly advanced in the reproductive year 2011 relative to 2010 as a consequence of high precipitation in 2011. Advances were greatest in the growth period, as early rain advanced the onset of resprouting by 12 weeks in 2011 relative to 2010 (Table 3). As phenological stages progressed, advances in phenology declined: the onset of the production of flower buds and flowering were advanced by 6 weeks respectively, fruiting was advanced by 3 weeks and fruit dehiscence by 1 week relative to 2010. Phenological observations in January 2005 suggest that similar advances in phenology occurred during the extremely wet year of 2004-2005 (Rundel et al. 2010).

The precipitation differences that advanced the timing of phenological stages also lengthened their duration in 2011; the total *A. jaegerianus* activity period was extended by 12 weeks in 2011, and the total reproductive period was extended by 6 weeks (Table 2). As in the timing of phenological stages, increases in the duration of phenological stages diminished as stages progressed; growth increased by 11 weeks, flower budding and flowering increased by 5 weeks respectively, fruiting increased by 2 weeks, and fruit dehiscence by 1 week (Table 2).

The interval of time between the start of consecutive phenological stages is a measure of the minimum time required for an individual plant to complete a stage. Unlike the duration and timing of phenological stages, the inter-stage interval did not proceed in a predictable, diminishing pattern (Table 4); *A. jaegerianus* growth required an additional 7-week before producing flower buds in 2011. The time necessary to

mature flower buds into flowers, 3 weeks, was the same in 2011 as it was in 2010 (Table 4). The time required for flowers to produce fruits, 5 weeks, increased by 2 weeks in 2011, and the time necessary for the maturation of fruits increased by 4 weeks, from 6 weeks in 2010 to 10 weeks in 2011 (Table 4).

Herbivory

On the week of 21 February 2011, 7 study plants experienced moderate to heavy herbivory, in which unknown herbivores consumed part or all of the emergent stems and racemes of *A. jaegerianus* study plants; stems within the canopy of host shrubs remained more or less intact. Emergent stems are *A. jaegerianus* stems outside of the host shrub canopy. Study plants 131, 132, 579, and 601 were in bud or flower, and were completely sterilized by herbivory (i.e. all reproductive tissue removed). Study plant 134 was partially sterilized by herbivory ($\approx 50\%$), and plants 458 and 459 had emergent stems partially consumed ($\approx 50\%$) while still in their growth phase without reproductive tissue. Plants with heavy herbivory experienced delays in reproduction by as much as 4 weeks, as renewed growth was initiated and new reproductive structures produced. Despite the complete sterilization, study plants produced flowers and seed pods after a 2 to 4 week delay, although at a reproductive cost in seed production (see Section 3).

DISCUSSION

Bagley (1998) noted that in *A. jaegerianus* most or all of the above ground plant dies back annually, but in some individuals new growth starts on stems produced during the previous season or seasons. The results of this study confirm Bagley's observations; what we are calling persistent green stems (PGSs), remain green (though leafless)

through summer dormancy. We found PGSs on all 20 study plants, and two study plants produced shoots exclusively from PGSs. Furthermore, PGSs became active 3 weeks before shoots from caudices were observed. The cause of differences in the timing of resprouting between caudices and PGSs is not clear, but *A. jaegerianus* stems are capable of photosynthesis (Gibson et al. 1998), and may remain metabolically active during the plant's dormant period. This metabolic activity may explain why PGS resprouting is more responsive to precipitation than caudices. Because shoots from PGSs are produced above superficial or subterranean caudices (sensu. Barneby 1964), the distance shoots must travel to reach the canopy of its host shrub may be greatly reduced, potentially increasing photosynthesis and pollinator access to flowers. Elevated caudices may be derived from PGS nodes that have produced multiple stems for multiple years and have themselves become swollen and woody.

The results of this study support our previous suggestion that between-year differences in *A. jaegerianus* phenology might be pronounced, and controlled by annual differences in precipitation (Rundel et al 2010). Phenological evidence from the reproductive seasons 2005, 2010, and 2011, suggest that the seasonal initiation of *A. jaegerianus* growth is cued by the first winter storm of sufficient magnitude (i.e. a rainfall trigger, Rundel et al. 2010). In 2005, precipitation in the central Mojave Desert was as high as three times mean precipitation. That year, two *A. jaegerianus* population surveys were carried out by UCLA in the winter and spring; the first survey, conducted on 27 January 2005, found *A. jaegerianus* flowering months before its previously reported flowering period (April to May, Bagley 1998, Charis Professional Services 2002; possibly March, Charis Professional Services 2003). In comparison to 2005, many study

plants were still dormant during January 2010, with the first signs of resprouting observed the week of January 25. In 2010, we found that flowering occurs 8 weeks (15 weeks in 2011) after the initiation of resprouting (Rundel et al. 2010). This 8-week interval could be used to estimate the time of *A. jaegerianus* resprouting in 2004/2005 as late October or early November, a period preceded by the first significant rainfall of the season: 94 mm of rainfall between October 20 and 27 (Table 1). Similarly, resprouting in 2010 began the week of 25 January, and was preceded by 50.6 mm of precipitation between January 18 and 22 (Fig. 1). In both cases, rainfall events that immediately preceded resprouting were the first rainfall events of the season. These observations suggested that the timing of *A. jaegerianus* resprouting was controlled by a precipitation cue, and that rainfall events of 56 mm are sufficient to trigger population-wide resprouting.

The initiation of resprouting in 2011, which began 1 to 2 weeks after the first winter storm of the season, suggests that a precipitation event of as little as 20.6 mm is sufficient to trigger resprouting (Table 1). While 20.6 mm of rainfall appears to be sufficient to trigger resprouting in most *A. jaegerianus* study plants, 3 study plants remained dormant until the next major rain event, between 17 and 22 December 2010, triggered their resprouting the week of 3 January 2011. This supports our previous supposition that individual *A. jaegerianus* plants differ in their sensitivity to precipitation, and that these differences in rainfall sensitivity may control the pattern of drought dormancy between years (Rundel et al. 2010); presumably, the three relatively rainfall-insensitive study plants that resprouted in January may have remained dormant in 2011 if precipitation had remained low the rest of the season, as occurs in drought years.

A precipitation trigger such as this could also explain the mechanism of drought dormancy between years; during years without sufficient rainfall such as 2012, plants would remain dormant based on their individual sensitivities to a rainfall stimulus. Resprouting could be triggered when rainfall reaches a certain root depth that may vary between plants depending on their root morphologies or root distributions, as well as the heterogeneous nature of water availability in the soil based on micro-topographic effects on water movement. In such a scenario, the rainfall trigger (the precise amount of rainfall necessary to stimulate resprouting) could be different in different plants.

The quantity and timing of precipitation during the 2012 reproductive season (low rainfall, relatively late) had a strong effect on *A. jaegerianus* phenology relative to 2010 and 2011. From October through March, precipitation was not only low, but no single precipitation event exceeded 11 mm of precipitation, far below the 20–30 mm event necessary for population-wide resprouting. As a result, nearly half the population of study plants failed to resprout. If individual *A. jaegerianus* vary in their resprout-sensitivity to precipitation then the plants that remained dormant during the low precipitation of 2012 represent individuals that require larger precipitation events to resprout than occurred during the 2012 reproductive season. The timing of precipitation also had a strong effect on phenology; relatively high precipitation in March and April (33 mm) failed to stimulate dormant plants into resprouting, or active plants into flowering. This suggests that winter rains in excess of 30 mm are necessary for complete population resprouting and flowering. This pattern is similar to that described by Beatley (1974) for most Mojave Desert herbaceous perennials, but not the congener *Astragalus*

lentiginosus, which Beatley reports is capable of flowering with spring precipitation regardless of winter drought.

The quantity and timing of precipitation during the 2011 reproductive season (high rainfall, relatively early) also had a strong effect on the duration and timing of *A. jaegerianus* phenology relative to 2010, a year of average precipitation. The total phenological period from initiation of resprouting to final dehiscing of seedpods was 12 weeks longer in 2011 (Table 2) and began 12 weeks earlier than resprouting in 2010 (Table 3). Both the onset and duration of all phenological stages were advanced and lengthened (Tables 2 and 3), but the effect was more pronounced earlier in the season when temperatures were low; study plants may have required more time to complete stages because low temperatures reduced plant productivity.

This early resprouting had a appreciable effect of the timing of reproduction: the initiation of flower buds began the week of 17 January 2011; both flower-budding and flowering in 2011 was advanced by 6 weeks (Table 3). These results suggest that the timing of phenological stages is strongly influenced by the initiation of resprouting, and is more or less independent of temperature, in the sense that phenological stage transitions are not cued by ambient temperatures. Instead, phenological stage transitions occur when the plant has reached some required level of physiological development. Temperature plays a role in phenology, because the rate at which the plant reaches the required level of development for phenological stage transitions is a function of ambient temperature (i.e. physiological rates are controlled by temperature). This would explain the pattern of differences in stage duration observed in Table 2; early stages such as the growth stage were disproportionately lengthened in 2011 compared to 2010 because they

occurred under lower ambient temperatures due to early resprouting. Temperature-independent cueing of phenological transitions explains early transition from the growth to reproductive stage in 2011; though *A. jaegerianus* growth may have been slowed by low temperatures in November, December, and January as indicated by an increase in the duration of growth (Table 2), the initiation of flower and raceme development commenced the week of 17 January 2011, despite a monthly mean temperature below 9° C in January with lows below freezing.

Phenological shifts of the magnitude observed in 2011 could have substantial negative effects on *A. jaegerianus* reproduction. For example, in 2011 the flowering of study plants began the week of February 7, six weeks earlier than flowering in 2010, and during a period in which pollinator activity was low (Fig. 2, Fig. 3). Also, seedpods required 4 more weeks of maturation before dehiscence in 2011 (Table 4), suggesting that conditions for seed production were suboptimal, despite the increase in productivity associated with increased precipitation in arid ecosystems. Furthermore, increases in the quantity and timing of precipitation in 2011 appear to have played a significant role in *A. jaegerianus* herbivory, which negatively affected its reproduction (see Section 3).

Because early rains initiated *A. jaegerianus* growth in November 2010, study plants were conspicuously leafy in February when host shrubs were leafless and other forage for herbivores was low. Significant herbivory of study plants was not observed in 2009 and 2010, but the effect of two consecutive years of average and above average precipitation (Table 1) may have elevated the populations of herbivores responsible for *A. jaegerianus* herbivory in 2011.

SUMMARY

The results of this study support our previous suggestion that between-year differences in *A. jaegerianus* phenology might be pronounced, and controlled by annual differences in precipitation (Rundel et al 2010). The initiation of resprouting in 2011, which began 1 to 2 weeks after the first winter storm of the season, suggests that a precipitation event of as little as 20.6 mm is sufficient to trigger resprouting. Differences between plants in their sensitivity to precipitation could explain differences in the timing of resprouting between plants, and could explain why some plants resprout during years of low rainfall, and others remain dormant. A precipitation cue to resprouting could cause plant and pollinator mismatch if *A. jaegerianus* precipitation cues and insect temperature cues are not synchronized. The results of this study demonstrate that the quantity and timing of seasonal precipitation can have a strong effect on *A. jaegerianus* phenology. Precipitation during the 2011 reproductive season (high rainfall, relatively early) resulted in appreciable phenological shifts in the duration and timing of *A. jaegerianus* phenology relative to 2010, a year of average precipitation. Phenological shifts of the magnitude observed in 2011 could have substantial negative effects on *A. jaegerianus* reproduction. Precipitation during the 2012 reproductive season (low rainfall, relatively late) resulted in substantial dormancy and reproductive failure. Long-term, multi-year studies of the effects of interannual variation in precipitation on *A. jaegerianus* phenology will help wildlife managers anticipate the possible effects of climate change on *A. jaegerianus* phenology and reproductive success.

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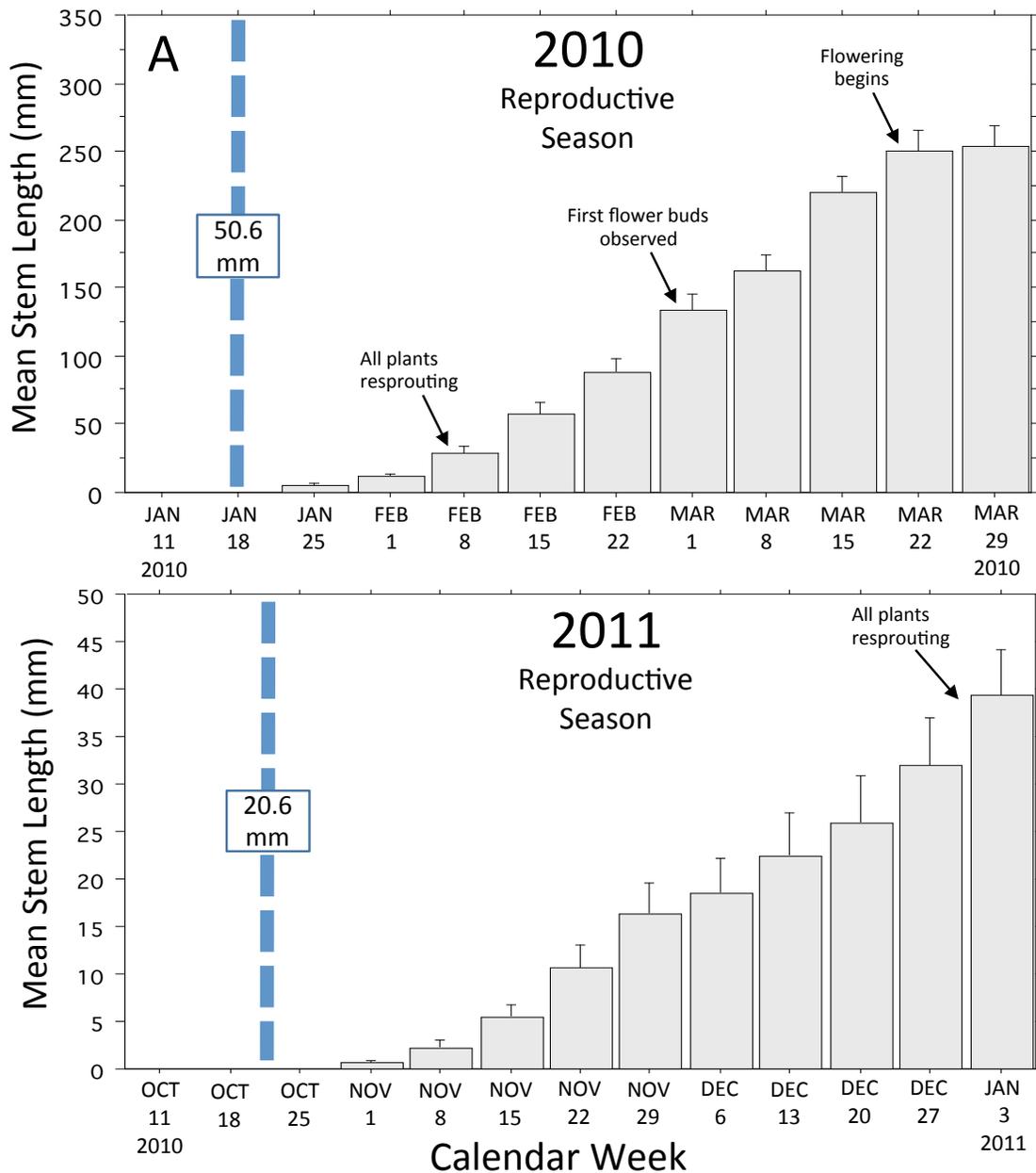


Figure 1. The first 10 weeks of *Astragalus jaegerianus* stem elongation, 2010 and 2011. Stem length is the length of longest shoot measured weekly in mm ($n = 22$ plants). Bars are means (+SE). (A) In 2010, resprouting of study plants was observed 1 week after the first major rainfall event of the year (50.6 mm, dashed blue line); stem elongation was rapid, but slowed after 9 weeks. (B) In 2011, resprouting of study plants was observed 2 weeks after the first major rainfall event of the winter (20.6 mm, dashed blue line), and stem elongation proceeded at a far slower pace than in 2010.

Astragalus jaegerianus

Phenology 2010

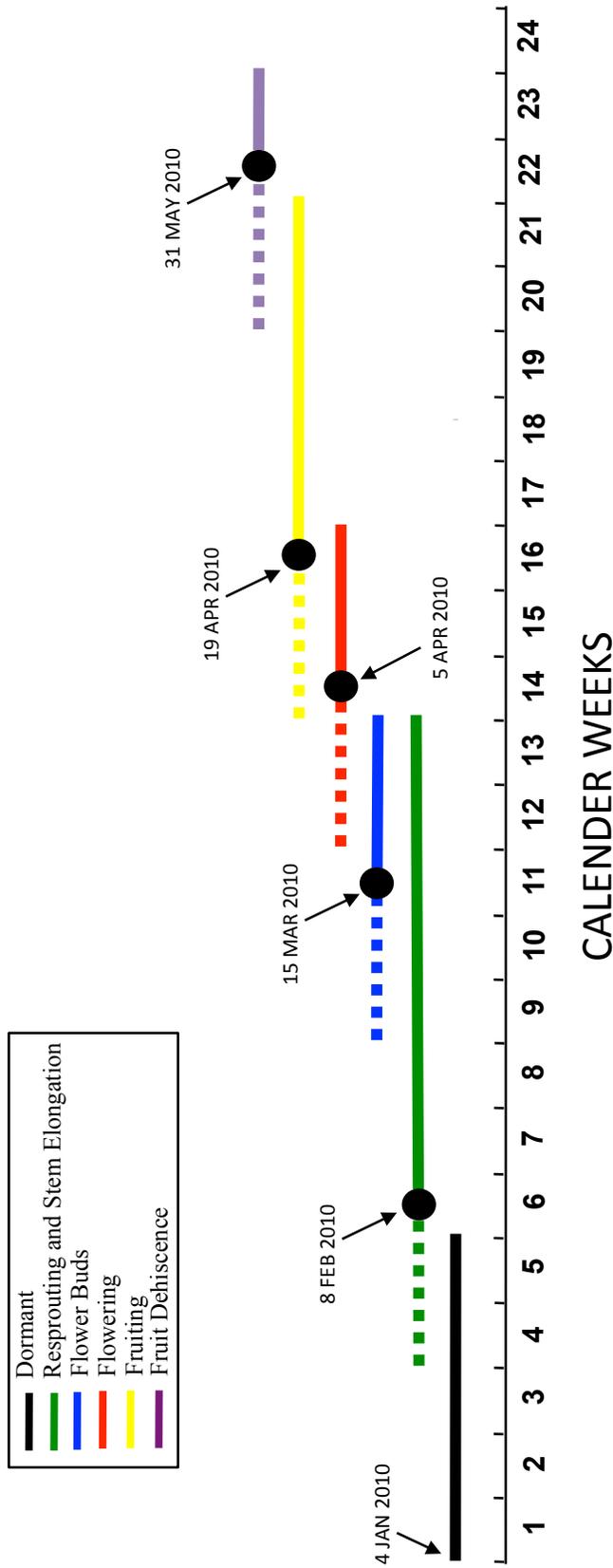


Figure 2. Phenology of *Astragalus jaegerianus* in 2010. *Astragalus jaegerianus* is a herbaceous perennial of the Mojave Desert that is active during the winter and dormant during the summer. Weekly observations were made on 20 *A. jaegerianus* resprouts starting January 4, 2010. Colored lines represent different phenological stages: dormancy, growth and stem elongation, flower bud production, flowering, fruiting, and fruit dehiscence. Black ovals represent the week all 20 plants reached the same phenological stage. Dashed lines represent weeks in which only a subset of study plants show a particular phenological stage.

Astragalus jaegerianus

Phenology 2011

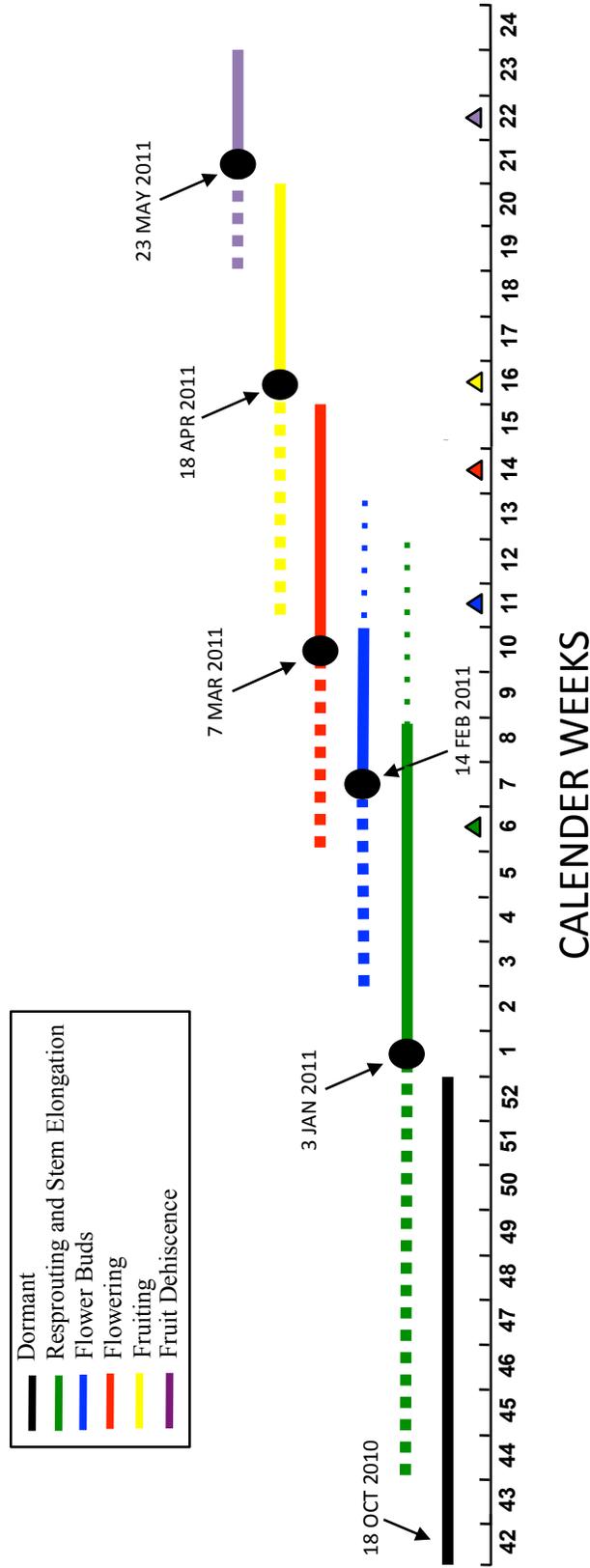


Figure 3. Phenology of *Astragalus jaegerianus* in the reproductive season of 2011. *Astragalus jaegerianus* is a herbaceous perennial of the Mojave Desert that is active during the winter and dormant during the summer. Weekly observations were made on 22 *A. jaegerianus* resprouts starting October 18, 2010. Colored lines represent different phenological stages: dormancy, growth and stem elongation, flower bud production, flowering, fruiting, and fruit dehiscence. Black ovals represent the week in which the majority of the 22 plants reached the same phenological stage; colored triangles represent the same point in the previous season. Dashed lines represent weeks in which only a subset of study plants show a particular phenological stage; thick dashes represent variation in the onset of phenological stages, and thin dashes represent delays in phenology due to heavy herbivory 6 study plants beginning week eight (February 21, 2011).

TABLE 1. Precipitation (mm) per month from October to May, in 2004-5, 2008-09, 2009-10, and 2010-11 and 2011-2012 at the remote automated weather station at Opal Mountain, CA (E 35°09'15"; W 117°10'32"; 3240 ft.). Years represent the season in which *A. jaegerianus* was reproductive. The data was adjust to better approximate precipitation at *A. jaegerianus* study sites (see methods in Section 1). Red numbers represent months with rain events over 20 mm that served as “rainfall triggers” to population-wide resprouting of *A. jaegerianus* (2004, October 18 – 27, 98.04 mm; 2010, January 18 – 22, 55.6 mm; 2010, October 17-20, 20.6 mm).

Opal Mountain		Precipitation				
Reproductive Year	2005	2009	2010	2011	2012	
Month	(mm)	mm	(mm)	(mm)	(mm)	
Oct	94.1	0.0	0.0	23.2	12.2	
Nov	26.3	15.6	0.5	10.2	9.5	
Dec	41.5	15.6	15.8	153.1	5.4	
Jan	88.8	0.7	58.5	0.7	4.4	
Feb	65.1	32.2	38.0	30.7	0.7	
Mar	42.9	2.2	10.7	13.4	11.0	
Apr	3.2	0.0	6.1	0.5	22.2	
May	0.0	0.2	0.0	1.2	0.0	
October-May Total	378.0	66.5	135.1	233.1	65.3	

TABLE 2. Duration of *Astragalus jaegerianus* phenological stages in weeks for 2010 and 2011. The total activity period is the number of weeks between the initiation of resprouting and the end of fruit dehiscence. The total reproductive period is the number of weeks between the beginning of flower budding and fruit dehiscence. The total duration of a phenological stage is a population-wide measure that includes all of the phenological variation in the study population.

Year	Total		Total		Flower		Fruit	
	Activity	Reproductive	Growth	Budding	Flowering	Fruiting	dehiscing	dehiscing
	Period	Period						
2010	20	15	10	5	5	8	4	
2011	32	21	21	10	10	10	5	
Difference	+12	+6	+11	+5	+5	+2	+1	

TABLE 3. The degree to which phenological stages were advanced by early precipitation during the 2011 *Astragalus jaegerianus* reproductive year.

	Growth	Flower budding	Flowering	Fruiting	dehiscence
Weeks Advanced	12	6	6	3	1

TABLE 4. The intervals in weeks between the initiation of *A. jaegerianus* phenological stages in 2010 and 2011. The interval of time between the initiation of phenological stages is a measure of the minimum time required for an individual plant to complete a stage.

Year	Resprouting to Flower Budding		Flower Budding to Flowering		Flowering to Fruiting		Fruiting to Dehiscing	
	Resprouting to Flower Budding	Flower Budding to Flowering	Flower Budding to Flowering	Flowering to Fruiting	Flowering to Fruiting	Fruiting to Dehiscing	Fruiting to Dehiscing	
2010	5	3	3	3	3	6	6	
2011	12	3	3	5	5	10	10	
Difference	7	0	0	2	2	4	4	

SECTION 3

SEED PRODUCTION, 2011

INTRODUCTION

Reproductive output in the form of seed production is critical to the long-term viability of a sexual reproducing species such as *Astragalus jaegerianus*. Despite its endangered status, little is known of the reproductive ecology of this geographically restricted species. A number of studies show a reduction in pollinator visitation and fruit set in small, geographically isolated populations (e.g. Kunin 1993, Steffan-Dewenter and Tschardt 1999, Vazquez and Simberloff 2004, Waites and Agren 2004). In light of its restricted geographic distribution, the objective of this study was to quantify *A. jaegerianus* seed production to determine to what extent its reproductive output may contribute to its rarity, its conservation status, and its recent declines.

METHODS

Determining flower, fruit, and seed production

Five weeks after the onset of *A. jaegerianus* fruit production in 2010 and 2011, and after all unfertilized flowers had senesced, racemes on 22 study plants were inventoried for fruits and flowers. Study plants were part of our long-term monitoring study in two distinct areas: Montana Mine-Brinkman Wash (MMBW), and Gemini

Conservation Area (GCM). Flower number was determined by counting the number of pedicel scars on each rachis.

At least twelve mature fruit from each study plant were randomly harvested. Fruits were opened and examined under a dissecting microscope to determine the mean number of seeds per fruit per plant. Total seed production for each study plant (S) was calculated as:

$$S = F_p \times S_f,$$

where F_p is the number of fruits per plant, and S_f is the mean number of seeds per fruit per plant.

RESULTS

Flower, fruit, and seed production

In 2011, the mean number of flowers per raceme per plant was 6.5 (Table 1), down from 7.8 in 2010 (Table 2), but individual racemes had as many as 17 flowers and as few as 1 flower. The mean number of fruits per raceme per plant was 1.3, unchanged from 2010 (Table 1 and 2), and the maximum number of fruits per raceme was 6, but many racemes (28.7%) produced no fruits; in 2010, 39.2% of racemes produced no fruit. Mean fruits per flower, a measure of reproductive efficiency, was 0.21, up from 0.16 in 2010 (Table 1 and 2). Only 19% of flowers produced fruit, and within these fruit, only 41% of ovules ripened into viable seed (Fig. 1a). The majority of ovules in fruit (59%) failed to mature into viable seed through lack of fertilization and abortion of seed (Fig. 1a). No pre-dispersal predation was observed.

Seed production between study plants was highly variable in both 2010 and 2011; for example, in 2011, the highest seed production was 5914 seeds for plant 745, and the lowest was 121 seeds for plant 362 (Fig 2b, Table 1). Total seed production for all 22 plants in 2011 was 21,210 seeds, down 26% from 28,809 seeds in 2010. This decrease in seed production in 2011 is visible in figure 2b as a suppression of seed production in the first two-thirds of the distribution relative to 2010 (Fig. 2a), with the exception of plant 745, which produced the most seed in both years, and had a small increase in seed production in 2011 (Fig 2). In 2011, 13 out of 22 plants had reductions in seed production relative to 2010, and 10 of these plants had declines of more than 25% (Fig 2b). A number of these study plants experienced heavy declines in seed production associated with moderate to heavy herbivory (bars marked with “H” in Fig. 2b). Study plants that experienced herbivory had significant declines in seed production, while plants that did not experience herbivory had non-significant increases in seed production (Fig. 3). Nine plants had increases in seed production in 2010, and 6 of these had increases of more than 25%; notable examples include plants 138, 152, 304, and 736; Fig. 2a and 2b).

DISCUSSION

In both 2010 and 2011, *A. jaegerianus* study plants had significant reproductive potential that was unrealized (Fig. 1). For example, in 2011 the average *A. jaegerianus* study plant produced over 700 flowers and nearly 12,000 ovules, but only 142 fruits and 964 seeds were ultimately produced per plant (Fig. 1, Table 1). Study plants lost most of their reproductive potential through the loss of flowers (81%, Fig. 1a), and secondarily

through the loss of ovules due to lack of fertilization and aborted seed (59%, Fig 1a). Significant unrealized reproductive potential has been observed in other *Astragalus* species (Green and Bohart 1975, Karron 1989, Kaye 1999, Crone and Lesica 2006, Kozuharova and Firmage 2007). The similarity between basic reproductive metrics in 2010 and 2011 (Fig. 1a) suggests that these intrinsic features of *A. jaegerianus* reproduction may be more or less invariant when seasonal precipitation is high. While 2011 had substantially more precipitation than 2010, both years had above average precipitation (Section 2). While a seed production study was not conducted in 2012, low seasonal precipitation led to high dormancy and low flower production among *A. jaegerianus* study plants that did resprout. These circumstances must have led to substantial decreases in seed production among study plants and across the species range. Seed production studies like those described here in 2010 and 2011 should be undertaken in dry years to help anticipate the effects of the regional drying predicted by recent climate change models (Seager et al. 2007) on *A. jaegerianus* reproduction.

While seed production in 2011 cumulatively decreased among *A. jaegerianus* study plants, individual plants increased and decreased seed production independently suggesting that countervailing forces may be acting on plants simultaneously. The substantial increases in seed production seen in several study plants was likely to be result of the positive effects of increased precipitation on plant production. But ironically, the high precipitation in 2011 may also be responsible for the high herbivory not seen in previous years of lower precipitation (2009 and 2010). Herbivory had a strong negative effect on seed production, and is likely to be the primary reason for decreases in seed production in 2011. The timing of precipitation may also have contributed to decreases

in seed production: early precipitation initiated *A. jaegerianus* resprouting in early November, which advanced flowering by 6 weeks (Section 2). This advanced flowering may have affected the coordination of *A. jaegerianus* flowering with pollinator activity, leading to some degree of plant-pollinator asynchrony, and a subsequent decrease in seed production from 8.3 seed per fruit in 2010 to 6.4 seeds per fruit in 2011 (Table 1 and 2).

CONCLUSIONS

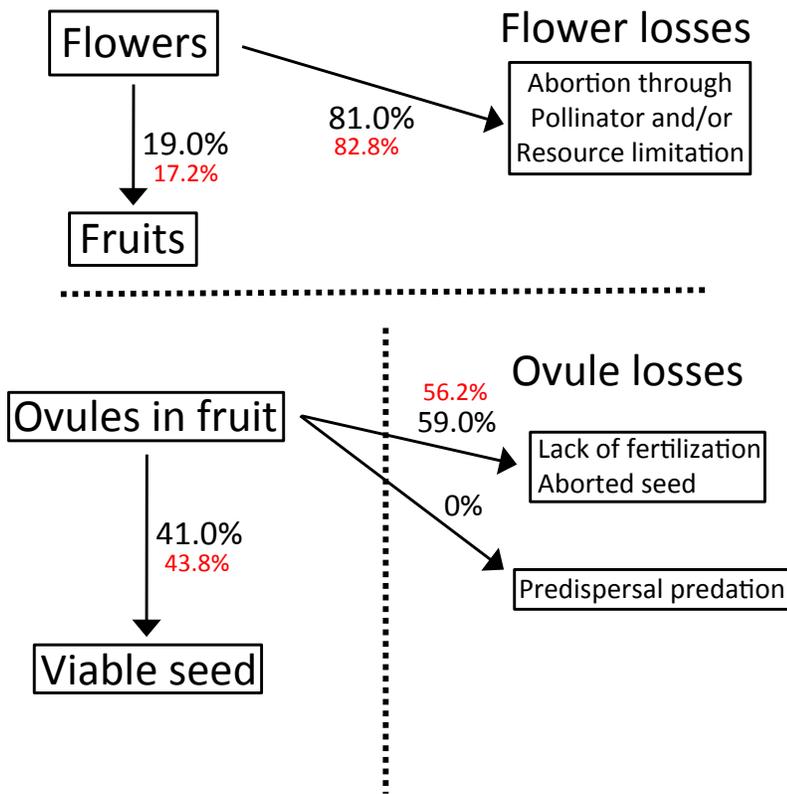
Seed production per plant in *A. jaegerianus* was highly variable in 2010 and 2011, and significant reproductive potential went unrealized in both years. The greatest loss in reproductive potential was flower abortion (81.0%), but of the 19.0% of flowers that matured into fruit, 59% of ovules were lost because of lack of fertilization and aborted seed. The similarity between basic reproductive metrics in 2010 and 2011 suggests that these intrinsic features of *A. jaegerianus* reproduction may be more or less invariant in wet years like 2010 and 2011, but more study is needed in dry years. While seed production in 2011 cumulatively decreased among *A. jaegerianus* study plants, individual plants increased or decreased seed production independently suggesting that countervailing forces may have been acting on plants simultaneously. High precipitation in 2011 is a likely explanation for increases in seed production in some plants, but the strong negative effect of herbivory on other plants appears to have overwhelmed the positive effect of precipitation on seed production. Early precipitation may also have contributed to decreases in seed production by advancing *A. jaegerianus* phenology, and leading to some degree of plant-pollinator asynchrony.

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2011
2010

A. Flower and ovule development



B. Total fecundity

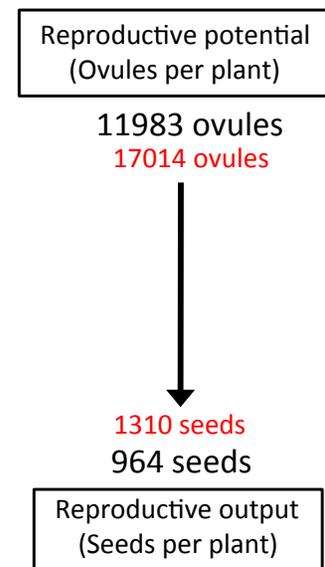


Figure 1. Diagram of (A) flower and ovule development, describing the ways in which the loss of flowers and ovules contribute to reduced reproduction, and (B) total fecundity as represented by the mean number of ovules produced per plant that develop into viable seeds. Black numbers are values in 2011, and red numbers are values in 2010. After Kaye 1999.

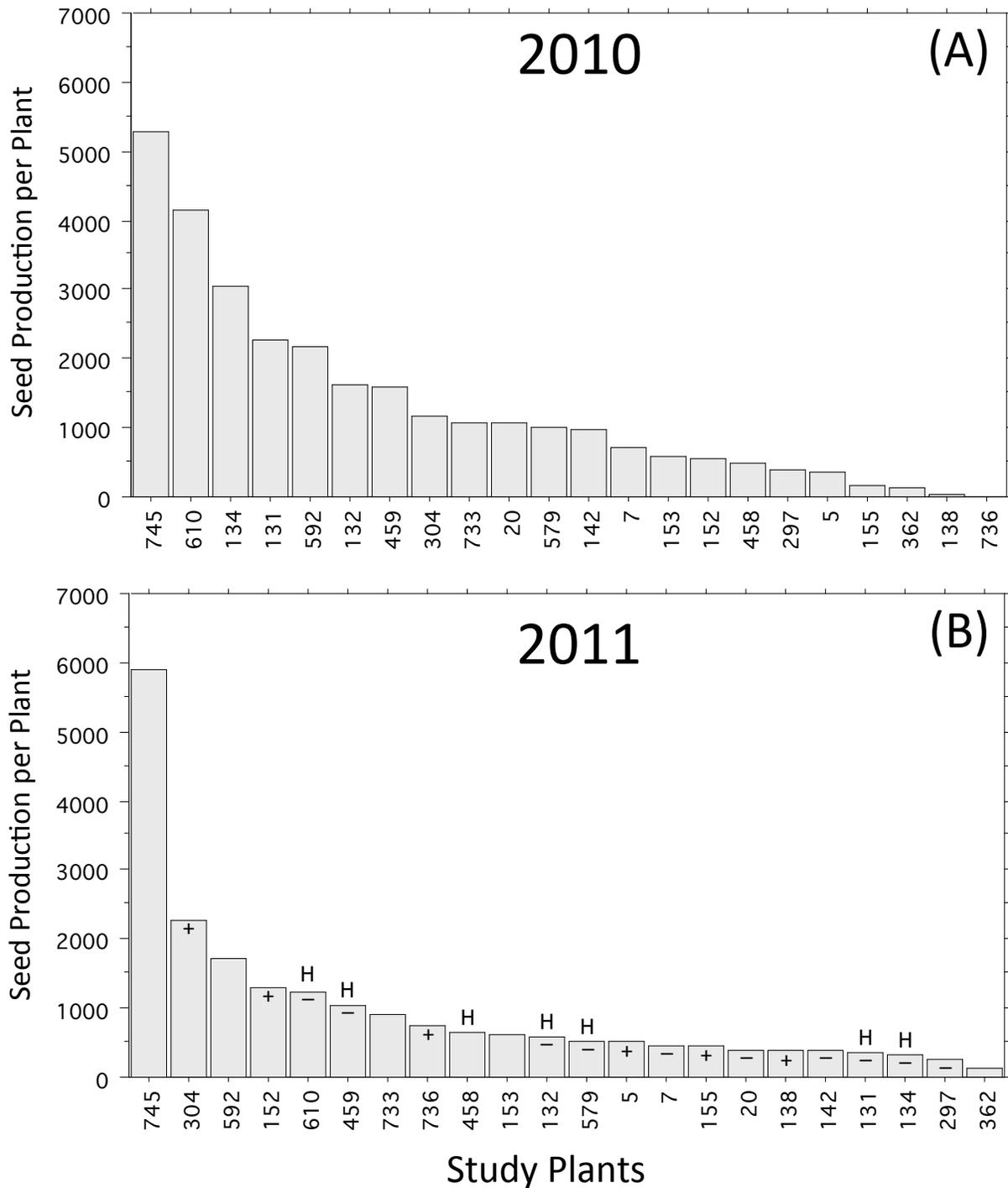


Figure 2. Seed production per plant in rank order of abundance in 2010 (A) and 2011 (B). Pluses and minuses indicate plants that increased or decreased seed production by more than 25% relative to the previous year, 2010. Plants that sustain moderate to severe herbivory damage are indicated with an H. Seed production is estimated as the product of the number of fruits per plant times the mean number of seeds per fruit. Seed production per plant was highly variable in both years. Mean seed production per plants was 1323 seeds in 2010 and 964 seeds in 2011 ($n=22$ study plants).

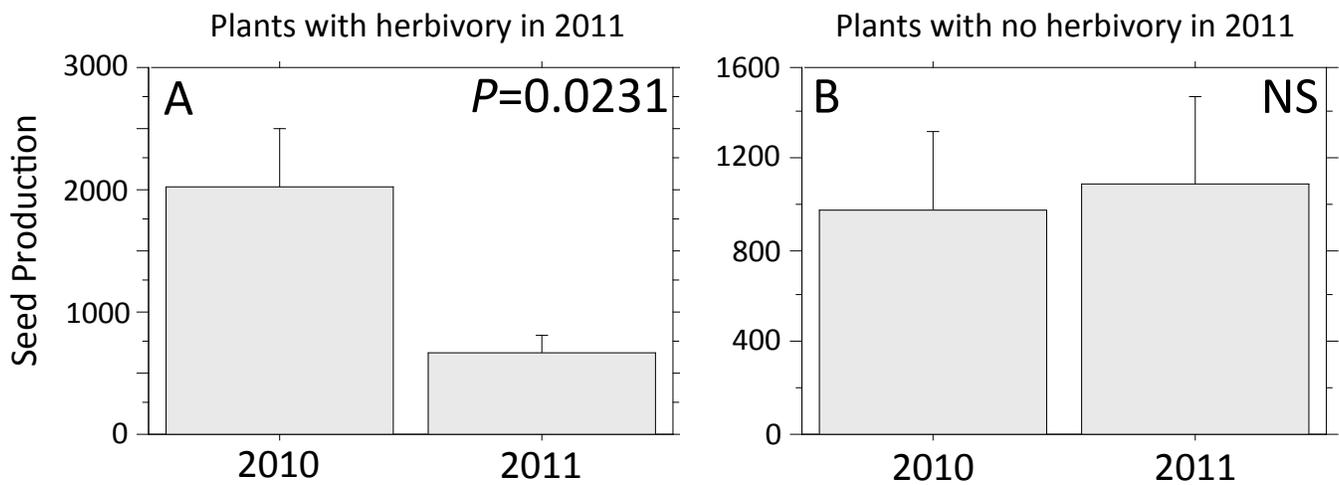


Figure 3. The negative effect of herbivory on seed production per study plant in 2011. (A) Plants with moderate to severe herbivory in 2011 (Paired t -test; $P=0.0231$, $n=7$ plants). (B) Plants with no herbivory in 2011(not significant; $n=15$ study plants). Bars are means plus 1 SE.

TABLE 1. Reproductive measures of 22 *Astragalus jaegerianus* long-term study plants active in 2011.

Study plant	Number of		Number of	Flowers per		Fruits per	Fruits per	Seeds per	Ovules	Total ovules	Total seeds
	raceme	flowers		fruits	raceme						
5	97	618	73	6.4	0.8	0.12	7.1	13.9	8590	518	
7	40	386	74	9.7	1.9	0.19	6.1	15.5	5983	451	
20	102	662	45	6.5	0.4	0.07	8.8	16.1	10658	396	
131	50	238	58	4.8	1.2	0.24	6.4	15.8	3760	371	
132	59	272	93	4.6	1.6	0.34	6.2	16.8	4570	577	
134	104	598	106	5.8	1.0	0.18	3.2	17.6	10525	339	
138	36	262	68	7.3	1.9	0.26	5.8	16.1	4218	394	
142	54	327	66	6.1	1.2	0.20	5.8	12.9	4218	383	
152	164	1110	225	6.8	1.4	0.20	5.8	15.4	17094	1305	
153	59	360	87	6.1	1.5	0.24	6.9	13.0	4680	600	
155	68	372	60	5.5	0.9	0.16	7.3	16.8	6250	438	
297	23	182	36	7.9	1.6	0.20	7.3	15.1	2748	263	
304	204	1804	368	8.8	1.8	0.20	6.2	14.5	26158	2282	
362	24	93	31	3.9	1.3	0.33	3.9	16.8	1562	121	
458	72	476	97	6.6	1.3	0.20	6.6	18.4	8758	640	
459	123	907	190	7.4	1.5	0.21	5.5	15.4	13968	1045	
579	213	1323	146	6.2	0.7	0.11	3.6	16.1	21300	526	
592	196	1107	326	5.6	1.7	0.29	5.3	17.4	19262	1728	
610	114	671	145	5.9	1.3	0.22	8.6	15.0	10065	1247	
733	88	592	110	6.7	1.3	0.19	8.3	18.3	10834	913	
736	104	667	223	6.4	2.1	0.33	3.4	14.1	9405	758	
745	468	3451	497	7.4	1.1	0.14	11.9	17.1	59012	5914	
Mean	112	749	142	6.5	1.3	0.21	6.4	15.8	11983	964	
Total	2462	16478	3124						263619	21210	

TABLE 2. Reproductive measures of 22 *Astragalus jaegerianus* long-term study plants active in 2010.

Study plant	Number of raceme	Number of flowers	Number of fruits	Flowers per raceme	Fruits per raceme	Fruits per flower	Seeds per fruit	Ovules per fruit	Total ovules per plant	Total seeds per plant
5	33	254	49	7.7	1.5	0.19	7.5	14.9	3785	370
7	57	538	103	9.4	1.8	0.19	6.9	18.2	9792	712
20	103	857	100	8.3	1.0	0.12	10.6	20.3	17397	1060
131	186	1357	222	7.3	1.2	0.16	10.2	19.3	26190	2264
132	167	1272	255	7.6	1.5	0.20	6.4	17.2	21878	1623
134	235	1743	409	7.4	1.7	0.23	7.5	21.6	37649	3052
138	78	562	24	7.2	0.3	0.04	0.8	12.5	7025	20
142	103	657	133	6.4	1.3	0.20	7.4	16.1	10578	986
152	46	323	54	7.0	1.2	0.17	10.1	15.6	5039	547
153	54	414	71	7.7	1.3	0.17	8.0	15.0	6210	568
155	24	186	22	7.8	0.9	0.12	7.7	18.3	3404	169
297	33	213	33	6.5	1.0	0.15	11.4	16.8	3578	376
304	89	752	118	8.5	1.3	0.16	10.0	16.3	12258	1180
362	10	105	19	10.5	1.9	0.18	6.8	17.7	1859	129
458	65	505	39	7.8	0.6	0.08	12.6	16.4	8282	492
459	142	1055	172	7.4	1.2	0.16	9.3	16.3	17197	1595
579	91	721	123	7.9	1.4	0.17	8.1	18.1	13050	994
592	189	1524	354	8.1	1.9	0.23	6.2	17.8	27127	2183
610	278	2326	398	8.4	1.5	0.17	10.4	16.1	37449	4133
733	60	441	119	7.4	2.0	0.27	9.1	17.1	7534	1081
736	28	158	0	5.6	0.0	0.00	NA	NA	0	0
745	524	4827	738	9.2	1.4	0.15	7.1	20.1	97023	5274
Mean	118	945	163	7.8	1.3	0.16	8.3	17.2	17014	1310
Total	2595	20790	3555						374301	28809

SECTION 4

RE-INTRODUCTION EXPERIMENT

INTRODUCTION

In Section 1 (Population Dynamics, 2010) we described the history of recent population declines of *Astragalus jaegerianus*, and hypothesized that these declines are the consequence of long-term drought in the Mojave Desert (1999-2010). Whether the current drought is part of a 20 to 30 year cycle, or the beginning of a shift to drier conditions associated with global climate change-type drought, our monitored *A. jaegerianus* population have dropped to critically low levels and are in danger of local extinction (Huggins et al 2010). Given the current state of long-term climate uncertainty, precautions should be taken to ensure that we have the methods necessary to reintroduce or facilitate the migration of *A. jaegerianus* if drought conditions worsen and population declines continue.

The object of this study is to develop methods of reintroduction through a pilot reintroduction of *A. jaegerianus* into a depleted population within the Gemini Conservation Area. Through an experimental approach, we can simultaneously develop practical methods of reintroduction, as well as investigate ecological factors that may affect the population dynamics of *A. jaegerianus*. A number of studies have detected a negative effect of drought (Casper 1996, Tielborger and Kadman 2000, Barchuk 2005), herbivory (Valiente-Banuet and Ezcurra 1991, Mandujano et al. 1998), and competition

from other plants (Ibanez and Schupp 2001, McAuliffe 1984, Callaway and D'Antonio 1991) on seedling establishment. In this study, we present the results of our pilot reintroduction in which we document the effect of supplemental watering, herbivore exclusion, and competition with annuals on the seedling establishment of *A. jaegerianus*.

METHODS

To test the effect of supplemental water and herbivore exclusion cages on the growth of *A. jaegerianus* seedlings (first year plants) we used a fully crossed, two factor, randomized block design with two levels for each factor (ambient rainfall vs. supplemental watering, and no cages vs. herbivore exclusion cages). To test the effect of annuals on *A. jaegerianus* growth, an addition supplemental water plus cage treatment with annuals removed was compared to supplemental water plus cage treatments where annuals were not removed.

At our Gemini Conservation Area (GCA) population 2 (G2), 40 shrubs were selected as seedling hosts, and assigned to eight blocks based on their position at the site (Fig 1). Each block contained five shrubs that were randomly assigned to five treatment groups: (1) no cage, ambient rainfall, (2) cage, ambient rainfall, (3) no cage, supplemental water, (4) cage, supplemental water, and (5) cage, supplemental water, annual removal, that was used exclusively for comparison with treatment (4) (Table 1). Under each experimental shrub, four *A. jaegerianus* seedlings were planted at the four cardinal compass directions, as far into the host shrub canopy as shrub branches would allow. Herbivore exclusion cages were constructed of ½ inch hardware cloth, and seated into the soil to a depth of 5 to 10 cm.

Seedlings were grown at UCLA from seed collected at GCA. Seeds were scarified on both sides using 180 grit sandpaper, and placed on damp filter paper in Petri dishes near a source of indirect sunlight. After 3 days, when seedling roots were between 1 and 2 cm long with developed cotyledons, seedlings were transplanted to 1.5 inch biodegradable pots in a 1:1 mixture of commercial seedling mix and native soil from the GCA. After 4 to 8 days of growth in a UCLA greenhouse, the most robust seedlings were transplanted under experimental host shrubs. Seedlings were measured on a monthly basis beginning on 16 February 2010 with the first supplemental watering. Seedlings stems were measured from the cotyledons to the distal internode of the longest stem. Initial stem lengths were very short, between 0 and 5 mm, with no more than 1 node. At the time of measurement, seedlings were examined for any signs of damage, including herbivory and wilting.

A watering schedule was designed to maintain optimal moisture around roots. To do this, the amount of water applied to host shrubs was increased as roots elongated and ambient temperatures increased (Table 2). Water runoff was minimized with 4 to 8 cm high berms around host shrubs constructed from cotton sleeves filled with local sand. Water was initially hand applied using a 2.5 gallon watering can (16 February through 4 May 2010), and the amount of water applied was determined using three rain gauges placed inside host shrubs; 2.5 gal. of hand watering produced approximately 3 cm of simulated rainfall. After ambient temperatures and root lengths increased, a combination of hand-watering and gravity-fed, drip irrigation was used (May 9 through June 21). The drip irrigation system consisted of 5 gal. jugs placed on cinder-blocks 60 cm high and adjacent to host shrubs. A siphon tube with an internal diameter of 3/8 in. was capable of

apply 10 gal. of water per hour with virtually no run-off, maximizing the effectiveness of water delivery to the root zone. Watering from 7 May through 21 June 2010 consisted of 2 gal. of hand watering plus either 6, 8 or 10 gal. of drip irrigation per plant (Table 2). The depth of water penetration was determined by digging shallow soil pits at the base of 3 non-experiment shrubs; mean penetration of 1 cm of hand watering was 7 cm.

Statistical analysis

Seedling growth data were analyzed using StatView (SAS 1999). *Astragalus jaegerianus* seedling growth was calculated as a seedling's greatest height measured during the experiment. For example, if a plant died during the first month, and its initial measurement was 3 mm, its total growth was also 3 mm. Statistical comparisons were based on the mean growth of all four seedlings per shrub. These growth data were not normally distributed, and a non-parametric test, the Mann-Whitney U , was employed in two group comparisons of factor levels such as "ambient rainfall" and "supplemental watering" treatments.

RESULTS

Seedling growth was significantly higher in water supplementation treatments (Fig. 2a; Mann-Whitney U , $U=52.5$, $n^1=n^2=16$, $P=0.0044$), and herbivore exclusion treatments (Fig. 2a; Mann-Whitney U , $U=69.0$, $n^1=n^2=16$, $P=0.0262$), but caging significantly increased seedling growth in supplemental water treatments only (Fig. 2b; Mann-Whitney U , $U=7.000$, $n^1=n^2=8$, $P=$). There was also a significant increase in

seedling growth when annuals were removed from “supplemental water plus cage” treatments (Fig. 3; Mann-Whitney U , $U=9.00$, $n^1=n^2=8$, $P=0.0157$).

Of the initial 160 *A. jaegerianus* seedlings, 55 survived to the end of the 2010 reproductive season (February 16 to June 20), and 24 of the 40 experimental host shrubs supported one or more seedlings. While a number of the larger plants emerged from their host shrubs canopy (10), none of these plants produced flowers in 2010. Surviving seedlings varied in size; 14 seedlings grew to a stem length greater than 200 mm, the longest was 340 mm (Fig. 4). One seedling (27 South) was measured at 370 mm in May, but was eaten back to 270 in June. As plants grew and matured, they first developed multiple stems, and then woody bases, such that large plants had a high proportion of both multiple stems and woody bases (Fig. 4).

Mortality among experimental seedlings was high: 65.6%. This mortality was not evenly distributed among treatments; host shrubs with ambient water and no herbivore exclusion cages (controls) had 97% seedling mortality, while shrubs with supplemental water, cages, and annual removal had 19% mortality. *Astragalus jaegerianus* mortality was highest among host shrubs without supplemental water, herbivore exclusion cages, or both (Fig. 5).

Seedling mortality could be categorized into four types: herbivory (31%), wilting (14%), digging (1%), and unknown causes (52%). Mortality by herbivory occurred by damage or removal of the apical meristem or by consumption of the whole plant leaving just the stem below the cotyledons. Often, the stem was eaten to the ground and difficult to see; much of the mortality due to unknown causes is likely to be this type of herbivory. Non-lethal herbivory, in which seedlings survived the removal of cotyledons (11

seedling) or leaves (12 seedlings) also occurred. In May and June, the last two months of the experiment, three large seedlings were denuded of leaves but their stems left intact, and three seedlings had the distal portion of stems consumed, reducing their height by as much as 10 cm (27 South). Caging reduced, but did not stop herbivory; lethal herbivory was observed 22 times in un-caged treatments and 11 times in caged treatments, and non-lethal herbivory was observed 15 times in un-caged treatments and 16 times in caged treatments. Darkling beetles (*Eleodes* sp.), blister beetles (*Lytta insperata*), as well as side-blotch lizards (*Uta stansburiana*) were frequently observed moving in and out of exclusion cages, and all are herbivores or facultative herbivores (Johnson and Triplehorn 2004, Nagy 1983). Wilting was a less ambiguous phenomenon to document than herbivory because, unlike some lethal herbivory in which all trace of the plant was removed, wilting occurs over several weeks, and the desiccated plant remains in place. Wilting was observed as a cause of mortality in 13 cases, and all were in ambient rainfall treatments (i.e. without supplemental water), suggesting insufficient precipitation was the cause of wilting.

In 2011, of the 55 plants that survived to the end of their first year, 34 resprouted. Of these 34 resprouts, 26 emerged from their host shrub's canopy, and 21 flowered and produced seed. Since 2011 was a wet year in the Mojave, we can assume that dormancy among these experimental plants was low. In 2012, 8 plants resprouted and none flowered. Since 2012 was a dry year in the Mojave with high dormancy and low flower production in natural *A. jaegerianus* population, we can assume that experimental plants also experience high dormancy. The larger the seedling its first year, the higher was the likelihood of it resprouting in subsequent years; for example, only 29% of the seedlings

under 100 mm resprouted in 2011, and 0% resprouted in 2012, while 92% of the seedlings above 200 mm resprouted in 2011, and 50% resprouted in 2012.

DISCUSSION

Our results demonstrate that for the purposes of *A. jaegerianus* reintroduction, the combination of supplemental water, herbivore exclusion, and the removal of annuals, provided the best conditions for growth and survival of *A. jaegerianus* seedlings (Fig. 2, Fig. 3, Fig.5). Using these methods, wildlife managers can expect 85% seedling survival the first year. In addition, seedling survival could be improved with more effective herbivore exclusion.

Our control treatments (ambient rainfall without anti-herbivore cages) had the lowest levels of growth (Fig. 2) and nearly complete mortality (Fig. 5), echoing the results of our long-term study of natural populations in which the recruitment of seedlings has been low and restricted to years with above average precipitation (Section 1). We have previously hypothesized that recruitment failure was a consequence of long-term drought (Huggins et al. 2010), and these results support this idea, in that recruitment in our control treatments is likely to be zero: only one, small, 50 mm seedling survived the control treatments, and is unlikely to resprout in 2011. In contrast, 15 seedlings in supplemental water treatments grew to lengths greater than or equal to 200 mm, and are therefore more likely to resprout. It is important to note that our working definition of recruitment is the addition of reproductive individuals into a population. Consequently, the recruitment success of each treatment can not be known until 2011 when experimental seedling grown in 2010 do or do not resprout and flower. However, we

hypothesize that larger, multi-stemmed seedlings with woody stem bases are more likely to survive dormancy and resprout because they have sequestered more resources and developed a viable caudex (woody stem base) prior to summer dormancy.

A number of studies have suggested that among other possible benefits, host plants may provide *A. jaegerianus* with protection from herbivores (Gibson et al. 1998, Sharifi et al. 2009, Huggins et al. 2010). The results of this study do not support this idea in the case of seedling. If host shrubs were protecting seedlings from herbivory, one would expect that caged and uncaged treatments would have similar seedling growth, and that mortality would be relatively low in uncaged treatments. Instead, mortality was high among uncaged treatments; 22 out of 64 seedling conservatively, and 54 out of 64 assuming “unknown causes” is in fact herbivory in which the entire plant is completely removed. In 2010, 14 of the 24 naturally occurring seedlings in our long-term study disappeared and were likely consumed by herbivores (see section 1). Furthermore, despite “leaky” herbivore exclusion cages, there was a significant increase in growth in cage treatments. Together, these results suggest that cages protected seedlings more effectively than host shrubs, a result found in other systems (Flores et al. 2004). This is not to say that host shrubs do not provide some herbivore protection, but rather, host shrub protection for seedlings is weak and does not appear to be a major benefit to its protégé *A. jaegerianus*. Ultimately, while seedling herbivory was high under host shrubs, we do not know that herbivory would have been even higher without host shrubs.

The reason why host shrubs may not be effective protection against herbivory is because herbivores are smaller than previously thought. Herbivore exclusion cages were designed to exclude mammalian and avian herbivores, but were only partially successful

in preventing herbivory to seedlings because insect and reptile herbivores were able to pass through the ½ inch hardware cloth from which the herbivore exclusion cages were constructed. Insects have been shown to be important herbivores in other host plant and protégé systems (Steenbergh and Lowe 1969, Flores et al. 2004), and side-blotched lizards, though typically carnivorous, eat plant leaf tissue (up to 43% of dry mass of stomach contents) in the late winter and early spring (Nagy 1983). Our group is presently testing the efficacy of anti-herbivore tubes: clear acrylic tubes 3 cm in diameter that fit over individual seedlings, protecting them from small insect and reptile herbivores.

SUMMARY

In this study, we presented the results of our pilot reintroduction study in which we document the effect of supplemental watering, herbivore exclusion, and competition with annuals on the seedling establishment of *A. jaegerianus*. Our results demonstrate that for the purposes of *A. jaegerianus* reintroduction, the combination of supplemental water, herbivore exclusion, and the removal of annuals, provided the best conditions for growth and survival of *A. jaegerianus* seedlings. Using these methods, wildlife managers can expect 85% seedling survival the first year. The results of this study suggest that host shrubs only weakly protect *A. jaegerianus* seedlings from herbivory; herbivory was high in uncaged treatments and herbivores were small and likely to be insects and possibly lizards. We have previously hypothesized that *A. jaegerianus* recruitment failure was a consequence of long-term drought (Huggins et al. 2010), and these results support this idea: without water supplementation, seedlings had low growth and high mortality from wilting even in a year of above average precipitation such as 2010.

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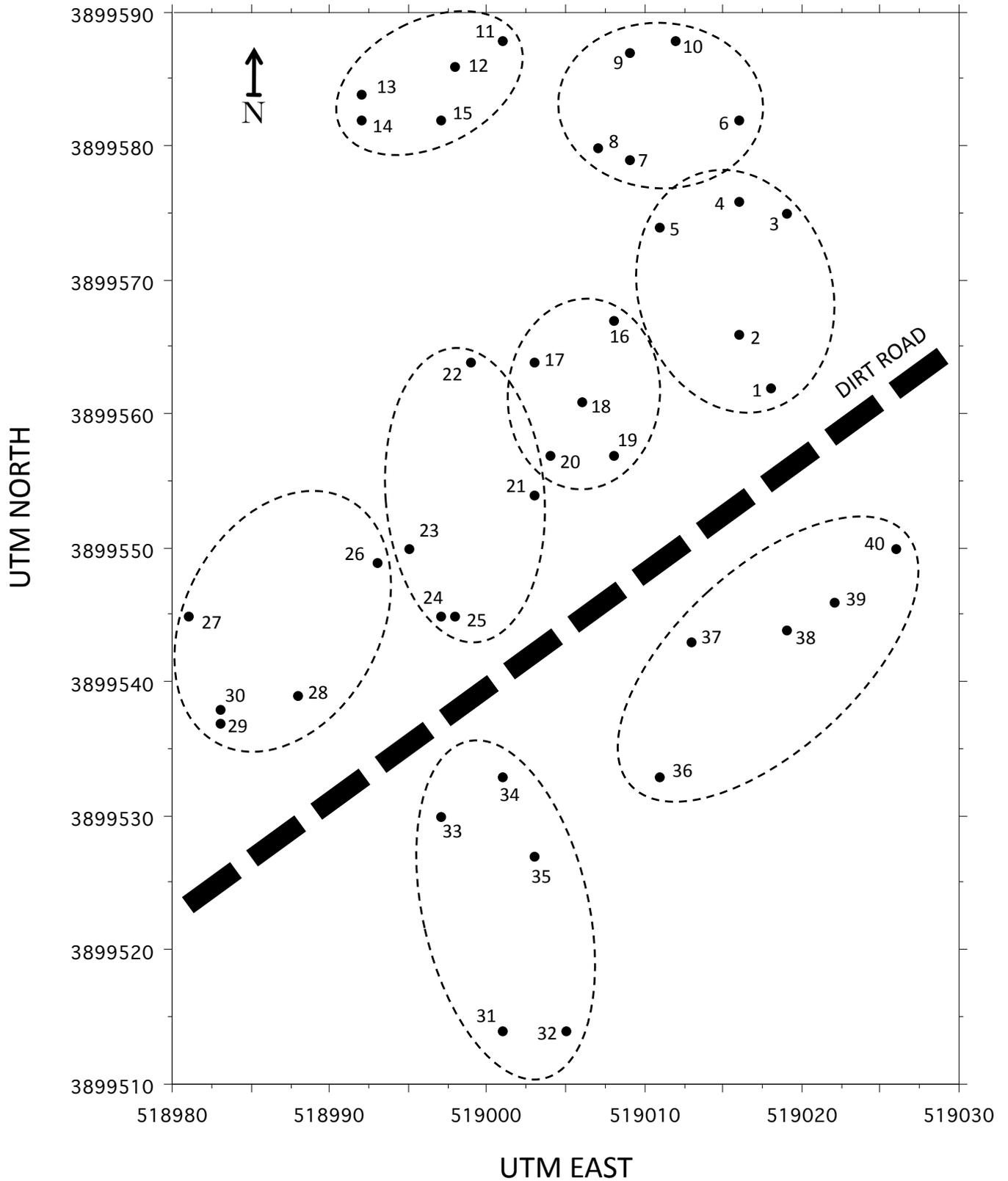


Figure 1. Areal view of GCA study site (G2) with numbered experimental host shrubs grouped into blocks (dashed circles). Each block contained 5 host shrub treatments. Each host shrub contained four experimental *Astragalus jaegerianus* seedlings.

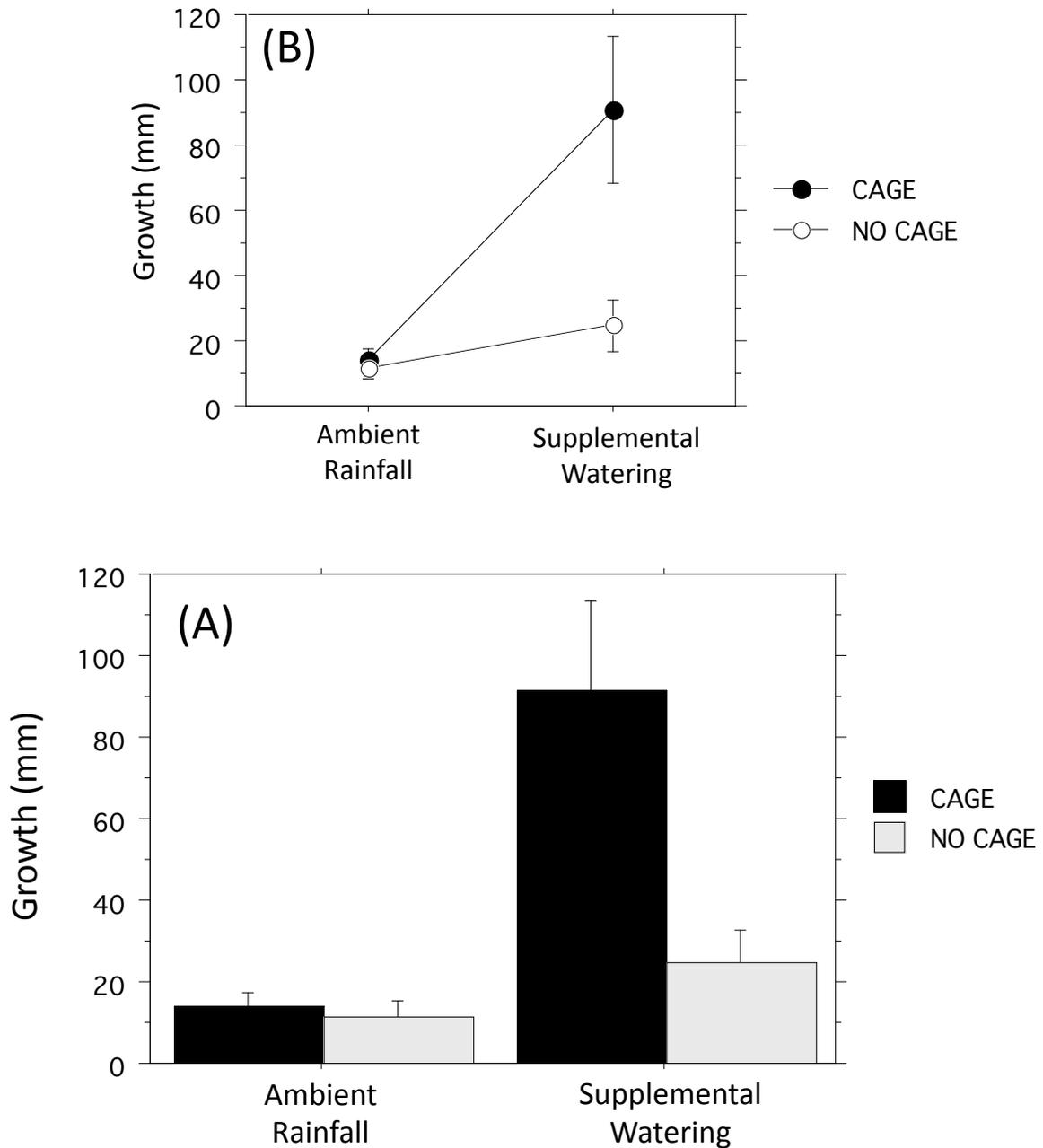


Figure 2. Mann-Whitney U tests of treatment effects on growth of *Astragalus jaegerianus*, 2010. Growth is mean growth of four experimental seedlings per host shrub (mm). (A) There was a significant effect of supplemental water ($U=52.50$, $n^1=n^2=16$, $P=0.0044$) and anti-herbivore cages ($U=69.00$, $n^1=n^2=16$, $P=0.0262$) on growth of experimental seedlings. Bars are means plus 1 SE (B) Interaction between cage and water treatments; caging significantly increased growth in supplemental water treatments only ($U=7.00$, $n^1=n^2=8$, $P=0.0087$). Points are means plus 1 SE.

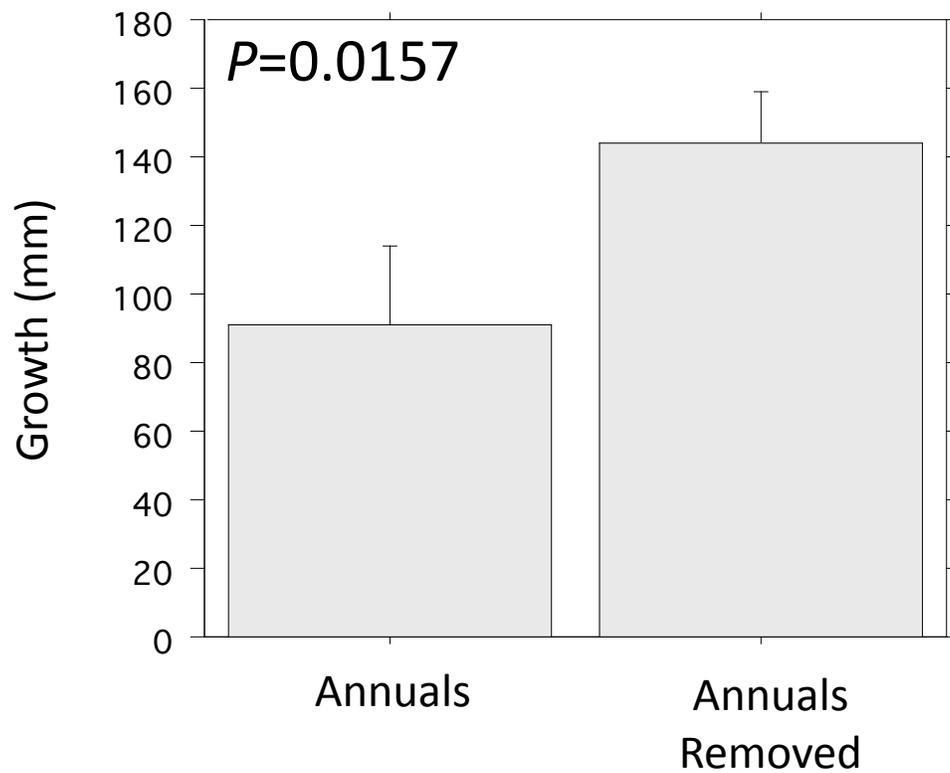


Figure 3. The effect of annuals on growth of *A. jaegerianus* in supplemental water treatments. There was a significant increase in growth when annuals were removed (Mann-Whitney U ; $U=9.00$, $n^1=n^2=8$, $P=0.0157$). Growth is mean growth of 4 experimental seedlings per host shrub (mm). Bars are means plus 1 SE.

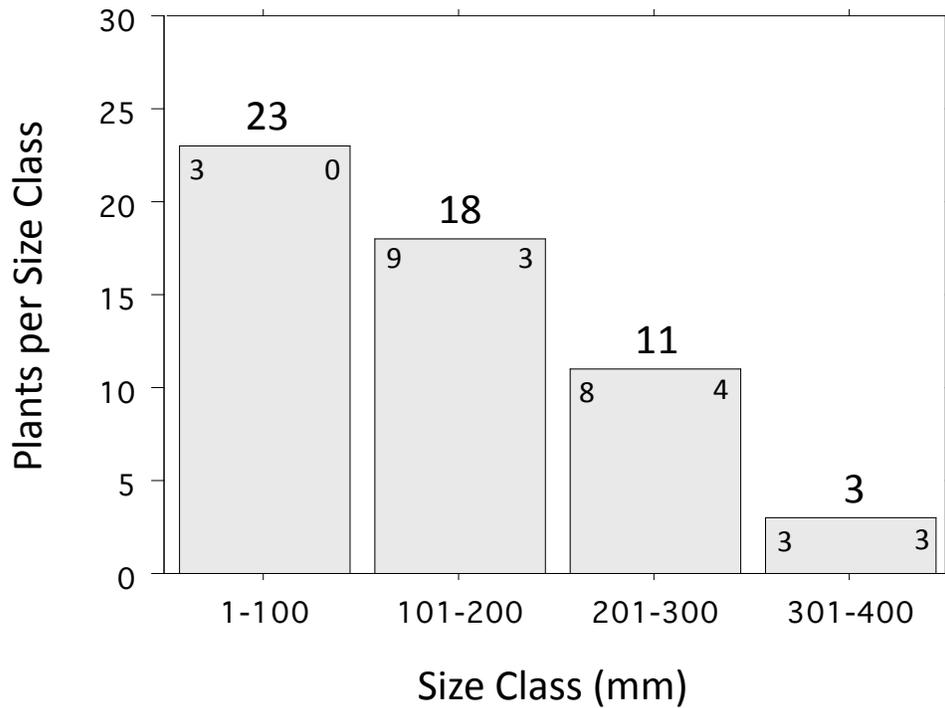


Figure 4. The number of surviving *A. jaegerianus* plants in four size classes. The number at top of bar is plants per size class. On the left side of each bars is number of plants with multiple stems, and at the right of each bar is number of plants with woody stem bases. One of the seedlings in the third size class (201-300) grew to a length of 370 mm in May, but was eaten down to 270 mm in June. This seedlings (27 South) would have been the longest surviving plant had it not been eaten.

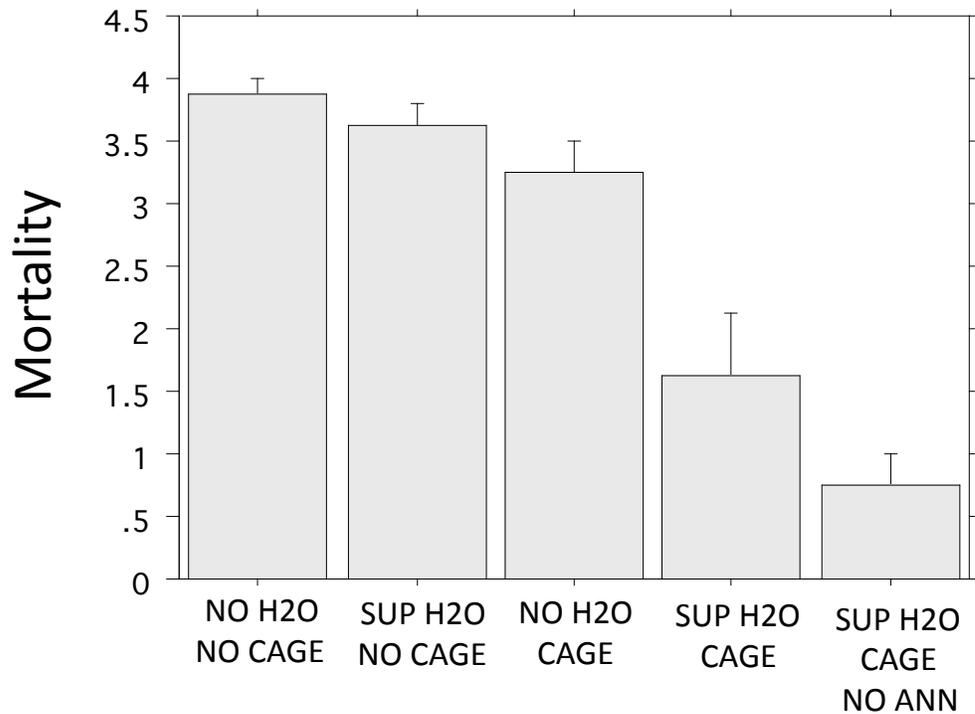


Figure 5. *Astragalus jaegerianus* seedling mortality and host shrub treatment. Mortality (dead seedlings per shrub) was highest among treatments that lacked supplemental water, anti-herbivore cages, or both (8 host shrubs per treatment, 4 seedlings per shrub).

Table 1. Experimental host shrub number, treatment assignment, host shrub species, and host shrub volume for experimental host shrubs at the Gemini Conservation Area, population G2, 2010. THMO=*Thamnosma montana*, EPNE=*Ephedra nevadensis*, ERFA=*Eriogonum fasciculatum*, ERCO=*Ericameria cooperi*, ENCA=*Encelia actonii*, AMDU=*Ambrosia dumosa*.

PLANT NUM.	TREATMENT	SPECIES	VOLUME
1	NO WATER, NO CAGE	THMO	0.130
2	NO WATER, CAGE	EPNE	0.150
3	WATER, NO CAGE	EPNE	0.183
4	WATER, CAGE, WEED REMOVAL	ERFA	0.279
5	WATER, CAGE	ENAC	0.063
6	WATER, CAGE, WEED REMOVAL	ERCO	0.030
7	WATER, CAGE	EPNE	0.158
8	NO WATER, NO CAGE	ERFA	0.076
9	NO WATER, CAGE	ERFA	0.039
10	WATER, NO CAGE	ERCO	0.038
11	NO WATER, NO CAGE	ERFA	0.180
12	NO WATER, CAGE	ERFA	0.098
13	WATER, CAGE, WEED REMOVAL	THMO	0.078
14	WATER, CAGE	ERCO	0.039
15	WATER, NO CAGE	ERFA	0.045
16	NO WATER, NO CAGE	ENAC	0.027
17	NO WATER, CAGE	ERFA	0.073
18	WATER, NO CAGE	THMO	0.078
19	WATER, CAGE, WEED REMOVAL	ERFA	0.085
20	WATER, CAGE	THMO	0.081
21	WATER, CAGE	ENAC	0.218
22	WATER, NO CAGE	THMO	0.052
23	WATER, CAGE, WEED REMOVAL	ERCO	0.042
24	NO WATER, CAGE	ERFA	0.039
25	NO WATER, NO CAGE	THMO	0.068
26	WATER, CAGE, WEED REMOVAL	AMDU	0.036
27	WATER, NO CAGE	ERCO	0.055
28	WATER, CAGE	THMO	0.065
29	NO WATER, CAGE	ERCO	0.028
30	NO WATER, NO CAGE	AMDU	0.062
31	WATER, CAGE, WEED REMOVAL	ERFA	0.045
32	NO WATER, NO CAGE	THMO	0.088
33	NO WATER, CAGE	ERCO	0.065
34	WATER, NO CAGE	ENAC	0.151
35	WATER, CAGE	EPNE	0.082
36	NO WATER, NO CAGE	ENAC	0.178
37	WATER, CAGE, WEED REMOVAL	AMDU	0.040
38	NO WATER, CAGE	THMO	0.043
39	WATER, NO CAGE	ERFA	0.025
40	WATER, CAGE	AMDU	0.040

Table 2. Watering schedule, including total gallons of water applied to host shrubs per watering, their equivalent in simulated rainfall, and depth soil penetration of watering for *Astragalus jaegerianus* restoration experiment. One gallon of applied water produced 1.2 cm of simulated rainfall, and 1 cm of simulated rainfall penetrates to a soil depth of 7 cm.

DATE	APPLIED WATER (gal.)	SIMULATED RAINFALL (cm)	SOIL PENETRATION (cm)
16 FEB	1	1.2	8.4
23 FEB	1	1.2	8.4
3 MAR	1	1.2	8.4
11 MAR	1	1.2	8.4
17 MAR	2	2.4	16.8
24 MAR	2	2.4	16.8
27 MAR	2	2.4	16.8
1 APR	2	2.4	16.8
7 APR	2	2.4	16.8
13 APR	3	3.6	25.2
19 APR	3	3.6	25.2
23 APR	4	4.8	33.6
29 APR	4	4.8	33.6
4 MAY	4	4.8	33.6
9 MAY	8	9.6	67.2
16 MAY	8	9.6	67.2
23 MAY	10	12	84.0
28 MAY	10	12	84.0
3 JUN	10	12	84.0
9 JUN	12	14.4	100.8
15 JUN	12	14.4	100.8
21 JUN	12	14.4	100.8

SECTION 5

SOIL SEED BANK, 2009-2011

INTRODUCTION

Since 1999, our long-term monitoring of six *A. jaegerianus* populations at the Gemini Conservation Area and Brinkman Wash has revealed significant population declines (see Section 1). These population declines have occurred simultaneously with severe drought conditions in the Mojave Desert (Hamerlynck and McAuliffe 2008, McAuliffe and Hamerlynck 2010). The drought conditions of the last decade are likely to represent the first part of a dry period in the Mojave Desert which typically last 20 to 30 years (Hereford et al. 2006, Huggins et al. 2010). Alternately, the current drought may be part of a more permanent shift to drier conditions driven by global climate change-type drought (Cook et al. 2004, Breshears et al. 2005, Seager et al. 2007). While many plant species are capable of adjusting their elevational range in response to climate change, *A. jaegerianus*' unique habitat requirements make dispersal to higher elevations difficult because *A. jaegerianus* habitat is patchy, and *A. jaegerianus* dispersal is low (Rundel et al. 2009, Prigge et al. 2011). Without the capacity to adjust its range in relation to climate, the recovery of *A. jaegerianus* must occur within existing population sites, which makes the condition of the *A. jaegerianus* soil seed bank at these sites critical to the long-term viability of the species. Understanding the density and distribution of the *A. jaegerianus* seed bank is important because, as *A. jaegerianus* populations contract

and the threat of local extinction increases, the *A. jaegerianus* seed bank represents the last refuge from which reproductive populations may regenerate after population collapse.

The objectives of our seed bank research program from were numerous: (1) document the vertical and horizontal distribution of the soil seed bank, (2) document the distribution of seed between shrubs with different histories of *A. jaegerianus* occupancy and dispersal distances, (3) and evaluate the stability and dynamics of the *A. jaegerianus* seed bank within and between years.

NATURAL HISTORY

Astragalus jaegerianus seed

Astragalus jaegerianus seeds are smooth, 1 to 3 mm long, typically weigh 3 to 6 mg, and are reniform to rhomboid in shape. The seed has an impermeable seed coat that controls germination and dormancy. Through weathering, the site of water entry, the striphiole, becomes permeable to water and the seed becomes capable of germination (Baskin and Baskin 1998). Unweathered *A. jaegerianus* seeds with intact seed coats may be germinated through mechanical scarification of the seed coat.

Astragalus jaegerianus seeds are without dispersal morphologies. The majority of seed is released when seed-pods dehisce and fall directly to the ground beneath host shrubs, where some portion is consumed by granivores (rodents, ants, birds). Seeds not consumed by granivores are buried beneath plant litter and soil particulate produced by host shrubs that act as traps for wind blown soil particles. Wind and rain can mechanically bury seed through mechanical agitation of the soil. Not all seed drops directly to the ground; a fraction of seeds remain within the partially opened seed-pods

which fall to the ground or are retained on the mother plant. Seed-pods that remain on the mother plant (aerial seed bank) may fall off weeks to several months later after primary dispersal. Seeds that remain in pods may be protected from weathering and scarification, and may therefore germinate later than seeds released individually at maturity. Detached seed-pod can disperse by wind or water several meters or more from their mother plant, but dispersal between populations is probably rare, and dispersal between the four geographic concentrations is likely to be extremely rare.

METHODS

Soil sample collection and treatment

Soil samples were collected under 22 host shrub canopies with actively growing *A. jaegerianus*. These study plants are part of our long-term monitoring program at GCA and Brinkman Wash described earlier (Section 1). Soil samples consisted of 10 by 10 cm samples collected from 0 to 1 cm in soil depth using a trowel and a 10 cm wire square as a guide to collection. Samples were placed in marked, resealable storage bags at the time of collection and transported to the University of California, Los Angeles for analysis. *Astragalus jaegerianus* seeds were removed from soil samples through sieving and visual inspection. Number 9 and 14 Tyler sieves were used to isolate that fraction of the soil sample that contained seeds. This process reduced the volume of the sample and made inspection faster and more accurate than inspecting the entire soil sample. Soil sample volumes were measured, and then spread evenly across an inspection surface marked with a 5 cm² grid. Each 5 cm square was then systematically inspected for *A. jaegerianus* seed.

Pre- and post-dispersal, 0 to 1 cm, soil samples were collected under host shrub canopies immediately before and after *A. jaegerianus* primary seed dispersal in 2009, 2010, and 2011. Additional soil samples were collected in a manner designed to answer specific questions about the distribution of the *A. jaegerianus* seed-bank. To determine the horizontal distribution of the seed-bank, pre-dispersal soil samples were collected in May 2009 along a transect extending away from the center of host shrubs with active *A. jaegerianus*; these soil samples were collected under the canopy, at the canopy edge, 50 cm outside the canopy, and 200 cm outside the canopy. To determine the vertical distribution of the seed-bank, an additional soil sample from 1 to 4 cm was collected underneath 0 to 1 cm samples. Soil samples (0 to 1 cm depth) were also collected under host shrub canopies that once contained an active *A. jaegerianus*, and under shrubs less than 2 m and more than 10 m away from an active *A. jaegerianus* study plant. To determine the dynamics of seed density within years, additional 0 to 1 cm, under-canopy soil samples were collected in September 2010 and January 2011.

Statistical analyses

Shrub and seed data were analyzed using Statview (SAS 1999a). Because many soil samples contained no seed, seed density data were zero-biased and not normally distributed. These data were resistant to transformation to normality, so nonparametric statistics were used to analyze seed density data (SAS 1999b). Kruskal-Wallis tests were used for multiple comparisons of horizontal samples and comparisons of seed density. Post-hoc comparisons were Wald-Wolfowitz runs tests with Bonferroni adjustments of significance for three pair-wise comparisons. Paired sign tests and Wilcoxon signed rank

tests were used for paired comparisons of seed density and soil depth, and seed density before and after primary seed dispersal.

RESULTS

The distribution of *A. jaegerianus* seed in the soil seed bank varied both vertically and horizontally. There were significant decreases in the density of seed with soil depth; 0 to 1 cm soil samples had roughly twice the seed density of 1 to 4 cm samples (Fig. 1). There were also significant decreases in seed density with horizontal distance from host plant canopies (Fig. 2); seed densities at the canopy edge were half those of the inner canopy, and densities outside the canopy, in the more or less un-vegetated areas between shrub, were negligible (0.2 seeds per 100 cm³ of soil at 50 cm outside the canopy, and zero seeds at 200 cm outside the canopy).

The distribution of seed across shrubs with different *A. jaegerianus* histories also varied significantly (Fig. 3). Shrubs with active *A. jaegerianus* had the highest densities. Shrubs that once supported an active *A. jaegerianus* had lower seed densities, roughly 70 percent of shrubs with active *A. jaegerianus* (Fig. 3). Host shrubs without recent histories of active *A. jaegerianus* had the lowest seed densities. Among these shrubs without *A. jaegerianus* histories, those less than 2 m from active *A. jaegerianus* had relatively low seed densities (0.2 seed per 100 cc soil sample), and no seed were observed in soil samples from shrubs 10 m from active *A. jaegerianus* (Fig. 3).

The pre- and post-dispersal seed bank exhibited a similar pattern of significant differences in 2009, 2010, and 2011, in which the post-dispersal seed-bank was 3 to 5 fold higher than the pre-dispersal seed bank (Fig. 4). While pre-dispersal soil seed

densities were nearly identical between years (134.5 seeds m^{-2} in 2009, 140.0 seeds $\cdot\text{m}^{-2}$ in 2010, and 124 seeds $\cdot\text{m}^{-2}$ in 2011), post-dispersal seed density tended to fluctuate, and in 2011 were 53% of their density in 2010 (Fig. 5; 857.7 seeds $\cdot\text{m}^{-2}$ in 2010 versus 401.4 seeds $\cdot\text{m}^{-2}$ in 2011; Wilcoxon signed rank test; $P=0.0186$, $Z=-2.354$, $n=22$).

In 2010 and 2011, two additional samplings were conducted in October and January to record the pace of declines in soil seed densities observed in post- and pre-dispersal soil samples between June 2010 and May 2011 (Fig. 6, starred bars). These interannual declines in soil seed density were significant (Fig. 6; Kruskal-Wallis Test: $n=22$, $H=19.520$, $P=0.0002$), and initially rapidly during the summer of 2010, with seed densities declining by 66 % between June and September of 2010. Declines in seed density between September 2010 and April 2011 occurred at a lesser rate than summer declines and were more or less constant (Fig. 6).

DISCUSSION

Results of this study demonstrate that *A. jaegerianus* seed density is low, and largely restricted to the area under host shrubs that support active *A. jaegerianus*. Roughly a third of seeds are found at a depth of 1 to 4 cm in the soil profile where it is unlikely that seed would germinate because of low light penetration (Harper 1977). Excluding seeds at 1 to 4 cm, the mean seed densities recorded in this study were 1.33 ± 0.05 seed per 100 cc of soil or 129 seeds $\cdot\text{m}^{-2}$ (pre-dispersal) and 6.36 seeds per 100 cc of soil or 636 seeds $\cdot\text{m}^{-2}$ (post-dispersal). These *A. jaegerianus* seed densities (133 to 636 seeds $\cdot\text{m}^{-2}$) are low to extremely low relative to desert shrubs (2485 to 6222 seed $\cdot\text{m}^{-2}$: Rundel and Gibson 1996). Furthermore, *A. jaegerianus* seed densities are much lower at

the landscape level because seeds are concentrated beneath active *A. jaegerianus* host shrubs, and drop to negligible densities under other shrubs and in the “un-vegetated” interstitial areas between shrubs.

The distribution of *A. jaegerianus* seeds in shrubs other than active *A. jaegerianus* host shrubs is limited. While our results indicate that seed may persist in the soil seed bank after active *A. jaegerianus* have died, recruitment of new plants to shrubs with once active *A. jaegerianus* has been observed only twice in 14 years of field surveys. Furthermore, the density of seeds beneath once active LMMV decreases each year as a result of seed predation and unproductive germination. The dispersal of seed beyond active *A. jaegerianus* host shrubs is rare and restricted to shrubs in the immediate vicinity of active LMMV host shrubs. Long distance dispersal of *A. jaegerianus* seed (greater than 10 m) was not detected in this study.

The *A. jaegerianus* post-dispersal seed bank is composed of two component seed populations: (1) seeds produced in previous reproductive seasons that are to some extent buried in the soil beneath host shrubs (the persistent seed bank), and (2) new seeds, produced that reproductive season, that are superficially distributed on the soil surface after seed release (the transient seed bank).

Within the Fabaceae, 32 genera and 65 species have been found to have persistent seed banks (Baskin and Baskin 1998). The *A. jaegerianus* persistent seed bank is more or less equivalent to pre-dispersal seed populations (Fig. 4). Persistent seed banks have been categorized as short-term persistent (1 to 5 years), or long-term persistent (> 5 years, Bakker et al. 1996). Although little is known about the long-term viability of *A. jaegerianus* seeds in the soil, seeds collected in 2001 were found to be viable after nine

years of storage at room temperature and ambient humidity (Sharifi and Huggins, unpublished data), suggesting that viability in the soil may exceed 5 years.

Based on the consistency of pre-dispersal seed densities in 2009, 2010, and 2011 (Fig. 4), the transient seed bank appears to be completely depleted before the next reproductive season, such that the mean density of the transient seed bank oscillated between approximately zero and $700 \text{ seeds} \cdot \text{m}^{-2}$ between reproductive periods (Fig. 4), while the persistent seed bank remains more or less constant at approximately $130 \text{ seeds} \cdot \text{m}^{-2}$ (Fig 4). In our second progress report (Rundel et al. 2010), we suggested that the *A. jaegerianus* persistent seed bank should be relatively insensitive to inter-annual variation in precipitation, because only a fraction of the transient seed bank is incorporated into the persistent seed bank each year. This idea was supported by our results in 2011: the persistent seed bank remained essentially unchanged in 2011 relative to 2009 and 2010 (Fig. 4). We also suggested in the same report, that the magnitude of the post-dispersal transient seed bank would likely to be controlled by climate, and that years with high precipitation should produce higher density transient seed banks than years with low precipitation. This hypothesis was not supported by our results in 2011: the transient seed bank, as represented by post-dispersal seed densities (Fig. 5), significantly declined in 2011 by 53% despite substantial increases in precipitation.

Part of the reason for this unpredicted decline in post-dispersal seed densities is likely to be the result of the reduction in the input of seed in 2011, which declined by 26% in 2011 relative to 2010, and was primarily the result of increased herbivory in 2011 (Section 2 & 3). These increases in herbivory were likely to be due to an increase in herbivore populations as a result of substantially above-average, wet-period precipitation

in 2010 and 2011. In addition, these same increases in precipitation may have increased seed predator populations (heteromyid rodents, birds and ants), resulting in an increase in the consumption of seed during the 5-week period in which seedpods were dehiscing (i.e. dropping their seeds). Furthermore, increases in the duration of phenological stages due to early precipitation and resprouting resulted in a period of dehiscence that was 1 week or 20% longer in 2011 than 2010 (Section 2). This increase in the period of dehiscing increased the time in which seeds were exposed to seed predators, which, together with an increase in seed predators, may have further reduced the post-dispersal, transient seed bank beyond losses attributable to decreases in seed production due to herbivory.

Annual depletion of the transient seed bank is likely to occur by three agents: (1) germination, (2) incorporation of seed into the persistent seed bank, and (3) seed predation by widespread granivores such as rodents, ants, and birds. An estimate of the magnitude seed predation 2010 can be derived from seed densities, seed germination, and some reasonable assumptions:

1. Germination. Since only 24 seedlings were observed under 22 study plants in 2010, a rough estimate of seeds lost to germination would be 1.1 seed per plant per year or 0.15% of the transient seed bank.

2. Incorporation. Since the persistent seed bank appeared to be more or less stable from 2009 to 2010, the number of seeds in the transient seed bank lost when incorporated into the persistent seed bank should approximately equal the number of seeds lost in the persistent seed bank due to all types of seed mortality. If we assume that 10% of the persistent seed bank in 2010 ($135 \text{ seed} \cdot \text{m}^{-2}$) was lost annually due to seed mortality (aging and predation), and that each host shrubs had a seed shadow of roughly 1

m⁻², then 13.5 seeds from the transient seed bank must be incorporated into the persistent seed bank to balance the loss due to seedling mortality. This estimate of seed mortality may be high; Martinez-Duro et al. 2009 found seed death due to pathogen attack and seed age was lower than 10% in an arid grassland ecosystem (3.0%, Martinez-Duro et al. 2009).

3. Predation. Based on the estimates above, 14.6 seeds per plant per year or only 2.0% of the transient seed bank is removed due to germination and incorporation of seed into the persistent seed bank. Consequently, these estimates suggest that 98% percent of the transient seed bank is removed due to seed predation by granivores such as rodents, ant, and birds. Rodent and ant granivores are efficient seed predators in North American Desert ecosystems (Brown et al. 1975, Nelson and Chew 1977, Inouye et al. 1980, Hulme 1998), but the intensity of predation is variable (Boyd and Brum 1983, Parmenter et al. 1984, Martinez-Duro et al. 2009)

In Section 3 (Seed Production) we showed that *A. jaegerianus* had significant unrealized reproductive potential: only 17.2% of flowers matured into fruit, and within these fruits only 43.8% of ovules produced viable seed. But, while these losses in reproductive effort are considerable, they are relatively small when compared to our estimates of post-dispersal seed predation. Future research should focus on directly quantifying post-dispersal seed predation (98%) through in situ granivore exclusion experiments. Because *A. jaegerianus* seed predation occurs before seed germination or incorporation of seed into the persistent seed bank, exclusion of seed predators should profoundly increase *A. jaegerianus* germination, seed densities in the persistent seed bank, and dispersal of seeds to other host shrubs. As a result, granivores exclusion is likely to

be the most effective method of maintaining and reintroducing *A. jaegerianus* populations that are now at very low levels.

SUMMARY

Soil seed bank sampling in 2011 confirmed sampling in 2009 and 2010 that suggests that *Astragalus jaegerianus* has a low density, long-term persistent seed bank of approximately $140 \text{ seeds} \cdot \text{m}^{-2}$, and a transient seed bank which fluctuates between a pre- and post-dispersal density of approximately zero and $700 \text{ seeds} \cdot \text{m}^{-2}$. While our results indicate that seed may persist in the soil seed bank after active *A. jaegerianus* have died, recruitment of new plants to shrubs with once active *A. jaegerianus* has been observed only twice in 14 years of field surveys. The dispersal of seed beyond host shrubs with actively growing *A. jaegerianus* is rare and restricted to shrubs in the immediate vicinity of host shrubs with actively growing *A. jaegerianus*. Long distance dispersal of seed to shrubs 10 m from host shrubs with actively growing *A. jaegerianus* was not detected in this study. An analysis of inter-seasonal decreases in seed density, suggested that seed predation occurs primarily during the summer, and that rates of seed consumption decline during the fall and winter, as the transient seed bank is depleted. Pre-dispersal seed densities in 2011 remained nearly identical to 2009 and 2010, but post-dispersal densities in 2010 increased, possibly because of increased precipitation. Our prediction that years with high precipitation should produce higher density transient seed banks than years with low precipitation was not supported by our results in 2011: the post-dispersal transient seed bank, significantly declined in 2011 by 53% despite substantial increases in precipitation. These decreases in soil seed density are attributable to two factors: (1) a

decrease in seed production due to increases in herbivory, and (2) a putative increase in seed predation due to high seed predator populations and an extended seed dispersal period. Rough estimates suggest that post-dispersal seed predation is high ($\approx 98\%$), and as a result, granivores exclusion is likely to be the most effective method of maintaining and reintroducing *A. jaegerianus* populations that are now at very low levels.

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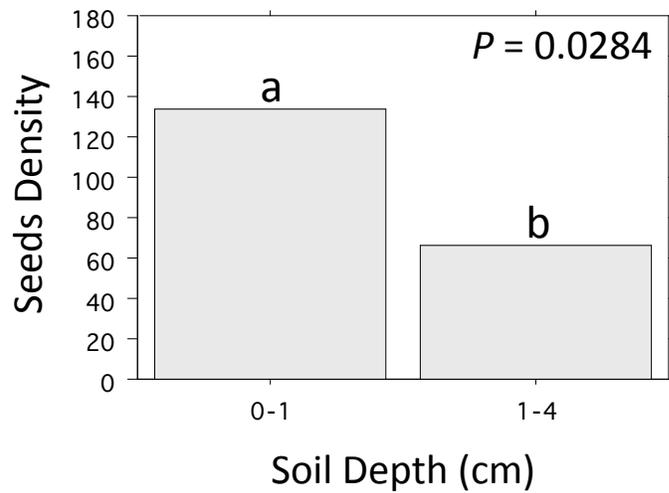


Figure 1. Mean seed density (seeds·m⁻² of soil) and soil depth, 2009. Soil samples were collected directly beneath *A. jaegerianus* canopy. Seed density decreases significantly with soil depth (Wilcoxon Signed Rank Test: $P = 0.0284$, $n = 20$).

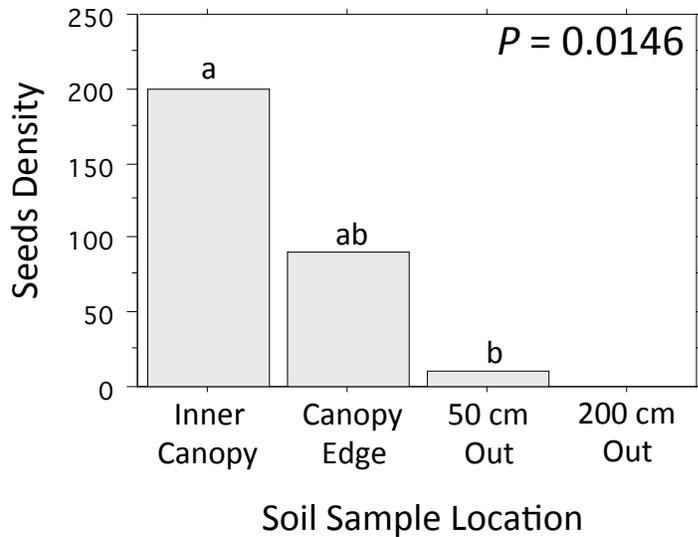


Figure 2. Mean seed density (seeds·m⁻² in top 1 cm of soil) versus distance from LMMV and its host shrub canopy, 2009. Soil samples were collected from a depth of 0 to 1 cm. There is a significant decrease in LMMV seed density with horizontal distance from LMMV (Kruskal-Wallis test: $P = 0.0146$, $n = 3$). Post-hoc comparisons were Wald-Wolfowitz runs tests with Bonferroni adjustments of significance for three pair-wise comparisons. No seeds were found in “200 cm out” samples.

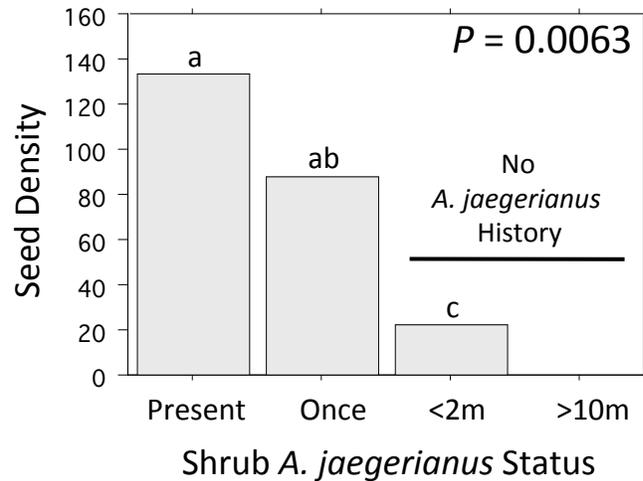


Figure 3. Mean seed density (seeds·m⁻² in top 1 cm of soil) under shrubs with different *A. jaegerianus* status in 2009: PRESENT = shrubs with active *A. jaegerianus*; ONCE = shrubs that supported an active *A. jaegerianus* in the last 10 years which is now dead; <2m = shrubs less than 2m from active *A. jaegerianus*, with no history of *A. jaegerianus*; >10m = shrubs great than 10m from active *A. jaegerianus*, with no history of *A. jaegerianus*. No *A. jaegerianus* seeds were found under >10m shrubs. Soil samples were collected directly beneath host shrub canopies, from a depth of 0 to 1 cm. Means were compared using a Kruskal-Wallis test ($P = 0.0063$, $n = 3$), and Wald-Wolfowitz runs tests for post-hoc analyses with Bonferroni adjustments of significance for three pair-wise comparisons.

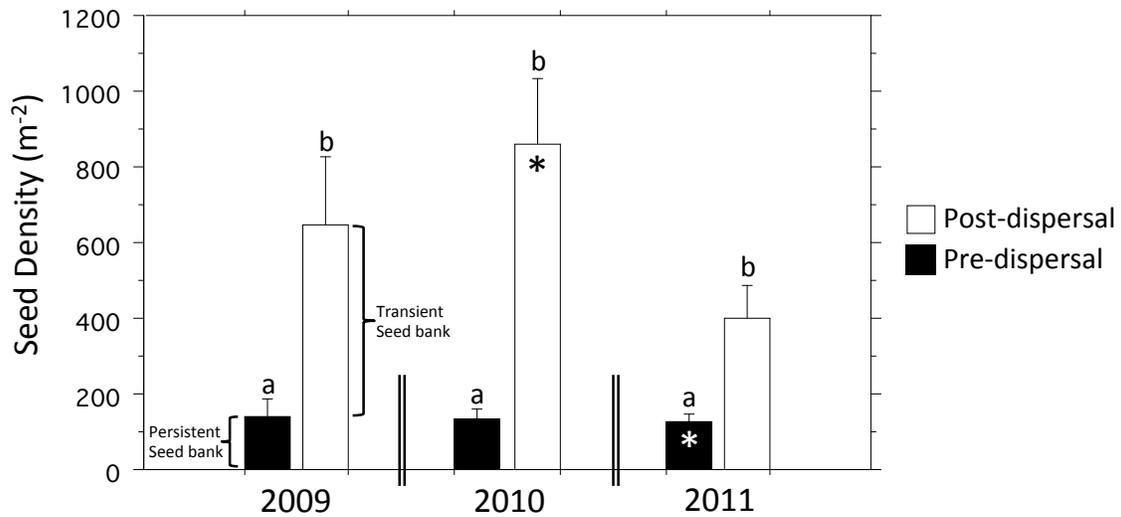


Figure 4. The *Astragalus jaegerianus* pre- and post-seed dispersal seed bank in 2009, 2010 and 2011, showing the approximate size of persistent and transient seed banks. Bars are mean seed density (seeds m⁻², converted from seeds per 100 cc soil) plus 1 SE. Within-year comparisons are Mann-Whitney *U* (**2009**, $P=0.0022$, $U=87.0$, $n=20$; **2010**, $P=0.0004$, $U=90.5$, $n=22$; **2011**, $P=0.0024$, $U=112.5$, $n=22$). Soil samples were between 100 cc and 250 cc, and included all soil and leaf litter to a soil depth of 1 cm. Pre-dispersal soil samples were collected as seed pods were ripening (April to May), and post-dispersal samples were collected immediately after pods had released all seed (June).

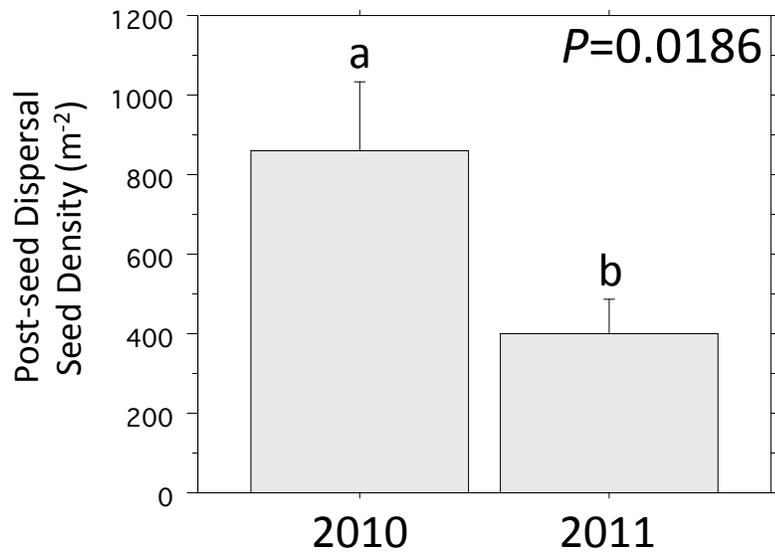


Figure 5. The *Astragalus jaegerianus* post-seed dispersal soil seed bank in 2010 and 2011; there was a significant decrease in seed density in 2011 (Wilcoxon Signed Rank Test: , $P=0.0186$, $Z=-2.354$, $n=22$). Bars are mean seed density (seeds m⁻², converted from seeds per 100 cc soil) plus 1 SE. Soil samples were between 100 cc and 250 cc, and included all soil and leaf litter to a soil depth of 1 cm. Post-dispersal soil samples were collected immediately after pods had released all seed (June).

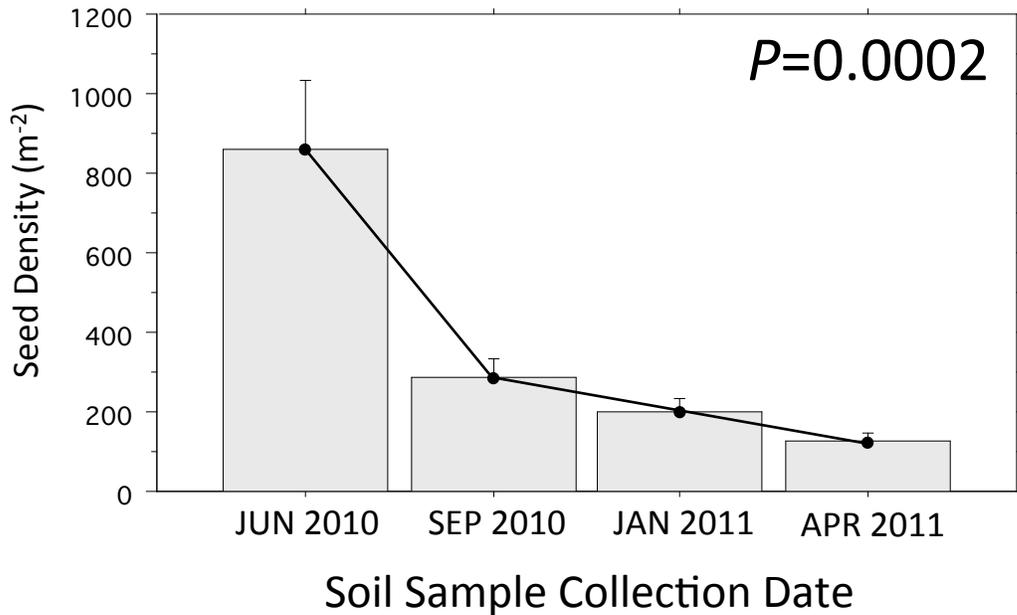


Figure 6. Decreases in the density of the *Astragalus jaegerianus* soil seed bank from post-seed dispersal (JUN 2010) to pre-seed dispersal (APR 2011). Soil samples were between 100 cc and 250 cc, and included all soil and leaf litter to a soil depth of 1 cm. Post-dispersal soil samples were collected immediately after pods had released all seed (June 2010), and pre-dispersal soil samples were collected as seed pods were ripening (April 2011). The between groups comparison is a Kruskal-Wallis Test ($n = 22$ plants per group; $H = 19.520$, $P = 0.0002$). Bars are mean seed density (seeds m⁻², converted from seeds per 100 cc soil) plus 1 SE.

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