STUDIES OF THE NATURAL HISTORY OF *ASTRAGALUS MAGDALENAE* VAR. *PEIRSONII*

(PEIRSON'S MILKVETCH)

FINAL REPORT

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ABSTRACT

Peirson's milkvetch, *Astragalus magdalenae* var. *peirsonii*, is a rare, state of California and federally protected species. Occurring on the Algodones dunes in Imperial County, California, this taxon has been the subject of great controversy, concerning the need for protection. In spite of the need for a greater understanding of the basic biology for the determination of protection need, little conclusive data exists. To help fill this void, we have investigated aspects of the natural history of Peirson's milkvetch, including static demographics, seedling fate in the wild, root system morphology and nodulation, germination, cultivation, pollination biology, breeding system, and several abiotic characteristics of soils. We show that Peirson's milkvetch is a perennial plant, which flowers in response to the winter rains. Individuals may require nine months of growth to flower or may flower in as little as three months. Presumably, this differential behavior is in response to differences in the timing of germination and correlated with the onset of the winter rains. Germination requires cool temperatures and scarification, the wearing away of the seed coat. Although it is perennial, Peirson's milkvetch has very high annual mortality, both adults and seedlings. High mortality in the first year life stages should not be confused with annual duration. High mortality in seedlings, coupled with late germination, can result in a near complete failure of recruitment, under certain conditions. The root system of Peirson's milkvetch is composed of a deep taproot (sometimes more than four meters deep) and shallow lateral roots that spread out less than a meter below the dune surface. This *Astragalus* apparently does not produce nitrogen-fixing root nodules. Peirson's milkvetch requires insect pollination for fruit production. Although a variety of insects visit flowers of this taxon, pollination is due largely to *Habropoda pallida*, the Digger bee. Peirson's milkvetch possesses a self-incompatibility system, and appears to be diallelic and sporophytic. The presence of a sporophytic self-incompatibility system has a profound influence on our expectation of population size. With this breeding system, populations must maintain a large number of individuals, in order for the species to maintain very high genetic diversity at the self-incompatibility loci. The number of individuals of Peirson's milkvetch present at Algodones Dunes is quite high; however, the number of

individuals is far less important and less meaningful than the genetic diversity of the individuals present. High measures of genetic diversity are good indicators of diversity at the SI loci. Peirson's milkvetch was cultivated at Rancho Santa Ana Botanic Garden for certain aspects of this research. We found that, even under greenhouse conditions, this taxon displays high mortality rates. The highest survival rates and survival to reproduction were associated with plants growing in an artificial dune, with fine sand, two meters deep.

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EXECUTIVE SUMMARY

Peirson's milkvetch, *Astragalus magdalenae* var. *peirsonii*, is a rare, state of California and federally protected species. Occurring on the Algodones dunes in Imperial County, California, this taxon has been the subject of great controversy, concerning the need for protection. In spite of the need for a greater understanding of the basic biology for the determination of protection need, little conclusive data exists. To help fill this void, we have investigated aspects of the natural history of Peirson's milkvetch. Our specific goals were to:

1. Develop a base-line understanding of age structure of populations, using static demographic approaches.
2. Estimate survival rates for the age (size) classes.
3. Character the morphology of the root system of Peirson's milkvetch, including the presence of nitrogen-fixing nodules.
4. Characterize germination requirements.
5. Cultivate individuals from germination to death in order to study duration (annual versus perennial).
6. Study pollination biology of Peirson's milkvetch.
7. Study breeding system of Peirson's milkvetch.

Age (size) structure of the Algodones dunes population tends to be bimodal. This bimodality represents two size-classes of reproductive adults (overlapping cohorts), but sometimes also represents seedling vs. reproductive adults.

We show that Peirson's milkvetch is a perennial plant, which flowers in response to the winter rains. Individuals may require nine months of growth in order to flower or may flower in as little as three months. Presumably, this differential behavior is in response to differences in the timing of germination and correlated with the onset of the winter rains.

Although it is perennial, Peirson's milkvetch has very high annual mortality, both for adults and seedlings. High mortality in the first year life stages should not be confused with annual duration. High mortality in seedlings, coupled with late

germination, can result in a near complete failure of recruitment, under certain conditions.

The root system of Peirson's milkvetch is composed of a deep taproot (sometimes more than four meters deep) and shallow lateral roots that spread out less than a meter below the dune surface. This *Astragalus* apparently does not produce nitrogen-fixing root nodules.

Germination requires cool temperatures and scarification, the wearing away of the seed coat. Under this treatment germination occurs in less than a week. Occasionally seed may germinate without scarification; however, this requires several weeks of constant moisture.

Peirson's milkvetch requires insect pollination for fruit production. Although a variety of insects visit flowers of this taxon, pollination is due largely to *Habropoda pallida*, the Digger bee.

Peirson's milkvetch possesses a self-incompatibility system, and appears to be diallelic and sporophytic. The presence of a sporophytic self-incompatibility system has a profound influence on our expectation of population size. With this breeding system, populations must maintain a large number of individuals, in order for the species to maintain very high genetic diversity at the self-incompatibility loci. The number of individuals of Peirson's milkvetch present at Algodones Dunes is quite high; however, the number of individuals is far less important and less meaningful than the genetic diversity of the individuals present. High measures of genetic diversity are good indicators of diversity at the SI loci.

Peirson's milkvetch was cultivated at Rancho Santa Ana Botanic Garden for certain aspects of this research. We found that, even under greenhouse conditions, this taxon displays high mortality rates. The highest survival rates and survival to reproduction were associated with plants growing in an artificial dune, with fine sand, two meters deep.

INTRODUCTION

Described in 1932 by Munz and McBurney in Munz (Munz 1932), the taxon currently known as *Astragalus magdalenae* E.L. Greene var. *peirsonii* (Munz & McBurney) Barneby was described at the species rank as A. *peirsonii* Munz and McBurney (Fig. 1). *Astragalus peirsonii* was compared to *A. coulteri* M.E. Jones, now treated as a variant of the widespread, *A lentiginosus* Dougl. It seems unlikely, however, that *A. magdalenae* var. *peirsonii* and *A. lentiginosus* are particularly closely related due to morphological differences between the two species.

Barneby (1958) recognized similarities between *A. peirsonii* and *A. magdalenae* and reduced *A. peirsonii* and *A. niveus* Rydberg to the varietal rank under *A. magdalenae*. Barneby's taxonomic treatment is far from irrefutable and there is good reason to question the reduction in rank. *Astragalus magdalenae* var. *peirsonii* is the only member of *Astragalus* section *Inflati* that possesses a terminal leaflet confluent with the rachis of the leaf (Fig. 1). Indeed, this is the only instance in *Astragalus* where this feature varies within a species (see Barneby 1964). The differences in such a distinctive and important trait in the genus serves to point out that even the taxonomic standing of *A. magdalenae* var. *peirsonii*, and the proposed relationship with *A. magdalenae*, are far from certain, and remain uninvestigated.

When described, *Astragalus magdalenae* var. *peirsonii* (Peirson's milkvetch) was known only from "sand dunes between Holtville and Yuma, Imperial County," California (Munz 1932). This geographic location corresponds to the Algodones Dunes system. Barneby (1964) reported a collection of Peirson's milkvetch from the Borrego Valley in San Diego County, but did not identify a collector nor an herbarium where the collection could be found, leaving the collection locality somewhat dubious. Several other reported localities have proved questionable or erroneous. A report of this taxon from the Yuma Dunes, near Yuma, Arizona (Shreve and Wiggins 1964; Wiggins 1980) was based on a misidentified collection of *A. aridus* A. Gray (P. Jenkins pers. comm. 2004). Reports of Peirson's milkvetch from the dunes north of San Felipe, Baja California, Mexico (Shreve and Wiggins 1964) were based upon misidentified collections of *A. magdalenae* var.

niveus (pers. obs., examination of specimens at JEPS, UC and RSA/POM). Two anecdotal reports (L. Olech, see CDFG Natural Diversity Data Base) of populations on the southwest margin of the Salton Sea are also dubious. No deep, unstabilized dunes presently occur at the cited locations and no populations are currently present (pers. obs.); but shallow barchan dunes occurred historically in this region (Smith 1978). The lack of recent collection at these localities does not necessarily mean that there are no other populations in California. Unfortunately, there is no evidence that natural populations, apart from those associated with the Algodones Dune system, occur in California. Beyond the boarders of the United States, Peirson's milkvetch is known to occur in the Gran Desierto of Sonora, Mexico, based largely on field studies by Dr. Richard Felger (Felger 2000); however, the extent of the population(s) in Sonora have never been assessed. Although the overall range is confused by misidentifications and complicated by unverified reports of occurrence, as far as is known, the natural distribution of *A. magdalenae* var. *peirsonii* is restricted to the Algodones Dune system in the United States and to Gran Desierto, Sonora, Mexico.

Peirson's milkvetch was listed as an endangered species under the California Endangered Species Act in November 1979 and as a threatened species, under the federal Endangered Species Act, on October 6, 1998. There is ongoing controversy over the protection afforded to listed species and land management at the Algodones Dunes. The Algodones Dunes are under federal jurisdiction, managed by the Bureau of Land Management (BLM). The dunes have been, and remain, a very popular site of off-road recreation. Conservationists with concerns over the impact of off-highway vehicle (OHV) activity upon Peirson's milkvetch and other sensitive species have pressed the BLM to enforce protection of rare species. At the same time, organizations promoting OHV recreation and OHV enthusiasts believe that protection of Peirson's milkvetch will restrict access to the dunes. As a result, a series of lawsuits have been files to enforce protection of *Astragalus magdalenae* var *peirsonii*, as well as to delist (remove protection from) this taxon. Potential resolution of this issue is confounded by the general lack of knowledge concerning the biology of Peirson's milkvetch.

The controversy surrounding *Astragalus magdalenae* var. *peirsonii* extends beyond issues of conservation, to basic characteristics of biology. Elucidation of biological aspects, such as life cycle, germination behavior, and pollination ecology, is critical for ascertaining what threats exist to Peirson's milkvetch, as well as determining what management approaches would be appropriate and necessary. A long-standing disagreement involves the life cycle of this taxon. Munz (1932) stated that *A. peirsonii* was annual (completing the life cycle, from seed to maturity and death, in one year or season). Felger (2000) echoed this perception, describing the duration as ephemeral (completing the life cycle in much less than a year). These observations contrast with those of Barneby (Barneby 1964; see also Munz 1974) who describes the species as having a comparatively robust stature and being perennial (living for several to many years although potentially reproducing the first year). Barneby later states that plants are "potentially perennial but mature rapidly, beginning to bear fruit some two months after germination of the seeds" (Barneby 1964. This blurring between annual and perennial duration is reflected in unpublished reports by Phillips et al. (2001) and Phillips and Kennedy (2002), who describe Peirson's milkvetch as a "facultative perennial, ...well adapted to flower and produce seeds during its first year" (Phillips and Kennedy 2001). The phrase, "facultative perennial," is used to describe an annual species that will persist into a second year, under exceptional growth conditions. It has also been used to describe monocarpic (flowering once then dying) species that sometimes require three or more years to flower (Imper 1997). Note that "facultative perennial" has been used differently by different authors, and as a result is somewhat ambiguous. It is important to determine if *A. magdalenae* var. *peirsonii* is an annual, facultative perennial, or perennial species. These differing life history strategies require different management considerations and approaches.

As is the case for species with different duration, species with different reproductive strategies and pollination biology necessarily will require different management strategies. The genus *Astragalus* includes species that self-pollinate as well as those that must cross-pollinate. For example, the narrowly restricted *Astragalus linifolius* Osterh. has been shown to be self-compatible and largely autogamous (Karron

1989). *Astragalus australis* (L.) Lam. var. *olympicus* Isely and *A. osterhouti* M.E. Jones have been shown to be self-compatible, capable of setting seed through self-pollination, but generally outcrossing (Karron 1989; Kaye 1999). In contrast, *A. cibarius* Sheldon and *A. utahensis* (Torrey) Torr. & A. Gray, two species of Utah, have been shown to be self-incompatible (Green & Bohart 1975) and require cross-pollination to set seed. One obvious difference in these examples is that some species of *Astragalus* require pollinators while others may not. For those protected species that require pollinators, it is important to recognize that managing the plant species also requires maintenance and possible management of the pollinator. In the case of Peirson's milkvetch, nothing is known concerning self-compatibility and pollination, making management blind to the reproductive biology.

Although there is a substantial literature concerning seed banks and germination of desert plants, little is published concerning *Astragalus magdalenae* var. *peirsonii*. In an unpublished report, Phillips and Kennedy (2002) demonstrate the presence of a seed bank; however, other factors of seed bank ecology were beyond the scope of their study. These factors include, but are not limited to, the viability and longevity of seeds in the seed bank, the depth structure of the seed bank (i.e., the percentages of seeds found at particular depths), and the genetics of the seed bank relative to the reproducing population. The complication and controversy comes in attempting to determine the relationship between the number of seeds in the seed bank and species longevity. It is unlikely, if not impossible, for all of the seeds in the seed bank to germinate and contribute through reproduction. The percentage of the seedbank that germinates at any one time and the average duration of seeds in the seedbank remain a mystery. For example, Bowers (1996) has shown that seeds of Peirson's milkvetch, while germinating, will not emerge if the seeds are more than 8 cm below the surface of the dune. Romspert and Burk (1979), in an unpublished report to the Bureau of Land Management, show that germination of Peirson's milkvetch is inhibited at higher temperatures. Such physical cues for germination are important aspects for seedbank dynamics. Therefore, it is critical to begin to develop an understanding of the dynamic of the seed bank.

ENVIRONMENTAL CONTEXT

A substantial amount of research has been dedicated to characterizing habitat of Peirson's milkvetch, among other rare plants, at Algodones Dunes (e.g., Romspert and Burk 1979; Ecos, Inc. 1990; Phillips et al. 2001). These studies have focused largely on features of vegetation, slope and aspect and, to a lesser degree, climate.

Vegetation

Algodones Dunes vegetation has previously been characterized (Westec Services Inc. 1977; BLM 1987; Ecos 1990; BLM 2002). In general, these reports describe four vegetative communities. These include Creosote bush scrub, Microphyll woodland, Psammophytic scrub, and a community that has been influenced by the All American and Coachella Canals, but including species of Creosote bush scrub and Microphyll woodland. Our field investigations confirm these earlier characterizations.

Creosote bush scrub is dominated by *Larrea tridentata* (Creosote bush), *Ambrosia dumosa* (Burrobush), and *Encelia farinosa* (Brittlebush). In the Algodones Dunes, this vegetation type has high vascular plant diversity (see Appendix 1). Many of the same understory species are shared with Microphyll woodlands. Although this vegetation covers only 23% of the Algodones Dunes management area covered in the ISDRA RAMP EIS (BLM 2003), it is one of the most common vegetation types in the Sonoran Desert. It occurs on stable, moderate- or well-drained soils along the edges of the dune system. Creosote scrub can also be found where winds have exposed the basement soil or very shallow sands are present within the dunes system.

Microphyll woodland is largely restricted to the braided washes and alluvial fans of the eastern side of the dune system. It is an open and sparse community, characterized be *Olneya tesota* (Desert ironwood), *Cercidium floridum* (Palo verde), *Psorothamnus spinosa* (Smoke tree), and *Prosopis glandulosa* (Honey mesquite). There is a variety of other shrubs that can occur, such as *Chilopsis linearis* (Desert willow), as well as a broad array of herbaceous species, such as *Asclepias subulata* (rush milkweed), *Sphaeralcea orcuttii* (Carrizo globe mallow), and *Oligomeris linifolia*. This vegetation type has the greatest diversity of trees and shrubs of any at the dunes.

The construction of the All American and Coachella Canals has resulted in a man-made, neo-riparian/aquatic assemblage of plants that follow the length of the canals. Common species that occur in these mesic habitats include *Typha domingensis* (Southern cattail), *Typha latifolia* (Broad-leaved cattail), *Polygonum persicaria* (Ladys thumb), *Arundo donax* (Giant reed), *Conyza canadensis* (Horseweed), *Helianthus annuus* (Sunflower), and *Pluchia sericea* (Arrow weed). In addition there are several submergent species, such as *Potamogeton pectinatus* (Fennel-leaf pondweed) and *Myriophyllum sibericum* (Thread-leaved water-milfoil). This is perhaps the most "weedy" of the communities, being made-up of largely alien species.

Psammophytic scrub occupies the greatest area, has the lowest plant cover, lowest vascular plant species diversity, but highest frequency of species of restricted distribution. It is characterized by *Eriogonum deserticola* (Desert buckwheat), *Helianthus niveus* subsp. *tephodes* (Algodones Dunes sunflower), *Tiquilia plicata* (Plicate coldenia), *Croton wigginisii* (Dunes croton), *Petalonyx thurberi* (Thurber's sandpaper plant), *Palafoxia arida* var. *gigantea* (Giant Spanish-needle), and *Panicum urvilleanum* (Dunes panic grass). However, none of these species truly dominate the landscape. It is in this vegetation type that Peirson's milkvetch occurs and only this vegetation (see Appendix 1 for associated species). This community is found between active faces (so-called slip-faces) of the dunes, in depressions commonly referred to as "bowls" (a colloquial description of barchan dune formations, see below), or on semi-stabilized shallow slopes, facing the slip-faces of active dunes.

Distribution within the dunes

Within the Algodones Dunes, Peirson's milkvetch is almost exclusively found in the western interior portions of the dunes. Occurrences are primarily in barchan formations of the deep dunes, but on the western ends of the transverse dunes. As a result, the population at Algodones Dunes forms a more or less semi-continuous line extending in a northwest-southeast direction. In the Wilderness area of the north colonies are smaller than those further south and become much less continuous. This distribution has been well characterized in previous studies and documents (e.g., Review for Critical Habitat, US Fish and Wildlife Service, Carlsbad, California).

Physical setting

The Algodones Dunes are located in the Colorado Phase of the Sonoran Desert, one of the hottest and driest regions in the United States. The dune system is approximately 64 km long and 3 to 8 km wide, running in a northwest-southeast direction. Lying over the southern extension of the San Andreas fault system (Kovach et al. 1962), the Algodones dune chain parallels the Imperial Valley and the Coachella Canal, extending from Mammoth Wash, approximately 70 km southeast to the Colorado River plain, just south of the Mexican boarder. It is composed of a series of large-scale longitudinal dunes, tens of kilometers long and linearly oriented along a northeast-southwest trajectory (Norris and Norris 1961; Smith 1978). These large-scale dune ridges are connected by a complex of coalesced domical dunes, megabarchans, and intradune hollows with gravel floors and sinuous dune ridges. At a smaller scale, these dune forms are covered with a series of smaller longitudinal dune ridges, barchans and transverse dunes. The barchan dunes, found on the interdune flats, have been shown to be migrating southeasterly at an average rate of five meters per year for large dunes and 20 meters per year for small dunes (Smith 1970; 1972; 1977).

The origin of the Algodones Dunes has been greatly debated (Brown 1923; Norris and Norris 1961; McCoy et al. 1967; Merriam 1969; van de Kamp 1973; Loeltz et al. 1975). There are two competing hypotheses: origin from the shores of the Holocene-aged Lake Cahuilla; and origin from the Colorado River delta. Lake Cahuilla was an intermittent lake that covered much of the Imperial Valley during the Holocene; its shoreline extended to the western edge of East Mesa (Fig 2). Norris and Norris (1961) suggest that Algodones Dunes are derived from a chain of megabarchan dunes formed at the lake margin from eroding sands from the adjacent mountains. By contrast, Loeltz et al. (1975) suggest that sands from the Colorado River delta were deposited along a higher shoreline of a lake more ancient than Lake Cahuilla and subsequently blown to the east to their present location. This later hypothesis is more consistent with Merriam's (1969) and van de Kamp's (1973) observations that the sands of Algodones Dunes are more similar to the sands of the Colorado River than those of the Salton Basin.

Climate

   In general, the Sonoran Desert is subtropical, characterized by a distinctive bimodal precipitation pattern, high summer temperatures, and mild winter temperatures, with few frost days. Much of the rainfall occurs in the fall/winter although a significant amount of precipitation occurs in association with summer monsoons. Long-term climate data are not available for Algodones Dunes; however, medium-term data (ca. 50 years) are available from weather stations nearby (Table 1). These data were used to extrapolate weather patterns at the dunes. Figure 3 shows the average precipitation at five nearby weather stations at Brawley, El Centro, Gold Rock Ranch, Yuma Valley, and Yuma Proving Grounds. Average annual precipitation for these sites is 2.67 in (67.8 mm), 2.60 in (66.0 mm), 3.9 in (99.1 mm), 2.86 in (72.6 mm), and 3.72 in (94.5 mm), respectively. The duration of these weather records range from 34 years at Gold Rock Ranch, to 74 years at Brawley. All of these stations report precipitation peaks in August and again in December/January. Similarly, there is a pronounced spring drought, in May and June. The eastern stations show nearly equal precipitation in the summer and winter events; however, to the west there is less summer precipitation and more winter precipitation. Due to the exceptionally high variance in rainfall, this overall pattern may not be evident if single year precipitation patterns are considered. For any specific year, all of the precipitation my result from monsoon rains, or there may a complete failure of summer rains, resulting in apparently unimodal precipitation (Fig. 4). It is critical to recognize that species adapt to long-term climatic patterns, not to patterns observed during any single year. It is therefore important to recognize these long-term patterns.

   Temperature shows a unimodal maximum. The highest average monthly high temperature, from four nearby long-term weather stations (Brawley, El Centro, Gold Rock Ranch, and Yuma Proving Grounds), occurs in the month of July at all of these stations (Fig. 5). The average monthly high temperatures at these weather stations are below 27 degrees C (80 degrees F) in the months of November, December, January, February, and March, while the remaining months have average high temperatures above 27 degrees C.

MATERIALS AND METHODS

Population sampling.

Population sampling of Peirson's milkvetch began in 29 February-2 March 2002, and 1-3 July 2002 under permit from U.S. Fish and Wildlife Service. Six populations were sampled (Table 2). A suite of population features were documented including associated plant species, herbivory, pollination vectors, direct human impacts, and static demographics (Appendix 1). During the contract period, field investigations were conducted on December 17, 2002, February 10-14, 2003, March 3-7, 2003, March 17-21, 2003, April 7-11, 2003, April 23-25, 2003, June 2-5, 2003, September 7-11, 2003, February 16-20, 2004, and March 1-4, 2004. Susan Hobbs, Orlando Mistretta, Valerie Soza, Patrick Griffith and J. Mark Porter conducted Field studies, with the assistance of Angela Gatto.

In total, 30 populations (local occurrences) were sampled (Table 2). Populations were examined both in areas open to OHV activity and those closed to such activity (e.g., administrative closures and wilderness designations). Seventeen populations were open to OHV activity, and 13 populations were closed to OHV activity.

Individuals were tagged at each site with a unique identification number, measured for maximum height, number of secondary stems, number of inflorescences per stem, number of flowers per inflorescence, number of fruit per inflorescence, exposed root length, and root diameter. A single voucher specimen was collected from one of the stems. Voucher specimens are housed at the RSA/POM herbarium. Each individual was tracked in subsequent visits.

Additional information was collected on associated species, patterns of herbivory, and evidence of OHV impacts within the populations; however, these data were not quantified. Rather, presence/absence of associated species were gathered, but not abundances or cover. Similarly, the presence and nature of herbivory was recorded for each population, but not the frequency or individual impacts. Likewise, the presence of

OHV tracks within the population were recorded as well as the number of Peirson's milkvetch adults evidently impacted.

Seedling Fate in the Wild

Two meter-by-two meter plots (Fig. 6) were established at eleven of the populations (Table 1), from April 7-11, 2003. Three plots were established in or near each bowl. Seedlings were counted measured, and the number of leaves was counted. In addition the amount of exposed root was determined. Seedling plots were revisited during April 23-25, 2003, June 2-5, 2003, and September 8-11, 2003. The overall health, height, number of leaves, and length of exposed root were recorded for each seedling.

Soil Characteristics

Surface soil samples (to a depth of 40 cm) were taken at populations one through thirty (1-30), using a soil sampling tube, 5 cm in diameter, and 40 cm long. At each site two soil samples were taken: one centrally located in the population, the second at an adjacent site, well outside of the population. Samples were characterized for percentages of sand, silt, clay, and organics, as well as soil moisture. Measures contrasting locations with Peirson's milkvetch present and those where it was lacking were analyzed using multivariate analysis of variance (MANOVA). At every population a soil penetrometer was used to measure soil compaction both within the population and at a nearby location where recent OHV activity had occurred, and also within our footprints. Because OHV activity was frequently observed within the study sites, nearly all of the OHV penetrometer readings are from the study sites. These sites were compared using analysis of variance (ANOVA). Soil surface temperatures were recorded at the time of site sampling of populations one through six.

Root system morphology and nodulation.

At three locations open to OHV activity, the root systems of two individuals were extracted from the dunes. Plants were sampled to show the range of variation present in the populations. The root system was measured, using a 30 cm rule, as well as plant height and the root diameter just below the vegetative growth. Tissue samples from both

shallow and deep roots were preserved in FPA solution. Tissues were examined for nodualation, using light microscopy.

Seed collection.

Staff of Bureau of Land Management provided seed collections that were collected by contract field biologists (Susan Hobbs and Fred Spraul) in the spring of 1999. These collections represent 18 localities that range in number from 17 seeds to 307 seeds. This seed collection was transferred to the log-term seed storage facility at Rancho Santa Ana Botanic Garden (RSABG). This facility is a recognized seed repository by the Center for Plant Conservation (CPC) and maintains CPC collections. The 18 populations are treated as separate sub-collections of a single accession (accession A), totaling 3666 seeds. Additional seed collections were made in 2003 at four populations: populations 3, 5, 14, and 21 (see Table 2). Each population is treated as a separate element of the accession (accession B). This will allow future analyses to track population level variation in viability and seed longevity, if such a phenomenon exists.

Germination.

Viability tests were preformed on the seed accessions. These include initial tests for viability of accessions A and B, in 2002 and 2003 respectively, as well as final viability tests in 2004. Two different protocols were used. The basic protocol employs 48 seeds, replicated three times, for a total of 144 seeds. The seeds were rinsed in 10% Clorox solution, to sterilize the seed coat. Fifty percent of the seeds received hard scarification (rupture of the seed coat), while the remaining 50% remained unscarified. Scarification treatment was employed because previous study of germination in *Astragalus magdalenae* var. *peirsonii* show enhanced germination following scarification (Romspert and Burk 1979; Bowers 1996) and germination rates of many *Astragalus* species are increased by scarification (M. Wall, RSABG, Long-term Seed Storage Program, pers. comm.). Seeds were placed on agar plates, with 24 scarified and 24 unscarified seeds per plate. The plates were stored in the dark (although darkness is not required for germination), at 20 degrees C. Seeds were checked every 24 hours, for three weeks.

For the second protocol, an artificial dune habitat was constructed, using a concrete planter 1.3 meters tall and 1.0 m in diameter (Fig. 7). The planter was filled to a depth of 1.2 m with silica sand. The surface of the "dune" was divided in half, using small stakes and string. On February 25, 2003, 100 scarified seeds (collected in 2003) were scattered over half of the approximately one square meter area. On the other half of the plot, 100 unscarified seeds (also collected in 2003) were scattered. No seeds were moved with the subplots and no seeds were removed from the entire plot.

To approximate rainfall patterns found in the Algodones Dunes, the artificial dune was provided a saturating watering on February 25, 2003, and supplemental watering was provided every three days for the first four two weeks. Following this period, supplemental watering was given on a monthly schedule. A saturating watering was also performed on 25 November 2003. The artificial dune was not protected from ambient rainfall.

Cultivation of Peirson's Milkvetch

Seedlings produced in the germination/viability studies were cultivated under greenhouse conditions at Rancho Santa Ana Botanic Garden. Twenty seedlings were transferred to 2-inch pots, in standard liner-mix soil. Two months later the plants were transplanted into 14-inch tall deep-root pots, in a high-sand soil mix. An additional set of 27 seedlings was allowed to grow in the artificial dune. Measurements of plant height and phenology were recorded on a periodic basis for these plants.

Pollination biology.

Methods used for the study of pollination biology of Peirson's milkvetch follow Kearns & Inouye (1993). Between 12 March 2002 and 8 March 2004, 600 person hours of field investigation were employed for the investigation of pollination at 21 locations, representing populations 1-21 (Table 1), throughout Algodones Dunes. Within the populations, plants were monitored for visitation. The number of visits and behavior of insects were documented. Insect visitors were collected, identified and examined for *Astragalus magdalenae* var. *peirsonii* pollen. Insect voucher specimens are housed at Rancho Santa Ana Botanic Garden.

Breeding system.

Timing of stigma receptivity, relative to anther dehiscence (gender expression during anthesis), was explored, using the plants cultivated at Rancho Santa Ana Botanic Garden. Pollinations were manually performed at anthesis at 24 hours and at 48 hours following anthesis. Pollination treatments involve both self-pollinations (N=12) and outcross pollinations (N=12). Examination of the stigmatic surface, using light microscopy, was performed six hours after pollination treatments.

Methods used to examine breeding system of Peirson's milkvetch follow Richards (1986). Inflorescences were bagged both in the field (within administrative closure areas; N=15) and using individuals under cultivation (N= 35). Hand pollinations were performed on cultivated plants only. Self-pollinations (same flower) were performed on 10 flowers each, from 6 individuals. Gietonogamous pollinations (same individual but different flowers) were performed on 10 flowers each, from 6 individuals. Outcross pollinations were performed on 10 flowers, each for all possible pairwise crosses of the same six individuals (300 pollinations). Successful crosses were considered to be those crosses that resulted in fruit production.

RESULTS AND DISCUSSION

Throughout this report, we use the term "population" to refer to the Peirson's milkvetch sample sites. In fact, these locations are merely local occurrences of individuals. As will be shown below, the potential distance that pollen is transferred is far greater than the distances among these local occurrences. It seems unlikely that either Interstate Highway 8 or California State Highway 78 provides an effective barrier to pollinator movement. Because the actual patterns of reproduction link all of the local occurrences that we have visited, we suggest that all of the occurrences of *Astragalus magdalenae* var. *peirsonii* at the Algodones Dunes represent a single, rather extensive, population.

In the late winter and spring of 2002, six sites were examined. The reproductive individuals at these sites varied in size; however, it was notable that seedlings were absent from all of the locations, except Population 6, where 15 seedlings occurred. A striking difference at Population 6 was the presence of moisture just below the surface of the dune. At all other sites, the dunes were dry to a depth of 18 cm. The increased moisture at Population 6 may be due to an upwelling of water to the northeast of this location. At the site of the upwelling, the surface of the dune was constantly wet.

Field investigations during 2003 provided an additional 24 occurrences (Fig. 8) of *Astragalus magdalenae* var. *peirsonii*. During the studies that took place between February 10 and 14, a substantial precipitation event occurred. It was also noted that there were abundant seeds on the dune surface at all of the populations sampled; however, no seedlings were present. Field studies between March 3 and 7 revealed that abundant seedlings were now found at nearly all of the locations previously visited, in addition to the new sites sampled during these dates. Therefore, these winter rains were responsible for the germinations observed in March 2003.

Static Demographics.

Due to the short duration of the study, a complete demographic study and analysis was not possible. As a result, we can provide only a glimpse in to the demographics of *Astragalus magdalenae* var. *peirsonii*, using static demography. A standard methodology in assessing static demographics in plants is the use of plant size as a proxy for age (Silvertown 1987). This procedure is somewhat problematic because the relationship between plant size and age is unknown for Peirson's milkvetch. While it is generally a safe assumption that plants less than 6 cm in height represent the seedling or pre-reproductive class, less than one year in age, individuals that are, for example, 24 cm tall may be one, two, or more years in age.

The size structure of pooled populations in 2002 show the dunes were dominated by taller individuals (Fig. 9A). The mean height was 44.14 cm, with a standard deviation of 20.96 cm, standard error of the mean of 1.59 cm, and a range of 2-90 cm. The distribution is not a standard normal distribution, as it is bimodal and negatively skewed. There is an overabundance of members in the larger height classes and, at the same time,

an overabundance of small individuals. Given the extremely low frequency of seedlings in the Fall 2001-Winter 2002 season (Phillips and Kennedy 2002; pers. obs.), the size class distribution largely reflects individuals one year or greater in age.

In an attempt to provide more meaningful data with respect to fruit and seed production, we generated a plant size index, using the product of the number of secondary branches and plant height. It is well recognized that annual seed crop is related to overall plant size (Silvertown 1987). The distribution of plant size index (Fig. 9B) reveals a strikingly different distribution. This distribution is highly positively skewed; that is, the most frequent membership is associated with the smallest size class. This pattern indicates that there are a large number of individuals that contributed to the seed bank; however, each individual relatively contributes very little (as opposed to a few individuals contributing a relatively great number of progeny.

Mean fruit production in 2002 was 628.93 fruits per plant, with standard deviation of 862.55, standard error of the mean of 112.30, and a range of 0-4311 fruits. A comparison of fruit production versus plant height and plant size index, using regression of log-transformed data reveals significant relationships between fruit production and both plant height (r= 0.412; r^2= 0.170) and size index (r= 0.627; r^2= 0.393). These analyses show that plant size index is a better predictor of fruit production than is height (Fig. 10). At the same time, plant size index explains only 39.3% of the variation in fruit production. The index suggests that most of the variation in fruit production is due factors other than plant size. These factors might include available moisture, plant vigor or pollinator effectiveness. We observed extended periods of time, during which no seed set occurred. These periods corresponded to extremely windy periods.

In 2003, height structure of pooled data provides a distinctly different pattern (Fig. 11A) than observed the previous year. The smallest height class (i.e., seedling and pre-reproductive individuals) dominates the populations. The mean height is 4.64 cm, with a standard deviation of 9.561 cm, and a range of 0.2-86 cm. This distribution remains largely unchanged if plant size index (plant height X number of branches) is used (Fig 11B). Figure 11C shows population size structure when the smallest size class is removed. The distribution of these larger individuals is similar, although, the absolute number of representatives is greatly reduced. The largest sample class is composed of

the smaller individuals; however, this is not reflected in the mean value, 39.97 cm (standard deviation= 15.048). This distribution (Fig. 11C) may, in fact, be bimodal, representing two cohorts of plants. The plant size-index possesses the same positively skewed distribution, dominated by small plants. It is critical to recognize that the smaller class of plants (seedling and pre-reproductive individuals) contributed little or no reproduction during this year, unlike the previous year. Only the large adults produced seed.

The period of time between March 2002 and March 2003 saw a significant reduction in the number of plants in all adult size classes. This reduction corresponds to a major drought event during the spring and summer of 2003. Likewise, the significant increase in seedlings is a function of the limited number of seedlings produced in 2002 during the drought and the relatively abundant seedlings of 2003. The frequency of individuals of different size classes, therefore, can differ substantially from year to year. The number of larger adult plants in a particular year may not be a good indicator of the number of adults in a subsequent year, and the number of seedlings in one year may not be a strong predictor of the number of larger adult plants the following year. More importantly, the relative importance of a particular size class to seed production may vary greatly from year to year. In some years, the smaller size class may contribute the bulk of seed production (due to the large overall numbers of individuals), while in other years; they may contribute little or nothing. The dynamic size structure of the population at Algodones Dunes may be due to variable precipitation patterns coupled with natural history features of Peirson's milkvetch.

Adult Survival

Survival and mortality estimates of *Astragalus magdalenae* var. *peirsonii* described here are derived from those plants that were reproductive in 2002, and therefore, represent adult survival rates. During the interval between March 2002 and March 2003, adult survival rates at populations 1-6 were 0.0818. The surviving cohort at populations 1-6 displayed a slight increase in survival rate during the interval of March 2003 to March 2004, to 0.2307. This survival rate is remarkably high given that survival rates of seedlings during the same time period were several orders of magnitude lower

(see below). The estimate may be biased as a result of the small number of surviving adults at these populations in March 2003 (i.e., 13 plants). Survival of adult class of individuals at populations 7-30, between March 2003 and March 2004, was 0.1064. Although adult mortality is apparently high in populations of Peirson's milkvetch, we find evidence that this species can persist for at least three years, even under severe drought conditions.

Seedling Fate in the Wild

Following the germination of *Astragalus magdalenae* var. *peirsonii* seed in late February 2003, the 33 seedling plots (2 m by 2 m) established at eleven of the populations from April 7-11, 2003, possessed abundant seedlings (Table 3). The initial average number of seedlings (and standard error of the mean) per plot was 41.26 ±5.93.

In late April, seedlings remained in generally good health. Strong winds from the previous weeks exposed the roots of many individuals; however, there did not appear to be great mortality as a result. In the resurveying process only one seedling plot could not be recovered. The average number of seedlings (and standard error of the mean) per plot was 31.42 ±4.20. The survival rate, averaged over all of the plots is 86.3%. Based on the Mann-Whitney-U test, there is no significant difference between seedling mortality in areas under administrative closure and those that have remained open ($U= 47.5$, $U'= 71.5$, $p= 0.4425$).

On the week of June 2-5, 2003, the seedling plots were again resampled. Mortality in the seedling plots was noticeably higher (Fig. 12). The exposure of the root system due to sand movement was one major cause of mortality. One plot was buried following the shifting of a dune, and the seedling did not emerge. The average number of seedlings per plot dropped to 6.98 ±1.68, representing a mean survival of 23.3%. Based on the Mann-Whitney-U test, there is no significant difference between seedling mortality in areas under administrative closure and those that have remained open ($U= 74$, $U'= 88$, $p= 0.7031$).

All of the seedling plots were revisited September 8-11, 2003. Survival decreased precipitously from June. Most of the plots showed no survival. The highest survival of any of the plots occurred at Population 8, with a survival of 7.33%. The mean

cumulative seedling survival across the 12 populations with seedling plots is 0.70%. This indicates that only 7 seedlings out of a thousand survived the summer. Although this seems an extraordinarily high mortality, it is not uncommon for desert plant to display high germination coupled with low survival. A contrast between seedling survival in areas open to OHV activity and those closed, using the Mann-Whitney-U test, reveals a significant decrease in the survival of seedlings (arcsine transformed survival frequencies) in areas open to OHV activity (U= 94.5, U'= 157.5, p= 0.0181). This result should be evaluated with caution, because only one plot (in a closed area) displayed any survival. This could have biased the results.

In general, these results demonstrate that Peirson's milkvetch seedlings can have exceptionally high mortality rates. All of the seedlings died prior to sexual reproduction. The high seed production (see Phillips and Kennedy 2002) coupled with high seedling mortality could be interpreted as a compensatory strategy. That is, a very large number of seeds are produced to compensate for the low number of survivors that reach reproductive age. At the same time, it is very important to recognize that this study encompasses only a single year. Therefore, we know little concerning year-to-year variance in seedling mortality, which may be very high. Phillips and Kennedy (2002) have observed high seedling survival during the 2001-2002 season. This suggests that there may be great variance in seedling survival, on an annual basis.

Soil Characteristics

Astragalus magdalenae var. *peirsonii* occurs in deep sands of the Algodones dunes. These sands lack the soil profiles that are commonly evaluated in soil studies. Surface soil samples, taken at the 30 populations, display little variance. Soils possess between 97.9 and 100 % sand. This sand is light brown in color with darker or black grains interspersed. It is a fine-grained, angular to polished sand, the grains mostly between 0.34 and 0.62 mm in diameter, but ranging from 0.06-1.14 mm. Sands have very little organic material, less than one percent at all of the sampled locations (0.00-0.37%). Silt is also rare, ranging from 0-2%. Clay was not found in any of the samples.

Soil moisture varied widely, depending on the date of sampling. Following precipitation events, the dune surface held considerable moisture. Within two to three

weeks, the surface of the dunes appears dry; however, moist sand can be found 3 cm below the dune surface. Later in the season, for example in April, the dune surface contains no measurable moisture, but moist sand can be found 19 cm below the surface.

On the deep sands along the western side of Algodones Dunes, we could detect no difference between the characteristics of sands of sites with *Astragalus magdalenae* var. *peirsonii* and those sites nearby that lacked this taxon (Table 4). There are many sites that lack *A. magdalenae* var. *peirsonii* with soil features indistinguishable from those found within populations of Peirson's milkvetch. This finding leads us to conclude that characteristics of the sand (soil features) are not determining factors for the presence of Peirson's milkvetch.

Soil penetrometer readings were used to measure soil compaction associated with undisturbed dunes, OHV traversed sands and dunes disturbed by foot traffic. The soil penetrometer measures the amount of force required to compress the soil. On dunes, this is more correctly the amount of force required to break the surface tension of the dune. There is a significant difference among the treatments, based on ANOVA ($F_{2,69}= 59.137$; p= 0.0001). Multiple pairwise comparisons tests, using Fisher's PLSD (Table 5) reveal that there is a significant difference between undisturbed dunes and OHV traversed and between undisturbed dunes and foot traversed, but detect no difference between OHV traversed and foot traversed. It is evident that neither OHV activity nor foot traffic causes soil compaction in these deep dunes. In fact, the undisturbed dunes have significantly higher surface tension. These results may appear counterintuitive; however, winds and rains cause the sand grains on the surface of the dune to sort and pack in undisturbed areas. The resulting tightly packed surfaces that may reduce evaporative water loss from the dunes. Disturbance of the dune surface, by either OHV activity or merely walking, disturbs the packing and results in a softer dune surface. It is possible that such disturbances will result in increased evaporative water loss in the dunes.

Root system morphology and nodulation.

The root system of *Astragalus magdalenae* var. *peirsonii* is composed of a narrow, primary taproot, descending into the dune. This primary root is often, but not always, branched, and usually bears some root hairs throughout, particularly in younger

plants. Secondary (lateral) root are also present. Frequently there are a series of secondary roots, 2-4 mm in diameter and generally bearing numerous root hairs, branching from 1-3 cm below the dune surface. These roots spread away from the plant and descent slightly into the dune. Younger plants (i.e., less than 1 year) usually possess secondary roots of similar size that radiate perpendicular to the taproot along its entire length. Older plants do not have many secondary roots other than just below the sand surface and at the deepest reaches of the primary root. Near the terminus of the root system, there are numerous secondary roots and branching of the primary root. In this region there are abundant root hairs. Root nodules, associated with nitrogen fixation, are not present on the roots of *A. magdalenae* var. *peirsonii*.

Root depth is largely a function of plant age. Seedlings may have roots descending only 10 cm, whereas old plants (e.g., 4 years or more) are likely to have roots many meters deep. Unfortunately, given the short duration of this study, the absolute age of the larger Peirson's milkvetch samples are not known. However, root depth can be related to plant height and the diameter of the exposed upper root, just below the vegetative portion Table 6, Fig. 13). In a multiple regression, the combination of plant height and upper root diameter explains 98.1 % of the variance in root length (r= 0.991; *F*= 77.834; p= 0.003).

Germination.

Phillips and Kennedy (2001) have demonstrated the presence of a seedbank for Peirson's milkvetch. However, seedbank dynamics remain unknown. Longevity of seeds in the seedbank is one important demographic parameter associated with seedbank dynamics. The seeds of Peirson's milkvetch collected in 1999, by contract field biologists, were used to examine long-term viability and longevity. Seeds were collected from 19 sites (Table 7) and stored at room temperature by BLM staff until provided to RSABG, in April 2002. In addition seeds collected in 2002 were used to examine short-term longevity of seeds (Table 8), as a control.

Astragalus magdalenae var *peirsonii* seed show high viability and longevity. Following a single season, all filled seeds that have not fallen prey to herbivores are

generally viable. After one year, we obtained 100% germination in scarified seed. Even after five years there is no drop-off in viability (Fig. 14). The longevity of Peirson's milkvetch seed is unknown, however it is certainly longer than five years.

The longevity of seeds may indicate that some dormancy mechanisms may be involved. As previously noted, Romspert and Burk (1978) have shown suppression of seed germination in Peirson's milkvetch by temperatures above 27° C. Annual variation in temperature (Fig. 5) guarantees that several months maintain temperatures below 27° C every year. Both Bowers (1996) and Romspert and Burk (1978) have suggested that scarification is important for germination of this species. The impermeability of the seed coat to water is an effective and common dormancy mechanism. The dune environment provides the materials for scarification, wind driven sand. Germination trials, therefore, contrasted two treatments: scarified versus unscarified. Our tests show that Peirson's milkvetch seeds possess a long-term seed dormancy mechanism, involving impermeability of the seed coat to water. Averaging over all germination trials, we find that seeds lacking scarification displayed 5.3% germination. By contrast, scarified seeds have 99.1% germination. There is a significant difference in germination rates of scarified and non-scarified seeds (p= 0.001).

In the artificial dune habitat, constructed using a concrete planter, germination rates were markedly lower. Germination began on March 6, 2003, and continued for four days. This germination event saw 27 scarified seeds germinate, and no unscarified seeds germinate. Following this bout, no germination occurred until November 28, 2003. The germination of November 28-December 3 resulted in 2 scarified seeds germinating, and no unscarified seed germination.

Results from this trial, in the context of previous germination trials, demonstrates that the germination rate of Peirson's milkvetch in native habitat (sand) may be considerably lower that the germination rates obtained for the previous trials, conducted using agar plates. However, even on agar, if seeds are unscarified (the seed coat is unbroken), the seeds will not imbibe water and germinate.

The variation in the timing (i.e., date) of germination in this trial, November/December and March, closely parallels the timing of flowering in Peirson's milkvetch. Flowering in cultivation at RSABG began in February/March 2002 and in

December 2002. The correspondence between germination and flowering may indicate that the same environmental queues or triggers are required for both initiation of flowering and germination. These triggers may include reduced temperature and/or short days, in addition to moisture availability. Multiple queues would prevent germination at times of the year when germination would almost certainly result in excessive mortality, such as following summer rains.

Cultivation of Peirson's Milkvetch and Duration

Seedlings cultivated in 2-inch pots, with standard liner-mix soil matured slowly and displayed high mortality. Following 30 days of growth, the average height was only 0.92 cm; the plants bearing on average only 8 leaves. By 60 days mortality reached 50%. One possible explanation for both the slow growth and the high mortality is that the soil mix was too high in organics, maintaining a lower pH than Peirson's milkvetch experiences in the wild. In addition, the four-inch pots did not permit growth of a deep taproot. After two months the surviving plants were transplanted into 14-inch tall deep-root pots, in a high sand soil mix. Following this treatment, growth increased but remained rates remained lower than observed in the field. After 90 days the average height was 5.26 cm ($\pm$0.8424 standard error), in 120 days height increased to 9.48 cm ($\pm$1.191 standard error), and in 210 days plants reached 13.3 cm ($\pm$1.312 standard error). At 210 days following germination all plants were entirely vegetative, no inflorescence primordial had been produced on any plant. Following nearly seven months in cultivation none of the plants were flowering. However, by the end of December 2003, nearly nine months after germination, floral primordia were beginning to appear. In cultivation, seedlings germinating in February and March do not flower until the following December, corresponding with the average timing of the winter rainy season.

Germination of a set of 27 seedlings, in a large concrete planter (artificial dune), with pure silica sand, 1.2 meters deep, began in March. Supplemental misting was used to keep the sand surface moist for the first 14 days. Growth rates were markedly higher in the deep sand; however, mortality remained high, with 45% mortality after 60 days. As observed with 14-inch deep tubes, plants in the deep sand developed only vegetatively through the spring and summer. In the late fall, during the final week of November,

primordial inflorescences were observed. Because of the vigor and the high number of lateral branches (and hence inflorescences), plants in the artificial dune were used for cross-pollination studies.

The cultivation of Peirson's milkvetch demonstrates that this taxon, while displaying high mortality during juvenile stages, delays reproduction until the next rainy season. This behavior is that of a perennial species and not of an annual species, consistent with the results from preliminary demographic study, noted above. It seems unlikely that Peirson's milkvetch occurs as both an annual species (Munz 1932; Phillips, Kennedy, and Cross 2001) and a perennial species (Barneby 1964) within the same populations. These data lead us to suggest that this taxon is a perennial species that displays high juvenile mortality. However, duration and age at first reproduction are two different phenomena, but two features that can be confused.

The pattern of germination, growth and flowering under cultivation corresponds precisely with observations of germination, growth and flowering in 2003. Germination occurred in late February. Seedlings slowly matured and did not flower until November or December of 2003. In this case the age at first reproduction was 9 months. During the 2004 season a different pattern was observed. Seed germination occurred in response to the same rains (i.e., those of November 2003) that initiated flowering. Growth rates of the young plants appeared to be higher than those of the previous year; however, no measurements were taken. By February 2004 many of the young plants were developing inflorescences, at least associated with the primary axis. In this case, the age at first reproduction was closer to 3 months. In both 2003 and 2004 mortality was high. As a result, some individuals behaved like annuals, but were succumbing to a premature death. This is consistent with Phillips, Kennedy, and Cross (2001), who suggested an "explosive germination event" in the fall, followed by flowering the same year and their perception of annual duration.

These two contrasting germination/flowering patterns lead us to hypothesize that Peirson's milkvetch displays different strategies (different ages at first reproduction) depending on the timing of rainfall events. Given the unreliability of rainfall in the desert, the first heavy rains may occur as early as October, or be delayed to March. If rains occur early then flowering can begin in as little as three months after germination.

Over the past 40 years, these conditions occurred in about 57% of the years. If, on the other hand, rains (and germination) do not occur until late February, then flowering is delayed until the next rainy season (32.5% of the years). This strategy prevents plants from flowering in the middle of summer. It is a very unusual dichotomy in age at first reproduction, and clearly warrants further investigation. At the same time this does not necessarily have a bearing on the perennial duration of this taxon.

Pollination biology.

Six hundred person-hours of field investigation were employed in the investigation of pollination, although pollination investigations were not the sole research task being performed. As a result, some insect visits could have been overlooked. The majority of insect visitors were bees with beeflies and microlepidoptera less frequent visitors (Table 9). The most frequent visitor and potentially the primary pollinator is *Habropoda pallida*, a sand dune native, frequently referred to as a "Digger bee" (Fig. 15). The behavior of *Habropoda*, probing nearly all of the flowers in an inflorescence, from the oldest flowers to the youngest (i.e., up the inflorescence), is consistent with pollinating behavior. The next most frequent visitors are *Bembix rugosa* and *Apis mellifera*. *Bembix* is a native dune wasp, known as the "Digger wasp"; whereas, *Apis* is the non-native European Honeybee. In both cases the behavior while on *Astragalus* is consistent with pollination behavior (i.e., probing flowers and visiting multiple flowers per inflorescence. *Bembix rugosa* is known to be the primary pollinator of *Pholisma sonorae*, in the Algodones Dunes (citation; Fig 16). Of the remaining visiting insects captured on *Astragalus magdalenae* var. *peirsonii,* only *Bombylius lancifer*, a common beefly, was determined to be carrying pollen. Though this species may affect some pollination, its low visitation rate and low pollen loads would mean that it is a less effective pollinator than the medium-sized bees. Two small solitary bees, *Perdita* and *Lasioglossum* (?), were collected; however, they did not actively probe the flowers as did the larger bees and were not found to be carrying pollen.

Table 9 lists only for those insects that were specifically visiting flowers and not all insects on *Astragalus magdalenae* var. *peirsonii*. For example, crab spiders (Thomisidae) were frequently observed on Peirson's milkvetch, capturing insects that

light on the flowers (Fig. 17). Likewise, a very frequent insect found on Peirson's milkvetch was an unidentified weevil (Curculionidae). This weevil strips the epidermis and chlorenchyma from the stems of *A. magdalenae* var. *peirsonii* (Fig. 18). During the drought year, 2003, stem damage by this insect was sufficient to result in mortality in several individuals.

Breeding system.

Determination of the timing of stigma receptivity, relative to anther dehiscence (anthesis), revealed two morphological features that are worthy of note. These are changes in pollen color associated with the age of the flower, and the adherence of pollen to the stigmatic surface in association with age of flower and pollination type (self versus cross). Anthers shed their pollen just before the banner petal (upper) reflexes upward. The anthers are adjacent to the stigmatic surface. At this time, the pollen is a bright golden to orange yellow in color (Fig. 19). After 24-48 hours, the pollen color changes to a very pale, yellow-white (Fig. 19). It is not known if this color shift is associated with a change in pollen viability.

Stigmatic surfaces were examined on flowers of differing ages (beginning of anthesis, 24 and 48 hours post-anthesis), and subjected to self-pollination and outcrossing, using pollen of two different ages (anthesis–golden yellow and 48 hours post-anthesis–pale yellow-white). Self-pollen does not adhere to the stigmatic surface, regardless of the age of the flowers or the age (color) of the pollen (Fig. 20). By contrast, outcrossed-pollen, regardless of its age (color) adheres to the stigmatic surface of young, old, and intermediate flowers. In other words, stigma receptivity does not appear to change over the life of the flower. Although pollen viability may decrease over the life of a flower, such a decrease has not been demonstrated.

Stigma receptivity and pollen presentation appear to be simultaneous events in Peirson's milkvetch. The inability of self-pollen to adhere to the stigma of the same flower in part prevents self-pollination and is consistent with a self-incompatibility mechanism.

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Self-incompatibility

Inflorescences bagged both in the field within administrative closure areas (N=15) and using individuals under cultivation (N= 35) fail to set fruit. Failure to set fruit demonstrates that Peirson's milkvetch is incapable of self-pollination. Hand pollinations of cultivated plants, involving self-pollinations (same flower), gietonogamous pollinations (same individual but different flowers), and outcross pollinations reveal a complex pattern of crossing success (Table 10). In all cases, self-pollinations fail to produce fruit. Outcross pollinations did result in fruit production, but not all outcross pollinations were successful. For example, in our crossing study, the pollen from plants three and five do not set fruit if placed on the stigmas of plant one. Pollen from plants three and five are successful in setting fruit if placed on the stigmas of either plants two or six. In most case the reciprocal crosses produce the same results, but not in all cases (see Table 10).

This pattern of fruit production is consistent with a sporophytic (diallelic) self-incompatibility system. However, the frequency of fruit set is somewhat lower than expected. The low fruit set in otherwise successful crosses may be the result of cross-pollination technique or a function of low sample size. Because only 10 crosses of each type were performed, any stochastic errors could significantly depress the frequencies.

SUMMARY

Several aspects of the natural history of Peirson's milkvetch have been investigated. Peirson's milkvetch is shown to be a perennial plant, which flowers in response to the winter rains. Individuals may require nine months of growth to flower or may flower in as little as three months. Presumably, this differential behavior is in response to differences in the timing of the onset of the winter rains. Similarly, germination also occurs in response to these same rains; however, rapid germination response requires scarification of the seed coat. Although it is perennial, Peirson's milkvetch has very high annual mortality, both adult and seedling. High mortality at all life stages should not be confused with annual duration. Further, high mortality in seedlings, demonstrated in this study, coupled with late germination, can result in a near

complete failure of recruitment, under some conditions. The frequency of such conditions is estimated to be 0.20, or 20 out of every one hundred years. Peirson's milkvetch requires insect pollination for fruit production. Although a variety of insects visit flowers of this taxon, pollination is due largely to *Habropoda pallida*, the Digger bee. Peirson's milkvetch possesses a self-incompatibility system, and appears to be diallelic and sporophytic. The presence of a sporophytic self-incompatibility system has a profound influence on our expectation of population size. With such a breeding system, populations must maintain a large number of individuals. This is because the species must maintain very high genetic diversity at the self-incompatibility loci. With sporophytic systems, if two individuals share even a single SI allele, they cannot successfully reproduce. The number of individuals of Peirson's milkvetch present at Algodones Dunes is quite high; however, the number of individuals is far less important and less meaningful than the genetic diversity of the individuals present. High measures of genetic diversity are good indicators of diversity at the SI loci.

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Table 1. Weather stations in southeastern California and southwestern Arizona used to estimate and characterize climatic patterns in the Algodones Dunes region. The station name, location (latitude, longitude), and the years for which records exist for precipitation (Ppt) and temperature (Temp) are provided.

Station	Location	Ppt Years	Temp Years
BRAWLEY2 SW	32° 57' N, 115° 33' W	1960-2002	1960-2002
CALEXICO2 NE	32° 41' N, 115° 28' W	1960-2002	1960-2002
COYOTE WELLS	32° 44' N, 115° 58' W	1960-1970	1960-1970
EL CENTRO2 SSW	32° 46' N, 115° 34' W	1960-2002	1960-2002
GLAMIS6 ENE	33° 03' N, 114° 59' W	1962-1963	1962-1963
GOLD ROCK RANCH	32° 53' N, 114° 52' W	1964-1996	1964-1996
IMPERIAL	32° 51' N, 115° 34' W	1960-2002	1960-2002
NILAND	33° 17' N, 115° 31' W	1960-2002	1960-2002
OCOTILLO2	32° 45' N, 116° 00' W	1960-2002	1960-2002
YUMA PROVING GROUNDS	32° 52' N, 114° 26' W	1958-2002	1958-2002
YUMA VALLEY	32° 39' N, 114° 35' W	1930-2002	1930-2002

Table 2. *Astragalus magdalenae* Greene var. *peirsonii* (Munz & McBurney.) Barneby populations sampled between December 2002 and March 2004. Latitude and longitude locations are provided, using degrees, minutes and seconds. A closure status of "Closed" indicates those populations that are either within the wilderness area or are within one of the administrative closure areas. A closure status of "Open" identifies those populations that are within areas open to ORV activity. For each population, the annual census of reproductive adults and seedlings surviving to September 2003 are provided. A dash indicates that the population was not sampled at the given date.

Name	Latitude	Longitude	Closure Status	# adults 2002	# adults Mar. 03	# adults Sep. 03	# prerep. Sep. 03	# adults Mar. 04
Pop 1	N32° 43' 44.8"	W114° 54' 12.4"	Closed	17	3	0	0	0
Pop 2	N 32° 43' 47.2	W 114° 53' 59.2"	Closed	1	0	0	0	0
Pop 3	N 32° 43' 40.1"	W 114° 54' 12.7"	Closed	123	5	2	2	0
Pop 4	N 32° 43' 41.0"	W 114° 54' 16.3"	Closed	7	0	0	0	0
Pop 5	N 32° 43' 36.3"	W 114° 54' 14.4"	Closed	8	2	2	2	1
Pop 6	N 32° 59' 07.4"	W 115° 08' 20.7"	Closed	3	3	3	3	2
Pop 7	N 32° 59' 07.0"	W 115° 08' 21.7"	Closed	-	5	0	3	1
Pop 8	N 33° 01' 51.2"	W 115° 12' 12.1"	Closed	-	1	0	16	11
Pop 9	N 32° 44' 51.3"	W 114° 56' 32.4"	Open	-	0	0	0	-
Pop 10	N 32° 45' 00.5"	W 114° 56' 20.9"	Open	-	0	0	0	-
Pop 11	N 32° 45' 04.2"	W 114° 56' 09.0"	Open	-	2	0	0	-
Pop 12	N 32° 45' 13.6"	W 114° 56' 29.6"	Open	-	7	2	2	1
Pop 13	N 32° 45' 29.5"	W 114° 56' 35.7"	Open	-	4	0	0	0
Pop 14	N 32° 46' 01.1"	W 114° 57' 15.4"	Open	-	4	2	0	1
Pop 15	N 32° 46' 07.4"	W 114° 57' 19.9"	Closed	-	9	4	0	2
Pop 16	N 32° 46' 10.7"	W 114° 57' 30.0"	Closed	-	2	2	0	2
Pop 17	N 33° 03' 22.8"	W 115° 14' 04.2"	Closed	-	2	1	0	-
Pop 18	N 32° 43' 04.5"	W 114° 53' 51.3"	Open	-	26	0	0	-
Pop 19	N 32° 55' 24.6"	W 115° 05' 45.4"	Open	-	3	0	0	0
Pop 20	N 32° 55' 27.6"	W 115° 05' 37.7"	Open	-	1	0	0	-
Pop 21	N 32° 45' 35.9"	W 114° 56' 40.8"	Open	-	14	2	0	0

Table 2. continued...

Name	Latitude	Longitude	Closure Status	# adults 2002	# adults Mar. 03	# adults Sep. 03	# prerep. Sep. 03	# adults Mar. 04
Pop 22	N 32º 54' 34.3"	W 115º 05' 39.8"	Closed	-	0	0	18	15
Pop 23	N 32º 59' 07.0"	W 115º 08' 17.8"	Closed	-	1	1	1	2
Pop 24	N 32º 59' 03.9"	W 115º 07' 55.0"	Open	-	-	4	14	11
Pop 25	N 32º 58' 53.8"	W 115º 07' 46.6"	Open	-	-	0	4	-
Pop 26	N 32º 45' 51.0"	W 114º 47' 05.5"	Open	-	-	0	2	-
Pop 27	N 32º 55' 20.9"	W 115º 05' 44.6"	Open	-	-	0	2	1
Pop 28	N 32º 54' 49.1"	W 115º 05' 37.3"	Open	-	-	0	1	0
Pop 29	N 32º 55' 01.4"	W 115º 05' 37.5"	Open	-	-	0	5	0
Pop 30	N 32º 55' 07.1"	W 115º 05' 39.8"	Open	-	-	0	10	-

Table 3. Seedling age class of populations of *Astragalus magdalenae* Greene var. *peirsonii* (Munz & McBurn.) Barneby, sampled between March 2003 and March 2004. Populations in bold indicate those sites where 2 × 2 m plots were established to examine the fate of seedlings. Latitude and longitude locations are provided, using degrees, minutes and seconds. A closure status of "Closed" indicates those populations that are either within the wilderness area or are within one of the administrative closure areas. A closure status of "Open" identifies those populations that are within areas open to ORV activity. For each population, the census of seedlings is provided. Numbers in parenthesis indicate the total number of seedlings within 2 × 2 m plots located at each site. A dash indicates that no count was made.

Name	Latitude	Longitude	Closure Status	Seedlings Mar. 03	Seedlings June 03	Seedlings Sept. 03	Seedlings Mar. 03
Pop 1	N32º 43' 44.8"	W114º 54' 12.4"	Closed	19	3	0	0
Pop 2	N 32º 43' 47.2	W 114º 53' 59.2"	Closed	7	0	0	-
Pop 3	N 32º 43' 40.1"	W 114º 54' 12.7"	Closed	309 (97)	7 (5)	0 (0)	2
Pop 4	N 32º 43' 41.0"	W 114º 54' 16.3"	Closed	90	0	0	0
Pop 5	N 32º 43' 36.3"	W 114º 54' 14.4"	Closed	81	0	0	9
Pop 6	N 32º 59' 07.4"	W 115º 08' 20.7"	Closed	77	7	0	0
Pop 7	N 32º 59' 07.0"	W 115º 08' 21.7"	Closed	31	3	0	2
Pop 8	N 33º 01' 51.2"	W 115º 12' 12.1"	Closed	493 (120)	- (-)	8 (8)	50
Pop 9	N 32º 44' 51.3"	W 114º 56' 32.4"	Open	1873 (136)	- (7)	0 (0)	-
Pop 10	N 32º 45' 00.5"	W 114º 56' 20.9"	Open	436 (62)	- (8)	0 (0)	-
Pop 11	N 32º 45' 04.2"	W 114º 56' 09.0"	Open	614 (165)	- (22)	0 (0)	-
Pop 12	N 32º 45' 13.6"	W 114º 56' 29.6"	Open	619 (74)	- (5)	2 (0)	231
Pop 13	N 32º 45' 29.5"	W 114º 56' 35.7"	Open	29	0	0	2
Pop 14	N 32º 46' 01.1"	W 114º 57' 15.4"	Open	512 (72)	- (25)	0 (0)	2146
Pop 15	N 32º 46' 07.4"	W 114º 57' 19.9"	Closed	550 (117)	- (17)	0 (0)	1655
Pop 16	N 32º 46' 10.7"	W 114º 57' 30.0"	Closed	-	-	0	1421
Pop 17	N 33º 03' 22.8"	W 115º 14' 04.2"	Closed	11	0	0	-
Pop 18	N 32º 43' 04.5"	W 114º 53' 51.3"	Open	729 (90)	1 (0)	0 (0)	-
Pop 19	N 32º 55' 24.6"	W 115º 05' 45.4"	Open	158 (50)	- (28)	0 (0)	128
Pop 20	N 32º 55' 27.6"	W 115º 05' 37.7"	Open	0	0	0	-

Table 3. continued...

Name	Latitude	Longitude	Closure Status	Seedlings Mar. 03	Seedlings June 03	Seedlings Sept. 03	Seedlings Mar. 04
Pop 21	N 32º 45' 35.9"	W 114º 56' 40.8"	Open	- (247)	- (2)	0 (0)	454
Pop 22	N 32º 54' 34.3"	W 115º 05' 39.8"	Closed	- (197)	- (75)	18 (0)	50
Pop 23	N 32º 59' 07.0"	W 115º 08' 17.8"	Closed	16	7	1	0
Pop 24	N 32º 59' 03.9"	W 115º 07' 55.0"	Open	-	-	14	2
Pop 25	N 32º 58' 53.8"	W 115º 07' 46.6"	Open	-	-	2	-
Pop 26	N 32º 45' 51.0"	W 114º 47' 05.5"	Open	-	-	2	-
Pop 27	N 32º 55' 20.9"	W 115º 05' 44.6"	Open	-	-	1	73
Pop 28	N 32º 54' 49.1"	W 115º 05' 37.3"	Open	-	-	5	5
Pop 29	N 32º 55' 01.4"	W 115º 05' 37.5"	Open	-	-	5	2
Pop 30	N 32º 55' 07.1"	W 115º 05' 39.8"	Open	-	-	10	-

Table 4. Multivariate analysis of variance comparing soil characteristics of sites supporting those populations of *Astragalus magdalenae* var. *peirsonii* (ASMAP) and those that lack this taxon. The means and, parenthetically, the standard errors of the means are provided for the two treatments.

	% Sand	**% Organics**	**%Silt**	**% Clay**
ASMAP Present	99.694 (±0.080)	0.140 (±0.020)	0.167 (±0.084)	0.0 (-)
ASMAP Absent	99.760 (±0.059)	0.123 (±0.017)	0.117 (±0.057)	0.0 (-)
F-value	0.435	0.410	0.241	n/a
p-value	0.5123	0.5244	0.6250	n/a

Table 5. Multiple comparisons tests, using Fisher's PLSD, comparing soil penetrometer readings on undisturbed, off highway vehicle (OHV) traversed, and foot-traffic traversed dunes.   The means, standard deviations (Std. Dev.), and standard errors of the means (Std. Err.) are provided for the three treatments. The mean difference (Mean diff.) and critical difference (Critical diff.), in addition to the probability are given for each of the comparisons.

Treatment	**Mean**	**Std. Dev.**	**Std. Err.**
Undisturbed	1.625	0.784	0.160
OHV traversed	0.333	0.159	0.030
Foot traversed	0.365	0.147	0.030

Comparison	**Mean diff.**	**Critical diff.**	*p*-value
Undisturbed vs. OHV	1.292	0.270	0.0001
Undisturbed vs. Foot	1.260	0.270	0.0001
OHV vs. Foot	-0.031	0.270	0.8183

Table 6. Descriptive statistics for the individuals sampled in the examination of root morphology. Sample size (N), minimum, maximum, mean, standard error of the mean and standard deviation are provided.

	N	Minimum (cm)	Maximum (cm)	Mean (cm)	Standard Error	Standard Deviation
Height	6	14.60	43.10	27.5833	3.9949	9.78558
Root diameter	6	0.21	1.71	0.5517	0.2356	0.57715
Root length	6	49.20	337.40	121.2833	45.1022	110.47741

Table 7. Populations (subpopulations) of Peirson's Milkvetch sampled by Bureau of Land Management contract personnel, in 1999, representing the source of seeds for lonf-term seed viability assessment. The location and the number of seeds recovered are provided.

Population number	Location	Number of seeds
1	32.98844º N, 115.13978º W	32
2	33.28449º N, 115.10807º W	75
3	33.09477º N, 115.28071º W	165
4	Transect 21, Cell 11	17
5	Transect 18, Cell 9	162
6	33.09518º N, 115.28316º W	33
7	32.84989º N, 115.00330º W	238
8	32.99854º N, 115.14317º W	15
9	32.98539º N, 115.13883º W	84
10	32.99029º N, 115.14214º W	35
11	32.99046º N, 115.13966º W	20
12	32.98640º N, 115.13555º W	307
13	32.85713º N, 115.04044º W	235
14	32.78288º N, 114.96432º W	287
15	32.98952º N, 115.14029º W	266
16	32.98693º N, 115.13695º W	125
17	Transect 17, Cell 6	180
18	32.81453º N, 114.99812º W	186
19	Near Hill 6	17

Table 8. Seed collection sites for *Astragalus magdalenae* var. *peirsonii* from the Year 2003 accession. Seed collections were made under our current USFWS permit. Seeds were collected from the surface of the sand, not to exceed 5% of the seeds present. The identity of specific source of the seeds (parent plant) could not be made due to the high mortality of adult plants from the previous year. The number of adult plants present at the collection site is noted, and the number of adult plants present the previous year is notes parenthetically, if known.

Name (Alt. Name)	Latitude	Longitude	Closure	adults03
Pop 2	N 32º 43' 47.2	W 114º 53' 59.2"	Closed	0 (1)
Pop 3	N 32º 43' 40.1"	W 114º 54' 12.7"	Closed	5 (127)
Pop 5 (2-N2)	N 32º 43' 36.3"	W 114º 54' 14.4"	Closed	2 (8)
Pop 8 (2-1)	N 33º 01' 51.2"	W 115º 12' 12.1"	Closed	1
Pop 9 (2-3)	N 32º 44' 51.3"	W 114º 56' 32.4"	Open	0
Pop 11 (2-5)	N 32º 45' 04.2"	W 114º 56' 09.0"	Open	2
Pop 13 (2-7)	N 32º 45' 29.5"	W 114º 56' 35.7"	Open	4
Pop 14 (2-8)	N 32º 46' 01.1"	W 114º 57' 15.4"	Open	4
Pop 18 (2-2)	N32º 43' 04.5"	W114º 53' 51.3"	Open	26
Pop 21	N32º 45' 35.9"	W114º 56' 40.8"	Open	14

Table 9. Insect visitors to *Astragalus magdalenae* var. *peirsonii*, in Algodones Dunes, Imperial County, California. The family, species (if determinable), frequency of capture (N), and the presence of pollen consistent in morphology with *A. magdalenae* var. *peirsonii* are noted. Vouchers are housed at RSABG.

Family	Species	N	Pollen
Anthophorideae	*Habropoda pallida*	52	present
Bembibinae	*Bembix rugosa*	12	present
Apidae	*Apis mellifera*	12	present
Bombyliidae	*Bombylius lancifer*	7	present
Andrenidae	*Perdita* sp.	6	absent
Halictidae	*Lasioglossum* sp. (?)	3	absent
Unidentified Microlepidoptera		3	absent

Table 10. Fruit production frequencies based on bi-directional crosses among six individuals of *Astragalus magdalenae* var. *peirsonii*. The parent providing an ovule (seed parent) is denoted by "Ovule" and the parent providing pollen (pollen parent) is denoted "Pollen." The individuals are identified with numbers one through six.

		Ovule					
		1	2	3	4	5	6
	1	0.0	0.6	0.0	0.0	0.0	0.4
	2	0.3	0.0	0.4	0.4	0.5	0.3
Pollen	3	0.0	0.1	0.0	0.1	0.1	0.1
	4	0.2	0.1	0.3	0.0	0.0	0.3
	5	0.0	0.3	0.3	0.0	0.0	0.4
	6	0.3	0.2	0.0	0.0	0.3	0.0
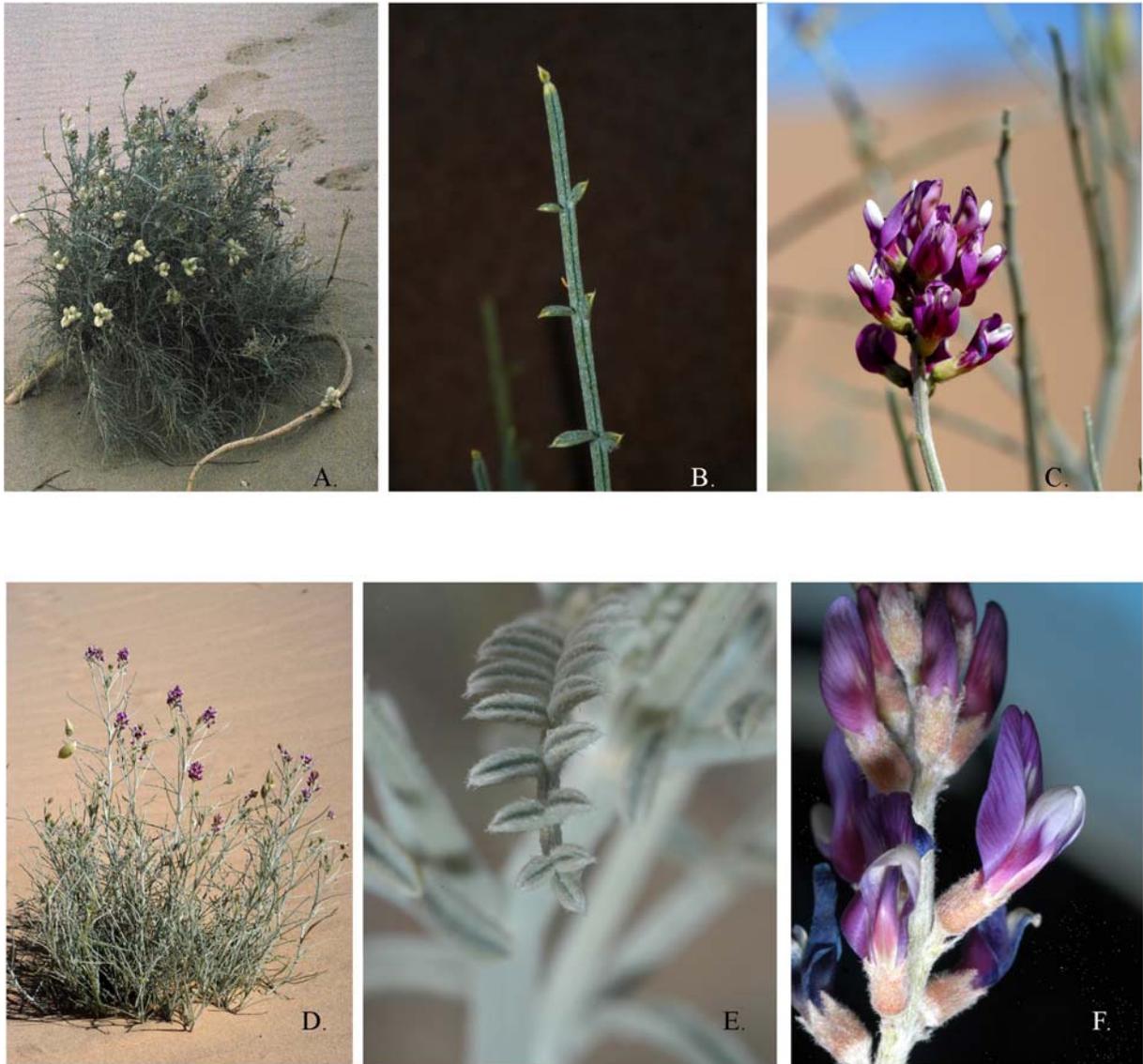
Figure 1. *Astragalus magdalenae* var. *peirsonii* growing at Algodones Dunes, Imperial County, California. The individual shown in A was present in 2002, when the study began, and was photographed in 2004, at the end of the study. Although the age of the plant is unknown, it was observed for three years. B shows the leaf morphology of Peirson's milkvetch, illustrating the prolongation of the rachis associated with the terminal leaflet. C is the inflorescence of Peirson's milkvetch. D is a flowering and early reproductive adult. E and F illustrate the leaf morphology and inflorescence of *Astragalus magdalenae* var. *magdalenae*, respectively.
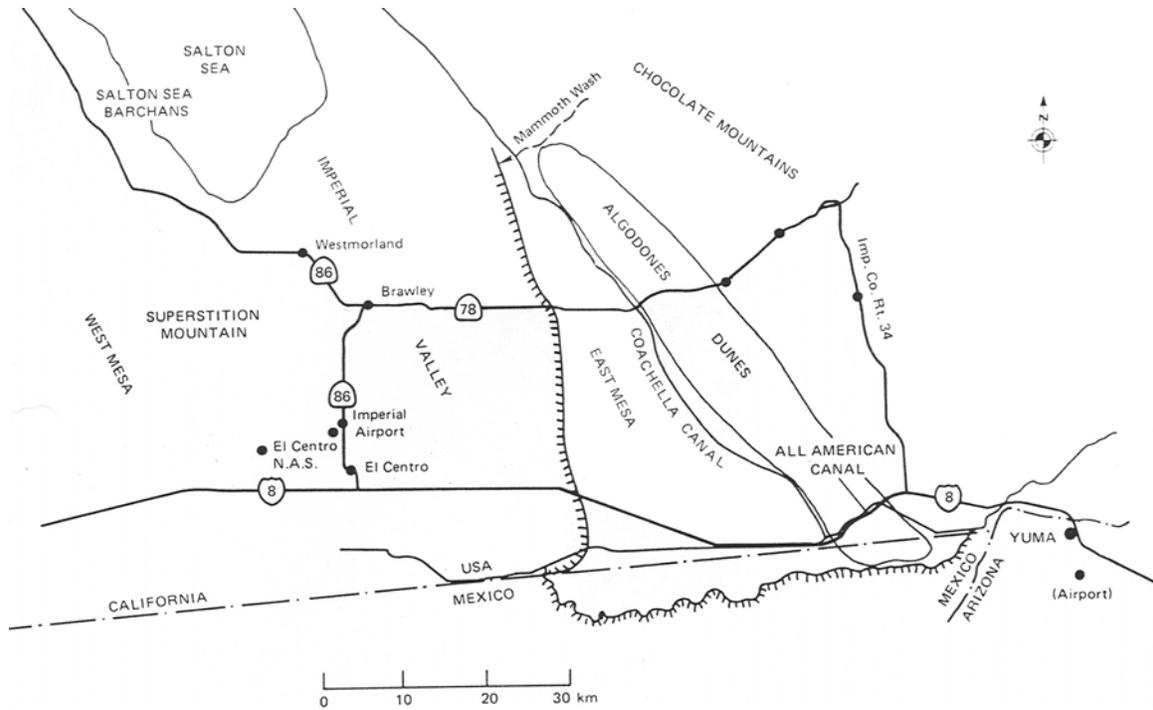
Figure 2. Physiographic features of southeastern California, illustrating the relative relationship of Algodones Dunes to these features as well as highways and major cities, redrawn from Norris and Norris (1961). Note that the hatched line represents the western edge of East Mesa and the southeastern margin of the ancient Lake Cahuilla
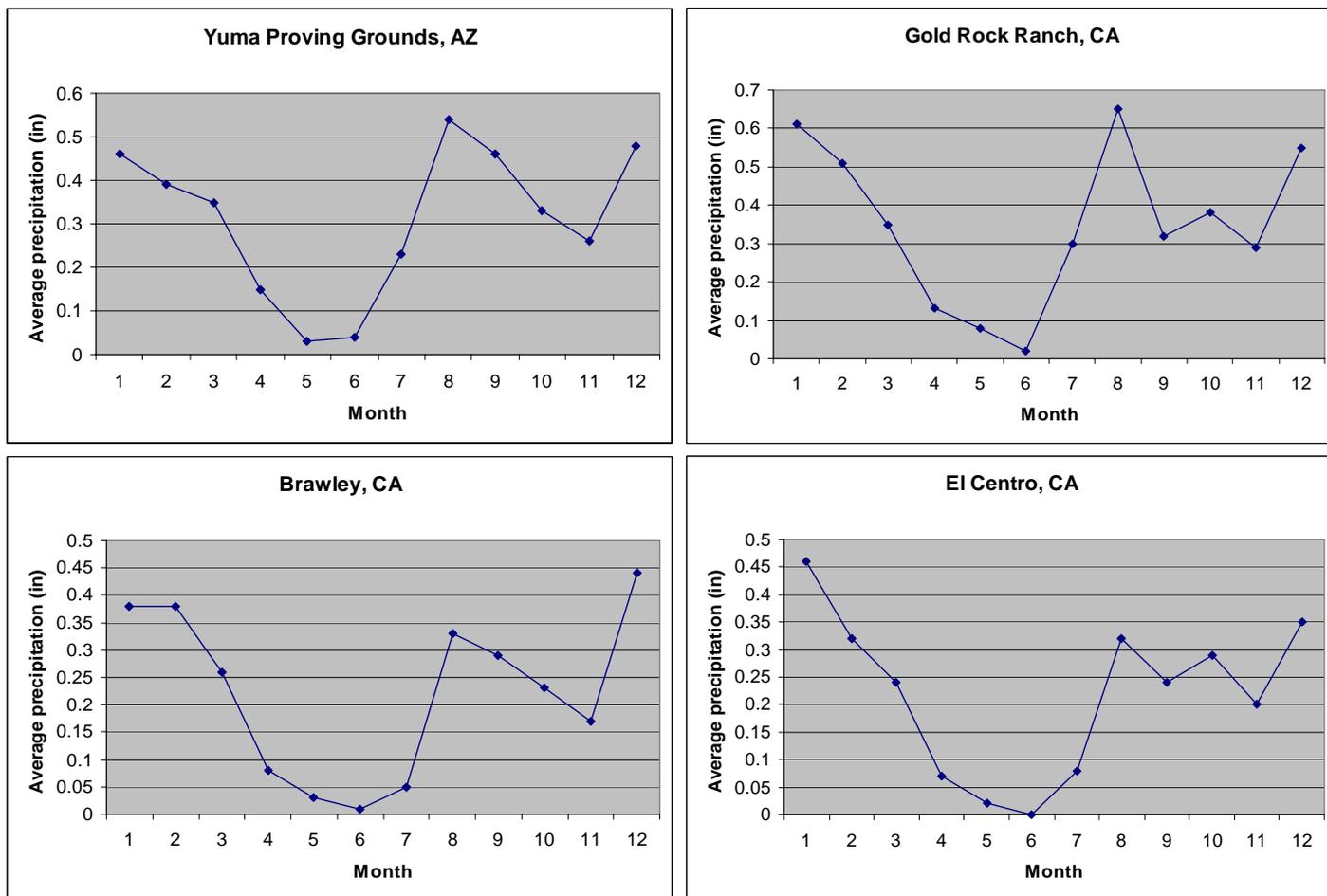
Figure 3. Average precipitation at Yuma Proving Grounds, Arizona, Gold Rock Ranch, near Algodones Dunes, California, Brawley, California, and El Centro, California, with respect to month, is portrayed in a series of graphs. Months are represented numerically, e.g., January= 1, and December = 12. Precipitation is shown in inches of precipitation per month.
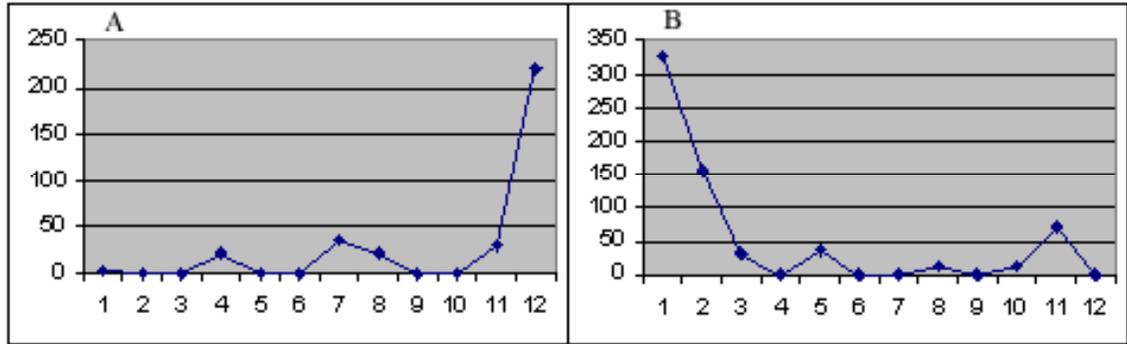
Figure 4. Examples of severe deviations from the typical bimodal precipitation pattern. Annual patterns of precipitation (millimeters of rain per month) at Gold Rock Ranch, during the years 1984 (A) and 1993 (B) portrayed as graphs. Months are represented numerically, e.g., January= 1, and December = 12. These patterns reflect unimodal rather than bimodal rainfall, in which maximum rains occur either in December or January, but the summer rains fail.
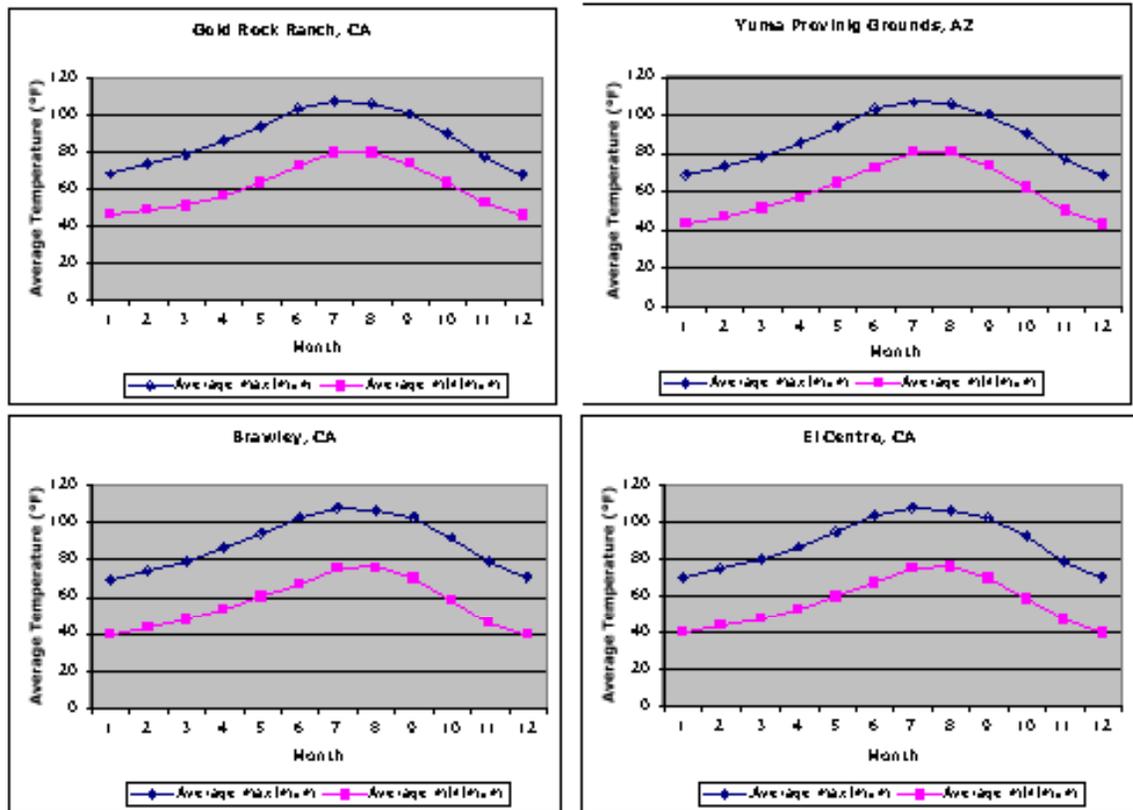
Figure 5. Average monthly temperatures at four long-term weather stations near Algodones Dunes. These sites are Brawley, El Centro, Gold Rock Ranch, and Yuma Proving Grounds. Months are represented numerically, e.g., January= 1, and December =12. Temperature is given in degrees Fahrenheit.
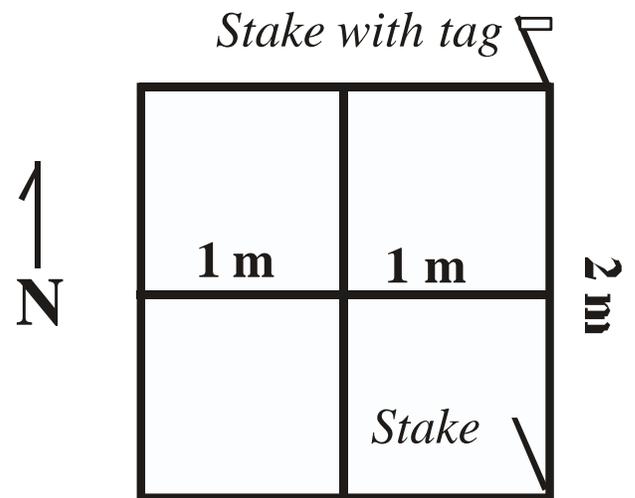
Figure 6. Design of the 2 m by 2 m seedling plots, indicating the location of the metal stake and tag and secondary stake.

Figure 7. Concrete planter filled with silica sand, used as an artificial dune for germination and growth of *Astragalus magdalenae* var. *peirsonii*. Set-up for germination trial in which one-half of the planter was seeded with scarified seed and the other with unscarified seed.
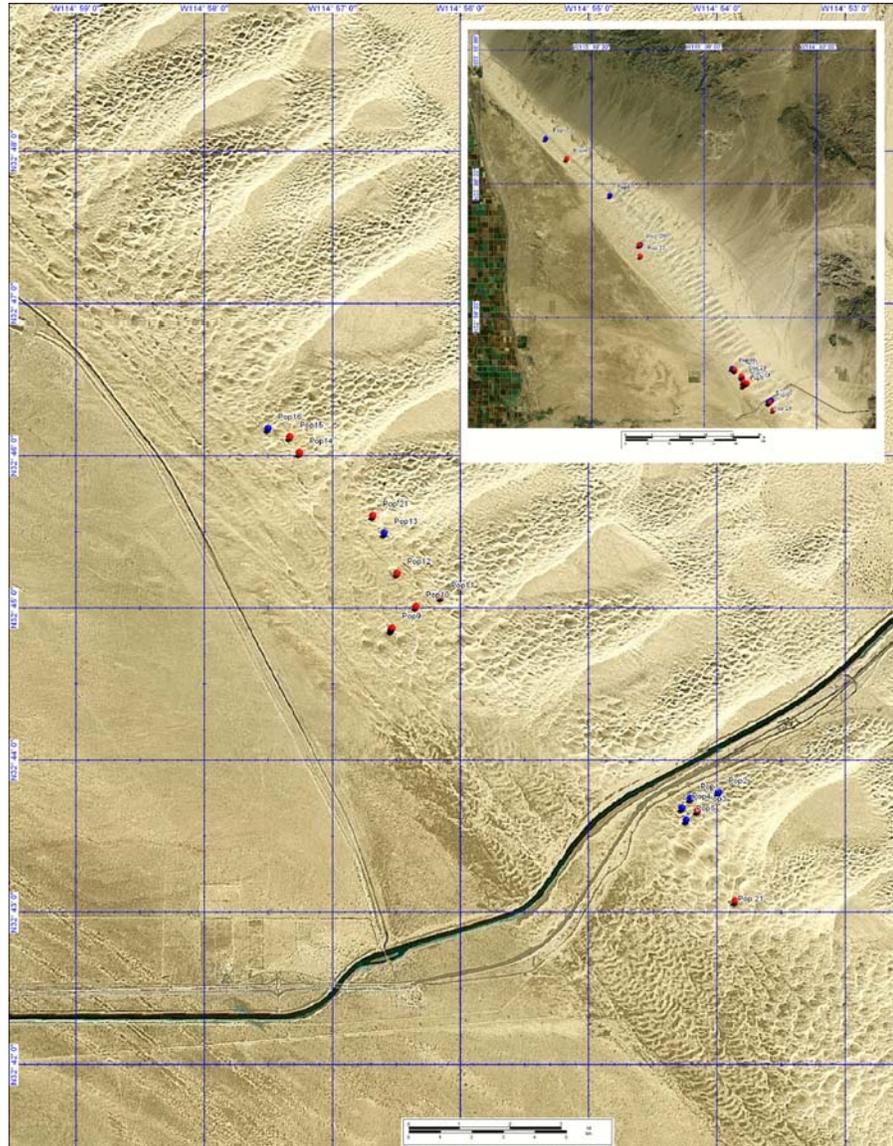
Figure 8. The distribution of sampling sites across Algodones Dunes (inset) with special attention to the high density sampling areas in the southern dunes. Red dots indicate those sites with seedling plots and blue are those without. Mapping utilizes a satellite image.
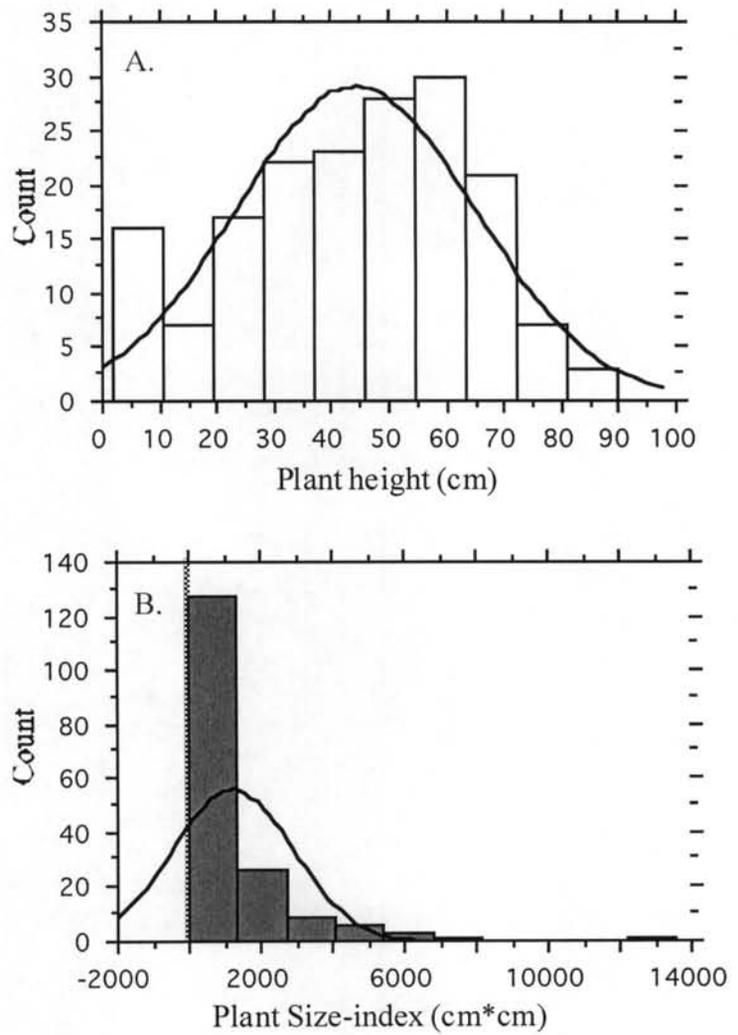
Figure 9. Static demographic frequency distribution of height classes (A) and plant-size index (B) during the 2002 sample year. Plant size index is calculated as plant height X number of branches.
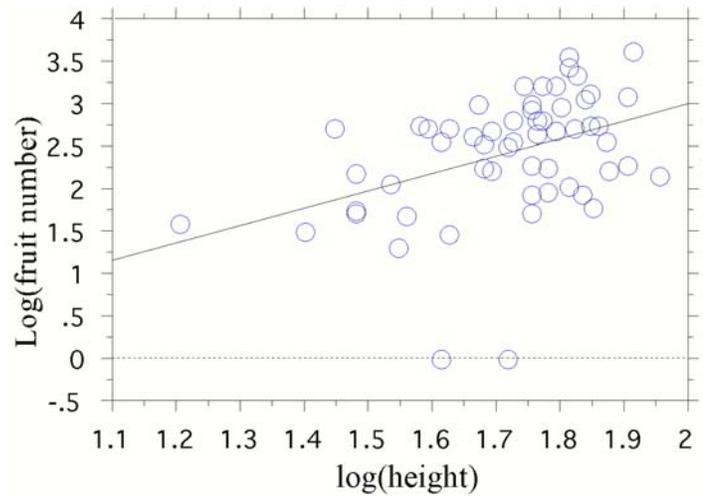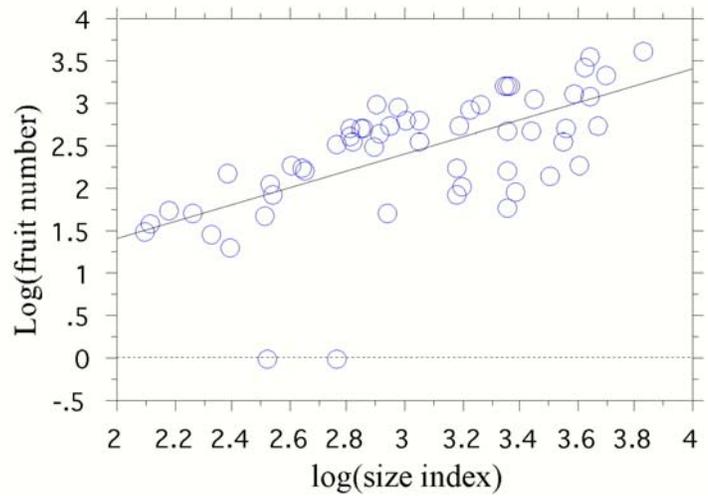
Figure 10. The relationship between plant height (upper graph) and plant size index (plant height X number of branches; lower graph) and fruit production is displayed in a general linear regression. Data are from the 2002 census of *Astragalus magdalenae* var. *peirsonii* and are log transformed.
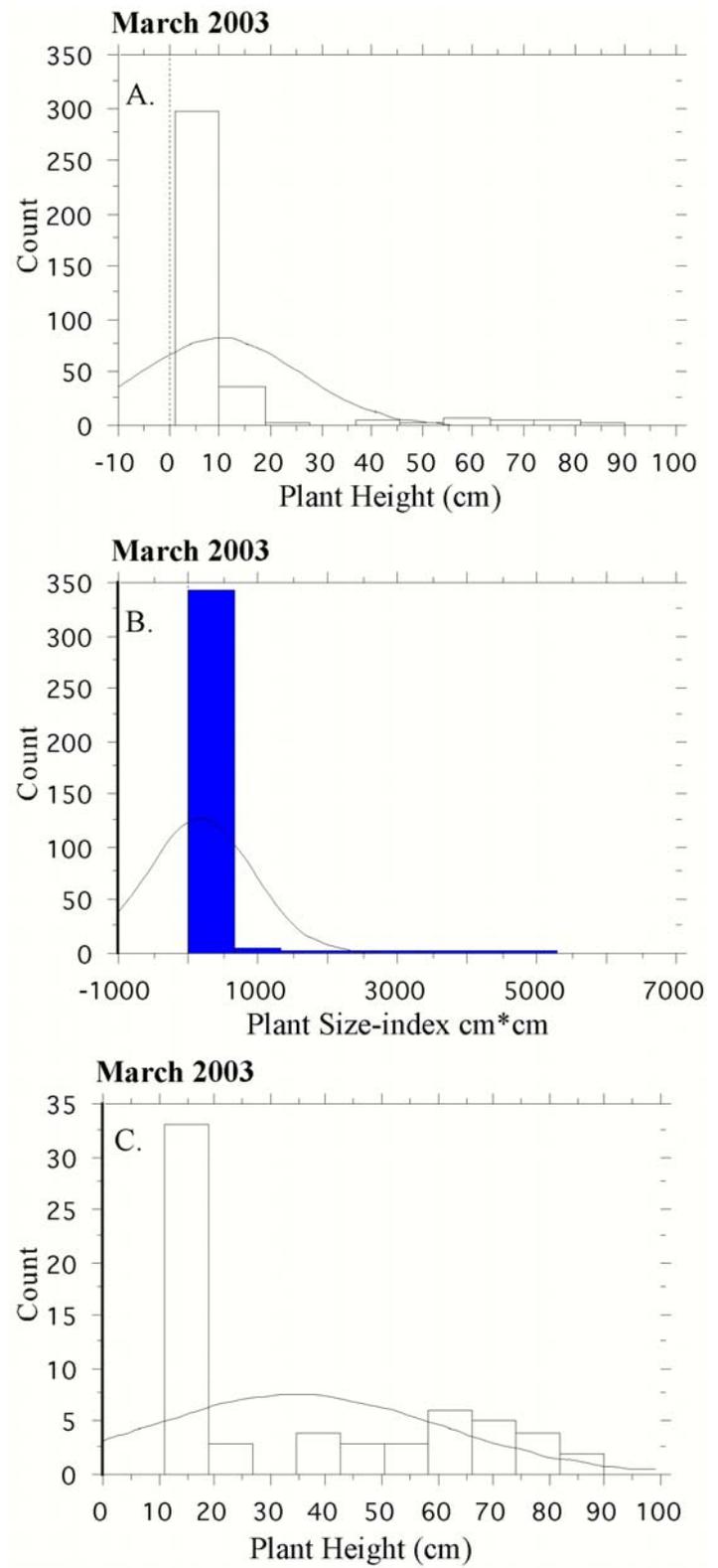
Figure 11. Static population height structure (A), distribution of plant size index (B), distribution of plant height when the smallest height class is removed, in 2003.
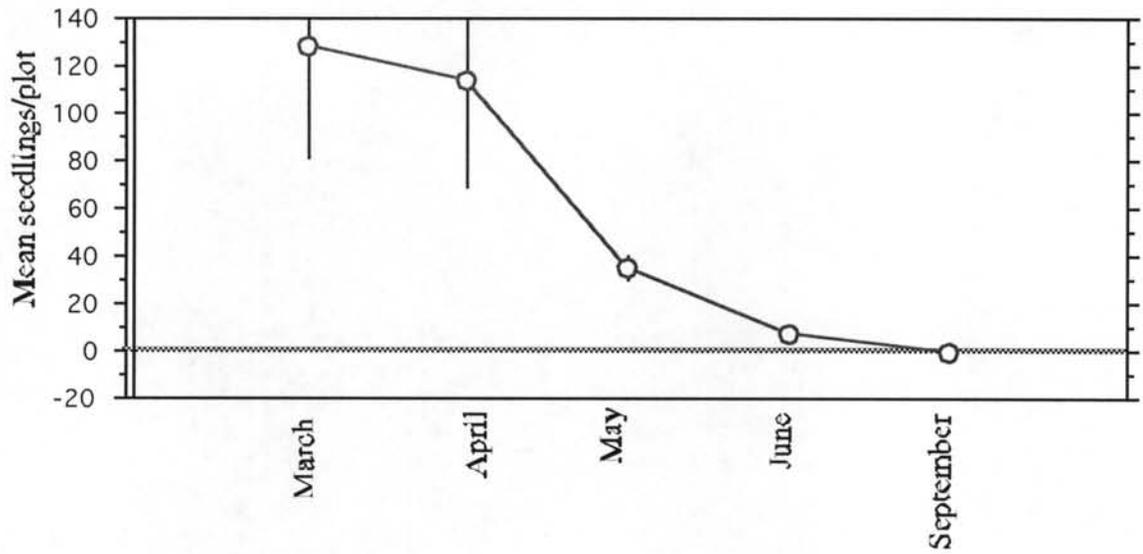
Figure 12. Pattern of seedling survival/mortality at Algodones Dunes, during 2003. Mean values are represented with bars representing standard errors of the mean. These errors were very small in May, June, and September.
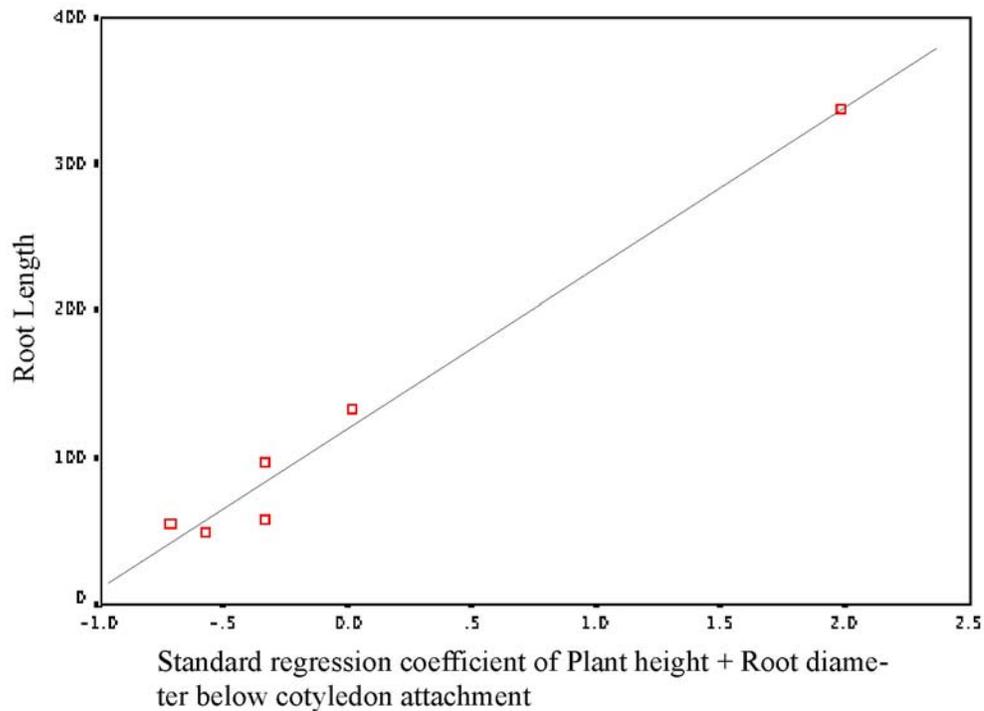
Figure 13. Regression, describing the relationship between combination of plant height and the diameter of the root just below the point of cotyledon attachment (x) and root length (y). The regression shows that plant height and the root diameter have highly significant explanatory power (r-square= 0.981) in predicting root length.

Figure 14. Germination trial of *Astragalus magdalenae* var. *peirsonii*. Scarified seed (labeled at the bottom) have 95.8% germination, whereas unscarified seeds (labeled at the top) show 0% germination.

Figure 15. *Habropoda pallida* on flower of *Astragalus magdalenae* var. *peirsonii*.

Figure 16. *Bembix rugosa*, a frequent visitor of Peirson's milkvetch, on *Pholisma sonorae* at Algodones Dunes.

Figure 17. Crab spider on the inflorescence of Peirson's milkvetch. The spider, moments after capturing a small solitary bee (c.f. Halictidae), as the prey landed on a flower.s

Figure 18. A. Photograph of the most common herbivore on Peirson's milkvetch, a species of weevil. B. Pattern of damage to the stems resulting from the activity of this insect species.

Figure 19. Change in pollen color associated with the age of the flower. The anthers on the right are from a flower that has recently reached anthesis; whereas, the anthers on the left are from a flower that began anthesis three days earlier.
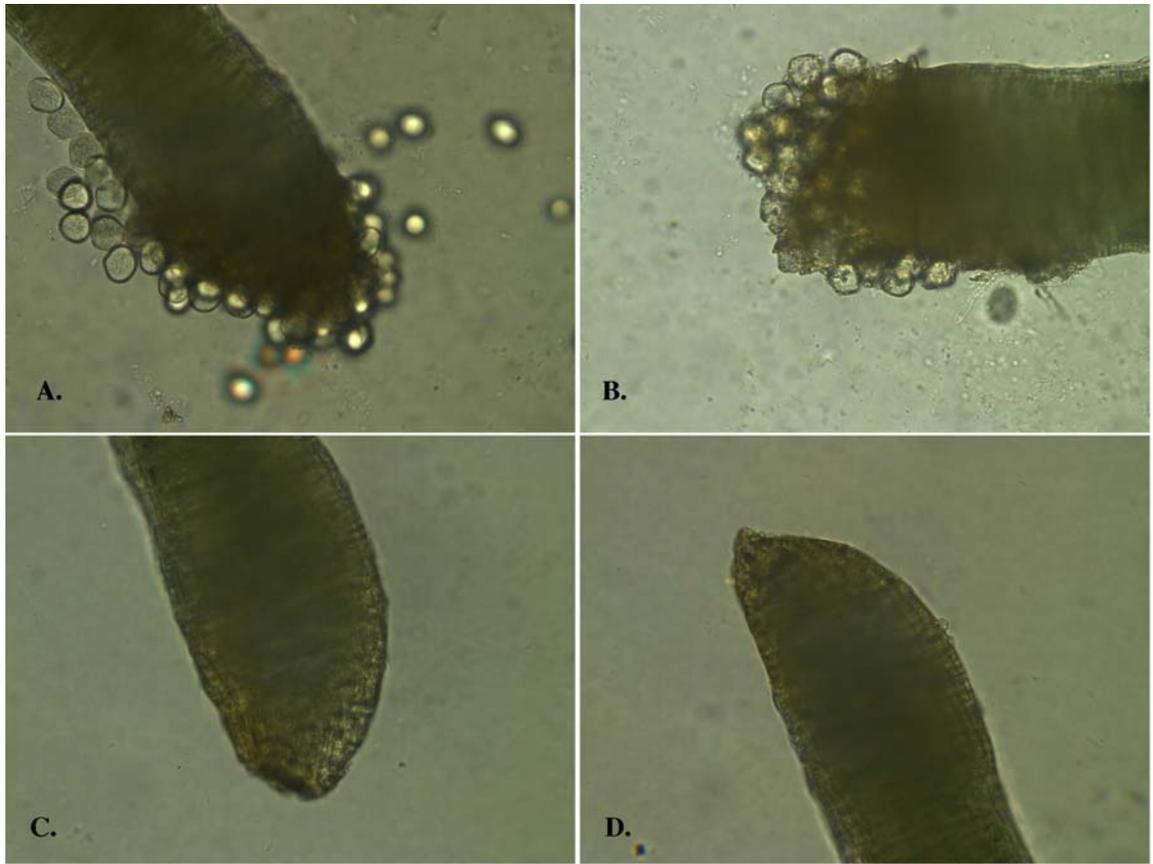
Figure 20. Stigmatic surface of *Astragalus   magdalenae* var. *peirsonii* three hours after pollination. A. Outcrossed pollen on the stigma of a flower that has just reached anthesis. B. Outcrossed pollen on the stigma of a flower that is three days old. C. Self pollen on the stigma of a flower that has just reached anthesis. D. Self pollen on the stigma of a flower that is three days old.

Appendix I. Preliminary Flora of Algodones Dunes.

The following is a preliminary listing of species encountered in Algodones, during the process of conducting this research. The list in organized alphabetically by plant family. Under each family, species are also arranged alphabetically by generic name and then by specific epithet. Authorities of each name are provided. A general summary of the habitat or plant community in which the species was found is given: CS= Creosote scrub, E= east side (e.g., along Ted Kipp Road), W= west side (between the Coachella canal and the dunes); MW= Microphyll woodlands; SD= shallow dunes, sandy areas; DD= deep dunes, psammophytic scrub; Canal= canal influenced habitat, along the All American or Coachella canals. An asterisk before the name identifies those species growing with *Astragalus magdalenae* var. *peirsonii*.

Amaranthaceae
      Amaranthus fimbriatus (Torr.) Benth. CS
      Amaranthus palmeri S. Wats. CS
      Tidestromia oblongifolia (S. Wats.) Standl. CS

Asclepiadaceae
      Asclepias subulata DC. CS-E

Asteraceae
      Ambrosia dumosa (A. Gray) Payne. CS-W
      Atrichoseris platyphylla A. Gray. CS
      Chloracantha spinosa (Benth.) G. Nesom var. *spinosa* CS
      Baccharis emoryi A. Gray. Canal
      Baccharis sarothroides A. Gray. SD-E
      Baileya pleniradiata A. Gray. SD, CS-E mostly
      Baileya pauciradiata A. Gray. SD, CS-W mostly
      Calycoseris wrightii A. Gray. CS-E
      Chaenactis stevioides Hook. & Arn. CS-E
      Conyza canadensis (L.) Cronq. Canal
      Conyza coulteri A. Gray. MW
      *Dicoria canescens A. Gray. SD, DD
      Eclipta prostrata (L.) L. Canal
      *Encelia farinosa Torr. & A. Gray. CS-E
      Encelia frutescens (A. Gray) A. Gray. CS
      Geraea canescens A. Gray. CS-E, washes
      Helianthus annuus L. var. *lenticularis*(Douglas) Cockerell. Canal
      *Helianthus niveus (Benth.) Brandegee subsp. *tephodes* (A. Gray) Heiser. DD
      Hymenoclea salsola A. Gray. CS-E
      Lactuca serriola L. Canal
      Monoptilon bellioides (A. Gray) H.M. Hall. CS-E
      Palafoxia arida Turner & Morris var. *arida* CS-W & E
      *Palafoxia arida Turner & Morris var. *gigantea* (M.E. Jones) Turner & Morris. SD, DD
      Pectis papposa Harvey & A. Gray. CS-W
      Perityle emoryi Torr. CS-E
      Pluchea sericea (Nutt.) Cov. Canal
      Psathyrotes ramosissima (Torr.) A. Gray. CS
      Rafinesquia californica Nutt. CS
      Sonchus asper (L.) Hill var. asper CS-E

Sonchus oleraceus L. CS-E
Stephanomeria pauciflora (Nutt.) Nelson var. *pauciflora* CS-E

Bignoniaceae
Chilopsis linearis (Cav.) Sweet subsp. *arcuata* (Fosb.) Henrickson. SD-E

Boraginaceae
Amsinckia tessellata A. Gray var. *tesselata* MW-E
Cryptantha angustifolia (Torr.) E. Greene. CS-W
Cryptantha barbigera (A. Gray) E. Greene. CS
Cryptantha costata Brandegee. CS
Heliotropium curassavicum L. CBS
Pectocarya platycarpa (Munz & I.M. Johnston) Munz & I.M. Johnston. CS-E
Tiquilia palmeri (A. Gray) A. Richardson. CS
Tiquilia plicata (Torr.) A. Richardson. SD-W, DD

Brassicaceae
Brassica tournefortii Gouan. SD, CS-E
Dithyrea californica Harvey. SD
Lepidium lasiocarpum Torr. & A. Gray. CS-E
Lyrocarpa coulteri Hook. & Harvey var. *palmeri* (S. Wats.) Rollins. CS
Sisymbrium altissimum L. CS-E

Cactaceae
Opuntia acanthocarpa Engelm. & J. Bigelow var. *coloradensis* L. Benson. CS
Opuntia basilaris Engelm. & J. Bigelow var. *basilaris* CS-E
Opuntia ramosissima Engelm. CS

Caryophyllaceae
Achyronychia cooperi Torr. & A. Gray. CS-E

Chenopodiaceae
Atriplex elegans (Moq.) D. Dietr. var. *fasciculata* (S. Wats.) M.E. Jones. CS
Chenopodium murale L. Canal
Salsola tragus L. SD-E

Cucurbitaceae
Brandegea bigelovii (S. Wats.) Cogn. CS-E
Cucurbita palmata S. Wats. DMW, CS

Ephedraceae
Ephedra trifurca Torr. SD-W, DD

Euphorbiaceae
Croton wigginisii Wheeler. SD,DD
Ditaxis neomexicana (Muell. Arg.) A.A. Heller. CS
Ditaxis serrata (Torr.) A.A. Heller. CS-E
Euphorbia parishii E. Greene. CS
Euphorbia polycarpa Benth. CS
Stillingia linearifolia S. Wats. MW-E
Stillingia spinulosa Torr. CS

Fabaceae

Astragalus aridus A. Gray. CS-E

Astragalus lentiginosus Hook. var. *borreganus* M.E. Jones. SD, CS

Astragalus magdalenae E. Greene var. *peirsonii* (Munz & McBurney) Barneby. DD

Cercidium floridum A. Gray subsp. *floridum* SD, MW, CS wash

Cercidium microphyllum (Torr.) Rose & I.M. Johnst. SD, MW, CS wash

Dalea mollis Benth. CS-W & E

Lupinus arizonicus (S. Wats.) S. Wats. CS-E washes

Melilotus albus Medikus. Canal

Olneya tesota A. Gray. SD, MW

Prosopis glandulosa Torr. var. *torreyana* (L. Benson) M. Johnson. CS, MW

Prosopis pubescens Benth. MW CS

Psorothamnus emoryi (A. Gray) Rydb. SD-W

Psorothamnus spinosa (A. Gray) Barneby. CS-E washes

Fouquieriaceae

Fouquieria splendens Engelm. subsp.*splendens* CS-E

Haloragaceae

Myriophyllum sibiricum V. Komarov. Canal

Hydrophyllaceae

Nama demissum A. Gray var. *demissum* CS

Nama hispidum A. Gray var *spathulatum* (Torr.) C. Hitchc. CS

Phacelia crenulata Torr. var. *crenulata* CS-E

Krameriaceae

Krameria grayi Rose & Painter. CS-E

Lennoaceae

*Pholisma sonorae (A. Gray) G. Yatskievych. DD

Liliaceae

Hesperocallis undulata A. Gray. SD-W mostly

Loasaceae

Mentzelia albicaulis Hook. CS-W

Mentzelia multiflora (Nutt.) A. Gray. *longiloba* SD

*Petalonyx thurberi A. Gray subsp. *thurberi* SD, DD

Malvaceae

Eremalche rotundifolia (A. Gray) E. Greene. CS-E

Sphaeralcea emoryi Torr. var. *arida* (Rose) Kennedy. CS, MW

Sphaeralcea orcuttii Rose. MW-E, next to SD

Hibiscus denudatus Benth. CS-E

Martyniaceae

Proboscidea althaeifolia (Benth.) DC. CS, MW, SD

Proboscidea parviflora (Wooton) Wooton subsp. *parviflora* CS, MW, SD

Nyctaginaceae

    Abronia villosa S. Wats. var. villosa SD, (DD- W)

    Allonia incarnata L. CS-E

    Boerhavia coulteri (Hook.) S. Wats. CS, SD

Onagraceae

    Camissonia arenaria (Nelson) Raven. CS

    Camissonia boothii (Dougl.) Raven subsp. *condensata*(Munz) Raven. CS

    Camissonia cardiophylla (Torr.) Raven subsp. *cardiophylla* CS

    Camissonia claviformis (Torr. & Fremont) Raven subsp. *yumae* (Raven) Raven. CS, SD

    Epilobium glaberrimum Barbey subsp. *glaberrimum* CS-E

    *Oenothera deltoides Torr. & Fremont subsp. *deltoides* SD

Orobanchaceae

    Orobanche cooperi (A. Gray) A.A. Heller. SD-W

Papaveraceae

    Argemone corymbosa E. Greene. CS-E

    Argemone munita Durand & Hilg. subsp. *argentea* Ownbey. CS

    Eschscholzia minutiflora S. Wats. CS-W & E

    Eschscholzia glyptosperma E. Greene. CS, MW

Plantaginaceae

    Plantago ovata Forsskal. CS-W & E

    Plantago patagonica Jacq. CS

Poaceae

    Aristida adscensionis L. CS

    Aristida californica Thurber var. *californica* CS-W

    Arundo donax L. Canal

    Avena fatua L. Canal

    Bouteloua barbata Lagasca var. *barbata* CS

    Cynodon dactylon (L.) Pers. Canal

    Echinochloa crus-pavonis (Kunth) Schultes. Canal

    Lolium perenne L. Canal

    *Panicum urvilleanum Kunth. SD, DD-E

    Phalaris aquatica L. CS-E

    Pleuraphis rigida Thurber. CS-E

    Schismus arabicus Nees. CS-W & E

    Schismus barbatus (L.) Thell. CS

Polemoniaceae

    Langloisia setosissima (Torr. & A. Gray) E. Greene subsp. *setosissima* CS

    Loeseliastrum matthewsii (A. Gray) S. Timbrook. CS

    Loeseliastrum schottii (Torr.) S. Timbrook. CS-E, SD

Polygonaceae

    Chorizanthe brevicornu Torr. var. *brevicornu* CS-E

    Chorizanthe corrugata (Torr.) Torr. & A. Gray. CS-E

    Chorizanthe rigida (Torr.) Torr. & A. Gray. CS-E

    Eriogonum deflexum Torr. var. *deflexum* CS

Eriogonum deserticola S. Wats. SD,DD
Eriogonum inflatum Torr. & Frem. var. *deflatum* I.M. Johnst. CS
Eriogonum thomasii Torr. CS
Polygonum persicaria L.Canal
Rumex hymenosepalus Torr. CS
Rumex violacens Rech. f. Canal

Potamogentonaceae
Potamogeton pectinatus L. Canal

Resedaceae
Oligomeris linifolia (M. Vahl.) J.F. Macbr. CS-E

Solanaceae
Datura discolor Bernh. CS, MW

Simaroubaceae
Castela emoryi (A. Gray) Moran & Felger. MW

Tamaracaceae
Tamarix aphylla (L.) Karsten. CS, MW
Tamarix parviflora DC. Canal

Typhaceae
Typha domingensis Pers. Canal
Typha latifolia L. Canal

Viscaceae
Phoradendron californicum Nutt. CS, MW

Zygophyllaceae
Fagonia laevis Standley. CS, MW
Fagonia pachyacantha Rydb. CS
Kallstroemia californica (S. Wats.) Vail. MW
Larrea tridentata (DC.) Cov. CS, SD, MW