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ECOPHYSIOLOGICAL OBSERVATIONS ON LANE MOUNTAIN MILKVETCH, *ASTRAGALUS JAEGERIANUS* (FABACEAE), A PROPOSED ENDANGERED SPECIES OF THE MOJAVE DESERT

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ABSTRACT

Astragalus jaegerianus, the Lane Mountain milkvetch, a perennial herbaceous legume, is a rare and very narrow endemic of the central Mojave Desert in San Bernardino County, California, and currently proposed to be listed as an endangered species. This herb grows in the protection of low shrubs. Anatomical observations revealed that leaflets are amphistomatic and have isolateral mesophyll, typical of full-sun desert leaves, and the green stem is an important photosynthetic organ, having abundant stomata and a cylinder of cortical chlorenchyma. Ecophysiological studies showed that this species requires high PFD (1400-1500 μmol m^{-2} s^{-1}) to achieve maximum photosynthetic rates and, therefore, is probably not utilizing the nurse shrub for shade but, instead, as a trellis for upper shoots to intercept high PFD. A study of $\delta^{15}N$ indicated that this legume is a nitrogen fixer, with higher tissue nitrogen content than other associated species (3.1% versus 1.8%). The herb-shrub association is speculated to be mutualistic, in that the shrub may benefit from higher soil nitrogen when it grows with a nitrogen-fixing legume, and *A. jaegerianus* likely uses the nurse shrub for protection from herbivores.

Key words: *Astragalus,* ecophysiology, endangered species, Fabaceae, milkvetch, Mojave Desert.

INTRODUCTION

In the most recent flora of California, Spellenberg (1993) recognized 94 species for the genus *Astragalus,* including 144 varieties, of which 41 taxa (29%) were described as rare, endangered, or presumed extinct. In a separate analysis on the same species, the California Native Plant Society judged 66 taxa (46%) to be either rare or endangered (Skinner and Pavlik 1994). Both lists included the Lane Mountain milkvetch, *A. jaegerianus* Munz, which was first collected by Edmund Jaeger on 16 April, 1939, a few kilometers north of the Paradise Range in San Bernardino County, California (Munz 1941). Field studies have confirmed the rarity and highly restricted distribution of this species on the northern and eastern outwash plain of the Paradise Range, where fewer than 150 individuals have ever been observed within an area of 20 km^2 around its type locality at the southwestern corner of the U.S. Army National Training Center at Fort Irwin (Barneby 1964; Bagley 1986; Brandt, Rickard, and Caboret 1993, referencing unpublished report of M. Bagley). *Astragalus jaegerianus* is one of the few endemic taxa of the Central Mojave Desert Region (Prigge 1996), as formally defined (Rowlands et al. 1982), and has been proposed by the U.S. Fish and Wildlife Service (1990, 1996) to be a federally endangered species, to protect this extremely narrow endemic from military and other off-road vehicle traffic.

The known habitat of *A. jaegerianus* is creosote bush desert scrub growing on gravelly sandy loam at 960 to 1180 m elevation (Brandt et al. 1993). This milkvetch is a thin-stemmed herbaceous perennial that typically scrambles into the uppermost canopy of the woody shrubs and subshrubs of the habitat; however, *Larrea tridentata* (DC.) Cov., a codominant species, has never been observed as a nurse plant, and tends to be present at low densities within the known microhabitat of *A. jaegerianus* (Brandt et al. 1993). Nurse plants may be either living or dead, and in 1992, during a relatively wet spring, several small individuals were found in open areas, without a nurse plant. *Astragalus jaegerianus* has been found growing within the canopy of the common woody species, but sample sizes have been too small to detect a statistically significant association of this legume with particular nurse species (Brandt et al. 1993).

To understand physiological adaptations of this rare legume and the role of fertile islands or nurse shrubs in the life of *A. jaegerianus,* the U.S. Department of Agriculture Natural Resources Conservation Service (late spring, 1994), requested an initial ecophysiological study to elucidate ecological and physiological performance, especially to determine if nitrogen fixation occurs. A follow-up study was commissioned by Natural and Cultural Resources, Directorate of Public Works at Fort Irwin, to complete the ecophysiological profile of this species during an early spring.

MATERIALS AND METHODS

Field studies of *A. jaegerianus* were conducted near the western boundary of the U.S. Army Fort Irwin National Training Center north of Barstow, California at 35°42′30″N 116°48′40″W (Grids NJ1695, NJ1696, NJ1794, and NJ1795; T13N, R2E Sec 19 and 24) and an elevation of 1040–1080 m. Mean annual precipitation was about 170 mm, recorded nearby at Echo Tracking Station on the Fort Irwin-Goldstone complex, mostly occurring from November through March. The site was visited on 12 May, 1994, during a very dry late spring, when five persons searching for two hours could only locate four individuals of *A. jaegerianus* growing within leafless canopies of *Ambrosia dumosa* (A. Gray) Payne, and on 20 March, 1997, when three persons searching for 30 minutes located six plants, several having flowers and immature fruits. In 1997, the three most robust individuals were found growing within large individuals of *Thamnosma montana* Torr. & Frem., an aphyllous shrub with photosynthetic stems, on a south-facing slope. Other perennials in the microhabitat were *Ambrosia dumosa, Encelia actoni* Elmer, *Ephedra nevadensis* S. Wats., *Ericameria cooperi* (A. Gray) H. M. Hall, *Eriogonum fasciculatum* Benth. var. *polifolium* (A. DC.) Torr. & A. Gray, *Hymenoclea salsola* A. Gray, *Krameria erecta* Schultes, *Larrea tridentata, Salazaria mexicana* Torr., *Tetradymia stenolepis* E. Greene, *Xylorhiza tortifolia* (Torr. & A. Gray) E. Greene, and *Yucca brevifolia* Engelm. The 1997 site had not received a soaking rainstorm since late December, 1996.

Gas exchange measurements were made in 1994 on leafy shoots of two individuals and adjacent shrubs of *Encelia actoni.* Assimilation, leaf conductance, transpiration, and dark respiration were determined under ambient field conditions using a LI-6200 portable photosynthesis system (LI-COR Inc., Lincoln, Nebraska). Neutral filters were used to alter ambient light intensities to provide a light response curve of photosynthesis in relation to photon flux density (PFD, 400–700 nm), and the chamber was enclosed in aluminum foil to obtain rates of dark respiration. Leaf-to-air vapor pressure deficit (VPD) was obtained by subtracting ambient vapor pressure from saturation vapor pressure at ambient air temperature, assuming that, for desert plants with small leaves, leaf temperature is close to air temperature (Nobel 1991). In 1997, four individuals of *A. jaegerianus* were used for similar physiological measurements; however, the drought-deciduous shrubs, e.g., *Encelia actoni,* had no mature leaves and were not measured, because such leaves would not have been comparable with young mature leaves of the legume. Gas exchange measurements taken with the same methods were obtained in the spring of 1995 for the annual *A. acutirostris* S. Wats. from near California City, California, and the very common perennial *A. lentiginosus* Hook. var. *fremontii* (A. Gray) S. Wats. from near Barstow, so that some comparisons within the genus could be made.

Permission to harvest a limited number of vegetative shoots in 1994 and 1997 was granted by the Natural and Cultural Resources Office, Directorate of Public Works at Fort Irwin, and cleared with the U.S. Fish and Wildlife Service, to be able to measure photosynthetic rates and water potential. Water potential measurements were taken at midday using a Scholander-type pressure chamber (PMS Instrument Corp., Corvallis, OR) immediately after gas exchange measurements were completed. To obtain leaf and green stem area enclosed within the 250-ml leaf chamber for photosynthesis measurements, outlines of shoots were carefully traced under fresh conditions and later photocopied. Photocopied leaflets were cut and fed through a LI-3100 leaf area meter (LI-COR Inc., Lincoln, Nebraska). Stem area was calculated geometrically assuming cylindrical form. To assess the accuracy of the tracing method, in 1997 shoots were traced in the field when fresh and then subsequently sealed in Ziploc plastic bags containing wet tissue paper and brought to the laboratory. Both traced and fresh leaflets were measured with an LI-3100 leaf area meter, and a close correlation between traced and fresh samples was found.

An effective and relatively nondestructive means of quantifying nitrogen fixation was used (Virginia et al. 1988). From the severed upper shoots in 1994, small samples of fully mature leaf tissues were obtained for *A. jaegerianus* and the three respective nurse plants of nonfixing *Ambrosia dumosa* to perform nitrogen isotope analysis. These leaves were oven-dried, ground, and sent to Boston University, where analyses were carried out using a Finnigan Delta-S isotope ratio mass spectrometer. In principle, nitrogen isotope ratios ($\delta^{15}N$) of the nurse plant were to be used as a nonfixing control, while the 100% nitrogen-fixing control was taken from hydroponically grown, nodulated plants of another herbaceous desert legume, *Dalea mollissima* (Rydb.) Munz, grown in a nitrogen-free solution. Leaf tissues of *D. mollissima* has a $\delta^{15}N$ value of -2.5. Soil was collected in the vicinity of the roots of *A. jaegerianus* and under three individuals of *Ambrosia dumosa* and analyzed for nitrogen content. An attempt was made to look for root nodules on one individual, but that trial was aborted when the vertical root disappeared into cracks of solid granite about 0.4 m below the surface, and it was prudent to permit the plant to remain intact rather than to threaten its life.

Calculations of nitrogen fixation typically are based on the discrimination against the heavier ^{15}N isotope during soil nitrogen transformation. These processes usually result in soil inorganic nitrogen that is enriched in ^{15}N in comparison with atmospheric nitrogen. Atmospheric nitrogen has a relatively stable value of about -1.0 ‰ for $\delta^{15}N$, as compared with more positive values for soil nitrogen (Mariotti 1984). A simple linear model can then be used to estimate relative symbiotic nitrogen fixation by ratioing the difference between $\delta^{15}N$ of nonfixing controls and the $\delta^{15}N$ of control fixers grown in a nitrogen-free medium (Shearer and Kohl 1986; Virginia et al. 1988). This ratio provides the proportionality of nitrogen fixation in the putative fixers between the poles of no fixation, i.e., pure soil nitrogen used by control plants, and 100% fixation, i.e., control fixers grown without nitrogen.

The stems and leaflets not used in the nitrogen analyses were examined from razor blade sections with a light microscope to record anatomical observations relevant to the ecophysiological study, in particular, measurements of stomatal distributions and densities and anatomical designs of chlorenchyma.

RESULTS

Astragalus jaegerianus, a scandent hemicryptophyte, was found scrambling upward within the shrub canopy. Its green stems were thin, cylindrical, and somewhat wiry, but showed no twining. Vigorous vegetative shoots and inflorescences reached the uppermost canopy but did not project above the nurse plant. Foliage was comparatively sparse, consisting of pinnately compound leaves typically with 11 or 13 (5–15) widely spaced, narrow leaflets (to 20 mm in length), and separated by internodes up to 5 cm in length. Leaflets were dark green with a grayish hue due to the presence of a L-shaped trichomes. Each leaf possessed a pair of minute, recurved, leafy stipules. Range of leaf area was 1.6–2.2 cm^2, and each robust plant had fewer than 50 mature leaves.

Leaflets were amphistomatic, with stomatal densities of up to 185 mm^{-2} on the abaxial surface and 85 mm^{-2} on the adaxial surface, because of the greater density of trichomes. Leaflet thickness was 230–255 μm, and laminae had isolateral organization of mesophyll.

The photosynthesizing stem had a uniseriate epidermis with tangentially thickened cell walls and a uniseriate hypodermis that covered the cylinder of chlorenchymatous outer cortex, composed of isodiametric cells. Mean stomatal density was as high as 71 mm^{-2}, and stomata were slightly sunken (<5 μm). Toughness of the wiry stem was attributable mostly to a nearly continuous ring of primary phloem fibers, which had thick secondary walls but little lignin.

Contrary to expectations, *A. jaegerianus* did not show physiological adaptations to low levels of PFD (Fig. 1). The light compensation point was at about 250 μmol m^{-2} s^{-1}, relatively high for any plant, and light saturation in 1994 and 1997 was 1400–1500 μmol m^{-2} s^{-1}, which exceeds that of many desert species. Dark respiration rates of 3.2 μmol m^{-2} s^{-1} were measured in this species, a relatively high value.

In 1997, shoots of *A. jaegerianus* had surprisingly low rates of net photosynthesis, with a midmorning maximum rate measured at only 9.6 μmol m^{-2} s^{-1} for leaflets and stems combined, substantially lower than even mean values for leaves of the other two species of *Astragalus* that were sampled (Table 1). For the three species, leaves of the annual *A. acutirostris* had the highest assimilation rate (mean 34.4 μmol m^{-2} s^{-1}) and stomatal conductance (mean 0.842 mol m^{-2} s^{-1}), while exhibiting the lowest intrinsic water-use-efficiency (A/g_s = 44 ±3). *Astragalus jaegerianus* had lowest values of assimilation and stomatal conductance with the highest intrinsic WUE, whereas *A. lentiginosus* var. *fremontii* held the intermediate position for all measured parameters (Table 1). For *A. jaegerianus,* the stem was an important photosynthetic organ, because it comprised a substantial part of shoot surface area (35%). By midday, when light response curves were taken, photosynthetic rate had dropped nearly in half to below 5.8 μmol m^{-2} s^{-1} (Fig. 1), indicating severe effects of increased VPD toward late afternoon. Photosynthesis declined steadily with increasing VPD, from 3.6 to 7.3 kPa, but the slope of this relationship was much more gradual than in neighboring plants of *Encelia actoni* (Fig. 2). However, leaf conductance was relatively insensitive to VPD in *A. jaegerianus* (Fig. 2). Air temperature and leaf-to-air VPD were highest during May, 1994, for *A. jaegerianus,* whereas the lowest values were achieved in March, 1995, at the site of *A. acutirostris.*

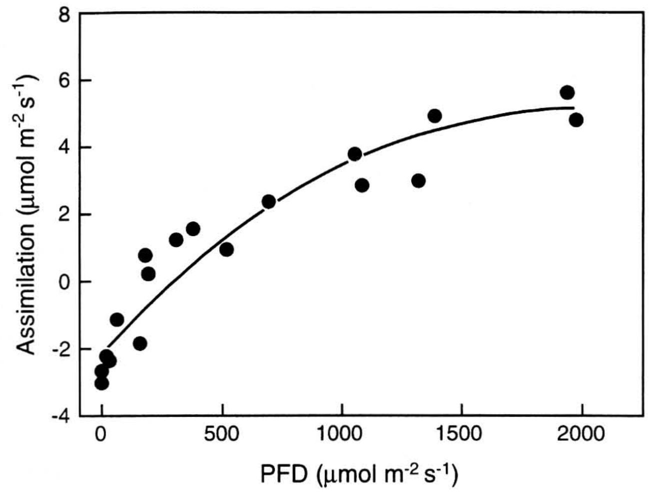

Fig. 1. Light response curve of *Astragalus jaegerianus* performed at the Fort Irwin study site on 20 March, 1997, showing the increase in assimilation with increasing photon flux density (PFD, μmol m^{-2} s^{-1}) to light saturation above 1400 μmol m^{-2} s^{-1}. A similar curve, but having a lower maximum assimilation rate (3.8 μmol m^{-2} s^{-1}), was obtained on 12 May, 1994, within the same population.

Mean midday shoot water potential ranged from −1.9 to −2.4 MPa in May, 1994, and −2.4 to −2.7 in March, 1997. Overlooking, for the moment, small sample size for this rare species, these values would typically indicate moderate amount of water stress,

Table 1. Gas exchange parameters at midmorning for three Mojave Desert species of *Astragalus*. For all measurements, PFD exceeded 1400 μmol m^{-2} s^{-1}. Mean ambient temperature was 27.9 C for *A. acutirostris* (30 March, 1995), 32.5 C for *A. lentiginosus* var. *fremontii* (28 March, 1995), and 33.7 C and 33.1 C for *A. jaegerianus* on the two sampling dates (12 May, 1994 and 20 March, 1997, respectively). On sampling date 12 May, 1994, five leaves per plant and on 20 March, 1997, two to three leaves per plant were measured. Measured and calculated parameters are: *A*, assimilation (μmol m^{-2} s^{-1}); g_s, stomatal conductance (mol m^{-2} s^{-1}); *E*, transpiration (mmol m^{-2} s^{-1}); VPD, vapor pressure deficit (kPa); A/g_s, intrinsic water-use efficiency. All readings are reported to document the range of variability, in particular for the endangered species. Mean and standard error is given.

Species	*A* (μmol m^{-2} s^{-1})	g_s (mol m^{-2} s^{-1})	*E* (mmol m^{-2} s^{-1})	VPD (kPa)	A/g_s
A. acutirostris	26.9	0.513	14.1	2.61	53
	26.5	0.551	15.4	2.62	48
	26.5	0.489	14.7	2.88	54
	38.0	0.790	18.8	2.41	48
	37.2	1.011	22.3	2.32	37
	38.3	1.134	28.1	2.64	34
	47.4	1.407	34.0	2.77	34
Mean ± SE	34.4 ± 3.03	0.842 ± 0.134	21.0 ± 2.87	2.61 ± 0.70	44 ± 3
A. jaegerianus (1994)	3.75	0.037	1.85	3.68	101
	4.21	0.042	2.10	3.72	100
	3.73	0.040	2.09	3.85	93
	3.44	0.044	2.31	3.88	79
	3.19	0.037	2.38	4.18	86
	2.97	0.037	2.43	4.24	79
	2.58	0.028	1.77	4.34	93
	2.56	0.034	2.25	4.38	75
	2.52	0.041	2.73	4.56	62
	2.73	0.028	1.92	4.62	97
Mean ± SE	3.17 ± 0.59	0.037 ± 0.005	2.18 ± 0.29	4.15 ± 0.34	87 ± 5
A. jaegerianus (1997)	5.60	0.058	3.23	4.79	97
	4.25	0.056	3.31	4.82	76
	4.91	0.051	2.55	4.40	96
	5.05	0.053	2.61	4.82	95
	4.17	0.035	1.99	4.50	121
	9.57	0.085	4.20	4.10	112
	8.21	0.079	4.19	4.40	104
	8.32	0.074	3.95	4.50	113
	9.14	0.084	4.89	4.30	109
Mean ± SE	6.58 ± 1.10	0.064 ± 0.007	3.40 ± 0.80	4.50 ± 0.24	103 ± 13
A. lentiginosus var. *fremontii*	22.4	0.316	10.9	3.35	71
	17.0	0.218	8.8	3.83	78
	13.4	0.173	7.3	3.99	78
Mean ± SE	17.6 ± 2.6	0.236 ± 0.042	9.0 ± 1.0	3.72 ± 0.13	76 ± 3

even though leaves appeared to be fresh and turgid during morning readings, and, during 1997, flowers and fruits were observed on those plants, usually a sign of good water status.

Analyses of $\delta^{15}N$ clearly indicated that *A. jaegerianus* is an active nitrogen fixer. Mean $\delta^{15}N$ for leaf tissue of this species was 0.6 ‰ for leaves as compared with 2.9 ‰ for leaves of *Ambrosia dumosa,* the nonfixing control plant from the same microhabitat (Table 2). Soil nitrogen below the canopies of paired *Astragalus* and *Ambrosia* had a $\delta^{15}N$ of 2.7 ‰, virtually identical to the values of *Ambrosia* tissue. These values, used together with the $\delta^{15}N$ of *Dalea mollissima* grown in a nitrogen-free medium, provide an estimate that 43% of the nitrogen in samples of *A. jaegerianus* was fixed from the atmosphere. Also an indicator of nitrogen fixation, mean nitrogen content of leaflets of *A. jaegerianus* was 2.93%, substantially higher than in leaves of *Ambrosia dumosa* (1.81%) and nearly 50 times higher than the soil.

DISCUSSION

Before this study was undertaken, one might have hypothesized that a desert hemicryptophyte like *A. jaegerianus,* growing within shrub canopies, uses a nurse shrub to avoid high solar radiation (Valiente-Banuet and Ezcurra 1991; Silverton and Wilson 1994). In contradiction to this hypothesis, we found that this legume does not reach light compensation until 250 μmol m^{-2} s^{-1} and requires at least two-thirds full sun to reach light saturation and its highest net photosynthetic rates. Such data support an interpretation that the nurse shrub acts as a trellis, to position the upper shoots in rela-

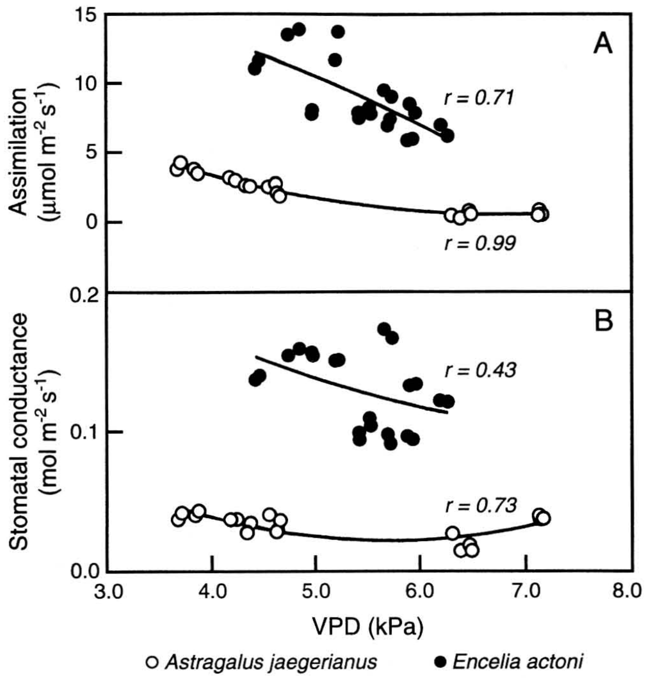

Fig. 2. Assimilation (A, µmol m^{-2} s^{-1}) and stomatal conductance to water vapor (B, mol m^{-2} s^{-1}) versus vapor pressure deficit (VPD, kPa) of *Astragalus jaegerianus* (n=2) and a neighboring shrub of *Encelia actoni* (n=2), measured at the Fort Irwin study site on 12 May, 1994.

tively high PFD, i.e., a light-harvesting strategy. Leaf and stem anatomy fit the typical characters of desert adaptations to high irradiance (Gibson 1996), not those of shade-adapted plants. It would be worthwhile to model PFD penetration into canopies of different species of desert shrubs, to determine which design permits highest PFD interception by milkvetch leaves while providing a strong branching network for shoot support. A revegetation program could use such information to improve establishment of new *Astragalus* plants. In this regard, the nearly aphyllous *Thamnosma montana,* which has nonsucculent stems as the chief photosynthetic organ, is an excellent candidate to serve as a nurse shrub.

Astragalus jaegerianus appears to be a desert species that achieves its maximum photosynthetic rate and stomatal conductance during early spring, when the air temperature and VPD are both low. Maximum assimilation and stomatal conductance declined sharply for all species with increases in air temperature and leaf-to-air VPD. However, increases in air temperature and leaf-to-air VPD resulted in increases in intrinsic WUE. A consequence of these characters would be to limit the growth season of *A. jaegerianus* to spring weeks when soil moisture, air temperature, and leaf-to-air VPD are not limiting for growth.

Nurse plants appear to play a variety of critical roles in the development and survival of the protected plant species (Turner et al. 1966; Nabham 1987). To date, clear examples of nurse plants of North American deserts have been described mostly between a nonsucculent perennial nurse plant and its succulent protégé (Nobel 1980; Vandermeer 1980; McAuliffe 1984*a,* 1984*b*; Franco and Nobel 1988, 1989; Cody 1993). In such cases, beneath the canopy of a nurse plant a protégé avoids extreme air temperatures and experiences different soil water potentials and nutrient levels than the same plant growing in an adjacent exposed site; however, the consequence is that growth rate of the protégé is substantially reduced due to shading by the nurse plant, i.e., substantially lower PFD (Franco and Nobel 1988, 1989). Many of these studies have also suggested that herbivore protection is another benefit from a nurse plant.

Table 2. Comparison of $\delta^{15}N$ (‰) and nitrogen content (%) in leaf tissues of a nitrogen-fixing legume, *Astragalus jaegerianus,* and a control nurse plant *Ambrosia dumosa,* which does not fix nitrogen, and soil collected beneath the canopy of the nurse plant at the Fort Irwin National Training Center on 12 May, 1994. Mean and standard error is given.

	Astragalus	*Ambrosia*	Soil
$\delta^{15}N$	0.6 ± 0.4	2.9 ± 0.3	2.7 ± 0.6
Nitrogen content (%)	2.93 ± 0.10	1.81 ± 0.20	0.06 ± 0.01

Several methods in this study indicated that *A. jaegerianus,* is, like other species of *Astragalus,* a nitrogen fixer (Allen and Allen 1981; Schulman, Lewis, Tipping and Bordeleau 1988). The value measured is similar to estimates of nitrogen fixation in *A. coquimbensis* (Hook. and Arnott) Reiche, a widespread herbaceous species of the Atacama Desert in northern Chile (Evans and Ehleringer 1994) and within the range of relative fixation for nitrogen-fixing legumes at sites in the Sonoran Desert of California and Baja California, Mexico (Shearer et al. 1983).

Leaves of leguminous species that have augmented levels of nitrogen are in another respect a liability, because they may be preferred food for herbivores cueing on nitrogen-rich plants (Lindroth 1989), and thus vegetatively impact plant production and reproductive output. Whereas *A. jaegerianus* rarely has been found in the open, such open sites would be unprotected from lagomorphs and rodents, which are likely excluded from foraging within highly branched shrub canopies. Studies of *Polygala desertorum* Brandeg. in the Sonoran Desert of northern Baja California have shown that this species thrives only when growing in cactus or shrub canopies, where it cannot readily be eaten by vertebrate herbivores (Meehan et al. 1977). The occurrence of *A. jaegerianus* within canopies of desert shrubs is possibly a case of mutualism, wherein the herbaceous legume can use a relatively leafless upper canopy as trellis-like support to avoid herbivory and intercept high irradiance, thereby to maximize photosynthesis, and the nurse shrub could be benefitting from higher soil nitrogen, from litter and roots of the nitrogen fixer, and hence improved growth (Franco and Nobel 1989). This very rare species probably is not a good model for testing, but among the highly specialized taxa of *Astragalus* in California there likely are other cases where these herbs use nurse plants, and there the hypothesis could be tested.

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