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COMPARATIVE ECOLOGY OF *SARCOBATUS BAILEYI* AND *SARCOBATUS VERMICULATUS* IN EASTERN CALIFORNIA

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ABSTRACT.—Greasewood (*Sarcobatus*) is a succulent-leaved, halophytic shrub of North American origin. The genus comprises 2 species: *Sarcobatus baileyi* and *Sarcobatus vermiculatus*. *Sarcobatus vermiculatus* is common throughout much of western North America, but *S. baileyi* is much more limited in distribution and was previously thought to be endemic to Nevada. Here we document and describe a *S. baileyi* population in eastern California, comparing its morphology and ecology to an adjacent *S. vermiculatus* population. Morphologically, *S. baileyi* is smaller in stature but produces larger seeds; however, fewer *S. baileyi* seeds germinated and survived a 20-day laboratory incubation compared to seeds of *S. vermiculatus*. *Sarcobatus baileyi* has higher leaf Na concentrations and operates at much lower plant water potentials than *S. vermiculatus* under field conditions; however, no significant differences were observed between the 2 species in long-term water-use efficiency as measured by leaf $\delta^{13}\text{C}$. Leaf Na concentrations were very low in both species. Overall, these species differ greatly in a number of traits that are consistent with the upland, nonphreatophytic character of *S. baileyi*, which is in stark contrast to the phreatophytic character of *S. vermiculatus*. Both species, however, are very salt tolerant and have low leaf N concentrations, indicating the low nutrient availability and the potentially high salinity of their extreme habitats. Further investigation of comparable desert ridge environments should be conducted to determine the extent of *S. baileyi* in eastern California, and common garden comparisons of the 2 species should be conducted to compare their ecophysiological traits.

RESUMEN.—El "greasewood" (*Sarcobatus*) es un arbusto halofítico de origen norteamericano con hojas suculentas. El género consta de dos especies: *Sarcobatus baileyi* y *Sarcobatus vermiculatus*. Aunque *S. vermiculatus* es común en gran parte del oeste de Norteamérica, *S. baileyi* tiene una distribución mucho más limitada. Se pensaba anteriormente que *S. baileyi* era endémico a Nevada, pero aquí documentamos y describimos una población en el este de California, comparando su morfología y ecología con las de una población adyacente de *S. vermiculatus*. Morfológicamente, *S. baileyi* es más pequeña de altura, pero produce semillas más grandes. Sin embargo, menos semillas de *S. baileyi* germinaron y sobrevivieron a una incubación en laboratorio de 20 días, comparado con *S. vermiculatus*. *Sarcobatus baileyi* opera con potenciales de agua mucho más bajos que los de *S. vermiculatus* en condiciones de campo y tiene mayores concentraciones de Na en sus hojas. No obstante, no se observaron diferencias significativas en la eficiencia del uso de agua a largo plazo, medida en términos de $\delta^{13}\text{C}$ entre las 2 especies. Las concentraciones de N en las hojas fueron muy bajas en ambas especies. En general, estas especies difieren mucho en varios rasgos que son consistentes con el carácter no freatófito de *S. baileyi* de tierras altas, el cual contrasta claramente con el carácter freatófito de *S. vermiculatus*. Ambas especies, sin embargo, son bastante tolerantes a la sal y tienen concentraciones bajas de N en hojas, lo cual indica la baja disponibilidad de nutrientes y la potencial alta salinidad en sus hábitats extremos. Investigaciones adicionales en ambientes comparables de bordes desérticos deberán llevarse a cabo para determinar la extensión *S. baileyi* en el este de California, además de comparaciones de las dos especies en jardín para comparar sus rasgos ecofisiológicos.

Greasewood (*Sarcobatus* Nees.) is a salt-tolerant, monoecious shrub of North American origin. Traditionally classified within the Chenopodiaceae, more recently it has been recognized as the sole genus within Sarcobataceae (Behnke 1997). The genus *Sarcobatus* is composed of 2 species: *Sarcobatus baileyi* Coville and *Sarcobatus vermiculatus* (Hooker) Torrey. Although early taxonomic accounts describe *S. baileyi* as restricted to Esmeralda and Nye Counties in Nevada and Mono and Inyo Counties in California (Coville 1893), more recent accounts consider

S. baileyi to be endemic to Nevada (Sanderson et al. 1999, Hils et al. 2004). Recently, 2 separate populations in Mono and Inyo Counties, California (M. Hils personal communication), one of which is described in this manuscript, have been identified. Unlike the limited distribution of *S. baileyi*, *S. vermiculatus* is common and wide-spread throughout much of western North America, where its range spans from western Canada to northern Mexico and from the Great Plains to California (Hickman et al. 1993).

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Based on taxonomic descriptions and field observations, *S. baileyi* and *S. vermiculatus* differ in both morphology and ecology. Typically, *S. baileyi* shrubs have a shorter stature than *S. vermiculatus* shrubs (5–10 dm versus 5–21 dm; Hils et al. 2004), and branches of *S. baileyi* are composed of short shoots arising from cushion-like pads, with the branch architecture forming an overall rounded appearance (Hils et al. 2004). The leaves of *S. baileyi* are grayish-green, and the flowers produce larger fruits with wider wings than do the flowers of *S. vermiculatus* (Hils et al. 2004). Rooting depth also differs between the species, with *S. baileyi* being more shallowly rooted than the phreatophytic *S. vermiculatus*. This morphological difference should translate into significant differences in the species' water relations. The ecological breadth of these species also differs. *Sarcobatus baileyi* has been documented only at elevations above 1200 m asl, typically in monoculture or in association with *Atriplex confertifolia*, whereas *S. vermiculatus* may be found at elevations as low as 100 m asl in saline lowlands, in dune systems, and around playas (Sanderson et al. 1999). Although *S. vermiculatus* often is the dominant shrub in more-saline areas, it can be codominant with other salt-tolerant shrub species including *Allenrolfea occidentalis*, *Atriplex confertifolia*, *Atriplex lentiformis*, and *Atriplex parryi* (Blank et al. 1998, James et al. 2005). In less saline areas, *S. vermiculatus* can be found in association with *Artemisia tridentata*, *Chrysothamnus nauseosus*, *Tetradymia tetrameres*, and *Tetradymia glabra* (Toft and Elliott-Fisk 2002, Aanderud et al. 2008). We know of no common garden or reciprocal transplant experiments comparing *S. baileyi* and *S. vermiculatus*. Moreover, there are no detailed comparisons of the species where they are growing in adjacent populations. While some differences in species traits may be due to site conditions, comparisons of adjacent populations will be useful for developing hypotheses regarding genetically versus phenotypically based ecological differences between the species.

In the Coso Mountains south of the Owens (dry) Lake playa, California, we documented stands of *S. baileyi*. In subsequent forays, we collected data on community characteristics and individual shrub traits. Our goal in this research was to compare multiple traits of *S. baileyi* and *S. vermiculatus* growing in adjacent populations

to illustrate ecological differences between the 2 species.

STUDY SITE

The *S. baileyi* community and individual shrubs were sampled on a broad upland ridge in the Coso Mountains, Inyo County, California, just south of Owens (dry) Lake (36.3°N, 117.9°W, 1225 ± 20 m elevation asl). This population is representative of the *S. baileyi*-dominated communities prevalent across the northern Coso Mountains. The closest *S. vermiculatus* shrubs were sampled from a wash (1150 ± 20 m elevation asl) just below the *S. baileyi* site. *S. vermiculatus* is a dominant shrub in the washes and lower bajadas of the northern Coso Mountains, as well as all around the margins of Owens (dry) Lake and in the Owens Valley (Manning 1997, Elmore et al. 2003).

METHODS

Community Assessment

During June 2009, all shrubs in an area totaling 250 m² at the *S. baileyi* study site were identified to species. Their reproductive status was noted and canopy volume measured (height and 2 perpendicular diameters). Cover was calculated as the sum of elliptical canopy areas divided by total ground area. Canopy volumes were calculated as ellipsoids. The natural logarithm of canopy volume was used, as this value is proportional to shrub biomass within species (Messina et al. 2002, Snyder et al. 2004).

Physiological Measurements

Within the adjacent populations of *S. baileyi* and *S. vermiculatus*, stem xylem pressure potentials were measured for branched leafy stems (approximately 10 cm; one sample each for 3–4 shrubs per species) with a pressure chamber (PMS Instrument Company, Corvallis, OR) at late afternoon, predawn, and midday on 17–18 June 2009. We followed rigorous field procedures, including prebagging stems before cutting and immediate reading to minimize errors (Turner 1988, Boyer 1995). Air temperatures at the time of sampling were 31 °C, 18 °C, and 28 °C with clear skies and very light breeze conditions.

Leaf samples (two 5-g samples each from 4 shrubs per species) were rinsed with distilled water to remove surface salts and air-dried in the field. In the lab they were oven-dried and finely

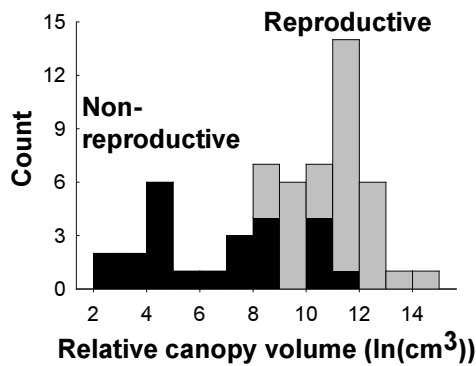


Fig. 1. Size structure and reproductive status of a population of *Sarcobatus baileyi* on a broad upland ridge in the Coso Mountains, Inyo County, California, in June 2009. Data from all shrubs within a 250-m² area ($n = 24$ for nonreproductive and $n = 33$ for reproductive shrubs). Natural log of canopy volume is correlated with shrub biomass. Black bars represent nonreproductive shrub frequency, and gray bars represent reproductive shrub frequency.

ground before analyses. Stable isotope composition and C and N content were determined using an elemental analyzer and isotope ratio mass spectrometer at the U.C. Davis Stable Isotope Facility (<http://stableisotopefacility.ucdavis.edu>). C isotope composition ($\delta^{13}\text{C}$) is given relative to the PeeDee Belemnite standard, and N isotope composition ($\delta^{15}\text{N}$) is given relative to atmospheric N_2 . Total leaf ash content was determined after dry-ashing at 550 °C. Na was determined on resuspended ash samples using atomic emission spectroscopy with a KCl matrix. Standards contained NaCl in a KCl matrix.

Fruit Collection and Measurement

During October 2006, we collected fruit from 10 randomly selected shrubs of *S. baileyi* and *S. vermiculatus* and composited them for each species. Fruit wingspan, length, and mass were measured on a subsample of 100 seeds for each species. In November 2007, fewer shrubs with fruit were available, particularly for *S. baileyi* (many had dispersed by wind at the time of sampling). In 2007, we collected fruit from 4 individuals of each species, keeping each collection separate. We measured the same variables as in 2006, as well as the percent of filled fruit and germinability. Fruits from each shrub were measured as subsamples, and the average of the subsamples was compared between shrub species. For the germinability studies, we plated

seeds from each shrub individual separately. Depending on the number of filled seeds available per shrub, 2–10 seeds were placed in petri dishes on filter paper moistened with one-tenth strength modified Hoagland's solution (Epstein and Bloom 2005). Since filled seed number varied between shrubs, 1–4 petri plates were monitored per individual. A total of 100 seeds per shrub species were plated. We sealed the plates with parafilm to prevent desiccation and placed them on a table in the John Carroll greenhouse. We checked plates daily for 20 days and recorded germination and survivorship.

Statistics

For all variables, following tests for normality and homogeneity of variance, population differences between the species were determined with t tests. If the assumptions were not met, we used a Mann–Whitney rank sum test. We analyzed data using SAS for Windows (SAS 2001).

RESULTS

Community Assessment

The sampled upland desert shrub community where *Sarcobatus baileyi* dominates in the Coso Mountains had total plant cover ranging from 6.4% to 9.9%, and of this cover, *S. baileyi* represented 85%–92%. Subdominants in the community were *Suaeda moquinii* and *Atriplex confertifolia* (5%–8% and 1%–4% of the total cover, respectively). Other shrubs (*Atriplex parryi*, *Chrysothamnus nauseosus*, and an unknown species) were very minor components ($\leq 1\%$ of the total cover) of this community. Some nearby *S. baileyi*-dominated communities were observed with a much greater importance of *A. parryi*, however. Common short-lived annuals observed in the community in mid-June 2009 included *Chaenactis douglasii*, *Cleomella obtusifolia*, and *Endolepis covillei*.

Reproductive *S. baileyi* individuals ($n = 33$) had a median $\ln(\text{canopy volume cm}^3)$ of 11.5 while nonreproductive plants ($n = 24$) were approximately half as large, with a median $\ln(\text{canopy volume cm}^3)$ of 6.6 (Mann–Whitney rank sum test, $U = 738$, $P < 0.001$) (Fig. 1). In contrast to *S. baileyi*, the *S. vermiculatus* individuals in the adjacent population were much larger, with a median $\ln(\text{canopy volume cm}^3)$ of 15.8, a size typical of this species. These large differences in canopy volume (i.e., relative biomass) between the 2 species resulted from large differences in

TABLE 1. Leaf C and N content, C:N ratio, and stable isotope composition of leaves of *Sarcobatus baileyi* and *Sarcobatus vermiculatus* in the Coso Mountains, Inyo County, California on 18 June 2009. Values are means (SE; $n = 4$), and significant differences between the 2 species' populations are indicated with boldface type.

Trait	<i>S. baileyi</i>	<i>S. vermiculatus</i>	<i>t</i>	<i>P</i>
Leaf C content (%)	33.4 (0.53)	35.5 (0.60)	2.66	0.04
Leaf N content (%)	1.09 (0.15)	1.24 (0.15)	0.73	0.5
C:N mass ratio	33.0 (5.6)	29.9 (3.5)	0.46	0.66
$\delta^{13}\text{C}$ (‰)	-23.3 (0.31)–24.2 (0.34)	1.83	0.12	
$\delta^{15}\text{N}$ (‰)	2.64 (0.16) 4.16 (0.61)	2.41 0.05		

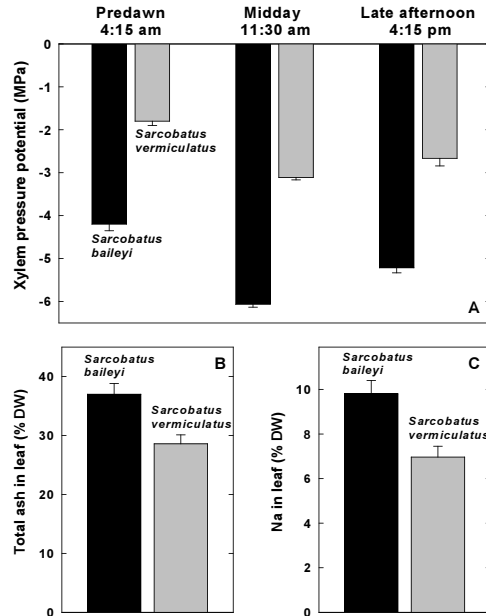


Fig. 2. Diurnal xylem pressure potentials (A), leaf ash (B), and leaf Na concentrations (C) of *Sarcobatus baileyi* and *S. vermiculatus* plants in adjacent populations in the Coso Mountains, Inyo County, California, on 17–18 June 2009. The *S. baileyi* population was on a broad ridge just above the wash population of *S. vermiculatus*. Average solar time is given for each pair of measurements. Values are means with standard errors, $n = 3-4$ (xylem pressure potentials) or $n = 4$ (leaf ash and Na).

both height and diameter. Comparing reproductive shrubs only, median height and diameter were 33 cm and 72 cm, respectively, for *S. baileyi* and 140 cm and 267 cm for *S. vermiculatus*.

Physiological Measurements

The 2 species differed significantly in stem water potential when measured at predawn, mid-day, and afternoon (t tests: all $t > 12$, $P < 0.001$; Fig. 2A). The water potential of *S. baileyi* was consistently 2-fold more negative than that of *S. vermiculatus*. Leaf ash (t test: $t = 3.56$,

$P = 0.012$; Fig. 2B) and Na concentration (t test: $t = 3.67$, $P = 0.010$; Fig. 2C) were greater in *S. baileyi* than in *S. vermiculatus*, but leaf C was significantly lower in *S. baileyi* (Table 1). Leaf N, C:N ratio, $\delta^{13}\text{C}$ (Table 1), and Na as a percent of ash weight (overall mean = 25.5%, SE = 1.1%) were not significantly different between the 2 species. Leaf $\delta^{15}\text{N}$, however, was 1.6-fold greater in *S. vermiculatus* than in *S. baileyi* (Table 1).

Seed Traits and Seed Germination

Wingspan did not differ between the 2 populations in 2006, but in 2007, wingspan was approximately 1.6-fold greater in *S. baileyi* than in *S. vermiculatus* (Table 2). Fruit length and mass were approximately 2-fold greater for *S. baileyi* fruit than for *S. vermiculatus* fruit in both 2006 and 2007 (Table 2). There was a trend for a lower percentage of filled seeds in *S. baileyi*, but this trend was not significant (Table 2). Fewer filled *S. baileyi* seeds germinated and fewer *S. baileyi* seedlings survived the 20-day greenhouse incubation period compared to seeds of *S. vermiculatus* (Table 2).

DISCUSSION

The population size structure of *S. baileyi* indicates multiple recruitment events and suggests a minimum canopy size before plants become reproductive (Fig. 1). Seedlings of *S. baileyi* were observed in the field population in mid-June 2009, following a relatively moist, cool spring. Although these particular seedlings may not have survived the summer, observations of many small individuals in the population suggest that at least occasional recruitment of *S. baileyi* is occurring in this population. However, if we compare *S. baileyi* and *S. vermiculatus* seeds from 2007, fewer *S. baileyi* seeds were filled, and the filled seeds were less likely to germinate and had lower survivorship under greenhouse conditions. Together, these traits suggest potentially

TABLE 2. Seed traits for *Sarcobatus baileyi* and *Sarcobatus vermiculatus* from the Coso Mountains, Inyo County, California in 2006 and 2007. In 2006, 100 seeds from a total of 10 shrubs were measured. In 2007, seeds were collected from 4 shrubs; seeds from each shrub were measured as subsamples, and the average of the subsamples was compared between shrubs. Data are means (SE), and significant differences among the populations are indicated in boldface type.

Trait	<i>S. baileyi</i>	<i>S. vermiculatus</i>	<i>t</i>	<i>P</i>
2006 (<i>n</i> = 100 seeds)				
Wing span (mm)	10.7 (0.2)	11.4 (0.2)	-2.88	1.0
Fruit length (mm)	7.4 (0.1)	4.6 (0.1)	21.14	<0.0001
Fruit mass (mg)	5.8 (0.2)	2.5 (0.1)	18.43	<0.0001
2007 (<i>n</i> = 4 shrubs)				
Wing span (mm)	9.3 (0.3)	5.6 (0.8)	4.46	0.0022
Fruit length (mm)	6.2 (0.2)	3.5 (0.2)	8.62	<0.0001
Fruit mass (mg)	4.3 (0.3)	2.2 (0.2)	6.87	0.0002
Filled seed (%)	19.3 (11.7)	48.2 (13.6)	-1.61	0.15
Germination (%)	66.7 (10.2)	95.6 (1.9)	-2.801	0.03
Survivorship (%)	27.9 (12.0)	73.2 (6.7)	-3.284	0.01

lower fitness in the *S. baileyi* population than in the nearby *S. vermiculatus* population. We know from work in the Mono Basin (approximately 240 km away) that N limitation can influence seed fill in *S. vermiculatus* (Drenovsky and Richards 2005). Additionally, work at the Owens (dry) Lake playa indicates that water and nutrient limitations influence seed germinability, as well as seed and seedling quality in *S. vermiculatus* (Breen and Richards 2008). The very low leaf N concentrations observed in *S. baileyi* are indicative of N limitation at this site, which likely has ramifications for seed production and seed fill in this species. However, greenhouse work suggests that the quality of the seedling environment may have a greater influence than seed traits on seedling germination and survivorship (Breen and Richards 2008). Therefore, annual variability in environmental conditions may have a large influence on seedling survivorship. Higher rainfall years, such as 2009, promote greater germination and potentially support higher survivorship.

Sarcobatus baileyi shrubs had a full complement of green, succulent leaves and maturing fruits, despite midday xylem pressure potentials averaging less than -6.1 MPa. The large difference between predawn and midday xylem pressure potentials, as well as the late-afternoon recovery, indicates that stomata were open and that plants were actively transpiring and photosynthesizing, despite these very low xylem pressure potentials. *Sarcobatus baileyi* was operating at much more negative water potentials than *S. vermiculatus*, which had xylem pressure potentials more than 2.6 MPa higher (less negative) throughout the diurnal cycle. Greater leaf Na concentration in *S. baileyi*

compared to *S. vermiculatus* is consistent with the lower plant water potentials in *S. baileyi*. Higher leaf Na also would yield leaves with greater leaf ash content and lower C content in *S. baileyi* compared to *S. vermiculatus*, as we observed. However, despite approximately 40% higher Na content and much lower xylem pressure potentials in *S. baileyi*, there was no difference in $\delta^{13}\text{C}$ between the species, suggesting that the 2 species were operating at approximately the same water-use efficiency. Nevertheless, a larger sample size may have allowed us to detect a difference between the species for this variable. We did observe differences in leaf $\delta^{15}\text{N}$ between the species, which may suggest different N sources, different biocycling of N, or different magnitudes of nitrate reduction between the species (Evans 2001).

Overall, these species differ greatly in a number of variables that are consistent with the upland, nonphreatophytic character of *S. baileyi*, a stark contrast to the phreatophytic character of *S. vermiculatus*. Both species, however, are very salt tolerant and have extremely low leaf N concentrations, indicating the low nutrient availability and potential high salinity of their extreme habitats. It appears that *S. baileyi* accumulates Na early in the growing season (approximately 10% by mid-June). This accumulation contributes to a low osmotic potential, helping *S. baileyi* to operate at very low plant water potentials and acquire necessary water from dry upland soils. Leaf Na concentrations nearly as high as 10% have been reported for *S. vermiculatus*, but these levels were not reached until much later in the summer, and water potentials as low as recorded

here for *S. baileyi* have not been recorded for *S. vermiculatus* (Donovan et al. 1996).

Our documentation of the *S. baileyi* population supports early taxonomic accounts of its distribution in eastern California. Other populations likely exist in similar ridge habitats in Inyo and Mono counties. Further exploration of other mountains near the Coso Range, such as the Inyo and Panamint mountains as well as the Death Valley area, should be conducted to determine the extent of *S. baileyi* in eastern California. Additionally, common garden or reciprocal transplant experiments should be carried out to determine the relative importance of genetic versus environmental variation on phenotypic variability in these 2 species.

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