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COMMUNITY STRUCTURE AND DEMOGRAPHY IN A SALINE PAN-DUNE MOSAIC IN THE WESTERN MOJAVE DESERT

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ABSTRACT

A unique saline ecological system formed by an extensive mosaic of small clay pans and low stable dunes exists within Edwards Air Force Base in the western Mojave Desert of California. This ecosystem lies between the large Rosamond and Rogers dry lakes on the old Pleistocene lakebed of Lake Thompson. Plant communities on the low and relatively stable dunes were broadly classed as saltbush scrub, with a total canopy cover of 30–36%. *Atriplex confertifolia* was the typical dominant, with *Ericameria nauseosa* as an important associate. Taller dunes of younger age and less saline soils had similar plant cover, but a distinct plant community with *Atriplex canescens* and *Krascheninnikovia lanata* as dominants and *Yucca brevifolia* as a common associate. Flat areas adjacent to the dunes were dominated by a virtual monoculture of *Atriplex confertifolia*. Aboveground shrub and bunchgrass biomass including dead material varied from 503 to 1204 kg ha^{-1}, low in comparison to similar plant communities in the Great Basin. The absence of small saplings and seedlings of many shrub species suggests successful establishment is highly episodic. Seedlings were abundant only in *Isocoma acradenia*.

Key words: *Atriplex*, Edwards Air Force Base, dune, Lake Thompson, salt pan, saltbush scrub.

INTRODUCTION

While most desert soils are only mildly alkaline, markedly saline habitats are widespread although scattered and local in occurrence throughout the Great Basin and, less frequently, in the Mojave Desert and western Sonoran Desert. These saline areas are typically associated with dry playa lakes and topographic sinks, as well as the flood plains of the Mojave, Amargosa and Colorado rivers. Poor drainage and subsequent evaporation rather than elevation are the key elements accounting for the presence of these saline habitats (West 1983; Caldwell 1985). Although more typical of the Great Basin, unique but poorly described saline habitats can be seen in the Antelope Valley located in the western margin of the Mojave Desert in Los Angeles and Kern counties of southern California. These unusual habitats have a significant conservation value because of the presence of a number of rare, threatened and/or endangered plant and animal species (EAFB 2008).

A major area of relatively undisturbed saltbush scrub communities can be found on Edwards Air Force Base (EAFB) in the Antelope Valley. The valley is a closed endorheic basin which was the site of the large Pleistocene Lake Thompson (Charlton and Rundel 2017). Surface-water runoff in most of the basin ultimately terminates in topographical depressions, most notably Rogers and Rosamond Dry Lakes. These lie entirely within the boundaries of EAFB, with the larger Rogers Dry Lake having a long history of aviation use ranging from the development of special aircraft for the U.S. Air Force to its service as a recovery site for early Space Shuttle landings.

The two large playas and associated salt pan and dune ecosystems cover over 20,000 ha, which is 16% of the total area of EAFB (Lichvar and Sprecher 1996; Lichvar et al. 2004*b*). The greatest portion of this area is comprised of Rogers Dry Lake (11,453 ha), Rosamond Dry Lake (5589 ha), Buckhorn Dry Lake (739 ha) and playa complexes north and northeast of Buckhorn Dry Lake (690 ha). In addition, however, there is a unique ecological system formed by a mosaic of small clay pans and low stable dunes lying on the old Pleistocene lakebed between Rosamond and Rogers dry lakes. A total of 2732 such pans were delineated in a survey, ranging in size from 0.005 ha to 124 ha in size. The mean size of these small clay pans was only 0.48 ha, and most pans fell in the 0.01–1.0 ha size class (Lichvar and Sprecher 1996).

Our broad objectives in this study were to provide baseline ecological data relevant to the resource management of this unusual geomorphic pan-dune ecosystem on EAFB. The fragility of this ecosystem was of paramount concern to the resource management of the base as it includes listed rare and endangered species (EAFB 2008) as well as extensive ground cover of environmentally significant but fragile biotic crusts (Brostoff et al. 2005). Our studies in this paper focus on plant processes and plant/soil relationships, with quantitative data relevant to plant community structure, plant productivity and biomass, and the interrelationships between soil chemistry and structure and microhabitat distributions of dominant plant species.

MATERIALS AND METHODS

Study Site

Rogers and Rosamond dry lakes and the smaller playas and numerous clay pans are situated at an elevation of 700 m, just above the old Lake Thompson lakebed, in an area of low shifting sand dunes (34°50′N, 117°55′W). The small dunes of the pan-dune system are comprised of windblown sands interbedded with fine silts from the lakebeds. Small clay pans develop in the interdune areas where the fine texture and compacted surfaces provide ponding of winter rains and increased deposition of fine evaporates (Orme 2008). Patterns of differential establishment of microbial crusts and vascular plants on dune, flats and pan soils help to reinforce sharp vegetation zonation around clay pans. Nevertheless, there is strong evidence that this geomorphic surface is a dynamic one rather than representing a paleo-landscape of the old Lake Thompson lakebed (Lichvar et al. 2004*b*; Orme 2008).

An area within the pan-dune complex between Rogers and Rosamond dry lakes was the focus for our study. This pan-dune study site was located about 1 km west of Lancaster Boulevard and 2.5 km north of Branch Memorial Park (or about 5 km north and slightly west of the South Entrance Gate to EAFB). A study plot of 0.25 km^2 was laid out in a natural area having small and medium-sized pans, flats with little topography, washes, low and relatively stable sand dunes, and younger dunes of moderate height. This site was selected after extensive field reconnaissance as being representative of the range of habitat types existing over the broader pan-dune ecosystem. The majority of larger pans held water in the spring of 1996 when field studies began and intermittently after that time. The northwest and southeast ends of the plot included moderately large dunes, while the central area consisted primarily of low dunes overlaying clay soils (Orme 2008). Human impacts occurred through the area in the latter half of the 19^{th} century as the area within the current base boundaries was used for crops, grazing and transportation corridors for wagon trains heading northward across the valley. As the later part of the century arrived, so did many settlers raising livestock (EAFB 2008). The site shows very few signs of recent anthropogenic disturbance as it is in a military restricted access area and at least 200 m from the nearest unimproved road. The site was likely subject to cattle grazing as recently as the 1940's.

Within the primary study site located in an area of low topography near Buckhorn Dry Lake, we chose small areas for intensive study. Five areas were used for soil surveys, selected for differences in topography and structure. Two of these, low-lying flat areas adjacent to small clay pans, were termed Flat 1 and Flat 2. These were relatively small areas with sparse vegetation cover. These were characterized for soil characteristics as part of a broader study of the pan-dune system which is described in a companion paper on phenology and plant water relations (Sharifi et al. 2017). Vegetation sampling was concentrated at three other nearby habitat types. Two low dunes, relatively stable and presenting no more than 2–3 m of topography above the surrounding flats and pans, were designated Dune 1 and Dune 2. A large dune of wind-blown sand at the northwestern margin of the plot was termed Dune 3. This dune, with a sandy structure suggesting a young age and aeolian movement of sediments, showed distinctive plant cover that differed sharply from that on the lower dunes. A flat area immediately to the southeast of Dune 3 with scattered vegetation was termed Flat 3. The southeastern margin of this area was bounded by a shallow wash used for limited vegetation sampling.

The climate of the pan-dune ecosystem within EAFB is typical of the western Mojave Desert with a precipitation regime dominated by winter precipitation (Rundel and Gibson 1996). Cyclonic winter storms bring the majority of precipitation, with 80% falling from November through March. A summer weakening of the subtropical high pressure center of the eastern Pacific, however, can occasionally allow low pressure systems from the Gulf of Mexico or tropical storms from the subtropical Pacific Ocean to penetrate and bring August or September rains. Mean annual precipitation at Rogers Dry Lake was 125 mm for the period 1944–2003 (EAFB 2008; Charlton and Rundel 2017). Precipitation at the study site during 1996 was 200 mm, well above mean amounts over the historical record. Seasonal temperature variation is high, with mean summer high temperatures of 36°C, but record extremes up to 45°C. Winter lows at night average −1°C, but record lows are −15°C.

Soil Physical and Chemical Characteristics

We made a preliminary survey to characterize the physical and chemical characteristics of soils at the study site. Soils in the study area have broadly been mapped by Benedict et al. (1988) in the context of a USDA Soil Conservation Service mapping survey. Soil samples, consisting of subsampled portions of the <2-mm soil fraction, were collected from 0–30 cm depth, and where possible from 30–60 cm and 60–100 cm depth under shrub canopies and open areas away from shrub canopies in Dune 1, Dune 2, Dune 3 and Flat 3. The data presented are analyses of a composite sample of five separate collection sites for each set of analyses. Soil samples were also collected from a salt pan adjacent to Dune 2. Soils were analyzed for texture (clay, silt and sand fraction), pH, electrical conductivity, sodium content, sodium accumulation ratio (SAR), total carbon, ammonium-nitrogen content, nitrate-nitrogen content and total Kjeldahl nitrogen content using standard laboratory procedures at the Soil Testing Laboratory of the Division of Agriculture and Natural Resources, University of California, Davis (see *http://anlab.ucdavis.edu/methods-of-analysis* for methods).

Community Structure and Demography

We studied demography, canopy structure and community biomass for 18 perennial plant species present within the study pan-dune area, with intensive work on the five most common species (Table 1). These included *Atriplex canescens* (four-wing saltbush), *A. confertifolia* (shadscale) and *A. torreyi* (Torrey's saltbush) in the Chenopodiaceae. These species all exhibit C_4 metabolism (Osmond and Björkman 1980). Also common and studied were *Ericameria nauseosa* subsp. *mohavensis* (rabbitbrush) and *Tetradymia stenolepis* (Mojave cottonthorn) in the Asteraceae. Less intensive studies of coverage and population size structure were carried out with *Acamptopappus sphaerocephalus* (goldenhead, Asteraceae), *Allenrolfea occidentalis* (iodine bush, Chenopodiaceae), *Artemisia spinescens* (bud sage, Asteraceae), *Atriplex parryi* (Parry's saltbush, Chenopodiaceae), *Ephedra nevadensis* (Mormon tea, Ephedraceae), *Forestiera pubescens* (desert olive, Oleaceae), *Isocoma acradenia* (alkali goldenbush, Asteraceae), *Krascheninnikovia lanata* (winterfat, Chenopodiaceae), *Lepidium fremontii* (desert pepperweed, Brassicaceae) and *Yucca brevifolia* (Joshua tree, Agavaceae). All plant names and family classification follow Baldwin et al. (2012).

We sampled the canopy cover of individual shrub and bunchgrass species in four habitats: Dune 1, Dune 2, Dune 3 and

Table 1. Perennial plant species utilized in studies of phenology, demography, and community cover and biomass in the pan-dune ecosystem of Edwards Air Force Base, California. Taxonomy follows Baldwin et al. (2012).

Species	Common name	Life form	Height (m)	Range
Agavaceae				
Yucca brevifolia Engelm.	Joshua tree	C_3 tree	1.0–15	Mojave Desert
Asteraceae				
Acamptopappus sphaerocephalus (Harv. & A. Gray) A. Gray	goldenhead	C_3 shrub	<1.0	Mojave Desert, Arizona
Artemisia spinescens D.C. Eaton	budsage	C_3 shrub	<0.3	widespread
Ericameria nauseosa (Pall. ex Pursh) G.L. Nesom & G.I. Baird	rabbitbrush	C_3 shrub	0.5–2.8	widespread
Isocoma acradenia (Greene) Greene	alkali goldenbush	C_3 shrub	0.5–1.3	Mojave and western Sonoran Desert
Tetradymia stenolepis Greene	Mojave horsebrush	C_3 shrub	0.5–1.2	western Mojave Desert
Brassicaceae				
Lepidium fremontii S. Watson	bush peppergrass	C_3 shrub	0.4–1.0	Mojave Desert
Chenopodiaceae				
Allenrolfea occidentalis (S. Watson) Kuntze	iodine bush	C_3 shrub	0.5–2.0	widespread
Atriplex canescens (Pursh) Nutt.	four-wing saltbush	C_4 shrub	<2.0	widespread
Atriplex confertifolia (Torr. & Frém.) S. Watson	shadscale	C_4 shrub	<1.0	widespread
Atriplex parryi S. Watson	Parry saltbush	C_4 shrub	0.2–0.5	Mojave Desert, Arizona
Atriplex torreyi (S. Watson) S. Watson	Torrey saltbush	C_4 shrub	0.8–3.0	Mojave Desert, Arizona
Krascheninnikovia lanata (Pursh) A. Meeuse & A. Smit	winter fat	C_3 shrub	0.5–1.0	widespread
Ephedraceae				
Ephedra nevadensis S. Watson	Mormon tea	leafless C_3 shrub	0.3–1.5	widespread
Oleaceae				
Forestiera pubescens Nutt.	desert olive	deciduous C_3 shrub	0.5–2.5	widespread
Poaceae				
Stipa hymenoides Roem. & Schult.	Indian ricegrass	perennial C_3 bunchgrass	0.2–0.7	widespread
Distichlis spicata (L.) Greene	saltgrass	C_4 rhizomatous grass	0.1–0.5	widespread
Sporobolus airoides (Torr.) Torr.	alkali sacaton	erect perennial C_3 grass	0.3–2.0	widespread

Flat 3. The Flat 1 and 2 areas were not sampled for species because of a low plant cover. In each of the study areas, four 25-m line transects were sampled, recording canopy interception along that line for all perennial species. Dead shrub canopies were recorded separately. These intercepts were totaled for each species within each of the four habitats, and the species totals summed to provide a measure of total plant canopy cover, both living and dead. No attempt was made to sample plant coverage or density of ephemerals. This cover was generally low, with only moderate diversity in the spring of 1996.

Large sample sizes of canopy diameter (two measurements at right angles to each other), mean maximum height and calculated canopy volume were recorded for each of the dominant shrub species to provide an estimation of population distribution by size class. Canopy volumes were grouped into nine volume classes ranging from <0.002 m^3 at the smallest to 2–5 m^3 and >5 m^3 in the largest volume classes. These samples represented a virtually complete census of all shrubs in the areas of approximately 1 ha for each habitat sampled, but the sample numbers were not designed to represent densities. Canopy measurements were made as follows: *Atriplex confertifolia* (Flat 3, Dune 1), *A. torreyi* (Wash), *Ericameria nauseosa* (Dune 2), *Lepidium fremontii* (Dunes 1 and 2), *Tetradymia stenolepis* (Dune 1), *Acamptopappus sphaerocephalus* (Dune 1) and *Isocoma acradenia* (Wash, Dune 2).

We randomly selected 10–12 individuals of four *Atriplex* species during the early summer of peak growth for biomass analysis. These studies were carried out using four groups of *A. confertifolia* (two on Flat 3, two on Dune 3), *A. canescens* (Dune 3), *A. torreyi* (Wash) and *A. parryi* (mixed sites). After measuring canopy top and bottom diameter and length, 25–100% of the canopy was harvested, depending on canopy size.

Fresh weight of the total harvested biomass was measured promptly in the field. Subsequently, subsamples were placed in double Ziploc bags in a cooler and brought to the lab for fresh weight and oven dry weight measurements. The dried samples were separated into individual components (leaves, shoots, flowers and fruit). We calculated mean values of aboveground dry weight biomass per unit canopy area from these canopies and biomass measurements on individual shrubs. These values were combined with habitat coverage measurements to provide an estimate of aboveground biomass on a stand basis. Because measurements of mean biomass per square meter of canopy cover were not made for all species encountered, we estimated this mean canopy biomass as follows: *Ephedra nevadensis* (Ephedraceae), 0.80 kg ha^{-1}; *Lycium andersonii* A. Gray (Solanaceae), 0.80 kg ha^{-1}; *Sporobolus airoides* (Poaceae), 0.20 kg ha^{-1}; and dead shrub canopies, 0.20 kg ha^{-1}.

Table 2. Physical and chemical characteristics of soil in the pan-dune ecosystem of Edwards Air Force Base, California. UC = under canopy, BC = between canopies; EC = electrical conductivity, Na = sodium, SAR = sodium absorption ratio, C = carbon, NH_4-N = ammonia nitrogen, NO_3-N = nitrate nitrogen, TKN = total Kjeldahl nitrogen.

Location	Habitat	Soil depth cm	Clay %	Sand %	Silt %	pH	EC Mmhos/cm	Na meq/L	SAR	C %	NH_4-N ppm	NO_3-N ppm	TKN %
Dune 1	UC	0–30	1	89	10	8.7	1.84	32.3	25	0.72	1.7	12.6	0.047
	BC	0–30	1	94	5	8.5	0.27	0.8	<1	0.21	0.8	0.6	0.012
Dune 2	BC	0–30	1	78	21	7.9	0.83	2.7	2	0.57	7.5	1.4	0.023
Dune 3	UC	0–30	1	78	21	8.3	2.45	36.4	28	0.75	1.3	18.2	0.041
	BC	0–30	1	73	26	8.7	0.54	1.4	1	0.57	1.5	1.3	0.037
Flat 3	UC	0–30	3	68	29	8.8	1.68	26.3	37	1.11	1.0	4.9	0.038
	BC	0–30	4	67	29	8.7	1.22	21.0	15	1.30	0.9	14.4	0.031
	BC	30–60	7	72	21	8.2	0.49	1.6	2	1.79	0.9	1.9	0.032
	BC	60–100	10	68	22	7.7	11.13	323	65	<0.005	4.7	109.4	0.008
Pan	PAN	0–5	20	40	40	9.1	12.62	418	836	1.14	0.9	8.1	0.014
	PAN	5–30	18	51	31	10	6.04	233	598	0.76	0.4	5.3	0.013

RESULTS

Habitat Soil Characteristics

Soil texture (of the <2 mm fraction) was strongly dominated by sand in all three dune sites. The sand fraction varied from 78 to 94% in Dunes 1 and 2, with a slightly lower mean value ranging from 73 to 78% in the larger Dune 3 (Table 2). The clay fraction was virtually absent from all the dune sites, while silt fractions varied from 5–21% in Dunes 1 and 2 to 21–26% in Dune 3. The surface soils of Flat 3 were similar, but with a slightly higher clay fraction of 3–4%. In all these sites, there was no consistent pattern of soil textural difference under shrub canopies and in open areas. Soil texture in the pan site was distinctly different from that of dune and flat sites, with a clay fraction of 18–20%, and a relatively low sand fraction of 40–51%.

Soil chemical characteristics were found to differ sharply between the dune and flat sites and the pan. Within the dunes and flats, a strong impact of plant canopy on soil chemistry was generally seen. Soil pH was found to be alkaline in all areas sampled. Dune and flat sites had a pH range of 7.7–8.8. In most but not all cases, soil pH was more alkaline in open sites than under shrub canopies (Table 2). Soil pH of the pan was extremely alkaline. We found surface soil pH to be 9.1 and subsoils to have pH 10.0 due to increased calcite content at depth as indicated by CO_3 and HCO_3 values.

The effect of organic matter collection and decomposition under shrub canopies or "fertile islands" (Rundel and Gibson 1996) is evident in analysis data for soil organic carbon, inorganic nitrogen and electrical conductivity. Soil carbon was consistently higher under shrub canopies in all the dune sites, but not in Flat 3. This absence of a shrub canopy effect in Flat 3 suggests that this surface may be frequently flooded and reworked following winter rains. Nitrate nitrogen, although consistently low, was always found to be higher under canopies than in the open on the dunes, but again not in Flat 3. Electrical conductivity (EC) showed the same pattern. EC values were 2–7 times higher under shrub canopies than in the open on-dune sites, but little different under and between canopies on Flat 3. Under-canopy and between-positions on Dune 3 differed from the low Dune 1 in a pattern of higher levels of soil organic carbon, nitrate nitrogen and electrical conductivity values. Smaller differences in sodium concentration and SAR are likely not significant. For the pan, soil carbon and inorganic nitrogen differed little from values on the dunes and flats, but EC values were higher.

Measures of soil salinity showed the strongest differentiation between the pan soils and other sites. The SAR of surface pan soil was 836, nearly 25 times higher than any SAR measured in dunes or flats. The sodium concentration in these surface pan soils was found to be 418 meq L^{-1}, eight times higher than any value found in the dune or flat soils (Table 2).

Plant Community Structure

Dune and pan habitats sampled within the pan-dune study site are broadly characterized as halophytic-phase saltbush scrub but each had a distinctive community structure and composition, although dominated by plants with C_4 metabolism (Table 3). The

Table 3. Canopy cover of individual species within four sample habitats in the pan-dune ecosystem of Edwards Air Force Base, California. All values are in % total ground area covered, based on four 25-m line transects sampled within each habitat.

Species	Dune 1	Dune 2	Dune 3	Flat 3
Acamptopappus sphaerocephalus	1.2	0	0	0
Artemisia spinescens	0.7	0	0	0
Atriplex canescens	0	0	11.3	0
Atriplex confertifolia	6.2	3.2	3.6	14.8
Atriplex torreyi	0	1.8	0	0
Ephedra nevadensis	0.9	0	2.5	0
Ericameria nauseosa	0	9.9	0.8	0
Isocoma acradenia	2.9	1.0	0	0
Krascheninnikovia lanata	0	0	5.9	0
Lepidium fremontii	0	0.5	0	0.8
Lycium andersonii	0	0	0.7	0
Sporobolus airoides	7.3	13.2	0.4	1
Tetradymia stenolepis	0.9	0.4	0.6	0
Total live cover	20.1	30.0	29.4	16.6
Dead shrub canopy	8.4	6.4	9.9	28.4
Total plant cover	28.5	36.4	39.3	45.0

Table 4. Relative frequency (%) of individuals in nine canopy volume classes for important shrub species in the pan-dune ecosystem of Edwards Air Force Base, California.

Habitat	*Acamptopappus sphaerocephalus* Dune 1	*Atriplex confertifolia* Flat 3	*Atriplex confertifolia* Dune 1	*Atriplex torreyi* Wash	*Ericameria nauseosa* Dune 2	*Isocoma acradenia* Wash, Dune 2	*Lepidium fremontii* Dunes 1, 2	*Tetradymia stenolepis* Dune 1
Sample size	22	82	65	100	62	100	25	25
Shrub volume (m^3):								
<0.002	0	0	0	0	0	33	0	0
0.002–0.01	0	9	0	2	0	16	0	0
0.011–0.05	9	20	0	16	15	16	12	0
0.051–0.20	64	34	26	22	16	16	72	4
0.21–0.50	27	16	37	13	21	15	16	20
0.51–1.00	0	13	29	21	18	4	0	28
1.01–2.0	0	5	8	12	15	0	0	36
2.01– 5.0	0	4	0	13	15	0	0	12
>5.0	0	0	0	1	2	0	0	0

dominant species on Dune 1 were the bunchgrass *Sporobolus airoides* (7.3% cover) and *Atriplex confertifolia* (6.2% cover), with *Isocoma acradenia* third in importance (2.9% cover). This community is classified as azonal dune and playa habitat (EAFB 2008), or more broadly as shadscale scrub. Total live cover on this site was 20.1%, with an additional 8.4% cover by dead shrub canopies. Seven perennial species were sampled.

On Dune 2 the two dominant species were *Sporobolus airoides* (13.2% cover) and *Ericameria nauseosa* (9.9% cover), with a smaller importance of *Atriplex confertifolia* (3.2%). The community is classified as a shadscale-rabbitbrush community. Total cover by live perennials on this dune was higher, at 30.0%, with an additional 6.4% cover by dead shrub canopies (Table 3). Seven perennial species were present in our samples.

Dune 3, the large aeolian dune, exhibited a strikingly different community, with many shrub and ephemeral species that were absent from the other dunes. It is classified as four-wing saltbush scrub. The two dominant species were *Atriplex canescens* with 11.3% cover, followed by *Krascheninnikovia lanata* with 5.9% cover. *Atriplex confertifolia* was present with 3.6% cover. *Sporobolus airoides* was scarce, with just 0.4% cover. Although not specifically sampled in our transects, *Yucca brevifolia* was common on this dune, indicating higher water availability. Total live canopy cover on Dune 3 was 29.4%, with an additional 9.9% cover by dead shrubs (Table 3). Eight perennial species were sampled.

Flat 3 was dominated by a near-monoculture of *Atriplex confertifolia* with 14.8% cover, characterizing it as shadscale scrub. Small numbers of *Lepidium fremontii* and *Sporobolus airoides* were also present. Total live canopy cover was only 16.6%, lower than the 28.4% cover by dead shrub canopies. Seedlings and young *Atriplex confertifolia* were notably absent from this habitat.

In addition to these plant community types, narrow belts of strongly salt-tolerant species requiring access to ground water existed around many of the pans at EAFB. These communities were generally dominated by species of Chenopodiaeae, including *Allenrolfea occidentalis*, *Suaeda nigra* (Raf.) J.F Macbr. (bush seepweed), *Kochia californica* S. Watson (rusty molly) and *Nitrophila occidentalis* (Moq.) S. Watson (boraxweed), as well as *Sarcobatus vermiculatus* (Hook.) Torr. (greasewood, Sarcobataceae). Also present were saline grasses such as *Distichlis spicata*.

Shrub Canopy Characteristics

Four shrub species had canopy volumes over 1 m^3 (Table 4). The largest were *Atriplex torreyi* and *Ericameria nauseosa* which each had individuals reaching canopy volumes of 5 m^3. Although usually smaller, a few individuals of *Atriplex confertifolia* exceeded 1 m^3 in volume. A less common shrub species, *Tetradymia stenolepis*, also commonly reached this size.

The modal canopy volume among shrubs was highest in *Tetradymia stenolepis* where nearly half of the shrubs sampled had volumes greater than 1 m^3 (Table 4). Modal shrub volumes exceeded 0.5 m^3 in *Atriplex torreyi*, *Ericameria nauseosa* and *Tetradymia stenolepis*. Other shrub species were much smaller. Modal shrub volume was less than 0.5 m^3 in *Atriplex confertifolia* and less than 0.2 m^3 in *Acamptopappus sphaerocephalus* and *Lepidium fremontii*. While larger shrub volumes between 0.5 and 1.0 m^3 were occasionally present in *Isocoma acradenia*, small individuals were plentiful with half of the plants sampled having canopy volumes less than 0.01 m^3. *Isocoma acradenia* was the only perennial species with abundant individuals in the smallest volume classes. Absences of small plants were notable in *Acamptopappus sphaerocephalus*, *Atriplex confertifolia*, *Ericameria nauseosa*, *Lepidium fremontii* and *Tetradymia stenolepis* on the dune site.

Canopy area biomass for individual plants is a measure based only on the mean aboveground biomass within the canopy area itself. By combining these data with the stand coverage values, stand biomass values for carbon sequestration can be calculated, as described below (Table 5). Canopy area biomass was highest in *Atriplex torreyi* and *Ericameria nauseosa* which each exceeded 0.5 kg m^{-2} in the biomass samples taken. A large group of shrub species was only slightly lower in biomass per unit of canopy area with means of 0.40–0.45 kg m^{-2}. These included *Acamptopappus sphaerocephalus*, *Artemisia spinescens*, *Atriplex canescens*, *A. confertifolia*, *Krascheninnikovia lanata* and *Tetradymia stenolepis*. Two shrub species were lower in canopy biomass: *Isocoma acradenia* (0.33 kg m^{-2}) and *Lepidium fremontii* (0.08 kg m^{-2}).

Table 5. Aboveground biomass (kg dry weight ha^{-1}) of individual species in three dune and one flat habitat at Edwards Air Force Base, California. See text for habitat descriptions.

Species	Dune 1	Dune 2	Dune 3	Flat 3
Acamptopappus sphaerocephalus	6	0	0	0
Artemisia spinescens	8	0	0	0
Atriplex canescens	0	0	497	0
Atriplex confertifolia	229	118	133	548
Atriplex torreyi	0	115	0	0
Ephedra nevadensis	0.9	0	200	0
Ericameria nauseosa	0	544	44	0
Isocoma acradenia	38	13	0	0
Krascheninnikovia lanata	0	0	49	0
Lepidium fremontii	0	4	0	6
Lycium andersonii	0	0	0.7	0
Sporobolus airoides	14	26	1	1
Tetradymia stenolepis	40	18	26	0
Total aboveground biomass	335	828	1005	555
Dead shrub canopy	168	128	198	568
Total plant biomass	503	956	1204	1123

Samples of canopy biomass for the ecologically widespread *Atriplex confertifolia* demonstrated that this species could achieve large sizes and biomass in wash habitats where soil water availability is present. There was no major difference in canopy biomass of this species in populations sampled in two flat habitats (Flat 1 and Flat 3) and two dune habitats (Dune 1 and Dune 3), with a mean biomass of about 0.35 kg m^{-2} of canopy area. For the Wash habitat, however, mean canopy biomass was nearly double this amount at 0.76 kg m^{-2}.

Community Biomass

Data on canopy cover by perennial species and mean biomass per unit canopy area have been combined in Table 5 to provide an estimate of aboveground dry weight biomass in each of the three dune communities and flat community sampled. The smallest biomass was found on Dune 1, with an estimated 335 kg ha^{-1}. Dead shrub canopies raised this figure to a total biomass of 503 kg ha^{-1}. The second low dune habitat, Dune 2, had a much larger shrub biomass of 828 kg ha^{-1} owing largely to *Ericameria nauseosa*, which contributed nearly two-thirds of this value. A relatively small amount of dead shrub canopy provided for a total biomass of 956 kg ha^{-1}. The extensive Dune 3 habitat had a larger shrub biomass, with 1005 kg ha^{-1}. *Atriplex canescens* contributed half of this total. Flat 3 had a relatively small biomass of 555 kg ha^{-1}, almost all of which was formed by *Atriplex confertifolia*. Dead shrub canopies, however, contributed a large additional biomass of 568 kg ha^{-1}, for a combined total of 1123 kg ha^{-1}.

DISCUSSION

Plant species diversity in the pan-dune system is lower than that of other nearby upland plant communities such as creosote bush scrub and Joshua tree woodland because of the strong environmental stresses which prevail. Drought, winter frosts, high summer temperatures, high winds, salinity and alkalinity all combine to provide difficult conditions for survival. For deeply rooted species, lowering of water tables can also be an added stress.

Desert playas in the southwestern United States are generally defined by a series of rings of vegetation formed around their margins, with salinity as the key selection factor (Vasek and Lund 1980; Rundel and Gibson 1996). As you move along the lower bajada slopes or sandy flats approaching a playa, *Larrea tridentata* typically drops out quite abruptly, and this transition is quite evident around the Lake Thompson lakebed. This boundary for creosote bush closely approximates the geologic lakebed (Orme 2008) and lies well beyond the existing playa. While residual salinity may be one factor in limiting the occurrence of creosote bush (Brehme et al. 2009), also important is the fine texture of the lakebed soils which provides poor mixing of soil gases (Lunt et al. 1973). Below this boundary, creosote bush is replaced by a saltbush scrub community with a dominance of mixed species of *Atriplex*. These saltbush habitats typically exhibit loamy soils with low levels of residual salinity originating from evaporation out of the geologic lakebed. Our soils follow this model with high sand and moderate silt content but almost no clay fraction. These soils are highly alkaline and saline, as well as low in available nitrogen, making them difficult habitats for plant growth.

Species of saltbush in the genus *Atriplex*, all of ours with C_4 metabolism, have a global pattern of distribution in saline coastal and interior arid habitats (Osmond and Björkman 1980) and the saline area of pans and dunes in our study site is no exception. *Atriplex confertifolia* is the most abundant species of saltbush at our sites, often forming pure stands with few or no associated species. Although shadscale is widely present around playas across the Mojave Desert, its tolerance of low temperatures allows it to range into areas too cold for many other Mojave Desert species of saltbush (Billings 1949; West 1983: Caldwell 1985).

One of the morphological characteristics common to most species of *Atriplex*, which is critical to their ecological success in saline soils, is the presence of specialized multicellular bladder cells on the leaf surfaces which limit the effects of the potentially toxic accumulation of salts in their tissues (Osmond and Björkman 1980). The eventual rupture of bladder cells releases these salts back into the environment. Light reflectance from the surface of bladder cells covering the leaf surface gives saltbush species their characteristic silvery color. The dominance of salt-accumulating halophytes in the Chenopodiaceae over our study area has reinforced strong differences in salinity between soils under shrub canopies and in the open. Sodium concentrations were found to often be 30–40 times higher under shrubs than outside of these canopies.

In a broader context than our study, vegetation structures within the old Lake Thompson lakebed have been described and mapped (Charlton 1992; Lichvar et al. 2004*a*,*b*) and are similar to salt-desert shrublands which have been described in detail for the Great Basin (Billings 1949; West 1983). For the Lake Thompson lakebed, the halophytic phase of saltbush scrub covers the largest portion of this area (45%; Lichvar et al. 2004*b*). Although the patterning of the pan-dune ecosystem at EAFB is unusual, the saltbush scrub communities are similar in many respects to saltbush scrub communities dominated by *Atriplex confertifolia* in the Great Basin of Nevada and Utah. Aboveground biomass at Curlew Valley in Utah varies from almost zero to a maximum of about 6000 kg ha^{-1} (Holmgren and Brewster 1972; West 1983), a range reaching five times higher than that which we measured. Although we were not able to investigate root biomass, research in Utah suggests that these communities have 50–80% of their biomass belowground (Holmgren and Brewster 1972; West 1983; Bjerregaard et al. 1984). This is among the highest for plant communities in the world (Rodin and Bazilevich 1967).

We can estimate net production in the pan-dune ecosystem at EAFB by extrapolating from literature studies on *Atriplex confertifolia*. A monospecific stand of this species in Curlew Valley had about 4200 kg ha^{-1} in aboveground biomass and 13,100 kg ha^{-1} belowground (Bjerregaard et al. 1984). Aboveground net primary production in this stand had a mean of about 840 kg ha^{-1} yr^{-1}, with three-fourths of this amount belowground (Caldwell and Camp 1974; Caldwell et al. 1977). If we extrapolate these figures to a stand of *A. confertifolia* in the pan-dune ecosystem with 1000 kg ha^{-1} in above-ground biomass, we would predict above-ground net primary production of about 200 kg ha^{-1} yr^{-1}. In the Curlew Valley studies, the stand of *Atriplex confertifolia* had an aboveground biomass that was 60% more than that in a less saline community dominated by *Krascheninnikovia lanata.* However, net aboveground primary production was only 20% higher (Bjerregaard et al. 1984).

Establishment of seedlings in our pan-dune ecosystem is clearly a highly episodic event as seen in the virtual absence of small plants of most species in our survey. Assuming that a rough correlation exists between shrub size and age, there is clear evidence from the population samples that many of the common shrub species are not reproducing well. Seedlings and small shrubs are rare in most species. The smallest of the shrub volume categories, those <0.002 m^{-3}, would include young seedlings. Only one species, *Isocoma acradenia*, had seedlings in this size category (Table 3). These seedlings were common, particularly in the Wash habitat where this species was reproducing well. One third of all the individuals sampled were in this seedling size class. From single season studies, however, it is impossible to predict whether or not there will be good survivorship of these seedlings.

Other shrub species showed a marked absence of small individuals, particularly *Acamptopappus sphaerocephalus*, *Atriplex confertifolia* and *Lepidium fremontii* whose individuals were generally clustered in larger size classes. Two other species, *Atriplex torreyi* and *Ericameria nauseosa*, were lacking in seedlings in the smaller size classes but otherwise showed a broad range of shrub volumes and thus putatively shrub ages. These species and ecologically similar taxa with deep rooting systems are generally less tolerant of water stress than shallow-rooted species and require wet years for successful seedling establishment (Donovan et al. 1993; Donovan and Ehleringer 1994).

Our results are consistent with a detailed study of interannual seedling survival in *Ericameria nauseosa* in a Great Basin site (Donovan et al. 1993). Patterns of episodic seedling establishment are well documented in many desert shrub species (Goldberg and Turner 1986; Bowers et al. 2004; Meyer and Pendleton 2005). This is not surprising, given that most desert shrub species are relatively long-lived and do not depend on regular seedling recruitment for their persistence. Favorable conditions for establishment may occur only with good soil moisture availability for one or more years.

Implications for Resource Management

Topographic, edaphic and hydrographic differences create opportunities for specialized habitats that allow a diversity of species to exist. The primary habitats within the pan-dune ecosystem at EAFB include washes, flats, low and relatively stable dunes, larger and deeper dunes, and clay pans. These habitats differ not only in their water availability, salinity and alkalinity, but also in the nature of their stability and natural disturbance regimes. Episodic disturbance may well be a critical driver of demographic factors such as reproductive success, seedling establishment and/or mortality.

The geomorphic history of erosional events in and around the old Lake Thompson lakebed has been of critical importance in determining the structure and stability of existing dune and pan areas today. Strong winds represent an important geomorphic force in the pan-dune ecosystem and have clearly shaped much of its origin and dynamics. The presence of a well established shrub cover enhances sand capture and accumulation over time and promotes dune stability and stable habitat niches. These niches are important components of species diversity for populations of vertebrates and invertebrates at EAFB.

Large mosaics of open pan surfaces are typically devoid of flowering plants, but a band of halophytic shrub and perennial grass species grow around the margins. These pans typically collect standing water for one to several months following winter and spring rains (Lichvar et al. 2004*a*). Once evaporative drying commences, extensive areas of microbiotic crusts on the pan surface play an important role in restricting wind erosion (Brostoff et al. 2002, 2005). Pan surface stability may be negatively impacted by physical disturbance, including foot traffic. Seasonal pools of water in the pans form an ephemeral habitat for remarkable density of invertebrates, especially desert shrimp, and act as a critical resource for migratory water birds.

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LITERATURE CITED

BALDWIN, B. G., D. H. GOLDMAN, D. J. KEIL, R. PATTERSON, T. J. ROSATTI AND D. H. WILKEN. 2012. The Jepson manual: vascular plants of California, 2nd edition. University of California Press, Berkeley.

BENEDICT, P. W. 1988. Soil survey of Edwards Air Force Base, California, Interim Report. U.S.D.A. Soil Conservation Service, U.S. Department of Defense Air Force Systems Command, in cooperation with the University of California Agricultural Experiment Station. 137 p. Unpublished report, Edwards Air Force Base, California.

BILLINGS, W. D. 1949. The shadscale vegetation zone of Nevada and eastern California in relation to climate and soils. *Amer. Midl. Naturalist* **2**: 87–109.

BJERREGAARD, R. S., N. E. WEST, M. M. CALDWELL AND H. F. MAYLAND. 1984. Standing crops and dynamics of phytomass and minerals in two salt desert shrub communities. *Great Basin Naturalist* **44**: 327–337.

BOWERS, J. E., R. M. TURNER AND T. L. BURGESS. 2004. Temporal and spatial patterns in emergence and early survival of perennial plants in the Sonoran Desert. *Pl. Ecol.* **172**: 107–119.

Brehme, C. S., W. I. Boarman, S. A. Hathaway, A. Herring, L. Lyren, M. Mendelsohn, K. Pease, M. Rahn, C. Rochester, D. Stokes, G. Turschak and R.N. Fisher. 2009. Spatial and temporal patterns across an ecological boundary: allochthonous effects of a young saltwater lake on a desert ecosystem. *J. Arid Environm.* **73**: 811–820.

Brostoff, W. N., M. R. Sharifi and P. W. Rundel. 2002. Photosynthesis of cryptobiotic crusts in a seasonally inundated system of pans and dunes at Edwards Air Force Base, western Mojave Desert, California: laboratory studies. *Flora* **197**: 143–151.

———, ——— and ———. 2005. Photosynthesis of cryptobiotic soil crusts in a seasonally inundated system of pans and dunes in the western Mojave Desert, California: field studies. *Flora* **200**: 592–600.

Caldwell, M. M. 1985. Cold desert, pp. 198–212. *In* B. F. Chabot and H. A. Mooney (eds.), *Physiological ecology of North American plant communities*. Chapman and Hall, New York.

——— and L. B. Camp. 1974. Belowground productivity of two cool desert communities. *Oecologia* **17**: 123–130.

———, R. W. White, R. T. Moore and L. B. Camp. 1977. Carbon balance, productivity, and water use of cold-desert shrub communities dominated by C_3 and C_4 species. *Oecologia* **50**: 14–24.

Charlton, D. 1992. Plant species of Edwards Air Force Base. Document on file at Environmental Management (AFFTC/EM), Edwards AFB, CA.

——— and P. W. Rundel. 2017. The vegetation and flora of Edwards Air Force Base, western Mojave Desert, California. *Aliso* **35**: 51–68 (this issue).

Donovan, L. A. and J. R. Ehleringer. 1994. Water stress and use of summer precipitation in a Great Basin shrub community. *Funct. Ecol.* **8**: 289–297.

———, J. Mausberg and J. R. Ehleringer. 1993. Seedling size and survival for *Chrysothamnus nauseosus. Great Basin Naturalist* **53**: 237–245.

Edwards Air Force Base [EAFB]. 2008. Integrated natural resources management plan for Edwards Air Force Base, California. Plan 32-7064. Rosamond, CA. *adminpress.jllpress.com/Continental_Group/documents/INRMP2008.pdf* (16 Apr 2016).

Goldberg, D. E. and R. M. Turner. 1986. Vegetation change and plant demography in permanent plots in the Sonoran Desert. *Ecology* **67**: 695–712.

Holmgren, R. C. and S. F. Brewster. 1972. Distribution of organic matter reserve in a desert shrub community. USDA Forest Research Paper INT-30. Intermountain Forest and Range Experiment Station, Ogden, UT.

Lichvar, R. and S. Sprecher. 1996. Delineation and characterization of "Waters of the United States" at Edwards Air Force Base. U.S. Army Corps of Engineers Waterways Experiment Station, Vicksburg, MS.

———, G. Gustina and R. Bolus. 2004*a*. Ponding duration, ponding frequency, and field indicators: a case study on three California, USA, playas. *Wetlands* **24**: 406–413.

———, W. Spencer and J. Campbell. 1999. Distribution of winter annual vegetation across environmental gradients within a Mojave Desert playa, California. *Madroño* **45**: 231–238.

———, S. Sprecher, D. Charlton, G. Gustina, M. Ericsson and J. Campbell. 2004*b*. Ecosystem classification and relationships for Pleistocene Lake Thompson Bed, Mojave Desert, California. Technical Report 04-21, U.S. Army Engineer Research and Development Center, Hanover, NH.

Lunt, O. R., J. Letey and S. B. Clark. 1973. Oxygen requirements for root growth in three species of desert shrubs. *Ecology* **54**: 1356–1362.

Meyer, S. E. and B. K. Pendleton. 2005. Factors affecting seed germination and seedling establishment of a long-lived desert shrub (*Coleogyne ramosissima*: Rosaceae). *Pl. Ecol.* **178**: 171–187.

Orme, A. R. 2008. Lake Thompson, Mojave Desert, California: the late Pleistocene lake system and its Holocene desiccation. *Special Pap. Geol. Soc. Amer.* **439**: 261–278.

Osmond, C. B. and O. Björkman. 1980. Physiological processes in plant ecology: toward a synthesis with Atriplex. Springer Verlag, Berlin, Germany.

Rodin, L. E. and N. I. Bazilevich. 1967. Production and mineral cycling in terrestrial vegetation. Oliver and Boyd, London, UK. 288 p.

Rundel, P. W. and A. C. Gibson. 1996. Ecological communities and processes in a Mojave Desert ecosystem: Rock Valley, Nevada. Cambridge University Press, Cambridge, UK.

Sharifi, M. R., W. N. Brostoff and P. W. Rundel. 2017. Plant phenology and water relations in a saline pan-dune mosaic in the western Mojave Desert. *Aliso* **35**: 87–96 (this issue).

Vasek, F. C. and L. J. Lund. 1980. Soil characteristics associated with a primary plant succession on a Mojave Desert dry lake. *Ecology* **61**: 1013–1018.

West, N. E. 1983. Intermountain salt-desert shrubland, pp. 375–397. *In* N. E. West (ed.), Temperate deserts and semi-deserts. Elsevier Scientific Publ., Amsterdam, The Netherlands.