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NATURAL HISTORY OF A SALINE MOUND ECOSYSTEM

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ABSTRACT.—Along the margins of playas in northwestern Nevada, a salt-tolerant plant community occupies mounds that dot a largely unvegetated landscape. In this environment we studied soil development and plant-soil relationships. The mounds, averaging 0.3 m in height, are occupied by the shrubs *Allenrolfea occidentalis* (iodine bush), *Sarcobatus vermiculatus* (black greasewood), and *Atriplex lentiformis* ssp. *torreyi* (Torrey saltbush). *Distichlis spicata* (desert saltgrass) is the only herbaceous plant occupying this community. Soil salinity decreases with depth in this environment, and content of aqueous-extractable solutes is significantly influenced by site-specific vegetation. Content of silt, clay, and salt in mound surface horizons suggests a chronosequence of mound formation, with the youngest at the barren playa interface and the oldest at the upland vegetation border. Plant demography and mound soil stratigraphy suggest that a pulse of plant recruitment and mound building occurred during a time of neoglacial cooling. As a substrate for plant recruitment, mounds have a limited lifespan because deposition of eolian-transported salts and geochemical cycling by plants quickly render them too saline for seed germination. The apparent periodicity of mound formation precludes definitive conclusions regarding those mound characteristics favorable for plant recruitment and survivorship.

Key words: Allenrolfea occidentalis, Atriplex lentiformis *spp.* torreyi, *eolian dust,* Sarcobatus vermiculatus.

Vegetated mounds, hummocks, or hillocks occur in desert climates worldwide (Shantz and Piemeisel 1940, Bendali et al. 1990, Danin 1991). The origin of these features is generally thought to be capture of eolian sediment by vegetation (Gile 1966, Vasek and Lund 1980), thus the term pythogenic hillock (Batanouny and Batanouny 1968). Plants occupying these mounds often have adaptive growth characteristics such as aerial structures and roots and runners favoring the capture and stabilization of eolian materials (Bendali et al. 1990). Colonization of mounds by cryptogamic organisms lends further stability to the soil (Danin 1991).

During the Pleistocene the Lahontan Basin of northwestern Nevada consisted of numerous interconnected lakes (Russell 1885). At the onset of the Holocene, these pluvial lakes receded leaving a complex of highly saline, fine-textured lacustrine sediments intermixed with coarser-textured, less saline, deltaic, beach, and offshore bar deposits. Fluviatile sands and eolian-reworked material offered a favorable substrate for plant colonization culminating in the presently diverse plant community (Young et al. 1986).

Post-pluvial recruitment on the very saline playa sediments, however, was problematic. Neal and Motts (1967) suggested that plant recruitment on playas may hinge on the formation of large desiccation cracks. These cracks accumulate sediment, presumably of low osmotic potential, capture seeds, have higher available water content for establishing seedlings, and begin the process of mound building. Another pathway of plant recruitment on saline playas occurs when phreatophytic species are able to tap into low osmotic potential groundwater and then begin mound building (Neal and Motts 1967). Assumed in the previous recruitment process is a favorable establishment phase sufficiently long to allow plant roots to reach the water table; this process likely hinges on optimal climatic conditions and a high water table. Jacobson and Jankowski (1989) present another mechanism for plant recruitment on saline playas. At discharge spots, evaporative concentration establishes dense brine pools. Crystallization of gypsum in capillary zones heaves the ground, which can then be colonized by halophytic plants.

Research was initiated to understand plant-soil relationships and the history of mound development in this arid, saline environment. Two basic questions were asked: (1) Is mound formation a prerequisite to the establishment and evolution of plant communities? (2) Conversely, are mounds happenstance, a natural

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consequence of aerodynamic baffling by vegetation in an environment with a high flux of wind-transported material? Working hypotheses developed during initial fieldwork postulated that the principal pedogenic processes operating were eolian dust capture by vegetation to form mounds, and that new mounds form in upland positions while mounds closest to the barren playa are eroding.

METHODS

The study was conducted in Eagle Valley (39°44′N, 119°2′W), 64 km east-northeast of Reno, Nevada. Eagle Valley is a small embayment of pluvial Lake Lahontan bounded to the northwest by the Truckee Range and to the southeast by the Hot Springs Mountains. The western boundary of the playa was the terminus of the Truckee River during pluvial periods and consists of coarse-textured deltaic and reworked eolian sands. Elevation of the barren playa surface in the study area is 1234 m. At maximum lake levels during pluvial cycles of the Pleistocene (Morrison 1964), water covered Eagle Valley to a depth of approximately 100 m. Presently, water ponds on the barren playa surface only during years of heavy runoff. Our principal study area is at the eastern end of the playa (Sec. 26, T22N, R26E). The location is a gradient from barren, flat, fine-textured, salt-encrusted sediments to a higher, coarser-textured, and less saline complex of reworked beach material, eolian sands, and alluvial colluvial material emanating from Hot Springs Mountains. This transitional area where halophytic plant communities exist on mounds is the focus of this study (Fig. 1). Nearby Fallon, Nevada (elevation 1209 m), with average precipitation of 12.5 cm yr^{-1}, had the following precipitation (cm) during the study period: 1988 = 12.9, 1989 = 12.2, 1990 = 14.5, 1991 = 8.3, 1992 = 10.4, 1993 = 14.0, 1994 = 13.3. Based on data from monitor wells installed throughout the study area, the water table is <3 m in most years. Mounds are dominated by *Allenrolfea occidentalis* ([S. Watson] Kuntze), *Atriplex lentiformis* ssp. *torreyi* ([S. Watson] H.M. Hall & Clements), and *Sarcobatus vermiculatus* ([Hook.] Torrey) and by the grass *Distichlis spicata* ([L.] Greene) (Young et al. 1986). In the less saline and coarse-textured beach and colluvial deposits, vegetation is dominated by *Atriplex confertifolia* and *Sarcobatus baileyi* (Billings 1945).

Six mounds, each supporting *A. occidentalis*, *S. vermiculatus*, *A. lentiformis* ssp. *torreyi*, and *D. spicata*, were randomly selected in 1989. From each mound we collected soil samples beneath each individual plant microsite (approximately 10 cm deep excluding the surface crust). We also collected composite soil samples from (1) barren mound surfaces, to 10 cm, (2) the surface 10 cm of lacustrine material beneath the mound centers, and (3) interdune sediment immediately adjacent to the mounds, 0–10 cm. A saturation extract was prepared for each soil sample (U.S. Salinity Laboratory Staff 1954). Electrical conductivity was measured with a salinity drop tester. Ion chromatography was used to quantify Na^+, K^+, Cl^-, NO_3^-, and SO_4^{-2}.

To explore the spatial distribution patterns of soluble salts in mound environments, we randomly selected 3 mounds in 1990. A grid pattern was overlain on the mounds. At nodes of the grid, we collected a 7.6-cm-diameter core to the depth at which lacustrine sediments were encountered or to 30 cm, whichever was shallower; the surface crust was excluded. Samples were placed in bags, brought to the laboratory, air-dried, and stored until analyzed. Extraction of soluble species was facilitated by placing 10 g of the homogenized original sample in 50-mL centrifuge tubes, adding 10 mL deionized water, and shaking for 1 h. The tubes were centrifuged and subsamples tested for electrical conductivity with a salinity drop tester and for pH with a glass electrode. Other subsamples were diluted with deionized water to appropriate levels for analyses by the ion chromatograph for Cl^-, Br^-, NO_3^-, SO_4^{-2}, Na^+, K^+, Mg^{+2}, and Ca^{+2}. Boron was determined using the azomethine-H colorimetric procedure (John et al. 1975). For one of the mounds, particle size analysis was done as described below. The spatial distribution of each individual attribute is presented in an XYZ contour fill chart facilitated by a commercial graphics program.

In 1990 we described a sequence of 7 soils along a transect encompassing the width of the mounded area from the barren playa surface southeast to the less saline upland interface (transect distance ≈ 1.2 km). A backhoe was used to excavate to a depth of approximately 3 m. Soils were described using established

Fig. 1. Landscape photograph of study areas showing mounds occupied by *Allenrolfea occidentalis*. For 50 mounds measured, the average length was 3.1 m (s = 1.8), average width was 1.9 (s = 1.1), and average height was 0.3 m.

protocols (Soil Survey Staff 1984). Samples of each horizon were returned to the laboratory for further characterization. We quantified the following attributes: (1) organic carbon by the dichromate digestion procedure (Nelson and Sommers 1982); (2) particle-size distribution after removal of organic matter and soluble salts (Gee and Bauder 1986); (3) saturated paste extraction (U.S. Salinity Laboratory Staff 1954) with quantification of anions and cations by ion chromatography. Clay-sized fractions reserved from particle-size analyses were prepared for and examined by X-ray diffraction using standard procedures (Moore and Reynolds 1989). The very fine sand fraction was examined with a petrographic microscope to identify its mineralogy (Brewer 1976). The silt-sized fraction was isolated by dry-sieving of original samples and examined by X-ray diffraction.

At approximately 1-mon intervals in 1991, we collected soil samples at depths of 20, 40, and 60 cm from 4 randomly selected mounds. After transport to the laboratory in sealed glass vials on ice, the samples were immediately analyzed for gravimetric water content and total soil water potential (Decagon SC-10 thermocouple psychrometer). Calibration of the psychrometer was facilitated using saturated salt solutions of LiCl (–294.4 MPa), NaCl (–38.0 MPa), KCl (–21.7 MPa), and KNO_3 (–7.5 MPa), and NaCl solutions with potentials of –3.2 MPa and –1.8 MPa.

To quantify eolian dust fluxes and chemical content, we placed marble dust collectors (3 replicates) on the barren playa surface approximately 8 km southwest of the study area. The marble dust collectors consisted of approximately a 5-cm depth of glass marbles placed in 33 × 24-cm teflon-coated cake pans placed on the soil surface. Collectors were sampled bimonthly from June 1994 through June 1995, at which time dust weight was recorded. A subsample of the dust was dissolved in deionized water (1-g sample 25 mL H_2O) and analyzed for Cl^-, NO_3^-, SO_4^{-2}, Na^+, and K^+ using ion chromatography and for Boron using the azomethine-H colorimetric procedure.

RESULTS

Soils

Except for the soil described on a large dune (soil 5), soils along the transect have grossly similar morphology and stratigraphy even between mound and intermound microsites (Table 1). Vesicular surface crusts overlying soft, sandy loam layers are common to all soils. Hues are 2.5Y in surface layers grading to 5Y in lower layers (Munsell color system). A textural discontinuity exists in all soils examined: sandy loam surface layers overlie silty clay loam varved lacustrine sediments. The upper several centimeters of the lacustrine unit contain many indurate nodules ranging from 1 to 5 cm in diameter. Tubular pores are abundant in the finer-textured material. These pores are in places peripherally coated by what appears to be organic material, perhaps old root channels. The proportion of sand in surface horizons decreases from the barren playa surface to the higher portion of the landscape at soil 7; silt and clay content correspondingly increases. In excavated sections of mounds, graded-bedding and cross-bedding were evident in the surface coarse-textured material.

Organic carbon levels are very erratic among soil horizons (Table 1). There is a slight increase in organic carbon in the lower mottled, reduced horizons. Organic carbon is highest in the surface crust of soil 7. Visual inspection of this layer did not show any evidence of rooting activity, but the crust had encased seeds and fruits of halophytic species that occupy the mounds.

Saturation paste extracts show the extreme salinity of this environment (Table 1). Complete solubilization of some salts may not have occurred for some samples given the soil-to-water ratios used. These systems are dominated by Na^+ and Cl^-. Levels of Na^+ and Cl^-, as well as other solutes, generally decline with depth. Extractable SO_4^{-2} values are erratic among soils and among soil horizons. Soils on the lowest part of the landscape (1, 2, 3, and 4) have a secondary bulge in profile SO_4^{-2} levels, which is absent in soils 5, 6, and 7. Levels of K^+ are inconsistent among soils and among horizons. Levels of NO_3^- are extraordinarily high in the surface crust of all soils, generally declining rapidly with depth.

Clay-sized mineralogy is similar among the soils examined. In the coarse-textured material overlying varved lacustrine materials, K-saturated treatments produce reflections corresponding to lattice spacings for kaolin, mica, and a poorly crystalline, randomly interstratified smectite-illite. With Mg^{+2} saturation and glycol intercalation, the randomly interstratified component expands to 1.6 nm with very broad reflections. Lacustrine sediments are dominated by smectite. One unusual X-ray trace was for the 5th layer of soil 3, the horizon with anomalously low pH (Table 1). The pattern was completely amorphous save for a very broad maximum centered at 0.40 nm, which is indicative of opaline silica (Jones and Segnit 1971).

X-ray diffraction was used to examine the silt-sized mineralogy of soils 1, 3, and 6. Samples were dry-sieved from original material to conserve water-soluble minerals. A peak matching algorithm was used to detect minerals in the samples. The principal evaporite mineral identified in the silt-fraction was halite (NaCl), which occurred in all soil layers above the lacustrine sediments. The only other evaporite mineral identified was bloedite ($Na_2MgSO_4 \cdot 4H_2O$), which occurred in layer 1 of soil 3. Other principal minerals in all horizons in decreasing order of abundance were plagioclase feldspar, quartz, calcite, and mica. Gypsum ($CaSO_4 \cdot 2H_2O$) was a major mineral component in layers 4 and 5 of soil 3 and the surface horizon of soil 5, both vegetated. Diagnostic peaks for sepiolite (ideal = $Si_{12}Mg_8O_{30}(OH)_4(OH_2)_4 \cdot 8H_2O$) were found in the 5th layer of soil 1. No zeolites were identified in the silt fraction even though saline playa environments are known to foster their formation (Ming and Mumpton 1989).

Mineralogy of the very fine sand fraction was determined by optical methods and quantified using the line count method (Brewer 1976). Samples were washed with water to remove soluble salts. The mineralogy of soil above lacustrine sediments is dominated by plagioclase feldspar and quartz with minor volcanic glass, hornblendes, mica, and carbonates. Much of the lacustrine material consisted of diatom tests partially or completely cemented by an isotropic material that appears to be silica.

Plant-Soil Relationships

The content of aqueous extractable solutes varied significantly among collection microsites (Fig. 2). The most saline microsites were unvegetated areas atop mounds and the soil beneath greasewood. Soil collected in the unvegetated zone adjacent to mounds and the playa material directly beneath the mounds had in general the lowest levels of extractable solutes among the collection microsites.

Using a backhoe, we were able to uncover a root system of *A. occidentalis* that emanated from a mound and extended over 10 m into the unvegetated interspace. The directionality of the root systems suggests linkages among mounds, although we did not excavate a complete root system from one mound to another. The diameter of larger roots was over 5 cm. Most large-diameter roots had over 90 growth rings, the oldest having 120 rings. Soil-water relations data collected in 1991, a wetter than normal year, show the extremely negative total soil water potentials characteristic of this environment (Table 2).

Soil samples from 3 spatially separated mounds were collected in a grid pattern to determine the spatial distribution of aqueous-soluble solutes. Canopy coverage of the mounds by *A. occidentalis* ranged from approximately 1/2 (Fig. 3a) to much less than 1/2 occupied (Fig. 3c). Spatial distribution of aqueous-soluble solutes differs considerably among the 3 mounds. There is a correspondence between levels of aqueous-soluble solutes and location of plant canopies for mounds a and b. In mound a the highest electrical conductivity and K^+ occur beneath *S. vermiculatus* plants; for mound c, levels of Mg^{+2} and SO_4^{-2} are especially high beneath *A. occidentalis* plants on the south side of the mound. Mound b, which has the greatest canopy coverage by *A. occidentalis*, generally has the lowest solute concentration near the top of the mound corresponding roughly to a nonvegetated area. There is also a directional aspect of solute distribution. Many solutes are highest in the southwest quadrant (all mounds). Coarse sand content shows a gradient from north to south (mound a). Very fine sand content is highest at the top of the mound, and silt and clay are highest at mound edges (mound a).

Eolian Dust

The bimonthly eolian dust flux on the barren playa surface averages over 130 g m^{-2} (Table 3). The dust is dominantly composed of Na^+ and Cl^- (nearly 40% by weight) with very high levels of water-soluble SO_4^{-2}, K^+, and NO_3^-. Concentration of phytotoxic boron averages over 1400 mg kg^{-1}.

DISCUSSION

Mound Pedogenesis

Particle-size distribution indicates that soil development began on a surface that was relatively coarse textured in comparison to the underlying lacustrine material. Depositional fabrics such as cross- and graded-bedding and the areal extent of the coarse-textured veneer suggest it is a remnant offshore bar likely reworked by beach and wind action as the pluvial lake receded. Thus, mounds are a composite of eolian material overlying offshore beach deposits.

In the Lake Lahontan basin, given geomorphic surface stability, the proportion of fines (silt and clay) increases with time via the steady capture of eolian dust in the soil skeletal framework of sand- and gravel-sized particles (Chadwick and Davis 1990). In our study the proportion of fines in mound surface layers increases from the barren playa interface to the surrounding upland. Based on the Chadwick and Davis model, youngest mounds are closest to the barren playa, which is supported by mound stratigraphy. Mounds closest to the barren playa show greater relief and have more visual evidence of recent eolian sand deposition. Moreover, as expected, there is a general increase in mound salinity from the playa to the upland because, as time increases, cumulative additions of salt-rich eolian dust (Table 4) and plant geochemical cycling of salts also increase (Robert 1950, Charley and West 1977). Expansion of vegetated mounds into barren playa surfaces is opposite the general conclusion that playas in western United States have generally enlarged during the Holocene (Blackwelder 1931, Malek et al. 1990). However, Eagle Valley may be unique due to the immense volume of coarse-textured deltaic sediments generally upwind of the study area (prevailing winter storm winds from the northwest).

The controlling factors of pedogenesis in this environment are eolian erosion and deposition,

TABLE 1. Soil descriptions and selected attributes by horizon.

Horizon	Depth (cm)	Munsell color (dry)	Roots	Efferves-cence HCl	pH	OC (%)	Size distribution Sand	Silt	Clay	Saturated paste Na^+	Cl^-	SO_4^{-2}	K^+	NO_3^-	Field notes
							---------- %	----------		---------- mM				----------	
BARREN PLAYA SURFACE—SOIL 1, approximately 200 m southwest of Eagle Rock															
C1	0–8	2.5Y 7/2	absent	slight	7.4	0.42	77.6	14.9	7.5	3480	3410	46.4	20.1	1.40	surface salt efflorescences
Bk1	8–30	2.5Y 7/2	absent	violent	7.3	0.36	62.8	26.3	10.9	2670	2550	20.8	16.1	0.27	platy structure
Bk2	30–51	2.5Y 6/2	absent	strong	7.2	0.45	44.5	30.1	25.4	2540	2490	20.2	23.8	0.21	platy structure
C2	51–64	2.5Y 7/2	absent	slight	7.3	0.44	48.1	30.4	21.5	1870	2360	20.4	21.6	0.26	many vesicles and tubular pores
2Cg1	64–91	5Y 5.5/3	absent	slight	7.4	0.72	2.5	44.4	53.1	1460	1630	34.0	36.7	0.12	varved; streaks of 2.5YR 6/8; pyrite coatings
2Cg2	91+	5Y 5.5/3	absent	slight	7.4	0.82	3.9	45.7	50.4	2810	1540	17.2	28.3	0.03	extremely hard when dry; mottles of 5YR 7/8
ALLENROLFEA MOUND—SOIL 2, approximately 200 m southeast of soil 1															
A	0–8	2.5Y 6.5/2	absent	slight	7.9	0.43	73.3	12.8	13.8	2810	2620	82.5	21.1	0.44	stolons of *Distichlis spicata*
C1	8–23	2.5Y 6.5/2	common	strong	8.1	0.30	83.0	5.8	11.1	380	420	34.9	7.7	5.78	roots concentrated at bottom of horizon
Bk	23–56	2.5Y 7/2	few	violent	8.2	0.17	65.0	18.7	16.3	400	410	6.2	3.8	0.07	forms granules when dry that easily pulverize
Cc	56–91	5Y 7/2	v. few	strong	8.2	0.13	54.3	26.3	19.4	220	200	3.0	4.9	0.17	strong local cementation
C2	91–127	5Y 7/2	v. few	strong	8.2	0.21	62.4	20.4	17.2	210	220	11.0	3.4	0.83	
2Cg	127+	5Y 8/0	v. few	strong	8.0	0.47	7.8	45.4	46.8	220	250	3.5	7.6	nd	pyrite coatings
ALLENROLFEA-SARCOBATUS MOUND—SOIL 3, 12 m south of soil 2															
A	0–1.5	2.5Y 6/3	absent	strong	7.8	0.32	78.8	7.1	14.1	990	960	33.0	7.3	6.61	slightly hard surface crust; vesicular porosity
C1	1.5–20	2.5Y 6.5/2	common	strong	8.1	0.20	75.6	12.6	11.7	540	550	12.7	5.9	0.05	pulverizes easily
C2	20–76	2.5Y 6.5/2	few	strong	8.3	0.65	85.7	5.8	8.5	310	300	43.1	4.6	0.49	very soft
By	76–86	2.5Y 6/2	v. few	strong	8.0	0.21	nd	nd	nd	270	280	41.6	4.0	0.08	gypsum crystals; seams of calcium carbonate
C3	86–122	5Y 6/3	common	none	5.2	0.74	68.0	16.0	16.0	380	410	12.3	3.4	0.01	decaying root debris
2C	122–157	2.5Y 7/2	v. few	strong	8.0	0.20	48.2	28.0	23.8	160	170	16.5	2.6	0.11	pulverizes easily; many tubular pores
2Cg	157+	2.5Y 7.8/2	v. few	violent	8.1	0.45	8.1	54.9	37.0	120	140	6.5	3.2	0.02	varved structure; black coatings of pyrite
UNVEGETATED INTERSPACE—SOIL 4, approximately 350 m southeast of soil 3															
A	0–2.5	2.5Y 6.5/2	absent	strong	7.8	0.65	69.5	15.0	15.5	3710	3860	56.6	14.9	7.70	surface crust; vesicular porosity
Bk	2.5–30	2.5Y 6.5/2	v. few	violent	7.9	0.22	69.1	14.1	16.7	630	650	3.0	9.5	0.09	very soft

TABLE 1. Continued.

Horizon	Depth (cm)	Munsell color (dry)	Roots	Effervescence HCl	pH	OC (%)	Size distribution Sand	Silt	Clay	Saturated paste Na^+	Cl^-	SO_4^{-2}	K^+	NO_3^-	Field notes
							---------- %	----------		-------------- mM	--------------				
UNVEGETATED INTERSPACE—SOIL 4, approximately 350 m southeast of soil 3															
C1	30–51	5Y 6.5/2	few	strong	8.1	0.31	37.5	35.1	27.4	330	330	1.8	4.3	0.08	pulverizes easily
C2	51–64	2.5Y 7/2	few	violent	7.6	0.30	44.8	27.3	27.9	1070	1130	37.4	13.1	0.58	many tubular pores
2Cc	64–81	2.5Y 6.5/2	v. few	violent	8.0	0.40	18.5	51.7	29.8	170	190	1.7	3.4	0.03	strong local cementation
2C	81–112	5Y 7/2	v. few	strong	8.3	0.58	nd	nd	nd	110	150	2.9	3.1	0.03	strong fine blocky structure
2Cg	112+	5Y 8/2	v. few	slight	8.2	0.49	1.4	56.3	42.4	100	130	1.1	7.0	0.01	varved structure; few black pyrite coatings
VEGETATED LARGE DUNE—SOIL 5, approximately 50 m east of soil 4															
A	0–2.5	2.5Y 7/2	absent	strong	7.9	0.39	61.4	16.0	22.5	2480	2240	210.4	12.1	0.32	gypsum crystals
C1	2.5–15	2.5Y 6.5/2	few	strong	7.7	0.33	74.4	5.4	20.2	3770	3800	177.6	11.0	8.51	graded bedding
C2	15–43	2.5Y 6/2	few	strong	8.2	0.15	76.8	9.7	13.6	830	780	86.2	7.3	2.52	graded bedding
C3	43–76	2.5Y 6/2	few	moderate	8.0	0.11	77.7	7.5	14.7	230	190	68.3	1.5	0.11	graded bedding
C4	76–132	2.5Y 6/2	v. few	slight	8.0	0.10	81.6	6.8	11.6	110	110	52.3	1.2	0.14	graded bedding
2Bt	132+	10YR 6/3	v. few	slight	8.2	0.10	71.0	16.7	12.3	80	110	6.9	1.7	0.20	common clay films
UNVEGETATED INTERSPACE —SOIL 6, approximately 280 m southeast of soil 4															
A	0–5	2.5Y 6/2	absent	strong	7.5	0.57	53.7	24.2	22.1	4010	4150	48.0	14.1	1.23	surface crust; vesicular porosity
C1	5–10	2.5Y 6/2	absent	strong	7.9	0.46	47.3	29.0	23.7	1760	1460	28.2	12.8	0.30	shiny ped faces
C2	10–33	2.5Y 6.5/2	few	violent	8.2	0.20	60.3	21.6	18.1	490	460	7.9	4.0	0.04	many tubular pores
C3	33–51	5Y 8/1.5	v. few	violent	7.6	0.47	9.0	56.1	34.9	720	730	5.2	12.7	0.05	many tubular pores
2Cc	51–69	5Y 8/1	v. few	strong	7.7	0.52	3.6	49.9	46.4	640	660	4.4	16.3	0.08	strong local cementation; many tubular pores
2C	69–99	5Y 8/2	v. few	strong	7.8	0.43	3.5	47.4	49.0	310	330	2.1	8.4	0.08	varved structure; many tubular pores
2Cg	99–127	5Y 7/3	v. few	slight	7.7	0.38	5.5	50.8	43.7	190	220	1.7	5.1	0.07	black pyrite coatings; many tubular pores
2Cg2	127+	5Y 7/3	v. few	slight	7.6	0.38	4.4	49.4	46.1	210	250	2.6	5.8	0.03	coating of rustlike 5.0 YR 5/6
ALLENROLFEA MOUND—SOIL 7, approximately 400 m south of soil 6															
A	0–8	2.5Y 7/2	absent	violent	7.0	1.03	46.9	31.4	21.7	4630	5550	20.3	18.8	4.17	puffy surface crust; vesicular porosity
2C1	8–13	2.5Y 7/2	v. few	strong	8.0	0.87	12.2	60.9	26.8	2510	2520	15.8	46.3	4.70	pulverizes easily
2C2	13–46	2.5Y 7/2	v. few	strong	7.5	0.60	11.2	60.9	27.9	1130	1360	5.0	22.4	1.41	pulverizes easily
2C3	46–86	2.5Y 8/2	v. few	strong	7.8	0.46	5.5	56.0	38.5	450	450	1.0	12.2	0.08	strong, fine, angular blocky structure
2Cg1	86–112	5Y 8/1.5	v. few	strong	8.1	0.38	12.3	49.0	38.7	80	120	0.9	2.3	0.03	hard when dry; many tubular pores
2Cg2	112+	5Y 8/1.5	v. few	strong	8.1	0.49	6.2	48.7	45.0	150	170	1.0	6.0	0.05	a few pyrite coatings; many tubular pores

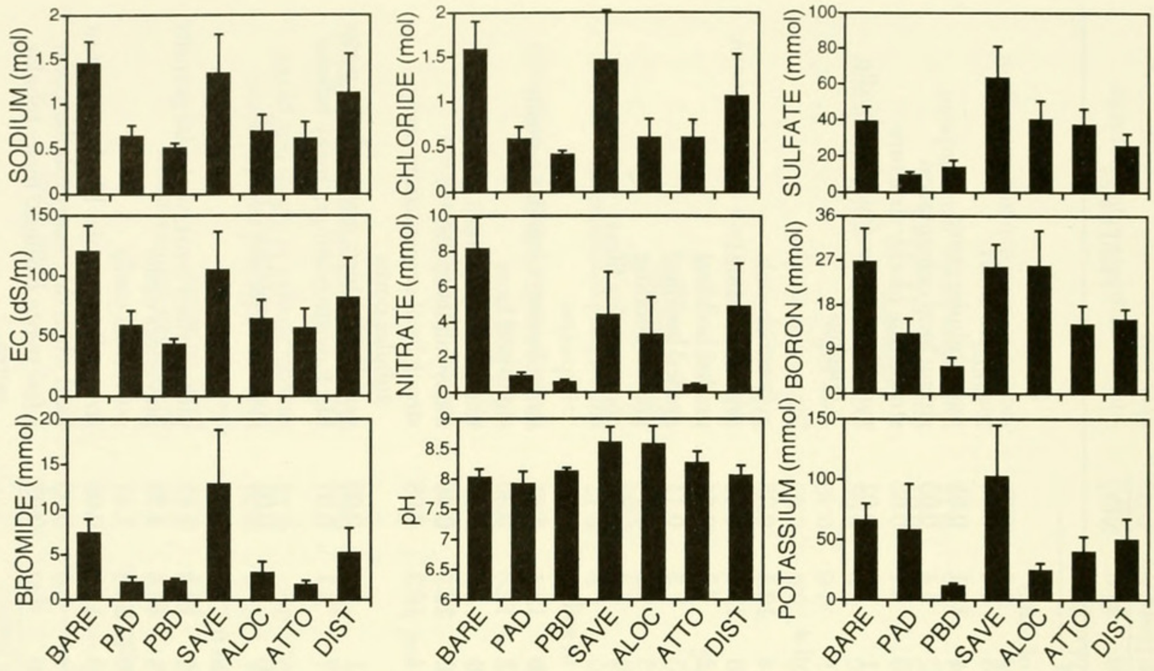

Fig. 2. Aqueous extractable solutes as influenced by collection microsite. Codes are as follows: BARE = top of mound with no vegetation; PAD = surface soil of unvegetated mound interspace; PBD = lacustrine sediment beneath mound; SAVE, ALOC, ATTO, and DISP = collected beneath *S. vermiculatus*, *A. occidentalis*, *A. torreyi*, and *D. spicata*, respectively. Values are means ±1 $s_{\bar{x}}$.

extreme aridity, high salinity, halophytic vegetation, and aeration status of the lower lacustrine sediments. Erosion and deposition via wind action are a constant in these salt desert environments (Young and Evans 1986). The magnitude of eolian transport in the study area is immense (Table 3). Moreover, deposition of dust in obstructions such as plant canopies would rapidly increase their salt content to levels too high for future seedling recruitment. The situation thus exists where eolian materials both build the vegetated mounds and are also partially responsible for their demise at some later date due to excessive salt accumulation and eventual plant death. As will be discussed later, we are not sure mound building is contemporaneous with steady salt accumulation from dust, or whether the mound-building phase requires some different climate from that present when less saline, coarser-textured eolian dust is more plentiful.

The study area's scant precipitation precludes extensive leaching of solutes through the soil. Steady additions of salt-rich eolian dust and plant deposition of salts on the soil surface appear to quickly make mounds extremely saline.

One of the consequences of extremely high salt content in soils is the accelerated physical breakdown of sand-sized particles to silt-sized particles by salt weathering (Goudie et al. 1970). In addition, the high salt content in conjunction with aridity and plant processes leads to extreme alkalinization such as seen in *S. vermiculatus* microsites (Robertson 1983). The locally high pH condition enhances the weathering of primary minerals via increased solubility of aluminum, iron, and silicon (Loughnan 1969).

At present, plant factors come into play only on the mounds themselves. One plant pedogenic aspect is the biogeochemical concentration of elements that accelerates mound salinization due to the capture of eolian dust alone. The yearly fall of leaves and seeds becomes incorporated, enriching the mound surface horizon with organic matter. Vegetation seems to play a role in the formation of gypsum, as only vegetated mounds contain measurable quantities. Gypsum formation may be a function of plant concentration of calcium and sulfur in mound soil to such levels that gypsum can precipitate. Alternatively, mound microclimate may foster the crystallization of gypsum via salt exclusion from ice (Marion and Grant 1997).

Another factor in the genesis of these soils is the extremely reduced nature of the lacustrine sediments as indicated by gley soil colors, mottling, and the presence of pyrite (FeS)

TABLE 2. Water relations, by depth, of mounds (values are means with standard errors in parentheses; n = 4).

Date	Gravimetric water content by depth (cm)			Total soil water potential by depth (cm)		
	20	40	60	20	40	60
	%			MPa		
5/30/91	13.2 (6.5)	20.9 (6.5)	24.8 (5.4)	−22.7 (3.7)	−11.2 (3.2)	−8.3 (2.2)
6/10/91	13.7 (6.0)	26.5 (13.0)	27.1 (5.9)	−15.2 (3.4)	−12.7 (5.1)	−5.2 (0.8)
7/8/91	9.4 (5.1)	27.6 (10.3)	23.1 (11.1)	−14.6 (4.3)	−6.8 (1.5)	−6.3 (1.3)
8/30/91	5.0 (1.4)	23.9 (10.6)	28.7 (7.3)	−22.1 (2.7)	−8.0 (1.8)	−8.0 (2.1)
9/30/91	4.8 (0.8)	29.5 (6.7)	29.0 (7.0)	−18.8 (1.5)	−5.1 (0.4)	−4.5 (0.3)

TABLE 3. Average bimonthly dust flux from June 1994 through June 1996, and water-soluble composition of dust collected on the barren playa surface just west of the study area. Standard errors in parentheses.

Months	Dust flux ($g\ m^{-2}$)	Sodium	Sulfate	Nitrate	Potassium	Boron
		$g\ kg^{-1}$ dust		$mg\ kg^{-1}$ dust		
Jul–Aug	81 (14.6)	171 (44)	27 (5.8)	704 (245)	2128 (462)	1302 (232)
Sep–Oct	17 (2.5)	120 (27)	33 (6.0)	884 (304)	1600 (429)	1547 (401)
Nov–Dec	172 (9.9)	193 (20)	94 (4.7)	565 (240)	2215 (140)	1712 (181)
Jan–Feb	159 (66.1)	150 (46)	45 (15.4)	6 (2.6)	2076 (629)	1592 (92)
Mar–Apr	157 (32.8)	151 (59)	41 (17.3)	293 (159)	1880 (159)	1414 (68)
May–Jun	239 (53.7)	136 (42)	21 (6.3)	23 (158)	1690 (355)	1316 (85)

coatings. Reduced conditions are likely facilitated by a shallow water table, but subdued oxygen diffusion rates through the fine-layered sediments may play a role. Lack of oxygen for root respiration will retard root growth of many plants (Marchner 1986). In addition, strongly reduced conditions will increase the solubility of metals such as Fe and Mn (Stumn and Morgan 1996). The unusually low pH in the 5th layer of vegetated soil 3 may be a consequence of changes in aeration status of the soil. If this horizon previously contained reduced sulfur minerals such as pyrite, its subsequent oxidation could lead to the low pH observed (Nordstrom 1982).

Natural History of Mounds

Vasek and Lund (1980) present a model of mound evolution on a playa that involves vegetation succession. Primary mound establishment on a playa begins with eolian dust entrapment by species of *Kochia*, which have high sodium tolerance. As mounds enlarge and accumulate nutrients, conditions are favorable for the establishment of *Atriplex lentiformis* ssp. *torreyi*, which promulgates mound expansion to a critical size at which time they coalesce. These complex mounds are favorable for the recruitment of new species such as *Atriplex confertifolia*, *Haplopappus acradeniaus*, and *Stanleya pinnata*. Further biogeochemical enrichment of the mound in Na^+, Cl^-, K^+, Ca^{+2}, and Mg^{+2} from litter fall and eolian dust leads to eventual death of plants and mound erosion. Soil pH and solute content are controlling factors in plant distribution in arid environments of the western United States (Gates et al. 1956, Skougard and Brotherson 1979).

There is no evidence to suggest plant succession occurs on mounds at Eagle Valley playa. Mounds begin and end with occupation by *A. occidentalis* and/or *S. vermiculatus*, and occasionally by *Atriplex confertifolia* and *Atriplex lentiformis* ssp. *torreyi*.

Mound establishment potentially could have begun sometime in the latest Pleistocene as pluvial Lake Lahontan dried (Mifflin and Wheat 1979, Morrison 1991). The mounds, however, are far younger because they lack profile differentiation indicative of nearly 10,000 yr of pedogenesis. For example, in a similar playa margin environment, a clay-rich, differentiated soil horizon formed in less than 3500 yr (Peterson 1980). Moreover, field research in the Lake

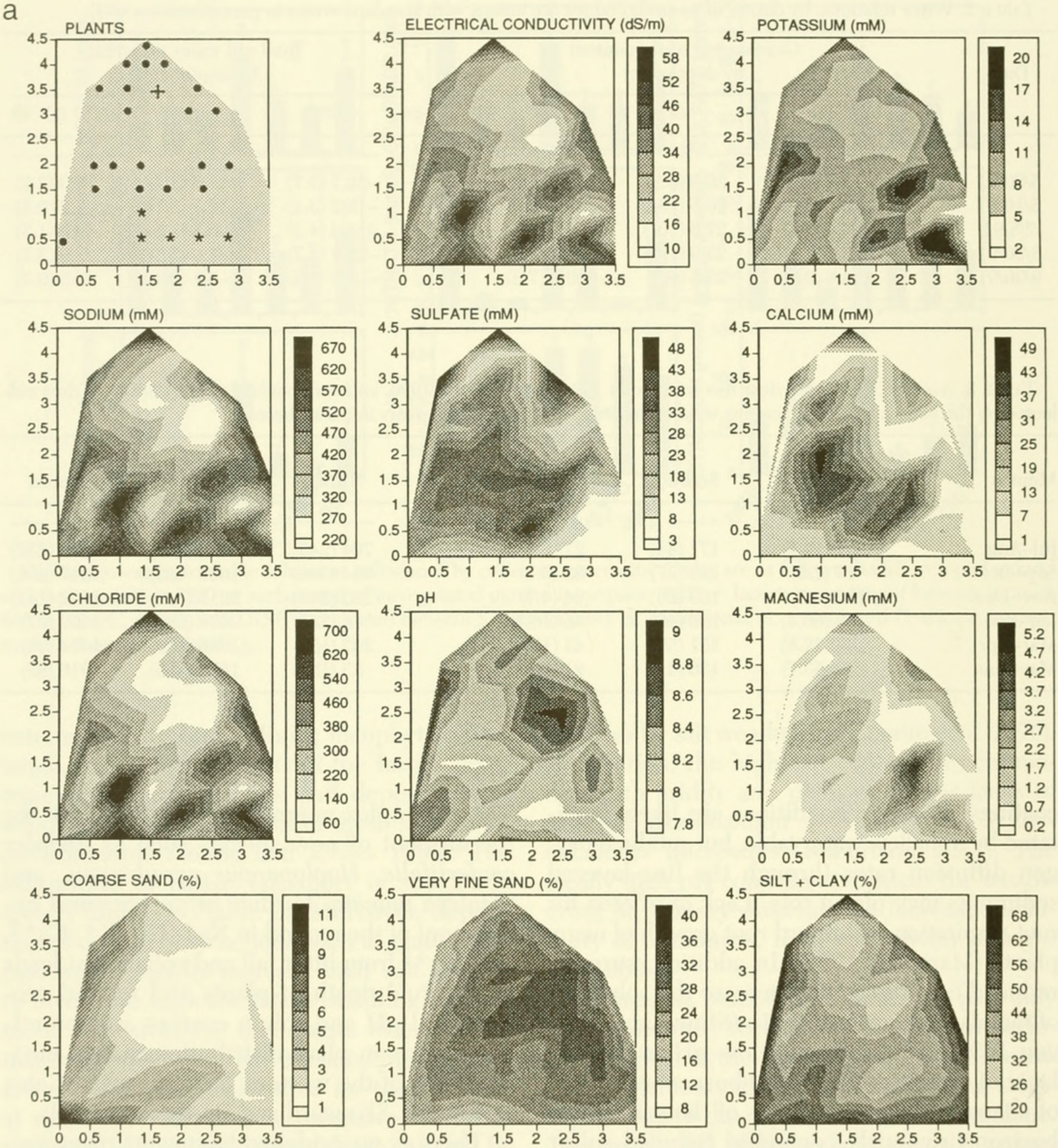

Fig. 3. Spatial distribution of aqueous extractable attributes for 3 mounds. If a portion of a plant canopy intercepted the grid sampling pattern, it is listed in the plants panel in the upper left-hand corner. Symbols used: ● = *A. occidentalis*, * = *S. vermiculatus*, and + = *A. torreyi*. Axes of graphs are in m. All panels are oriented north (top) to south (bottom).

Lahontan basin by Morrison (1964) shows that pedogenesis since the middle Holocene produces an oxidized B horizon.

The Holocene in the western United States has been marked by profound shifts in climate and vegetation patterns (Antevs 1938, Davis 1982, Wigand 1987, Anderson and Smith 1994). The latest Holocene has seen extended periods of drought lasting >100 yr (Stine 1994) and cooler and wetter periods where glaciers in the Sierra Nevada expanded considerably (Curry 1969). The late Holocene cool and wet periods or neoglacials contributed to the rise in pluvial lakes (Morrison 1964). Heights of neoglacial pluvial lake maximums are uncertain, but in all likelihood water at times completely covered the Eagle Valley embayment, further reducing the potential age of the mounds. Neal and Motts (1967) believe that most geomorphic features on and adjacent to playas in

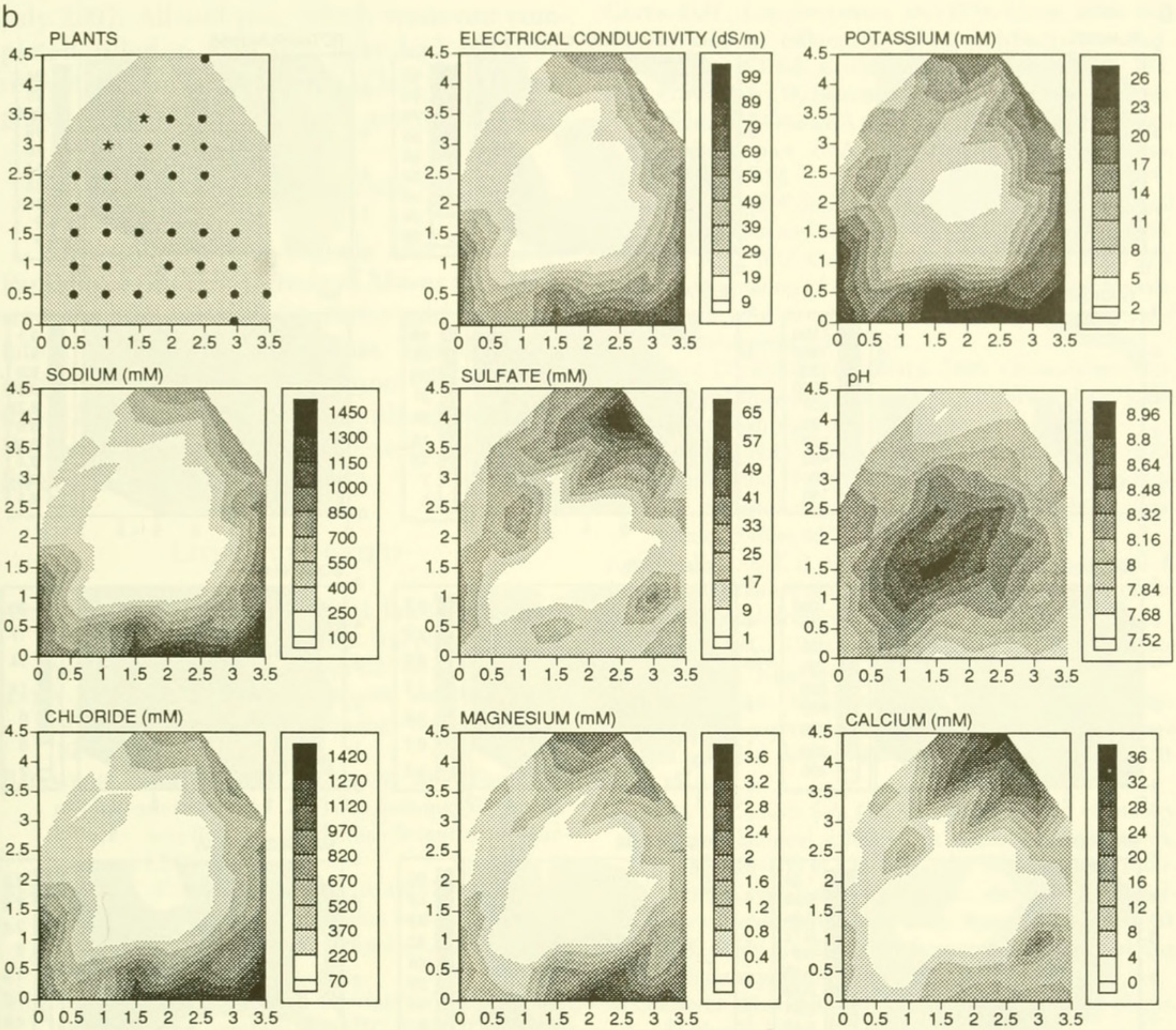

Fig. 3. Continued.

the western United States were formed within the last 100 yr, a result of a lowered water table caused by man's activities. The most recent glacial advance in the Sierra Nevada occurred from 1880 to 1908 (Curry 1969), which correlates with rings of *A. occidentalis* in the study area. Phytogenic hillocks can form and enlarge in this time frame (Gile 1966).

Present osmotic potentials of these playa margins are a magnitude too high for seed germination and suggest that large-scale plant recruitment may hinge on rare climatic events (Romo and Haferkamp 1987, Blank et al. 1994). What were those conditions in the past 90–120 yr that initiated mound formation? Present plant recruitment occurs rarely in small, flood-caused channels; however, mound plant demography suggests pulses of large-scale recruitment. If mound initiation began during a neoglacial cycle, then long-term increases in effective precipitation may have leached soluble salts deeper into the soil, thereby favoring plant recruitment. This scenario is problematic because long-term increases in effective precipitation would promulgate playa flooding. Perhaps plant recruitment on the playa margin began at the end of the neoglacial period. There would be greater sources of unconsolidated material at the delta of the Truckee River for mound building. Moreover, the neoglacial lake may have reduced the salt content of sediments along the playa margin.

Do mounds provide benefits for plants or are they happenstance, simply a result of inescapable physical processes? Phreatophytes such as *S. vermiculatus*, which dominantly root in the underlying lacustrine material, would seem not to require mound formation for continual survival. Potentially beneficial aspects of mound formation could include the following:

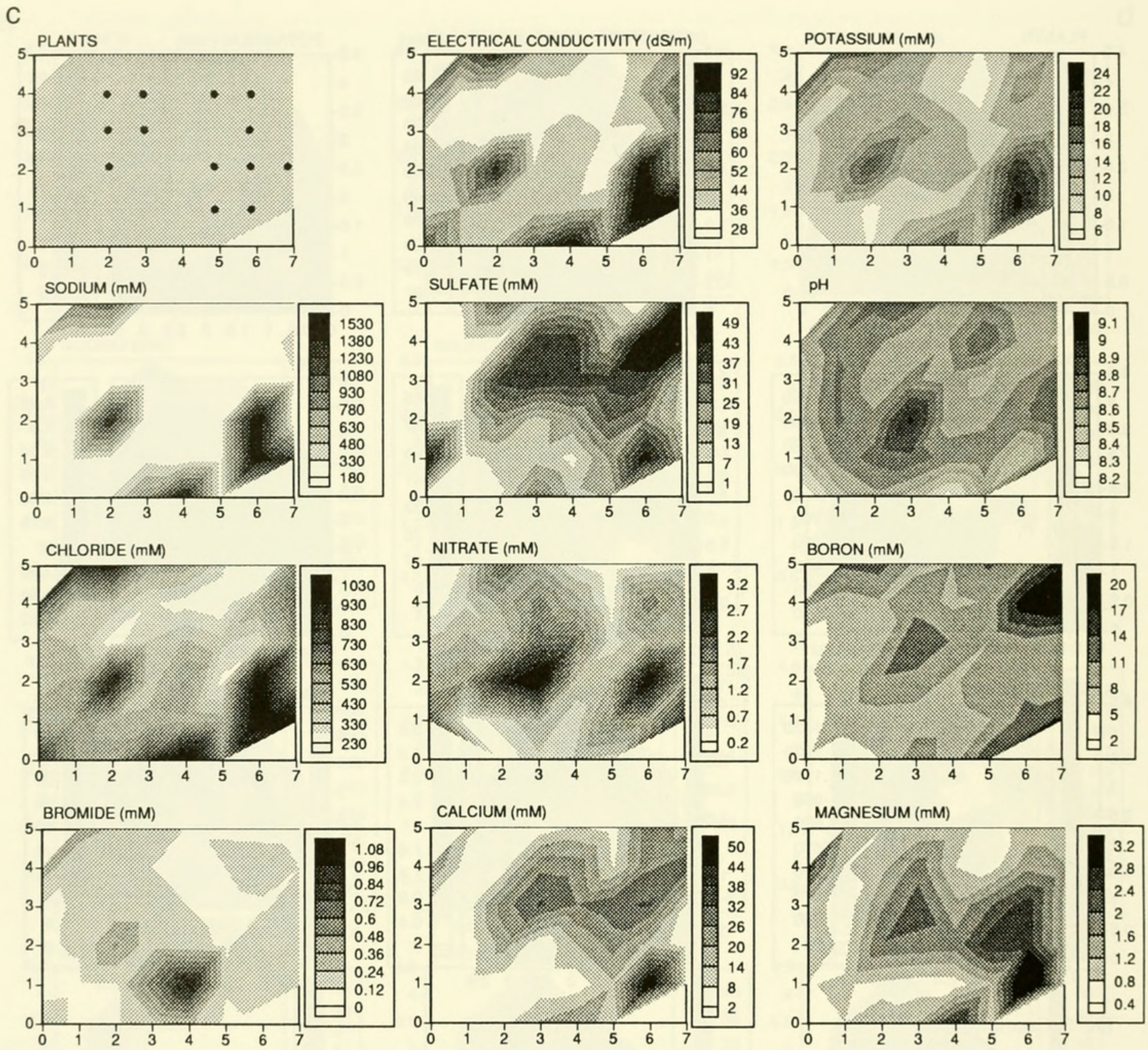

Fig. 3. Continued.

(1) a seedbed with superior physical characteristics and lower salt content favoring the recruitment of a host of plant species; (2) more favorable rooting media compared to the dense lacustrine sediments; (3) favorable bio-meteorological properties in portions of the mound due to aspect, i.e., cooler soil temperatures in midsummer on the north side of the mound or warmer temperatures in early spring on the south side of the mound.

At present, mounds function very poorly as seedbeds given the extraordinary levels of salt which would seem to negate beneficial aspect 1 listed above. Early in the life history of the mounds, however, they may have been far less saline. Throughout this study the salt content of recent eolian sand deposits on large dune fields and on the lee sides of mounds was measured. Electrical conductivity values of saturation extracts were always below 4 dS m^{-2}, indicating no osmotic limitation for germination of seeds of native plants. In the years of study, however, plant recruitment was never seen on the small eolian veneer on the sides of mounds, possibly because the veneers are too thin to allow a rooting mantle. It appears, then, that early in the life history of mounds, recruitment of plant species was not limited by salinity. Because of extreme periodicity of mound formation, we are witnessing mounds in Eagle Valley at an advanced age when extreme salinity prevents new plant recruitment. As established plants die, the no-longer-protected mounds will erode and new recruitment must await the next rare mound-building phase. Interestingly, soil description sites were revisited in

July 1997. All soil pits, which were not completely filled in with soil, have had extensive recruitment of plants. One pit has very robust plants of *A. lentiformis*, and *S. vermiculatus*.

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