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DISTRIBUTION OF WINTER ANNUAL VEGETATION ACROSS ENVIRONMENTAL GRADIENTS WITHIN A MOJAVE DESERT PLAYA

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ABSTRACT

Discovery of distinct bands of winter annual vegetation on dry playas in the Mojave Desert caused us to investigate the relationships between edaphic factors and plant distribution. We established three transects across the band of vegetation in Deadman Dry Lake and measured soil and plant characteristics. *Monolepis nuttalliana,* (Schultes) E. Greene *Oligomeris linifolia,* (M. Vahl) J. F. Macbr. and *Schismus barbatus,* (L.) Thell., all psuedohalophytic winter annuals, were encountered within the band. Soil texture and salinity appeared to be the primary determinants of the presence of vegetation. Distribution of winter annual vegetation within Deadman Playa appeared to be constrained by low soil moisture towards the outer edge, and high soil salinity towards the inner edge of the vegetation band.

Dry lakes and playas have primarily been classified according to soil chemistry, groundwater, surface features, and vegetation (Forshag 1926; Thompson 1929). Motts (1965) described six different playa types according to surface and hydrogeomorphic conditions. Stone (1956) also developed a classification scheme which divides playas into three categories: wet, dry, and mixed. Wet playas, which have groundwater within 10 m of the surface throughout most of the year, are further grouped into either clay-encrusted, salt-encrusted, or crystal body. Dry playas are divided into two main groups: clay pan or lime pan. Mixed playas have an occurrence of both dry and wet features distributed across the playa. Seasonal ponded water is mostly associated with dry playas due to the hard and impenetrable surface while wet playas pond water less frequently because on gentle slopes and hummocky surfaces resulting from ground water influences.

Phreatophytic species, those possessing extremely long roots to reach the water table, are most often associated with wet playas (Hunt 1966). Likewise, bands of halophytic plants, associated with areas with high salt concentrations, and xerophytic shrubs are often found adjacent to dry clay pan playas (Shreve 1925). Halophytic shrubs, which create centimeter high and higher soil mounds, have also been observed on one centimeter high and higher soil mounds located near the edges on dry, clay pan playas (Vasek 1983; Barbour et al. 1990). Similarly, Dahlgren et al. (1997) noted plant communities established on small dust dunes on the playas at Owens Lake, California. Indeed, these dust dunes offer plants an area of decreased salinity and increased rooting zone. Nevertheless, both dry and wet playas within the Mojave Desert are usually devoid of any vegetation (Stone 1956). While delineating the boundaries of several playas during the winter of 1992, we observed the remnants of vegetation in a band along one particular dry clay pan playa (Deadman Dry Lake) (Lichvar and Pringle 1993). During February 1993, winter annual vegetation was again observed growing in a distinct band on Deadman Dry Lake. This playa lacked both soil mounds and phreatophytic species within the band of vegetation. While vegetation literature from other parts of the country and the world described different types of vegetation patterns ranging from playas that are entirely vegetated to dominated by shrub communities along the edges (Wondzell et al. 1990; Smettan et al. 1993; Hoagland and Collins 1997), this particular distribution pattern of vegetation in relation to environmental gradients within playas of the Mojave Desert has not been well described. The objective of this research was to investigate edaphic factors that may influence the distribution of winter annual vegetation within Deadman Dry Lake, San Bernardino County, CA.

MATERIALS AND METHODS

Study site. The study area (Deadman Dry Lake or Playa) is located within the Marine Corps Air-Ground Combat Center (MCAGCC) at 34°18′36″ latitude and 116°08′06″ longitude, 12 miles north of the town of Twentynine Palms, San Bernardino County, CA (Fig. 1). Deadman Playa results from local fault block activity and is located near the bottom of a 56,860 ha watershed (Londquist and Martin 1991). The playa itself is 6300 m long along its greatest axis, has an average width of 960 m, and is approximately 361 ha in size (Lichvar and Pringle 1993). Deadman Playa has an active wash that enters from the northwest and diffuses at the

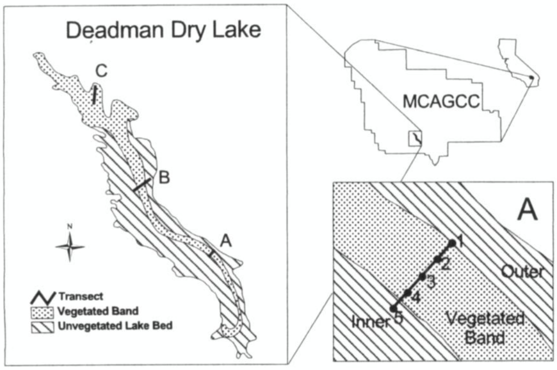

FIG. 1. Location of vegetation band within Deadman Dry Lake, San Bernardino County, CA, and locations of Transects A, B, and C. Also shown is the location of sampling points in relation to the vegetation band of Transect A. Vegetation band is not drawn to scale (MCAGCC = Marine Corps Air–Ground Combat Center).

northern part of the playa where the water remains until it evaporates. Deadman Playa is connected to Mesquite Dry Lake to the east by an inactive dry wash located at the southeast corner. Therefore, there is no evidence that surface water currently flows out of the southeast side of the playa. Thus, the association of plant occurrence with allochothonous soil material from the active wash is uncertain.

The elevation at Deadman Playa is 554 m. Adjacent areas reach elevations of 1062 m and are gently sloping on all sides except to the north, where the playa abuts a bajada. This bajada is dominated by Creosote series (*Larrea tridentata* [DC.] Cov.), while the remaining areas are dominated by the halophytic saltbushes (*Atriplex canescens* [Pursh] Nutt. and *A. polycarpa* [Torrey] S. Watson). The playa itself is unvegetated except for the here-described annual plant community and is classified as a dry, hard, clay-type playa by Stone (1956).

Deadman Playa is located in a region characterized by a warm, hyperarid climate with hot summers and mild winters (Minnich 1991). Freezing temperatures occasionally occur at Deadman Playa during December and January; summer temperatures often exceed 35°C. The temperature between January and March 1993 ranged from 25 to 33°C, while annual precipitation averages from 50 to 150 mm each year. A total of 89 mm of precipitation was received between January and March 1993.

Plant and soil sampling. Three transects were established during March 1993 across the winter annual vegetation band within Deadman Playa, CA (Fig. 1). Transects were located by selecting representative locations within the vegetated band. Transects A and B contained five sampling locations, while Transect C contained three sampling locations. Three replicate 1 m^2 quadrats, spaced 1 m apart, were placed at each sampling location along the three transects (Fig. 1). The length of each transect was 160 m, 280 m, and 200 m, respectively. Density, richness, and percent cover of all species were recorded and surface soil samples (0–10 cm deep) were taken within each quadrat. Plant densities were recorded for each species as the number of individuals per m^2, while species richness was recorded as number of species per m^2. Percent cover values were estimated for each species in each m^2. Voucher specimens were verified by and deposited at UCR. Soil samples collected from each of the three replicate quadrats at all sampling locations were pooled and subsequently analyzed for texture, electrical conductivity (EC), Water Content (WC), Ca^{+2}, Mg^{+2}, Na^{+1}, and Sodium Absorption Ratio (SAR) by the U.S. Department of Agriculture, Natural Resources Conservation Service, National Soil Laboratory, Lincoln, NE (Soil Survey Laboratory Staff 1992). Water content was obtained by analyzing double bagged soil samples measured at 15 bars. In addition, SAR, a derived salinity measure using a sodium paste extract soil solution, was calculated following direct soil analysis. Salinity and sodic status of the soils were classified using criteria established by the Soil Science Society of America (Terminology Committee 1979).

Data analysis. Pearson Product-Moment Correlation coefficients were calculated to assess the relationships among the ten environmental variables and the three vegetation variables (species richness, density, and percent cover). In addition, Canonical Correspondence Analysis (CCA: ter Braak 1988) was used to determine the relationship between the species density values, composition, and environmental variable values. Only identified species were input into this analysis. CCA is a direct gradient analysis technique that relies on the assumption of unimodal relationships between species and environmental variables. To determine the components that explained the greatest proportion of variance in the species data, stepwise forward selection of environmental variables was employed. Finally, Monte Carlo permutation analysis was performed on the first ordination axis to determine its' significance (Manly 1990). Subsequent to CCA, species density data for the 39 sampling locations were classified using TWINSPAN (Hill 1979). TWINSPAN is a polythetic, divisive classification technique which bases groupings on percent similarity. To facilitate interpretation of the dendrogram, species data in the three replicate quadrats in each of the 13 sampling locations were averaged.

RESULTS

Soils parameters. Particle size distribution of soils within Deadman Playa varied within transects (Table 1). Clay and silt content was lower at the outer edge and increased toward the inner edge of the band within each transect, while sand content

TABLE 1. MEANS (±1 SD) FOR CLAY, SILT, SAND, AND COARSE MATERIAL (>2m) CONTENT AND WATER CONTENT OF THE THREE POOLED REPLICATE QUADRATS FOR EACH SAMPLING LOCATION WITHIN DEADMAN PLAYA, CA.

Sampling location	% clay	% silt	% sand	% coarse	WC (%)
Transect A					
1	33.6	14.3	52.1	2.33	15.73
	(0.44)	(0.6)	(0.7)	(0.58)	(0.63)
2	40.9	16.4	42.7	0.83	19.40
	(2.0)	(1.1)	(3.1)	(0.29)	(0.94)
3	39.2	15.8	45.3	0.50	19.00
	(0.7)	(0)	(0.4)	(0.9)	(1.02)
4	41.7	17.1	41.2	0.50	20.07
	(3.4)	(1.2)	(4.1)	(0)	(1.05)
5	43.6	16.2	40.2	0	20.37
	(2.7)	(0.7)	(2.8)	(0)	(0.25)
Transect B					
1	17.3	10.2	72.5	25.7	7.90
	(3.50)	(1.10)	(4.50)	(3.78)	(1.50)
2	35.3	14.4	50.2	3.7	16.10
	(0.7)	(1.1)	(0.5)	(2.08)	(0.60)
3	42.5	14.2	43.0	0	18.70
	(2.8)	(1.4)	(4.2)	(0)	(3.4)
4	43.6	14.7	41.0	0	20.60
	(1.6)	(1.3)	(2.4)	(0)	(1.5)
5	50.4	20.9	28.7	0	24.2
	(1.7)	(1.0)	(2.7)	(0)	(1.1)
Transect C					
1	12.6	7.1	80.3	7.3	5.37
	(1.3)	(1.3)	(1.9)	(0.6)	(0.31)
2	28.3	32.0	30.0	0.7	15.23
	(1.9)	(5.2)	(5.3)	(1.0)	(1.82)
3	37.3	32.0	30.7	0.7	19.40
	(3.1)	(3.4)	(5.7)	(0.6)	(0.56)

was higher at the outer edge and decreased toward the inner edge. The percent coarse material, although generally low, was highest at the outer edge of the vegetation band, particularly in Transect B. EC and SAR varied widely within each of the transects (0.7 to 10.2 mmhos cm^{-1} and 8.3 to 67.5, respectively). Both EC and SAR were higher near the outer and inner edge of the vegetation band, and lower in the center of the vegetation band along Transect A (Table 2). In Transect B and C, both EC and SAR were lower along the outer edge and center of the band and increased toward the inner edge.

The salinity and sodic status of soils within Deadman Playa varied between normal (non-saline, non-sodic) and saline-sodic (Table 2). Soils were generally sodic to normal at the center of the vegetation band and saline-sodic at the inner and outer edges of the band. Soil moisture content (WC) in Deadman Playa ranged from 5.4% to 24.2%, and exhibited similar trends in each of the transects. Soil moisture was lowest at the outer edge of the vegetation band and increased towards the inner edge of the band.

Plant parameters. Six winter annual species were encountered within the vegetation band of Deadman Playa. *Monolepis nuttalliana* (Schultes) E. Greene, native species considered as a facultative wetland species (FACW) (Reed 1988) that occurs primarily in alkaline areas with clay soils, was dominant and occurred in each of the three transects. *Oligomeris linifolia* (M. Vahl) J. F. Machr. and *Schismus barbatus* (L.) Thell. also occurred, but less frequently. *Oligomeris linifolia,* a native facultative wetland species (FACW), is normally found in areas ranging from creosote scrub to alkaline sinks, while *S. barbatus,* an upland species (UPL), is an alien grass occurring primarily in dry areas associated with sandy soils. *Nama demissum* A. Gray var. *demissum* was observed on the vegetated band but was not present in any quadrat. Two additional species were observed within the quadrats, but could not be identified because the material was immature.

Subsequent to averaging the replicates within each sampling locations, species richness of winter annuals observed in Deadman Playa was greatest

TABLE 2. MEANS (±1 SD) FOR ELECTRICAL CONDUCTIVITY (EC), SODIUM ABSORBANCE RATIO (SAR), CA:MG RATIO, AND SALINITY TYPE MEASURED AT 15 BARS FROM SOILS OF THE THREE POOLED REPLICATE QUADRATS FOR EACH SAMPLING LOCATION WITHIN DEADMAN PLAYA, CA. [a] Terminology Committee (1979).

Sampling location	EC (mmhos/cm)	SAR (mol/mol)	Ca:Mg	Salinity type[a]
Transect A				
1	10.15 (2.91)	54.33 (8.99)	8.18	saline-sodic
2	2.40 (0.88)	24.33 (6.85)	3.32	sodic
3	1.16 (0.87)	21.33 (1.25)	3.35	sodic
4	1.50 (0.14)	20.00 (3.27)	4.35	sodic
5	5.99 (4.69)	37.33 (9.84)	7.68	saline-sodic
Transect B				
1	0.74 (0.092)	12.22 (4.22)	2.09	normal
2	1.10 (0)	16.00 (2.65)	3.33	sodic
3	0.98 (0.33)	14.67 (5.13)	3.35	sodic
4	1.18 (0.40)	18.00 (9.64)	3.35	sodic
5	6.15 (0.08)	67.50 (10.61)	5.00	saline-sodic
Transect C				
1	0.84 (0.19)	12.00 (4.58)	4.00	normal
2	0.95 (0.13)	8.33 (2.08)	4.65	normal
3	2.59 (1.15)	18.93 (8.05)	6.76	sodic

at the outer edge of the vegetation band in Transects A and B and lowest at the inner edge (Table 3). Richness along Transect C was greater than the richness observed along all sampling locations of Transects A and B. Average plant density was lowest at the outer and inner edges and greatest at the center of the vegetation band in Transects A and B. Transect C maintained disproportionately higher density values at all sampling locations. The average percent area covered by vegetation was lowest at the outer and inner edges of the vegetation band in Transects A and B. While, average vegetation cover was low at the inner edge of Transect C along the vegetation band and increased toward the outer edge, percent cover was greater in all zones of Transect C than in Transects A and B.

Correlations among soil and plant parameters. Pearson Product Moment Correlation coefficients suggested species density and percent cover exhibited a negative relationship with the salinity parameters of the soil (Table 4). In addition, species richness was correlated with soil texture and soil moisture parameters.

Canonical Correspondence Analysis (CCA) indicated the overall amount of variation in the species matrix accounted for by the environmental variables was 61.1% on the first axis and 10.5% on the second axis. However, initial CCA results suggested high multicollinearity existed between environmental variables. Indeed, Variable Inflation Factors were greater than the threshold amount of 20 for most variables (ter Braak 1988). A stepwise forward selection of environmental variables reported that two variables (percent clay and EC) accounted for over 90% of the variance explained on the first ordination axis (Fig. 2). In addition, Monte Carlo permutation analysis indicated that the first axis of the ordination was significant when only percent clay and EC were used ($P < 0.01$). The first ordination axis was negatively correlated with both soil texture (percent clay) and salinity parameters (EC) (Table 5). The second ordination axis, while similarly negatively correlated with percent clay was positively correlated with EC.

TWINSPAN classified the 13 pooled sampling locations into three groups which were biologically

TABLE 3. MEANS (± 1 SD) FOR THE PLANT PARAMETERS OF THE THREE POOLED REPLICATE QUADRATS FOR EACH SAMPLING LOCATION ON DEADMAN PLAYA, CA.

Transect distance (m)	Richness (No./m²)	Density (No./m²)	Cover (%)
Transect A			
1	2.3 (0.6)	25.7 (18.5)	3.7 (2.1)
2	1.7 (0.6)	267.3 (76.8)	55.7 (5.5)
3	1.0 (0)	233.3 (28.9)	50.0 (8.7)
4	1.0 (0)	58.3 (16.1)	10.0 (2.0)
5	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Transect B			
1	2.33 (1.53)	75.67 (25.5)	5.67 (2.52)
2	1.00 (0)	283.33 (14.43)	18.33 (2.89)
3	1.67 (0.58)	142.67 (62.53)	43.33 (12.58)
4	1.00 (0)	141.67 (52.04)	27.67 (11.24)
5	0 (0)	0 (0)	0 (0)
Transect C			
1	4.67 (0.58)	301.67 (114.73)	59.67 (9.29)
2	4.33 (1.16)	290.00 (101.89)	82.33 (4.51)
3	3.67 (1.16)	181.00 (36.37)	82.00 (5.57)

meaningful (Fig. 3). Initially, the two innermost sampling locations (sampling location 5) on Transects A and B were excluded from the analysis as they were unvegetated. TWINSPAN then calculated the first major division in the remaining sampling locations based on spatial orientation. The three sampling locations at Transect C were separated from Transects A and B. *Schismus barbatus,* found primarily along Transect C, was an indicator of sandy conditions at those sampling locations. The second major division extracted by TWINSPAN indicates differences in soil texture and salinity. The outer sampling locations were recognized as having either lower WC or higher percent clay values than those seen in the center of the vegetation band. Such conditions may allow *M. nuttalliana* to be more prevalent at the central sampling locations while the upland species, *O. linifolia,* was found exclusively in the outer sampling locations.

DISCUSSION

Distinct horizontal gradients in EC, SAR, and other salinity factors were observed within transects across the vegetation band within Deadman Playa. Vegetation was largely restricted to normal or sodic (non-saline) sites that generally exhibited higher soil moisture. Three saline-sodic sites were observed in this study. Of those three sites, one was sparsely vegetated and the other two were unvegetated.

Among the salinity parameters examined in this study, EC was described by CCA to be the factor related to salinity that explains the greatest amount of variation in the species richness, density and percent cover. EC was negatively correlated with total species density. Plant distribution seems to be restricted to sites with an EC of less than 5 mmhos/cm. Normally, plant distribution decreases toward the center of the playa due to increasing salt concentrations (Egbahl et al. 1989). Indeed, the average EC value on the unvegetated inner sampling locations was 6.07 mmhos cm^{-1}. While one vegetated site did exceed an EC of 5 mmhos cm^{-1}, this site also had a relatively high percent sand content and WC. The occurrence of low EC at the outer edge of Transect B may be related to the extremely high sand content of this sampling location. It is

TABLE 4. PEARSON PRODUCT MOMENT CORRELATION COEFFICIENTS AMONG SOIL AND PLANT PARAMETERS OF POOLED REPLICATE QUADRATS WITHIN DEADMAN PLAYA, CA. Levels of significance are indicated by * P = 0.05 and P = 0.001, all other correlations are insignificant (% coarse percent of coarse fragments, EC = Electrical Conductivity, SAR = Sodium Absorbance Ratio, WC = Water Content in Soil, Ca:Mg = ratio of Calcium to Magnesium).

	% clay	% silt	% sand	% coarse	EC	SAR	WC	Ca:Mg	Richness	Density	% cover
% clay	—	0.30	−0.81**	−0.71*	0.35	0.50	0.98**	0.22	−0.76*	−0.41	−0.28
% silt		—	−0.78*	−0.42	0.07	0.02	0.44	0.35	0.24	0.09	0.53
% sand			—	0.72*	−0.25	−0.31	−0.88**	−0.33	0.34	0.18	−0.14
% coarse				—	−0.24	−0.27	−0.73*	−0.40	0.23	−0.06	−0.21
EC					—	0.88**	0.38	0.80**	−0.28	−0.67*	−0.48
SAR						—	0.48	0.57*	−0.49	−0.68*	−0.55*
WC							—	0.27	−0.68*	−0.38	−0.18
Ca:Mg								—	0.27	−0.46	−0.11
Richness									—	0.54*	0.72*
Density										—	0.78*
% cover											—

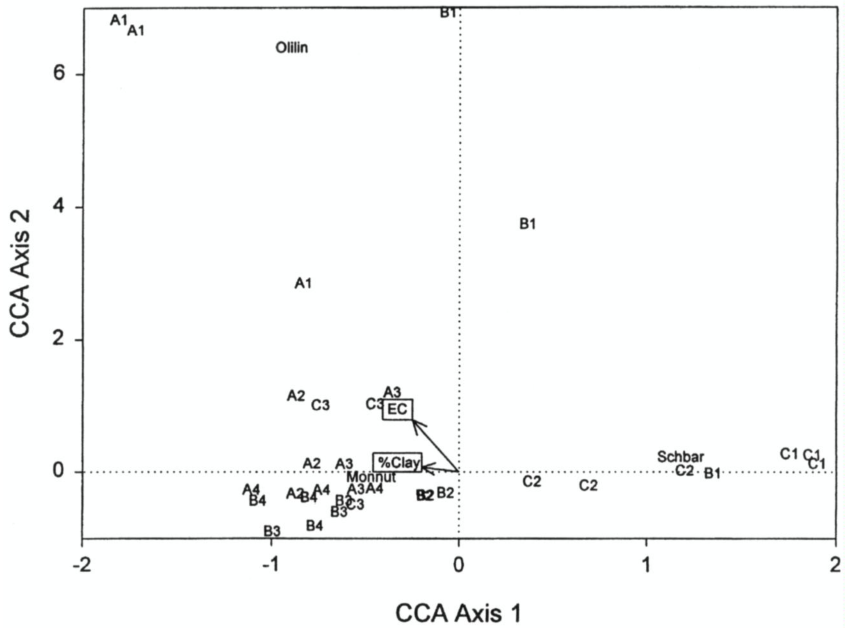

FIG. 2. CCA triplot of samples, species, and environmental variables (extracted via stepwise forward selection). Monnut = *Monolepis nuttalliana,* Olilin = *Oligomeris linifolia* and Schbar = *Schismus barbatus.*

possible that percolation of surface water through the soil profile in the outer edge of Transect B is great enough to prevent the accumulation of salts at the surface. Additional hydrologic and soil porosity studies are needed to quantify the movement of water through the soil profile.

The distribution of winter annual vegetation in Deadman Playa was also constrained by percent clay and soil moisture. Percent clay was extracted by CCA as the environmental variable which explained the most variance in the species data. As one might expect, percent clay was highly correlated with WC (Table 4). Both percent clay and WC were negatively correlated with species richness. *Monolepis nuttalliana* was clearly the most common species in the vegetated sites (>90% relative density), so variation in plant density primarily represents variation in the distribution of *M. nuttalliana.* The relationship of *M. nuttalliana* cover to salinity parameters suggests that this species is a pseudohalophyte (a species present at moist. non-saline sites within larger saline locations) rather than a true halophyte (Waisel 1972).

TABLE 5. INTRA-SET CORRELATIONS OF ALL ENVIRONMENTAL VARIABLES WITH CCA ORDINATION AXES.

Variable	Axis 1	Axis 2
% clay	−0.92	−0.15
% silt	0.04	−0.10
% sand	0.44	0.16
% coarse	0.38	0.39
Electrical Conductivity (EC)	−0.42	0.57
Sodium Absorption Ratio (SAR)	−0.59	0.41
Water Content (WC)	−0.85	−0.16
Species Richness	0.91	0.04
Density	0.53	−0.33
% cover	0.56	−0.22

The xerophytic grass, *Schismus barbatus,* was found primarily on Transect C. Transect C, had lower average values for all salinity parameters than Transects A and B. These relatively normal soils may have allowed *S. barbatus* to outcompete the more halophytic species, *M. nuttalliana* and *O. linifolia* in many sampling locations. Finally, *O. linifolia* was uncommon in most of the sampling locations. However, it was found in four of the six quadrats in the outer sampling locations. Although there are no clear indicators which explain *O. linifolia* association with the outer quadrats, it does appear to be found in areas with relatively high EC and percent sand.

In summary, the winter annual taxa encountered within Deadman Playa during the winter of 1993 appear to be pseudohalophytes distributed largely within a non-saline area within a larger saline location. The distribution of these annual taxa appears to be limited by salinity near the inner edge of the band and low water availability at the outer edge of the band. The vegetation band represents a window of suitable conditions for growth in an otherwise stressful location. It appears that, given sufficient precipitation during the winter, soil conditions are suitable for the germination and establishment of winter annual vegetation within non-saline locations of Deadman Playa.

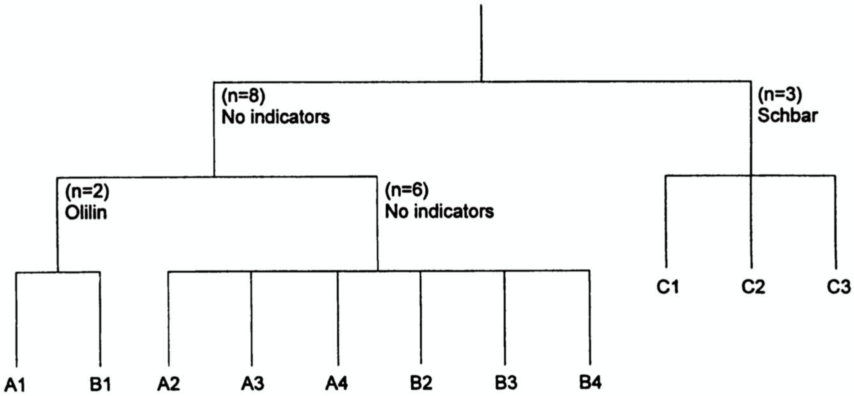

FIG. 3. Results of TWINSPAN analysis of sampling locations expressed as pooled averages of replicate quadrats. Groups distinguished at each level are shown (n = number of sampling locations per group) with indicator species. Olilin = *Oligomeris linifolia* and Schbar = *Schismus barbatus.*

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