

Vegetation patterns, microtopography, and soils on a Chihuahuan desert playa

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Abstract. Spatial patterns of vegetation on an ephemeral lake bed (playa) in the northern Chihuahuan desert were closely correlated with elevation. Distributions of species along a 265 m transect from the center to the edge of the playa showed abrupt boundaries at 110 m and 220 m. These boundaries seem related to the maximum elevation covered with standing water following complete flooding, and to an edaphic boundary between heavy clay soils at the center of the playa and adjacent soils.

The complete turnover in species composition across this transect, with an elevation change of only 85 cm, indicates that environmental gradients resulting from flooding and soil development are steep. Vegetative patterns within the lowest part of the playa were patchy, with patch diameters ranging from 2 to 5 m. These patches appear to be produced by differences in the duration and frequency of flooding between small knolls and depressions resulting from gilgai microtopography.

Keywords: Ephemeral lakebed; Flooding; Gilgai microtopography; Spatial pattern; Topo-edaphic gradient.

Abbreviations: DCA = Detrended Correspondence Analysis; OSL = Observed Significance Level.

Nomenclature: Correll & Johnston (1970).

Introduction

Most of the Chihuahuan desert lies within the Mexican Highlands section of the Basin and Range physiographic province (Fenneman 1931; Hawley 1975). Broad basins, bordered by north-south trending ranges, constitute approximately 80% of the land area. Most basins are internally drained, with the bed of a shallow ephemeral lake (locally named a playa) at the lowest point. Playa lakes are non-saline when flood water is lost via deep

percolation to a water table, but saline when primary loss is through evaporation. The surfaces of both saline and frequently flooded non-saline playas are usually barren (Peterson 1981), but occasionally support low covers of either salt tolerant or ephemeral species, respectively. Infrequently flooded fresh water playas are unique within this arid environment, supporting covers of perennial grasses and forbs which may exceed 90% following flooding (Wondzell unpubl.). Obviously, these areas have increased water availability following flooding, however, floods are episodic and much drier conditions prevail between flood events. This situation is extreme in infrequently flooded playas which may fill only once or twice a decade.

The supply of water available for plant growth is often limiting in semi-arid and arid regions. Thus, patterns of water availability produced by horizontal redistribution (White 1971; Noy-Meir 1973; Ludwig 1986) or by differences in soil texture (Wilson & Leigh 1964) often determine vegetation patterns. However, localized ponding within playas might also function as a disturbance to established plants (Kozlowski 1984).

Vascular plant species show fine scale distributional patterns within these playas. Abrupt changes in species composition on a fine spatial scale have also been observed on river flood plains (Menges & Waller 1983), drained marshland (Zedler & Zedler 1969), heathland (Kashimura 1985), and arctic tundra (Peterson & Billings 1980). These changes frequently result from large differences in soil moisture across microtopographic gradients resulting from shallow water tables or differential redistribution of water.

The objective of this study was to identify factors causing general patterns of species distributions across the surface of an infrequently flooded fresh water playa, and factors resulting in smaller scale, patchy distributions within the center of this playa.

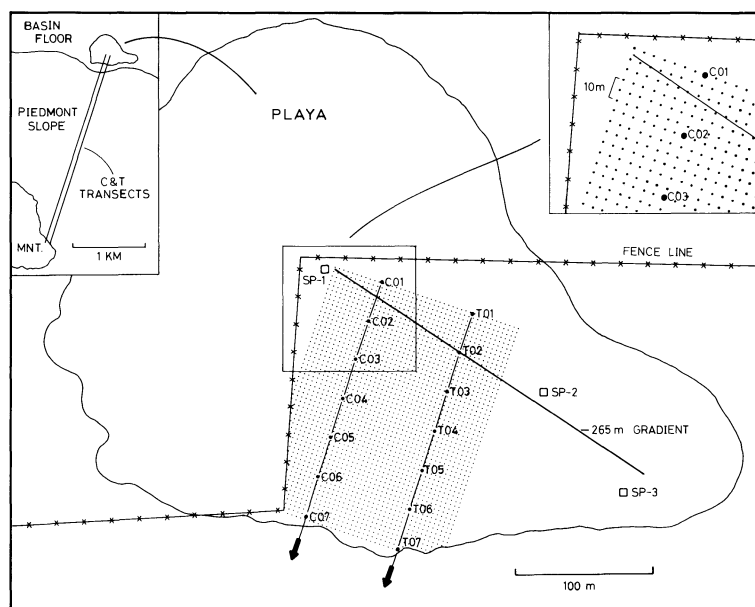


Fig. 1. The Jornada LTER site is depicted at the top left. At center are shown the outline of the playa, the location of the control (C) and treatment (T) transects, the area sampled by the 5 × 5 m grid (shaded by fine dots), the 265 m transect composed of contiguous quadrats, and the location of soil pits (SP-1, SP-2, and SP-3). A portion of the 5 × 5 m grid is enlarged at the top right showing the location of sample points.

Study site

The study was conducted ca. 40 km north of Las Cruces, Dona Ana County, New Mexico, USA, on the National Science Foundation / Jornada Long Term Ecological Research Site (32° 32' N, 106° 47' W). The study playa is at the low point of an internally drained basin in the northern Chihuahuan desert (elevation 1300 m) (Fig. 1). The playa is underlain by the Jornada I surface, a soil surface formed during the mid- to late Pleistocene in sediments deposited by the ancestral Rio Grande River (Fig. 2). This surface, represented by an argillic horizon of highly oxidized clays with some rounded gravels of mixed lithology, has been exposed by erosion in areas adjacent to the playa. Within the playa, Holocene aged lacustrine deposits of the Lake Tank surface, derived mainly from monzonite, rhyolite, and andesite, have buried the Jornada I surface (Gile & Grossman 1979). These deposits are thicker than 4.5 m near the playa center but are only 1.5 m deep near the playa edge.

Lacustrine deposits at the center of the playa are subject to increased rates and depths of weathering due to greater frequency and duration of flooding. This weathering has resulted in a high content of primary clays that shrink and swell during cycles of flooding and desiccation. During dry seasons, desiccation cracks several centimeters wide and greater than a meter deep form in the soil at the lowest part of the playa and gradually fill with loose surface material. The hydration of the clays following flooding causes soil swelling and the cracks

close. However, the presence of sediments deposited within the cracks results in the dissipation of forces generated by the swelling clays through vertical displacement of the soil. Repeated wetting and drying over many years has produced a type of patterned ground composed of a complex surface of small knolls and depressions commonly referred to as gilgai microtopography.

As elevation increases from the center of the playa, the depth and rate of weathering decreases as does the frequency and duration of flooding, eventually resulting in a soil in which the depth and content of clay is insufficient to form a vertisol. Elevations greater than 50 to 55 cm within the playa are rarely flooded (a major flood in May 1984 inundated the playa to an elevation of 53 cm above the lowest point). Soils in this region are subject to sheet flow during floods.

The climate of south central New Mexico is characterized by high temperatures, high evaporation, and low rainfall. Three distinct seasons can be identified: Winter - from November to March, a period of cool temperatures and variable precipitation resulting from broad frontal storms; Spring - from April to June, a period of high temperatures and low rainfall; and Summer - from July to October, a period of high temperatures and high rainfall resulting from localized convective storms (Table 1). These intense thunderstorms occasionally flood the playa, resulting in either partial inundation where only the lowest micro-depressions hold standing water, or, more rarely, the filling of the entire playa. Following flooding, standing water percolates to a deep water

Table 1. Statistical summary of long-term climatic data. Data are from the U.S.D.A. Jornada Experimental Range, Headquarters Station, located 7 km NE of the study site. Precipitation and temperature data are averaged from July 1914 through December 1983, and evaporation is averaged from 1930 to 1978 (Walt Conley, unpubl.).

	Winter	Spring	Summer	Year
Precipitation (mm)	54.2	28.4	150.8	233.4
Coefficient of variation	61 %	76 %	40 %	
Percent of total	23 %	12 %	64 %	
Free surface evaporation (mm)	103.2	303.2	227.7	634.1
Coefficient of variation	22 %	11 %	10 %	
Percent of total	16 %	48 %	36 %	
Maximum temperature (°C)	16.4	29.6	30.9	24.5
Coefficient of variation	9 %	5 %	6 %	
Minimum temperature (°C)	-5.4	6.9	10.3	2.9
Coefficient of variation	135 %	88 %	98 %	

table, thereby preventing the high levels of soil salinity common to many playas in arid regions (Gile & Grossman 1979). The playa flooded once in 1970, three times in 1972, twice in 1974, and partially in both 1977 and 1980 (Walter G. Whitford, pers. comm.). During the current study the playa flooded completely in May 1984, partially in August 1984, and re-flooded during both October and December 1984.

The playa is surrounded by a narrow band of shrubs, the most common of which is *Prosopis glandulosa* var. *torreyana*. This band of shrubs approximates the maximum extent of flood waters. 39 vascular plant species have been recorded on the playa. 16 of these occur only infrequently along the margin of the playa but are quite common outside the playa.

Methods

The Jornada Long Term Ecological Research Site was established in 1982, when approximately one third of the playa was fenced to exclude cattle (Fig. 1). At this time two parallel transects 70 m apart and 2.7 km in length with sampling stations at 30 m intervals were also established (Wierenga et al. 1987). These transects traverse several landscape elements, from the rocky slopes of a small isolated mountain range to the center of the playa (Wondzell, Cunningham & Bachelet 1987; see also Orlóci & Orlóci 1990). The playa contains the first seven stations of both transects. Vegetation data from these stations showed extreme differences in the cover and composition of plant species, which appeared to be related to elevation. To test this relationship we established a systematic grid of 1021 sampling points at

5 m intervals centered around these 14 stations in August 1985 (Fig. 1). Ocular estimates of the vegetative cover of each plant species were recorded from quadrats (0.2 × 0.5 m) centered on each point (Daubenmire 1959). The elevation of each point (reported relative to the lowest point encountered) was measured to the nearest centimeter using a level and rod. The maximum elevation recorded from this grid was 55 cm.

Samples were subset into 5 elevation classes: 0 - 10 cm, 11 - 20 cm, 21 - 30 cm, 31 - 40 cm, and greater than 40 cm. Species with overall average covers of less than 1% were excluded from the analysis. Using the General Linear Model Procedure (PROC GLM) of SAS Institute, Inc. (Anon. 1985) a one-way analysis of variance for unbalanced sampling designs was conducted to test for differences in species cover between elevation classes. Significant differences ($p < 0.05$) were further analyzed using a pairwise least significant difference range test.

These data allowed examination of broad-scaled relationships between species cover and elevation, but not finer-scaled resolution of plant species composition patterns along a gradient. Therefore, we also established a 265 m transect oriented to include the entire range of vegetative variability within the playa (Fig. 1). In November 1985 (end of the growing season) ocular estimates of plant species covers were made within 531 contiguous quadrats (0.2 × 0.5 m) centered along the transect line with their long axis parallel to it. Elevation measurements were taken along the transect at 50 cm intervals. The maximum elevation along the transect was 85 cm above the lowest point measured within the playa.

Detrended correspondence analysis (DCA) was used to examine the relationship between patterns in species composition and a topo-edaphic gradient. Species with a frequency less than 5% were excluded from the analysis (Hill & Gauch 1980). We used simple linear regression to test for an overall relationship between elevation and DCA axis sample scores.

Changes in DCA scores indicate changes in species composition, with complete species turnover occurring in approximately 4.0 standard deviations (Hill & Gauch 1980). Since our data were collected from contiguous quadrats, we plotted sample scores against sample position to produce an ordination trace (Shmida & Whittaker 1981). We examined the resulting trace for indication of change in species composition along the transect. A gradual change in composition would appear as a continuous change in sample scores along the trace, while an abrupt change in composition would appear as an abrupt change in sample scores. Further, high sample to sample variability would indicate compositional changes occurring within only a few sample units, while low inter-sample variability would appear as a relatively smooth line (Olsvig-Whittaker, Shachak

& Yair 1983).

Both field observations and the analysis of the ordination trace showed two vegetative boundaries along the transect. Soil pits were centered between these vegetative boundaries. The first soil pit (SP-1) was in a gilgai-depression, 18 cm above the lowest point in the playa (Fig. 1). The next soil pit (SP-2) was 41 cm above the lowest point, and the last soil pit (SP-3) was 65 cm above the lowest point in the playa. Also, a 2 m trench was dug from the top of a gilgai-knoll to the center of a gilgai-depression to check for differences in soil properties associated with changes in microtopography. Soil profiles were examined in each pit, and along the trench. Diagnostic horizons were identified, thick horizons were subdivided, and soil samples were collected from each horizon within the top meter of soil. There were no apparent differences in soil properties between the gilgai-knoll and gilgai-depression along the trench; consequently, soil horizons were not sampled. Soil samples were analyzed at the New Mexico State University Soil and Water Testing Laboratory for texture, organic matter, pH, electrical conductivity, nitrate plus nitrite, and ammonium. Due to low variability between subdivided horizons, data were averaged, weighted by the thickness of each subdivided horizon. Soils were classified according to Gile & Grossman (1979) and Soil Survey Staff (Anon. 1975).

Differences in gravimetric soil moisture with respect

to elevation were measured at four sites along the transect described above: in a gilgai-depression, 10 cm above the lowest point in the playa; on a gilgai-knoll, 25 cm above the lowest point; at an intermediate elevation, 41 cm above the lowest point; and near the playa edge, 65 cm above the lowest point. Five samples were collected from each site using a 5 cm by 20 cm soil corer. On the first sampling date only two samples were collected from both the gilgai-depression and gilgai-knoll due to clays clogging the corer, four samples were collected from each of the other sites. Samples were sealed in plastic bags, transported to the laboratory, weighed, oven dried at 70 °C for 48 h and reweighed to determine water content. Soil cores were collected weekly, starting the first day that standing water was no longer observed in gilgai-depressions following a minor flood in August 1985, and continued until water contents converged four weeks later.

Results

Soils

The first soil pit (Fig. 1) was located near the center of the playa on the Dalby Clay soil series (Gile & Grossman 1979) in an area of gilgai microtopography, with a maximum vertical amplitude of approximately 30

Table 2. Soil horizons and physical properties from soil pits.

Hor.	Depth (cm)	Sand (%)	Silt (%)	Clay (%)	O.M. (%)	pH	E.C. (mmhos/cm)	NO ₂ NO ₃ (mg /kg)	NH ₄
A. Soil Pit SP-1, Typic Torrt									
A	0 - 5	20	20	60	1.69	7.57	0.93	4.06	1.21
AC	5 - 10	20	19	61	1.06	7.74	0.48	0.56	0.29
C	10 - 98+	22	17	61	0.87	7.67	0.31	0.16	0.30
B. Soil Pit SP-2, Vertic Haplargid									
A	0 - 12	28	24	48	3.69	7.65	0.75	10.52	2.09
B _{tk}	12 - 66	30	19	51	1.18	7.73	0.30	0.64	0.67
B _{tkb}	66 - 122	63	11	26	0.31	7.81	0.33	0.16	0.09
B _{tb}	122 - 170	-	-	-	-	-	-	-	-
C. Soil Pit SP-3, Ustollic Haplargid									
A	0 - 10	28	28	44	7.23	7.89	0.84	8.13	2.10
B _t	10 - 40	52	11	37	0.84	7.53	0.43	0.92	0.56
B _{tk}	40 - 110	61	12	26	0.47	7.75	0.26	0.47	0.99
2B _t	110 - 137	-	-	-	-	-	-	-	-
3B _k	137 - 170+	-	-	-	-	-	-	-	-

Hor. = horizon; O.M. = organic matter; E.C. = electrical conductivity; '-' = not sampled.

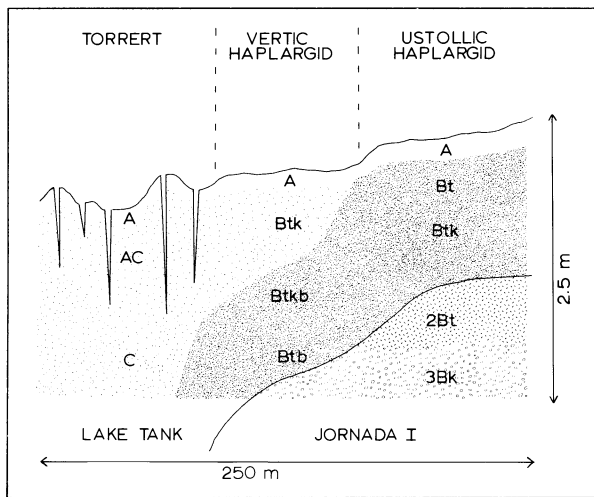


Fig. 2. Idealized cross sectional profile of the playa showing the edaphic gradient from the playa edge (right) to the center (left).

cm over horizontal distances of 1 to 5 m (Fig. 2). Clay contents were 60 % or greater in all horizons (Table 2A). Cracks up to 5 cm wide were visible at depths of 1 m. Smaller cracks, extensive polished surfaces (where surfaces of soil fragments had been smoothed by rubbing during shrinking and swelling), and tilting of major structural units 30° from the vertical were also observed. Repeated wetting and drying cycles have caused churning and prevented development of diagnostic soil horizons in which silicate clay or carbonate accumulated (Buol, Hole & McCracken 1973; Gile & Grossman 1979). This soil is classified as a typical torrert.

The upper soil horizons of the soil pit located near the margin of the playa (Figs. 1 and 2) on the Headquarters variant of the Dalby Clay soil series had reduced clay contents compared to the other soils. Also, calcic and argillic horizons were well developed (Table 2C). A buried argillic horizon was present at 110 to 137 cm depth which was underlain by a layer of rounded gravels, marking a discontinuity to the older sediments of the Jornada 1 surface. This soil is classified as an ustollic haplarginid.

The second soil pit (Figs. 1 and 2) was located between the soil pits described above. Here, weathering resulted in a layer of clays 66 cm deep (Table 2B) in which polished surfaces were rare but clay skins were common. The presence of small cracks, averaging 35 cm apart but not open to the surface nor exceeding widths of 1 cm at 50 cm depth, indicated that these clays also expanded and contracted with repeated wetting and drying. However, both the clay content and depth of clays were insufficient to result in churning, thus

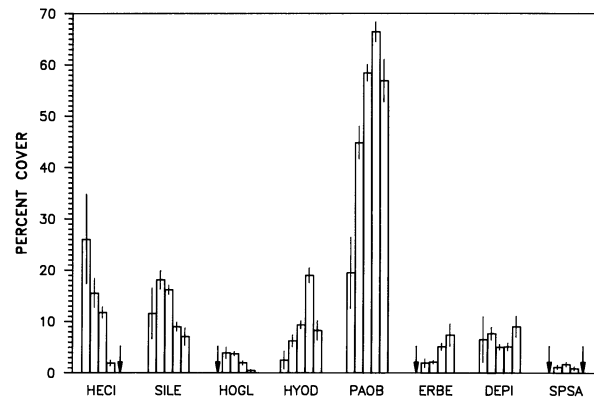


Fig. 3. cover of the eight dominant vascular plant species $\bar{X} \pm SE$ for five elevation classes within the playa. From left to right, each cluster of bars represents the 0 - 10 cm, 11 - 20 cm, 21 - 30 cm, 31 - 40 cm, and greater than 40 cm classes, with $N = 20, 131, 553, 253,$ and $64,$ respectively. Arrows indicate mean covers of 0.0 except for HOGI with a cover = 0.05 and S.E. = 0.05. HECI = *Helianthus ciliaris*; SILE = *Sida leprosa*; HOGI = *Hoffmanseggia glauca*; HYOD = *Hymenoxis odorata*; PAOB = *Panicum obtusum*; ERBE = *Erigeron bellidistrum*; DEPI = *Descurainia pinnata*; and SPSA = *Sphaerosphysa salsula*.

diagnostic horizons were present. A layer of rounded gravels, similar to those described for the previous pit, was present at a depth of 170 cm and also marked a discontinuity to the older sediments of the Jornada I surface. This soil is intermediate between the two described above and is classified as a vertic haplarginid.

Flooding

Following the flood of May 1984, evapo-transpiration and infiltration of standing water exposed the highest portions of the playa within a week, but took more than three weeks to expose the micro-depressions at the center of the playa. Several minor floods during 1984 and 1985 only filled micro-depressions.

Soil water contents at four microsites were compared following one minor flood event. Initially, the soils in the micro-depressions were saturated with water, while soils from higher elevations were drier. This inverse relationship between elevation and soil water content was maintained for several weeks, with water contents beginning to converge by the fourth week.

Vegetation

A total of 32 vascular plant species were encountered in the grid samples, of which only eight species had an overall average cover greater than 1 %. Analysis of variance showed that all species, except the perennial

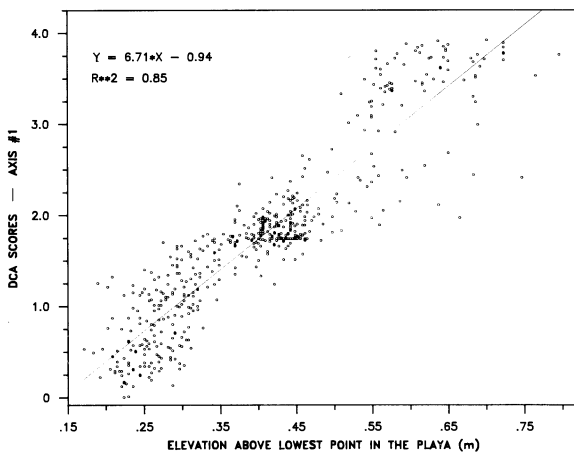


Fig. 4. Regression of sample scores on the first DCA axis against elevation.

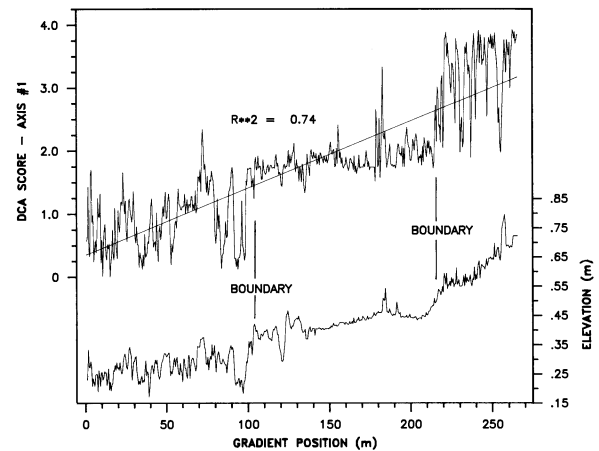


Fig. 5. Ordination trace of sample DCA scores on the first axis (upper line), and a surface profile of the playa showing sample elevations (lower line), graphed against gradient position.

forb, *Sphaerosphysa salsula*, had significant differences in cover between elevation classes. The perennial forb, *Helianthus ciliaris*, reached maximum cover in the 0 - 10 cm elevation class (Fig. 3). Two perennial forbs, *Sida leprosa* and *Hoffmanseggia glauca*, reached maximum cover in the 10 - 20 cm and 20 - 30 cm elevation classes. The annual forb *Hymenoxes odorata* and the perennial grass *Panicum obtusum*, reached maximum cover in the 30 - 40 cm elevation class. However, *Panicum obtusum* dominated all but the lowest and highest elevations within the playa (the highest portions of the playa were only sampled on the 265 m transect). *Erigeron bellediastrum*, a perennial forb, reached maximum cover in the 40 - 50 + cm elevation class. Only the annual forb, *Descurainia pinnata*, lacked an interpretable trend with elevation (Fig. 3).

Eigenvalues of the first four DCA axes were 0.74, 0.29, 0.16 and 0.12 respectively. Because eigenvalues of the second, third, and fourth DCA axes were small relative to the first axis, and there were no significant relationships between elevation and these DCA scores, only the results from the first axis are reported. There was a significant linear relationship between sample scores on the first DCA axis and elevation along the 265 m transect ($n = 529$, $r^2 = 0.85$, $OSL < 0.0001$) (Fig. 4). DCA scores ranged from 0.0 to 4.0 standard deviation units over the length of the 265 m transect, indicating a nearly complete turnover in species composition. However, the change in DCA scores is not gradual; rather, two abrupt transitions are apparent in the ordination trace (Fig. 5) ca. 110 m and 220 m from the center of the playa.

The ordination trace shows a relatively high degree of sample to sample variability in DCA scores within the first 110 m of the transect (Fig. 5). The surface profile of the playa also shows high sample to sample variation in elevation due to the gilgai microtopography. A comparison between the surface profile and the ordination trace shows that micro-knolls roughly correspond to peaks in DCA scores, while micro-depressions roughly correspond to troughs in DCA scores. Within this region three species, *Panicum obtusum*, *Helianthus ciliaris* and *Sida leprosa*, co-dominant, showing strong microsite preferences. *Panicum obtusum* is most common on relatively high and wide micro-knolls, less common on smaller knolls, and least common in micro-depressions. The distribution patterns of *Helianthus ciliaris* and *Sida leprosa* are the opposite, being most common on relatively low and broad micro-depressions, and becoming less common on micro-knolls.

The abrupt change in the ordination trace at 110 m occurs at the boundary between the gilgai microtopography of the typical torrert and the relatively smooth surface of the adjacent vertic haplargid. The region between 110 and 220 m has a relatively low sample to sample variability in DCA scores indicating low microsite variation (Fig. 5). Within this region only one species, *Panicum obtusum*, is dominant, maintaining nearly continuous cover. Though the soil boundary is not as sharp as the vegetative boundary, the dominance of high gilgai-knolls between 110 m and 140 m creates an abundance of microsites dominated by *Panicum obtusum*.

The second abrupt change in the ordination trace

occurs at 220 m on the transect. At this point the surface of the playa begins to slope upwards at a relatively steep angle, increasing in elevation from 45 cm to 55 cm above the lowest point over a horizontal distance of 10 m (Fig. 5). At elevations above 55 cm, *Hilaria mutica* replaces *Panicum obtusum* as the dominant species, with *Calliandra humilis* becoming sub-dominant. Beyond 220 m, the ordination trace shows high sample to sample variability (Fig. 5). The low points in the ordination trace in this region corresponded to samples with high *Panicum obtusum* cover. However, there were no indications of microsite differentiation. Apparently, the sampling scale was fine enough to detect the natural grain of the vegetation.

Discussion

Differences in the frequency and duration of flooding are the most obvious factors which vary with elevation in the playa and could regulate species distributions. Field data were collected following two growing seasons during which the playa was frequently flooded, therefore direct influences from flooding were to be expected. However, plant distributions were also related to soil properties, as they changed from aridisols at the playa margin to vertisols in the central portion of the playa. The effects of flooding and soils are not independent. Flooding often leads to increased denitrification but also to the addition of dissolved nutrients and the deposition of organic matter. Over longer time periods, flooding is one of the primary factors regulating the deposition and weathering of sediments which has led to the edaphic gradient within the playa.

Helianthus ciliaris, *Sida leprosa*, and *Panicum obtusum* appear tolerant of flooding and are quite successful within the lowest portions of the playa. The dominance of *Panicum obtusum* at slightly higher elevations, such as gilgai-knolls, may be indicative of a somewhat lower tolerance to anoxic soils or disturbance by soil cracking. The increased dominance of *Panicum obtusum*, absence of *Helianthus ciliaris*, and decreased abundance of *Sida leprosa*, at intermediate elevations on the vertic haplargids located between 110 m and 220 m along the 265 m transect is also likely a result of both reduced flooding and soil cracking. In any case, the rapid change in species composition indicates a sharp change in environmental conditions across the transition from the gilgai microtopography of the typical torret to the smooth and slightly higher surface of the vertic haplargid.

The rapid change in species composition at 220 m along the 265 m transect also indicates a sharp change in environmental conditions. At this point, the elevation of the playa surface increases rapidly to heights greater

than 55 cm above the playa's lowest point. Following complete flooding of the playa in May 1984, the maximum extent of flood water was approximately 53 cm above the playa's lowest point, indicating that this boundary separates those portions of the playa occasionally holding standing water from those areas which are only subject to sheet flow during floods. *Hilaria mutica* and *Calliandra humilis* are uncommon at elevations lower than 55 cm, indicating that these species are intolerant of flooding. In contrast, *Panicum obtusum* is frequent at elevations greater than 55 cm, and is occasionally found outside the playa indicating that it does not require flooded conditions for growth.

During long, flood-free time periods moisture available for plant growth would be in very low supply. In addition, according to the reverse textural relationship proposed by Noy-Meir (1973), under the same precipitation inputs, arid soils with high clay contents (such as the playa) would have less water available for growth than the adjacent, more coarsely textured soils. Therefore, during long flood-free periods biomass (and cover) of perennial plants should decrease relative to the immediate post-flood environment. Observations made during 1986 and 1987 suggest this to be true. As a consequence of this reduced cover of perennials, more open space becomes available for colonization by ephemerals and short-lived perennials, and spatial patterns become less clearly defined. Flooding, however, kills these intolerant species, and open spaces are once again available for colonization by flood-tolerant perennials.

Therefore, the rate at which species can colonize open space on the surface of the playa following flooding may be an important determinant of spatial distributional patterns. The stoloniferous growth habit of *Panicum obtusum* would allow rapid colonization of open space following flooding when soils are saturated. In contrast, the rhizomatous growth habit of *Hilaria mutica* would be inhibited by these conditions. Therefore, a combination of differential soil moisture regimes caused by soil texture differences and differential growth habits between these two species may account for their separation along the gradient.

The soils in portions of the playa dominated by *Hilaria mutica*, which absorb water from sheet flow when the playa floods, are seldom saturated. Also, following small storms, these areas frequently receive run-on water that is absorbed within 40 or 50 m of the playa edge, never flooding any portion of the playa (Wondzell pers. obs.). The combination of increased soil moisture availability for loamy soils of this portion of the playa under ambient precipitation (Noy-Meir 1973) and additions of run-on water increase the total soil moisture available for plant growth during flood free intervals. The cover of *Hilaria mutica* seldom decreases during

these periods, and open spaces are not formed. Therefore, the rate at which open space is colonized, following flooding, is of decreased importance in this area.

Conclusions

The differences in species distributions between elevation classes (Fig. 3) and the strong linear relationship between first axis DCA scores and elevation (Fig. 4) indicate that elevation is a complex variable closely related to factors controlling the distribution of plant species within the playa. Differences in the frequency and duration of flooding across the topographic gradient, and differences in the physical and chemical properties of soils across the edaphic gradient, are both strong environmental factors, either of which is sufficient to control distributions of plant species. Undoubtedly, both of these factors contribute to the observed patterns.

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