The distribution of vascular plant species and guilds in space and time along a desert gradient

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Abstract. We studied distribution patterns of vascular plant species and environmental variables for three years along a permanent transect traversing a closed-drainage watershed in the northern Chihuahuan Desert of south-central New Mexico, USA. The transect extended for 2.7 km from a basin floor playa (1310 m elevation, fine-textured soil), across a piedmont slope, and onto the base of a granitic mountain (1410 m elevation, coarse-textured soil). The gradients in elevation and soils across our transect, along with variable seasonal rainfall, downslope redistribution of water and organic matter, and soil texture-related variation in infiltration, water holding capacity, and moisture release characteristics, interact to generate a complex spatial and temporal gradient of available soil water and nitrogen. We grouped plant species into guilds according to growth form and photosynthetic pathway type. These guilds are spatially and temporally differentiated along the transect such that particular groups utilize particular seasonal phases or spatial regions of the gradient. We identified six distinct plant communities along the transect. C_4 perennial grasses dominated the mesic/high nitrogen portion of the gradient, which occurred at the highest (upper piedmont grassland, dominated by *Bouteloua eriopoda*) and lowest (playa, dominated by *Panicum obtusum*) elevations along the transect. C_3 shrubs were dominant in the xeric/low nitrogen portion of the gradient located near the middle of the transect (bajada shrubland, dominated by *Larrea tridentata*). C_3 shrubs also dominated a narrow zone of vegetation located adjacent to the playa (playa fringe, dominated by *Prosopis glandulosa*). C_4 perennial grasses, C_3 subshrubs, and C_3 and C_4 perennial forbs and annuals were co-dominant in the intermediate locations along the gradient, which occurred below (mixed basin slopes) and above (lower piedmont grassland) the bajada shrubland. Life-form distribution patterns at the small scale of our study reflect some of the patterning that occurs at larger scales in response to climate gradients. The distributions of some species and guilds along the transect are apparently modified by competitive interactions.

Introduction

Although the deserts of the Southwest USA are characterized by low plant productivity and low cover relative to other ecosystems in North America (Webb et al. 1978), these desert plant communities have a greater diversity of growth forms than other North American ecosystems (Shreve 1942; Whittaker & Niering 1965). Extremely arid desert ecosystems are characterized by low species diversity, but, semi-arid ecosystems within the North American deserts often have higher species diversity than more mesic ecosystems (Whittaker 1975). We hypothesize that this variety is due to the occurrence of sharp environmental gradients and small-scale heterogeneity within the desert landscape which is exploited by species having widely different structural and functional adaptations.

We are interested in how photosynthetic pathway type (physiological trait) and growth form (morphological traits) vary with respect to environmental gradients in space and time. Our rationale for looking at these attributes is that both morphological and physiological traits determine the capacity for resource acquisition, and these two particular traits are recognized as adaptations

to environment on broad geographic scales. As an example, C_3 photosynthesis is often characteristic of temperate climates while C_4 or CAM photosynthesis is favored in warm or arid climates (Teeri & Stowe 1976; Ting 1976; Stowe & Teeri 1978; Hattersley 1983). Similarly, specific growth forms are characteristic of certain environments (Raunkiaer 1934; Whittaker 1975), such as shrubs in extreme arid and Mediterranean type climates (Schulze 1982; Danin & Orshan 1990), or ephemerals in desert environments (Noy-Meir 1979/ 80). Other studies have documented changes in growth form distributions over large regions (e.g. Danin & Orshan 1990; Floret et al. 1990); Orlóci & Orlóci (1990) similarly described the distribution of growth form characteristics along the same Jornada transect; Montaña (1990) studied life-form distribution along a land form gradient in the southern part of the Chihuahuan Desert. However, many desert plant communities are composed of species with a variety of growth forms and all of the three photosynthetic pathway types (Shreve 1942; Whittaker & Niering 1965; Syvertsen et al. 1976; Kemp 1983) growing in relatively close proximity to one another.

Our study examines the small-scale spatial and temporal distribution patterns of vascular plant species and guilds along a transect traversing a northern Chihuahan desert landscape by (1) classifying the plant communities along the transect, (2) defining the affinity of particular guilds to specific community types, (3) quantifying the gradients in species distributions along the transect, and (4) correlating these gradients to environmental variables measured along the same transect.

Methods

Study site

In February 1982 a 2.7 km transect was established on the Jornada Long-term Ecological Research (LTER) site located on the New Mexico State University Ranch on the Jornada del Muerto Basin of south-central New Mexico, USA (Dona Ana County). The transect is centered at UTM 3 599 500 m N, 331 200 m E, zone 13. The study site is located within the Mexican Highlands Section of the Basin and Range Physiographic Province (MacMahon & Wagner 1985). The transect traverses a 1500 ha closed-basin watershed draining the slopes of an isolated, granitic mountain (Mount Summerford), and extends in a SSW direction from an ephemeral lake or playa located on the basin floor, across a fan piedmont and alluvial fan located on the piedmont slope, and onto the base of the mountain (Wondzell, Cunningham & Bachelet 1987). Elevation along the transect ranges

Table 1. Seasonal distribution of rainfall (mm) at the LTER Jornada research site (data courtesy of W. G. Whitford). Average is based on 1941-1970 NOAA Jornada Experimental Range weather data.

Year	Winter	Spring	Summer	Total
1982	36	14	125	175
1983	56	38	127	221
1984	27	69	220	315
Average	52	20	143	215

from 1310 m in the playa basin to 1410 m at the upper end. Soils range from fine-textured, clay soils (vertisols) within the playa basin to coarse-textured gravely, sandy soils at the base of Mt. Summerford (Wierenga et al. 1987). The geomorphology of the region and site has been described in detail by Gile, Hawley & Grossman (1981), Wondzell, Cunningham & Bachelet (1987) and Lajtha & Schlesinger (1988). Historical records indicate that the Jornada del Muerto was dominated by grassland ecosystems at the time of European settlement, but during the late 1800's to early 1900's these grasslands became desertified into ecosystems dominated by desert shrubs, which has been attributed to climate change and/or overgrazing (Buffington & Herbel 1965; Pieper et al. 1983; Schlesinger et al. 1990). Our study site contains both remnant desert grassland and desert shrub plant communities. Since the 1920's the study site has been only moderately to lightly grazed, and, there has been no grazing since the establishment of the LTER site in 1981. No fences have ever crossed the transect, thus, grazing pressure differences were likely unimportant in causing any of the observed vegetation zonation patterns.

The climate of the northern Chihuahuan Desert is arid to semi-arid with a mean annual precipitation of 215 mm. There are three rather distinct seasons (Walt Conley unpubl.; Table 1): (1) hot, dry springs (April-June); (2) hot, moist summers (July-October), with fairly predictable annual occurrence of rainfall, most of which occurs as intense convective thunderstorms that are highly localized and of intense duration (Schmidt 1986); and (3) cold, moderately dry winters (November - March), with highly variable annual rainfall, most of which occurs as low intensity rainfall over large areas (Schmidt 1986). Precipitation was below average in about 2/3 of all years from 1916-1972 (Pieper et al. 1983). Droughts, in which both summer and winter rainfall were deficient for two or more consecutive years, have occurred four times since 1900: 1908-1913, 1934-1935, 1951-1956, and 1963-1965 (Neilson 1986).

Sampling

91 sampling stations were located at 30 m intervals along the transect. At each station a 30 m line was positioned perpendicular to the transect and cover (percent of line intercepted by living plant canopy) of all vascular plant species was measured twice a year for three years (1982 - 1984); during late March - early April (following winter rains, if any) and during mid October (after the summer rainy season). These sampling times provided a record of maximum cover accumulated during the winter and summer seasons, respectively. In addition to the vegetation cover data, other investigators associated with the Jornada LTER program measured several additional environmental variables at the same permanent stations along the transect, including soil physical characteristics and volumetric soil water content (Wierenga et al. 1987), soil nitrogen (Whitford, Reynolds & Cunningham 1987), elevation, soil water potential, rainfall, and maximum and minimum air temperatures (unpubl. Jornada LTER data). Because two stations (90 and 91) extended onto the base of the mountain and had extremely different species composition relative to the other transect stations, we elected to exclude them from our analyses.

Vascular plant guilds

We grouped all vascular plant species ($n = 125$) into guilds (functional groups) based on similar methods of resource acquisition in time and space. We defined guilds with a combination of photosynthetic pathway type (C_3, C_4, or CAM) and growth form class (shrub, subshrub, and perennial or annual grass or forb). Photosynthetic pathway determinations follow Syvertsen et al. (1976) and Kemp & Gardetto (1982). Growth form determinations were based on observations of the species phenologies for three years, and on information in Correll & Johnston (1970). Nine photosynthetic pathway / growth form guilds occurred along the transect (Table 2, below):
C_3 annual forbs;
C_4 annual forbs;
C_4 annual grasses;
C_3 perennial forbs;
C_4 perennial forbs;
C_4 perennial grasses;
C_3 subshrubs;
C_3 shrubs;
CAM stem succulents
(there were no C_3 annual or perennial grasses, or woody C_4 plants along the transect). We analyzed patterns of vegetation distribution using cover abundances of both species and guilds.

Community classification

Our samples were from ordered locations along a transect with obvious zonation of vegetation. We used split moving - window boundary analysis - SMW (Webster 1978; Ludwig & Cornelius 1987) as a tool for locating natural discontinuities, or boundaries between adjacent groups of relatively homogeneous sample units (stations). We conducted our analysis using squared Euclidean distance (SED), which emphasizes differences between the most abundant species. We report results from a window width of six transect stations, which revealed the major discontinuities along the transect with a minimum of noise (Ludwig & Cornelius 1987).

We classified the stations from each data set (spring and fall of 1982, 83, 84) using divisive, hierarchical cluster analysis via the Cornell Ecology Program, Two-way Indicator Species Analysis (TWINSPAN; Gauch & Whittaker 1981). We used these results, along with the locations of discontinuities provided by SMW, to define the plant community types along the transect. We also used the TWINSPAN analysis to examine how the groups of stations cluster together through time.

We derived a geometric model depicting the association of guild types with particular plant communities by conducting a discriminant ordination (Pielou 1984) using canonical discriminant functions analysis (Proc CANDISC; SAS Institute, Inc. 1985). We conducted this analysis using cover abundances of plant guilds averaged over all three summer sampling periods. We defined groups of stations according to their community classification. We treated the derived canonical discriminant functions as orthogonal coordinate axes and plotted the community types according to mean scores on the first two canonical variates (Klecka 1980). We drew confidence circles around the group centroids according to Pimentel (1979). We then projected the original variables as vectors into the two-dimensional canonical space with the vector direction being determined by the between-groups correlations of the original variables (i.e. guild cover) with the derived canonical variables (Pimentel 1979; Klecka 1980). Such projected vectors tend to point toward the vegetation zones having the highest mean level for that particular guild. We made the relative lengths of the projected guild vectors proportional to the univariate F ratio for that guild. Thus, the directions and lengths of guild vectors relative to the location of vegetation zone centroids indicate the relative dominance of particular guilds within specific plant community types.

Gradient analysis

We ordinated sample stations using detrended correspondence analysis (DCA; Hill & Gauch 1980) to quantify relationships among stations along the topo-edaphic gradient without regard to location, and to examine the gradient along which the plant species were distributed. We conducted our ordination using cover abundances of plant species for data averaged over all three summer sampling periods. To determine which environmental factors were most closely associated with the species distributions we correlated (Spearman's product moment correlation coefficient) scores on the DCA axes with the environmental variables. We only included 19 of the 89 stations (1, 5, 10, 15,..., 85, 89; ordered from the playa) that had measurements for all the environmental variables in the correlation analysis.

Results

Community classification

Split moving-window boundary analysis

We analyzed each winter and summer data set separately. SED distance peaks from summer cover data were generally more prominent than those from winter, probably due to the higher cover of most perennial species in summer. The locations of boundaries in summer data from the different years were very similar, thus, we only present results from a pooled data set consisting of average cover values for the 1982 - 1984 summer sampling periods. The SED distance profiles showed three very prominent discontinuities distinguishing four vegetation zones (Fig. 1A). The sharpest discontinuity (i.e. the boundary with the highest SED peak) occurred at transect position 7, and separated the vegetation of the playa basin from the remainder of the transect. A very distinct discontinuity also occurred at transect position 72, which separated the grassland vegetation of the upper piedmont slope from the vegetation below. A third distinct discontinuity was located at transect position 81, which divided the piedmont slope grassland into two communities, which we refer to as the upper and lower piedmont grassland vegetation zones. No other distinct SED peaks were present in the SMW distance profile graph.
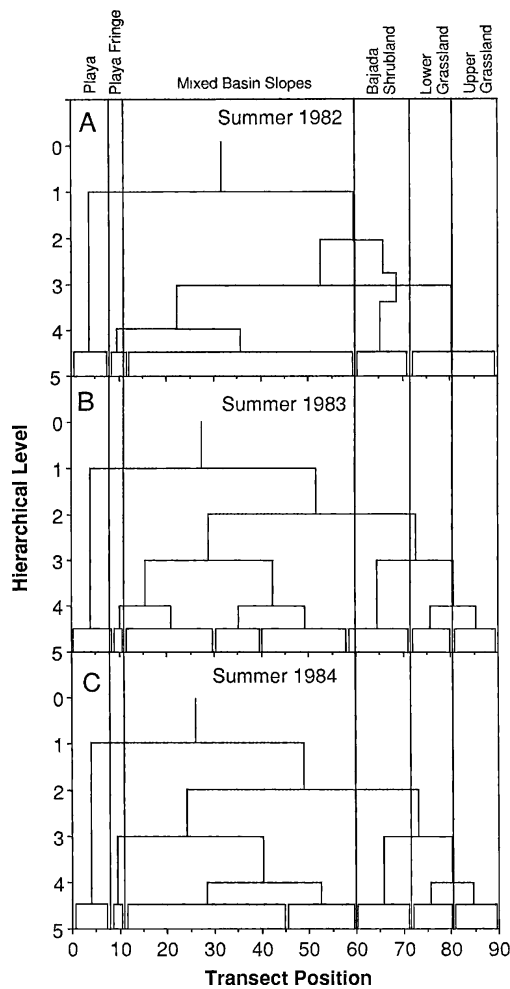
TWINSPAN classification

Transect positions from each summer and winter data set for 1982, 83 and 84 were individually classified using cover abundances of species (Fig. 2). Winter and summer data classified similarly, thus, we only include results from summer here. The first hierarchical level
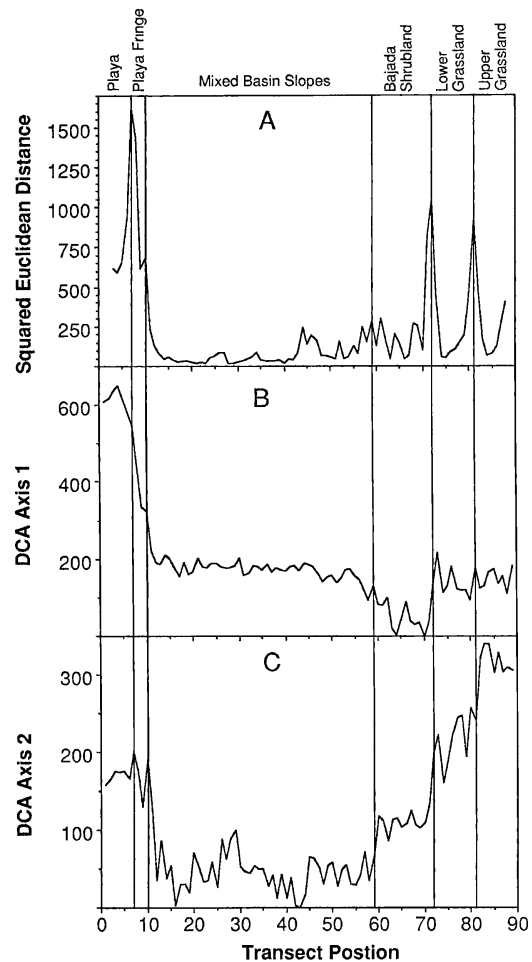
Fig. 1. Traces of (A) squared euclidean distances from split moving - window boundary analysis (window size = 6), and ordination scores on (B) the first and (C) the second DCA axes, of summer 1982-84 average species cover for each transect position. Distance along the transect (m) may be found by multiplying the transect station number by 30. Vertical lines through graphs indicate the locations of boundaries between vegetation zones. Vegetation zone names are given across the top.

always separated the playa transect stations from the rest. Further hierarchical divisions produced slightly different clustering of stations depending on the season and year. When the analysis was carried out to four hierarchical levels, five to eight clusters of stations were created. Clusters which were always created included the playa (stations 1 - 7), playa fringe (stations 8 - 10), mixed basin slopes (stations 11 - 59), bajada shrubland (stations 60-71), and piedmont grassland (stations 72 - 89). Lower (stations 72 - 81) and upper (stations 82 - 89) piedmont grassland zones were separated in 1983 and 1984. The basin slopes were found to be heterogeneous
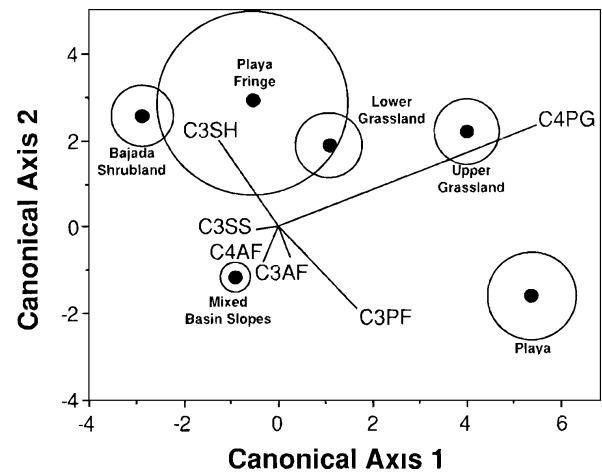
Fig. 2. Dendrograms summarizing the first four split levels from TWINSPAN classification of species cover from summer (A) 1982, (B) 1983 and (C) 1984. Distance along the transect (m) may be found by multiplying the transect station number by 30. Vertical lines through graphs indicate the locations of boundaries between vegetation zones. Vegetation zone names are given across the top.


Fig. 3. Orthogonal plots of vegetation zone group centroids on the first two canonical axes from canonical discriminant functions analysis of summer 1982-84 average guild cover. Lines extending outward from the origin are projections of the most prominent discriminator variables; circles represent confidence circles around group centroids. Vascular plant guilds: C3SH = C_3 shrubs, C3SS = C_3 subshrubs, CAM = CAM succulents, C4PG = C_4 perennial grasses, C3PF = C_3 perennial forbs, C4PF = C_4 perennial forbs, C4AG = C_4 annual grasses, C3AF = C_3 annual forbs, C4AF = C_4 annual forbs.

in the TWINSPAN analyses and were variously divided into one, two, or three zones, depending on year and season, hence, we considered them to belong to one community type in all our other analyses.

Canonical discriminant functions analysis

Based on lengths of the projected guild vectors, canonical discriminant functions analysis showed that the most prominent discriminating variables among zones were C_4 perennial grasses, C_3 shrubs, C_3 perennial forbs, C_4 annual forbs, C_3 annual forbs, and C_3 sub-shrubs (Fig. 3). Vector directions indicated that: (1) C_4 perennial grasses had their greatest cover in the playa and upper

piedmont grassland zones; (2) C_3 shrubs had their greatest cover in the playa fringe and bajada shrubland zones; (3) C_3 perennial forbs were most abundant in the playa and mixed basin slopes zones; and (4) C_3 subshrubs and C_3 and C_4 annual forbs were most abundant in the mixed basin slopes zone. With the exception of the playa fringe zone (because of its small sample size; $N = 3$), all vegetation zones were quite distinct from each other in guild composition (i. e. all Mahalanobis' distances between groups are significant at $p < 0.05$).

Vegetation zones

Playa (stations 1-7): This vegetation zone was the most distinct in all our analyses. In addition to having sharply different soil texture (see Fig. 5A), the playa differs from the rest of the transect in that it is occasionally flooded. The species found in the playa are virtually absent from elsewhere on the transect. These species must have the capacity to tolerate (e. g. perennials), and/or respond to (e.g. annuals) (1) disturbance from flooding, sometimes for extended periods, (2) disturbance from swelling - heaving and shrinking - cracking associated with wet-
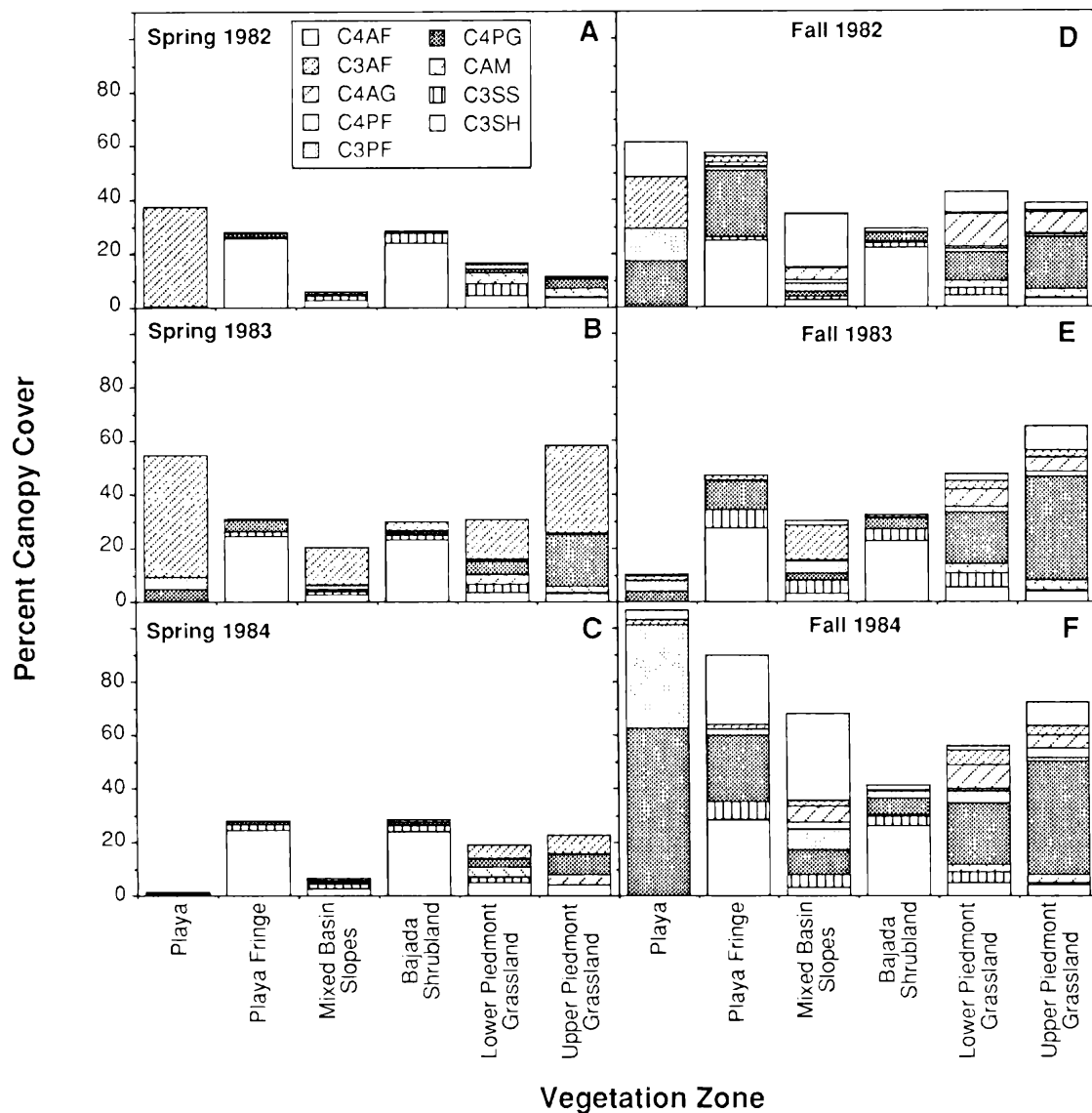
Fig. 4. Mean cover of vascular plant guilds in the six vegetation zones occurring along the transect from winter (A - C) and summer (D - F) of 1982, 83 and 84. Vascular plant guilds: C3SH = C_3 shrubs, C3SS = C_3 subshrubs, CAM = CAM succulents, C4PG = C_4 perennial grasses, C3PF = C_3 perennial forbs, C4PF = C_4 perennial forbs, C4AG = C_4 annual grasses, C3AF = C_3 annual forbs, C4AF = C_4 annual forbs.

ting-drying cycles in vertisols (Buol, Hole & McCracken 1980), and (3) competition from close neighbors (the playa had greater than 100% cover in summer 1984) - characteristics which set species in the playa apart from those on the rest of the transect. The three most prominent guilds of plants in the playa were C_3 annual forbs that germinate after late summer rains and grow through winter and spring, and C_3 perennial forbs and the C_4 grass, *Panicum obtusum*, which are tolerant of disturbances in the playa and which grow mostly in summer (Fig. 4, Table 2). Wondzell, Cornelius & Cunningham

(1990) give a detailed discussion of vegetation patterns relative to microtopography and soils on the same playa.

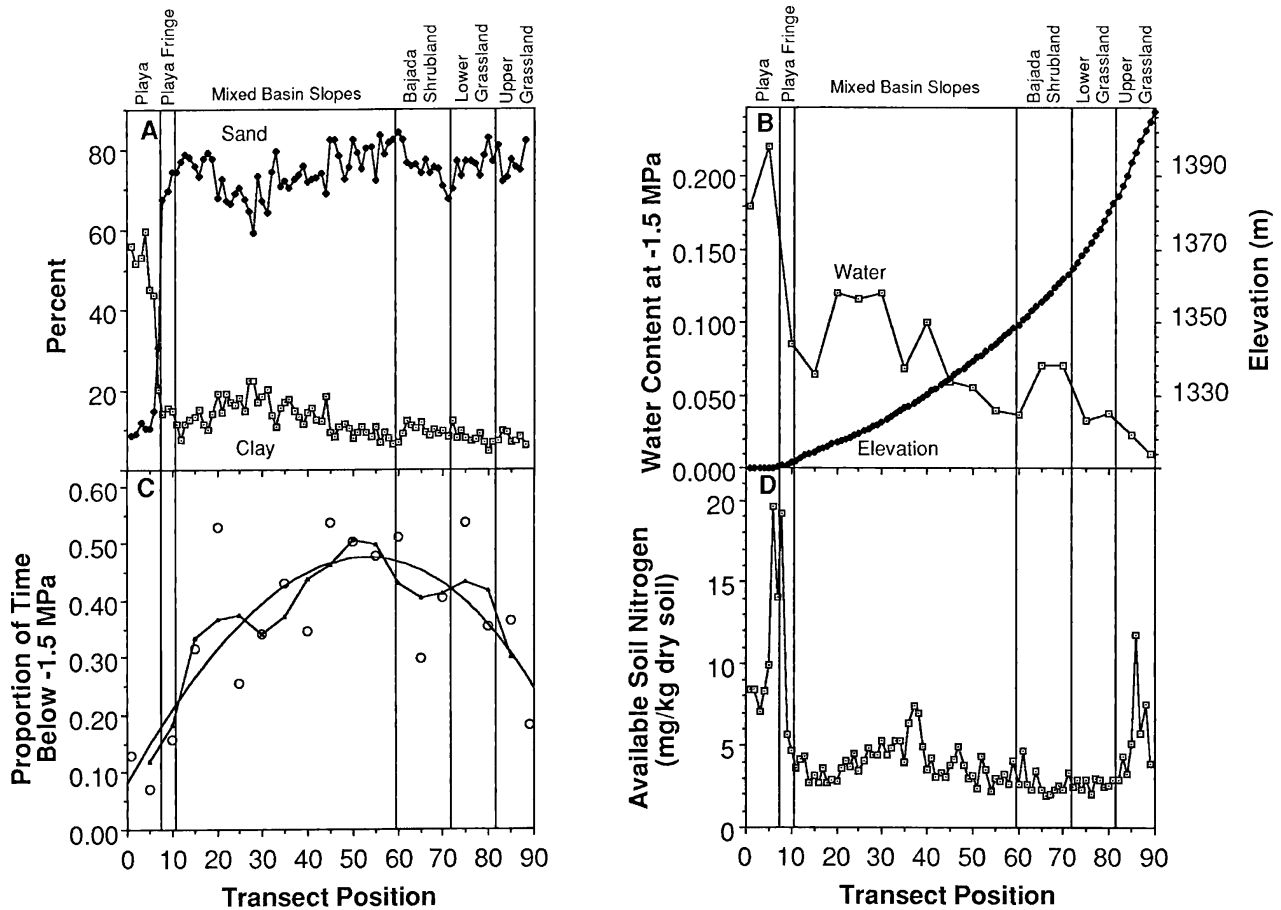*Playa fringe* (stations 8-10): This narrow vegetation zone is a transition zone between the playa and the mixed basin slopes. It is dominated by the C_3 shrubs, *Prosopis glandulosa* and *Ephedra trifurca* (Fig. 4, Table 2). Two other functional groups develop high cover during summer in this zone: C_4 grasses (primarily *Muhlenbergia porteri*), and C_3 subshrubs (primarily *Xanthocephalum sarothrae*).

Table 2. The distribution of summer cover abundance classes (1982-1984) for the most dominant species within each photosynthetic pathway/life-form guild occurring along the Jornada LTER transect. Cover classes are as follows: – = 0%, 1 = > 0-2%, 2 => 2-5%, 3 = > 5-10%, 4 = > 10-20%, 5 = > 20-40%, 6 = > 40%.

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Transect position          11111111112222222222333333333344444444445555555555666666666677777777778888888888
                           12345678901234567890123456789012345678901234567890123456789012345678901234567890123456789
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C₃ Shrubs

Species	Distribution
Ephedra trifurca	————————4311———121—2—1–2———1————111–232—212211–1–231–1——————12—1111–222—232–
Larrea tridentata	——————————————————————————2—1—325345644544564———————————2–2–2–
Prosopis glandulosa	————————6443————————————————————————12——1—23–3—1————————1–
Yucca elata	————————1231———————————2—————————32—22——————2————————423————

C₃ Subshrubs

Species	Distribution
Xanthocephalum microcephalum	————————————————————1——112111—1—2111–11221111—113221221–33122421——1–1–1
X. sarothrae	——————332232332223222331211221212–1–11222223322221121–1—1——1——1————
Zinnia acerosa	————————————————————————————————————1111–3——2–1————
Z. grandiflora	————————1—1——111–1–11—1111111111111—11–11—11–1—11————————2—1–11111–11–1—1————

C₃ Perennial forbs

Species	Distribution
Bahia absinthifolia	————————1–211111121111111–11111112111111121211———1111222132221111111111111111121111—11—
Cassia bauhinioides	————————————111211111–1——1————1–11–1111111111———————————1————
Croton pottsii	————————1121111111122322332122221111111111———22–111—111—1–1111–1—12–22112–21——111
Helianthus ciliaris	3315————
Hoffmanseggia glauca	1321—21—1————————1–1————————————————————1————
Hybanthus verticillatus	————————1——1–1111–1111—————————1—————————1——11–1–1—
Perezia nana	————————1111111111—1111111111111—111112221111—11————————11————
Sida leprosa	4441431————
Solanum elaeagnifolium	————————111——1—11–11—1111–11111–111——1–11–1111———1————11—11–1—111—11
Sphaeralcea subhastata	——————111–1–11112211232112112121211112111–11————
Talinum angustissimum	——————————————1——1———1————————————————1—111—

C₃ Annual forbs

Species	Distribution
Astragalus nuttallianus	——————2———11111–11111–1—1–11———1–1—————1————
A. tephrodes	——————11–1——11————
Bahia pedata	——————————111—1—11————————————1–1————
Baileya multiradiata	——————11111111111—1–1——11–11111—111–111121–1111————1–11————
Chenopodium incanum	21——————1–13121313233314321–22122121211112231222122212232121—11————
Eriogonum abertianum	——————1————11111–111——1–111—1—1112211221111111–11——————11211111—1—121111
Eriogonum trichopes	——————1—12222————————————2———1—————
Happlopappus gracilis	————————————————1——————————————11122211——1221
Hymenoxys odorata	–23442————
Verbesina encelioides	——————1——————————222——111–221————
Xanthocephalum spaerocephalum	——————1—1—21–2——————1———1————

C₄ Perennial grasses

Species	Distribution
Aristida longiseta	—————————1112111—1–11111221112121–1———1————1–1111–1111——
A. ternipes	——————————————————————————————————11221221——1–1–1
A. wrightii	—————————————————————111————1–1111–1————1————1–
Bouteloua eriopoda	——————1——1–1————11—12–11111—1–111—1111———————332234422355555555
Cyperus esculentus	113211————
Eragrostis lehmaniana	—————————————————————————————————12112–1111—
Erioneuron pulchellum	——————1—21111312232222222122121121111111111121111111111111111111111111122122222111—111
Muhlenbergia porteri	——————43322212111——1—1221—1————1———1–1—221111132111333–13—21421–1122–
Panicum obtusum	44455655————
Sporobolus contractus	——————————1—11——111–1——1—11211—11—11—1–1–1111—1————
Sporobolus cryptandrus	——————1111–111111111–11232123122111111–111111–111–11–1——1————12121231–11111—11

C₄ Perennial forbs

Species	Distribution
Allionia incarnata	————————213——1–1—1–1–111–1–11–11111——1–1——111112222211————————121–1—111–111112
Ammocodon chenopodioides	——————1111111111—11111111111—111111–11111–11–1111111————————11——1—1–1—1
Euphorbia albomarginata	——————1–1——121—1–1—1–1111–1——111–111————————1————111–1————

C₄ Annual grasses

Species	Distribution
Aristida adscenionis	——————1———————11111111111121112–1–221211121–111–111–1–1111————————1122112331—121–3
Bouteloua aristidoides	————————111–111—1—1——11–11111–11111–112123322222224121————————1132214311–32313
B. barbata	——————11–1——11111111111111—11111111—112121111111113121211————————111–1222111–2–1—
Tragus berteronianus	——————11————————————1–1111–11—1—11–1————1————

C₄ Annual forbs

Species	Distribution
Amaranthus palmeri	—1–113——————————1–11—1————11121–2211221————————1——1———1332214
Boerhavia intermedia	——————1——2——————2—2–11111–1–111——1–1——1–2132—112————13231222112—212–1
B. spicata	——————132—2–1——1————1—11–1–2——111–112123133332331–1————————211—1——1——
Euphorbia micromera	——————————————1——————————1–1–1—1–1———1————1–11–1—11–2—11
E. serpyllifolia	——————1–12111121111121211211111111111111122–222111211211—11——1——1—1——
Kallstroemia parviflora	——————1—11—1–1111–12–112–121—2——1–1—21–1222——————————————1–1–1–
Pectis angustifolia	——————————————————1111111111–1111233124132111–1————————1————
Portulaca oleracea	–111251————
Salsola kali	——————433–12——2——11–21222122212122222–111—22–2132——1————
Tidestromia lanuginosa	——————12–12322211–21111111313112323222332345344445534343131——1–111————
Tribulus terrestris	——————2——————1–1—21–2222333234444444434442312—211121–1————————1————

CAM Succulents

Species	Distribution
Opuntia phaecantha	——————————————————1————————————1————————5–221—14–
O. violacea	——————————————1——1————————————1———2——3–1–1–1—

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                           11111111112222222222333333333344444444445555555555666666666677777777778888888888
Transect position          12345678901234567890123456789012345678901234567890123456789012345678901234567890123456789
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Fig. 5. Environmental characteristics from stations along the Jornada LTER transect: (A) percentage sand and clay in soil at 30 cm depth (from Wierenga et al. 1987); (B) elevation and soil water content at -1.5 MPa water potential (estimated for 30 cm soil depth from unpubl. Jornada LTER data, courtesy of W. G. Whitford); (C) proportion of 1982-86 sample dates with soil water content estimates below the -1.5 MPa water content (estimated from 121 neutron probe readings taken at approximately biweekly intervals, unpubl. Jornada LTER data, courtesy of W. G. Whitford) - open circles are actual estimates, line with small triangles is three-term moving average through actual values, line without symbols is predicted values from third order polynomial regression of proportion versus transect position ($R^2 = 0.654$); (D) 1982-86 average available soil nitrogen (NH_4-N + NO_3-N, mg/kg dry soil, from nine sample dates, unpubl. Jornada LTER data, courtesy of W. G. Whitford). Distance along the transect (m) may be found by multiplying the transect station number by 30. Vertical lines through graphs indicate the locations of boundaries between vegetation zones. Vegetation zone names are given across the top.

Mixed basin slopes (stations 11-59): This broad, diverse vegetation zone is characterized by high cover of annual species, but, there is also a low, rather uniform cover of C_3 subshrubs, C_4 perennial grasses, and C_3 perennial forb species (Fig. 4). The basin slopes have a great amount of seasonal and annual change in cover and species composition because of the high cover of annual species. The winter annual species are exclusively C_3 plants that depend on precipitation during the winter period (November through March). Both 1982 and

1984 had only about one-half of the winter precipitation received in 1983 (Table 1), resulting in sparse germination and survival of winter annual species in those years. The summer annual species composition was quite different between years. In 1982 and 1984 summer seasons these annual species were nearly all C_4 species, whereas in 1983 the cover was primarily from two C_3 annual species, *Chenopodium incanum* and *Eriogonum abertianum* (Table 2).

Bajada shrubland (stations 60-71): At the upper end of the mixed basin slopes zone there is a rather abrupt decline in annual species accompanied by an increased abundance of C_3 shrubs, primarily *Larrea tridentata* (Fig. 4, Table 2). Associated with *L. tridentata* within the bajada shrubland vegetation zone is low to moderate cover of C_3 subshrubs and C_4 perennial grasses.

Lower (stations 72-81) and *Upper* (stations 82-89) *Piedmont grasslands*: At higher elevation, adjacent to the bajada shrubland, are two grassland vegetation zones, which have the highest guild diversity of all plant communities along the transect (Fig. 4, Table 2). Both communities are dominated by C_4 perennial grasses, but the lower piedmont grassland, co-dominated by *Bouteloua eriopoda* and *Erioneuron pulchellum*, has only about half the grass cover found in the upper piedmont grassland, dominated solely by *B. eriopoda*. Both communities also have low cover of C_3 shrubs, CAM stem succulents, and seasonally high cover of annual species. The lower piedmont grassland also has moderate cover (4 to 7%) of C_3 subshrubs not found in the upper piedmont grassland. The highest cover of C_4 perennial forbs occurs within the upper piedmont grassland zone. The high diversity of functional groups within the piedmont grasslands is probably related to the relatively steep slopes and rocky terrain that provides a number of slightly different moisture micro-habitats through differential drainage and evaporation. Also, given equal moisture inputs, the upper piedmont grassland should be the most productive plant community along the transect because it has the most coarse-textured soil (see Fig. 5A) (inverse texture hypothesis - Noy-Meir 1973). In addition, seasonal moisture inputs would be amplified in the upper piedmont grassland by run-on from the adjacent rocky mountain (Wondzell, Cunningham & Bachelet 1987), thus providing a more reliable moisture resource for the C_4 grasses.

Gradient analysis

DCA ordinations were conducted using cover abundances of species and functional groups for data averaged over all three summer sampling periods. Axes from the ordination based on functional group cover were not as strongly related to environmental variables as the ordination using cover by species, hence, we only include the latter results here. The eigenvalues for the first four DCA axes were 0.91, 0.52, 0.24, and 0.21 respectively. The eigenvalues for DCA axes three and four were quite small relative to the first two, so only axes one and two are reported. There are several sharp transitions in DCA scores in the traces of the first two axes (Fig. 1B, C), with the locations of these sharp transitions corresponding to the locations of the discontinuities identified by SMW (Fig. 1A). The first DCA axis essentially characterizes the sharp gradient from the playa and playa fringe zones to the remainder of the transect. The stations of the bajada shrubland zone also separate from the other vegetation zones along this axis. The second DCA axis generally characterizes the gradient from the mixed basin slopes to the upper piedmont grassland, with the stations from each vegetation zone recognizable as relatively homogeneous groups.

The transect has gradients in soil texture (Fig. 5A) and elevation (Fig. 5B), with the sand fraction of soil increasing and clay decreasing as elevation increases from the playa to the upper piedmont grassland. We defined the –1.5 MPa water content at 30 cm depth from systematic locations along our transect (Fig. 5B) using soil psychrometer estimates of water potential and neutron probe tube estimates of water content taken at various overlapping time intervals during 1986 (unpubl. Jornada LTER data, water content data described in Wierenga et al. 1987). We then calculated the proportion of biweekly neutron probe readings taken from the same locations along the transect from 1982 - 1986 ($n = 121$) which had water contents below the estimated –1.5 MPa water content (Fig. 5C). These data showed that over the long-term the middle of the transect has the least available water, while the two ends have the most. We also summarized the average available soil nitrogen (NO_3-N + NH_4-N) of all transect stations from nine sample dates over the same five year period (1982 - 1986 - unpubl. Jornada LTER data, chemical analyses as in Fisher et al. 1987) (Fig. 5D). The greatest available soil nitrogen was found in the playa fringe, playa and upper piedmont grassland vegetation zones, with the middle of the transect (especially the bajada shrubland and lower piedmont grassland vegetation zones) having the least (with the exception of stations 35 - 40).

The first DCA axis was significantly correlated ($N = 19$, $p < 0.05$) with available soil nitrogen ($R = 0.90$), elevation ($R = -0.71$), soil coarse fragment fraction ($R = -0.62$), proportion of time water potential was below -1.5 MPa ($R = -0.60$), soil clay fraction ($R = -0.60$), water content at field capacity (–0.033 MPa) ($R = 0.57$), and soil organic carbon ($R = 0.55$). The second DCA axis was not significantly correlated with any environmental variable.

Discussion

Our study has demonstrated significant associations between landscape-level patterns of environmental heterogeneity and the distribution patterns of vascular plant guilds and species across a desert landscape. Previous

studies in the northern Chihuahuan Desert have demonstrated relationships between vegetation, soils and landscape features (Stein & Ludwig 1979; Wierenga et al. 1987; Wondzell, Cunningham & Bachelet 1987). We suggest that the primary causal factors underlying these relationships are the generation and maintenance of gradients in the most limiting resources: nitrogen and water; and the separation of vascular plant guilds and species along these gradients due to specific groups being better adapted to utilize specific windows of resource availabilities.

Distribution patterns of water and nitrogen

Our analyses and assessments of the pattern and zonation along the transect suggest that the most important environmental gradients and boundaries across the landscape are associated with downslope movement of water, soil particles, and organic matter. Over a period of five years we found that the two ends of the transect had the greatest amounts of both available water and nitrogen, while the middle had the least. These patterns seem best explained by interactions between (1) differences in soil texture and their effect on infiltration, water holding capacity, and moisture release characteristics, and (2) the downslope redistribution of water that occurs across the landscape during rain events, such that certain locations (e.g. the upper piedmont grassland and playa) gain water from run-on, while other locations lose water to run-off (see Wondzell, Cunningham & Bachelet 1987). Similarly, the observed patterns in available soil nitrogen seem related to long-term redistribution of organic matter within the watershed that occurs during large rainfall events, as soil organic matter and total nitrogen have similar distributions along the transect (Whitford, Reynolds & Cunningham 1987). Nitrogen fixation inputs account for the elevated soil nitrogen in the playa fringe (Fig. 5D), which is dominated by *Prosopis glandulosa*, a symbiotic nitrogen-fixer (Jenkins, Virginia & Jarrell 1988).

Distribution patterns of vascular plant guilds

C_3 shrubs were dominant in two plant communities: the playa fringe and bajada shrubland. The playa fringe zone was dominated by *Prosopis glandulosa*, which commonly occupies sites where run-on water accumulates (e.g. edges of arroyos and playas). At our playa fringe site, *P. glandulosa* has roots that extend below 10 m, exploiting subsurface reservoirs of soil moisture that are recharged by occasional playa flooding (Jenkins, Virginia & Jarrell 1988), and essentially decoupling it from the arid conditions affecting most other species along the transect. In contrast, *Larrea tridentata* was dominant in the bajada shrubland vegetation zone, the location along our transect with the least available water and nitrogen.

C_3 subshrubs were broadly and relatively uniformly distributed across the middle of the transect, having little or no cover within the playa and the upper piedmont grassland vegetation zones. Thus, they occupied the relatively dry/low nitrogen locations along our transect. There was evidence of niche differentiation within the C_3 subshrub guild along the moisture gradient of our transect, suggesting that competitive interactions may be important in determining species distributions within certain guilds. *Xanthocephalum sarothrae* occurred in the more mesic lower portion of the transect whereas *X. microcephalum* occurred in the drier upper part, with only a small amount of overlap. *Zinnia acerosa* occurred only in the dry bajada shrubland zone, while *Z. grandiflora* occurred in more mesic sites both below and above this zone. These patterns correspond to broadscale generalizations that *X. microcephalum* and *Z. acerosa* seem restricted to dry locations (Lane 1985; Correll & Johnston 1970).

C_4 perennial grasses had highest cover in the upper piedmont grassland and playa vegetation zones, which had the highest amounts of available water and nitrogen (Fig. 5C, D). However, C_4 perennial grasses had significant cover in every vegetation zone of our transect in summer (Fig. 4, Table 2), reflecting their adaptation to the relatively reliable summer rainfall of the northern Chihuahuan Desert.

C_3 perennial forbs had maximum cover in the playa vegetation zone, but had significant cover all along the transect. C_4 perennial forbs were most abundant in the upper piedmont grassland, but also had a low and uniform cover all along the transect, (except for the playa and bajada shrubland). Thus as a group, perennial forbs were most abundant in the mesic / high nitrogen locations along our transect.

As a group, annual species (C_3 and C_4 forbs and C_4 grasses) were most abundant in the mixed basin slopes and lower piedmont grassland zones, locations with intermediate amounts of available water and nitrogen. They were least abundant in the upper piedmont grassland, playa fringe, and playa, locations with the most available water and nitrogen, and in the bajada shrubland, with the least available water and nitrogen. Even though there were apparent landscape-level patterns in the distribution of annual species during our study, annuals exhibited complex seasonal and annual variation in cover, apparently due to (1) predictable seasonal patterns of rainfall, (2) great year-to-year variation in the amount of rainfall within a season, and (3) high spatial variation in the amount of rainfall for individual rainfall events. Seasonal variation in abundance is due to offset

activity as a function of photosynthetic pathway type, with C_4 annual forbs and grasses having measurable cover only in summer and C_3 annual forbs having much greater cover in winter than summer. Year-to-year variation in the cover of desert annual species is partially related to seasonal total rainfall amounts. For example, C_3 annual forb cover was low within the mixed basin slopes and lower and upper piedmont grasslands following the dry winters of 1982 and 1984, and high following the wet winter of 1983. Also, for the transect as a whole the greatest cover of C_4 annuals occurred in 1984, which had the greatest summer rainfall. However, there were specific locations along the transect in both 1982 and 1983 (years with relatively low summer rainfall) that had C_4 annual cover equal to or greater than the same locations in 1984. In addition, in summer 1982 the basin slopes were dominated by C_4 annual forbs and grasses with no C_3 annual cover, but in summer 1983 cover of C_3 annual forbs was greater than that of C_4 annuals, the reverse of the typical pattern for desert annual species (Mulroy & Rundel 1977; Kemp 1983). The C_3 annual forb species that were present during summer 1983 belonged to a small group of species that germinated in winter and flowered in early spring along with other C_3 annuals. However, because both winter and spring rainfall in 1983 were above average (Table 1), these species persisted through spring and early summer, and flowered again in late summer. At the same time there were no summer rainfall events large enough to induce germination in C_4 annuals (about 15 mm; Freas & Kemp 1983) within the mixed basin slopes (unpubl. Jornada LTER rainfall data).

Comparisons with previous studies

The distribution patterns of vascular plant guilds relative to gradients in soil environment identified in our study allow comparisons to previous studies, where gradients in climate were the principal component along which guilds were separated. These studies usually involved large elevation changes with relatively steep gradients in meso-scale climate, in which distributions of photosynthetic pathway types and life forms were found to be correlated with temperature and/or aridity (e.g. Raunkiaer 1934; Teeri & Stowe 1976; Eickmeier 1978; Boutton, Harrison & Smith 1980; Rundel 1980; Wentworth 1983; Cavagnaro 1988; Danin & Orshan 1990). Along our transect there is essentially no gradient in meso-scale climate, but, there is a rather steep gradient in available water.

There are striking similarities in the small-scale, distribution patterns of vascular plant life forms relative to the moisture gradient of our transect, and the large-scale distribution of lifeforms along meso-scale climatic

gradients within the arid and semi-arid regions of Israel (Danin & Orshan 1990). Danin & Orshan (1990) found that hemicryptophytes and geophytes were most abundant in regions with the highest precipitation; similarly, we found the greatest abundance of perennial grasses and forbs within the most mesic locations along our transect. They found that phanerophytes and chamae phytes were most abundant in regions with the lowest precipitation; similarly, we found the greatest abundance of shrubs and subshrubs within the driest locations along our transect. They also found that therophytes were least abundant in regions of low and high rainfall, and most abundant in regions with intermediate amounts of rainfall; similarly, we found the greatest abundance of annual species at locations of intermediate moisture availability along our transect. These similarities indicate that certain life-form types are better adapted to certain patterns of resource availabilities at both large (regional) and small (landscape) scales.

Several studies have shown that over large, regional scales C_4 plants tend to dominate more arid environments relative to C_3 (e.g. Winter, Troughton & Card 1976; Eickmeier 1978; Tieszen et al. 1979; Wentworth 1983). Along our transect we, in fact, found the opposite-C_4 species were most abundant in the two vegetation zones that had the most available water, while C_3 species were most abundant in the vegetation zone with the least available water. Teeri & Stowe (1976) developed a regression model for predicting proportional composition of C_3 and C_4 perennial grasses within North America based on climatic data. Using weather data from Las Cruces, NM their model predicts that 74 % of the grass species from our study site should be C_4, in comparison to 97% actual occurrence (29 of 30; *Vulpia octoflora*, an annual, was the only C_3 grass found on our site). This difference is rather paradoxical, considering that in the neighboring Sonoran Desert the predicted percentage was in perfect agreement both regionally (Teeri & Stowe 1976) and at a specific location (Wentworth 1983). The occurrence of both groups of grasses is due to seasonally offset patterns of growth, with C_4 grasses growing principally in summer and C_3 grasses growing principally in winter (Mulroy & Rundel 1977; but see also Gurevitch 1986). The Sonoran Desert has reliable winter moisture and high winter temperatures, providing a window of resource availability for C_3 perennial grasses that is apparently lacking in the northern Chihuahuan Desert.

The gradients and associated vegetation pattern described in our study contrast with the general view of desert plant community structure that has been developed from studies of bajadas in the Sonoran Desert (cf. MacMahon & Schimpf 1981). These studies have consistently found relatively unidirectional gradients in soil

texture and available water, which were associated with a decline (from top to bottom) in species and growth form diversity (e.g. Barbour & Diaz 1973; Phillips & MacMahon 1978) and usually two distinct community types: a tree dominated community at the upper elevations of the bajada, and a shrub dominated community at lower elevations (e.g. Yang & Lowe 1956; Phillips & MacMahon 1978). In our study the gradient is more heterogeneous and the vegetation zonation more complex than the generalized Sonoran Desert model, as we found changes in guild dominance and distribution that were related to a complex distribution of water and nitrogen. These differences are probably due to our study site having much steeper environmental gradients over a relatively short distance in comparison to the Sonoran Desert studies.

Conclusions

The patterns of distribution of photosynthetic pathway / growth form guilds observed in our study reveal that these characteristics act as adaptations to local habitats associated with small differences in the environment. Gradients in elevation and soils along our study transect, together with variable seasonal rainfall, downslope redistribution of water and organic matter, and soil texture-related variation in infiltration, water holding capacity, and moisture release characteristics, interact to generate a complex spatial and temporal gradient of available soil water and nitrogen, such that the upper and lower ends of the transect have the most available water and nitrogen and the middle has the least. Particular guilds of vascular plants seem adapted to utilize particular spatial and temporal windows of resources along this complex gradient, as C_4 perennial grasses and C_3 and C_4 perennial forbs were most abundant in the mesic / high nitrogen locations along the transect, C_3 shrubs and sub-shrubs were most abundant in the xeric / low nitrogen locations along the transect, and annual species (C_3 in winter, mostly C_4 in summer) were most abundant in the intermediate locations along the water/nitrogen gradient. The distribution patterns of life forms along the moisture gradient of our transect were similar to patterns observed in response to larger-scale climatic gradients, however, the distribution patterns of photosynthetic pathway types were different. Competitive interactions apparently modify the distribution patterns of species within certain guilds.

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