PAIRWISE SPECIES ASSOCIATIONS IN THE PERENNIAL VEGETATION OF THE NORTHERN CHIHUAHUAN DESERT

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ABSTRACT—We analyzed pairwise species associations based on presence/absence data from transects of perennial vegetation at 129 sites located in the northern Chihuahuan Desert. The sites were chosen to represent the range of commonly encountered desert vegetation types from grassland to shrubland. Twenty-four significant associations were found, all of which were positive (i.e., the species pairs co-occurred more frequently than would be expected by chance). Some of the species associations identified by our analysis have been noted in the literature previously, but others have not and warrant further investigation. Given the nature and scale of the data used in our analysis, the associations we uncovered most likely represent species with similarities in ecological requirements or tolerances, but might or might not indicate strong interaction at the scale of individual plants.

RESUMEN—Analizamos las asociaciones de pares de especies, usando datos de presencia/ausencia provenientes de transectos de la vegetación perenne en 129 sitios en el norte del desierto Chihuahuense. Elegimos los sitios para representar toda la variación de tipos de vegetación desértica que se encuentra frecuentemente, desde pastizal hasta matorral. Se encontraron 24 asociaciones significativas, todas positivas (es decir, la concurrencia de los pares de especies fue más frecuente que la esperada al azar). Algunas de las asociaciones de especies identificadas en el análisis han sido reportadas previamente en la literatura, pero otras no, sugiriendo más investigación. Dada la naturaleza y la cantidad de los datos usados en nuestro análisis, es muy probable que las asociaciones detectadas representen especies similares en tolerancias o requerimientos ecológicos, que pueden, o no, indicar una intensa interacción al nivel de plantas individuales.

The northern Chihuahuan Desert is a region that is both dynamic and floristically diverse. Historical accounts describe the region as predominantly grassland in the 1800s (Buffington and Herbel, 1965; York and Dick-Peddie, 1969). Throughout the 1900s, there was an increasing dominance by woody vegetation, particularly the perennial shrubs *Larrea tridentata* (creosotebush) and *Prosopis glandulosa* (honey mesquite). The extent of shrub encroachment and ecological factors leading to it were reviewed by Grover and Musick (1990). Multiple causal factors apparently played a role in the observed vegetation changes, including effects of extensive grazing by domestic livestock (primarily cattle), suppression of the normal fire regime (which might in part be a related to grazing), fluctuations in the amount and seasonality of precipitation, and shifts in the impact of granivores (Neilson, 1986; Brown and Heske, 1990; Chew and Whitford, 1992; Brown et al., 1997).

The vegetation of the northern Chihuahuan Desert has recently been characterized by Johnson et al. (2000) through multivariate ordination techniques. They found that the shrubs *L. tridentata* and *P. glandulosa* were not only dominant in terms of total cover over the study area, but they also largely defined the first ordination axis of both principal components and detrended correspondence analyses. A clear gradient from grassland to shrubland sites was evident in the ordination analyses. Heavily shrub-dominated sites varied primarily in the relative proportions of *L. tridentata* and *P. glandulosa*. These sites tended to have low diversity and low cover of other perennial species. In contrast, grassland sites, or sites with

Species 1

		present	absent	row totals
Species 2	present	a	b	m
	absent	c	d	n
	column totals	r	s	

$m = a + b$
$n = c + d$
$r = a + c$
$s = b + d$

$N = $ total number of sites
$= a + b + c + d$
$= m + n$
$= r + s$

Jaccard Index: $J = \dfrac{a}{a + b + c}$

Log odds ratio: $\log \left(\dfrac{ad}{bc}\right)$

Yule's V (or tetrachoric point correlation):

$V = \dfrac{ad - bc}{+(mnrs)^{1/2}}$

FIG. 1—Illustration of the notation for a 2 × 2 contingency table based on species presence/absence data, and formulas for 3 measures of association.

a) *complete*

Species 1
		pres	abs	
Species 2	pres	25	25	50
	abs	0	50	50
		25	75	100

b) *absolute*

Species 1
		pres	abs	
Species 2	pres	50	0	50
	abs	0	50	50
		50	50	100

c) *independent*

Species 1
		pres	abs	
Species 2	pres	25	25	50
	abs	25	25	50
		50	50	100

d) *negative*

Species 1
		pres	abs	
Species 2	pres	0	25	25
	abs	25	50	75
		25	75	100

	Jaccard	Yule's V	log odds ratio
a) *complete*	0.5	0.58	undefined
b) *absolute*	1.0	1.0	undefined
c) *independent*	0.33	0.0	0.0
d) *negative*	0.0	-0.33	undefined

FIG. 2—Examples of contingency tables showing various types of association, with the corresponding values of the measures of association: a) complete association, b) absolute association, c) independence, and d) negative association.

minimal shrub cover, were often more diverse at a site and varied compositionally from site to site.

Tests or measures of pairwise species association have been used in ecology to characterize community structure. At times, the existence of a particular association might be used as evidence for a particular ecological process (e.g., a negative association in the case of interspecific competition). However, such inference of mechanism must be made with considerable caution, because multiple causal factors can usually be hypothesized that logically might lead to a given association. Still, the investigation of species associations can be useful for identifying patterns of co-occurrence that are in need of mechanistic explanation. Additionally, repeated investigations of species associations are valuable in identifying changes in community structure over time, which might indicate accompanying changes in ecological function.

Many factors influence the selection of an appropriate measure of species association. A bewildering array of measures has been proposed in the literature. Janson and Vangelius (1981) reviewed 20 of these measures, and Hubálek (1982) reviewed 43 measures. Topham et al. (1991) investigated the statistical properties of 9 commonly used measures of association. Figure 1 illustrates the computation of selected measures of association and identifies the notation used to refer to entries in the 2 × 2 contingency table.

One major issue is the treatment of joint absences—those sites at which neither species is present. If both species are regionally common (i.e., occur at a high percentage of sites), then a greater than expected frequency of joint absences might convey ecologically relevant information. However, if one or both of the species are uncommon, a large value for joint absences (d in the formulae of Fig. 1) might unduly inflate the measure of association. If one wanted joint absences and joint presences to contribute equally to the measure of association, Sokal and Michener (1958) recommended the simple matching coefficient, $(a + d)/N$.

However, Ludwig and Reynolds (1988) concluded that, for most ecological data, it is better to ignore joint absences and recommended Jaccard coefficient, $a/(a + b + c)$, which makes no use of joint absences.

Another issue influencing the choice of a measure of association is the ability to distinguish between complete versus absolute association (Pielou, 1977). A complete association is one in which all occurrences of one species are at a subset of the sites where the other species is present (Fig. 2a). Thus, a complete as- sociation implies that either $b = 0$ or $c = 0$. An absolute association implies that neither species is ever present without the other (Fig. 2b), in which case both $b = 0$ and $c = 0$. Some measures of association fail to distinguish these cases (i.e., they yield the same maximal value for either a complete or absolute association). Jaccard's and Yule's V coefficients each yield a maximal value of 1 in the case of absolute association and a lesser value for complete association (Fig. 2). The log odds ratio is undefined when any of the frequencies equal zero,

so it cannot be computed for complete or absolute associations. To correct this problem, the log odds ratio is sometimes modified by adding 0.5 to each of the frequencies (Upton, 1978). The modified measure becomes:

$$\log\left[\frac{(a + 0.5)(d + 0.5)}{(b + 0.5)(c + 0.5)}\right] \quad (1)$$

This procedure, although pragmatic, must be considered rather ad hoc.

In choosing a measure of association, it is instructive to consider the value it yields in the case where frequencies equal those expected given independence (i.e., the case of no association, Fig. 2c). Yule's V is related to the χ^2 statistic, which is often used to test for independence, by $V^2 = \chi^2/N$. Yule's V takes on an expected value of zero in the case of independence. The log odds ratio also yields a value of zero when the frequencies conform to independence. The behavior of the Jaccard coefficient is more complex. The value it yields depends on the proportion of sites at which each species occurs. Specifically, given independence, the expected value for the Jaccard coefficient is:

$$\left(\frac{N}{m} + \frac{N}{r} - 1\right)^{-1} \quad (2)$$

which can vary, approaching 1 if both species are common and approaching 0 if both species are rare.

In the case of a negative association (i.e., when the frequency of joint occurrences is less than expected under independence), both Yule's V and the log odds ratio yield negative values (Fig. 2d). In the extreme case of $a = 0$, Yule's $V = -1$ and the log odds ratio is undefined unless modified as described in equation (1) above. The Jaccard coefficient is zero if (and only if) $a = 0$, but in general it takes on positive values for negative associations. For negative associations, the value of the Jaccard coefficient will be less than the expected value given by equation (2).

In this paper, we report the pairwise species associations apparent in the perennial vegetation of the northern Chihuahan Desert. This analysis complements the multivariate ordination approach of Johnson et al. (2000). The ordination analyses were based on cover data. Our analysis of species associations is based on presence/absence data, and therefore seeks to discover those pairs of species that consistently co-occur at a higher (or lower) frequency than expected by chance, regardless of the absolute cover of either species.

The concept of species co-occurrence is inherently scale dependent. In this study, species are said to co-occur if they were observed at the same site, where a site is defined by 3 radiating 100-m transects. Thus, species recorded as co-occurring at this scale are in the same general location, but might or might not be in direct proximity. Also, because only overstory vegetative cover was analyzed, host/nurse-plant relationships are unlikely to be revealed in this study. Rather, this paper focuses on species associations of the sort that are important in defining vegetation community types, such as those in Dick-Peddie (1993).

METHODS—*Field Methods*—Vegetation data were collected at 129 sites as part of an accuracy assessment (ground-truthing) for a vegetation classification based on remotely sensed (AVHRR) imagery. This classification has been proposed as a useful tool for assessing degradation of rangelands (Eve et al., 1999). The study area included much of south-central New Mexico, ranging from 32.00° to 34.21°N and from 105.74° to 107.78°W. Non-desert areas (including montane forests, woodlands, irrigated croplands, and urban areas) were not included in the classification.

We selected 100 study sites by a stratified random sampling of the classified satellite image. The locations of randomly selected pixels within each class were plotted on the most recent 1:100,000-scale BLM Surface Management Status maps (United States Bureau of Land Management, various dates). Most of the study area was accessible to us as public lands (United States Bureau of Land Management, State of New Mexico), under United States military management (White Sands Missile Range, Fort Bliss), or as a research area (United States Department of Agriculture, Jornada Experimental Range). We also were able to work on the largest tracts of patented land in our study area, the Armendaris and Ladder ranches. Those few sites more than 3.2 km from any mapped road or sites located on small tracts of patented land were considered inaccessible and another pixel was chosen at random. A few sites initially chosen could not be reached due to eroded roads or locked gates, and 5 sites were eliminated because of spatial heterogeneity in the vegetation at a scale that would not be adequately characterized by our survey techniques. Shrubs dominated most of the randomly selected sites. To better characterize the grassland end of the vegetation spectrum, 20 ad-

ditional sites with substantial grass cover were selected. The locations of these study sites were determined based on inspection of the classified satellite image, existing vegetation maps, and the expertise of local ecologists. We also conducted vegetation surveys at 9 sites (6 shrubland, 3 grassland) that had been used as training sites in the image classification procedure.

The end result of this site selection procedure was a set of 129 sites, ranging from desert grassland through shrubland. We used a global positioning system (GPS) with differential correction to record the location of each of our study sites. This information ensures that we will be able to return to the same field sites with a high degree of accuracy for future research.

Vegetation surveys were conducted from April through July of 1996. Most of the study area experienced moderate to severe drought, starting approximately July 1995 and lasting through May 1996 (National Oceanic and Atmospheric Administration, 1998). Perennial vegetative cover was measured at each site on 3 transects that radiated out from the central point identified at random and located with the GPS. We chose a starting direction at random for the first transect and all transects were placed 120° apart. Each of the radiating transects was 100 m long, and intercepts were recorded to the nearest 1 cm. Measurements were made by recording the identity of the plant species (living or standing dead) or bare patch and the horizontal linear dimensions of the plant or bare patch intercepting the transect (Canfield, 1941; de Soyza et al., 1997). Plants could usually be identified to species, but in some cases, only genus could be determined. Binomial nomenclature follows that of Kartesz (1999). In cases of overlapping canopies (e.g., grass under a shrub), intercepts of both overstory and understory plants were recorded. The present analysis, however, is based solely on overstory cover.

Statistical Methods—Only those species that occurred at 10 or more sites were included in the analysis, because it was deemed unreliable to infer patterns of association based on few actual occurrences. Based on this criterion, of the 85 perennial plant species recorded in the study, 29 were included in the analysis. Pairwise species associations were statistically evaluated in 2 distinct steps. First, all pairwise combinations of species were subjected to a test of independence. Second, in cases where a statistically significant association was indicated (i.e., when the null hypothesis of independence was rejected), selected indices were calculated to measure the degree and nature (positive vs. negative) of the association.

Three tests of independence are used for analysis of 2 × 2 contingency tables (such as our species presence/absence tables, Fig. 1): the G-test, Fisher's exact test, and the Chi-square (χ^2) test. The theoretical foundations of each of these tests differs somewhat, although in practice, they usually yield similar results (Ludwig and Reynolds, 1988). The literature is characterized by debate and conflicting recommendations regarding the best choice for a test statistic. Yates (1984) and Cressie and Read (1989) provided discussions of the technical issues involved. Based on our consideration of the alternatives, we chose to use the χ^2-statistic with Yates' continuity correction, which has considerable history of use in ecology (Pielou, 1977).

Because our analysis involved calculation of many χ^2-statistics to test for independence or association in all possible species pairs, we adjusted the rate of Type I errors (rejection of the null hypothesis of independence) by applying a Bonferroni correction (Sokal and Rohlf, 1995). An association was deemed significant if the null hypothesis could be rejected at a Type I error rate $\alpha' = 1 - (1 - \alpha)^{1/k}$, where α is the experimentwise error rate, α' is the adjusted error rate for a single comparison, and k is the number of comparisons. For N species, the number of unique comparisons of non-identical species is $(N^2 - N)/2$. In our case (all pairwise comparisons between 29 species), $k = 406$.

For those species pairs that showed a statistically significant association, 3 measures of the strength of the association were calculated. Based on the considerations discussed above, which are more fully treated in Pielou (1977) and Ludwig and Reynolds (1988), we chose to calculate 1) the Jaccard coefficient, 2) Yule's V (also known as the tetrachoric correlation coefficient), and 3) the log odds ratio (Fig. 2).

Each coefficient has its advantages and disadvantages. The Jaccard coefficient is the only 1 of the 3 we present that was recommended both by Janson and Vegelius (1981) and Hubálek (1982). However, the Jaccard coefficient does not readily distinguish between positive and negative associations, whereas our other measures do. Yule's V is cited as a useful supplement to the Jaccard coefficient by Ludwig and Reynolds (1988). The log odds ratio was included because it arises naturally in the context of log-linear models, and because its statistical properties are well characterized (Fienberg, 1977; Topham et al., 1991).

A plexus technique, as described by McIntosh (1978), was used to present significant associations graphically. Each species is represented as a node in a graph, with lines linking species pairs that show a statistically significant association. Different thicknesses of lines are used to roughly characterize the strength of the association. Conventionally, solid lines are used for positive associations and dashed lines for negative associations (e.g., Bartha, 1992).

RESULTS—Of the 29 plant species included in the analysis, 19 entered into at least 1 statis-

TABLE 1—Species included in the analyses (i.e., perennial vegetation occurring in at least 10 sites). Shorthand codes (used in the plexus graph of Fig. 3) are given for each species that exhibited a significant pairwise association.

Species	Code
Aloysia wrightii Benth.	ALWR
Artemisia filifolia Heller ex Abrams	—
Aristida purpurea Nutt.	ARPU
Atriplex canescens (Pursh) Nutt.	—
Bouteloua curtipendula (Michx.) Torr.	BOCU
Bouteloua eriopoda (Torr.) Torr.	BOER
Dalea formosa Torr.	DAFO
Dasyochloa pulchella (Kunth) Willd. ex Rydb.	DAPU
Ephedra torreyana S. Wats.	EPTO
Ephedra trifurca Torr. ex S. Wats.	—
Flourensia cernua DC.	FLCE
Gutierrezia sarothrae (Pursh) Britt. & Rusby	—
Larrea tridentata (Sessé & Moc. ex DC.) Coville	LATR
Lycium pallidum Miers	—
Muhlenbergia arenacea (Buckl.) A.S. Hitchc.	MUAR
Muhlenbergia porteri Scribn. ex Beal	MUPO
Opuntia santa-rita (Griffiths & Hare) Rose	OPSA
Parthenium incanum Kunth	PAIN
Pleuraphis mutica Buckl.	PLMU
Prosopis glandulosa Torr.	—
Rhus microphylla Engelm. ex Gray	RHMI
Scleropogon brevifolius Phil.	SCBR
Sphaeralcea hastulata Gray	SPHA
Sporobolus airoides (Torr.) Torr.	—
Thymophylla acerosa (DC.) Strother	THAC
Tiquilia canescens (DC.) A. Richards.	TICA
Yucca elata (Engelm.) Engelm.	—
Zinnia acerosa (DC.) Gray	—

tically significant pairwise association (Table 1). Table 2 summarizes the results of χ^2 tests for all species pairs that showed statistically significant associations (experimentwise $P < 0.05$, with Bonferroni adjustment). An interesting fact apparent from the inspection of Table 2 is that all of the significant associations are positive (i.e., joint occurrences are more common than would be expected by random, independent assortment).

Focusing on the strongest species associations (experimentwise $P < 0.0001$), various clusters of positively associated species were apparent in the plexus graph (Fig. 3, species codes are from Table 1). One cluster involved 3 grass species (*Bouteloua eriopoda, Aristida purpurea,* and *Dasyochloa pulchella*) along with the subshrub *Thymophylla acerosa*. Another cluster

involved a positive association of 3 shrub species: *Larrea tridentata, Flourensia cernua,* and *Parthenium incanum*. The final cluster defined by associations with $P < 0.0001$ involved the grass *Bouteloua curtipendula,* which was linked to the subshrubs *Dalea formosa* and *Tiquilia canescens*. If slightly weaker ($P < 0.001$) relationships are considered, *B. curtipendula* also was associated with the shrubs *Aloysia wrightii* and *Rhus microphylla*. A new cluster was evident with the shrub *Ephedra torreyana* being linked to the herbaceous *Sphaeralcea hastulata*. Also at this level of significance, new pairwise associations between existing cluster members were detected (*B. eriopoda* was linked to *D. pulchella,* and *D. formosa* was linked to *T. canescens*). When $P < 0.01$ and $P < 0.05$ associations were considered, the web of associations became more

TABLE 2—Results of tests of independence and measures of association for pairwise species comparisons that showed statistically significant association. Species codes (Sp. 1, Sp. 2) are defined in Table 1. Contingency table entries ($a, b, c,$ and d) as defined in Fig. 1 Other entries are the chi-square statistic (χ^2), experimentwise Bonferroni-adjusted significance probability (P) for tests of independence, strength of the association measured by Jaccard's coefficient (J), Yule's V, and the log odds ratio (LOR).

Sp. 1	Sp. 2	a	b	c	d	χ^2	P	J	V	LOR
ARPU	DAPU	44	20	5	60	48.48	1.36×10^{-9}	0.638	0.629	3.27
FLCE	LATR	30	2	25	72	42.72	2.56×10^{-8}	0.526	0.594	3.77
BOCU	DAFO	9	4	6	110	40.66	7.37×10^{-8}	0.477	0.602	3.72
ARPU	BOER	43	21	9	56	35.95	8.22×10^{-7}	0.589	0.544	2.54
BOCU	TICA	7	6	4	112	31.88	6.66×10^{-6}	0.412	0.543	3.49
LATR	PAIN	23	32	2	72	28.44	3.92×10^{-5}	0.404	0.489	3.25
DAPU	THAC	21	28	3	77	28.16	4.53×10^{-5}	0.404	0.488	2.96
DAFO	TICA	7	8	4	110	26.36	0.000115	0.368	0.495	3.18
ALWR	BOCU	6	4	7	112	24.14	0.000364	0.353	0.481	3.18
BOCU	RHMI	8	5	10	106	23.04	0.000646	0.348	0.460	2.83
BOER	DAPU	33	19	16	61	22.23	0.000983	0.485	0.431	1.89
EPTO	SPHA	9	17	3	100	21.12	0.00175	0.310	0.438	2.87
LATR	MUPO	33	22	15	59	19.65	0.00377	0.471	0.406	1.77
BOCU	PAIN	9	4	16	100	19.58	0.00390	0.310	0.422	2.64
DAFO	DAPU	14	1	35	79	19.50	0.00409	0.280	0.414	3.45
BOER	PLMU	35	17	21	56	18.65	0.00634	0.479	0.392	1.70
DAFO	RHMI	8	7	10	104	18.37	0.00736	0.320	0.412	2.48
PLMU	SCBR	29	27	11	62	18.29	0.00769	0.433	0.393	1.80
MUAR	SCBR	10	1	30	88	17.22	0.0134	0.243	0.395	3.38
LATR	RHMI	16	39	2	72	16.17	0.0233	0.281	0.377	2.69
DAFO	LATR	14	1	41	73	15.57	0.0318	0.250	0.372	3.22
ALWR	RHMI	6	4	12	107	15.21	0.0383	0.273	0.385	2.59
DAFO	PAIN	9	6	16	98	15.10	0.0405	0.290	0.373	2.22
MUPO	OPSA	14	34	3	78	14.92	0.0444	0.275	0.364	2.37

connected, with most of the discrete clusters defined by strong associations joined by weaker links (Fig. 3).

DISCUSSION—The most important factor to consider in interpreting these results is the scale of the observations. An observational data set can be characterized by 2 aspects of scale: grain and extent (Wiens, 1989; Allen and Hoekstra, 1992; Ahl and Allen, 1996). Grain is defined as the smallest units that can be resolved within the data. Our analysis made use of species presence or absence at a site, where a site was characterized by 3 radiating 100-m transects. Thus, our analysis was unable to resolve spatial relationships on scales less than approximately 100 m. Positive or negative associations between individuals or small groups of plants (on the scale of centimeters to a few meters) would not be apparent in this analysis. Given the grain of our analysis, it is most likely that we are detecting species pairs that have

similar ecological requirements or tolerances, but which might or might not exhibit strong interactions between individual plants. We most certainly were not exploring nurse plant relationships, which are well documented in this and other desert ecosystems (e.g., Niering et al., 1963; Welsh and Beck, 1976; Yeaton, 1978; McAuliffe, 1988; de Soyza et al., 1997; Livingston et al., 1997), but which involve overstory-understory relationships and occur at a much finer spatial scale than our analysis would detect.

Study sites were scattered through a region approximately 180 km by 240 km in extent. Thus, our results characterized patterns of species co-occurrence at a regional scale, roughly the northern Chihuahuan Desert. Different patterns might emerge if the extent of observations were expanded to the entire Chihuahuan Desert or the North American continent.

The associations we identified at site and regional scales represented a recent snapshot of
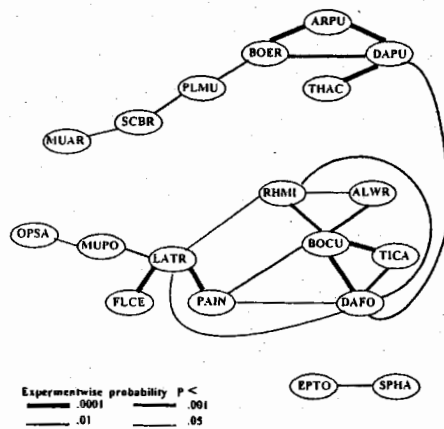
FIG. 3—Plexus diagram summarizing network of statistically significant pairwise species associations for perennial plants of the northern Chihuahuan Desert. The thickness of lines connecting nodes of the graph is proportional to the strength of the association. Nodes are labeled with species codes defined in Table 1.

patterns that we know to be changing (Buffington and Herbel, 1965; York and Dick-Peddie, 1969; Grover and Musick, 1990). Time scales relevant to these dynamics (decades to centuries) were not considered. However, we suspect from previous work (Johnson et al., 2000) that some of the reported associations might be the fairly recent result of shrub encroachment in the northern Chihuahan Desert, driven by changes in land use, whereas other associations might reflect long-term regional geo-ecological processes.

The clusters defined by significant pairwise species associations, as illustrated in Fig. 3, provided the best summary of the relationships detected by our analysis. The strong associations of *B. eriopoda–A. purpurea* and *A. purpurea–D. pulchella* were to be expected, given the ecological similarity of these grasses. The association of *D. pulchella* with the subshrub *T. acerosa* was less obvious and has not to our knowledge been previously noted. The strong association of *L. tridentata* with *F. cernua* and *P. incanum* was not surprising, because these are all long-lived, deep-rooted shrubs with similar ecological niches. The associations involving *B. curtipendula, A. wrightii,* and *R. microphylla* involved plants of differing life forms and would

not necessarily have been predicted a priori. Further research is needed to delineate the ecological factors responsible for the frequent co-occurrence of these species pairs.

The plant associations identified in our analysis were broadly concordant with, but not identical to, vegetation series described by Dick-Peddie (1993) in his classification of vegetation communities of New Mexico. Within the Desert Grassland vegetation type, he recognized several Shrub-Mixed Grass Series, one of which reflects the associations we observed: *Larrea tridentata–Bouteloua eriopoda–Erioneuron pulchellum* (=*Dasyochloa pulchella*)–*Muhlenbergia porteri*–Mixed Forbs. Within the Chihuahuan Desert Scrub vegetation, Dick-Peddie (1993) recognized a Creosotebush Series (*Larrea tridentata–Erioneuron pulchellum*) and a Creosote-Mixed Shrub Series (*Larrea tridentata–Flourensia cernua–Erioneuron pulchellum*). These series involve several of the species that figured predominantly in the clusters identified by our analysis. The fact that our quantitative analyses did not exactly mirror the vegetation series defined by Dick-Peddie (1993) was probably attributable to differences in the spatial scale and methods of data analysis.

Bartha (1992) referred to clusters of associated species, such as those in Fig. 3, as "multispecies coalitions." The spatial scale of vegetation analysis by Bartha (1992) was markedly finer than ours, focusing on interspecific associations within 15-m × 22-m plots, representing variously aged stands of successional plant communities. Even within the limits imposed by this small spatial extent, Bartha (1992) documented considerable variation in the delineation of multispecies coalitions depending upon the size of the sampling units used in the analysis of pairwise associations. Bartha (1992) also noted that, within a multispecies coalition defined by positive associations at the broader scale, it is reasonable to expect that particular pairs will exhibit strong negative interactions (e.g., competition or alleopathy) at finer spatial scales.

The comments of Bartha (1992) regarding the scale-dependence of pairwise and multispecies patterns of association seem to apply broadly to ecological communities. The patterns of association we documented describe the vegetation of the northern Chihuahan Desert over an extent of approximately 200 km

and at spatial resolution (grain) of 100 m. This is the only study we are aware of to investigate these patterns of association at such a broad scale. Considerably more data are available to describe species associations at relatively fine scales (with a resolution of 1 to 100 cm). The remaining challenges are: 1) to document the variation in apparent species associations across a range of spatial scales, providing a bridge from fine-grained to coarse-grained analyses, and 2) to elucidate the ecological mechanisms responsible for generating the observed patterns.

LITERATURE CITED

AHL, V., AND T. F. H. ALLEN. 1996. Hierarchy theory: a vision, vocabulary, and epistemology. Columbia University Press, New York.

ALLEN, T. F. H., AND T. W. HOEKSTRA. 1992. Toward a unified ecology. Columbia University Press, New York.

BARTHA, S. 1992. Preliminary scaling for multi-species coalitions in primary succession. Abstracta Botanica 16:31–41.

BROWN, J. H., AND E. J. HESKE. 1990. Control of desert-grassland transition by a keystone rodent guild. Science 250:1705–1707.

BROWN, J. H., T. J. VALONE, AND C. G. CURTIN. 1997. Reorganization of an arid ecosystem in response to recent climate change. Proceedings of the National Academy of Science USA 94:9729–9733.

BUFFINGTON, L. C., AND C. H. HERBEL. 1965. Vegetational changes on a semidesert grassland range from 1858 to 1963. Ecological Monographs 35:139–164.

CANFIELD, R. H. 1941. Application of the line inter-

ception method in sampling range vegetation. Journal of Forestry 39:388–394.

CHEW, R. M., AND W. G. WHITFORD. 1992. A long-term positive effect of kangaroo rats (*Dipodomys spectabilis*) on creosote bushes (*Larrea tridentata*). Journal of Arid Environments 22:375–386.

CRESSIE, N., AND T. R. C. READ. 1989. Pearson's χ^2 and the loglikelihood ratio statistic G^2: a comparative review. International Statistical Review 57:19–43.

DE SOYZA, A. G., W. G. WHITFORD, AND J. E. HERRICK. 1997. Sensitivity testing of indicators of ecosystem health. Ecosystem Health 3:44–53.

DE SOYZA, A. G., W. G. WHITFORD, E. MARTINEZ-MEZA, AND J. W. VAN ZEE. 1997. Variation in creosotebush (*Larrea tridentata*) canopy morphology in relation to habitat, soil fertility and associated annual plant communities. American Midland Naturalist 137:13–26.

DICK-PEDDIE, W. A. 1993. New Mexico vegetation: past, present, and future. University of New Mexico Press, Albuquerque.

EVE, M. D., W. G. WHITFORD, AND K. M. HAVSTAD. 1999. Applying satellite imagery to triage assessment of ecosystem health. Environmental Monitoring and Assessment 54:205–227.

FIENBERG, S. 1977. The analysis of cross-classified categorical data. MIT Press, Cambridge, Massachusetts.

GROVER, H. D., AND H. B. MUSICK. 1990. Shrubland encroachment in southern New Mexico, U.S.A.: an analysis of desertification processes in the American Southwest. Climatic Change 17:305–330.

HUBÁLEK, Z. 1982. Coefficients of association and similarity, based on binary (presence-absence) data: an evaluation. Biological Review 57:669–689.

JANSON, S., AND J. VANGELIUS. 1981. Measures of ecological association. Oecologia 49:371–376.

JOHNSON, A. R., S. J. TURNER, W. G. WHITFORD, A. G. DE SOYZA, AND J. W. VAN ZEE. 2000. Multivariate characterization of perennial vegetation in the northern Chihuahan Desert. Journal of Arid Environments 44:305–325.

KARTESZ, J. T. 1999. A synonymized checklist and atlas with biological attributes for the vascular flora of the United States, Canada, and Greenland, first edition. In: Kartesz, J. T., and C. A. Meacham. Synthesis of the North American flora, version 1.0. North Carolina Botanical Garden, Chapel Hill.

LIVINGSTON, M., B. A. ROUNDY, AND S. E. SMITH. 1997. Association of overstory plant canopies and native grasses in southern Arizona. Journal of Arid Environments 35:441–449.

LUDWIG, J. A., AND J. F. REYNOLDS. 1988. Statistical

ecology: a primer on methods and computing. Wiley, New York.

McAuliffe, J. R. 1988. Markovian dynamics of simple and complex desert plant communities. American Naturalist 131:459–490.

McIntosh, R. P. 1978. Matrix and plexus techniques. In: Whittaker, R. H., editor. Ordination of plant communities. Dr W. Junk Publishers, The Hague, The Netherlands. Pp. 151–184.

Neilson, R. P. 1986. High-resolution climatic analysis and Southwest biogeography. Science 232:27–34.

Niering, W. A., R. H. Whittaker, and C. H. Lowe. 1963. The saguaro: a population in relation to environment. Science 142:15–23.

National Oceanic and Atmospheric Administration. 1998. Palmer Drought Severity Index data. http://www.ncdc.noaa.gov/onlineprod/drought/xmgr.html. Accessed: July 2000.

Pielou, E. C. 1977. Mathematical ecology. Wiley, New York.

Sokal, R. R., and C. D. Michener. 1958. A statistical method for evaluating systematic relationships. University of Kansas Science Bulletin 38:1409–1437.

Sokal, R. R., and F. J. Rohlf. 1995. Biometry: the principles and practice of statistics in biological research. W.H. Freeman, New York.

Topham, P. B., B. Boag, and J. W. McNicol. 1991. An assessment of some measures of association between species based on presence/absence and applied to plant-parasitic nematode data. Nematologia 37:470–480.

Upton, G. J. G. 1978. The analysis of cross-tabulated data. Wiley, Chichester, United Kingdom.

United States Bureau of Land Management. Various dates. Surface Management Status maps, 30 × 60 minute quadrangles (1:100,000): Carrizozo, NM, 1989 edition; Crow Flats, NM-TX, 1980 edition; Deming, NM, 1984 edition; Hatch, NM, 1984 edition; Las Cruces, NM, 1992 edition; Oscura Mountains, NM, 1984 edition; San Mateo Mountains, NM, 1981 edition; Truth or Consequences, NM, 1981 edition; Tularosa, NM, 1984 edition; White Sands, NM, 1983 edition.

Welsh, R. G., and R. F. Beck. 1976. Some ecological relationships between creosotebush and bush muhly. Journal of Range Management 29:472–475.

Wiens, J. A. 1989. Spatial scaling in ecology. Functional Ecology 3:385–397.

Yates, F. 1984. Tests of significance for 2 × 2 contingency tables. Journal of the Royal Statistical Society, A 147:426–463.

Yeaton, R. I. 1978. A cyclical relationship between *Larrea tridentata* and *Opuntia leptocaulis* in the northern Chihuahuan Desert. Journal of Ecology 66:651–656.

York, J. C., and W. A. Dick-Peddie. 1969. Vegetation changes in southern New Mexico during the past hundred years. In: McGinnies, W. G., and B. J. Goldman, editors. Arid lands in perspective. University of Arizona, Tucson. Pp. 155–166.

LIGHT EFFECT ON SEED GERMINATION OF FOUR *MAMMILLARIA* SPECIES FROM THE TEHUACÁN-CUICATLÁN VALLEY, CENTRAL MEXICO

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ABSTRACT—Seed germination of 4 species of *Mammillaria* (Cactaceae) from the Tehuacán-Cuicatlán Valley in central México were compared at 4 light treatments (red, far-red, white light, and darkness) at 25°C and at 2 light treatments (white light and darkness) at 2 alternating temperatures (15/30°C and 20/35°C). Seeds were positive photoblastic, but germinated at far-red light. For all species, best germination results were obtained at 25°C with white and red light, and there were no significant differences among treatments. Higher germination percentages were obtained at 25°C than at alternating temperatures. None of the species exhibited any morphophysiological mechanisms of dormancy.

RESUMEN—La germinación de 4 especies del género *Mammillaria* (Cactaceae) del Valle de Tehuacán-Cuicatlán, México, se comparó en 4 tratamientos: luz roja, roja lejana, blanca y oscuridad a 25°C y en luz blanca y oscuridad a 2 temperaturas alternantes (15/30°C y 20/35°C). Las semillas resultaron ser fotoblásticas positivas, aunque germinaron en rojo lejano. Para todas las especies la mejor germinación se obtuvo a 25°C con luz blanca y luz roja, y no hubo diferencias significativas entre tratamientos. Se obtuvieron porcentajes más altos de germinación a 25°C que a temperaturas alternantes. Las semillas no presentaron ningún mecanismo de latencia morfofisiológica.

Several environmental factors, including water, temperature, light, and salinity, interact in the soil interface and regulate seed germination in arid environments (Bewley and Black, 1985; Gutterman, 1993). Germination of many desert species is influenced by light; its effect on inducing seed germination in arid and semiarid regions has been demonstrated with annual and perennial species, such as *Atriplex patula*, *Picris galilaea*, *Artemisia tridentata*, and *Artemisia scoparia* (Kigel, 1995). Within the Cactaceae, the effect of light on the induction of seed germination has been studied for several species. Several species, including *Carnegiea gigantea* and *Stenocereus thurberi* (Alcorn and Kurtz, 1959; McDonough, 1964), *Aztekium ritterii* and *Epithelantha micromeris* (Maiti et al., 1994), *Ferocactus recurvus*, *F. robustus*, and *F. flavovirens* (Rojas-Aréchiga et al., 1997), *Oreocereus maximus* and *Epiphyllum anguliger* (Zimmer and Buttner, 1982), *Melocactus caesius* (Arias and Lemus, 1984), and *Harrisia martinii* (Campbell, 1988), show an absolute light requirement in temperatures close to the optimum (i.e., between 20 and 33°C). Other species, including *Pereskia aculeata* (Dau and Laboriau, 1974; Campbell, 1988), *Neobuxbaumia tetetzo*, *Cephalocereus chrysacanthus*, and *Pachycereus hollianus* (Rojas-Aréchiga et al., 1997), are indifferent to light conditions close to the temperature optimum.

It has been demonstrated for seeds of many desert species that alternating temperatures can substitute for the light requirement for germination. Temperature changes that occur in arid environments can interfere with the active phytochrome form (P_{fr}) (Toole et al., 1955; Takaki et al., 1981; Pons, 1992; Probert, 1992). This has been shown for *Hyoscyamus muticus*, *Erucaria microcarpa*, *Artemisia abyssinica*, and *Rhazya stricta*, among others (Hammouda and Bakr, 1969; Mahmoud et al., 1983, 1984). However, few experiments have been done to assess the effect of alternating temperatures on cactus seed germination (see Rojas-Aréchiga and Vázquez-Yanes, 2000).