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Vegetation-environment relationships based on a life-forms classification in a semiarid region of Tropical Mexico

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Abstract: Taking the view that morphological characteristics represent behavioral strategies of plants to cope with environmental pressures, we defined 18 life-forms, using multivariate classification techniques in a tropical semiarid ecosystem in Central Mexico. A multiple discriminant analysis confirmed the existence of these groups. A null model of random membership of species to life-forms was significantly different from our classification. Vegetation-environment relationships were examined with Detrended Canonical Correspondence Analysis (DCCA). Ordination axes were interpreted mainly by altitude and soil moisture. Response curves of life-forms along these gradients were explored fitting generalized linear models (GLIM's). We believe that the life-forms approach for the study of vegetation-environment relationships is a valid alternative to the traditional species approach usually used in phytosociological research because: i) life-forms number was found to be an excellent species diversity predictor, ii) this approach enables considerable reduction in the bulk of data without losing ecological information, and iii) life-forms represent ecological strategies per se and, they constitute an index of the number of different ways the desert's resources are utilized.

Key words: Morphological attributes; morphological strategies; ordination; multiple discriminant analysis; response curves; xerophyllous scrub; desert plants.

The occurrence of structural similarities among desert plants, independent of their phylogenetic relationships and geographical distribution, is well known . There is a preponderance of certain growth forms in desert floras that are rare or restricted in other types of ecosystems. Nevertheless, the causes of these presumed convergences are not well understood (Solbrig *et al.* 1977, Bowers and Lowe 1986, Cody 1989). A fundamental problem is to understand how the environment acts as a selection pressure on the shape and function of plants. How do desert plants coexist interacting with each other and with the physical environment?

There have been several attempts to define morphological strategies of desert plants in relation to environmental pressures (Shreve 1942, Cody 1989, Leishman and Westoby 1992). These attempts vary widely in the number and nature of the morphological traits used and in the number of life-form groups produced.

In this paper we describe a multivariate classification of 107 perennial plant species based on morphological characteristics in a semiarid region of tropical Mexico. The basic assumption is that plant species would be naturally clumped in a few morphological categories each of which represents a convergence of strategies to cope with the desert environment. Our aim was to describe vegetation-environment relationships based on these life-form categories.

Vegetation-environment relationships are usually studied along gradients. The concept of environmental gradients has been a cornerstone in the development of ecological theory (Okland 1992). Austin *et al.* (1984) recognize three basic environmental gradients types: (i) indirect gradients, those which do not have a direct influence on plant growth (*e.g.*, altitude); (ii) direct gradients, those which have a direct influence on plant growth, but are not resources potentially subject to competition (*e.g.*, pH); and (iii) resource gradients, those environmental variables which are direct resources influencing plant growth (*e.g.*, soil nutrients). Using certain assumptions, direct environmental gradients can be regarded as dimensions of the Hutchinsonian niche concept. Following this, species response curves along direct gradients would represent their realized niches in one dimension (Austin *et al.* 1990) and, hence, would provide measurements of niche amplitude and overlap.

Taxonomical nomenclature in this paper follows Davila *et al.* (1993).

MATERIAL AND METHODS

Our study site was located in the semiarid valley of Zapotitlán (18° 20' N, 97° 28' W), a local basin in the Pueblan- Oaxacan region in the Mexican State of Puebla (Vite *et al.* 1990). This is a unique region because of its biological richness. About 30% of its species are endemic and it is especially rich in columnar cacti (Villaseñor *et al.* 1990).

The climate is dry with summer rains. Annual mean temperature is 18-22°C and precipitation is around 400 mm/yr. The soils are shallow, stony, and halomorphic (Byers 1967). Arid conditions are produced by the rain shadow of the Sierra Madre Oriental. The vegetation has been classified as xerophyllous scrub (Rzedowski 1978) or as thorn scrub cactus (Smith 1965), and is a well-preserved example of this vegetation type, that supposedly covered the region some 10,000 years ago (Smith 1967, Zavala-Hurtado 1982). Zavala-Hurtado (1982) described four vegetation units in the Zapotitlan Valley: thorn scrub (dominated by thorny shrubs and trees, mainly legumes, agavaceae and low cacti), cardonal (thorn scrub with the columnar cactus *Cephalocereus columna-trajani* Weber), izotal (thorn scrub with *Yucca periculosa* Baker or *Beaucarnea gracilis* Lem., and tetechera (thorn scrub with the columnar cactus *Neobuxbaumia* spp.). There are permanent sites for research on vegetation dynamics in the tetechera, izotal and cardonal units.

The study site utilized for the vegetation-environment relationships is a protected area adjacent to the 'Helia Bravo Hollis' Botanic Garden, located in the middle of the Zapotitlan Valley, 28.5 Km SW of Tehuacan city. The study site occupies an area of 1 Km^2 and consists of the tetechera vegetation unit.

Five 10 x 10 m permanent plots have been established at each site where vegetation dynamics studies are carried out. In these 15 plots we recorded 107 perennial plants. We selected ten individuals of each species in every 10 x 10 m plot that it was present, and recorded the presence or absence of 30 morphological attributes (Table 1). These attributes have clear adaptive significance in terms of photosynthesis optimization (presence of leaves, photosynthetic stems, etc.), water storage and conservation (waxy leaves and stems, succulence, etc.), and thermic regulation (morphology of stems, hairy leaves, etc.).

TABLE 1

Morphological attributes used for classification and multiple discriminant analysis

1 Spines present
2 Succulent stem
3 Exfoliant cortex
4 Perennial stem
5 Spiny stem (*)
6 Photosynthetic stem
7 Waxy stem
8 Woody stem
9 Erect stem
10 Flattened stem
11 Solitary stem
12 Globose stem
13 Candelabrous shape (*)
14 Ribs present
15 Tubercles present
16 Branched
17 Extensive branching
18 Plagiotrophic branching
19 Wide base
20 Leaves present (*)
21 Rosetophyllous leaves (*)
22 Simple leaves
23 Microphyllous leaves
24 Hairy leaves
25 Succulent leaves
26 Glabrous leaves
27 Waxy leaves
28 Perennial leaves
29 Caudex present
30 Epiphytic habit

(*) Attributes not entered by multiple discriminant analysis.

On the species-attributes matrix (107 x 30) we carried out an agglomerative cluster analysis using Ward's method (1963) with the SPSS+Pc package (Norusis 1988). The number of groups in the species classification was chosen subjectively, based on a visual inspection of the dendrogram obtained (Fig. 1). Each of these groups was regarded as a life-form (LF).

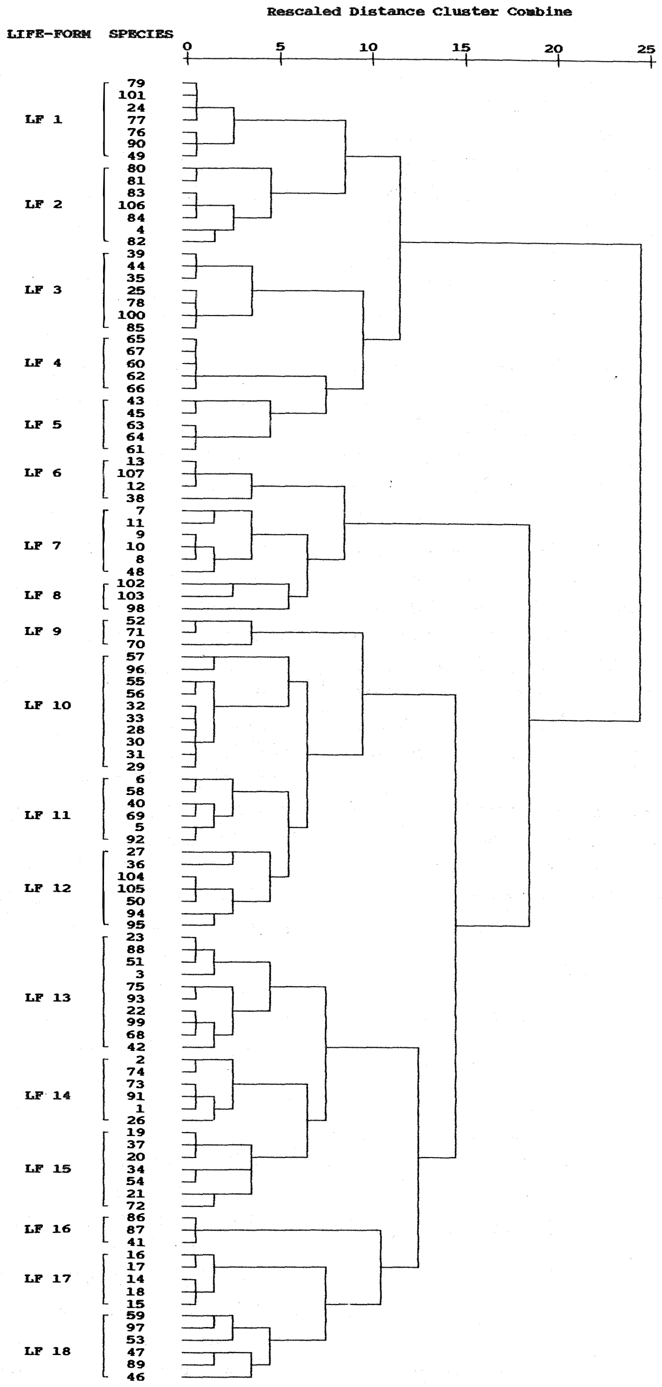

Fig. 1. **Dendrogram with the agglomerative schedule of the classification of** 107 **species from the semiarid valley** of Zapotitlan, Mexico into 18 life-forms (indicated by LF#) using Ward's method. See App. 1 for species names.

Results of the classification were evaluated by a stepwise multiple discriminant analysis using SPSS+PC. This method was also applied to a null model of random assignment of species to the same number of groups detected with the cluster analysis. The objective of this comparison was to test the null hypothesis of random membership to life-forms.

The null model was constructed permuting at random the life- form constituency of each species (maintaining its own morphological attributes).

Analysis of vegetation-environment relationships was carried out in the protected area of the 'Helia Bravo Hollis' Botanic Garden where we set-out a grid of one hundred 100 x 100 m squares in an area of 1 Km^2. In the southeast corner of each of the 100 resulting squares we located a 5 x 5 m plot. As 22 edge sites were occupied by cultivars, we were left with 78 5 x 5 m plots. Within each plot we recorded presence/absence data for perennial plants, and took into account their life-forms membership according to the classification analysis. Also, we recorded 11 continuous and 12 categorical environmental variables for each plot (Table 2).

Incident radiation was estimated using the computer package INSOL (Sánchez-Colón 1987 unpubl.) considering geoposition of the plots and topographical interferences.

TABLE 2

Environmental variables used for ordination by DCCA

Continuous	Categorical
1 Altitude m.a.s.[1].	1 North eastern aspect
2 Winter incident radiation MJ/m^2	2 South-eastern aspect
3 Spring incident radiation MJ/m^2	3 South-western aspect
4 Summer incident radiation MJ/m^2	4 North-western aspect
5 Fall incident radiation MJ/m^2	5 Indeterminate aspect
6 Yearly incident radiation MJ/m^2	6 Concave topography
7 Soil moisture at 10 cm depth (%)	7 Plain topography
8 Soil moisture at 20 cm depth	8 Convex topography
9 Soil pH at 10 cm depth	9 Stoniness (0-25%)
10 Soil pH at 20 cm depth	10 Stoniness (25-50%)
11 Slope (°)	11 Stoniness (50-75%)
	12 Stoniness (75-100%)

Soil moisture was estimated as a percentage of the soil dry weight (Avery and Bascomb 1974). pH was measured in a water- saturation percentage preparation (Jackson 1958) using a pH-meter Chandos type M43.

Altitude, aspect and slope were measured using conventional methods. Topography (concave, plain and convex) and stoniness were estimated visually.

With these data, we built-up two matrices: life-forms x samples and environmental variables x samples. Both matrices were analyzed simultaneously with a Detrended Canonical Correspondence Analysis (DCCA) using the CANOCO package (ter Braak 1987).

To explore the relationship between the defined life-forms and the environmental variables considered, we made a biplot of the life-forms ordination on the sample space. The vectors show direction and relative importance of the environmental variables significantly correlated with the sample ordination axes.

The response of different life-forms to environmental gradients was estimated by fitting Generalized Linear Models (GLIMs, Baker and Nelder 1978) to the defined life-forms. Independent variables (gradients) tried were the environmental variables that explained significantly the sample ordination axes. This approach is useful to predict the probability of a life-form being present (in a quadrat of 5 x 5 m, in this case) at a given point along the gradient. We assumed a binomial distribution for presence/absence data and used a logit transformation to link this distribution with the linear predictor (Austin *et al.* 1984).

RESULTS

Cluster analysis grouped the 107 species to 18 life-forms (Fig. 1). All morphological attributes listed in Table 1 were used for the definition of life-forms. The dendrogram in Fig. 1 shows the agglomeration schedule. Two large groups are evident: species with (life-forms 1 to 5) and without leaves (life-forms 6 to 18). All the latter life-forms have succulent stems.

The first group of life-forms consists entirely of members of the Cactaceae family (31 species). LF1 (seven species) includes branched columnar and candelabrous-like species, LF2 includes seven species with branched flattened stems, columnar nonbranched and barrel-like cacti are clumped in LF3 (seven species), whereas five species of solitary globose cacti (tubercles present) belong to LF4, and LF5 is formed by five species of gregarious globose plants (tubercles present). A single case of misclassification was found in this group: *Coryphanta palida* Brit. & Rose a solitary globose cactus was located in LF3 bearing more morphological affinity with members of LF5.

The second outstanding group (leaves present), with 77 species, is subdivided in two further groups: species with succulent leaves (LF's 6 to 8) and with non-succulent leaves (LF's 9 to 18). Within the life-forms possessing succulent leaves there is LF6 (four species) formed by arboreal rosette-like plants, LF7 (six species) with acaulescent rosette-like species, and LF8 (three species) with small rosette-like plants (some of them epiphytes). The group with non-succulent leaves is composed of a variety of trees and shrubs with and without spines. Life form 9 (three species) consists of climbing species, LF10 (ten species) of short shrubs with unarmed simple leaves, LF11 (six species) of medium-sized shrubs with microphyllous leaves. The LF12 (seven species) includes short shrubs with hairy leaves. Unarmed trees and shrubs, mainly with composed leaves were grouped in LF13 (ten species), whereas LF14 (seven species) includes thorny trees and shrubs. Medium sized unarmed shrubs with simple leaves are in LF15. Species with ephemeral leaves, succulent photosynthetic and unarmed stem were grouped in LF16 (three species). LF17 (five species) includes trees and shrubs with an exfoliant cortex, and LF18 (six species) consists of shrubs with simple waxy leaves.

Multiple Discriminant Analysis validated this 18 group classification (Fig. 2), with 99.07% of the species being correctly classified. The first two discriminant functions accounted for 55.25% of variance (39.99% and 15.26% for discriminant function 1 and discriminant function 2, respectively; $p < 0.001$). The structuring of groups shown in the dendrogram of Fig. 1 is clearly depicted in the discriminant space of Fig. 2. Although, according to the multiple discriminant analysis, segregation between the two main groups is not given by the presence or absence of leaves. The first discriminant function separates these two groups by the presence or absence of succulent stems, spines, ribs and tubercles.

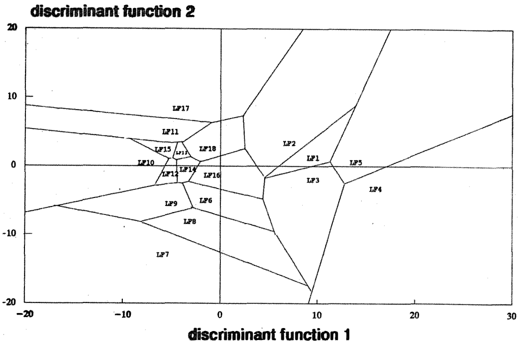

Fig. 2. **Centroids and poligonal territories of 18 life-forms in discriminant space given by the first and second functions of multiple discriminant analysis.**

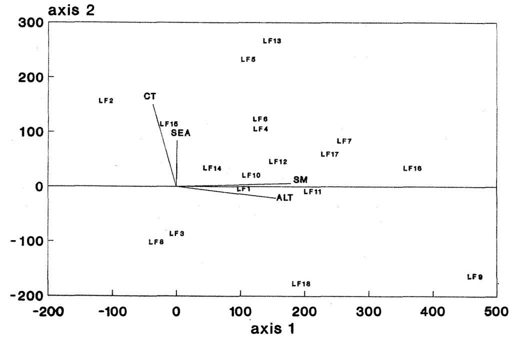

Fig. 3. **Biplot of life-forms ordination** in the sample space with respect to four enviromental variables (lines). CT=concave topography; ALT=altitude; SEA=south-eastern aspect; SM=soil moisture at 20 cm depth.

The Multiple Discriminant Analysis of the null classification model, revealed that only 15.89% of the species were classified correctly. Our life-forms classification differed significantly from this random assignation (Chi square = 1414.26; $p < 0.001$).

Fig. 3 shows the ordination of life-forms on axes 1 and 2 of DCCA. These axes accounted for 60.54% of variance (37.77% and 22.99%, respectively). The same Figure shows the biplot of life-forms ordination on the sample space and the direction and relative importance of the most influential environmental variates. Axis 1 was significantly explained by altitude ($r^2 = 0.55$; $p < 0.001$) and soil moisture at 20 cm depth ($r^2 = 0.44$; $p < 0.001$). Axis 2 was explained by concave topography ($r^2 = 0.80$; $p < 0.001$) and south-eastern aspect ($r^2 = 0.19$; $p < 0.001$). On

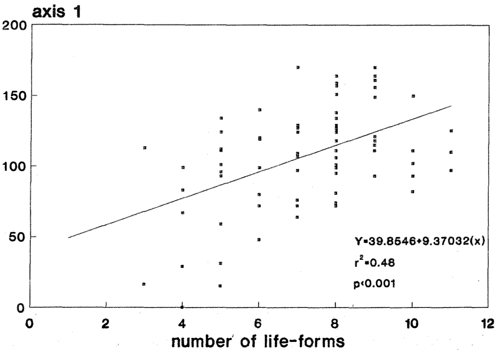

Fig. 4. Relationship between ordination axis 1 (exp. var=37.77%) and life-forms diversity.

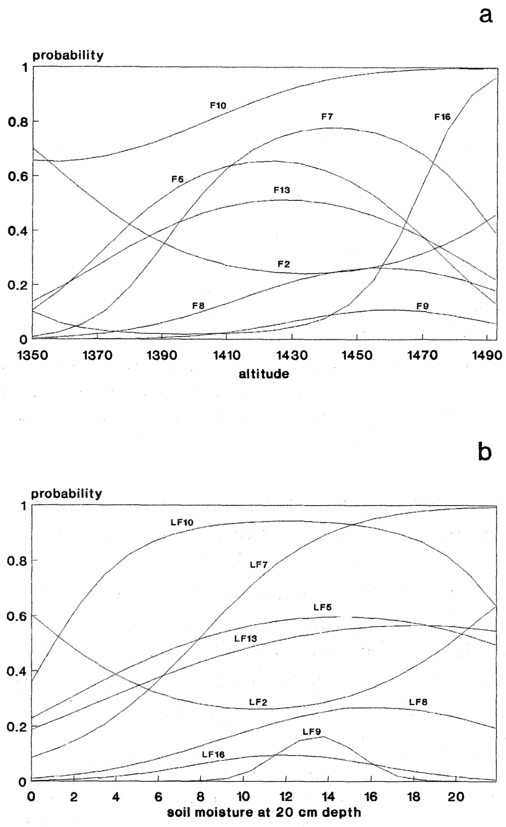

Fig. 5. **Significant (p<0.05) response curves of eight representative** life-forms to (a) altitude and (b) soil moisture at 20 cm depth. Response curves were fitted to GLIMs assuming a binomial distribution.

the other hand, axis 1 showed a significant relationship with number of life-forms ($r^2 = 0.48$; $p < 0.001$). Hence, this axis corresponded to a life-forms diversity gradient (Fig. 4).

It can be seen that climbing deciduous plants (LF9), unarmed shrubs with succulent stems and ephemeral leaves (LF16), trees and shrubs with simple leafs and waxy stems (LF18), acaulescent rosette-like succulents (LF7) and trees with microphyllous leaves and exfoliant stems (LF17) would be restricted to relatively high altitude and/or relatively high water soil content. On the other hand, unarmed trees with composite leaves (LF13) and small globose gregarious spiny succulents (LF5) would be found in lower and less humid sites. Succulents with spiny flattened photosynthetic stems (LF2), unbranched columnar cacti (LF3) and small rosette-like epiphytes (LF8) occupy moderately xeric sites. The other eight life-forms are expected to be found in intermediate conditions or to have a wider range of tolerance.

Fig. 5 shows significant ($p < 0.05$) response curves of eight representative life-forms to (a) altitude and (b) soil moisture at 20 cm depth, the most important environmental variables in the determination of sample ordination. Climbing deciduous plants (LF9) show low probabilities of occurrence along both gradients and are restricted to moderately high soil moisture contents and relatively high altitudes. Unarmed shrubs with succulent stems and ephemeral leaves (LF16) are restricted to high altitudes. Rosette-like acaulescent succulents (LF7), unarmed trees with composite leaves (LF13) and small rosette-like plant (some of them epiphytes, LF8) raise their probability of occurrence as both altitude and soil moisture increase, but become rarer in the upper part of the altitude gradient. Succulents with spiny flat photosynthetic stems (LF2) show bimodal response curves for both gradients with relatively high probabilities of occurrence at both ends of the soil moisture gradient and at low altitudes. Finally, short deciduous unarmed shrubs (LF10) and small globose gregarious spiny succulents (LF5) show wide bell-shaped response curves with highest probabilities of occurrence in the middle of both gradients.

DISCUSSION

The 18 defined life-forms represent different strategies to cope with the environmental pressures characteristic of this arid region in central Mexico. Although the considered attributes represent only structural traits, they also characterize the plants function (Bowers and Lowe 1986). Grouping of cacti into life forms 1 to 5, based on morphological attributes (succulent stem, absence of leaves and presence of spines) has important functional implications for water storage and type of photosynthetic pathway. For the rest of the life forms (LF6-18), attributes such as succulent, rosette-like, microphylous, waxy and deciduous leaves have an influence on both sun light interception and storage and also use of water (Fitter and Hay 1983). Cody (1989), reviewing several authors, notes the ecological implications on light interception resulting from stem geometry in cacti, and leaf shape in shrubs.

Our classification of 18 life-forms using multivariate techniques resembles, in some way, Shreve's (1942) life-forms described for the Sonoran Desert. In that study life-forms were classified subjectively using morphological and phenological characteristics, although the categories used were not completely equivalent with those in the present study. On the other hand, Leishman and Westoby (1992), using multivariate techniques, classified 300 semiarid Australian species in to only five functional life-forms. Such differences may be in part due to the absence of succulents and rosette-like forms in the region which they worked. Other life-form systems (*e.g.*, Raunkier 1934) are not considered adequate to investigate adaptations to environmental conditions of arid ecosystems (Montaña 1990).

Life-forms territories determined on discriminant space (Fig. 2) allows the classification, into their appropriate life- form, of species within the Zapotitlan region not considered in this study. This could be achieved by the simple substitution of their attribute values (1/0) into discriminant functions 1 and 2. Then, the species scores for these two functions could be plotted on the territories map and the assignation would be complete. The first two discriminant axes explain 55.25% of inter-group variability. Although, this figure is low for practical purposes, it would raise to 69.30% if the third discriminant function is considered as well. Also, it is expected that the inclusion of a greater number of species, and the use of dynamic traits (*e.g.*, phenology) would futher improve the classification.

Comparison of our life-forms classification with the random grouping (null model), provides supporting evidence that the former exhibits a non-random pattern. It is proposed that such a pattern reflects similarities and differences in morphological, and hence ecological, attributes of species with each other.

One major drawback of direct gradient analysis is the subjectivity involved in defining important environmental gradients. An indirect approach to the ordination of community data is likely to overcome this problem, because the extracted gradients are defined by the vegetation itself and are expected to reflect the effect of important environmental factors acting on the vegetation (Gauch 1982). A successful environmental interpretation of the major axes of vegetational variation could provide a bridge to return to the direct gradient analysis approach, but with less subjectively defined gradients. In this study, Canonical Correlation Analysis produced an interpretable ordination of the community data in environmental terms.

Although altitude is not a resource or direct gradient (*sensu* Austin 1980), it is associated with the water regime of a site (Ezcurra *et al.* 1987). The positive significant correlation between altitude and the first ordination axis, and between the later and life-forms diversity could be explained by an increment in the complexity of habitat structure (Noy-Meir 1985). So, higher altitudes could be associated with topographic heterogeneity (land forms) and micro topography (soil texture, rockiness, etc.). On the other hand, soil moisture is a direct gradient that represents available water for plants. So, it seems that differences in available soil moisture would be the main cause of life-forms distribution in our study site. This agrees with the widespread idea of water as the main controlling factor in arid ecosystems (Noy-Meir 1973).

Nevertheless, the environmental interpretation of the derived axes cannot be a completely satisfactory one because of intrinsic limitations of environmental ordinations caused by the open ended nature of environmental data (Greig-Smith 1983). Although CANOCO is a very popular and reliable method, it assumes Gaussian response curves (ter Braak 1985, 1987, ter Braak and Looman 1986, Austin *et al.* 1994) and its robustness of violations to this assumption remains to be proved (Minchin 1987, Austin *et al.* 1994).

The present study has no intention of contributing to the debate about shape of response curves (Gauch and Whittaker 1972, Austin

1985, 1987, Austin *et al.* 1984, Austin *et al.* 1994), but the interpretation of the ordination axes did allow us to get an insight into the performance of life-forms along explicit environmental gradients using a direct gradient analysis approach.

The simple quadratic models used revealed significant bell- shaped (mainly platykurtic, and bimodal in some cases) responses of life-forms to the environmental variates examined. Most of the life-forms response curves were wide, perhaps because they encompass realized niches of their constituent species. In this sense, life-form response curves would be a guild level analogous to the qualitative environmental realized niche (QERN) of species (Austin *et al.* 1994, Austin *et al.* 1990). Nevertheless, life-forms response curves should not be regarded simply as cumulative species response curves because these categories may behave in a quite different way to the same environmental gradient (Okland 1992).

The life-forms approach for the study of vegetation- environment relationships is considered a valid alternative to the traditional species approach usually used in phytosociological research: firstly because, life-forms number was found to be an excellent predictor of species richness ($r^2 = 0.65$, $p < 0.001$). Secondly, the life-forms approach enables a considerable reduction in the bulk of data (18 LF's << 107 spp) without losing ecological information. Thirdly, life-forms represent ecological strategies *per se* and, as Cody (1989) states, they constitute an index of the number of different ways that the desert's resources are utilized.

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RESUMEN

Bajo la consideración de que las características morfológicas representan estrategias conductuales de las plantas para enfrentar presiones ambientales, definimos 18 formas de vida utilizando técnicas multivariadas de clasificación en un ecosistema semiárido del trópico mexicano. Un análisis discriminante múltiple confirmó la existencia de estos 18 grupos. Esta clasificación fue significativamente diferente de la esperada por una asignación aleatoria de formas de vida. Se exploraron relaciones vegetación-medio ambiente utilizando un análisis de correspondencia canónico sin tendencia (DCCA). Los ejes de ordenación fueron interpretados principalmenmte en términos de altitud y humedad del suelo. Se exploraron las curvas de respuesta de las formas de vida a lo largo de estos gradientes ajustando modelos lineales generalizados (GLIM). Consideramos que el planteamiento de formas de vida para el estudio de las relaciones vegetación-medio ambiente es una alternativa válida al tradicional uso de categorías taxonómicas en estudios fitosociológicos porque: (i) se encontró que el numero de formas de vida es un buen predictor de la diversidad de especies, (ii) este planteamiento permite una reducción considerable de la base de datos sin pérdida de información ecológica y (iii) las formas de vida representan estrategias ecológicas *per se* y constituyen un índice del número de formas diferentes en que son utilizados los recursos del desierto.

REFERENCES

Austin, M.p. 1980. Searching for a model for use in vegetation analysis. Vegetatio 42: 11-21.

Austin, M.P. 1985. Continuum concept, ordination methods and niche theory. Ann. Rev. Ecol. Syst. 16: 39-61.

Austin, M.P. 1987. Models for the analysis of species' response to environmental gradients. Vegetatio 69: 35-45.

Austin, M.P., R.B. Cunningham & P.M. Fleming. 1984. New approaches to direct gradient analysis using environmental scalars and statistical curve-fitting procedures. Vegetatio 55: 11-27.

Austin, M.P., A.O. Nicholls & C.R. Margules, 1990. Measurement of the realized qualitative niche:environmental niches of five *Eucalyptus* species. Ecol. Monogr. 60: 161-177.

Austin, M.P., A.O., Nicholls, M.D. Doherty, & J.A. Meyers, 1994. Determining species response functions to an environmental gradient by means of a ß-function. J. Veg. Sci. 5: 215-228.

Avery, B.W. & C.L. Bascomb. 1974. Soil survey laboratory methods. Adlar, Harpenden. U.K.

Baker, R.J. & J.A. Nelder. 1978. The GLIM system. Release 3. Numerical Algorithms Group, Oxford.

Bowers, M.A & C.H. Lowe, 1986. Plant-form gradients on Sonoran Desert bajadas. Oikos 46: 284-291.

Byers, D.S. 1967. Climate & hidrology, p. 48-65. *In* Byers, D.S. (ed.) The prehistory of the Tehuacan valley. Environment and subsistence, Vol. 1. University of Texas. Austin, Texas.

Cody, M.L. 1989. Growth-forms diversity and community structure in desert plants. J. Arid Environ. 17: 199-209.

Dávila, P., J.L. Villaseñor, Medina, R. Ramírez, A. Salinas, A., Sánchez-Ken, J. & Tenorio, P. 1983. Listado Florístico de México X. Flora del Valle de Tehuacán-Cuicatlán. Instituto de Biología, UNAM, México, D.F.

Ezcurra, E., M. Equihua & López-Portillo, J. 1987. The desert vegetation of El Pinacate, Sonora, México. Vegetatio 71: 49-60.

Fitter, A.H and R.K.M. Hay, 1983. Environmental physiology of plants. Academic, London.

Gauch, H.G. 1982. Multivariate analysis in community ecology. Cambridge University, Cambridge.

Gauch, H.G. & R.H. Whittaker, 1972. Coencline simulation. Ecology 53: 446-451.

Greig-Smith, P. 1983. Quantitative plant ecology. Blackwell Scientific, Oxford.

Jackson, M.L. 1958. Soil chemical analysis. Constable, London.

Leishman, M. & M. Westoby, 1992. Classifying plants into groups on the basis of associations of individuals traits. evidence from Australian semi-arid woodlands. J. Ecol. 80: 417-424.

Michin, P.R. 1987. An evaluation of the relative robustness of techniques for ecological ordination. Vegetatio 69: 89-107.

Montaña, C. 1990. A floristic-structural gradient related to land forms in the southern Chihuahuan Desert. J. Veg. Sci. 1: 669-674.

Norusis, M. J./SPSS Inc. 1988. SPSS/PC+ Advanced Statistics V 2.0 for the IBM PC/XT/AT and PS2. Statistics Guide. SPSS, Chicago.

Noy-Meir, I. 1973. Desert ecosystems: environment and producers. Ann. Rev. Ecol. Syst. 4: 25-51.

Noy-Meir, I. 1985. Desert ecosystems structure and function, p. 93-103. *In* Evenari, M.,Noy-Meir, I. and Goodall, D.W. (eds.). Hot Deserts and Arid Shrublands. Vol. A. Elsevier, Amsterdam.

Okland, R.H. 1992. Studies in SE Fennoscandian mires: relevance to ecological theory. J. Veg. Sci. 3: 279-284.

Raunkiaer, C. 1934. The Life Forms of Plants and Statistical Plant Geography. Oxford University, Oxford.

Rzedowski, J. 1978. Vegetación de México. Limusa. México.

Shreve, F. 1942. The desert vegetation of North America. Bot. Rev. 8: 195-246.

Smith Jr., C.E. 1965. Flora, Tehuacan valley. Fieldiana Botany 31: 105-144.

Smith Jr., C.E. 1967. Plant remains, p. 220-255. *In* Byers, D.S. (ed.) The prehistory of the Tehuacan valley. Environment and subsistence, Vol. 1. University of Texas. Austin, Texas.

Solbrig, O.T., M.A. Barbour, J. Cross, Goldstein, C.H., Lowe, C.H., Morello, J. & Yang T.W. 1977. The strategies and community patterns of desert plants, p. 67-107. *In* Orians, G.H. and O.T. Solbrig, (eds.). Convergent evolution in warm deserts: examination of strategies and patterns in deserts of Argentina and the United States. Dowden, Hutchingson & Ross. Stroudsburg, Pennsylvania.

ter Braak, C.J.F. 1985. Correspondence analysis of incidence and abundance data: properties in terms of an unimodal response model. Biometrics 41: 859-873.

ter Braak, C.J.F. 1987. CANOCO a FORTRAN program for canonical community ordination by [partial] [detrended] [canonical] correspondence analysis, principal component analysis and redundancy analysis (version 2.1). ITINO. Agriculture Mathematics Group, Wageningen, Netherlands.

ter Braak, C.J.F. & C.W.N. Looman, 1986. Weighted averaging, logistic regression and the Gaussian responce model. Vegetatio 65: 3-11.

Villaseñor, J.L., P. Dávila & F. Chiang, 1990. Fitogeografía del Valle de Tehuacán-Cuicatlán. Boletín de la Sociedad Botánica de México, No. 50: 135-149.

Vite, F., Zavala-Hurtado, J.A., M.A. Armella, & M.D. García-Suárez, 1990. Regionalización y caracterización macroclimática del Matorral Xerófilo. *In* Atlas Nacional de México, Vol. II, Carta IV.8.3.B. Instituto de Geografía, UNAM. México, D.F.

Ward, J. 1963. Hierarchical grouping to optimise an objetive function. J. Amer. Stat. Ass. 58: 236-244.

Zavala-Hurtado, J. A. 1982. Estudios ecológicos en el valle semiárido de Zapotitlán, Pue. I. Clasificación numérica de la vegetación basada en atributos binarios de presencia o ausencia de las especies. Biótica (México) 7: 99-120.

Appendix 1. Plant species used for the definition of life-forms in the semiarid valley of Zapotitlan, Mexico

	Species	Life-form
79	*Neobuxbaumia tetetzo* (Web. ex K. Sch.) Backeb.	**1**
101	*Stenocereus stellatus* (Pffei.) Riccob.	**1**
24	*Cephalocereus chrisacanthus* (Weber) Britt & Rose	**1**
77	*Neobuxbaumia macrocephala* (Weber) Dawson	**1**
76	*Myrtillocactus geometrizans* (C. Martius) Console	**1**
90	*Polaskia chichipe* (Gosselin) Backeb.	**1**
49	*Polaskia chende* (Gosselin) Gibson & Horak	**1**
80	*Opuntia decumbens* Salm-Dyk	**2**
81	*Opuntia depressa* Rose	**2**
83	*Opuntia pumila* Rose	**2**
106	*Peniocereus viperina* (Weber) Buxb.	**2**
84	*Opuntia rosea* De Candolle	**2**
4	*Acantothamnus aphyllus* (Schldl.) Stanley	**2**
82	*Opuntia pilifera* Weber	**2**
39	*Echinocactus platyacanthus* Link & Otto	**3**
44	*Ferocactus recurvus* (Miller) Lindsay	**3**
35	*Coryphanta palida* Britt. & Rose	**3**
25	*Cephalocereus columna-trajani* Sch.	**3**
78	*Neobuxbaumia mezcalaensis* (Bravo-Holl.) Backeb.	**3**
100	*Pachycereus marginatus* (De Candolle) Britt & Rose	**3**
85	*Pachycereus hollianus* (Weber) Buxb.	**3**
65	*Mammillaria compressa* De Candolle	**4**
67	*Mammillaria pectinifera* (Ruempler) Weber	**4**
60	*Mammilaria carnea* Zucc. ex Pfeiffer	**4**
62	*Mammilaria myxtax* Martius	**4**
66	*Mammillaria elegans* De Candolle	**4**
43	*Ferocactus flavovirens* (Scheidw.) Britt. & Rose	**5**
45	*Ferocactus robustus* (Pfeiffer) Britt. & Rose	**5**
63	*Mammilaria sphacelata* Martius	**5**
64	*Mammilaria viperina* Purpus	**5**
61	*Mammilaria haageana* Pfeiffer	**5**
13	*Brahea dulcis* Cooper	**6**
107	*Yucca periculosa* Baker	**6**
12	*Beaucarnea gracilis* Lemm.	**6**
38	*Echeveria* sp.	**6**
7	*Agave karwinskii* Zucc.	**7**
11	*Agave potatorum* Zucc.	**7**
9	*Agave macroacantha* Zucc.	**7**
10	*Agave marmorata* Roezl.	**7**
8	*Agave kerchovei* Lemm.	**7**
48	*Hechtia podantha* Mez.	**7**
102	*Tillandsia pueblensis* Liman Smith	**8**
103	*Tillandsia recurvata* L.	**8**
98	*Sellaginella* sp.	**8**
52	*Ipomoea conzatii* Greenman	**9**
71	*Metastelma* sp.	**9**
70	*Maximowitzia* sp.	**9**
57	*Lippia gratissima* (Gill.) Troncoso	**10**
96	*Sanvitalia fruticosa* Hemsley	**10**
55	*Lantana camara* L.	**10**
56	*Lantana* sp.	**10**
32	Asteraceae 1	**10**
33	Asteraceae 2	**10**
28	Asteraceae 3	**10**
30	Asteraceae 4	**10**
31	Asteraceae 5	**10**
29	Asteraceae 6	**10**
6	*Aeschenomene compacta* Rose	**11**
58	*Lippia graveolens* Kunth	**11**
40	*Echinopteryx eglandulosa* Small.	**11**
69	*Mascagnia seleriana* Loes.	**11**
5	*Actinocheita filicina* (Sesse & Moc.) Barkley	**11**
92	Asteraceae 7	**11**
27	*Cnidoscolous tehuacanensis* Breckon	**12**
36	*Croton ciliato-glandulosus* Ortega	**12**
104	*Turnera difussa* Willd ex Schult.	**12**
105	*Viguiera* sp.	**12**
50	*Hibiscus* sp.	**12**
94	*Ruellia* sp.	**12**
95	*Salvia* sp.	**12**
23	*Celtis pallida* Torr.	**13**
88	*Phitecellobium acatlense* Benth.	**13**
51	*Ipomoea arborescens* Sweet	**13**
3	*Acacia subangulata* Rose	**13**
75	*Morkillia mexicana* Rose & Painter	**13**
93	*Pseudosmodingium multifolium* Rose	**13**
22	*Ceiba parvifolia* Rose	**13**
99	*Senna pringlei* Rose	**13**
68	*Manihot* sp.	**13**
42	*Eysenhardtia polystachia* Sarg.	**13**
2	*Acacia* sp.	**14**
74	*Mimosa luisana* Brandg.	**14**
73	*Mimosa lacerata* Rose	**14**
91	*Prosopis laevigata* (Humb. & Bonpl ex Willd.) Johnst.	**14**
1	*Acacia constricta* Benth	**14**
26	*Cercidium praecox* Harms	**14**
19	*Caesalpinia melanadenia* Standl.	**15**
37	*Dalea* sp.	**15**
20	*Calliandropsis* sp.	**15**
34	*Cordia cylindrostachya* Roem. & Schult.	**15**
54	*Karwinskia humboldtiana* Zucc.	**15**
21	*Castela tortuosa* Liebm.	**15**
72	*Megastigma galiottii* Baill	**15**
86	*Pedilanthus aphyllus* Boiss	**16**
87	*Pedilanthus* sp.	**16**
41	*Euphorbia antisiphyllitica* Zucc.	**16**
16	*Bursera fagaroides* Engl.	**17**
17	*Bursera hindsiana* Engl.	**17**
14	*Bursera* sp.	**17**
18	*Bursera* sp.	**17**
15	*Bursera arida* Standl.	**17**
59	*Lycium* sp.	**18**
97	*Schaefferia stenophylla* Standl.	**18**
53	*Jatropha spathulata* Muell. Arg.	**18**
47	*Gymnosperma glutinosa* Spreng.	**18**
89	*Plumeria rubra* L.	**18**
46	*Fouquieria formosa* Kunth	**18**