UNIVERSIDAD DE GUADALAJARA

Centro Universitario de Ciencias Biológicas y Agropecuarias

Postgrado en Ciencias Biológicas
Orientación en Sistemática Vegetal

ORDENACIÓN DEL BOSQUE MESÓFILO EN EL CERRO LA MONA, SIERRA DE COALCOMÁN, MÉXICO, EN EL CONTEXTO DEL CAMBIO CLIMÁTICO

TESIS

Presentada como requisito parcial
para obtener el grado de

DOCTOR EN CIENCIAS BIOLÓGICAS ORIENTACIÓN EN SISTEMÁTICA VEGETAL

Presenta

EDUARDO SAHAGÚN GODÍNEZ

Las Agujas, Zapopan, Jalisco, 10 de Junio, 2004

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por

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Fecha 02 de Junio de 2004

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DEDICATION

I dedicate this dissertation to my wife, Ma. Elena Romo Limón, for her love and patience

and to my daughter Andrea, for her sheer innocence

CHAPTER 1

Ordination of cloud forest at cerro La Mona, Sierra de Coalcomán, México

Keywords: ammonium and nitrate nitrogen; community-environment relationships; NMS/NMDS ordination; soil moisture and nutrients; tropical montane vegetation; western Mexico.

ABSTRACT

The cloud forest at cerro La Mona was studied using circular quadrats on a stratified random design and Varimax-rotated non-metric multidimensional scaling (NMS) ordination. Eighty-one species in 68 genera and 42 families of woody vascular plants occurred within nine 0.1 ha samples. Species richness averaged 21.4 species/sample (range 10-35). It was negatively correlated with aluminum and elevation and positively correlated with cation exchange capacity (CEC) and nitric-nitrogen. Species richness also showed a nearly significant correlation with soil moisture. Species richness, evenness and diversity (H') were higher in bottomland samples than in ridge samples. Density averaged 99.6 individuals/sample (range 49-221) and was positively correlated with dry-season soil moisture and species richness. On average, ridge sites showed lower densities than bottomland sites. The NMS ordination successfully recovered three axes which cumulatively explained 94.8% of the variance. Axis 1 of the NMS ordination was correlated positively with dry-season soil moisture, electrical conductivity, calcium and organic matter, but negatively so with elevation and soil aluminum. The second axis was positively correlated with CEC and nitrates and the third axis was positively correlated with ammonium-nitrogen. Nitrogen forms independently explained community organization; nitrate possibly associated to leaching and ground water dynamics and ammonium probably related to soil microbial activity. Here the hypothesis that CEC could significantly explain community organization of cloud forest communities is advanced, perhaps through a relationship with small-scale patterns of germination and seedling establishment.

INTRODUCTION

Studies of vegetation in Mexico have been mostly qualitative, relying largely on floristic and physiognomic data (Miranda and Sharp 1950; Miranda and Hernández-Xolocoztli 1963; Rzedowski 1983). Only recently have multivariate methods been applied in vegetation studies of various tropical regions in Mexico (Vázquez-García 1993, 1995; Santiago and Jardel 1993; Aguado *et al.* 1996; Zavala *et al.* 1996; Vargas-Rodríguez 1998; Huerta *et al.* 1999; Vázquez-García and Givnish 2000; Ramírez 2001; Cuevas 2002; Luquín 2003). However, no multivariate vegetation studies are known from any part of Sierra de Coalcomán. Existing studies of plant communities in this region are qualitative (i.e., Turner 1960; Rzedowski and McVaugh 1966; Guerrero 1985).

Also, as far as known, no information on soil nutrient or dry-season soil water content is available for cloud forest or other plant communities in Sierra de Coalcomán, notwithstanding the well known dependence of cloud forest for high humidity conditions (Grubb and Whitmore 1966; Vogelmann 1973; Rzedowski 1983; Cavelier 1996) and the importance of soil nutrient and moisture variations for the outcome of plant competition and survival (Grime and Curtis 1976; Bunce *et al.* 1977, 1979; Chapin 1980; Grime 1977, 2001).

Rzedowski (1991a) reported a considerable richness of endemic species in cloud forest and he also (Rzedowski 1991b) regarded cloud forests as the most diverse per surface unit of all Mexican plant communities, comprising about 10% of that nation's flora. The understanding of the ways in which cloud forest interacts with environmental variables such as soil moisture and nutrients is essential to devise appropriate strategies for its management and conservation.

Ordination by means of multivariate techniques is aimed at identifying major community axes and the environmental factors they represent. This explains the variation observed in the plant communities by reducing the many dimensions of the system to only two or three, with a minimum loss of useful information (Beals 1984).

Nonmetric multidimensional scaling (NMS) is a technique of sociological ordination that has proved to be robust under adverse conditions such as high beta diversity (Fasham 1977;

Prentice 1980; Beals 1984; Kenkel and Orloci 1986; Minchin 1987) and is currently considered the method of choice for the graphical representation of community relationships (Clarke 1993; McCune and Grace 2002).

The aims of this chapter are: 1) to describe the major community patterns of cloud forest at cerro La Mona, in western México, along a ridge-bottomland toposequence using direct gradient analysis, 2) to determine the major axes of variation in the cloud forest community using NMS ordination and 3) to investigate the relationships between those axes and measured environmental variables using Pearson's correlations.

METHODS

Arriaga *et al.* (2000) described Sierra de Coalcomán as an isolated, plant-relict region in southern Jalisco and northwestern Michoacán occupying a surface of approximately 5,500 km^2 with tropical deciduous and semi deciduous forest, pine-oak forest and smaller areas covered by mesophytic mountain forest (i.e., cloud forest). The vegetation typology in western Mexico has been described by Rzedowski and McVaugh (1966).

Cerro La Mona (Fig. 1) lies on the northwest part of Sierra de Coalcomán, in Michoacán, near Puerto del Caimán and Villa Victoria, the latter functioning as the municipal capital of Chinicuila.

Undisturbed cloud forest stands at La Mona are remote or located on highly inclined slopes with brittle calcareous rock that are prone to landslides. Crime in the area is high mostly due to illegal crops, making access to remote sites dangerous. These difficulties have made Sierra de Coalcomán a little explored region of Mexico, despite its high biological richness and endemism and the fact that The National Commission for Knowledge and Use of Biodiversity (CONABIO) has selected it as priority region for conservation (Arriaga *et al.* 2000). This is particularly important given that deforestation for cattle pasture and agriculture have already removed much of the original vegetation. Deforestation was first recognized as a major threat to conservation in the Coalcomán region about 60 years ago (Hinton and Rzedowski 1975).

The climate near cerro La Mona is described as warm, temperate sub-humid (García 1997a; Arriaga *et al.* 2000), with a mean annual temperature of 18-22°C (García 1997b) and total annual precipitation of approximately 1200 mm (García 1997c). Climatic data for mountains in the Americas are imprecise because of the lack of a station network (Barry and Seimon 2000).

The rainy season in western Mexico extends from June to October, a period when cerro La Mona is covered intermittently with fog at an elevation of about 1300 m and above. No thematic maps on the geology, soils or vegetation cover of cerro La Mona were available during the course of this study.

Selection of the study area

Cerro La Mona was selected for study as it is one of the few places that still have much of their original montane arboreal vegetation in the explored area of northwestern Sierra de Coalcomán (Fig. 1), although the line of deforestation is actively moving forward. The vegetation shows a strong ridge-bottomland effect throughout the mountain, apparently due to edaphic differences. Oak forest commonly covers the ridges while cloud forest or tropical semi deciduous forest develop in the ravines. The selected sampling area started at 1320 m and proceeded up along an elevational range of about 300 m to the highest available cloud forest sites. Most cloud forest at La Mona is found within this small elevation interval (1300 to 1650 m), as it is replaced by tropical semi deciduous forest at lower elevations. Given the small altitudinal range, edaphic factors were expected to play a major role in community organization of cloud forest (Vázquez-García and Givnish 2000) and thus particular emphasis was placed on sampling along a ridge-bottomland topographic sequence.

Field sampling

The cloud forest of cerro La Mona was sampled using the circular quadrat method (Curtis and McIntosh 1951) and a stratified random design (Matteuci and Colma 1982). Nine 0.1 ha samples were taken along an elevation interval of 300 m as topography and forest stand dimensions permitted.

To investigate the relationships between edaphic factors and the cloud forest community, five samples were located on ridges and four samples were placed on bottomlands near creeks. Bottomland sites were marked as "B" sites whereas those located on a ridge were marked as "R" sites (Table 1).

Each of the nine sampling sites was subdivided into 20 equal squares of 11.5 x 11.5 m. Ten of the squares were randomly selected and their centers were marked with stakes. A measuring tape was used to measure a radius of 5.64 m around the stakes. The combined sampled area of the 10 circular quadrats marked in any one sampling site totaled 0.1 ha. Thus, a total of nine 0.1 ha samples were surveyed at cerro La Mona.

Sampling of circles was accomplished by recording the species of trees, shrubs and lianas that were rooted in them as well as their diameter at breast height (d.b.h.), i.e., at 1.3 m above the ground. Only woody plants whose diameter was at least 2.5 cm d.b.h. were considered. If they were on the edge, they were recorded only when at least half of their base was within the circular plot. Sampling took place between 1999 and 2000, except for site R5 which was sampled in 2002.

At least one voucher specimen of each recorded species of trees, shrubs and lianas found within the plots was collected and subsequently deposited at local herbaria (GUADA and IBUG) (Holmgren & Holmgren 2003). Identifications were performed by the author or by specialists at Universidad de Guadalajara and elsewhere. Online specimen databases (IEB 2004; MO 2004; NY 2004; TEX-LL 2004; XAL 2004), especially those with images of type specimens were useful tools to confirm some determinations. Nomenclature of species names follows Missouri Botanical Garden's w3-TROPICOS (MO 2004). Nomenclatural equivalents of cloud forest have been discussed in the literature (i.e., Rzedowski 1983; Vázquez-García 1995; Ramírez 2001).

Environmental variables

The peak of the dry season was selected for soil sampling in order to study the relationship of vegetation and water stress. A soil sample of about 2 kg was taken 20 cm below the leaf litter layer from eight of the sampling sites in April, 2001. An additional soil sample was taken in late March of 2002 when site R5 was first visited. After collection, soil samples were taken to the laboratory to determine dry-season soil moisture gravimetrically. Nutrient content was assessed using standard soil fertility procedures as well as salinity tests in which a portion of soil was water-saturated and analyzed for water-soluble ions (Table 2).

Canopy openness, an indicator of the light environment in the understory of the sampling sites (Denslow *et al.* 1998; Brown *et al.* 2000), was measured in March 2002 by means of a canopy-scope. Measurements of the largest canopy gap were taken and averaged from five circular plots for each of the nine 0.1 ha sampling sites (Table 2). Measurements at the peak of the rainy season in July-August, when light stress becomes more prominent to tree seedlings because of canopy closure were not possible due to inaccessibility to most sampling sites at that time. The canopy-scope (Brown *et al.* 2000) is a simple instrument that consists of a transparent plastic screen with 25 1-mm diameter dots printed on it and spaced 3 cm apart in a 5 x 5 square arrangement, with a 20 cm cord attached to one of its corners to ensure a constant distance from the eye of the viewer.

Landform (i.e., ridge vs. bottomland) and aspect were introduced as categorical variables in the ordination to see whether they showed an important effect. Landform was expected to have a relationship with one or more of the ordination axes but not aspect, because north and east exposure are considered equivalent in terms of heat load received from the sun (McCune & Grace 2002).

Community patterns

Community patterns of variation were explored along the topographic sequence using a direct gradient analysis approach. Pearson's correlations were calculated in order to analyze the relationship of species richness and density of individuals with available environmental factors.

Community ordination

Prior to the ordination analyses, the data were scanned for outliers with an iterative use of PC-ORD's outlier analysis of both sample and species data using a cutoff value of 2 standard deviations. After removing outliers, Nonmetric Multidimensional Scaling (NMS) ordinations were performed on the remaining data using PC-ORD version 4.24, which uses the method described by Kruskal (1964) and Mather (1976). In order to assess the dimensionality of the data set, an NMS ordination was set up with six axes using the step down function and a Scree plot (not shown). A Monte Carlo test was also performed with 1500 runs in real data and 900 runs in randomized data to assess the probability that a 3-dimensional NMS ordination would achieve lower final stress than due to chance. The final NMS ordination was performed using the scores from a previous NMS ordination as starting configuration to increase stability, which was evaluated with up to 1500 runs in real data. Varimax rotation was used on the final ordination to maximize the correlation of variables with higher correlations and minimize those with lower correlations.

To evaluate the proportion of variance represented by each axis, correlations were used between ordination distances and distances in the original 3-dimensional space. To investigate the relationships of cloud forest and the environment, Pearson's correlations were used between the identified axes of the NMS ordination and the available environmental variables. The cutoff value used for graphing the ordination biplot was $r^2 = 0.444$. This figure was obtained by squaring the r value at $p < 0.05$ for $df = 7$. This process is used in PC-ORD for graphing environmental variables that are significantly correlated with ordination axes (see McCune and Grace 2002).

Sorensen's distance measure, which is based on the difference of floristic composition between each pair of samples, was used. This distance measure has proved to be more robust and efficient than others (Beals 1984; Faith *et al.* 1987). Also, Synthetic Importance Values (SIV) were used as abundance measures (Whittaker 1975). These were obtained for each species by averaging relative dominance (i.e., basal area), relative density (i.e., number of plants per sample) and relative frequency values (i.e., proportion of species in subplots). To investigate the relationships of cloud forest and the environment, Pearson's correlations between the identified axes of the sociological ordination and the available environmental variables were used. In order to better describe the ordination axes a number of representative species were selected based on a significant correlation with the corresponding axis and their presence in at least three 0.1 ha sites. This number was arbitrarily selected in an attempt to avoid spurious correlations based on fewer samples.

RESULTS

Environmental variables

Coefficients of determination below assume df = 7. Elevation was negatively correlated with dry-season soil moisture ($r = -0.917$), calcium concentration ($r = -0.705$), electrical conductivity (EC) ($r = -0.772$) and organic matter ($r = -0.694$) but it was positively correlated with aluminum concentration ($r = 0.735$). Concentrations of nitric nitrogen were quite different from those of ammonium nitrogen; the latter contributing more significantly to total nitrogen values in most soil samples (Table 2). With regard to slope, the least inclined sites were R1, B3 and R4 (i.e., 21-22°) whereas most other sites were slightly more inclined (i.e., 25-29°). Only site B2 had an unusually high inclination (i.e., 36°) (Table 2). The elevation interval studied was about 300 m, between 1320 m and 1645 m.

Community patterns

A total of 81 species in 68 genera and 42 families of woody vascular plants occurred within the nine 0.1 ha sites surveyed at cerro La Mona. Those that were more important (cumulative 90% of importance values) are listed in the appendix. Despite the small elevational range studied, the sampled woody species clearly showed a staggered distribution along the topographic sequence.

Species richness in the nine samples averaged 21.4 per 0.1 ha site and ranged from 10 species in the ridge site R2, to 35 species in the bottomland site B4. On average, bottomland sites showed higher richness values (i.e., 26 species) than ridge sites (i.e., 17.8 species) but evenness (0.63 vs. 0.52) and diversity averages (2.04 vs. 1.48), although higher, were not very different.

In addition, species richness was negatively correlated with elevation ($r = -0.793$) and aluminum ($r = -0.778$) and was positively related to soil fertility variables such as cation exchange capacity (r = 0.769) and nitric nitrogen (r = 0.706). Lastly, species richness had a nearly significant positive correlation with soil moisture (r = 0.655).

Density averaged 99.6 plants per sample in the nine 0.1 ha samples at cerro La Mona and ranged from 49 plants in sites B3 and R5, to 221 plants in site R1. This site was unusual when compared to the remaining ridge sites which averaged 60.3 individuals per sample. On average, ridge sites (i.e., 92.4 plants per sample) showed lower densities than bottomland sites (i.e., 108.5 plants per sample). Density of individuals was positively correlated with soil moisture (r = 0.881) and species richness (r = 0.797).

Community ordination

Using a cutoff value of 2 standard deviations, no sites were identified as outliers but three species were. *Chromolaena ovaliflora*, *Sapium lateriflorum* and *Arbutus xalapensis* were consequently removed from the ordination analysis.

A preliminary Nonmetric Multidimensional Scaling (NMS) ordination using the step down function showed that a 3-dimensional model was recommended for this study since it achieved a low final stress of 0.358. The Scree plot (not shown) also indicated that the first three axes accounted for most of the reduction in stress.

Using the 3-dimensional solution of the preliminary NMS ordination as starting configuration, a second NMS ordination was produced with a final stress of 0.358 and a final instability of 0.0005 with 452 iterations. Most stress was reduced after about 95 iterations.

The Monte Carlo Test also showed that a 3-dimensional solution was recommended for this data set as it achieved a reduction in stress that was significantly lower than would be attributable to chance. The mean stress in real data (1500 runs) was 1.222 whereas it was 4.492 in randomized data (900 runs) (P value = 0.0344).

The final Varimax-rotated NMS ordination thus successfully recovered three axes using abundance (SIV) data from 78 woody species. The first axis represented 44.6% of the variance and was correlated with six of the available environmental factors (Table 3, Figs. 2 and 3).

The environmental variables that were positively correlated with axis 1 were electrical conductivity ($r = 0.882$), soil moisture ($r = 0.858$) (Fig. 5), calcium ($r = 0.764$) and soil organic matter ($r = 0.734$) (Fig. 6). Conversely, axis 1 was negatively correlated with elevation ($r = -0.962$) and soil aluminum concentration ($r = -0.809$).

Representative species that were positively correlated with axis 1 on the NMS ordination (Table 4) were trees such as *Clusia salvinii* ($r = 0.805$) (Fig. 7) and *Styrax argenteus* ($r = 0.859$) as well as large woody climbers, i.e., *Canavalia hirsutissima* ($r = 0.850$) and *Marsdenia* aff. *macrophylla* ($r = 0.946$). Conversely, *Carpinus tropicalis*, a large tree, was negatively correlated with axis 1 ($r = -0.841$) (Fig. 8). All species were of cloud forest affinity.

The second axis represented 29.3% of the variance for a cumulative total of 74%. Axis 2 was positively correlated with cation exchange capacity ($r = 0.672$) (Fig. 9) and nitrate concentration ($r = 0.730$) (Fig. 10) (Table 3). Species that were positively correlated with axis 2 were trees of cloud forest affinity, i.e., *Guarea glabra* ($r = 0.967$), *Trichilia havanensis* ($r = 0.860$) and *Quercus uxoris* ($r = 0.800$) (Fig. 11). Conversely, species with negative correlations had an affinity with oak forest, i.e., *Clethra lanata* ($r = -0.789$) and *Quercus scytophylla* ($r = -0.804$) (Fig. 12) (Table 4).

The third axis represented 20.8% of the variance for a cumulative total of 94.8%. This axis was positively correlated with ammonium-nitrogen ($r = 0.685$), an important soil nutrient (Figs. 3, 4 and 13) (Table 3). Several cloud forest species were positively correlated with axis 3, i.e., *Dendropanax arboreus* ($r = 0.890$) (Fig. 14), *Sebastiania jaliscensis* ($r = 0.883$) (Fig. 15), *Persea hintonii* ($r = 0.878$) and *Cedrela odorata* ($r = 0.840$), whereas *Oreopanax peltatus* was negatively correlated with axis 3 ($r = -0.700$) (Table 4).

DISCUSSION

Community patterns

In terms of species richness of trees, shrubs and vines > 2.5 d.b.h. the La Mona sites are of comparable richness to average temperate forests and also to those of intermediate to high elevations at the calcareous cerro Grande, in Manantlán (Vázquez-García and Givnish 1998). However, they are less rich than average lowland forests of the cerro Grande transect and average forests of the volcanic western region of Manantlán. They are also less rich than most Mexican montane forests at similar elevations located south of La Mona (Gentry 1995). Certainly they are by far less rich than average tropical lowland dry or wet forests (Vázquez-García and Givnish 1998; Cuevas 2002). These differences may partly reflect lower rainfall in the Coalcomán gradient as predicted by Gentry (1988) or perhaps lower residual dry-season soil moisture.

Woody species richness at cerro La Mona decreased with increasing elevation. This agrees with the conclusions of Gentry (1988) and Vázquez-García and Givnish (1998). Also, in agreement with our results, there are reports of a positive relationship of species richness and soil nutrients (Gentry 1988; Givnish 1999), although a negative relationship has also been documented in more fertile soils (Huston 1980; Faber-Langendoen and Gentry 1991).

In addition, a nearly significant positive correlation between species richness and soil moisture was found. These small-scale results show a similar pattern as those relating rainfall and species richness at a large scale (Gentry 1982; Givnish 1999; Francis and Currie 2003). Dry-season soil moisture data should be used more in plant community studies, because it can provide small-scale detail in regions such as western Mexico where a prolonged dry season may have an effect on forest structure and composition through selection of tree seedling or even adult tree survival (Segura *et al.* 2003).

Community ordination

The analysis of aspect as a categorical variable, as expected, yielded no clear relationship with any of the axes of the ordination; i.e., they did not form two separate groups on any of the axes (Figs. 2-4). We concluded that the variation in east-north exposure is not a major factor that significantly explains community organization. Conversely, when land form was analyzed as a categorical variable, it showed a clear relationship with axis 2 of the ordination, with bottomland sites grouping on one side and ridge sites on the other (Fig. 2).

Inspection of axis 1 of the ordination showed an elevational trend wherein sample scores increased toward low elevations. Furthermore, axis 1 was negatively correlated with elevation and positively correlated with dry-season soil moisture (Table 3, Figs. 2, 3 and 5). This agrees with the observed susceptibility to drought reported for cloud forest communities elsewhere (Rzedowski and McVaugh 1966; Rzedowski 1983; Puig and Bracho 1987; Vázquez-García 1993, 1995; Hamilton *et al.* 1995; Luna *et al.* 1988). Also, axis 1 was negatively correlated with soil aluminum concentration. Toxicity of aluminum at low pH values has been known for a long time (i.e., Magistad 1925). The combination of low pH and high Al concentration in the ridge sites may partly explain their lower diversity and density.

The positive correlation of axis 1 with soil organic matter implies a greater proportion of deciduous species in the lowlands, as is the case in the Sierra de Manantlán (Vázquez-García and Givnish 1998), which is located northwest of our area. This is often the result of a soil fertility gradient (Montague and Givnish 1996). In addition, the analysis of the ordination also indicated a positive relationship between axis 1 and several soil chemical variables, (i.e., Ca and electrical conductivity) which were higher in low elevation samples (Table 3, Figs. 2 and 3). At least some of these trends may be the result of gradients in erosion, leaching and runoff (Raghubanshi 1992; Givnish 1999; Yavitt 2000), which may have caused low-elevation soils to be more humid and richer in solutes, including calcium. This would also partly explain their more alkaline pH.

Axis 1 is apparently related to an elevational gradient that may be climatic and/or edaphic in nature, where elevation appears to be of greater importance than the ridge-bottomland situation. Thus, species at higher elevations growing in a cooler climate with drier and less rich soil show higher abundances on the negative end of the axis, whereas those that grow at lower elevations in a warmer climate with more humid and richer soil show higher scores on the positive side of this axis.

The analysis of axis 2 indicated that sample scores increased from sample sites located on the ridges to those located on bottomlands near creeks and that soil fertility as indicated by cation exchange capacity (CEC) and nitrate concentration (Table 3 and Figs. 2, 4, 9 and 10) were related to this trend.

With regard to nitrates, Triska *et al.* (1989a) have demonstrated that under natural conditions these nutrients may be carried down by a waterway and thus become a mineral source for downstream communities and that such minerals (Triska *et al.* 1989b) may be transported through ground water to the riparian zone and made available to the plants rooted there. Furthermore, the small concentrations of nitric nitrogen that were found in this study agree well with the notion that nitrate is easily leached and mobilized in tropical montane ecosystems (Silver *et al.* 2001).

Cation exchange capacity (CEC) was significantly correlated with axis 2 (Fig. 9). It showed a tendency to increase in the bottomland samples while decreasing in most ridge samples. Differences in CEC could imply differences in seedling and sapling establishment, thus influencing forest regeneration. It is noteworthy that CEC has also been found to be an important environmental factor for the tropical dry forest of the lowlands in western Mexico, where it was correlated with the secondary axis of a sociological ordination using binary data for both adult trees or a combination of seedlings and saplings (Y. L. Vargas-Rodríguez, Louisiana State University, personal communication). Axis 2 thus seems to be soil-related, mostly linked to the ridge-bottomland situation. The negative end apparently representing poor soils on ridges, whereas the positive end representing richer soils on bottomlands (Figs. 2 and 4).

Axis 3 showed a trend in which sample scores increased toward sample sites in the bottomlands at higher elevations. This axis was related to soil ammonium concentration, which also increased in the high-elevation sample sites near creeks (i.e., samples B3 and B4). Ammonium was correlated with elevation, although the correlation was not significant (r = 0.528). The increase in soil ammonium concentration from low to mid elevations has also been reported in other tropical montane environments (Kitayama *et al.* 1998). Dissimilatory nitrate reduction to ammonium (DNRA) may be responsible for the increase of ammonium concentration with elevation in montane tropical forests (Silver *et al.* 2001). DNRA is an anaerobic microbial pathway that accounts for an important amount of nitrogen being transformed from nitrate to nitrite and then to ammonium. This transformation is beneficial as ammonium is more easily conserved than nitrate. This is consistent with the higher concentrations of ammonium relative to nitrate found in most soil samples in this study. Axis 3, like axis 2 above, seems to be soil related, except that in axis 3 this fact appears to be synergistic with elevation. The negative end represents poor soils at low elevations, whereas the positive end represents richer soils on bottomlands at high elevations (Figs. 3, 4, 13-15).

A better understanding of nitrogen dynamics in tropical montane environments is necessary, as our observations suggest that nitrogen rather than phosphorus plays a major role in community organization of cloud forest. Support for this also comes from other studies of Neotropical montane communities (Tanner *et al.* 1992) and pine-oak forest (Nieves and Vázquez-García, Universidad de Guadalajara, personal communication) where nitrogen was found to be the limiting nutrient in a small-scale gradient (within a contiguous 0.1 ha sample). Although sometimes both nitrogen and phosphorus have been found to limit plant growth in tropical montane communities (Tanner *et al.* 1990).

In summary, elevation and its implied covariables continue to be the major factors explaining cloud forest variation even over short gradients such as this one. However, in much shorter gradients, other factors such as possibly edaphic variables are expected to be more important than elevation. Nitrogen was more relevant than phosphorus for community organization, since it was related to both axes two and three. However, the relationship of nitrates and ammonium with the community were independent, the former possibly associated to leaching and ground water dynamics and the latter perhaps related to soil microbial activity. Here we advance the hypothesis that CEC and aluminum could play a major role explaining community organization of cloud forest communities.

APPENDIX

List of the most important species (Cumulative 90% SIV) in the 0.1 ha plots.

Species	Family	SIV (%)	CSIV
Quercus scytophylla Liebm.	Fagaceae	13.02	13.02
Sebastiania jaliscensis McVaugh	Euphorbiaceae	9.47	22.49
Styrax argenteus C. Presl	Styracaceae	8.76	31.25
Carpinus tropicalis (Donn. Sm.) Lundell	Betulaceae	6.87	38.12
Quercus uxoris McVaugh	Fagaceae	6.39	44.51
Inga vera ssp. *eriocarpa* (Benth.) Jorge León	Mimosaceae	4.37	48.88
Symplococarpon purpusii (Brandegee) Kobuski	Theaceae	3.44	52.32
Miconia glaberrima (Schltdl.) Naudin	Melastomataceae	3.33	55.65
Persea hintonii C.K. Allen	Lauraceae	3.30	58.95
Ficus velutina Humb. et Bonpl. ex Willd.	Moraceae	3.03	61.98
Ardisia compressa Kunth	Melastomataceae	2.93	64.91
Guarea glabra Vahl	Meliaceae	2.22	67.13
Quercus elliptica Née	Fagaceae	1.80	68.93
Lonchocarpus sp.	Papilionaceae	1.75	70.68
Quercus xalapensis Bonpl.	Fagaceae	1.68	72.36
Clethra lanata M. Martens et Galeotti	Clethraceae	1.65	74.01
Trichilia havanensis Jacq.	Meliaceae	1.58	75.59
Clusia salvinii Donn. Sm.	Clusiaceae	1.58	77.17
Clethra rosei Britton	Clethraceae	1.27	78.44
Canavalia hirsutissima J.D. Sauer	Papilionaceae	1.21	79.65
Calyptranthes pallens var. *mexicana* (Lundell) McVaugh	Myrtaceae	1.01	80.66
Vitis tiliifolia Humb. et Bonpl. ex Roem. et Schult.	Vitaceae	0.89	81.55
Oreopanax peltatus Linden	Araliaceae	0.88	82.43

Species	Family	SIV (%)	CSIV
Marsdenia aff. *macrophylla* (Humb. & Bonpl. ex Schult.) E. Fourn.	Asclepiadaceae	0.87	83.30
Conostegia xalapensis (Bonpl.) D. Don ex DC.	Melastomataceae	0.85	84.15
Prunus cortapico Kerber ex Koehne	Rosaceae	0.85	85.00
Sapium lateriflorum Hemsl.	Euphorbiaceae	0.78	85.78
Dendropanax arboreus (L.) Decne. et Planch.	Araliaceae	0.77	86.55
Pouteria sapota (Jacq.) H.E. Moore et Stearn	Sapotaceae	0.65	87.20
Piper villiramulum C. DC.	Piperaceae	0.61	87.81
Cedrela odorata L.	Meliaceae	0.61	88.42
Agonandra racemosa (DC.) Standl.	Opiliaceae	0.60	89.02
Bursera simaruba (L.) Sarg.	Burseraceae	0.52	89.54
Rondeletia leucophylla Kunth	Rubiaceae	0.50	90.04

SIV = Synthetic Importance Values. CSIV = Cumulative Synthetic Importance Values.

REFERENCES

Aguado G.A., García E., Velasco C. and Flores J.L. 1996. Importancia de los elementos climáticos en la variación florística temporal de pastizales semidesérticos. Acta Botánica Mexicana 35: 65-81.

Arriaga L., Espinoza J.M., Aguilar C., Martínez E., Gómez L. and Loa E. 2000. Regiones terrestres prioritarias de México. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, México City, México.

Barry R.G. and Seimon A. 2000. Research for mountain area development: Climatic fluctuations in the mountains of the Americas and their significance. Ambio 29 (7): 364-370.

Beals E.W. 1984. Bray-Curtis ordination: an effective strategy for analysis of multivariate ecological data. Advances in Ecological Research 14: 1-55.

Brown N., Jennings S., Wheeler P. and Nabe-Nielsen J. 2000. An improved method for the rapid assessment of forest understorey light environments. Journal of Applied Ecology 37: 1044-1053.

Bunce J.A., Miller L.N. and Chabot B.F. 1977. Competitive exploitation of soil water by five eastern north American tree species. Botanical Gazette 138 (2): 168-173.

Bunce J.A., Chabot B.F. and Miller L.N. 1979. Role of annual leaf carbon balance in the distribution of plant species along an elevational gradient. Botanical Gazette 140 (3): 288-294.

Cavelier J. 1996. Environmental factors and ecophysiological processes along altitudinal gradients in wet tropical mountains. In: Mulkey S.S., Chazdom R.L. and Smith A.P. (eds), Tropical Forest Plant Ecophysiology. Chapman & Hall, New York, USA.

Chapin F.S. 1980. The mineral nutrition of wild plants. Annual Review of Ecology and Systematics 11: 233-260.

Clarke K.R. 1993. Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology 18: 117-143.

Cuevas R. 2002. Análisis de gradientes de la vegetación de la cañada El Tecolote, en la Sierra de Manantlán, Jalisco, México. Tesis de Doctorado. Colegio de Postgraduados, Montecillo, Texcoco, Estado de México, México.

Curtis J.T. and P. McIntosh. 1951. An upland forest continuum in the prairie-forest border region of Wisconsin. Ecology 32: 476-496.

Denslow J.S., Ellison A.M. and Sanford R.E. 1998. Treefall gap size effects on above- and below-ground processes in a tropical wet forest. Journal of Ecology 86: 597-609.

Faber-Langendoen D. and Gentry H. 1991. The structure and diversity of rain forests at Bajo Calima, Chocó Region, western Colombia. Biotropica 23(1): 2-11.

Faith D.P., Minchin P.R. and Belbin L. 1987. Compositional dissimilarity as a robust measure of ecological distance. Vegetatio 69: 57-68.

Fasham M.J.R. 1977. A comparison of nonmetric multidimensional scaling, principal components and reciprocal averaging for the ordination of simulated coenoclines and coenoplanes. Ecology 58: 551-561.

Francis A.P. and Currie D.J. 2003. A globally consistent richness-climate relationship for angiosperms. The American Naturalist 161 (4): 523-536.

García E. 1997a. Carta de climas (clasificación de Koeppen, modificado por García). Escala 1: 1000 000. Jalisco. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, Mexico City, México.

García E. 1997b. Carta de isotermas medias anuales. Escala 1: 1000 000. Jalisco. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, Mexico City, México.

García E. 1997c. Carta de precipitación total anual. Escala 1: 1000 000. Jalisco. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, Mexico City, México.

Gentry A.H. 1982. Patterns of neotropical plant species diversity. Evolutionary Biology 15: 1-84.

Gentry A.H. 1988. Changes in plant community diversity and floristic composition on environmental and geographical gradients. Annals of the Missouri Botanical Garden 75(1): 1-34.

Gentry A.H. 1995. Patterns of diversity and floristic composition in Neotropical montane forests. In: Churchill S.P., Balslev H., Forero E. and Luteyn J.L. (eds), Biodiversity and conservation of Neotropical montane forests, The New York Botanical Garden, New York, USA.

Givnish T. 1999. On the causes of gradients in tropical tree diversity. Journal of Ecology 87: 193-210.

Grime J.P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. American Naturalist 111: 1169-1194.

Grime J.P. 2001. Plant strategies, vegetation processes and ecosystems properties. Wiley, West Sussex, England.

Grime J.P. and Curtis A.V. 1976. The interaction of drought and mineral nutrient stress in calcareous grassland. Journal of Ecology 64: 976-998.

Grubb P.J. and Whitmore T.C. 1966. A Comparison of montane and lowland rain forest in Ecuador: II. The climate and its effects on the distribution and physiognomy of the forests. Journal of Ecology 54 (2): 303-333.

Guerrero B. 1985. Reconocimiento botánico de Aquila, Michoacán (México). Tesis de licenciatura. Universidad Michoacana de San Nicolás de Hidalgo, Morelia, Michoacán, México.

Hamilton L.S., Juvik J.O. and Scatena F.N. 1995. Tropical montane cloud forests. Springer-Verlag, New York, USA.

Hinton J. and Rzedowski J. 1975. George B. Hinton, explorador botánico en el sudoeste de México. Anales de la Escuela Nacional de Ciencias Biológicas 21: 1-114.

Holmgren, P.K. and Holmgren N.H. 2003. Index Herbariorum Part I: The herbaria of the world. The New York Botanical Garden (available at: http://www.nybg.org/bsci/ih/ih.html).

Huerta F.M., García E., Flores J.L. and Pimienta E. 1999. Ordenación de las poblaciones silvestres de pitayo y cardón en la cuenca de Sayula, Jalisco. Boletín de la Sociedad Botánica de México 64: 11-24.

Huston M. 1980. Soil nutrients and tree-species richness in Costa Rican forests. Journal of Biogeography 7(2): 147-157.

IEB. 2004. Node of the Instituto de Ecología del Bajío Herbarium in the World Network of Biological Information (REMIB). National Commission for Knowledge and Use of Biodiversity (CONABIO). Project Q017 (available at: http://www.conabio.gob.mx).

Kenkel N.C. and Orloci L. 1986. Applying metric and nonmetric multidimensional scaling to ecological studies: some new results. Ecology 67: 919-928.

Kitayama K., Aiba S.I., Majalap-Lee N. and Ohsawa M. 1998. Soil nitrogen mineralization rates of rainforests in a matrix of elevations and geological substrates on Mount Kinabalu, Borneo. Ecological Research 13: 301-312.

Kruskal J.B. 1964. Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. Psychometrika 29: 1-27.

Luna I., Almeida L., Villers L. and Lorenzo L. 1988. Reconocimiento florístico y consideraciones fitogeográficas del bosque mesófilo de montaña de Teocelo, Veracruz. Boletín de la Sociedad Botánica de México 48: 35-63.

Luquín H. 2003. Ordenación de comunidades leñosas de bosque tropical caducifolio en la cuenca del Río Ayutla-Ayuquila, Jalisco, México. Tesis de Maestría. Centro Universitario de Ciencias Biológicas y Agropecuarias. Universidad de Guadalajara, Guadalajara, Jalisco, México.

Magistad O.C. 1925. The aluminum content of the soil solution and its relation to soil reaction and plant growth. Soil Science 20: 181-225.

Mather P.M. 1976. Computational methods of multivariate analysis in physical geography. Wiley, London, Great Britain.

Matteuci S.D. and Colma A. 1982. Metodología para el estudio de la vegetación. Secretaría General de la Organización de los Estados Americanos. Washington, D.C., USA.

McCune B. and Grace J.B. 2002. Analysis of ecological communities. MjM Software Design, Oregon, USA.

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

Miranda F. and Sharp A.J. 1950. Characteristics of the vegetation in certain temperate regions of eastern Mexico. Ecology 31 (3): 31-33.

Miranda F. and Hernández-Xolocoztli E. 1963. Los tipos de vegetación de México y su clasificación. Boletín de la Sociedad Botánica de México 28: 29-179.

MO. 2004. Missouri Botanical Garden's VAScular Tropical (VAST) nomenclatural database and associated authority files. w3-TROPICOS 1.7 (available at: http://www.tropicos.org).

Montague T.G. and Givnish T.J. 1996. Distribution of black spruce vs. eastern larch along peatland gradients: Relationship of relative stature, growth rate and shade tolerance and the significance of larch's deciduous habit. Canadian Journal of Botany 74: 1514-1532.

NY. 2004. The New York Botanical Garden Vascular Plant Types Catalog (available at http://www.nybg.org/bsci/hcol/vasc/).

Prentice I.C. 1980. Vegetation analysis and order invariant gradient models. Vegetatio 42: 27-34.

Puig H. and Bracho R. 1987. Climatología. In: Puig E. and Bracho R. (eds.). El bosque mesófilo de montaña de Tamaulipas. Instituto de Ecología, Mexico City, México.

Ramírez N. 2001. Diversidad florística del bosque mesófilo en el norte de Chiapas y su relación con México y Centroamérica. Boletín de la Sociedad Botánica de México 69: 63-76.

Raghubanshi A.S. 1992. Effect of topography on selected soil properties and nitrogen mineralization in a dry tropical forest. Soil Biology and Biochemistry 24: 145–150.

Rzedowski J. 1983. La vegetación de México. Limusa, Mexico City, México.

Rzedowski J. 1991a. El endemismo en la flora fanerogámica mexicana: una apreciación analítica preliminar. Acta Botánica Mexicana 15: 47-64.

Rzedowski J. 1991b. Diversidad y orígenes de la flora fanerogámica de México. Acta Botánica Mexicana 14: 3-21.

Rzedowski J. and McVaugh R. 1966. La vegetación de Nueva Galicia. Contributions from the University of Michigan Herbarium 9: 1-123.

Santiago A.L. and Jardel E. 1993. Composición y estructura del bosque mesófilo en la Sierra de Manantlán; Jalisco-Colima. Biotam (5)2: 13-26.

Segura G., Balvanera P., Durán E. and Pérez A. 2003. Tree community structure and stem mortality along a water availability gradient in a Mexican tropical dry forest. Plant Ecology 169: 259-271.

Silver W.L., Herman D.J. and Firestone M.K. 2001. Dissimilatory nitrate reduction to ammonium in upland tropical forest soils. Ecology 82 (9): 2410-2416.

Tanner E.V.J., Kapos V., Freskos S., Hearley J.R. and Theobald A.M. 1990. Nitrogen and phosphorus fertilization of Jamaican montane forest trees. Journal of Tropical Ecology 6 (2): 231-238.

Tanner E.V.J., Kapos V. and Franco W. 1992. Nitrogen and phosphorus fertilization effects on Venezuelan montane forest trunk growth and litterfall. Ecology 73 (1): 78-86.

TEX-LL. 2004. Node of the University of Texas Herbarium in the World Network of Biological Information (REMIB). National Commission for Knowledge and Use of Biodiversity (CONABIO). Project Q047 (available at: http://www.conabio.gob.mx).

Triska F.J., Kennedy V.C., Avanzino R.J., Zellweger G.W. and Bencala K.E. 1989a. Retention and transport of nutrients in a third-order stream in Northwestern California: Channel Processes. Ecology 70 (6): 1877-1892.

Triska F.J., Kennedy V.C., Avanzino R.J., Zellweger G.W. and Bencala K.E. 1989b. Retention and transport of nutrients in a third-order stream in Northwestern California: Hyporheic processes. Ecology 70 (6): 1893-1905.

Turner B.L. 1960. Phytogeographic reconnaissance: The western segment of the Michoacán coast. In Brand D.D., Bullard F.M., Corona J., Duellman W.E., Howard M.J., Miller E., Peters J.A., Porter G.W., Ross D.I., Singletary C.E., Storer R.W. and Turner B.L. Coalcomán and Motines del Oro, an ex-distrito of Michoacán, México. The Institute of Latin American Studies. The University of Texas, M. Nijhoff, The Hague, The Netherlands.

Vargas-Rodríguez Y.L. 1998. Ordenación sociológica de la comunidad arbórea del bosque tropical caducifolio en El Aguacate, Zenzontla, Sierra de Manantlán, Jalisco. Tesis de

Licenciatura, Centro Universitario de Ciencias Biológicas y Agropecuarias, Universidad de Guadalajara, Guadalajara, Jalisco, México.

Vázquez-García J.A. 1993. Cloud forest archipelagos: preservation of fragmented montane ecosystems in tropical America. In: Hamilton L.S., Juvic J.O. and Scatena F.N. (eds). Tropical montane cloud forest. Proceedings of an international symposium, 31 May-5 June 1993. East-West Center, Honolulu, Hawaii.

Vázquez-García J.A. 1995. Cloud forest archipelagos: preservation of fragmented montane ecosystems in tropical America. Ecological Studies 110: 315-332.

Vázquez-García J.A. and Givnish T.J. 1998. Altitudinal gradients in tropical forest composition, structure and diversity in the Sierra de Manantlán. Journal of Ecology 86: 999-1020.

Vázquez-García J.A. and Givnish T.J. 2000. Vegetation of the cerro Grande Massif, Sierra de Manantlán, Mexico: Ordination of a long altitudinal gradient with high species turnover. Boletín del Instituto de Botánica de la Universidad de Guadalajara 6 (2): 227-250.

Vogelmann H.W. 1973. Fog precipitation in the cloud forests of eastern Mexico. BioScience 23 (2): 96-100.

Whittaker R.H. 1975. Communities and ecosystems. 2nd. ed. Macmillan, New York, USA.

XAL. 2004. Node of the Instituto de Ecología de Xalapa Herbarium in the World Network of Biological Information (REMIB). National Commission for Knowledge and Use of Biodiversity (CONABIO). project K004 (available at: http://www.conabio.gob.mx).

Yavitt J.B. 2000. Nutrient dynamics of soil derived from different parent material on Barro Colorado Island, Panama. Biotropica 32(2): 198-207.

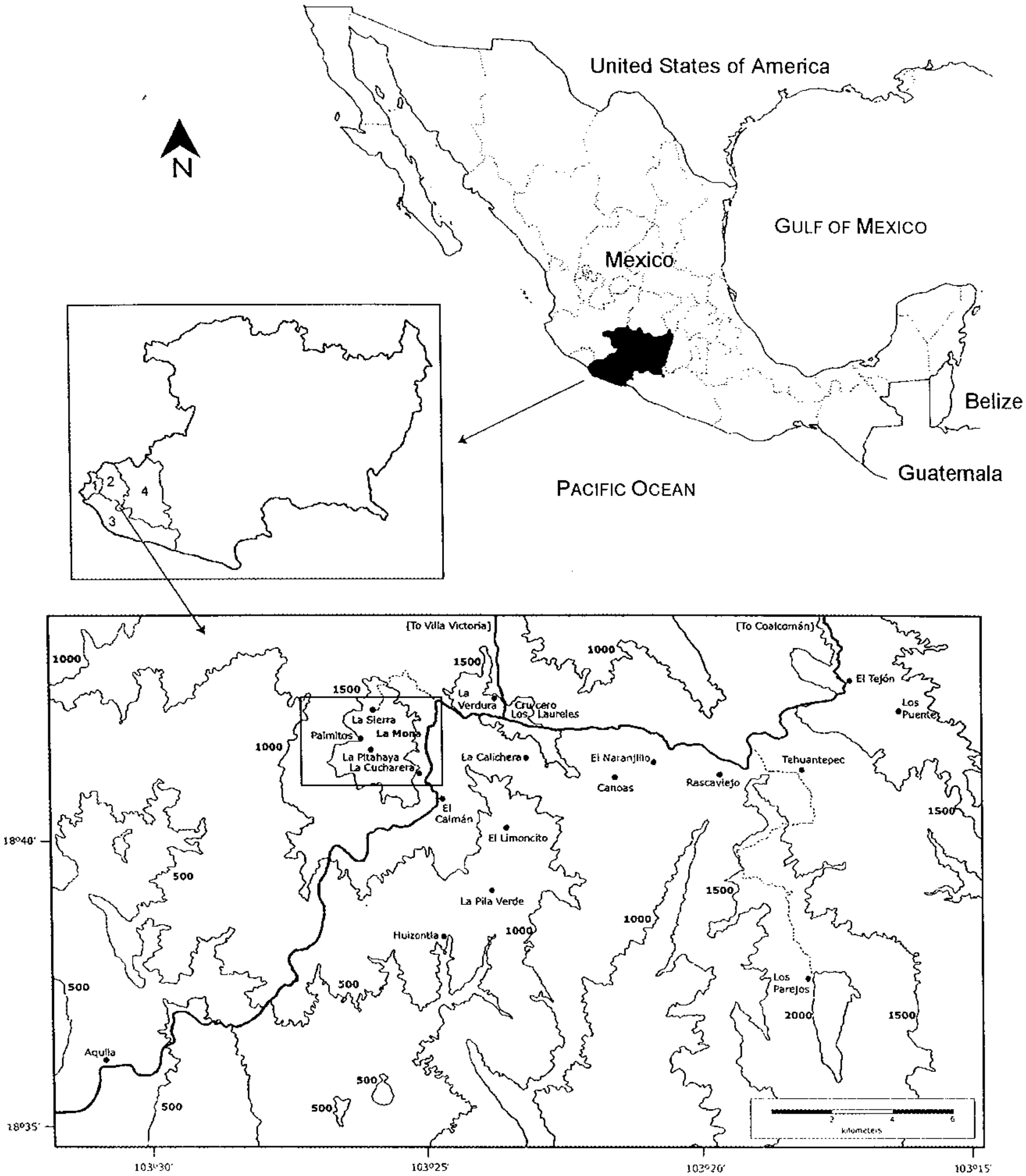
Zavala J.A., Valverde P.L., Díaz A., Vite F. and Portilla E. 1996. Vegetation-environment relationships based on a life-forms classification in a semiarid region of tropical Mexico. Journal of Tropical Biology 44 (2A): 581-590.

FIGURES

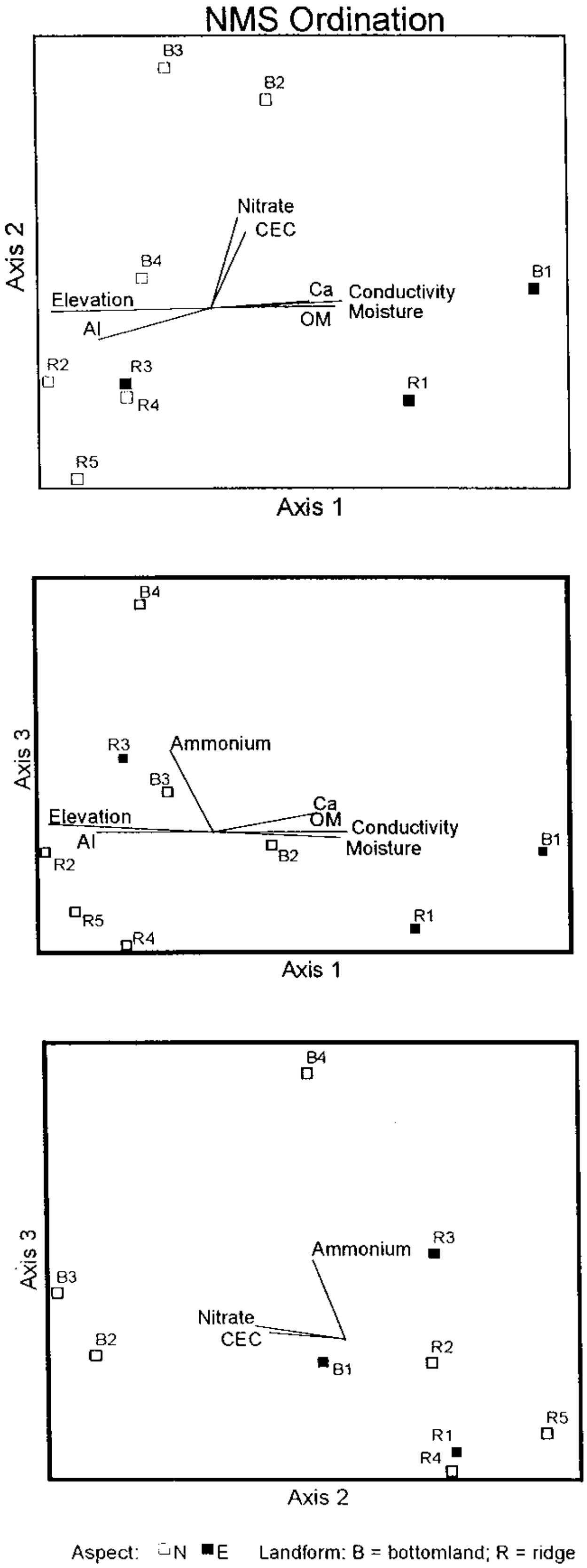
FIGURE ABBREVIATIONS

Al = soil aluminum concentration; Amm. N = soil ammonium concentration; Ca = soil calcium concentration; CEC = cation exchange capacity; Cond. = Electrical conductivity; Elevat. = Elevation; Moisture = Dry-season soil moisture; Nitric N = soil nitrate concentration; OM = Organic Matter.

Fig. 1. Map of cerro La Mona and vicinity in Sierra de Coalcomán, Mexico. Above right, map of Mexico, with the state of Michoacán highlighted in black. Inset at left, outline of Michoacán showing the current limits of the four municipalities of the former district of Coalcomán: (1) Coahuayana, (2) Chinicuila, (3) Aquila and (4) Coalcomán. Inset at bottom, explored area in cerro La Mona and vicinity. Rectangle = cerro La Mona, filled circles = town or named location, dotted line = dirt road, thick line = paved road, thin line = elevation line (in meters).

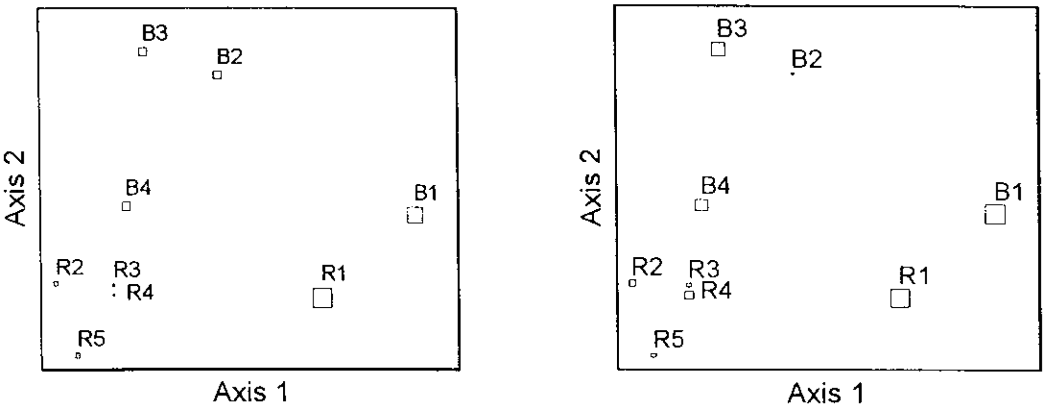

United States of America
N
GULF OF MEXICO
Mexico
Belize
PACIFIC OCEAN
Guatemala
1
2
3
4
[To Villa Victoria]
[To Coalcomán]
1000
1500
1500
1000
La Sierra
Palmitos
La Mona
La Pitahaya
La Cucharera
La Verdura
Crucero Los Laureles
El Tejón
Los Puentes
La Calichera
El Naranjillo
Canoas
Rascaviejo
Tehuantepec
El Calmán
El Limoncito
La Pila Verde
Huizontla
1000
1000
1500
1500
500
500
500
Los Parejos
2000
1500
Aquila
500
500
500
kilometers
2
4
6
18°40'
18°35'
103°30'
103°25'
103°20'
103°15'

Figs. 2-4. Biplots of proportion of Max relationships of environmental variables on the Varimax-rotated NMS ordination of cloud forest at cerro La Mona, Michoacán, with an r^2 cutoff value of .444. Vectors were scaled down to 70% to fit the ordination space. 2. Axes 1 & 2. 3. Axes 1 & 3. 4. Axes 2 & 3.


NMS Ordination
Axis 2
Axis 1
B3
B2
Nitrate
CEC
B4
B1
Elevation
Ca
Conductivity
Moisture
OM
Al
R2
R3
R4
R1
R5
Axis 3
Axis 1
B4
R3
Ammonium
B3
Ca
OM
Elevation
Conductivity
Moisture
Al
B2
B1
R2
R5
R4
R1
Axis 3
Axis 2
B4
R3
Ammonium
B3
Nitrate
CEC
B2
B1
R2
R5
R1
R4
Aspect: □N ■E Landform: B = bottomland; R = ridge

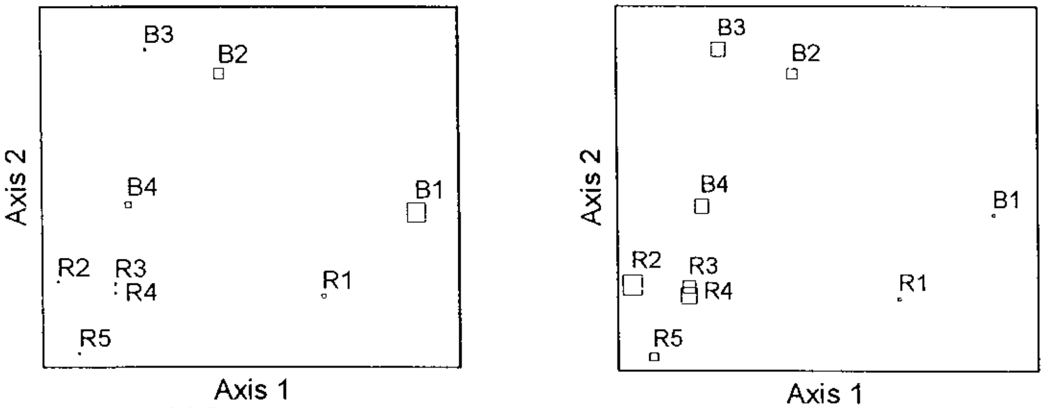
Figs. 5-8. Overlays of proportion of Max relationships of selected environmental variables and taxa on the Varimax-rotated NMS ordination of cloud forest at cerro La Mona, Michoacán, with special reference to axis 1. 5. Dry-season soil moisture. 6. Organic matter. 7. *Clusia salvinii*. 8. *Carpinus tropicalis*.

NMS Ordination



Moisture.
Axis 1, r = 0.858

Organic matter.
Axis 1, r = 0.734

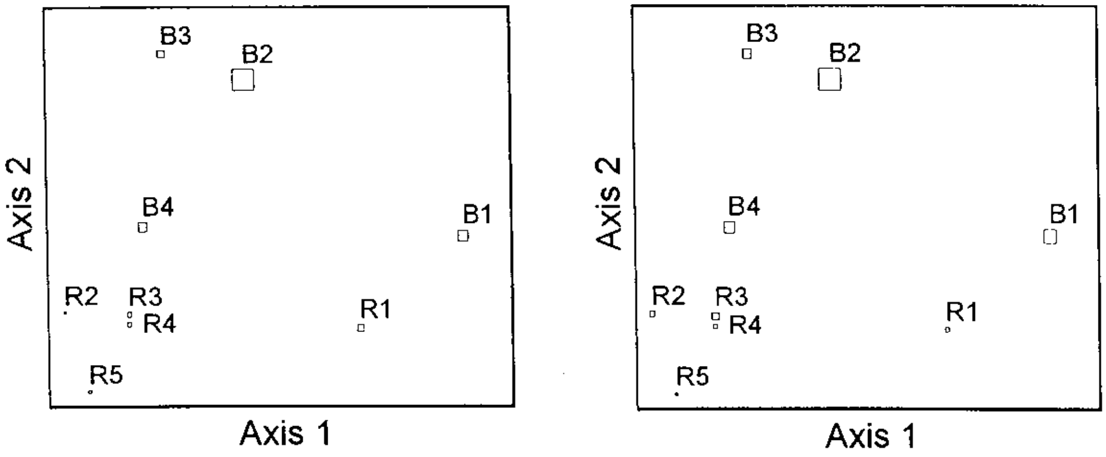


Clusia salvinii
Axis 1, r = 0.805

Carpinus tropicalis
Axis 1, r = -0.841

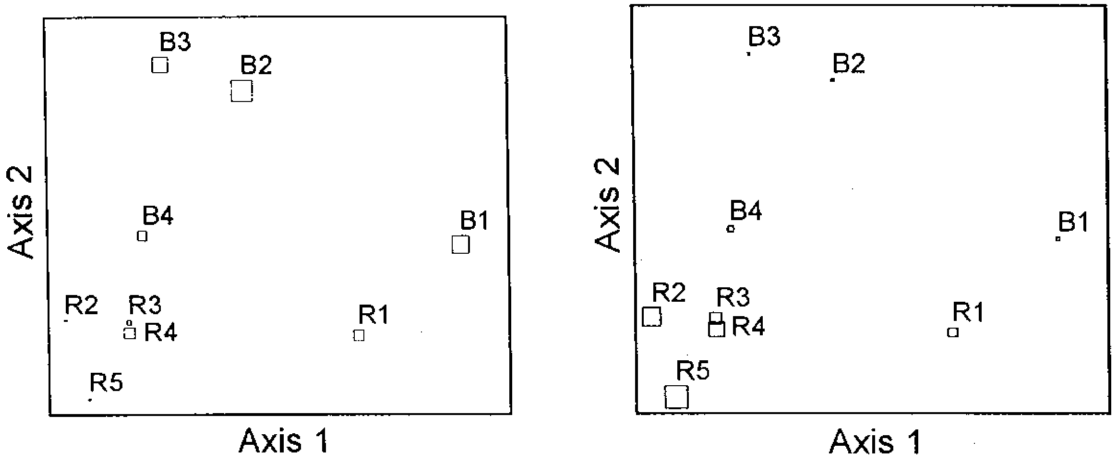
Figs. 9-12. Overlay of proportion of Max relationships of selected environmental variables and taxa on the Varimax-rotated NMS ordination of cloud forest at cerro La Mona, Michoacán, with special reference to axis 2. 9. Cation exchange capacity. 10. Nitrate. 11. *Quercus uxoris*. 12. *Quercus scytophylla*.

NMS Ordination



Cation exchange capacity
Axis 2, r = 0.672

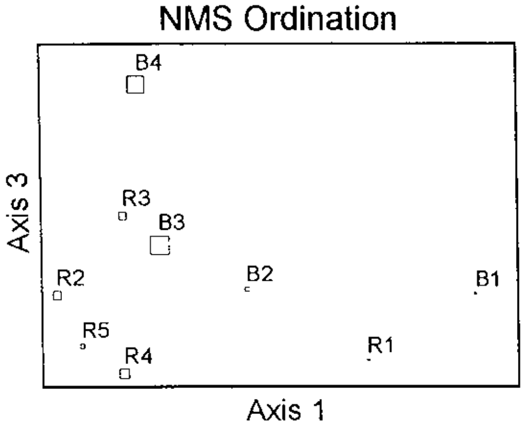
Nitrate
Axis 2, r = 0.730



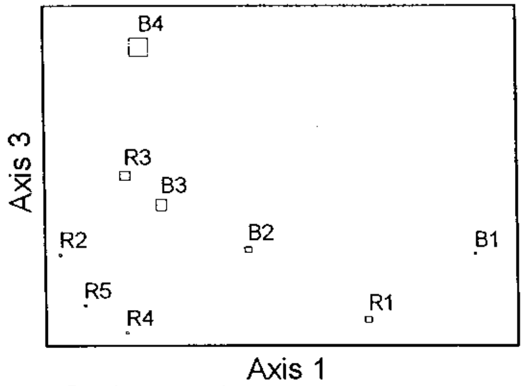
Quercus uxoris
Axis 2, r = 0.800

Quercus scytophylla
Axis 2, r = -0.804

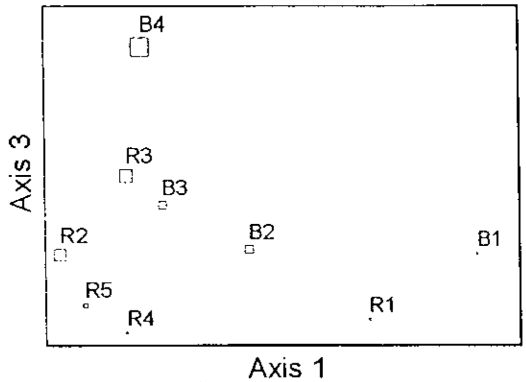
Figs. 13-15. Overlay of proportion of Max relationships of selected environmental variables and taxa on axes 1 and 3 of the Varimax-rotated NMS ordination of cloud forest at cerro La Mona, Michoacán, with special reference to axis 3. 13. Ammonium. 14. *Dendropanax arboreus*. 15. *Sebastiania jaliscensis*.



Ammonium
Axis 3, r = 0.685



Dendropanax arboreus
Axis 3, r = 0.890



Sebastiania jaliscensis
Axis 3, r = 0.883

TABLES

Table 1. Description of sample sites at cerro La Mona, in Sierra de Coalcomán, Michoacán, western Mexico.

Sample site	Description
B1	Cerro La Mona. La Cucharera, on bottomland. 1320 m asl. 18° 41' 02"N 103° 24' 46"W
B2	Cerro La Mona. Palmitos, on bottomland. 1470 m asl. 18° 41' 38"N 103° 25' 51" W
B3	Cerro La Mona. La Pitahaya, on bottomland. 1580 m asl. 18° 41' 26"N 103° 25' 39"W
B4	Cerro La Mona. La Pitahaya, on bottomland. 1575 m asl. 18° 41' 28"N 103° 25' 40"W
R1	Cerro La Mona. La Cucharera, on ridge. 1320 m asl. 18° 41' N 103° 25' W
R2	Cerro La Mona. La Pitahaya, on ridge. 1590 m asl. 18° 41' 26"N 103° 25' 42"W
R3	Cerro La Mona. La Pitahaya, on ridge. 1590 m asl. 18° 41' 27"N 103° 25' 43"W
R4	Cerro La Mona. La Pitahaya, on ridge. 1610 m asl. 18° 41' 26"N 103° 25' 43"W
R5	Cerro La Mona. La Pitahaya, on ridge. 1645 m asl. 18° 41' 22"N 103° 25' 42"W

Table 2. Environmental variables used in the NMS ordination.

Variable	Units	B1	B2	B3	B4	R1	R2	R3	R4	R5
Aluminum	µg/g	7.99	270.00	105.00	350.00	28.50	800.00	425.00	625.00	447.00
Apparent density	g/cm^3	1.56	1.57	1.56	1.57	1.46	1.54	1.54	1.58	1.41
Boron	µg/g	2.15	1.90	2.04	2.75	0.22	1.97	2.44	2.37	0.10
Calcium	µg/g	4665.00	2024.00	2108.14	4048.00	3305.00	1214.40	1518.00	2024.00	999.00
Canopy openness	%	20.00	16.00	28.80	16.00	16.00	14.40	14.40	16.00	23.32
Cation exchange capacity	--	25.18	48.44	13.38	22.18	13.95	7.82	9.52	8.57	5.80
Copper	µg/g	0.10	0.30	0.10	0.10	0.10	0.10	0.74	0.30	0.68
Electrical conductivity	mmhos/cm	0.27	0.07	0.09	0.09	0.11	0.04	0.06	0.06	0.03
Elevation	m	1320	1470	1580	1575	1320	1590	1590	1610	1645
Iron	µg/g	0.43	0.10	0.10	0.10	0.10	0.29	17.29	7.55	16.54
Magnesium	µg/g	177.00	982.20	1841.60	859.40	354.00	982.20	1104.90	1166.30	179.20
Manganese	µg/g	30.79	15.62	16.66	16.92	14.34	18.55	19.04	18.13	17.90
Nitrogen (Ammonium)	µg/g	19.10	96.12	659.14	616.04	40.94	248.65	257.12	279.87	92.30
Nitrogen (Nitric)	µg/g	10.06	19.25	5.35	8.87	2.51	2.54	3.22	2.84	0.00
Organic matter	%	9.56	1.72	6.84	5.94	8.58	3.26	2.40	4.70	2.32
pH	--	6.30	5.02	5.78	6.65	6.12	5.48	5.58	5.28	4.89
Phosphorus	µg/g	22.55	11.75	35.75	38.00	10.28	114.42	191.84	77.09	30.70
Potassium	µg/g	250.00	187.50	275.00	273.89	212.50	350.00	312.50	387.50	90.40
Slope	degrees	27	36	21	28	21	27	25	22	29

Table 2 (continued)

Variable	**Units**	**B1**	**B2**	**B3**	**B4**	**R1**	**R2**	**R3**	**R4**	**R5**
Soil moisture (dry-season)	%	19.66	10.02	10.07	9.45	25.85	6.30	2.52	3.07	6.40
Sulfate	μg/g	50.71	47.99	27.29	26.75	56.81	21.85	59.75	47.55	33.69
Sum of water soluble anions	meq/l	6.28	4.05	9.06	5.00	5.19	5.97	5.41	5.77	3.15
Sum of water soluble cations	meq/l	6.08	5.36	7.60	6.13	5.61	7.85	8.39	5.29	3.25
Texture, clay	%	0.06	0.70	0.00	0.00	17.06	3.26	3.26	3.26	0.52
Texture, sand	%	86.02	87.66	85.66	89.66	58.02	79.82	79.46	95.46	87.48
Texture, silt	%	13.92	11.64	14.34	10.34	24.92	16.92	17.28	1.28	12.00
Water soluble Ca++	meq/l	3.63	0.19	2.03	2.03	0.73	1.01	3.05	1.01	2.00
Water soluble Cl-	meq/l	0.62	0.92	7.35	1.99	2.41	1.99	6.79	1.79	0.48
Water soluble HCO3-	meq/l	0.88	1.08	0.62	0.79	0.88	1.41	1.93	0.40	2.12
Water soluble K+	meq/l	0.64	0.45	0.32	0.51	0.38	0.58	0.45	0.26	0.11
Water soluble Mg++	meq/l	1.44	0.26	1.01	0.10	0.59	2.03	0.10	0.10	1.00
Water soluble Na+	meq/l	0.37	4.46	4.24	3.59	3.91	4.23	4.89	4.02	0.14
Water soluble SO4=	meq/l	1.39	2.05	1.09	2.22	1.40	2.57	1.87	3.58	0.55
Zinc	μg/g	1.18	0.50	0.64	1.01	0.46	0.45	0.37	0.72	0.20

Table 3. Pearson's correlations of environmental variables and the axes of the NMS ordination.

	Axis 1	**Axis 2**	**Axis 3**
Variable	*r*	*r*	*r*
Aluminum	-0.809		
Calcium	0.764		
Electrical Conductivity	0.882		
Elevation	-0.962		
Organic matter	0.734		
Soil moisture	0.858		
Cation exchange capacity		0.672	
Nitrates		0.730	
Ammonium			0.685

(N = 9, df = 7).

Table 4. Pearson's correlations of species scores* and the axes of the NMS ordination.

Species	*r*	Nz	**Axis**
Canavalia hirsutissima	0.850	3	1
Carpinus tropicalis	-0.841	7	1
Cedrela odorata	0.840	3	3
Clethra lanata	-0.789	5	2
Clusia salvinii	0.805	4	1
Dendropanax arboreus	0.890	5	3
Guarea glabra	0.967	6	2
Marsdenia aff. *macrophylla*	0.946	3	1
Miconia glaberrima	-0.636	7	2
Oreopanax peltatus	0.700	4	3
Persea hintonii	0.878	7	3
Quercus scytophylla	-0.804	6	2
Quercus uxoris	0.800	7	2
Sebastiania jaliscensis	0.883	7	3
Styrax argenteus	0.859	5	1
Trichilia havanensis	0.860	4	2

*Only correlations of species with three or more non-zero abundance values are shown.

Nz = number of non-zero abundance values. ($N = 9$, df = 7).

CHAPTER 2

Potential effects of climate change on the cloud forest of cerro La Mona, Sierra de Coalcomán, western México

Keywords: ammonium and nitrate nitrogen; community-environment relationships; NMS/NMDS ordination; soil moisture and nutrients; tropical montane vegetation; western México.

ABSTRACT

The cloud forest at cerro La Mona was studied using circular quadrats on a stratified random design and Varimax-rotated non-metric multidimensional scaling (NMS) ordination. Using a framework of drought induced by regional climate warming in western México, and correlations of species data with ordination axes, we generated testable hypotheses of possible range expansion or retraction. Species that may hypothetically recede as a result of drought induced by climate warming were *Clusia salvinii* and the woody vines *Canavalia hirsutissima*, *Marsdenia* aff. *macrophylla* and possibly *Smilax moranensis*. Conversely, species with potential to invade new ground were *Carpinus tropicalis* and *Vitis tiliifolia*. Using a framework of nitrogen disruption and impoverishment induced by climate warming, we hypothesized a possible range expansion of *Oreopanax peltatus* and a potential retraction of *Dendropanax arboreus*, *Persea hintonii* and *Sebastiania jaliscensis*. Research focusing on the nutrient and water relations of these species are necessary to test these hypotheses. The ordination analysis revealed an interesting niche separation of *Quercus scytophylla* and *Q. uxoris* on geomorphic / edaphic grounds which presents an opportunity for ecological studies. Also, *Dendropanax arboreus* and *Oreopanax peltatus* were found to form a similarly interesting pair of species, as they showed opposing trends along axis 3 of the ordination despite their classification in the same family (Araliaceae).

INTRODUCTION

Climate change has recently raised concerns due to signs of alterations in the cold regions of the world. Food web stability in Antarctica is threatened (Hickley *et al.*, 2002), and bird range (Thomas and Lennon, 1999) and shrub abundance (Sturm *et al.*, 2001) have increased northwards in the northern hemisphere. Also, reduced growth in a North American boreal forest tree species has been attributed to temperature-induced drought stress (Barber *et al.*, 2000).

Effects of climate warming have also been detected in tropical mountains. The lifting of the cloud base and the alteration of the dry-season mist frequency has upset animal communities in highland forests in Costa Rica (Pounds *et al.*, 1999) and an increase in the severity of the dry season has contributed to the loss of shrubs and small trees adapted to moist (Condit *et al.*, 1996a) or even seasonally dry (Segura *et al.*, 2003) microhabitats.

It is believed that in the tropics, climate change will have a pronounced impact on vegetation, and that this will be mostly attributable to changes in precipitation rather than to shifts in temperature (Condit *et al.*, 1996b). In addition, research anticipates a substantial decrease in water availability and agricultural production as a result of climate change in the tropics, even after considering the fertilization effect of increasing CO_2 concentrations (Rind *et al.*, 1997; Weltzin *et al.*, 2003).

Ruiz (2000) in a study spanning the last three decades, reports an increase of 0.23 °C in the mean annual temperature and a decrease of 33 mm in the total annual precipitation in western México, and points out that these alterations have affected corn agriculture significantly. He attributes these shifts to global change based on a spatial and temporal analysis of the growing season and meteorological data.

Cloud forest remnants in western México are restricted to mountainous areas where relatively low temperature and high humidity are prevalent during most of the year (Rzedowski and McVaugh, 1966; Rzedowski, 1983; Vázquez-García, 1993, 1995; Velázquez *et al.*, 2000). In México, fog contributes a significant amount to total precipitation in areas with cloud forest, and may be especially important in the dry season (Vogelmann, 1973). It has been argued that the presence of fog and high humidity in the dry season may be the key factor limiting the distribution of cloud forest (Grubb and Whitmore, 1966; Rzedowski, 1983). Thus, communities that develop under moist and cool conditions such as tropical cloud forest are expected to be adversely affected by climate change in western and parts of central México (INE, 2000; Williams *et al.*, 2000). Perhaps even the highlands may not be cool and humid enough to sustain cloud forest if current temperature and humidity trends continue. This is particularly relevant given the prolonged dry season that occurs from November to May in western México.

On a geologic time scale, changes in the elevation of the boundary between various plant communities in response to climate change have been known to occur (Ambrose and Sikes, 1991; Gentry, 1995). On ecological time scales, ecotone studies have provided much insight on vegetation dynamics in temperate regions (i.e., Hessl *et al.*, 1996; Allen and Breshears, 1998; Bossuyt *et al.*, 1999) and although not as frequently used, also in the Neotropics (i.e., Grau and Veblen, 2000). Shifts in importance values of dominant species have been recorded in as little as 10 years (Herwitz and Young, 1994). Even if changes in vegetation resulting from climate change will probably take place throughout the plant community, they are expected to occur more rapidly and intensely at ecotones (Neilson, 1993; Allen and Breshears, 1998), providing an early warning. Thus, the possibility of ecotone displacement between cloud forest and adjacent plant communities is an indirect threat that climate change poses to cloud forest permanence and should be investigated. This is important because the thermophilous trees in neighboring tropical semi deciduous forest are presently restricted to the lowlands by the cooler temperatures prevalent on mountain tops (Rzedowski and McVaugh, 1966; Rzedowski, 1983; Puig and Bracho, 1987) and lowland tropical trees have shown greater carbon gains in dry years than in wet years presumably due to higher light availability under a lower cloud cover (Clark and Clark, 1994; Condit *et al.*, 2004). Thus this type of trees would be expected to migrate upwards, mix and compete with montane cloud forest species for space and resources as the temperature and the cloud-induced light limitations become more moderate.

The possibility that oaks (*Quercus* spp.) may also outcompete cloud forest species in a potentially warmer and drier situation should also be considered. This case seems critical, as the long and narrow ecotones shared by cloud forest with oaks coupled with the high abundance of the latter, would allow rapid population shifts. Vegetation changes become particularly important in view of the high rate of deforestation in the region (Hinton and Rzedowski, 1975) which could imply that regeneration after logging cloud forest may speed ecotone displacement.

México is a megadiverse country. With about 22000 species of flowering plants, it holds nearly 10% of the magnoliophytes known in the world (Villaseñor, 2003). On the other hand, cloud forest has been identified as the most diverse plant community per surface unit in México, with about 10% of the flora in that country (Rzedowski, 1991a). Also, cloud forest is the habitat of numerous endemic species (Rzedowski, 1991b), therefore its conservation is a priority. In addition, Sierra de Coalcomán has been designated a priority region for conservation by the National Commission for Knowledge and Use of Biodiversity (CONABIO) (Arriaga *et al.*, 2000). However, despite its importance, this region remains poorly known. Exploration has been historically limited by floods and landslides that block roads, and by high crime rates. There are no quantitative assessments that emphasize the interactions of climate change and cloud forest in Sierra de Coalcomán. The aim of this work is to analyze the potential effects of climate change on the woody plants of cloud forest at cerro La Mona in western México, and to select indicator species for future testing of proposed hypotheses related to climate alterations in that area.

STUDY SITE DESCRIPTION

Cerro La Mona, a part of Sierra de Coalcomán, is located in northwestern Michoacán, near the limits with the states of Jalisco and Colima (Fig. 1). The mountain is mostly covered with oak forest and to a lesser extent by pine forest. Also, strips of cloud forest and tropical semi deciduous forest occur in the ravines along an elevation gradient. Cloud forest occupies ravine bottomlands of the top 300 m (i.e., 1300-1600 m) of the mountain and is gradually replaced by tropical semi deciduous forest along the gullies toward lower elevations and by oak forest sideways toward the ridges. The tropical semi deciduous vegetation is much disturbed near the highway, where several small settlements are established along its border. Fog, known as "chubasco" by the local residents, commonly prevents access to locations above 1500 m in the summer. It covers the mountain top during the rainy season, which takes place from June to November. The climate in the region of cerro La Mona is warm, temperate sub-humid (García, 1997a; Arriaga *et al.*, 2000), with a mean annual temperature of 18-22°C (García, 1997b) and total annual precipitation of approximately 1200 mm (García, 1997c). The lack of a station network in the mountains of Latin America results in imprecise data (Barry and Seimon, 2000).

METHOD

Field sampling

The cloud forest of cerro La Mona was sampled using the circular quadrat method (Curtis and McIntosh, 1951) and a stratified random design (Matteuci and Colma, 1982). To analyze the effect of climate on cloud forest, nine 0.1 ha samples were taken along an elevational gradient of the top 300 m of Cerro La Mona, where cloud forest occurs. To account for landform variation, five samples were located on ridges and four on bottomlands (Table 1). Each sample comprised 10 circular subsamples, each with a radius of 5.64 m.

Sampling of circles was accomplished by tallying the species of trees, shrubs and lianas that were rooted in them as well as recording their diameter at 1.3 m above the ground. Only woody plants with a diameter of at least 2.5 cm were considered. If they occurred on the edge, they were recorded only if at least half of their base was inside the circular plot. Sampling took place between 1999 and 2000. Site R5 was sampled in 2002 when it was first visited.

At least one voucher specimen of each recorded species of trees, shrubs and lianas found in the plots was collected. Identifications were performed by the author and by specialists at the Instituto de Botánica, Universidad de Guadalajara, and elsewhere. Species nomenclature follows Missouri Botanical Garden's w3-Tropicos (available at: http://www.tropicos.org). Vegetation nomenclature follows Rzedowski and McVaugh (1966).

A sociological ordination of cloud forest using non-metric multidimensional scaling (NMS) was performed in PC-ORD 4.24, which uses the method described by Kruskal (1964) and Mather (1976). A random starting configuration was first used, and in order to increase stability, the scores obtained were later used as starting configuration for a subsequent ordination as recommended by McCune and Grace (2002). Stability was evaluated with up to 1500 runs in real data.

To determine the dimensionality of the data set, an NMS ordination with six axes was set up using the step down function and a Scree plot (not shown). A Monte Carlo test was also used with 1500 runs in real data and 900 runs in randomized data to evaluate the probability that a 3-dimensional NMS ordination would attain lower final stress than attributable to chance alone.

Sorensen's distance measure was used. It is based on the difference of floristic composition between each pair of samples. This distance measure has been recommended by Beals (1984) and Faith *et al.* (1987) as more robust and efficient than others for ordination analyses. Synthetic Importance Values (SIV) were calculated (Whittaker, 1975) as abundance measures by averaging relative dominance (i.e., basal area), relative density (i.e., number of plants) and relative frequency (i.e., proportion of species in subplots).

Ordination results may be used to generate hypotheses which may, after suitable experimentation and testing, help support or reject cause-effect relationships. In this fashion, we selected plant species whose scores were correlated with the ordination axes and generated hypotheses of possible range expansion or retraction under the current trends of climate change in western México. The hypothetical behavior of these species was fine-tuned using habitat preferences reported for them in the literature. Only species with at least three non-zero abundance values were used. This threshold was arbitrarily selected in an attempt to avoid correlations based on too little information.

Many of the correlated plants were physically found on the ecotones of cloud forest and adjoining vegetation types as defined with the criteria of Rzedowski (1983) and Rzedowski and McVaugh (1966). The species for which we had more information were evaluated as indicator species of climate change alterations on cloud forest ecotones.

RESULTS

In a parallel study using 34 environmental variables, Sahagún *et al.* (unpublished data) found that elevation and moisture were climate-related variables that explained the variance in axis 1; nitrate nitrogen and cation exchange capacity explained axis 2, whereas ammonium nitrogen was related to the pattern observed for axis 3 of the NMS ordination. In general terms, soil residual moisture was higher in low elevation sites than on high elevation ones, and soil was richer and deeper in bottomlands than on ridges, where it was nearly nonexistent.

Five species were significantly correlated with axis 1 of the NMS ordination and had at least 3 non-zero abundance values (Table 2). Only *Carpinus tropicalis* was negatively correlated with this axis. This species showed high abundances at high elevations, in the drier soil of the ridges (Fig. 2), on the ecotone with oak forest. On the other hand, the remaining four species that had positive correlations with axis 1 (Table 2) were *Canavalia hirsutissima*, *Clusia salvinii*, *Marsdenia* aff. *macrophylla* and *Styrax argenteus* (Figs. 3-6). The abundances of these species increased at low elevations. They were greatest on the more mesic extreme of the gradient, which corresponds to the bottomlands at mid to low elevations, on the ecotone with tropical semi deciduous forest.

Clethra lanata and *Quercus scytophylla* were negatively correlated with axis 2 (Figs. 7 and 8). These species had higher abundances on the poor, eroded soils of the ridges than on the deep, rich soils of the bottomlands. On the other hand, four species were positively correlated with axis 2 of the NMS ordination (Table 2); namely, *Guarea glabra, Piper villiramulum, Quercus uxoris* and *Trichilia havanensis* (Figs. 9-12). These species showed higher abundances in the bottomlands than on the ridges.

Cedrela odorata, Dendropanax arboreus, Oreopanax peltatus, Persea hintonii and *Sebastiania jaliscensis* were positively correlated with axis 3 (Table 2). These plants showed greater abundances in the bottomlands at high elevations than on the ridges or low elevation bottomlands (Figs. 13-17). Conversely, *Oreopanax peltatus* was negatively correlated with axis 3 and showed the opposite trend.

DISCUSSION

The individualistic approach to community organization has received much support (Gleason, 1926; Curtis and McIntosh, 1951). This includes the tropical highland and lowland vegetation in western México (Vázquez-García and Givnish, 1998). Therefore each species may respond differently to changes in the environment. A slight change in average annual temperature or drought may go unnoticed for species with an ample tolerance, but may be catastrophic for species near their tolerance limits or yet unleash others for invasion into new habitats. Thus, as far as it is possible, the discussion of community shifts that may be induced by climate change includes species-specific considerations.

Carpinus tropicalis is a large tree that had a negative correlation with axis 1 (Table 2). This species is regarded as an element of cloud forest (Table 3) and showed high abundances in the dry upslope ground of the ridges on the ecotone with oak forest (Fig. 2), which suggests it could advance under a drier situation.

On the other hand, various species had positive correlations with axis 1 and were found on the mesic end of the gradient, which corresponds to the ecotone of cloud forest and tropical semi deciduous forest. These species could be hypothetically advancing or receding in that area, depending on their adaptations to drought and cold. *Clusia salvinii* is a plant positively correlated with axis 1 (Fig. 4) that is commonly reported as an element of cloud forest (Table 3). Despite the fact that this species is commonly seen as an epiphyte, a habit that is often associated with drought resistance, the ordination overlay shows a preference of this species for humid sites near creeks (Fig. 4). It is not known whether *C. salvinii* presents any CAM activity, but other species of *Clusia* show ample photosynthetic flexibility, switching from C_3 to CAM as needed (Borland *et al.*, 1992; Franco *et al.*, 1994; Zotz and Winter, 1994; Haag-Kerwer *et al.*, 1996). The water use efficiency brought about by CAM should allow plants of *Clusia* to live in drier sites, but this is probably counteracted by the fact that C_3 is more prevalent in seedlings than in adults of *Clusia* (Ball *et al.*, 1991), a stage when most tropical plant populations are commonly subjected to strong selection and high mortality (Clark and Clark, 1992). Also, *Clusia* species have been shown to have inefficient xylem water transport (Patiño *et al.*, 1995) and high vulnerability to drought-induced cavitation (Zotz *et al.*, 1994). This is particularly relevant since xylem resistance to cavitation and ensuing embolism is probably the most important trait that determines drought resistance in woody plants (Tyree and Ewers, 1991). This suggests that *C. salvinii* is susceptible to drought and would probably recede if the climate becomes drier.

Styrax argenteus, a cloud forest species (Table 3), clearly shows a higher abundance on the low elevation end of axis 1 (Fig. 6) which suggests affinity for high humidity according to the hypothesis stated above. But its presence in many of the ridge samples (i.e., R2-R5) (Table 2) and its absence from bottomland samples at similar elevations (i.e., B2-B4) contradicts this idea. Additionally, Frankie *et al.* (1974) reported *Styrax argenteus* as an element of dry forest in Central America, while Kappelle *et al.* (1996) considered it a primary forest species with maximum abundances and densities in old forests, which are also contradictory findings. At Cerro La Mona, *S. argenteus* is a common species and appears to benefit from small amounts of disturbance, which probably explains in part its greater abundance at low elevations. Vázquez-García (Universidad de Guadalajara, personal communication) has seen a similar behavior for this species in Manantlán. It appears that its pioneer-like behavior confounds ecological observations. Given the above circumstances, it seems unlikely that *S. argenteus* will be affected negatively by climate warming, but more studies are needed for a clearer hypothesis of the role of this species in a climate change scenario.

Woody vines were mostly found in moist sites. Their abundances commonly increased as residual soil moisture increased. *Canavalia hirsutissima* was correlated with axis 1 of the ordination (Fig. 5) which suggests a vulnerability to drought. This liana was found in sites B1 and R1 (Table 2); its abundance in the ridge sample was half that of the bottomland sample. It was also found in a high elevation ridge site (i.e., R4), where it had an even lower abundance. *Marsdenia* aff. *macrophylla* showed a similar pattern (Table 2). It was found in sites R1 and B1, and its abundance in the bottomland sample was more than twice that of the ridge site. But the drier high elevation bottomland sample B2 had the lowest abundance value. This species, like *C. hirsutissima* above, was correlated with axis 1 of the NMS ordination ($r = 0.946$) (Fig. 5).

Vitis tiliifolia was not correlated with any of the axes and thus it was unusual in that it did not show the strong affinity for moist sites near creeks displayed by other woody vines (see raw data in the Appendix, Chapter 3). Rather, it seemed to thrive in well-lit sites opened by tree falls, a pioneer-like behavior common to many *Vitis* species (Siccama, *et al.*, 1976; Morano and Walker, 1995). For instance, there was a tree fall in site R1 after data collection. A year later the grapevine had taken over the fallen branches and trunks. Although the abundance distribution of *V. tiliifolia* may be an artifact of a low number of observations, it may also reflect a better adaptation to water stress than other lianas. *Smilax moranensis*, the remaining woody vine, had too few sample observations for correlations with axis 1 of the

NMS ordination to be informative. Nevertheless, it was found in site B1, a low elevation site near a creek.

Lianas are commonly recognized as elements of relatively humid communities such as cloud forest or tropical semi deciduous forest (Table 3). Also, woody vines become progressively less common and diverse as one proceeds from humid communities to drier ones (Rzedowski and McVaugh, 1966; Frankie *et al.*, 1974; Gentry, 1982; Gentry and Dodson, 1987). Although vessel dimensions are not the only factor determining vulnerability to cavitation (Sperry *et al.*, 1988), Putz (1983) showed that wide vessels in lianas are associated to water-stress-induced cavitation, and Gartner *et al.* (1990) found that vines that develop in wet sites have wider vessels than similar vines growing in drier areas. The decrease in the diversity of woody vines from tropical to temperate communities has been attributed to their vulnerability to cavitation induced by cold (Carlquist, 1984). In this regard it is noteworthy that many *Vitis* species have been able to colonize the temperate zone, and that *V. tiliifolia* showed indications of a higher resistance to drought than other woody vines at Cerro La Mona. Water storage in the larger trunks of trees in addition to their narrower vessels may make them better able to resist xylem cavitation (Tyree and Ewers, 1991), which may explain the greater tolerance to drought displayed by many trees when compared to woody vines. This suggests that, with the possible exception of *Vitis tiliifolia*, lianas at Cerro La Mona would recede if drought becomes more prevalent.

The nitrogen cycle has been undoubtedly affected by climate change, and its effects will be observed in both natural and agricultural regions (Vitousek, 1994). Due to its high complexity (Vitousek, 1977), nitrogen will only be discussed in general terms because of the limited information available for cerro La Mona. Since both axes 2 and 3 are nitrogen related according to the ordination-generated hypotheses, they will be discussed together. However, axis 3 will be emphasized due to its relationship with elevation, which suggests a more rapid response to climate alterations.

The pattern of increasing soil ammonium concentration from low to mid elevations observed at cerro La Mona was also reported for Mount Kinabalu (Kitayama *et al.*, 1998). Various explanations have been proposed for the accumulation of ammonium at higher elevations, including microbial processes such as dissimilatory nitrate reduction to ammonium (Silver *et al.*, 2001) or abiotic immobilization through the ferrous wheel hypothesis (Davidson *et al.*, 2003). No comparable patterns were observed for nitrate at cerro La Mona nor were similar reports found in the literature. Apparently nitrate is very easily leached or transformed into other chemical forms of nitrogen in tropical montane environments (Silver *et al.*, 2001).

If ammonium accumulation depends on the "temperate" climate of the mountains, it is evident that it will be disrupted by the regional climate warming ongoing in western México. Based on the trend observed on the axis 3 of the ordination of higher ammonium content at higher elevations, it is here hypothesized that regional climate warming could bring about an alteration of the cloud forest community through an impoverishment of soil nitrogen. This would result in the possible reduction of the competitive ability of the species that were correlated with axis 3, namely: *Cedrela odorata, Dendropanax arboreus, Persea hintonii* and *Sebastiania jaliscensis*. Conversely, *Oreopanax peltatus* would possibly be benefited. It is noteworthy that, with the possible exception of *Cedrela odorata,* which is not a good example due to the widespread planting programs that it has undergone in tropical regions of México, *O. peltatus* is the only species in this group that thrives in environments that are decidedly drier than that at cerro La Mona such as the Rio Santiago Canyon near Guadalajara, in Jalisco (Sahagún, Personal Observation). Research emphasizing the nitrogen requirements of these species are necessary to test this hypothesis. Also, research focusing on understanding the details of the biogeochemical pathways of major plant nutrients in the cloud forest of western México is sorely needed.

The species correlated with axis 2 did not make "ecological sense" in terms of their relationship with climate change, as did those correlated with the other axes. For instance, when considering the two negatively correlated species, *Clethra lanata* is reported from dry environments (Robertson, 1967) but *Quercus scytophylla* is said to grow in moist habitats (Rzedowski and McVaugh, 1966; Vázquez-García and Cuevas, 1995). A similar situation is seen among the positively correlated species. As suggested in the ordination, landform was apparently more important than climate-related variables such as elevation or soil moisture for these plants, so their relationships with climate change are not clear.

Drought vulnerability studies (see Tyree and Ewers, 1991), ecophysiological inquiries, and wood anatomy surveys of woody plants in the cloud forest and neighboring communities in western México are required to understand the limits of resistance of cloud forest species to water stress and their potential for dieback or invasion. Also, regeneration studies and effects of drought on seedlings and saplings in the context of climate change are much needed.

Finally, the ordination analysis revealed an interesting niche separation of *Quercus scytophylla* and *Q. uxoris* on geomorphic/edaphic grounds (Figs. 8, 11), which presents an opportunity for ecological studies. Also, *Dendropanax arboreus* and *Oreopanax peltatus* were found to form a similarly interesting pair of species, as they showed opposing trends along axis 3 of the ordination (Figs. 14 and 15), despite their classification in the same family (Araliaceae).

CONCLUSIONS

The analysis of the NMS ordination supported by available literature suggests the possibility that a number of plant species in the cloud forest of western México and adjoining communities may either increase or decrease their abundances as a result of climate change.

One of the tree species that are hypothesized to recede as a result of increased drought is *Clusia salvinii*. In addition, woody vine abundances would hypothetically decrease also, with the notable exception of *Vitis tiliifolia*, which apparently has a higher resistance to drought. Conversely, a species that would hypothetically invade new ground is *Carpinus tropicalis*.

Alterations of the nitrogen biogeochemical cycle brought about by climate change would also probably have negative effects on the cloud forest community. Species that are hypothesized to recede are *Cedrela odorata*, *Dendropanax arboreus*, *Persea hintonii*, and *Sebastiania jaliscensis*. Whereas *Oreopanax peltatus* would hypothetically be benefited by the change.

Field studies to assess the physiological resistance or tolerance to drought, population dynamics, nutrient and water relations, wood anatomy and regeneration rate of the species of interest in the context of drought induced by climate change are much needed.

REFERENCES

Allen, C. D. and D. D. Breshears. 1998. Drought-induced shift of a forest-woodland ecotone: Rapid landscape response to climate variation. Proceedings of the National Academy of Sciences of the United States of America 95 (25): 14839-14842.

Ambrose, S. H. and N. E. Sikes. 1991. Soil carbon isotope evidence for Holocene habitat change in the Kenya Rift Valley. Science 253 (5026): 1402-1405.

Arriaga, L., J. M. Espinoza, C. Aguilar, E. Martínez, L. Gómez and E. Loa (coordinators). 2000. Regiones terrestres prioritarias de México. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, México City, México.

Ball, E., J. Hann, M. Kluge, H. S. J. Lee, U. Luttge, B. Orthen, M. Popp, A. Schmitt, and I. P. Ting. 1991. Ecophysiological comportment of the tropical CAM-tree *Clusia* in the field. II. Modes of photosynthesis in trees and seedlings. New Phytologist 117 (3): 483-491.

Barber, V. A., G. P. Juday, and B. P. Finney. 2000. Reduced growth of Alaskan white spruce in the twentieth century from temperature induced drought stress. Nature 405: 668-673.

Barry, R. G. and A. Seimon. 2000. Research for mountain area development: Climatic fluctuations in the mountains of the Americas and their significance. Ambio 29 (7): 364-370.

Beals, E. W. 1984. Bray-Curtis ordination: An effective strategy for analysis of multivariate ecological data. Advances in Ecological Research 14: 1-55.

Borland, A. M., H. Griffiths, C. Maxwell, M. S. J. Broadmeadow, N. M. Griffiths, and J. D. Barnes. 1992. On the ecophysiology of the Clusiaceae in Trinidad: Expression of CAM in *Clusia minor* L. during the transition from wet to dry season and characterization of three endemic species. New Phytologist 122 (2): 349-357.

Bossuyt, B., M. Hermy and J. Deckers. 1999. Migration of herbaceous plant species across ancient-recent forest ecotones in central Belgium. Journal of Ecology 87: 628-638.

Breedlove, D. E. 1973. The phytogeography and vegetation of Chiapas, México. *In:* A. Graham (Ed.). Vegetation and vegetational history of northern Latin America. Elsevier Scientific. New York, USA.

Carlquist, S. 1984. Wood and stem anatomy of Lardizabalaceae, with comments on the vining habit, ecology and systematics. Botanical Journal of the Linnean Society 88: 257-277.

Clark, D. A., and D. B. Clark. 1992. Life history diversity of canopy and emergent trees in a Neotropical rainforest. Ecological Monographs 62: 315-344.

Clark, D. A., and D. B. Clark. 1994. Climate-induced annual variation in canopy tree-growth in a Costa-Rican tropical rain forest. Journal of Ecology 82(4): 865-872.

Condit, R., S. P. Hubbell, and R. B. Foster. 1996a. Changes in tree species abundance in a Neotropical forest: Impact of climate change. Journal of Tropical Ecology 12 (2): 231-256.

Condit, R., S. P. Hubbell, and R. B. Foster. 1996b. Assessing the response of plant functional types to climatic change in tropical forests. Journal of Vegetation Science 7: 405-416.

Condit, R., S. Aguilar, A. Hernández, R. Pérez, S. Lao, G. Angehr, S. P. Hubbell and R. B. Foster. 2004. Tropical forest dynamics across a rainfall gradient and the impact of an El Niño dry season. Journal of Tropical Ecology 20: 51-72.

Curtis, J. T. and P. McIntosh. 1951. An upland forest continuum in the prairie-forest border region of Wisconsin. Ecology 32: 476-496.

Davidson, E. A., J. Chorover and D. B. Dail. 2003. A mechanism of abiotic immobilization of nitrate in forest ecosystems: the ferrous wheel hypothesis. Global Change Biology 9 (2): 228-236.

Faith, D. P., P. R. Minchin, and L. Belbin. 1987. Compositional dissimilarity as a robust measure of ecological distance. Vegetatio 69: 57-68.

Franco, A. C., E. Olivares, E. Ball, U. Luttge and A. Haag-Kerwer. 1994. In situ studies of Crassulacean Acid Metabolism in several sympatric species of tropical trees of the genus *Clusia*. New Phytologist 126 (2): 203-211.

Frankie, G. W., H. G. Baker and P. A. Opler. 1974. Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. Journal of Ecology 62 (3): 881-919.

García, E. 1997a. Carta de climas (clasificación de Koeppen, modificado por García). Escala 1:1000,000. Jalisco. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad. México City, México.

García, E. 1997b. Carta de isotermas medias anuales. Escala 1:1000,000. Jalisco. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad. México City, México.

García, E. 1997c. Carta de precipitación total anual. Escala 1:1000,000. Jalisco. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad. México City, México.

García, I., J. Nava, R. E. Flores, M. Cházaro, J. A. Machuca and E. del Río. 2002. Flora del Parque Nacional Pico de Tancítaro, Michoacán. Secretaría de Urbanismo y Medio Ambiente. Morelia, México.

Gartner, B. L., S. H. Bullock, H. A. Mooney, V. B. Brown and J. L. Whitbeck. 1990. Water transport properties of vine and tree stems in a tropical deciduous forest. American Journal of Botany 77 (6): 742-749.

Gentry, A. H. 1982. Patterns of neotropical plant species diversity. *In*: M. K. Hecht, B. Wallace and G. T. Prance, (Eds.). Evolutionary Biology. 15. Plenum Press. New York, USA.

Gentry, A. H. 1995. Patterns of diversity and floristic composition in Neotropical montane forests. *In:* S. P. Churchill, H. Balslev, E. Forero and J. L. Luteyn, (Eds.). Biodiversity and conservation of Neotropical montane forests. The New York Botanical Garden. New York, USA.

Gentry, A. H. and C. Dodson. 1987. Contribution of non-trees to species richness of a tropical rain forest. Biotropica 19 (2): 149-156.

Gleason, H. A. 1926. The individualistic concept of the plant association. Bulletin of the Torrey Botanical Club 53 (1): 7-26.

Gómez-Pompa, A. 1973. Ecology of the vegetation of Veracruz. *In:* A. Graham (Ed.). Vegetation and vegetational history of northern Latin America. Elsevier Scientific. New York, USA.

Grau, H. R. and T. T. Veblen. 2000. Rainfall variability, fire and vegetation dynamics in Neotropical montane ecosystems in north-western Argentina. Journal of Biogeography 27: 1107-1121.

Grubb, P. J. and T. C. Whitmore. 1966. A comparison of montane and lowland rain forest in Ecuador: II. The climate and its effects on the distribution and physiognomy of the forests. Journal of Ecology 54 (2): 303-333.

Haag-Kerwer, A., T. E. E. Grams, E. Olivares, E. Ball, S. Arndt, M. Popp, E. Medina and U. Luttge. 1996. Comparative measurements of gas exchange, acid accumulation and chlorophyll a fluorescence of different species of *Clusia* showing C_3 photosynthesis, or Crassulacean Acid Metabolism, at the same field site in Venezuela. New Phytologist 134 (2): 215-226.

Herwitz, S. R. and S. S. Young. 1994. Mortality, recruitment and growth rates of montane tropical rain forest canopy trees on Mount Bellenden-Ker, Northeast Queensland, Australia. Biotropica 26 (4): 350-361.

Hessl, A. E., P. J. Weisberg and W. L. Baker. 1996. Spatial variability of radial growth in the forest-tundra ecotone of Rocky Mountain National Park, Colorado. Bulletin of the Torrey Botanical Club 123 (3): 206-212.

Hickley, G., R. Fullagar, K. Holden, M. Lee, K. McGhee, M. McLean, R. Sullivan and A. Thomas. 2002. Antarctic meltdown. Nature Australia 27 (4): 6.

Hinton, J. and J. Rzedowski. 1975. George B. Hinton, explorador botánico en el sudoeste de México. Anales de la Escuela Nacional de Ciencias Biológicas 21: 1-114.

INE (Instituto Nacional de Ecología). 2000. Estrategia Nacional de Acción Climática. Comité Intersecretarial de Cambio Climático. Secretaría del Medio Ambiente, Recursos Naturales y Pesca. México. Available at http://www.ine.gob.mx

Kappelle, M., T. Geuze, M. E. Leal and A. M. Cleef. 1996. Successional age and forest structure in a Costa Rican upper montane *Quercus* forest. Journal of Tropical Ecology 12 (5): 681-698.

Kitayama, K., S. I. Aiba, N. Majalap-Lee and M. Ohsawa. 1998. Soil nitrogen mineralization rates of rainforests in a matrix of elevations and geological substrates on Mount Kinabalu, Borneo. Ecological Research 13: 301-312.

Kruskal, J. B. 1964. Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. Psychometrika 29: 1-27.

Mather, P. M. 1976. Computational methods of multivariate analysis in physical geography. Wiley, London, Great Britain.

Matteuci, S. D. and A. Colma. 1982. Metodología para el estudio de la vegetación. Secretaría General de la Organización de los Estados Americanos. Washington, D.C. USA.

McCune, B. and J. B. Grace. 2002. Analysis of ecological communities. MjM Software Design. Oregon, USA.

McVaugh, R. 1987. Flora Novo-Galiciana. Vol. 5. Leguminosae. The University of Michigan Herbarium. Ann Arbor, USA.

McVaugh, R. 1989. Flora Novo-Galiciana. Vol. 15. Bromeliaceae to Dioscoreaceae. The University of Michigan Herbarium. Ann Arbor, USA.

Morano, L. D. and M. A. Walker. 1995. Soils and plant communities associated with three *Vitis* species. American Midland Naturalist 134 (2): 254-263.

Neilson, R. P. 1993. Transient ecotone response to climatic change: Some conceptual and modelling approaches. Ecological Applications 3 (3): 385-395.

Patiño, S., M. T. Tyree and E. A. Herre. 1995. Comparison of hydraulic architecture of woody plants of differing phylogeny and growth form with special reference to free-standing and hemi-epiphytic *Ficus* species from Panama. New Phytologist 129: 125-134.

Pounds, J. A., M. P. L. Fogden and J. H. Campbell. 1999. Biological response to climate change on a tropical mountain. Nature 398: 611-615.

Puig, H. and R. Bracho. 1987. Climatología. *In*: E. Puig and R. Bracho (Eds.). El bosque mesófilo de montaña de Tamaulipas. Instituto de Ecología. México City, México.

Puig, H. 1993. Árboles y arbustos del bosque mesófilo de montaña de la Reserva El Cielo, Tamaulipas, México. Instituto de Ecología, A. C. Xalapa, México.

Putz, F. E. 1983. Liana biomass and leaf area of a "tierra firme" forest in the Rio Negro basin, Venezuela. Biotropica 15: 185-189.

Rind, D., C. Rosenzweig and M. Stieglitz. 1997. The role of moisture transport between ground and atmosphere in global change. Annual Review of Energy and the Environment 22: 47-74.

Robertson, K. R. 1967. Clethraceae. Flora of Panama. Part VIII. Annals of the Missouri Botanical Garden 54 (3): 389-392.

Ruiz, J. A. 2000. Cambio climático y algunos impactos sobre las potencialidades agrícolas de Jalisco, México. DeVinci, Universidad de Guadalajara 2 (5): 4-15.

Rzedowski, J. 1983. La vegetación de México. Limusa. México City, México.

Rzedowski, J. 1991a. Diversidad y orígenes de la flora fanerogámica de México. Acta Botánica Mexicana 14: 3-21.

Rzedowski, J. 1991b. El endemismo en la flora fanerogámica mexicana: una apreciación analítica preliminar. Acta Botánica Mexicana 15: 47-64.

Rzedowski, J. and R. McVaugh. 1966. La vegetación de Nueva Galicia. Contributions from the University of Michigan Herbarium 9: 1-123.

Segura, G., P. Balvanera, E. Durán and A. Pérez. 2003. Tree community structure and stem mortality along a water availability gradient in a Mexican tropical dry forest. Plant Ecology 169: 259-271.

Siccama, T. G., G. Weir and K. Wallace. 1976. Ice damage in a mixed hardwood forest in Connecticut in relation to *Vitis* infestation. Bulletin of the Torrey Botanical Club 103 (4): 180-183.

Silver, W. L., D. J. Herman and M. K. Firestone. 2001. Dissimilatory nitrate reduction to ammonium in upland tropical forest soils. Ecology 82 (9): 2410-2416.

Sperry, J. S., M. T. Tyree and J. R. Donnelly. 1988. Vulnerability of xylem to embolism in a mangrove vs. an inland species of Rhizophoraceae. Physiologia Plantarum 74: 276-283.

Sturm, M., C. Racine and K. Tape. 2001. Climate change: Increasing shrub abundance in the Arctic. Nature 411: 546-547.

Thomas, C. D. and J. J. Lennon. 1999. Birds extend their ranges northwards. Nature 399: 213.

Tyree, M. T. and F. W. Ewers. 1991. Tansley Review No. 34. The hydraulic architecture of trees and other woody plants. New Phytologist 119 (3): 345-360.

Vázquez-García, J. A. 1993. Tropical montane cloud forest. *In:* L. S. Hamilton, J. O. Juvic and F. N. Scatena (Eds.). Proceedings of an international symposium, 31 May-5 June 1993. East-West Center. Honolulu, Hawaii.

Vázquez-García, J. A. 1995. Cloud forest archipelagos: Preservation of fragmented montane ecosystems in tropical America. Ecological Studies 110: 315-332.

Vázquez-García, J. A. and R. Cuevas. 1995. Fitogeografía y vegetación de la Sierra de Manantlán, Jalisco-Colima, México. *In*: J. A. Vázquez-García, R. Cuevas, T. S. Cochrane, H. H. Iltis, F. J. Santana and L. Guzmán. Flora de Manantlán. Sida Botanical Miscellany No. 13. Universidad de Guadalajara-IMECBIO/University of Wisconsin-Madison. Guadalajara, México.

Vázquez-García, J. A. and T. J. Givnish. 1998. Altitudinal gradients in tropical forest composition, structure and diversity in the Sierra de Manantlán. Journal of Ecology 86: 999-1020.

Velázquez, A., V. M. Toledo and I. Luna-Vega. 2000. Mexican Temperate Vegetation. *In:* M. G. Barbour and W. D. Billings, (Eds.). North American Terrestrial Vegetation, 2nd. ed. Cambridge University Press. New York, USA.

Villaseñor, J. L. 2003. Diversidad y distribución de las Magnoliophyta de México. Interciencia 28 (3): 160-186.

Vitousek, P. M. 1977. The regulation of element concentrations in mountain streams in the northeastern United States. Ecological Monographs 47 (1): 65-87.

Vitousek, P. M. 1994. Beyond global warming: Ecology and global change. Ecology 75 (7): 1861-1876.

Vogelmann, H. W. 1973. Fog precipitation in the cloud forests of eastern México. Bioscience 23 (2): 96-100.

Weltzin, J. F., M. E. Loik, S. Schwinning, D. G. Williams, P. A. Fay, B. M. Haddad, J. Harte, T. E. Huxman, A. L. Knapp, G. Lin, W. T. Pockman, M. R. Shaw, E. E. Small, M. D. Smith, S. D. Smith, D. T. Tissue and J. C. Zak. 2003. Assessing the response of terrestrial ecosystems to potential changes in precipitation. Bioscience 53 (10): 941-952.

Whittaker, R. H. 1975. Communities and ecosystems. $2^{nd.}$ ed. Macmillan Publishing. New York, USA.

Williams, G., M. S. Devall and C. Álvarez. 2000. A relict population of *Fagus grandifolia* var. *mexicana* at the Acatlán Volcano, México: Structure, litterfall, phenology and dendroecology. Journal of Biogeography 27: 1297-1309.

Zotz, G. and K. Winter. 1994. A one-year study on carbon, water and nutrient relationships in a tropical C_3-CAM hemi-epiphyte, *Clusia uvitana* Pittier. New Phytologist 127: 45-60.

Zotz, G., M. T. Tyree and H. Cochard. 1994. Hydraulic architecture, water relations and vulnerability to cavitation of *Clusia uvitana* Pittier: A C_3-CAM tropical hemiepiphyte. New Phytologist 127: 287-295.

TABLES

Table 1. Description of sample sites at cerro La Mona, in Sierra de Coalcomán, Michoacán, western México*.

Sample site	Description
B1	Cerro La Mona. La Cucharera, on bottomland. 1320 m asl. 18° 41' 02"N 103° 24' 46"W
B2	Cerro La Mona. Palmitos, on bottomland. 1470 m asl. 18° 41' 38"N 103° 25' 51" W
B3	Cerro La Mona. La Pitahaya, on bottomland. 1580 m asl. 18° 41' 26"N 103° 25' 39"W
B4	Cerro La Mona. La Pitahaya, on bottomland. 1575 m asl. 18° 41' 28"N 103° 25' 40"W
R1	Cerro La Mona. La Cucharera, on ridge. 1320 m asl. 18° 41' N 103° 25' W
R2	Cerro La Mona. La Pitahaya, on ridge. 1590 m asl. 18° 41' 26"N 103° 25' 42"W
R3	Cerro La Mona. La Pitahaya, on ridge. 1590 m asl. 18° 41' 27"N 103° 25' 43"W
R4	Cerro La Mona. La Pitahaya, on ridge. 1610 m asl. 18° 41' 26"N 103° 25' 43"W
R5	Cerro La Mona. La Pitahaya, on ridge. 1645 m asl. 18° 41' 22"N 103° 25' 42"W

*The sampled sites on ridges at cerro La Mona had oak forest (*Quercus* spp.) rather than pine forest (*Pinus* spp.) as seen elsewhere in Sierra de Coalcomán.

Table 2. Pearson's correlations* of species abundances (SIV) and the three axes of the NMS ordination ($N = 9$, df = 7).

Species	Axis	*r*	SIV
Canavalia hirsutissima	1	0.850	B1 = 4.02; R1 = 2.20; R4 = 1.58
Carpinus tropicalis	1	-0.841	B2 = 6.57; B3 = 10.23; B4 = 11.57; R2 = 16.23; R3 = 9.21; R4 = 12.53; R5 = 5.34
Clusia salvinii	1	0.805	B1 = 6.81; B2 = 2.72; B4 = 1.27; R1 = 0.55
Marsdenia aff. *macrophylla*	1	0.946	B1 = 2.99; B2 = 0.70; R1 = 1.23
Styrax argenteus	1	0.859	B1 = 23.62; R1 = 27.67; R2 = 1.96; R3 = 4.52; R4 = 1.68
Clethra lanata	2	-0.789	R1 = 3.89; R2 = 2.51; R3 = 1.26; R4 = 4.74; R5 = 5.32
Guarea glabra	2	0.967	B1 = 2.34; B2 = 6.27; B3 = 5.35; B4 = 2.40; R1 = 0.54; R3 = 1.26
Piper villiramulum	2	0.736	B2 = 1.73; B3 = 1.54; B4 = 2.39
Quercus scytophylla	2	-0.804	B4 = 5.07; R1 = 13.41; R2 = 36.01; R3 = 20.01; R4 = 30.92; R5 = 43.95
Quercus uxoris	2	0.800	B1 = 9.44; B2 = 12.75; B3 = 9.03; B4 = 4.30; R1 = 5.69; R3 = 1.26; R4 = 5.54
Trichilia havanensis	2	0.860	B1 = 0.84; B2 = 4.03; B3 = 8.42; R3 = 1.30
Cedrela odorata	3	0.840	B2 = 1.00; B3 = 1.54; B4 = 3.69
Dendropanax arboreus	3	0.890	B2 = 0.69; B3 = 1.75; B4 = 2.87; R1 = 0.61; R3 = 1.26
Oreopanax peltatus	3	-0.700	B1 = 1.09; R1 = 2.61; R4 = 1.58; R5 = 1.76
Persea hintonii	3	0.878	B1 = 1.39; B2 = 4.46; B3 = 4.72; B4 = 9.82; R2 = 2.03; R3 = 5.07; R5 = 4.73
Sebastiania jaliscensis	3	0.883	B2 = 11.36; B3 = 11.24; B4 = 33.19; R2 = 20.03; R3 = 21.89; R4 = 1.58; R5 = 3.54

*Only correlations of species with three or more non-zero abundance values are shown. SIV = Synthetic Importance Values. B1-B4 = bottomland samples; R1-R5 = ridge samples (see Table 1).

Table 3. Vegetation affinity of selected plant species from cerro La Mona and their hypothetical role in climate change-induced vegetation dynamics.

Species / Morphospecies	**Vegetation**	**Habit**	**Hypothetical behavior**
Canavalia hirsutissima	TDF[8], TSF[8], CF[8]	Liana	Recede
Carpinus tropicalis	CF[1,3,4,5,6,7]	Tree	Advance
Clusia salvinii	TRF[6], CF[1,3]	Tree	Recede
Marsdenia aff. *macrophylla*	CF[6]	Liana	Recede
Smilax moranensis	TSF[2], CF[2,4]	Liana	Recede
Styrax argenteus	CF[1,3,4,5,7]	Tree	Undefined
Vitis tiliifolia	CF[4]	Liana	Advance

Vegetation affinity: CF = cloud forest (includes fir forest); CV = coastal vegetation (includes coastal dunes and savannah-like vegetation); HGF = High elevation gallery forest; TDF = tropical deciduous forest (includes subtropical scrub); TF = thorn forest; TRF = tropical rain forest (tropical evergreen forest); TSF = tropical semi deciduous forest (includes palm forest). References: [1]Rzedowski and McVaugh (1966); [2]McVaugh (1989); [3]Vázquez-García and Cuevas (1995); [4]García *et al.* (2002); [5]Breedlove (1973); [6]Gómez-Pompa (1973); [7]Puig (1993); [8]McVaugh (1987).

FIGURES

Fig. 1. Map of cerro La Mona and vicinity in Sierra de Coalcomán, México. Above right, map of México, with the state of Michoacán highlighted in black. Inset at left, outline of Michoacán showing the current limits of the four municipalities of the former district of Coalcomán: (1) Coahuayana, (2) Chinicuila, (3) Aquila and (4) Coalcomán. Inset at bottom, explored area in cerro La Mona and vicinity. Rectangle = cerro La Mona, filled circles = town or named location, dotted line = dirt road, thick line = paved road, thin line = elevation line (in meters).

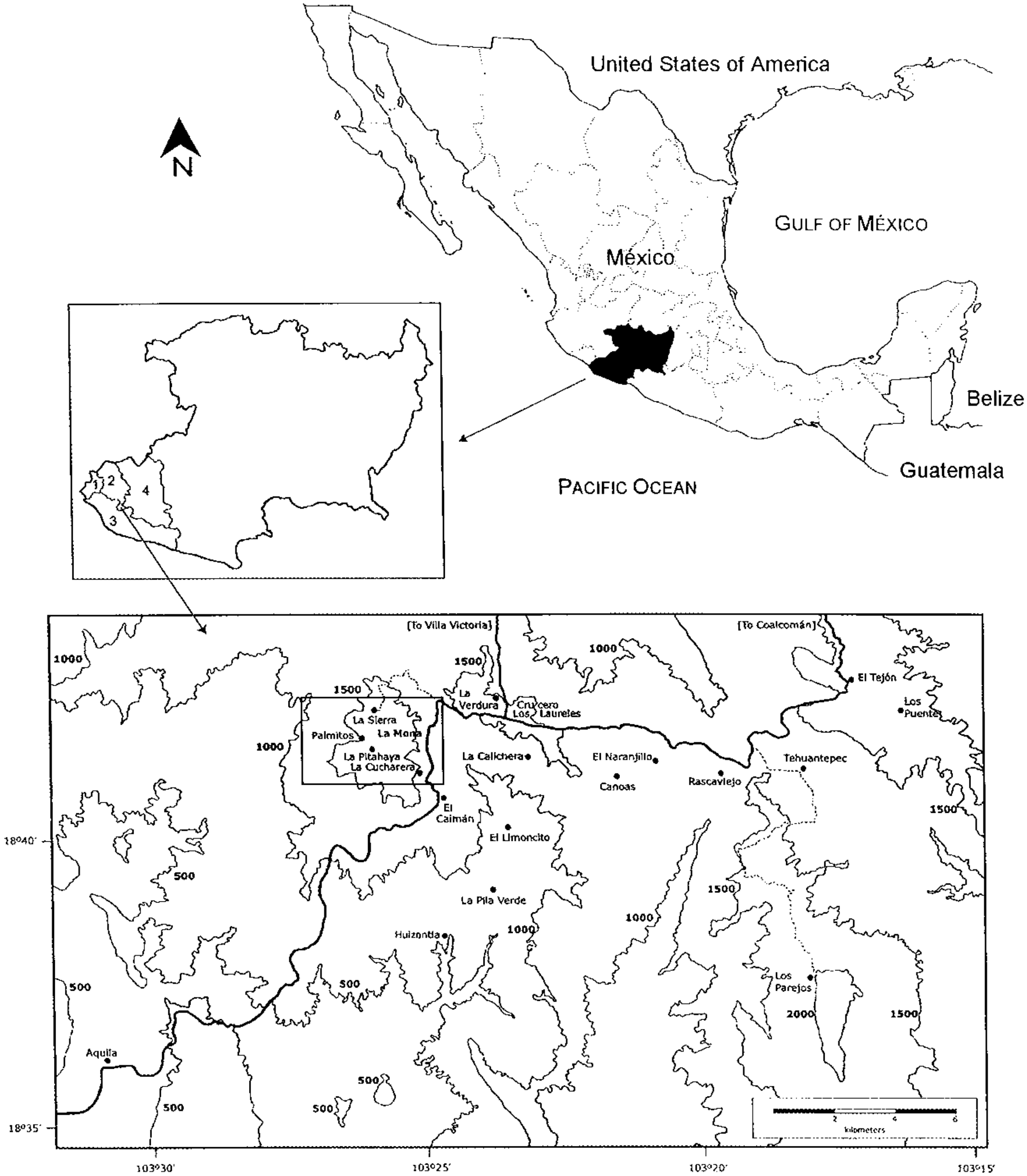
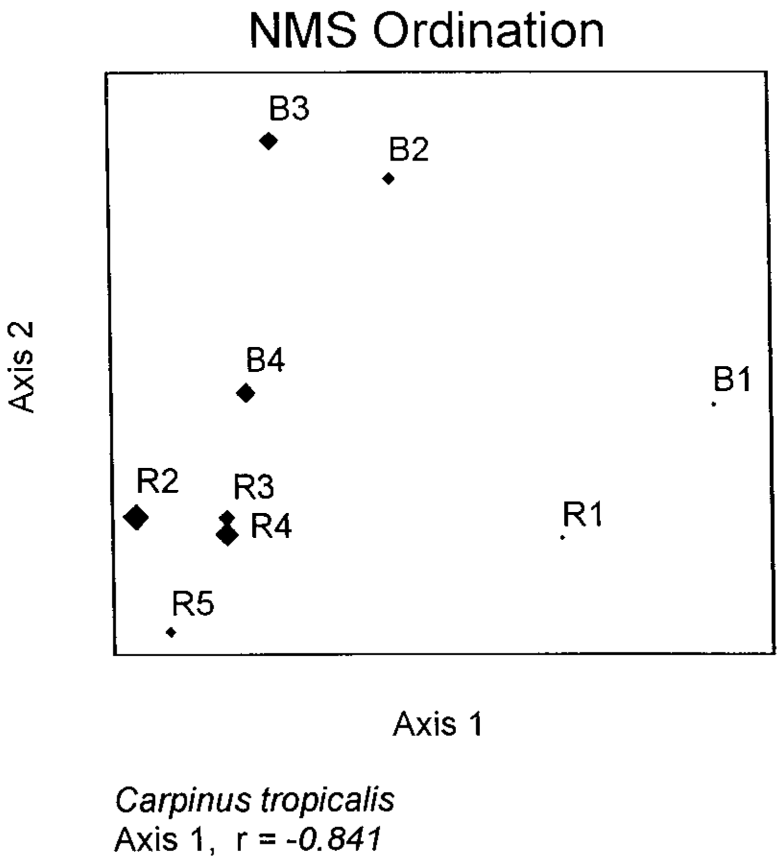
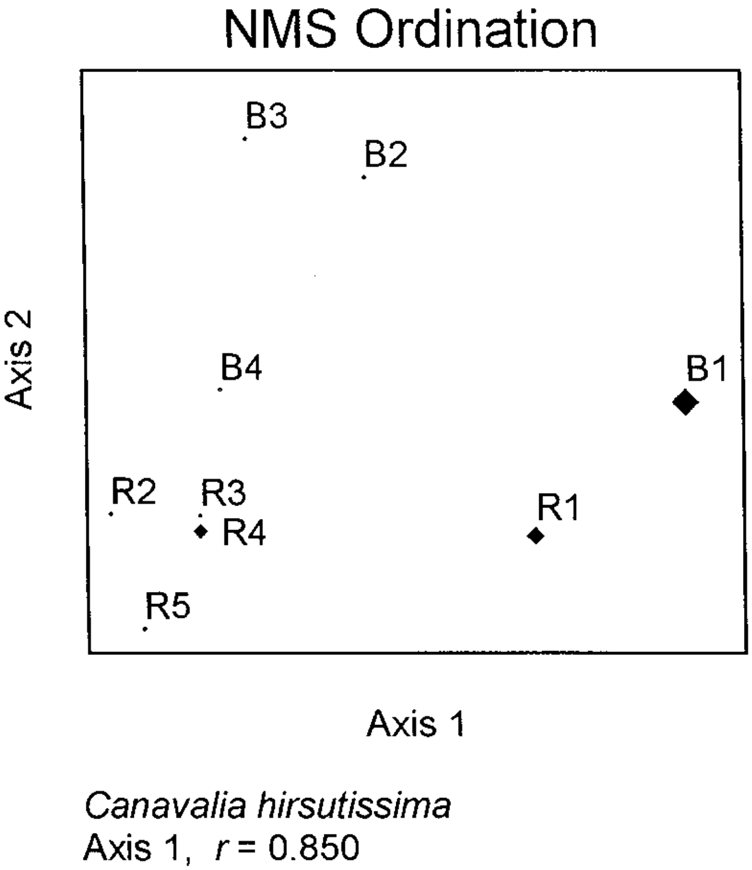

United States of America
N
GULF OF MÉXICO
México
Belize
Guatemala
PACIFIC OCEAN
1
2
3
4
[To Villa Victoria]
[To Coalcomán]
1000
1500
1500
1000
La Verdura
Crucero Los Laureles
El Tejón
Los Puentes
La Sierra
Palmitos
La Mona
1000
La Pitahaya
La Cucharera
La Calichera
El Naranjillo
Canoas
Rascavlejo
Tehuantepec
1500
El Caimán
El Limoncito
18°40'
500
La Pila Verde
1500
1000
Huizontla
1000
500
500
Los Parejos
2000
1500
Aquila
500
500
500
18°35'
2
4
6
kilometers
103°30'
103°25'
103°20'
103°15'

Fig. 2. Overlay of *Carpinus tropicalis* abundances on the NMS ordination of cloud forest in cerro La Mona, Michoacán.



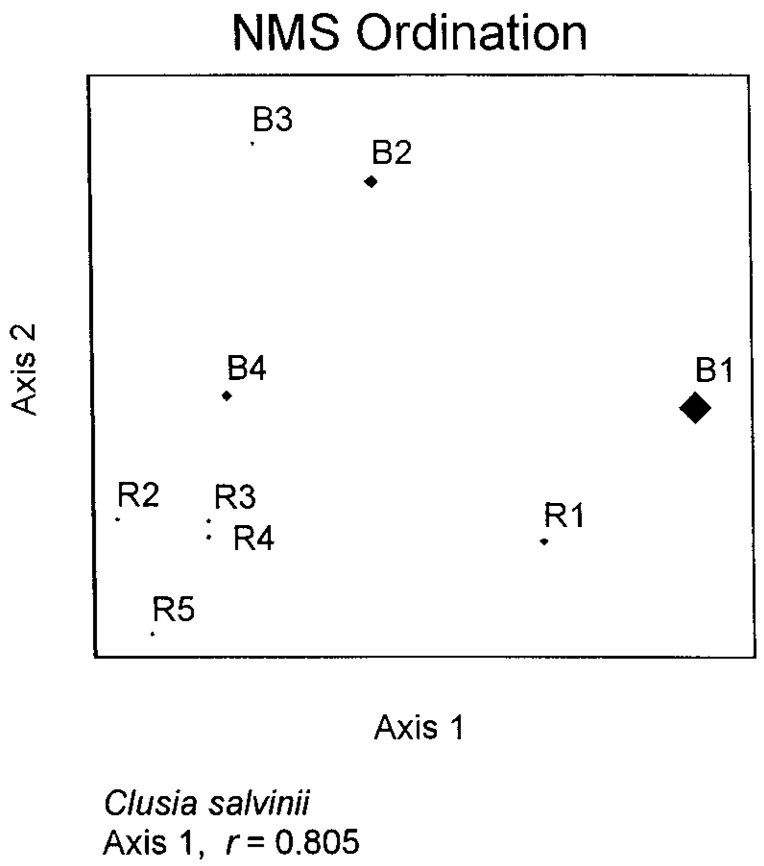
The plot shows Min-Max relationships of plant abundances to axis 1 of the ordination.

Fig. 3. Overlay of *Canavalia hirsutissima* abundances on the NMS ordination of cloud forest in cerro La Mona, Michoacán.



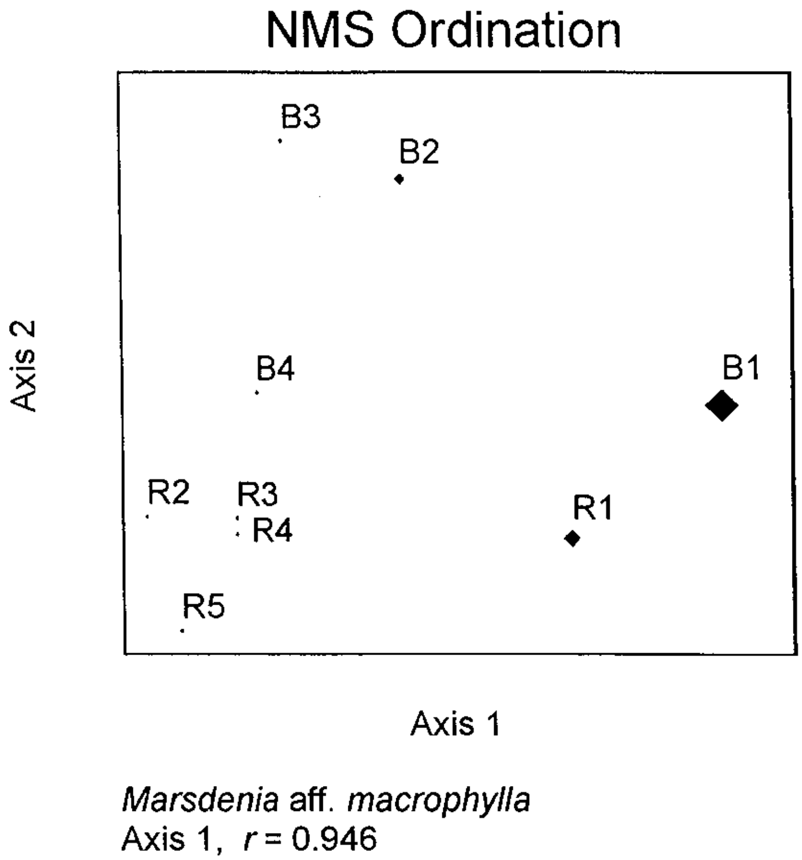
The plot shows Min-Max relationships of plant abundances to axis 1 of the ordination.

Fig. 4. Overlay of *Clusia salvinii* abundances on the NMS ordination of cloud forest in cerro La Mona, Michoacán.



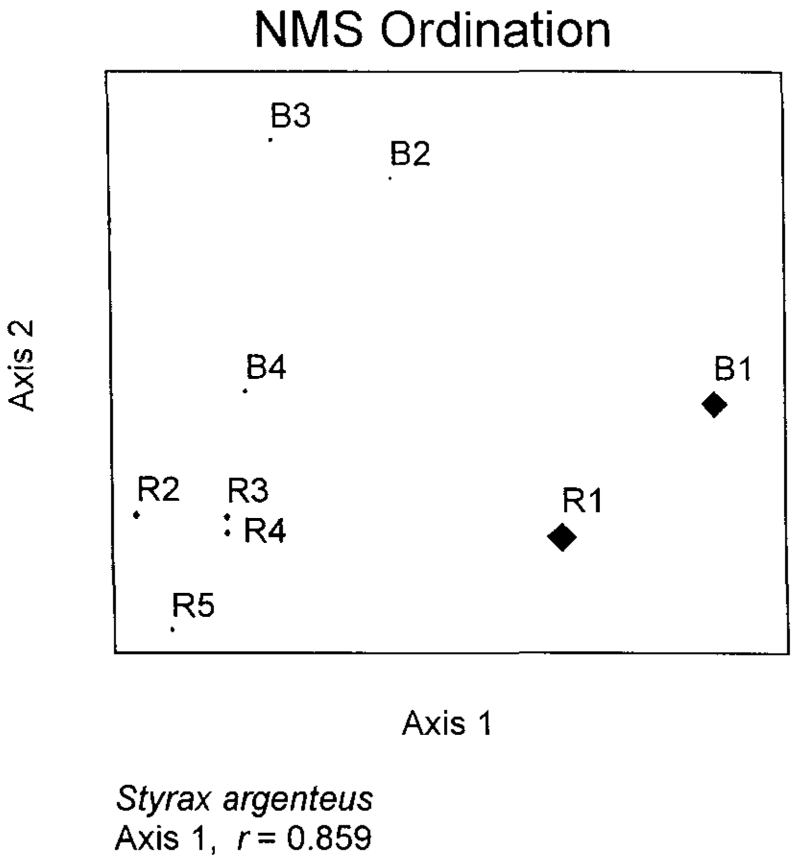
The plot shows Min-Max relationships of plant abundances to axis 1 of the ordination.

Fig. 5. Overlay of *Marsdenia* aff. *macrophylla* abundances on the NMS ordination of cloud forest in cerro La Mona, Michoacán.



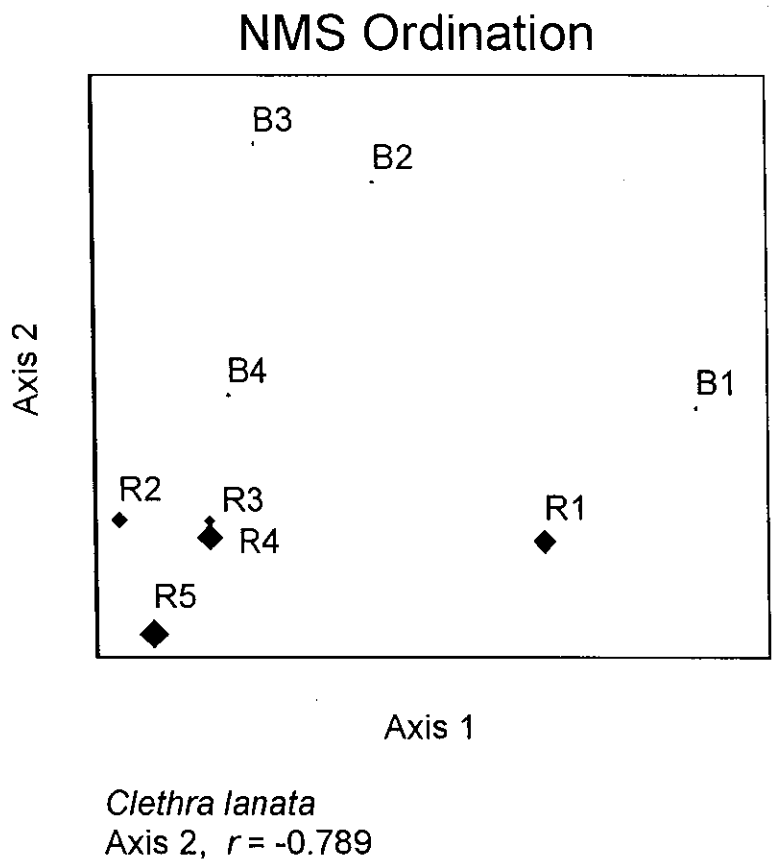
The plot shows Min-Max relationships of plant abundances to axis 1 of the ordination.

Fig. 6. Overlay of *Styrax argenteus* abundances on the NMS ordination of cloud forest in cerro La Mona, Michoacán.



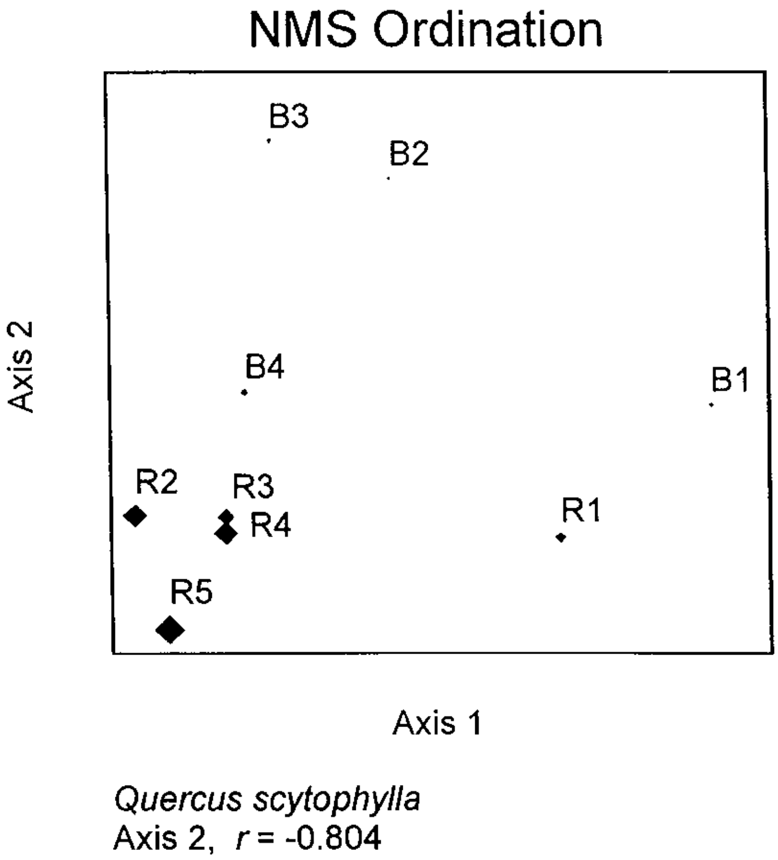
The plot shows Min-Max relationships of plant abundances to axis 1 of the ordination.

Fig. 7. Overlay of *Clethra lanata* abundances on the NMS ordination of cloud forest in cerro La Mona, Michoacán.



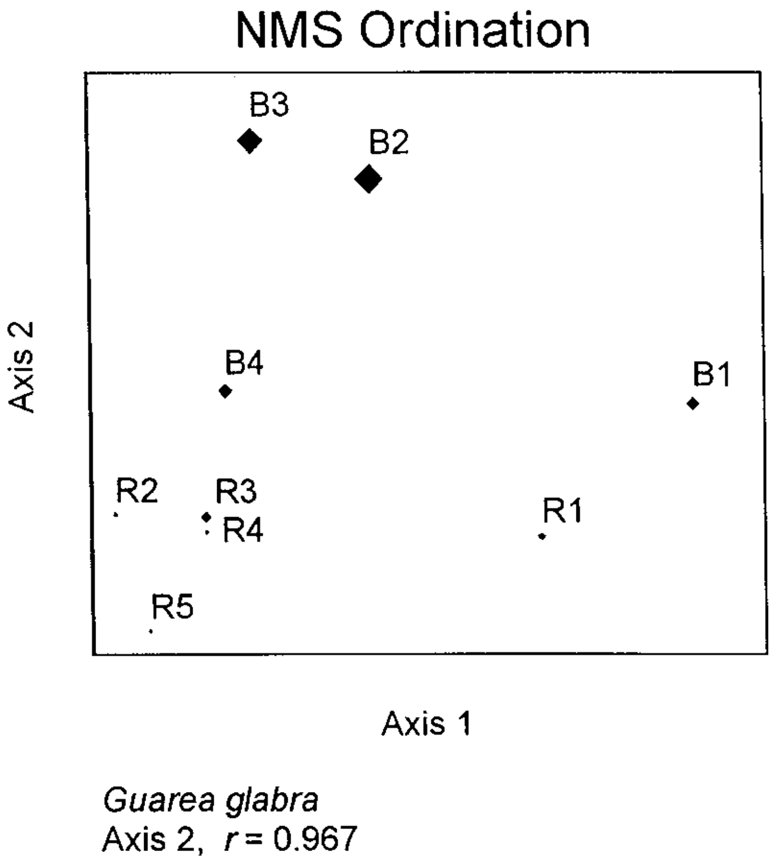
The plot shows Min-Max relationships of plant abundances to axis 2 of the ordination.

Fig. 8. Overlay of *Quercus scytophylla* abundances on the NMS ordination of cloud forest in cerro La Mona, Michoacán.



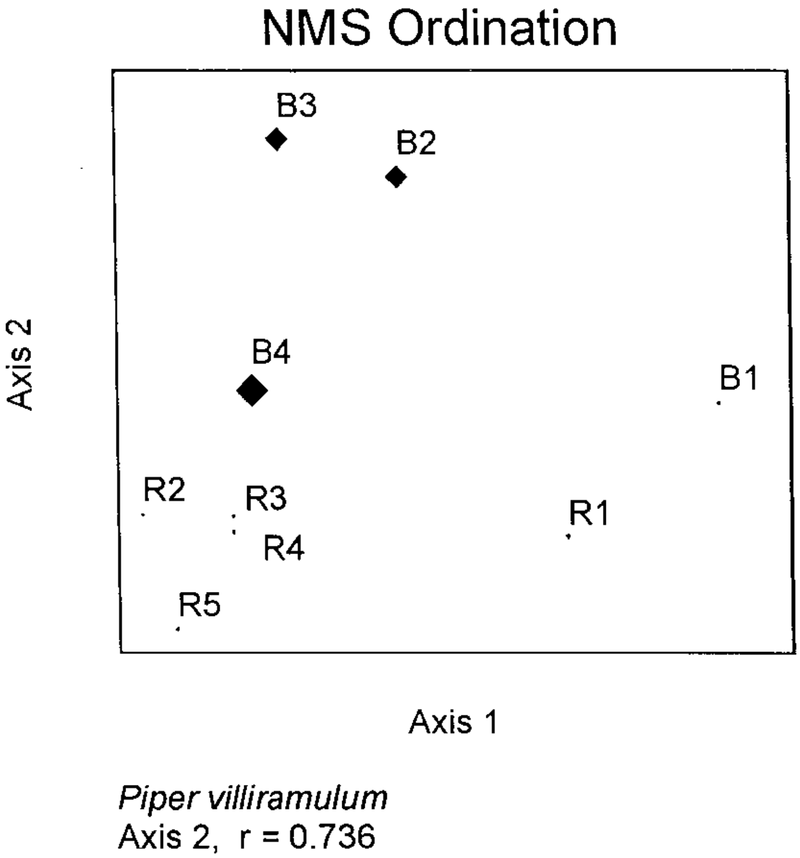
The plot shows Min-Max relationships of plant abundances to axis 2 of the ordination.

Fig. 9. Overlay of *Guarea glabra* abundances on the NMS ordination of cloud forest in cerro La Mona, Michoacán.



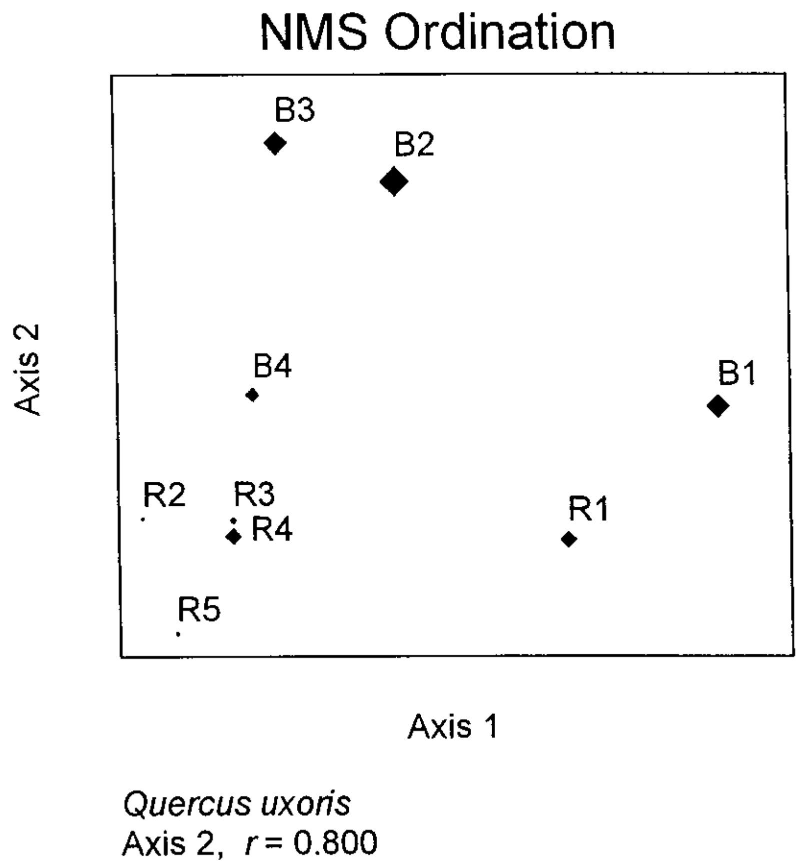
The plot shows Min-Max relationships of plant abundances to axis 2 of the ordination.

Fig. 10. Overlay of *Piper villiramulum* abundances on the NMS ordination of cloud forest in cerro La Mona, Michoacán.



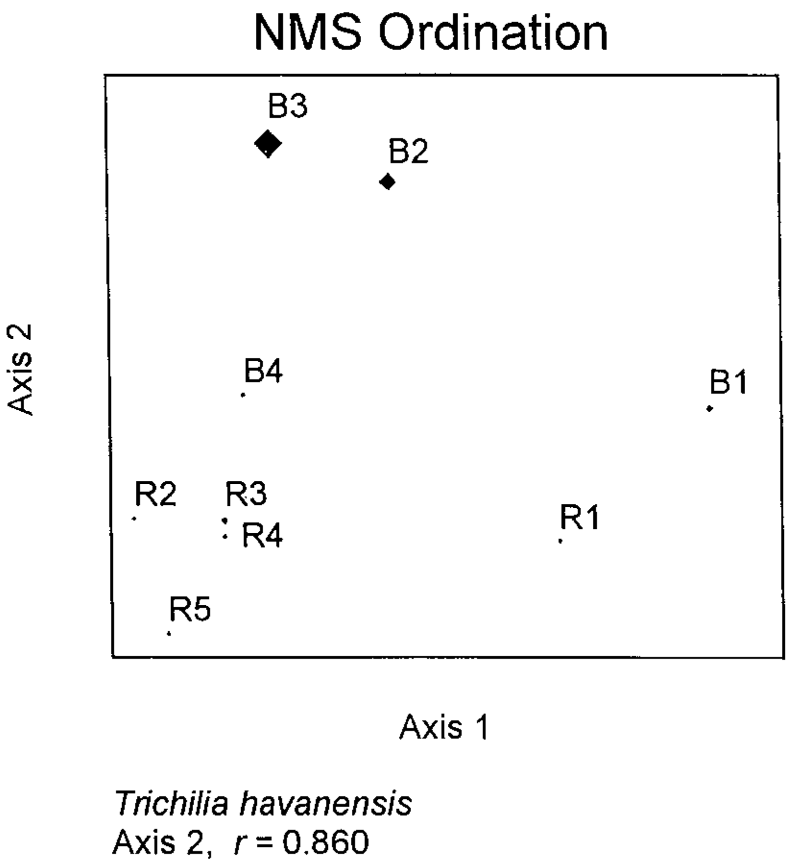
The plot shows Min-Max relationships of plant abundances to axis 2 of the ordination.

Fig. 11. Overlay of *Quercus uxoris* abundances on the NMS ordination of cloud forest in cerro La Mona, Michoacán.



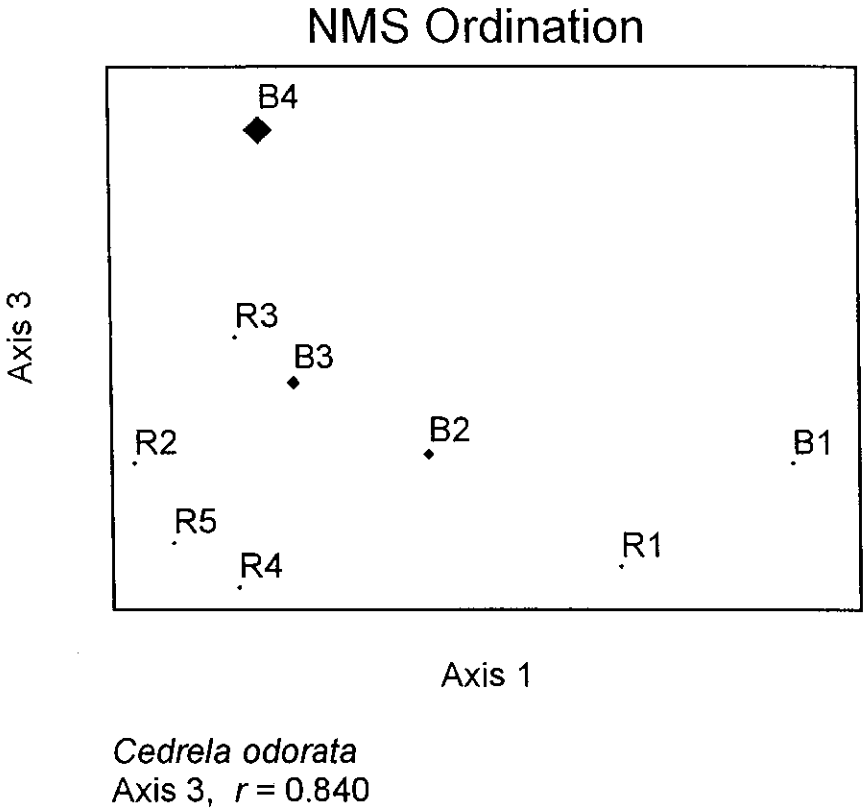
The plot shows Min-Max relationships of plant abundances to axis 2 of the ordination.

Fig. 12. Overlay of *Trichilia havanensis* abundances on the NMS ordination of cloud forest in cerro La Mona, Michoacán.



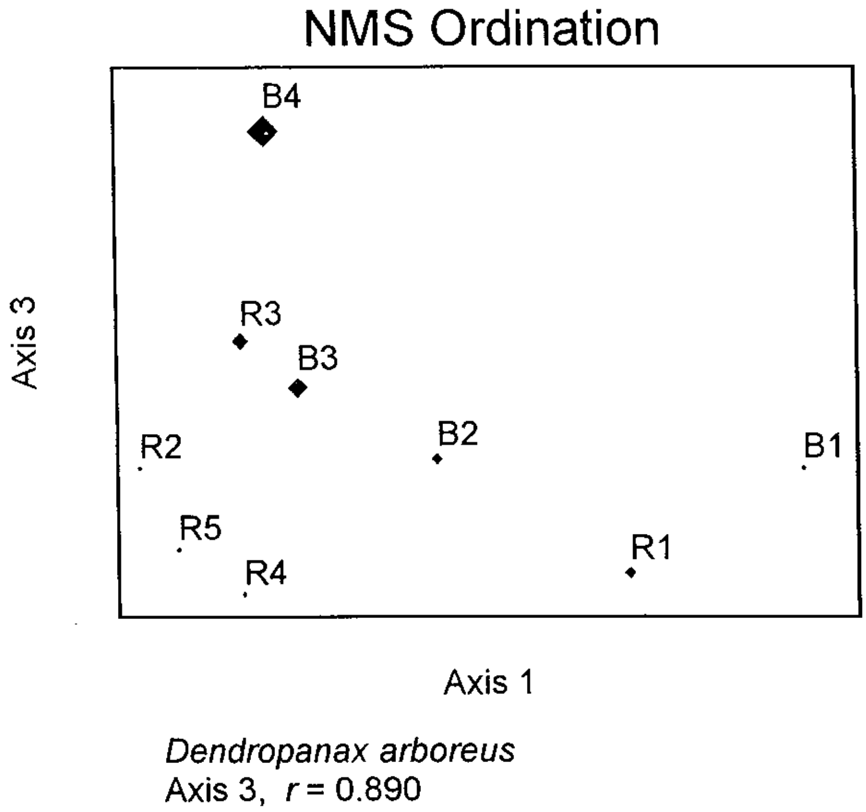
The plot shows Min-Max relationships of plant abundances to axis 2 of the ordination.

Fig. 13. Overlay of *Cedrela odorata* abundances on the NMS ordination of cloud forest in cerro La Mona, Michoacán.



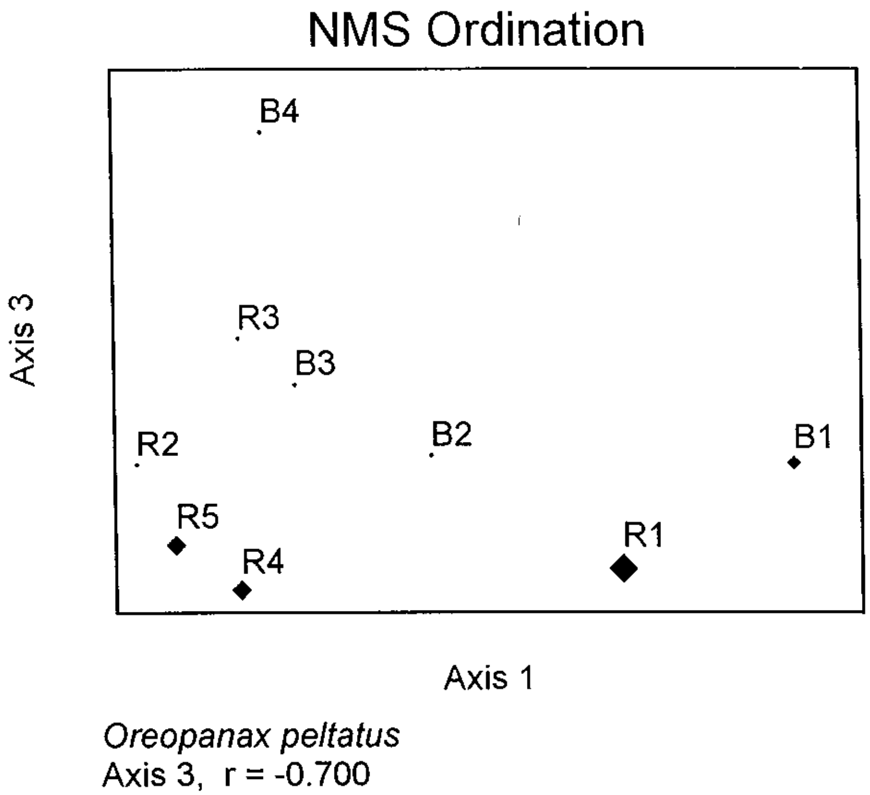
The plot shows Min-Max relationships of plant abundances to axis 3 of the ordination.

Fig. 14. Overlay of *Dendropanax arboreus* abundances on the NMS ordination of cloud forest in cerro La Mona, Michoacán.



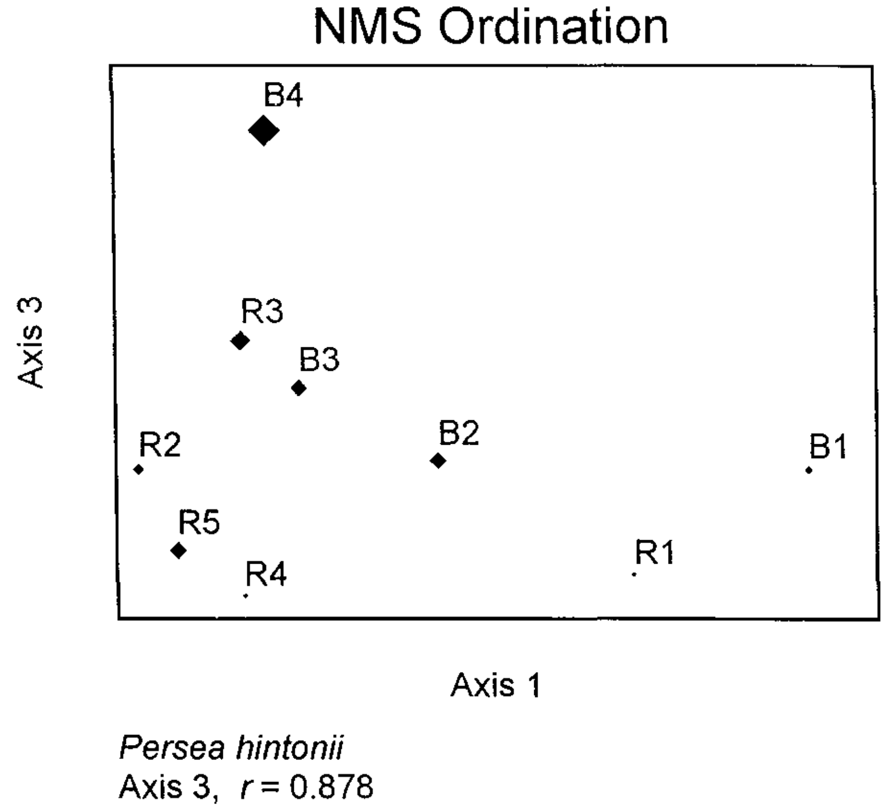
The plot shows Min-Max relationships of plant abundances to axis 3 of the ordination.

Fig. 15. Overlay of *Oreopanax peltatus* abundances on the NMS ordination of cloud forest in cerro La Mona, Michoacán.



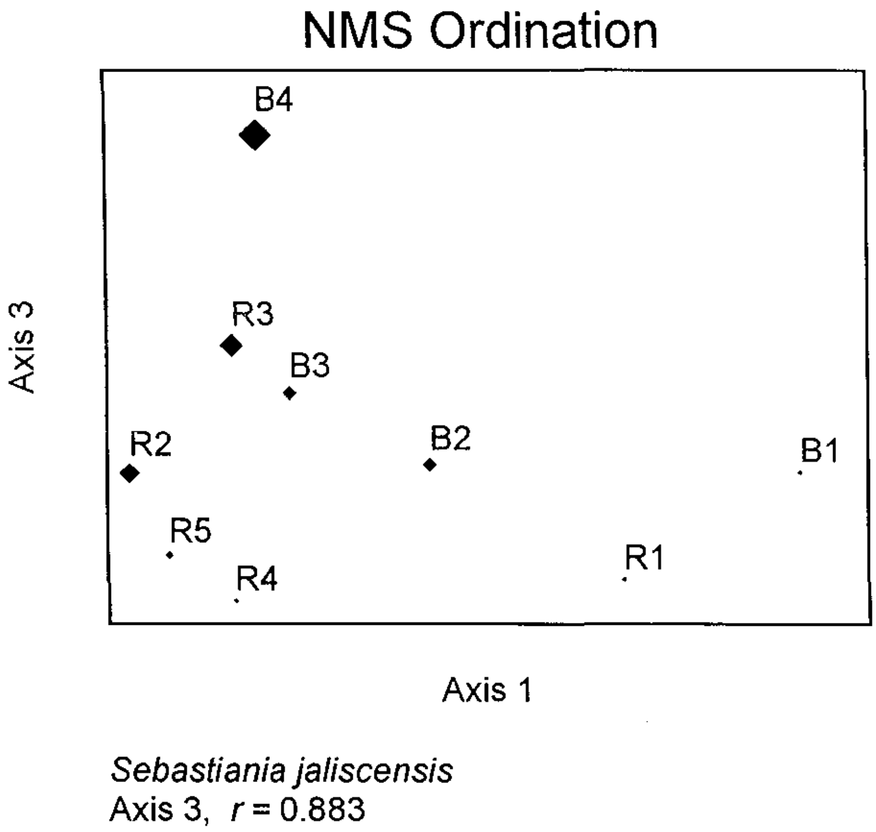
The plot shows Min-Max relationships of plant abundances to axis 3 of the ordination.

Fig. 16. Overlay of *Persea hintonii* abundances on the NMS ordination of cloud forest in cerro La Mona, Michoacán.



The plot shows Min-Max relationships of plant abundances to axis 3 of the ordination.

Fig. 17. Overlay of *Sebastiania jaliscensis* abundances on the NMS ordination of cloud forest in cerro La Mona, Michoacán.



The plot shows Min-Max relationships of plant abundances to axis 3 of the ordination.

CHAPTER 3

Annotated checklist of woody plants collected at cerro La Mona in western Mexico

INTRODUCTION

The presence of endemic plants and animals and its biological richness has made Sierra de Coalcomán a priority region for conservation (Arriaga *et al.* 2000). However, it remains superficially known. McVaugh (1961) called attention to the need of botanical exploration in western Michoacán over forty years ago, and his call remains valid to this day. The inaccessibility of the terrain and high crime rates have resulted in reduced exploration and few collections.

With the exception of a few recent botanical studies (i.e., Guerrero-Campanur 1985), floristic exploration in sierra de Coalcomán is mostly limited to the first half of the XX century or earlier. McVaugh (1972) credits the first record of botanical exploration in Nueva Galicia to Francisco Hernández, who traveled by Coalcomán searching for medicinal plants in 1570-1577. Sessé, Mociño and Castillo followed a route similar to that of Hernández in 1790-1792, but they passed through Coahuayana, north of Coalcomán (McVaugh 1977). These were the first scientists to contribute significantly to the modern botanical knowledge of western Mexico. Nelson collected botanical specimens in the high mountains of western Michoacán in 1902-1903 (McVaugh 1972). Brand *et al.* (1960) presented a detailed review of biological collecting, which was mostly marginal to the Coalcomán region prior to the Mexican revolution in 1910. Later on it was Hinton who made significant collections in the decade of 1930, specifically between Coalcomán and the Pacific coast to the west and as far as Aguililla to the south (Hinton and Rzedowski 1975). No floristic records from cerro La Mona have been located and thus the aim of this paper is to contribute to the floristic knowledge of this mountain in particular, and of the Sierra de Coalcomán in general.

RESULTS

A total of 81 species in 68 genera and 42 families of woody vascular plants occurred within the nine 0.1 ha sites studied at cerro La Mona, using a cutoff diameter at breast height of 2.5 cm. Most families had a few species, without strong dominance of any taxa. However, legumes had the most species (8) which corresponded to about 10% of the total. Of these, four were mimosoid and 4 papilionoid. Asteraceae was the second largest family with five species (6%), and the third position was occupied simultaneously by Euphorbiaceae, Fagaceae and Lauraceae, with four species each (5%). Regarding habit, most species, i.e., 45 (56%) were trees, 32 (39%) were shrubs and only 4 (5%) were lianas.

REFERENCES

Arriaga L., Espinoza J.M., Aguilar C., Martínez E., Gómez L. and Loa E. 2000. Regiones terrestres prioritarias de México. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, México City, México.

Brand D.D., Bullard F.M., Corona J., Duellman W.E., Howard M.J., Miller E., Peters J.A., Porter G.W., Ross D.I., Singletary C.E., Storer R.W. and Turner B.L. Coalcomán and Motines del Oro, an ex-distrito of Michoacán, México. The Institute of Latin American Studies. The University of Texas, M. Nijhoff, The Hague, The Netherlands.

Guerrero-Campanur, B. 1985. Reconocimiento botánico de Aquila, Michoacán. (México). Tesis de licenciatura. Universidad Michoacana de San Nicolás de Hidalgo. Morelia, México.

Hinton J. and Rzedowski J. 1975. George B. Hinton, explorador botánico en el sudoeste de México. Anales de la Escuela Nacional de Ciencias Biológicas 21: 1-114.

McVaugh, R. 1961. Euphorbiaceae Novae Novo-Galicianae. Brittonia 13: 145-205.

McVaugh, R. 1972. Botanical exploration in Nueva Galicia, Mexico from 1790 to the present time. Contributions from the University of Michigan Herbarium 9(3): 205-357.

McVaugh, R. 1977. Botanical results of the Sessé and Mociño expedition (1787-1803) I. Summary of excursions and travels. Contributions from the University of Michigan Herbarium 11(3): 97-195.

Appendix. Checklist of woody plants recorded in nine 0.1 ha sites at cerro La Mona, Sierra de Coalcomán, México.

No.	Family	Species	Common name / Morphospecies	Voucher specimen	Sample	DM	DN	FR	RDM	RDN	RFR	SIV
1	Actinidiaceae	*Saurauia serrata* DC.	"palo de barranca"	ESG-1618	B4	8.24	1	1	3.11	1.03	2.50	2.21
2	Annonaceae	[2]*Annona* sp. 1	"anonillo"	ESG-2132	R1	0.23	1	1	0.09	0.45	1.14	0.56
3	Araliaceae	*Dendropanax arboreus* (L.) Decne. & Planch.	"macarmina"	ESG-1398	B2	0.06	1	1	0.01	0.75	1.30	0.69
					B3	4.12	1	1	0.65	2.04	2.56	1.75
					B4	4.10	2	2	1.55	2.06	5.00	2.87
					R1	0.65	1	1	0.24	0.45	1.14	0.61
					R3	0.08	1	1	0.03	1.19	2.56	1.26
4	Araliaceae	*Oreopanax echinops* (Cham. & Schltdl.) Decne. & Planch.	"mano de león [pubescente]"	ESG-1948	B2	0.15	2	2	0.04	1.49	2.60	1.38
5	Araliaceae	*Oreopanax peltatus* Linden	"mano de león"	ESG-1313	B1	2.35	1	1	1.22	0.65	1.39	1.09
					R1	2.66	5	4	1.00	2.27	4.55	2.61
					R4	0.10	1	1	0.03	1.85	2.86	1.58
					R5	0.05	1	1	0.02	2.04	3.23	1.76
6	Asclepiadaceae	[1]*Marsdenia* aff. *macrophylla* (Humb. & Bonpl. ex Schult.) E. Fourn.	"huacuco"	ESG-1082	B1	0.32	5	4	0.17	3.25	5.56	2.99
					B2	0.17	1	1	0.04	0.75	1.30	0.70
					R1	0.18	3	2	0.07	1.36	2.27	1.23
7	Asteraceae	*Ageratina choricephala* (B.L. Rob.) R.M. King & H. Rob.		ESG-1537	B4	0.17	2	1	0.07	2.06	2.50	1.54
					R2	0.38	1	1	0.19	1.79	4.00	1.99
					R3	0.18	2	2	0.07	2.38	5.13	2.53
8	Asteraceae	*Ageratina areolaris* (DC.) Gage ex B.L. Turner	"vara amargosa"	ESG-1943	R1	0.42	1	1	0.16	0.45	1.14	0.58
9	Asteraceae	*Chromolaena ovaliflora* (Hook. & Arn.) R.M. King & H. Rob.		ESG-1544	R2	0.05	1	1	0.02	1.79	4.00	1.94
10	Asteraceae	*Critonia hebebotrya* DC.		ESG-1326	B1	1.61	1	1	0.84	0.65	1.39	0.96
11	Asteraceae	*Verbesina greenmanii* Urb.	"tacote amarillo"	ESG-1980	R1	0.57	6	2	0.21	2.73	2.27	1.74
12	Berberidaceae	*Berberis lanceolata* Benth.		ESG-2181	R4	0.22	1	1	0.06	1.85	2.86	1.59

No.	Family	Species	Common name / Morphospecies	Voucher specimen	Sample	DM	DN	FR	RDM	RDN	RFR	SIV
13	Betulaceae	*Carpinus tropicalis* (Donn. Sm.) Lundell	“margarito”	ESG-1552	B2	40.51	8	3	9.84	5.97	3.90	6.57
					B3	94.58	4	3	14.84	8.16	7.69	10.23
					B4	51.84	5	4	19.56	5.15	10.00	11.57
					R2	29.15	10	4	14.84	17.86	16.00	16.23
					R3	52.64	2	2	20.12	2.38	5.13	9.21
					R4	57.43	6	4	15.05	11.11	11.43	12.53
					R5	0.67	3	3	0.22	6.12	9.68	5.34
14	Burseraceae	*Bursera simaruba* (L.) Sarg.	“cuajiote”	ESG-1314	B1	1.83	5	2	0.95	3.25	2.78	2.33
					R1	1.06	2	1	0.40	0.91	1.14	0.81
15	Celastraceae	*Perrottetia longistylis* Rose	“alacrancillo”	ESG-1644	B3	19.57	3	2	3.07	6.12	5.13	4.77
16	Chloranthaceae	*Hedyosmum mexicanum* C. Cordem.	“achoque de ciénega”	ESG-1639	B3	0.20	1	1	0.03	2.04	2.56	1.55
17	Clethraceae	*Clethra lanata* M. Martens & Galeotti	“jaboncillo [hoja angosta]”	ESG-1538	R1	14.70	6	3	5.54	2.73	3.41	3.89
					R2	3.43	1	1	1.75	1.79	4.00	2.51
					R3	0.06	1	1	0.02	1.19	2.56	1.26
					R4	18.30	2	2	4.80	3.70	5.71	4.74
					R5	0.46	3	3	0.15	6.12	9.68	5.32
18	Clethraceae	*Clethra rosei* Britton	“jaboncillo”	ESG-1311	B1	7.74	1	1	4.03	0.65	1.39	2.02
					B4	83.32	1	1	31.44	1.03	2.50	11.66
19	Clusiaceae	*Clusia salvinii* Donn. Sm.	“siempreviva”	ESG-1260	B1	12.02	9	6	6.26	5.84	8.33	6.81
					B2	1.34	7	2	0.32	5.22	2.60	2.72
					B4	0.75	1	1	0.28	1.03	2.50	1.27
					R1	0.18	1	1	0.07	0.45	1.14	0.55
20	Cornaceae	*Cornus disciflora* DC.	“cenicillo”	ESG-1249	R4	1.91	1	1	0.50	1.85	2.86	1.74
					R5	0.84	1	1	0.28	2.04	3.23	1.85
21	Ericaceae	*Arbutus xalapensis* Kunth	“madroño”	ESG-1950	R5	18.07	2	2	5.98	4.08	6.45	5.50
22	Euphorbiaceae	[2]*Cnidoscolus* sp. 1	“chicle”		B2	0.99	1	1	0.24	0.75	1.30	0.76
23	Euphorbiaceae	*Gymnanthes riparia* (Schltdl.) Klotzsch		ESG-1959	B2	0.79	1	1	0.19	0.75	1.30	0.75

No.	Family	Species	Common name / Morphospecies	Voucher specimen	Sample	DM	DN	FR	RDM	RDN	RFR	SIV
24	Euphorbiaceae	*Sapium lateriflorum* Hemsl.	"higuerilla"	ESG-1245	B1	0.07	1	1	0.04	0.65	1.39	0.69
					B2	6.64	2	2	1.61	1.49	2.60	1.90
					R1	2.75	3	3	1.04	1.36	3.41	1.94
25	Euphorbiaceae	*Sebastiania jaliscensis* McVaugh	"lechosilla"	ESG-1617	B2	10.73	30	7	2.61	22.39	9.09	11.36
					B3	3.12	10	5	0.49	20.41	12.82	11.24
					B4	43.02	59	9	16.23	60.82	22.50	33.19
					R2	12.13	19	5	6.17	33.93	20.00	20.03
					R3	9.16	35	8	3.50	41.67	20.51	21.89
					R4	0.06	1	1	0.02	1.85	2.86	1.58
					R5	0.23	2	2	0.08	4.08	6.45	3.54
26	Fagaceae	*Quercus elliptica* Née	"encino colorado"	ESG-1530	R3	36.10	1	1	13.80	1.19	2.56	5.85
					R4	18.32	1	1	4.80	1.85	2.86	3.17
					R5	44.33	6	3	14.67	12.24	9.68	12.20
27	Fagaceae	*Quercus scytophylla* Liebm.	"encino rosillo"	ESG-1553	B4	28.23	2	1	10.65	2.06	2.50	5.07
					R1	88.74	5	4	33.42	2.27	4.55	13.41
					R2	115.99	14	6	59.04	25.00	24.00	36.01
					R3	115.11	7	3	44.00	8.33	7.69	20.01
					R4	199.87	11	7	52.39	20.37	20.00	30.92
					R5	225.37	17	7	74.57	34.69	22.58	43.95
28	Fagaceae	*Quercus uxoris* McVaugh	"encino cascarón"	ESG-1309	B1	24.87	13	5	12.95	8.44	6.94	9.44
					B2	132.15	3	3	32.11	2.24	3.90	12.75
					B3	100.99	3	2	15.84	6.12	5.13	9.03
					B4	15.46	2	2	5.83	2.06	5.00	4.30
					R1	19.34	9	5	7.28	4.09	5.68	5.69
					R3	0.06	1	1	0.02	1.19	2.56	1.26
					R4	27.48	2	2	7.20	3.70	5.71	5.54
29	Fagaceae	*Quercus xalapensis* Bonpl.	"encino saucillo"	ESG-1539	B3	55.55	1	1	8.71	2.04	2.56	4.44
					B4	2.91	1	1	1.10	1.03	2.50	1.54
					R2	32.37	1	1	16.48	1.79	4.00	7.42
					R3	16.98	1	1	6.49	1.19	2.56	3.42
30	Icacinaceae	*Calatola laevigata* Standl.		ESG-1955	B2	0.05	1	1	0.01	0.75	1.30	0.69

No.	Family	Species	Common name / Morphospecies	Voucher specimen	Sample	DM	DN	FR	RDM	RDN	RFR	SIV
31	Juglandaceae	*Juglans olanchana* var. *standleyi* W.E. Manning	"nogal"	ESG-2408	B2	23.59	1	1	5.73	0.75	1.30	2.59
32	Lauraceae	[3]*Nectandra* aff. *salicifolia* (Kunth) Nees	"carretero"	ESG-1425	R1	0.29	2	2	0.11	0.91	2.27	1.10
33	Lauraceae	[2]*Nectandra* sp. 1	"ondulado correoso"	ESG-1964	B2	0.09	1	1	0.02	0.75	1.30	0.69
34	Lauraceae	*Persea hintonii* C.K. Allen	"laurelillo"	ESG-1323	B1	0.15	2	2	0.08	1.30	2.78	1.39
					B2	26.73	4	3	6.49	2.99	3.90	4.46
					B3	31.49	2	2	4.94	4.08	5.13	4.72
					B4	1.68	11	7	0.63	11.34	17.50	9.82
					R2	0.62	1	1	0.32	1.79	4.00	2.03
					R3	0.95	6	3	0.36	7.14	7.69	5.07
					R5	2.26	5	1	0.75	10.20	3.23	4.73
35	Lauraceae	[2]*Persea* sp. 1	"cola de choncho"	ESG-1442	R1	0.24	3	3	0.09	1.36	3.41	1.62
36	Leguminosae	*Calliandra houstoniana* (Mill.) Standl.	"barba de viejo"	ESG-1646	B4	0.11	1	1	0.04	1.03	2.50	1.19
37	Leguminosae	*Calliandra laevis* Rose	"gallinero"	ESG-1307	B1	0.16	1	1	0.08	0.65	1.39	0.71
38	Leguminosae	*Canavalia hirsutissima* J.D. Sauer	"frijolillo"	ESG-1324	B1	1.08	7	5	0.56	4.55	6.94	4.02
					R1	0.60	4	4	0.23	1.82	4.55	2.20
					R4	0.13	1	1	0.03	1.85	2.86	1.58
39	Leguminosae	*Dalea leucostachys* var. *eysenhardtioides* (Hemsl.) Barneby	"cuernillo de venado"	ESG-1925	B3	0.38	1	1	0.06	2.04	2.56	1.56
40	Leguminosae	*Erythrina flabelliformis* Kearney	"colorín"	ESG-1641	B2	0.33	1	1	0.08	0.75	1.30	0.71
					B3	0.10	1	1	0.02	2.04	2.56	1.54
41	Leguminosae	[4]*Inga micheliana* Harms		ESG-1647	B3	5.31	2	2	0.83	4.08	5.13	3.35
42	Leguminosae	*Inga vera* ssp. *eriocarpa* (Benth.) Jorge León	"churin"	ESG-1318	B1	3.92	2	2	2.04	1.30	2.78	2.04
					B2	42.48	10	7	10.32	7.46	9.09	8.96
					B4	4.23	1	1	1.60	1.03	2.50	1.71
					R1	18.75	20	9	7.06	9.09	10.23	8.79
					R3	3.61	2	2	1.38	2.38	5.13	2.96
					R4	32.18	4	2	8.44	7.41	5.71	7.19

No.	Family	Species	Common name / Morphospecies	Voucher specimen	Sample	DM	DN	FR	RDM	RDN	RFR	SIV
43	Leguminosae	[2]*Lonchocarpus* sp. 1	"cuero de vaca"	ESG-1312	B1	42.54	11	5	22.14	7.14	6.94	12.08
					R1	12.35	3	3	4.65	1.36	3.41	3.14
44	Malpighiaceae	*Galphimia glauca* Cav.	"margarita"	ESG-1410	R3	0.10	1	1	0.04	1.19	2.56	1.26
45	Malvaceae	*Malvaviscus arboreus* Cav.	"monaguillo"		B2	0.05	1	1	0.01	0.75	1.30	0.69
46	Melastomataceae	*Conostegia xalapensis* (Bonpl.) D. Don ex DC.	"cerezo" "cerecillo"	ESG-2187b	B1	0.74	2	1	0.39	1.30	1.39	1.02
					R1	1.63	6	3	0.61	2.73	3.41	2.25
					R3	0.25	2	2	0.10	2.38	5.13	2.53
47	Melastomataceae	*Miconia glaberrima* (Schltdl.) Naudin	"cerezo"	ESG-1936	B2	0.70	2	2	0.17	1.49	2.60	1.42
					B3	0.11	1	1	0.02	2.04	2.56	1.54
					R1	2.27	7	4	0.86	3.18	4.55	2.86
					R2	2.15	6	4	1.09	10.71	16.00	9.27
					R3	0.58	2	2	0.22	2.38	5.13	2.58
					R4	2.24	11	5	0.59	20.37	14.29	11.75
					R5	9.13	7	6	3.02	14.29	19.35	12.22
48	Meliaceae	*Cedrela odorata* L.	"cedro rojo"		B2	3.98	1	1	0.97	0.75	1.30	1.00
					B3	0.05	1	1	0.01	2.04	2.56	1.54
					B4	19.95	1	1	7.53	1.03	2.50	3.69
49	Meliaceae	*Guarea glabra* Vahl	"cabo de hacha"	ESG-1405	B1	0.48	4	3	0.25	2.60	4.17	2.34
					B2	6.21	11	7	1.51	8.21	9.09	6.27
					B3	1.27	4	3	0.20	8.16	7.69	5.35
					B4	0.35	2	2	0.13	2.06	5.00	2.40
					R1	0.11	1	1	0.04	0.45	1.14	0.54
					R3	0.10	1	1	0.04	1.19	2.56	1.26
50	Meliaceae	*Trichilia havanensis* Jacq.	"cedrillo blanco"	ESG-1528	B1	0.92	1	1	0.48	0.65	1.39	0.84
					B2	18.35	5	3	4.46	3.73	3.90	4.03
					B3	14.19	5	5	2.23	10.20	12.82	8.42
					R3	0.40	1	1	0.15	1.19	2.56	1.30
51	Moraceae	[3]*Ficus* aff. *pertusa* L. f.	"camichín"	ESG-1674	R1	0.37	1	1	0.14	0.45	1.14	0.58

No.	Family	Species	Common name / Morphospecies	Voucher specimen	Sample	DM	DN	FR	RDM	RDN	RFR	SIV
52		*Ficus velutina* Humb. & Bonpl. ex Willd.	“higuera”	ESG-1426	B3	232.89	1	1	36.53	2.04	2.56	13.71
					R1	2.77	2	2	1.04	0.91	2.27	1.41
53	Moraceae	*Trophis racemosa* (L.) Urb.	“palo verde”	ESG-1525	R3	16.15	1	1	6.17	1.19	2.56	3.31
54	Myrsinaceae	*Ardisia compressa* Kunth	“arrayán”	ESG-1555	B1	1.72	17	5	0.89	11.04	6.94	6.29
					B2	0.48	4	2	0.12	2.99	2.60	1.90
					B3	0.72	2	2	0.11	4.08	5.13	3.11
					R1	0.99	10	5	0.37	4.55	5.68	3.53
					R3	1.01	10	3	0.39	11.90	7.69	6.66
55	Myrsinaceae	*Ardisia* sp. 1	“arrayán [morado]”	ESG-2185	R4	2.04	6	2	0.54	11.11	5.71	5.79
56	Myrsinaceae	*Rapanea myricoides* (Schltdl.) Lundell	“carretero [hoja angosta]”	ESG-1435	R1	0.06	1	1	0.02	0.45	1.14	0.54
57	Myrtaceae	*Calyptranthes pallens* var. *mexicana* (Lundell) McVaugh	“guayabillo”	ESG-1678	B1	0.19	3	3	0.10	1.95	4.17	2.07
					B2	3.58	8	3	0.87	5.97	3.90	3.58
					R1	0.08	1	1	0.03	0.45	1.14	0.54
58	Opiliaceae	*Agonandra racemosa* (DC.) Standl.	“suelda”	ESG-1316	B1	3.36	6	3	1.75	3.90	4.17	3.27
					R1	0.07	1	1	0.02	0.45	1.14	0.54
59	Piperaceae	*Piper pseudofuligineum* C. DC.	“achoque [cigarro]”	ESG-1436	R1	0.18	2	2	0.07	0.91	2.27	1.08
60	Piperaceae	*Piper villiramulum* C. DC.	“achoque”	ESG-1638	B2	0.64	5	1	0.15	3.73	1.30	1.73
					B3	0.09	1	1	0.01	2.04	2.56	1.54
					B4	0.26	2	2	0.10	2.06	5.00	2.39
61	Rosaceae	*Photinia parviflora* Cardot	“agrillo”	ESG-2104	B1	0.34	1	1	0.18	0.65	1.39	0.74
					B2	0.18	1	1	0.04	0.75	1.30	0.70
					B4	0.15	1	1	0.06	1.03	2.50	1.20
					R5	0.65	1	1	0.22	2.04	3.23	1.83
62	Rosaceae	*Prunus cortapico* Kerber ex Koehne	“ocás”	ESG-2356	B3	64.75	1	1	10.16	2.04	2.56	4.92
63	Rubiaceae	*Randia armata* (Sw.) DC.	“crucillo de lo frío”	ESG-1264	B1	0.25	2	2	0.13	1.30	2.78	1.40
64	Rubiaceae	*Rondeletia leucophylla* Kunth		ESG-1422	B2	0.44	4	3	0.11	2.99	3.90	2.33
					R4	0.57	1	1	0.15	1.85	2.86	1.62

No.	Family	Species	Common name / Morphospecies	Voucher specimen	Sample	DM	DN	FR	RDM	RDN	RFR	SIV
65	Rutaceae	*Zanthoxylum caribaeum* Lam.	"chicolillo"	ESG-1253	B1	1.25	4	2	0.65	2.60	2.78	2.01
66	Sapotaceae	*Pouteria sapota* (Jacq.) H. E. Moore & Stearn	"huizilacate"	ESG-1643	B2	22.14	2	2	5.38	1.49	2.60	3.16
					B3	2.22	2	1	0.35	4.08	2.56	2.33
67	Smilacaceae	*Smilax moranensis* M. Martens & Galeotti	"coalcomeca"	ESG-1083	B1	0.13	2	1	0.07	1.30	1.39	0.92
68	Solanaceae	*Cestrum tomentosum* L. f.		ESG-1310	B1	0.15	1	1	0.08	0.65	1.39	0.70
69	Solanaceae	*Lycianthes surotatensis* J.L. Gentry	"tomatillo"	ESG-1322	B1	0.06	1	1	0.03	0.65	1.39	0.69
					B3	0.14	1	1	0.02	2.04	2.56	1.54
70	Styracaceae	*Styrax argenteus* C. Presl	"cucharo"	ESG-1413	B1	62.56	44	7	32.56	28.57	9.72	23.62
					R1	73.12	97	10	27.54	44.09	11.36	27.66
					R2	0.19	1	1	0.10	1.79	4.00	1.96
					R3	3.38	6	2	1.29	7.14	5.13	4.52
					R4	1.23	1	1	0.32	1.85	2.86	1.68
71	Symplocaceae	*Symplocos citrea* Lex. ex La Llave & Lex.	"agrillo"	ESG-1089	R3	4.71	1	1	1.80	1.19	2.56	1.85
72	Theaceae	*Symplococarpon purpusii* (Brandegee) Kobuski	"zapotillo"	ESG-1558	B1	20.03	5	3	10.43	3.25	4.17	5.95
					B2	65.08	6	5	15.81	4.48	6.49	8.93
					B3	5.64	1	1	0.88	2.04	2.56	1.83
					R1	18.15	7	4	6.83	3.18	4.55	4.85
					R4	15.77	2	2	4.13	3.70	5.71	4.52
					R5	0.17	1	1	0.06	2.04	3.23	1.77
73	Theaceae	*Ternstroemia lineata* DC.		ESG-2182	B2	0.10	1	1	0.02	0.75	1.30	0.69
					R4	3.63	1	1	0.95	1.85	2.86	1.89
74	Tiliaceae	[2]*Heliocarpus* aff. *palmeri* S. Watson	"zicuito"	ESG-1966	B2	0.45	1	1	0.11	0.75	1.30	0.72
75	Urticaceae	*Gyrotaenia myriocarpa* Griseb.	"ortiga lisa"	ESG-1965	B2	0.21	1	1	0.05	0.75	1.30	0.70
76	Urticaceae	*Phenax hirtus* (Sw.) Wedd.	"ortiga lisa"	ESG-825	B2	0.44	2	1	0.11	1.49	1.30	0.97
					B4	0.07	1	1	0.03	1.03	2.50	1.19
77	Urticaceae	*Urera caracasana* (Jacq.) Griseb.	"ortiga"	ESG-1268	B1	0.51	1	1	0.27	0.65	1.39	0.77
					B2	0.27	1	1	0.07	0.75	1.30	0.70

No.	Family	Species	Common name / Morphospecies	Voucher specimen	Sample	DM	DN	FR	RDM	RDN	RFR	SIV
78	Verbenaceae	*Citharexylum glabrum* (S.Watson) Greenm.	"amargosilla"	ESG-1565	B1	0.79	1	1	0.41	0.65	1.39	0.82
79	Verbenaceae	*Lantana camara* L.	"siete colores"		R1	0.14	1	1	0.05	0.45	1.14	0.55
80	Vitaceae	*Parthenocissus quinquefolia* (L.) Planch.	"bembéricua"		B2	0.33	2	2	0.08	1.49	2.60	1.39
81	Vitaceae	*Vitis tiliifolia* Humb. & Bonpl. ex Roem. & Schult.	"uva de agua"	ESG-1557	B2	1.19	2	2	0.29	1.49	2.60	1.46
					B4	0.17	1	1	0.07	1.03	2.50	1.20
					R1	1.87	8	3	0.71	3.64	3.41	2.58

DM = Dominance (basal area – dm^2); DN = Density of individuals; FR = Frequency (proportion of species in subplots); RDM = Relative Dominance; RDN = Relative Density; RFR = Relative Frequency; SIV = Synthetic Importance Values = (relative basal area + relative frequency + relative density) / 3. R1-R5 = Ridge samples; B1-B4 = Bottomland samples (for sample site descriptions see Table 3 in Chapter 2).

[1] A woody liana with corky bark, elliptic leaves and ellipsoid, smooth follicles. [2] Lack of fertile material prevented complete determination. [3] Currently being studied; possibly an undescribed species. [4] Known in the literature as *Inga hintonii*.

CHAPTER 4

Rediscovery of *Pedilanthus coalcomanensis* (Euphorbiaceae), a threatened endemic Mexican species[1]

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[1] Lomelí-S. J. A. and E. Sahagún-G. 2002. American Journal of Botany 89(9): 1485-1490.

Keywords: biodiversity; Coalcomán, Michoacán, western México; conservation; extinction; George B. Hinton; *Pedilanthus coalcomanensis*; Euphorbiaceae.

ABSTRACT

Pedilanthus coalcomanensis was described from specimens collected by George B. Hinton in 1941 but was not collected again until 1999, when we found it in a tropical deciduous forest near Tehuantepec, in Chinicuila, Michoacán, Mexico. After analyzing Hinton's original collection notes, we concluded that this is the type locality. Based on the reduced geographic distribution presently known for this species (11 km^2), the level of disturbance of its habitat and the use of the method for the assessment of extinction risk in Mexican wild species (MER), we propose that *P. coalcomanensis* be covered by the appropriate Mexican legislation as a threatened species and be included in the Red List of Threatened Plants of the International Union for the Conservation of Nature. Our results help justify and delimit a local biosphere reserve in northwestern Michoacán, an area that is considered a center of endemism and that has largely been deforested. Our findings have implications for research on other historical specimens collected by Hinton in this region.

INTRODUCTION

Mexico is a center of biodiversity. With about 10% of all vascular plant species in the world, it ranks third among megadiverse countries (Mittermeier and Mittermeier, 1992). Nearly 30 000 species of plants are native in Mexico (Rzedowski and Equihua, 1987) and many are endemic (Rzedowski, 1973). The Pacific slope of Mexico has a particularly diverse flora (Rzedowski, 1993). The sierra of Coalcomán in Michoacán, where *Pedilanthus coalcomanensis* Croizat was rediscovered, is located in this highly biodiverse strip of land. This rugged and isolated mountain range has recently been granted conservation priority by the Federal Commission for Conservation and Use of Biodiversity in Mexico (CONABIO) (Arriaga-Cabrera et al., 2000). Unfortunately, a high rate of deforestation in the Coalcomán region was noted about 60 yr ago (Hinton and Rzedowski, 1975). Casual inspection today easily reveals that as much as 50% of the area is now pasture for cattle or is used for other agricultural endeavors.

Information on the location of endemic species is urgently needed to help delimit an area for protection of what may remain. The information reported here is timely because so far no biosphere reserves exist in northwestern Michoacán. And the fact that *P. coalcomanensis* is not yet extinct lends support to local conservation efforts.

The Euphorbiaceae, with nearly 8000 species (Jensen, Vogel-Bauer and Nitschke, 1994) and a cosmopolitan distribution, is divided into five subfamilies. Of these, the Euphorbioideae include the tribe Euphorbieae, in which *Pedilanthus* is classified. This tribe is characterized by a unique inflorescence, the cyathium (Webster, 1994). *Pedilanthus*, a genus of about 14 species, is further distinguished by having a spurred zygomorphic involucre (Dressler, 1957).

Knowledge of the collection sites of historical specimens of *P. coalcomanensis* is important because it has implications for research on the itinerary followed by Hinton in this region, where he collected other specimens that are nomenclaturally critical. However, after Hinton no other collectors found *P. coalcomanensis* again until we rediscovered it in July 1999.

The rediscovered population of *P. coalcomanensis* is located in tropical deciduous forest near Tehuantepec, in Chinicuila, northwestern Michoacán. It is possible that the population we documented is the same one that Hinton found in 1941.

Based on the reduced geographic distribution of *P. coalcomanensis*, the high propensity for the forests in that region to be cut and the results of the assessment of extinction risk in Mexican wild species (MER), we have concluded that this species is threatened with extinction.

The objectives of this paper are to document the rediscovery of a population of *P. coalcomanensis*, to provide its precise geographic location, to report the vegetation where it grows and to estimate the species' vulnerability to extinction.

MATERIALS AND METHODS

We reviewed the specimens of *P. coalcomanensis* that the curators of the following herbaria provided us: C, F, G, GH, MEXU, MICH, NY, P, RSA, S, US and W (herbarium abbreviations according to Holmgren, Holmgren and Barnett, 1990). Seven fieldwork trips were conducted in Aquila, Chinicuila and Coalcomán, in northwestern Michoacán, between May 1998 and June 2001. The plant material collected during these trips was deposited in the herbarium of the Universidad Autónoma de Guadalajara (GUADA).

To determine whether *P. coalcomanensis* is present in other parts of Mexico, we consulted several local herbaria (CIDIIR, CIMI, CREG, EBUM, FCME, IBUG, IEB, OAX and XAL; herbarium abbreviations according to Holmgren, Holmgren and Barnett, 1990), but no additional specimens were found. We also visited various regions in the vicinity of El Naranjillo (Fig. 1) in search of this species.

To delimit the distribution area, we used a global positioning system device (model 12XL, Garmin, Olathe, Kansas, USA) to record the geographic coordinates for the locations where *P. coalcomanensis* was found. We used two topographic maps (SPP, 1988, 1989) and a polar compensation planimeter (model KP-27 zero-setting device with optical tracer, Koizumi, Japan) to estimate the surface area where this species grows.

To determine the vulnerability of *P. coalcomanensis*, we applied a recently developed method for the assessment of the extinction risk in Mexican wild species (MER)(SEMARNAT, 2002). The method entails the evaluation of the following criteria: (1) distribution range of the taxon in Mexico, (2) condition of the habitat for favoring or limiting the permanence of the taxon, (3) intrinsic biological vulnerability of the taxon and (4) impact of human activities on the taxon. The evaluation of each criterion is then scored and the sum of scores is compared with a scale. A taxon with a score of 12-14 is considered endangered and one with a score of 10-12 is considered threatened. Published results of MER evaluations have legal implications in Mexico because they are currently used to propose the inclusion, exclusion, or change of status of a taxon in the lists of taxa under the legal protection of NOM-059-ECOL.

RESULTS

In May 1998 we first visited the only known location recorded by George B. Hinton for *P. coalcomanensis*: Sierra Naranjillo. From Villa Victoria, the capital of Chinicuila, we went to the small village El Naranjillo, where the residents told us the exact location of Sierra Naranjillo. Using sketches and features obtained from the botanical specimens we had previously examined, we asked about "candelilla," the local name Hinton recorded for *P. coalcomanensis*. However, although the local people associate this common name with other euphorbiaceous plants with white latex, such as *P. palmeri* Millsp. or *Cnidoscolus* spp., they seemed not to know *P. coalcomanensis*. This reaction initially made us think that the species was either extremely rare or already extinct.

We explored a number of sites in Sierra Naranjillo and its vicinity without success. Then in July 1999 we finally located a population near Tehuantepec, in Chinicuila, growing in tropical deciduous forest. Because the plants were vegetative, we took only a couple for cultivation in the botanic garden, where they bloomed in November that same year. We visited this population again during the winter-spring of the following two years to prepare herbarium specimens and to take photographs and field notes. The location of this population, is outside what local residents know as Sierra Naranjillo, although it is adjacent.

After exploring an extensive area in search of this elusive species, we believe that this population is the same one found by Hinton because we found plants growing at the same elevations (1440-1600 m) indicated on Hinton's plant labels, beside the old mule road that joined Coalcomán and Tehuantepec, next to a seasonal creek, near Los Puente [Las Fuentes] (Fig. 1) a former rest stop for travelers; the vegetation of what we take to be the type locality is taller than elsewhere, more suggestive of the "woods" referred by Hinton; there we found the largest plants of *P. coalcomanensis*, up to 9 m tall. (Hinton's potential type collection site is marked with an empty square in Fig. 1). On the other hand, most of Sierra Naranjillo in the modern sense lies below the elevation where Hinton's type specimen was collected and pine and oak forests cover most of the highest elevations in this Sierra (i.e., Canoas, Fig. 1), habitats where *P. coalcomanensis* has not yet been found. We believe that Hinton used the name "Sierra Naranjillo" for a broader region than currently delimited.

The application of MER methodology (Table 1) to evaluate the vulnerability of *P. coalcomanensis* produced the following results. (1) Distribution of the species is very restricted (score = 4) because its range is less than 5% of Mexican territory. (2) Although its habitat does not seem hostile, given the level of reproduction observed, we regard it as intermediate or limiting (score = 2), rather than favorable, because seemingly suitable habitat extends far beyond the small area where the species is restricted. Further studies are necessary to elucidate the factors that limit the distribution of this taxon. They appear to be environmental, given the altitudinal limit to the species' dispersal. (3) The intrinsic biological vulnerability of the taxon is low (score = 1), as evidenced by the high recruitment level. *Pedilanthus coalcomanensis* appears to reproduce well both by seed and by subterranean tubercles in situ and is easily cultivated ex situ. (4) Human activities greatly affect the species. It is cut and burned with the rest of the vegetation in areas used for crops or cattle grazing. However, it seems to benefit somewhat from occasional disturbance. Also, older trees are able to survive in rocky mounds that are of little use to farmers. We therefore gave it an intermediate-impact score of 3.

The scores for *P. coalcomanensis* total 10, which according to the MER vulnerability scale means the species is threatened.

Our observations of fresh material indicated the need to reevaluate details that had not been previously available. An updated description of *P. coalcomanensis* is available at (http://ajbsupp.botany.org/v89).

Horticultural uses

This species has potential as an ornamental plant because of its showy scarlet bracts. However, despite the spectacular color displayed at flowering time, residents of the area where it occurs apparently do not know this taxon. Flowering is conspicuous owing to the deciduous habit of the shrubs. Furthermore, flowering and fruiting last six months, spanning the winter, when there is much demand for red flowers. No other potential uses are known.

Phenology

Presence of foliage: May to November or up to January in specimens growing in shaded spots protected by the forest canopy; flowering: November to early June; fruiting: March to early June.

Distribution

A strict endemic in Chinicuila, Michoacán, in western Mexico. It is distributed over approximately 11 km^2, near the municipal limit with Coalcomán; at present it is known only from the locations cited in this report. Sierra Naranjillo, which George B. Hinton identified as the site of his collections, is located in Chinicuila (Fig. 1).

Pollination

Pedilanthus coalcomanensis appears to be pollinated by hummingbirds (Dressler, 1957). Also, we observed that black wasps commonly pierce cyathia to rob nectar, leaving characteristic scars in the medial lobes of the spur (Fig. 2). The wasps do not serve a pollination function, as the flowers are out of their reach; but wasps may be effective pollinators of other species of *Pedilanthus* (Sahagún and Lomelí, 1997).

Habitat

Tropical deciduous forest (see Rzedowski, 1983) near the ecotone with oak and pine forest, on areas with calcareous rocks. The tropical deciduous forest where this species develops appears to have relatively high humidity: there is an abundance of lichens and other epiphytes. Other species growing in the area are *Agave gypsophila* Gentry, *Calliandra laevis* Rose, *Cattleya aurantiaca* (Batem.) P. N. Don, *Clusia salvinii* Donn. Sm., *Hexadesmia sessilis* Reichb. f., *Laelia albida* Batem. ex Lindl., *Lysiloma acapulcense* (Kunth) Benth., *Meiracyllium wendlandii* Reichb. f., *Neobuxbaumia* sp., *Nyctocereus serpentinus* (Lag. et Rodr.) Britt. et Rose, *Oncidium cebolleta* (Jacq.) Sw., *Oreopanax peltatus* Linden ex Regel, *Pseudobombax* sp., *Psidium sartorianum* (Berg) Niedenzu and *Pittocaulon* (*Senecio*) *hintonii* H. Rob. et Brett. Elevation: 1400-1780 m.

DISCUSSION

Pedilanthus coalcomanensis was described by Leon Croizat in 1943 on the basis of specimens collected 2 yr earlier in northwestern Michoacán by George B. Hinton. McVaugh (1972) noted that some of Hinton's collection sites are difficult to locate on modern maps, because Hinton referred his collections to "distritos," large political subdivisions no longer used in Mexico. McVaugh also pointed out that in western Michoacán, most of Hinton's collections are referred to distrito Coalcomán, but they may actually come from one of various modern municipalities, i.e., Coalcomán, Chinicuila, Coahuayana, or Aquila, (Fig. 1) an area that totals approximately 6500 km^2. For this reason, McVaugh warned that the references to Coalcomán in the literature citing Hinton's collections must be considered with caution.

On his herbarium labels, Hinton referred to the habitat where *P. coalcomanensis* grows as "woods," failing to mention the conspicuous calcareous rocks. This imprecision complicated our search, as we did not know where to look for the species. Because the rocks have razor-sharp edges and at times make access difficult, areas with many of them are little used for crops or cattle pastures.

Additionally, Hinton's collection labels stated that *P. coalcomanensis* is a tree 5-7 m high. However, *P. coalcomanensis* trees at such heights are found only in few, very rocky places and also in humid ravines. By contrast, smaller shrubby plants, 1.5-2 m high, are relatively abundant on areas that are more open and have fewer rocks and less primary vegetation. Vegetation in such areas, we were told, had been cut and burned in the past. These smaller plants represent new growth produced from tubercles or from seed that germinated during the regeneration of the vegetation, favored by the new open space.

Croizat (1943) and Dressler (1957, p. 113) stated that the involucre of *P. coalcomanensis* is red, because they studied only pressed specimens. However, observations of living plants in the field and of cultivated specimens in the botanic garden showed that the cyathia are uniformly green when young, turning red in senescence.

When Dressler (1957) wrote his revision of the genus *Pedilanthus*, *P. coalcomanensis* was known only from Sierra Naranjillo. In the 1950s this region was inaccessible and had been explored botanically only by Hinton (Hinton and Rzedowski, 1975). Hinton collected this species at various elevations on five occasions, yet always referred them to the same location: Sierra Naranjillo. Dressler (1957, p. 114) thus concluded that when the area was better explored, additional collections would extend the species' distribution range. But the northwestern part of Michoacán has remained little explored by botanists mainly because the roads are prone to flooding and landslides and because of criminal activity in the area, including the cultivation of illegal plants, which has resulted in a large military presence. Not surprisingly, *P. coalcomanensis* remained uncollected until 1999, when we explored northwestern Michoacán.

Guerrero-Campanur (1985) compiled a checklist of the flora of Aquila that grows at elevations of 0-1100 m. Aquila neighbors Chinicuila and borders the Pacific ocean. Guerrero-Campanur reported only one species of *Pedilanthus*, *P. palmeri* Millsp. (*B. Guerrero C. 805* XAL!). On the basis of that report and our exploration of rocky areas in Aquila, we conclude that *P. coalcomanensis* is absent there. We also visited Mexican herbaria that were likely to have specimens and found none.

These findings plus the MER results lead us to believe that *P. coalcomanensis* is a narrow endemic species, growing only in a single small region and therefore vulnerable to extinction. We therefore propose its inclusion in the Mexican legislation (NOM-059-ECOL) with the status of threatened species. We also propose its inclusion in the Red List of Threatened Plants of the International Union for the Conservation of Nature (Walter and Gillett, 1997).

But not only *P. coalcomanensis* needs protection. By the 1930s Hinton already realized the threat to forests in northwestern Michoacán and other Mexican states from nomadic agriculture (Hinton and Rzedowski, 1975, p. 13). We emphatically agree with this observation. We have seen vast extensions of forest devastated by slash-and-burn agriculture, by unplanned forest exploitation and by the establishment of pasture for cattle. The need for protection of and research on what remains of the old-growth forests in this isolated region is critical.

Dressler (1957) suggests that the genus *Pedilanthus* may have originated on the Pacific slope of tropical Mexico, since the beginning of the Tertiary. A greater precision in the timing of this event is complicated by the absence of fossil records.

The Oaxaca region is a good candidate as the center of diversification of the genus, because it contains a high diversity of species of *Pedilanthus*, including some of the primitive moisture-loving arborescent ones. One such woody species is *P. pulchellus* Dressler, which is closely related to *P. coalcomanensis* (Dressler, 1957) and grows in tropical subdeciduous forest on the Pacific slope region of Oaxaca.

Pedilanthus pulchellus and *P. coalcomanensis* are known from isolated populations about 800 km apart. Judging from observations of their habitat, both species appear to be adapted to relatively high humidity conditions. This and the narrow altitudinal restriction of both species suggests that dispersion of *P. coalcomanensis* or its ancestor might have required a more humid paleoclimate than modern conditions.

Graham (1973) has presented evidence that a cooler, more humid climate was present in southern Mexico during the Miocene, which allowed the migration of temperate trees from North America to the south into Mexico as far as Chiapas. Such large vegetation changes and especially the global warming that marked the transition of the Miocene into the Pliocene, created an opportunity for many tropical plants to migrate and occupy the land freed by the receding temperate vegetation.

Pedilanthus pollen, if found among Miocene-Pliocene microfossils, would indicate that this genus might have spread at this time, but the mostly zoophilous flora that grows in areas with warm climate produce small amounts of pollen and there are a number of problems associated with its fossilization (Palacios and Rzedowski, 1993). Not surprisingly, the few available palaeobotanical reports provide no record of *Pedilanthus* pollen or other materials (Rzedowski and Palacios, 1977; Graham 1987; Palacios and Rzedowski, 1993; González-Medrano, 1996; Martínez-Hernández and Ramírez-Arriaga, 1996). However, Graham (1987) reports pollen that he tentatively attributed to *Tithymalus* from upper Miocene deposits of Paraje Solo in Veracruz, which he (Graham, 1993) later rectified as Pliocene. This report warrants further study to verify whether this pollen may be assigned to *Pedilanthus* or a closely related genus. In the absence of more direct information, our conclusions regarding the phytogeography of *P. coalcomanensis* must remain tentative.

APPENDIX

Updated description of *Pedilanthus coalcomanensis.*

Pedilanthus coalcomanensis Croizat. J. Wash. Acad. Sci. 33: 19. 1943. Fig. 2.

Type: México, Michoacán [municipio of Chinicuila]. Sierra Naranjillo, distr. Coalcomán, alt. 1550 m, tree 5 m, hab. woods, 3 Nov. 1941, *G. B. Hinton 15765* (holotype: US 1808071; isotypes: G!, NY!, P!, US!).

Local name: Candelilla.

Deciduous monopodial shrub or tree up to 9 m high, with white latex and tubercles able to generate new basal shoots. Main trunk gray, glabrous, smooth, and up to 9.5 cm diameter at breast height, with branches of up to fifth order; young branches light green, pubescent or tomentose, the tomentum on new shoots brown or pink (the latter seen only in fresh material), but whitish on previous year's shoots and flowering stalks, the nodes 1-4 cm apart; axilar buds with whitish vestiture. Leaves with inconspicuous stipules; petiole subterete, 4-10 mm long and 2-5 mm diameter, furrowed above, with dense whitish or brown tomentum; lamina elliptic to oblong or ovate, 5-17 cm long and 2.5-9.5 cm wide, membranous, dull green in pressed specimens or light green turning reddish pink with senescence in fresh material, margin entire, base of lamina obtuse, rounded or slightly cordate, apex of lamina acute, upper surface pilose or pilosulose, with 17-23 lateral conspicuous nerves, lower surface tomentose with yellowish-white tomentum, turning brown with age, midrib terete, most evident in the proximal third of its length, not carinate beneath. Dichasia terminal, internodes 0.8-3.6 cm long, the scape deep pink, tomentose, the tomentum yellowish white. Bracts deep pink when fresh, scarlet when pressed, long-ovate, 1.5-3 cm long and 0.9-1.8 cm wide, persistent, acuminate, acute, oblique at base or apiculate at apex, pilosulose adaxially, pilose or tomentose abaxially, the tomentum whitish (canescent). Cyathia pedunculate, the peduncle green to pinkish when fresh, reddish when dry, 4-14 mm long, filiform to terete, pilose or tomentose, canescent; involucre glabrous, green when young, becoming scarlet in senescence; spur glabrous, green when young, scarlet when pressed or in senescence, projecting 7-15 mm from involucral tube, 4 mm wide at apex, involucral tube 8-15 mm long, connate at base up to two-thirds of its length and with conspicuous mentum; main involucral lobes 15-20 mm long, green when young or red in senescence, foliaceous, acute at apex, glabrous outside, canescent inside on distal half and ciliate on margin, medial spur lobes green when young, red in senescence or when pressed, 7-12 mm long, 2-3 mm wide at base and ca. 1 mm wide at apex, glabrous outside and connate on central margin, with a 5-6 mm long suture, pale yellowish inside, where glabrous on proximal half, distal half with dense yellowish tomentum and a transversal callus 2-3 mm below apex, margin canescent-tomentose except at apex; accessory involucral lobes 6-15 mm long and somewhat > 1 mm wide, green when fresh or red when pressed and in senescence, canescent-tomentose, connate, lateral accessory involucral lobes with their proximal part glabrous inside, distal part with dense pale yellowish tomentum, acuminate at apex, adnate to main involucral lobes for almost their whole length, median accessory involucral lobe beneath the lateral ones; glands four, ca. 2 mm long, pale yellowish when fresh, lateral glands lenticular to obovoid, medial glands falciform. Staminate flowers 22-37; pedicels yellowish green when young, red in senescence and when pressed, 11-16 mm long, proximal half glabrous, distal half cottony; stamen filaments light to reddish yellow when fresh, 2-4 mm long, glabrous, villous, tomentose or cottony, anthers red when fresh, glabrous or gossypine to arachnoid, ca. 0.5-1 mm long and 1 mm in diameter. Pistillate flower with non elongating pedicel, glabrous or villous, 5-11 mm long and ca. 1.5 mm in diameter, yellowish green when young, reddish in senescence; ovary ovoid, triquetrous in pressed specimens, ca. 2.5 mm long and 2 mm thick, glabrous, light green when fresh, yellowish lines highlighting margin and central vein of carpels; style persistent, 9-11 mm long, red when fresh and in senescence, glabrous or sparsely hirsute in fruit; stigmas 1-2 mm long. Capsule glabrous, green to reddish when fresh, dull yellow to dark brown when pressed, 11-12 mm long and 8-11 mm in diameter, included in involucre because of its non accrescent pedicel, in predehiscence emerging between accessory involucral lobes and moving upward before exploding. Seeds dark brown, 5 mm long and 3.5-4 mm in diameter, concave or truncate basally, acute apically, the raphe brown, extending to the midpoint at base.

Additional specimens examined: MICHOACÁN: Municipio of Chinicuila: Sierra Naranjillo, distr. Coalcomán. *G. B. Hinton 12685* (F, GH, MICH, NY, RSA, S, US); *G. B. Hinton 13733* (G, GH, MICH, NY, RSA, S, US, W); *G. B. Hinton 13734* (C, F, MICH, NY); *G. B. Hinton 15130* (G, GH, MICH, NY, RSA, S, US). Immediately past the crossroad to Tehuantepec, on Aquila-Coalcomán paved road, 18°42'N & 103°18'W, *J. A. Lomelí et al. 3184* (GUADA); *ibid. 3239* (GUADA); Rancho El Tejón, ca. 3 km past the crossroad to Tehuantepec on Aquila-Coalcomán paved road, 18°42'N & 103°17'W, *J. A. Lomelí et al. 3240* (GUADA); ravine ca. 1 km SSW of Los Puente [Las Fuentes], 18°41'N & 103°16'W, *J. A. Lomelí et al. 3465* (GUADA); west of Las Fuentes, near the corral door [Spanish *falsete*], 18°42'N & 103°16'W, *E. Sahagún G. et al. 2270* (GUADA)

LITERATURE CITED

Arriaga-Cabrera, L., J. M. Espinoza-Rodríguez, C. Aguilar-Zúñiga, E. Martínez-Romero, L. Gómez-Mendoza and E. Loa-Loza. 2000. Regiones terrestres prioritarias de México. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, México City, México.

Croizat, L. 1943. *Pedilanthus*. Notes on American Euphorbiaceae. Journal of the Washington Academy of Sciences 33: 19.

Dressler, R. L. 1957. The genus *Pedilanthus* (Euphorbiaceae). Contributions from the Gray Herbarium of Harvard University 182: 1-188.

González-Medrano, F. 1996. Algunos aspectos de la evolución de la vegetación de México. Boletín de la Sociedad Botánica de México 58: 129-136.

Graham, A. 1973. History of the arborescent temperate element in the northern Latin American biota. *In* A. Graham [ed.], 301-314. Vegetation and vegetational history of northern Latin America. Elsevier, New York, USA.

Graham, A. 1987. Tropical American Tertiary floras and paleoenvironments: Mexico, Costa Rica and Panama. American Journal of Botany 74 (10): 1519-1531.

Graham, A. 1993. Historical factors and biological diversity in Mexico. *In* T. P. Ramamoorthy, R. Bye, A. Lot and J. Fa [eds.], 109-127. Biological diversity of Mexico, Oxford University Press, New York, USA.

Guerrero-Campanur, B. 1985. Reconocimiento botánico de Aquila, Michoacán (México). Bachelor's Degree Thesis, Universidad Michoacana de San Nicolás de Hidalgo, Morelia, México.

Hinton, J. and J. Rzedowski. 1975. George B. Hinton, explorador botánico en el sudoeste de México. Anales de la Escuela Nacional de Ciencias Biológicas 21: 1-114.

Holmgren, P. K., N. H. Holmgren and L. C. Barnett [eds.]. 1990. Index herbariorum, part I, The herbaria of the world, 8th ed. New York Botanical Garden, Bronx, New York, USA.

Jensen, U., I. Vogel-Bauer and M. Nitschke. 1994. Leguminlike proteins and the systematics of the Euphorbiaceae. Annals of the Missouri Botanical Garden 81: 160-179.

Martínez-Hernández, E. and E. Ramírez-Arriaga. 1996. Paleocorología de las angiospermas de la flora mexicana durante el Mesozoico y Terciario. Algunas evidencias palinológicas. Boletín de la Sociedad Botánica de México 58: 87-97.

McVaugh, R. 1972. Botanical exploration in Nueva Galicia, Mexico, from 1790 to the present time. Contributions of the University of Michigan Herbarium 9: 205-357.

Mittermeier, R. A. and C. G. Mittermeier. 1992. La importancia de la diversidad biológica de México. *In* J. Sarukhán and R. Dirzo [eds.], México ante los retos de la biodiversidad, 63-73. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, México City, México.

Palacios, R. and J. Rzedowski. 1993. Estudio palinológico de las floras fósiles del Mioceno inferior y principios del Mioceno medio de la región de Pichucalco, Chiapas, México. Acta Botánica Mexicana 24: 1-96.

Rzedowski, J. 1973. Geographical relationships of the flora of Mexican dry regions. *In* A. Graham [ed.], 61-71. Vegetation and vegetational history of northern Latin America, Elsevier, New York, USA.

Rzedowski, J. 1983. Vegetación de México. Limusa, México City, México.

Rzedowski, J. 1993. Diversity and origins of the phanerogamic flora of Mexico. *In* T. P. Ramamoorthy, R. Bye, A. Lot and J. Fa [eds.], 129-144. Biological diversity of Mexico: Origins and distribution, Oxford University Press, New York, USA.

Rzedowski, J. and M. Equihua. 1987. Colección atlas cultural: Flora. Secretaría de Educación Pública, Instituto Nacional de Antropología e Historia and Grupo Editorial Planeta, México City, México.

Rzedowski, J. and R. Palacios. 1977. El bosque de *Engelhardtia* (*Oreomunnea*) *mexicana* en la región de La Chinantla (Oaxaca, México). Una reliqua del Cenozoico. Boletín de la Sociedad Botánica de México 36: 93-123.

Sahagún-Godínez, E. and J. A. Lomelí-Sención. 1997. *Pedilanthus diazlunanus* (Euphorbiaceae): Pollination by hymenopterans in a bird-pollinated genus. American Journal of Botany 84 (11): 1584-1587.

SEMARNAT (Secretaría del Medio Ambiente y Recursos Naturales). 2002. Norma oficial mexicana NOM-059-ECOL-2001. Protección ambiental. Especies nativas de México de flora y fauna silvestres. Categorías de riesgo y especificaciones para su inclusión, exclusión o cambio. Lista de especies en riesgo. Anexo normativo I, método de evaluación del riesgo de extinción de las especies silvestres en México (MER). Diario Oficial de la Federación. México City, México.

SPP (Secretaría de Programación y Presupuesto). 1988. Topographic map, 1:50 000, El Ranchito, Michoacán, E13B65, 2nd printing. México City, México.

SPP (Secretaría de Programación y Presupuesto). 1989. Topographic map, 1:50 000, Tehuantepec, Michoacán, E13B66, 2nd printing. México City, México.

Walter, K. S. and H. J. Gillett. 1997. Red list of threatened plants. World Conservation Union, Gland, Switzerland.

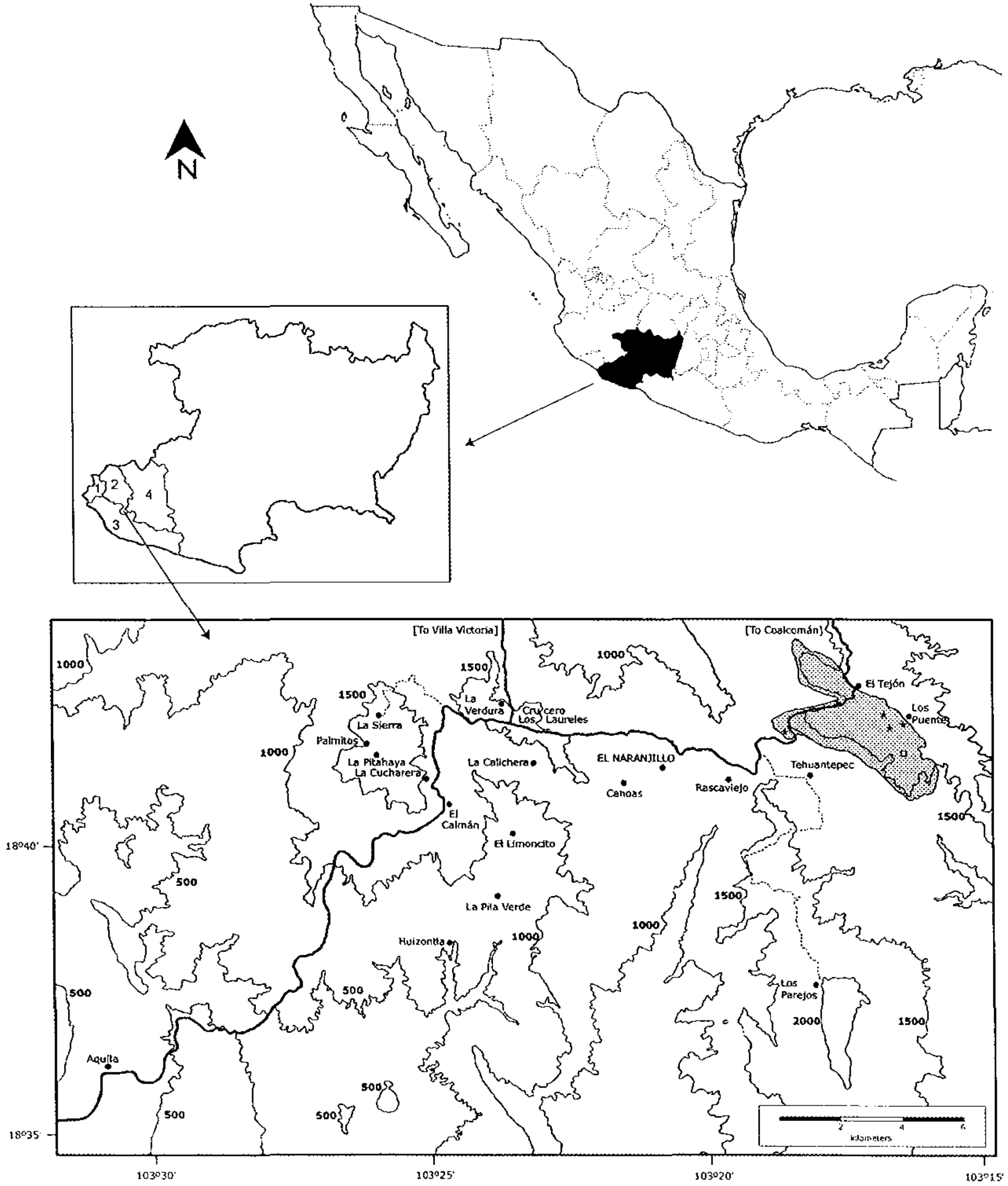
Webster, G. L. 1994. Synopsis of the genera and suprageneric taxa of Euphorbiaceae. Annals of the Missouri Botanical Garden 81: 33-144.

TABLE 1. MER (Method for the evaluation of the risk of extinction of Mexican native species of flora and fauna) criteria and scores used to propose the inclusion, exclusion, or change of status of taxa under the legal protection of NOM-059-ECOL.

Criteria	Evaluations	Score
Distribution range of the taxon in Mexico	<5%	4
	Between 5 and 15%	3
	>15% but <40%	2
	≥40%	1
Condition of the habitat for favoring or limiting the permanence of the taxon	Hostile or very limiting	3
	Intermediate or limiting	2
	Favorable or mildly limiting	1
Intrinsic biological vulnerability of the taxon	High	3
	Intermediate	2
	Low	1
Impact of human activities on the taxon	High	4
	Intermediate	3
	Low	2

FIGURE LEGENDS

Fig. 1. Study site for *Pedilanthus coalcomanensis*. Above right, map of México, with the state of Michoacán highlighted in black. Inset at left, outline of Michoacán showing the current limits of the four municipalities of the former district of Coalcomán: (1) Coahuayana, (2) Chinicuila, (3) Aquila and (4) Coalcomán. Inset at bottom, explored area in the vicinity of El Naranjillo. The shaded region shows the known distribution of *P. coalcomanensis*. star = collection site of *P. coalcomanensis,* rectangle = George B. Hinton's probable type collection site, filled circle = town or named location, thin line = elevation line (in meters), dotted line = dirt road, thick line = paved road.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La Cucharera
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Crucero Los Laureles
El Tejón
Los Puentes
La Calichera
EL NARANJILLO
Canoas
Rascaviejo
Tehuantepec
El Calmán
El Limoncito
La Pila Verde
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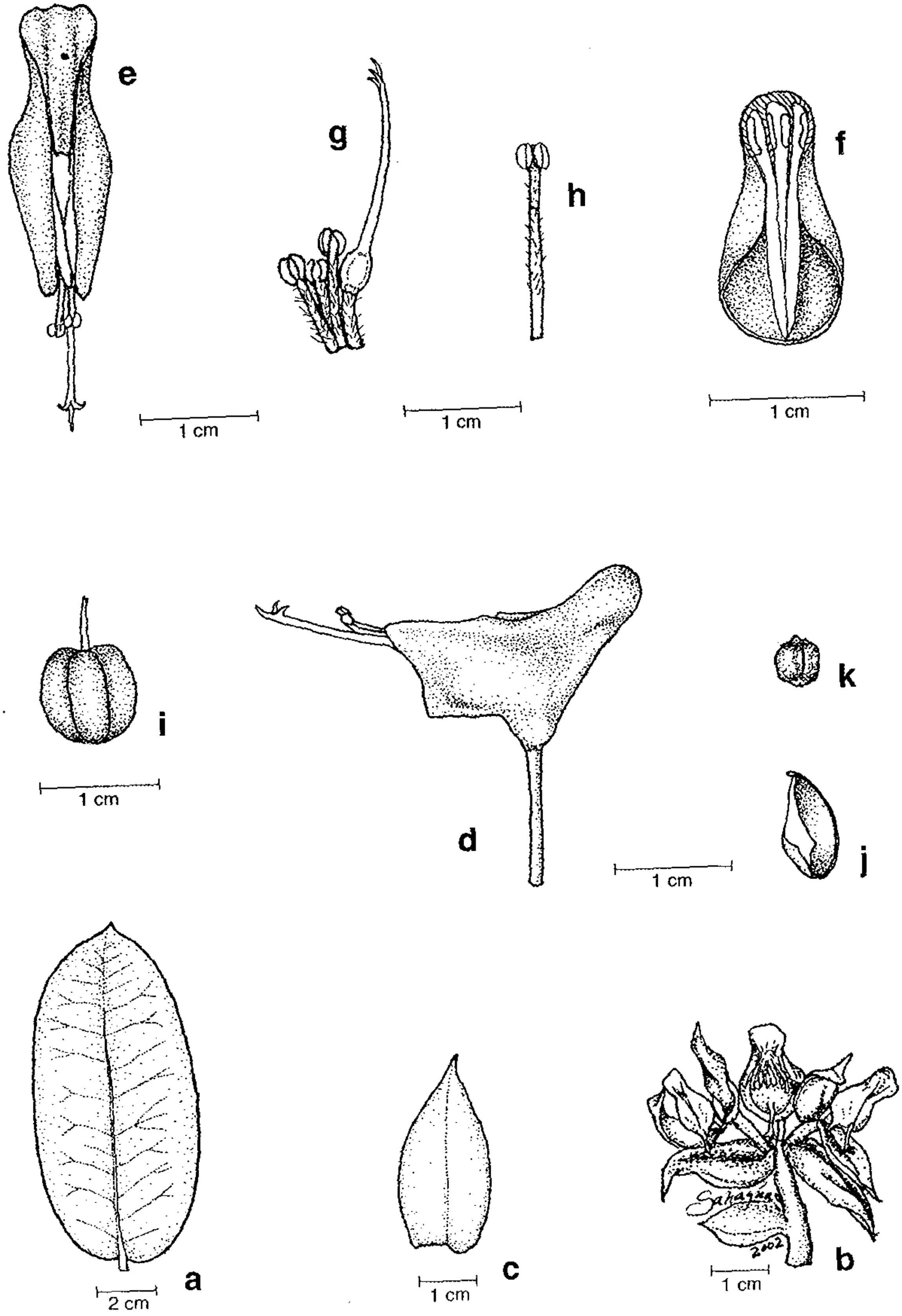
Fig. 2. *Pedilanthus coalcomanensis.* (a) Leaf, upper surface. (b) Apex of stem with bracts and cyathia. (c) Bract. (d) Lateral view of cyathium. (e) Dorsal view of cyathium. Note the puncture on dorsal lobes of spur made by wasps. (f) Involucre showing glands and accessory involucral lobes. (g) Pistillate flower and three immature staminate flowers. (h) Mature staminate flower. (i) Capsule with persistent style. (j) Valve showing inner part. (k) Seed, ventral view; a, j, k drawn from *Sahagún et al. s.n. 2-Jul-1999*; b-h from *Lomelí et al. 3184*; i from *Lomelí et al. 3239.*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