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Multivariate analysis of the vegetation of the volcanoes Tláloc and Pelado, Mexico

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Abstract. Multivariate analysis was used to describe the composition and distribution of vegetation types on the slopes of the volcanoes Tláloc and Pelado, Mexico. These volcanoes are situated in the transitional zone between the Holarctic and Neotropical floristic regions, which offers a partial explanation for the relatively high α and β diversities. Previous research argued that human activities, i.e. burning and grazing, rather than abiotic factors, play a major role in determining the distribution and floristic composition of the vegetation. TWINSPAN, Detrended Correspondence Analysis and Canonical Correspondence Analysis were used to test this hypothesis. Floristic and environmental data from 138 relevés and seven explanatory environmental variables were included: elevation, soil depth, soil moisture, percentage litter cover, percentage cover of bare ground, burning and grazing were included in the analysis. Soil moisture and elevation accounted for ca. 63 % of the residual inertia and none of the remaining explanatory variables proved to be correlated significantly with the first two axes. The present results suggest that burning and grazing operate on a finer scale. In conclusion, soil moisture and elevation are the most relevant variables to explain the distribution of the vegetation under study.

Keywords: Burning; Correspondence Analysis; Elevation; Gradient Analysis; Grazing; Soil moisture; Vegetation type.

Abbreviations: CCA = Canonical Correspondence Analysis; DCA = Detrended Correspondence Analysis; DGA = Direct Gradient Analysis; IGA = Indirect Gradient Analysis.

Nomenclature: Rzedowski & Rzedowski (1981, 1985, 1991).

Introduction

The montane zone on Mexican volcanoes shows a clear zonation with coniferous forests, deciduous forests and grasslands. On the volcanoes Pelado and Tláloc, just south of Mexico City, four main vegetation types have been described by Rzedowski (1988): (a) pine forest dominated by *Pinus montezumae* and *P. hartwegii*; (b) mixed pine and alder forest, dominated by *Pinus* spp. and *Alnus firmifolia*; (c) bunch-grassland characterized by *Muhlenbergia* spp., *Festuca tolucensis*, and *Calamagrostis tolucensis*; and (d) fir forest, characterized by *Abies religiosa*. Recent phytosociological studies (Velázquez & Cleef 1993) provide a detailed description of these plant communities.

Previous studies carried out by Miranda & Hernández-X (1963), Rzedowski & Rzedowski, (1981, 1985) and Rzedowski (1988) stated that the commonly found pine-alder-grassland community is maintained by burning and grazing. These authors supposed that without these disturbing activities, fir (*Abies religiosa*) forest, which is considered the local climax community, would replace it. This fir forest is restricted to humid places (Madrigal 1967; Rzedowski & Rzedowski 1981, 1985). Deciduous forest dominated by *Alnus firmifolia* has been considered a successional stage prior to the establishment of fir forest (Rzedowski & Rzedowski 1981). Concerning the grassland communities, Cruz (1969) and Rzedowski (1988) mentioned the establishment of meadow communities in places with poor soil drainage. Timbering, grazing, and burning promote the establishment of bunch-grass communities (Benítes 1987). In the study area fires are set to promote the regrowth of vegetation in order to provide forage for livestock production in the dry season (Velázquez 1992a). Such human disturbance, together with humidity seem to be the major factors governing the distribution of the plant communities on the slopes of these volcanoes. Rzedowski (1988) emphasized the need to carry out quantitative research in order to document this hypothesis. This study aims to do just that by means of multivariate analysis. It is based on the detailed description by Velázquez & Cleef (1993).

The purpose of this paper is to detect environmental variables that may be responsible for the distribution of the plant communities, and in particular to explore the role of burning and grazing as the key environmental factors. Multivariate analysis, especially ordination, is considered an important tool to achieve this purpose (c.f. Montaña 1990).

Methods

Study area

The volcanoes Tláloc and Pelado are situated within the transitional zone between the Holarctic and Neotropical regions in central Mexico; they are located between 19° 02' - 19° 13' N, and 98° 56' - 99° 16' W at an altitudinal range of 2500 - 3660 m. The volcanoes are relatively recent, i.e. from the Plio-Quaternary. The topography is irregular and consists of recent lava shoulders, lava ridges, a main cinder cone, a number of craters, and valleys. The dominant soil types are Andosol and Lithosol. The climate is temperate, sub-humid, mild to cool, with a mean annual temperature of ca. 11 °C. February is the coldest month, and June is the warmest. The mean annual rainfall is ca. 1000 mm. Thus, the climate can be characterized as $C\ (w^2)\ (w)$ according to Koeppen's classification as modified by García (1981).

Sampling

A set of aerial photographs (scale 1: 20 000) was used to stratify the study area into major vegetation units. Within every stratum a number of points were randomly selected. During 1987-1990, 152 relevés were made at the previously selected points, following the Braun-Blanquet approach (Mueller-Dombois & Ellenberg 1974; Westhoff & van der Maarel 1973). A stratified random sampling procedure was followed. The size of the relevés was as follows: 625 m^2 for forests, 200 m^2 for shrublands and 125 m^2 for grasslands.

Vegetation classification

13 plant communities were distinguished by classification analysis with the aid of the program TWINSPAN (Hill 1979). They were interpreted as associations and grouped in six groups, which were considered as alliances. A total of 332 plant species – belonging to 161 genera and 61 families – were included in the classification analysis. Details on the classification and a thorough description of the plant communities and their ecology are found in Velázquez & Cleef (1993). The major vegetation types of the study area described by Rzedowski (1988) and Miranda & Hernández-X (1963) resemble the types on the alliance level of Velázquez & Cleef (1993). This level was, therefore, used in order to compare previous and actual studies of the vegetation. Fig. 1 presents the dendrogram obtained and Table 1 summarizes the floristic composition of the six main groups.

Environmental variables

At each sample point, seven environmental variables were measured:

1. Elevation, which is an indirect measurement of precipitation and temperature.
2. Soil depth in cm. Shallow soils (< 30 cm) are of a Lithosol type, whereas deep soils are of Andosol or Regosol types (Velázquez 1992b).
3. Soil drainage class. This class was calculated from the amount of nodules (oxidation spots) quantified in the A1 horizon in the soil. It was assumed that the more nodules there were, the more oxidation would occur, hence the poorer the drainage (Foth 1984). Five classes were defined: class 1 = nodules absent; class 2 = nodules rare but present; class 3 = nodules present; class 4 = nodules present in moderate amounts; and class 5 = sample saturated with nodules.
4. Percentage cover of litter in the sample plot, as an estimation of organic matter in the soil.
5. Percentage cover of bare ground in the sample plot as an indication of potential erosion.
6. Burning.
7. Grazing. To quantify burning and grazing, a set of five subsamples, of 1 m^2 each, were randomly chosen within every plot. In each subsample the presence-

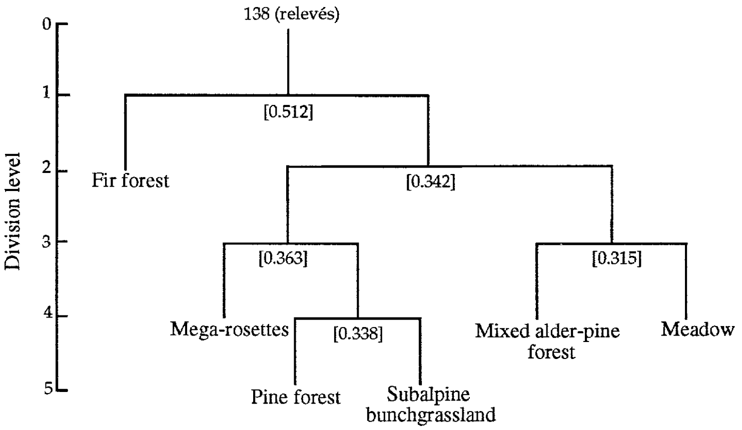

Fig. 1. Dendrogram of the two-way indicator species analysis (TWINSPAN) of the relevés at the Tláloc and Pelado volcanoes, Mexico. Groups indicated represent the alliance level (modified after Velázquez & Cleef 1993).

absence of traces of fire (ashes and charcoal) and traces of browsing (by domestic and wild herbivores) were recorded. A class value ranging from 0 to 5 of burning and grazing/browsing was assigned to every relevé based upon the number of subsamples with traces.

Gradient analysis

Indirect Gradient Analysis (IGA) was performed on the data matrix (species cover data). Since the data were collected along an environmental gradient, presuming the presence of a major coenocline, a unimodal model is appropriate (Pielou 1984; ter Braak 1987a,b). Detrended Correspondence Analysis (DCA: detrending by segments, nonlinear rescaling of axes; downweighting of rare species; Hill & Gauch 1980; ter Braak 1990) was used to help in the identification of outliers (Eilertsen et al. 1990). Two outlier types were distinguished: relevés from strata where agricultural use was obvious and relevés which were more than three standard deviations away from the mean. The first type ($n = 10$) had a substantially different floristic composition, likely induced by agricultural practices such as fertilization, ploughing and mowing. The second type ($n = 10$) included relevés with a large percentage cover of rare species and an absence of diagnostic species. 138 relevés and 273 species were included in the final analysis.

Direct Gradient Analysis (DGA) was used to find a linear combination of explanatory variables maximizing the dispersal of samples and species along axes. For this purpose Canonical Correspondence Analysis (CCA, no transformation of species data, no species and sample weights, and downweighting of rare species; ter Braak 1990) was used. The inertia of the most important explanatory variables to the total variance in the floristic data was calculated by invoking the forward selection option. A Monte Carlo permutation test was used to test the significance of the eigenvalue of the first axis, and to test the significance of the effect on the species of the explanatory variables. In all tests, 99 permutations were invoked (ter Braak 1990). Relations were considered significant at $P < 0.05$ throughout the analysis. The final results obtained by DCA and CCA were compared to see whether environmental variables had been overlooked, i.e. which could have explained a large part of the variation in the species data (ter Braak 1990). All analyses were performed with the help of the program package CANOCO version 3.10 (ter Braak 1990).

The results of both species and relevé ordinations are presented in biplots. The species biplot diagram shows the diagnostic species at the alliance level whereas the rare and constant species are indicated as a group. Relevés were pooled into their alliances and the mean and confidence intervals (95 %) were calculated per alliance. This procedure was conducted for the first and second axes. The environmental variables are represented by arrows pointing in the direction of maximum variation.

Table 1. Floristic composition of the six main plant community groups distinguished (after Velázquez & Cleef 1993). Only species with a frequency of at least 60% in any type are included. A = *Abies* forest; B = Mega-rosette vegetation; C = Pine forest; D = Subalpine bunch-grassland; E = Mixed *Alnus*-*Pinus* forest; F = Meadow. Life form symbols: P = phanerophyte; X = mega-rosette; C = cryptophyte (geophyte); H = hemicryptophyte; T = therophyte; m = moss.

	Life form	A	B	C	D	E	F
Abies religiosa	P	+	…	…	…	…	…
Senecio barba-johannis	P	+	…	…	…	…	…
Salix oxylepis	P	+	…	…	…	…	…
Festuca amplissima	C	+	…	…	…	…	…
Senecio callosus	H	+	…	…	…	…	…
Polytrichum juniperinum	m	+	…	…	…	…	…
Thuidium delicatum	m	+	…	…	…	…	…
Senecio angulifolius	P	+	+	…	…	…	…
Sibthorpia repens	H	+	+	…	…	…	…
Alnus firmifolia	P	+	+	…	+	+	…
Pinus spp.	P	+	…	…	+	+	…
Symphoricarpos microphyllus	P	…	+	…	…	…	…
Buddleia sessiliflora	P	+	…	…	…	…	…
Muhlenbergia macroura	C	+	+	+	+	+	…
Pinus montezumae	P	+	…	…	+	+	…
Calamagrostis tolucensis	H	…	…	+	+	+	…
Furcraea bedinghausii	X	…	+	…	…	…	…
Stipa ichu	C	…	+	…	…	…	+
Senecio cinerarioides	P	…	+	…	…	+	…
Muhlenbergia quadridentata	H	…	+	+	…	+	…
Festuca toluensis	H	…	…	+	+	…	…
Pinus hartwegi	P	…	…	+	…	…	…
Geranium potentillaefolium	H	…	…	+	…	…	…
Arenaria lycopodioides	T	…	…	+	…	…	…
Penstemon campanulatus	C	…	…	…	…	+	…
Trisetum spicatum	H	…	…	…	+	…	…
T. altijugum	H	…	…	…	…	+	…
Poa conglomerata	T	…	…	…	…	+	…
Castilleja arvensis	H	…	…	…	…	+	…
Agastache mexicana	H	…	…	…	…	+	…
Potentilla candicans	H	…	…	…	…	…	+

Final remarks regarding the actual distribution of the plant communities based upon the results of ordination analysis were given. The results were discussed and compared to previous observations (Benítes 1987; Miranda & Hernández-X 1963; Madrigal 1967; Cruz 1969; Rzedowski 1988).

Results

Fig. 2 shows the ordination of the species obtained by Canonical Correspondence Analysis (CCA). The eigenvalue ($\lambda = 0.420$, scaling $\alpha = 1$) of the first axis implied a good separation among plant communities, hence a turnover in ecological conditions along this first

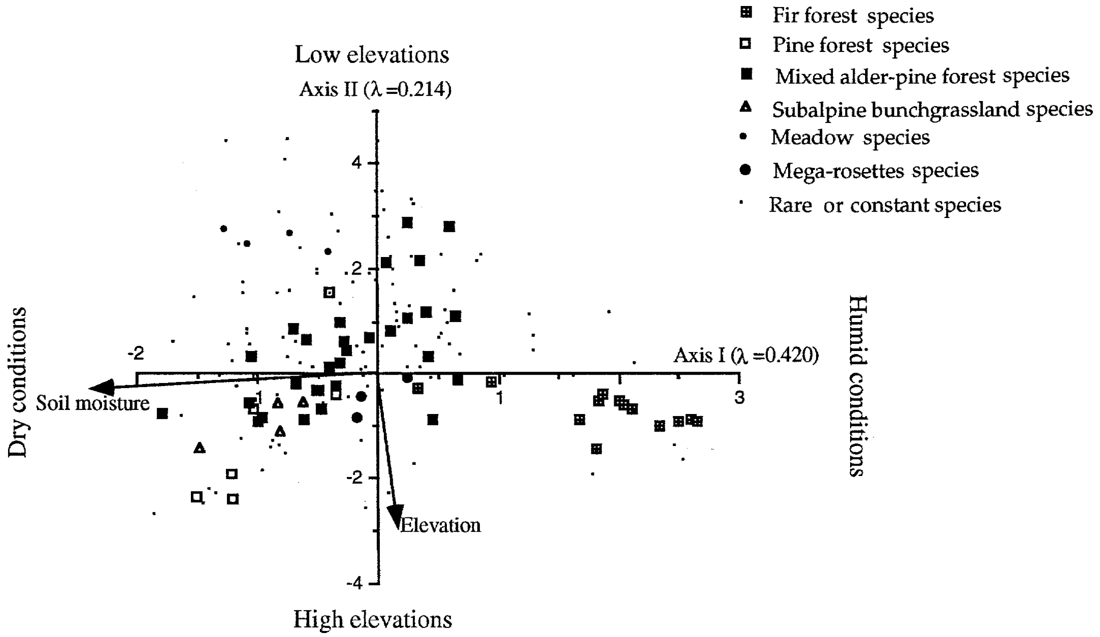

Fig. 2. Canonical Correspondence Analysis of 138 relevés with 273 plant species and seven environmental variables on the volcanoes Tláloc and Pelado, Mexico; position of species and the two most relevant explanatory environmental variables, moisture and elevation, are indicated.

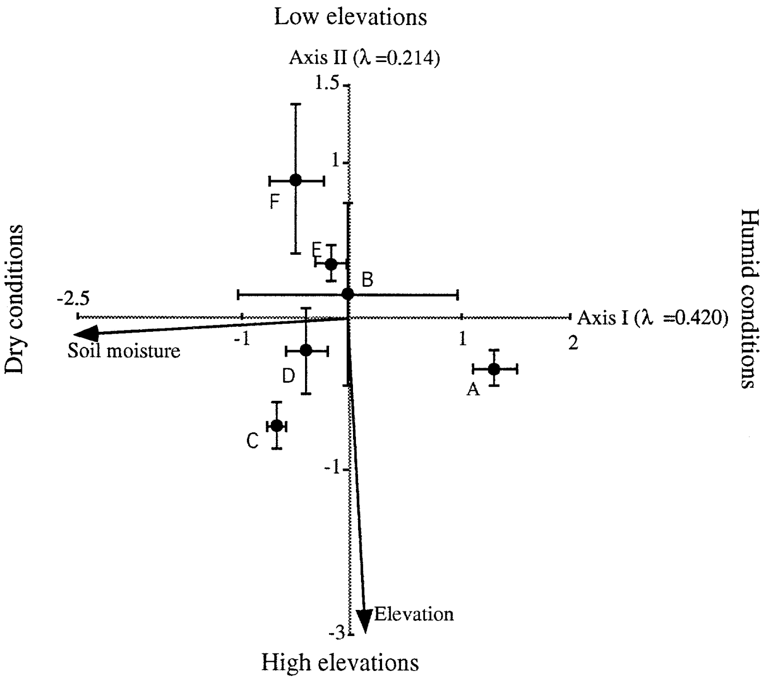

Fig. 3. Canonical Correspondence Analysis of 138 relevés with 273 plant species and seven environmental variables on the volcanoes Tláloc and Pelado, Mexico; position of the centroids of the vegetation types distinguished and the two most relevant explanatory environmental variables, moisture and elevation, are indicated. 95 % confidence intervals for the mean coordinates of each vegetation type are indicated as well. Vegetation types are: A = Fir forest; B = Mega-rosettes; C = Pine forest; D = Subalpine bunch-grassland; E = Mixed alder-pine forest; F = Meadow.

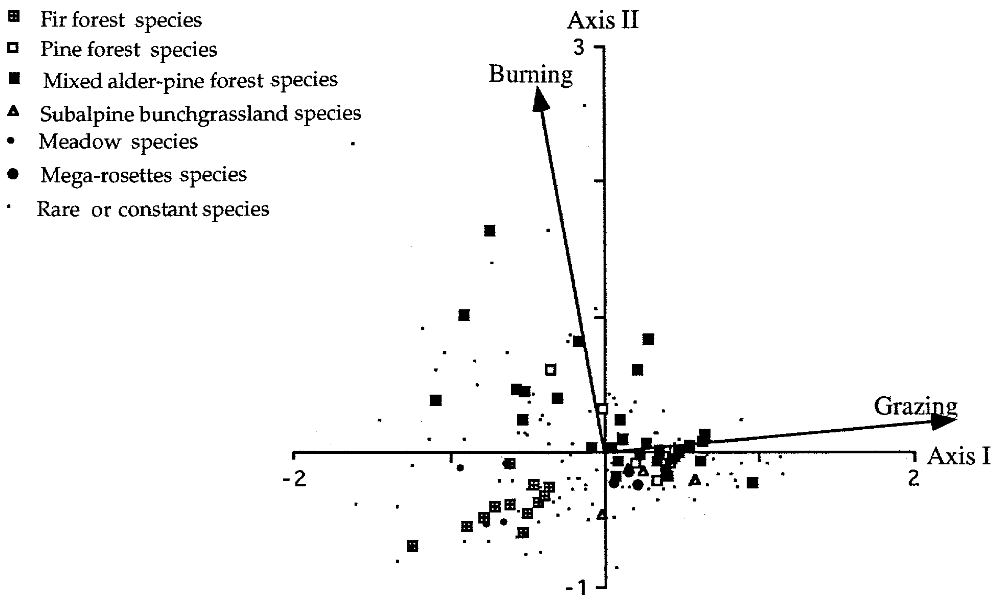

Fig. 4. Canonical Correspondence Analysis of 138 relevés with 273 plant species and five environmental variables (elevation and moisture excluded) on the volcanoes Tláloc and Pelado, Mexico; position of species and the variables burning and grazing are indicated.

axis (ter Braak 1987a). The seven environmental variables contributed independently to the overall ordination since none of the inflation variables reached higher scores than 9.3. The total inertia (total variance in the species data) was 5.704. The current explanatory variables explained ca. 65 % of the residual inertia. Out of the seven environmental variables involved in the analysis, only two, soil moisture and elevation contributed significantly to the total variance of the floristic data. The contribution by soil moisture was 42 %, of elevation 21 %. This indicated that the remaining 30.7 % of the variation was due to other environmental factors. Accordingly, a significant correlation was found between the first species axis and the first environment axis (0.874). The highest correlation coefficient of the first species axis with the environmental variables was obtained by soil moisture (– 0.872). Fir forest communities characterized by *Abies religiosa, Senecio platanifolius, S. barba-johannis, S. toluccanus,* and *Thuidium delicatulum* were positioned on the extreme right side of the first axis, representing the more humid and richer conditions. In contrast, pine forest characterized by *Pinus hartwegii* and the meadow type, characterized by *Potentilla candicans* and *Stipa ichu*, were positioned on the left end of the first axis. The latter species were mainly found on relatively dry and poor soils (Cruz 1969; Rzedowski & Rzedowski 1981; Rzedowski 1988). Regarding the second axis, elevation obtained the highest correlation coefficient (– 0.828) with the second species axis and with the second environmental axis (Table 1). Therefore, axis 2 ($\lambda = 0.214$, scaling $\alpha = 1$), suggests an elevation gradient (Figs. 2, 3). The diagnostic species of the meadow type, normally found at lower elevations, were positioned on the upper part of the diagram. The location of pine forest (*Pinus hartwegii*), and subalpine bunch-grassland (*Festuca tolucensis*) found on the lower side of the second axis supported this altitudinal gradient. These plant communities were mainly observed in the cones of the volcanoes above 3350 m elevation (Velázquez 1992b).

The random data-set generated by the Monte Carlo permutation test yielded an *F*-ratio of 10.73 ($P = 0.01$). This result indicated that the Canonical Ordination Analysis was unlikely to have been obtained by chance only. In brief, the ordination biplots (Figs. 2, 3) provide a

Table 2. Correlation coefficients between axes and variables obtained with CCA on all relevés and all environmental explanatory variables. * = $P < 0.05$.

	Species axis 1	Species axis II	Variables axis I	Variables axis II	Elevation
Species axis I	1				
Species axis II	– 0.095	1			
Variables axis I	0.874 *	0	1		
Variables axis II	0	0.829 *	0	1	
Elevation	0.019	– 0.828 *	0.022	– 0.999 *	1
Soil moisture	– 0.872 *	– 0.055	– 0.997	– 0.067	0.044

significant representation of the distribution of the plant communities and the environmental variables under study. Therefore, soil moisture and elevation seem to explain the present distribution of these communities in the best possible way (Table 2).

Discussion and Conclusions

The plant communities present on the volcano Tláloc do not differ substantially from those of Pelado, with the exception of the mega-rosette vegetation, which is restricted to Pelado. This vegetation type was positioned near the centroid of the ordination biplots and showed a large variation (Figs. 2, 3). A similarly large variation was observed in the meadow type. Apparently, the mega-rosette and meadow vegetation types are azonal communities (Rzedowski 1988; Cruz 1969). On the whole, the ordination reflected the zonal distribution of the vegetation. Previous studies documented the similarities in geology, topography, soil and vegetation between the two volcanoes (Velázquez 1992b) and the spatial distribution of the common vegetation types on the two volcanoes suggested similar relations to the major environmental factors (Velázquez 1992b). The present study provides quantitative documentation for this observation.

Miranda & Hernández-X (1963) and Rzedowski (1988), considered burning and grazing as two of the most important factors operating in the area, which favour *Pinus*, *Alnus* and grassland communities, whereas *Abies* forests would develop optimally in the absence of fire and grazing. Thus, it was expected that the variables burning and/or grazing in the present study would be significantly correlated with the first or second ordination axis. Also, species favoured by fire should be found at one of the extremes of an axis, and *Abies* forest species at the opposite end of that axis. However, burning and grazing did not attain correlation coefficients higher than 0.7 along any of the axes. The vegetation types supposed to be favoured by burning and grazing, e.g. pine forest and mixed alder-pine forest (Rzedowski & Rzedowski 1985) are relatively widely dispersed in the ordination diagram and occupy part of the centre (Figs. 2, 3). This contradicts the earlier hypothesis.

By excluding soil moisture and elevation from the ordination analysis, the influence of burning and grazing on the distribution of the plant communities became clearer (Fig. 4). With the exception of some species characteristic of the *Abies* forest and the meadows, most diagnostic species at the alliance level were positioned near the centre of the ordination diagram (Fig. 4). The similar position of fir forest and meadow species, which are ecologically quite different, indicates that burning and grazing activities operate at a finer scale than soil moisture and altitude. This does not agree with conclusions in previous studies (Benítes 1987; Miranda & Hernández-X 1963; Rzedowski 1988). In Fig. 4, the vector burning showed some correlation with mixed *Alnus-Pinus* forest. Vegetation types characterized by *Alnus firmifolia* have, as a matter of fact, been associated with burning activities (Rzedowski & Rzedowski 1981). Unlike burning, grazing seems to be more associated with the occurrence of the *Pinus hartwegii* community. The present results suggest no correlation between burning and grazing. In the study area, fires are often widespread and usually cover large surfaces. On the other hand, intensive grazing mostly takes place in vegetation types characterized by a dense grass layer. Consequently, some of the plant communities affected by burning will not be grazed intensively. Additionally, the grazing areas are frequently rotated and sometimes protected by roads against fires. This is done to ensure forage in different years, but non-grazing areas are frequently burned without any control.

Altitude has been considered important as an indicator of climatic conditions, particularly temperature and precipitation (Holdridge 1987; García 1981). The major changes along the altitudinal range on the Tláloc and Pelado volcanoes were correlated with temperature rather than precipitation (Velázquez 1992b), although both play a role. This indicated that the actual gradient represented by the second axis in Figs. 2 and 3 may be a temperature gradient, changing from cool in the lower part of the diagram to mild or even warm in the upper part. Retuerto & Carballeira (1991) suggested a similar temperature gradient related to elevation. In the present study, no climatic data were available to document the existence of this temperature gradient.

The present paper was aimed at assessing the role of fire and burning following an exploratory (statistical) approach. These results are still preliminary and should be confirmed by experimental studies on the impact of fire and grazing. Regarding fire, factors such as fuel availability, wind speed, seasonal changes, history of fire and recovery of vegetation should be included. Such studies should be long-term and differentiated as to vegetation type. They should also be related to the observation that most fires in the study area affect mainly the understorey, whereas the tree layer is seldom substantially damaged. This suggests that most of the impact of these disturbances concerns the herb and shrub layers and the tree saplings.

As to grazing, its impact has been proved to be important in determining the regeneration of pine forest communities, because cattle promote the rapid establishment of woody species (Gonzáles-Espinosa et. al. 1991). Further experimental research, taking into account other characteristics of burning and grazing, such as severity and frequency, is recommended in order to determine the actual role that these disturbing activities play. Multivariate techniques seem adequate to cope with the lack of data in order to postulate a sound hypothesis of vegetation-environment relationships (Montaña & Greig-Smith 1990). These are, however, recommended as exploratory tools since no deterministic conclusions can be obtained by any of the gradient techniques (Gauch 1982; Ludwig & Reynolds 1988; van Groenewoud 1992). In brief, experimental research is needed to gain insight into the causes and consequences in the relationships between plant distribution and environmental variables.

Ordination analysis along complex ecological gradients might lead to misleading interpretations, so that stratification is recommended (Krebs 1989). Similar recommendations have been suggested for classification analysis (van der Maarel et al. 1987). Discrete distribution patterns are primarily due to the dominance of few species which is reflected in relatively low α and β diversities. In recent volcanic formations, discrete borders among plant communities are less obvious, unless there are interruptions created by ecological changes or disturbances, forming a complex community continuum with gradual changes (Whittaker 1973; Austin 1985).

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