VARIATION IN TREE SPECIES STRUCTURE, COMPOSITION AND PHYTOGEOGRAPHICAL AFFINITIES OF THE CLOUD FOREST ALONG AN ALTITUDINAL GRADIENT IN VERACRUZ, MEXICO

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Résumé : La végétation de la forêt de nuages du Mexique est composée d'éléments phytogéographiques holartiques et tropicaux. Cependant, les familles tropicales peuvent être divisées en deux centres de distribution : taxa d'origine amazonienne et d'origine andine. Cette étude a été établie pour décrire les changements des espèces d'arbres en fonction de leur affinité phytogéographique et de la structure de la végétation le long d'un gradient altitudinal de la forêt de nuage du Centre de l'État de Veracruz. La densité, l'aire basale, les espèces d'arbres dominantes (plus de 10 % de l'aire basale) ont été estimées pour six sites, localisés entre 1 250 et 2 050 m d'altitude. La densité des arbres a varié de 510 à 1 340 individus ha^{-1}. et leur aire basale de 25.1 à 60.6 $m^2 ha^{-1}$. Les densités ont été semblables pour tous les sites, excepté pour le site 5 qui a eu la densité la plus haute. Les sites de basse altitude (sites 1, 2 et 3) ont eu une aire basale inférieure à celle des trois autres sites. La plus grande aire basale a été enregistrée dans le site le plus élevé. Dans toutes les localités les espèces dominantes d'arbres sont des éléments holartiques. Les trois sites de basse altitude possèdent les mêmes espèces dominantes (*Carpinus caroliniana, Liquidambar macrophylla, Quercus germana*, et *Q. xalapensis*). Le site 5 a trois espèces dominantes, mais il a en commun seulement une espèce avec les sites 1, 2 et 3 (*C. caroliniana*) et une avec le site 4 (*Ostrya virginiana*). Dans les sites 4 et 6, la seule espèce dominante est *O. virginiana* et *Q. salicifolia* respectivement. En altitude élevée, la plupart des espèces néotropicales appartiennent aux familles d'origine andine, et quelques espèces holartiques sont absentes : par exemple, *L. macrophylla* est absente des sites au-dessus de 1 800 m. *Ostrya virginiana* est absente du site le plus élevé. *Carpinus caroliniana* n'a pas été trouvée dans le site 4 et 6. D'autres espèces ont seulement été relevées dans les sites les plus hauts, e.g. *Alnus* spp., *Cleyera theaeoides, Drymis granadiensis, Ternstroemia sylvatica*, et *Weinmannia intermedia*. Néanmoins, les deux sites les plus élevés ont trois espèces en commun *Clethra mexicana, Ilex tolucana*, et *Saurauia leucocarpa*. Dans la forêt de nuages du Veracruz central, la diminution relative apparente d'éléments holartiques au profit d'éléments néotropicaux d'origine andine le long de l'accroissement en altitude doit être liée à la fragmentation de la forêt, au climat actuel et aux changements historiques ou géologiques de l'environnement.

Mots-clés : Forêt de nuages, gradient altitudinal, néotropical, Veracruz, Mexique.

Abstract: The vegetation of the Mexican cloud forest is composed of both holartic and tropical phytogeographical elements. Tropical families, however, can be divided into two major distributional groups: Amazonian-centered taxa and Andean-centered taxa. This study was designed to describe changes in tree species phytogeographical affinities and vegetation structure along an altitudinal gradient in the cloud forest of central Veracruz. Density, basal area, and dominant tree species (more than 10% of basal area) were estimated for six sites located between 1250 and 2050 m. Density of trees varied between 510 and 1340 individuals ha^{-1}. Basal area varied between 25.1 and 60.6 $m^2 ha^{-1}$. Densities were similar at all sites except site 5 which had the highest density. The sites at lower altitudes (sites 1, 2 and 3) had smaller basal area than the other three sites. The largest basal area was recorded at the highest altitude. In all the sites the dominant tree species were holartic elements. The three sites located at lower altitudes had the same dominant species (*Carpinus caroliniana, Liquidambar macrophylla, Quercus germana*, and *Q. xalapensis*). Site 5 had three dominant species, but only shared one with sites 1, 2 and 3 (*C. caroliniana*), and one with site 4 (*Ostrya virginiana*). At sites 4 and 6, the only dominant species were *O. virginiana* and *Q. salicifolia*, respectively. At the highest altitudes most of the neotropical species belong to Andean-centered families, and some holartic species were absent. For instance, *L. macrophylla* was absent from sites above 1800 m. *Ostrya virginiana* was absent from the site at the highest altitude. *Carpinus caroliniana* was not found at site 4 or 6. Other species were only recorded at the highest elevations, e.g. *Alnus* spp., *Cleyera theaeoides, Drymis granadiensis, Ternstroemia sylvatica*, and *Weinmannia intermedia*. However, the two sites at higher altitudes had three species in common which were also present at lower altitudes: *Clethra mexicana*, *Ilex tolucana*, and *Saurauia leucocarpa*. The apparent relative decrease of holartic elements and increase of Andean-centered neotropical elements with increase in altitude in the cloud forest of central Veracruz may be related to forest fragmentation, present climate, and historical or geological environmental changes.

Keywords: Cloud forest, altitudinal gradient, neotropics, Veracruz, Mexico.

Introduction

Variations in plant species composition along elevational gradients is well documented (KITAYAMA 1992), and can occur over small distances within what may be classified as a single vegetation type (TERBORGH 1971, LIEBERMAN *et al.* 1985, LEE *et al.* 1986, GENTRY 1988, WEAVER 1991). Mexican cloud forest is composed of both northern (holartic) and southern (tropical) elements (MIRANDA & SHARP 1950, GRAHAM 1976, RZEDOWSKI 1978, GENTRY 1982); the plant species composition of this forest varies with latitude, altitude and topography (RZEDOWSKI 1978). Where this variation occurs in the major Mexican mountainous zones needs to be investigated. This study was designed to describe changes in tree species composition along an altitudinal gradient, within a cloud forest region.

Study area

In central Veracruz, altitude varies from 0 to 4300 m over a distance of 100 km. The cloud forest (lower montane forest, HOLDRIDGE *et al.* 1971; "bosque mesofilo de montana", RZEDOWSKI 1978) occurs between 1200 and 2100 m. At present, this type of forest is represented by remnant patches surrounded by agroecosystems and human settlements.

Study sites

Six sites were selected with altitudes ranging from 1250 to 2050 m a.s.l. on the Sierra Madre Oriental around Xalapa, Veracruz (Figure 1). Each site had at least 10 ha of forest and a minimum core area of 2 ha of forest with no evidence of human disturbance. Site characteristics are presented in Figure 2.

Site 1. Rancho Guadalupe is a protected forest area, next to the Francisco Javier Clavijero Botanical Garden, at km 2.5 Xalapa-Coatepec road (19° 30' N, 96° 57' W).

Site 2. San Antonio Tlalnehuayocan is a forest patch (19° 32' N, 90° 80' W) surrounded by pasture, macadamia plantation and an old field.

Site 3. Rancho La Mesa is located 2 km north of Banderilla (19° 35' N, 96° 75' W). The protected forest patch is surrounded by pasture.

Site 4. This forest covers the NW slope of the crater in the Acatlàn volcano (19° 41' N, 96° 51' W).

Site 5. The site atop Acatlàn volcano is a forest remnant (19° 41' N, 96° 51' W). The volcano foothills have been transformed into *milpas* (corn fields) and pastures.

Site 6. The Planta del Pie forest (19° 44' N, 96° 48' W) lies 10 km west of Chiconquiaco. This forest is at the elevational agricultural frontier in this region.

Methods

At each site, randomly selected 10 x 10 m plots were located at least 20 m away from any forest edge. Because some sites are part of ongoing projects, the number of plots differed between sites. Sampled areas per site varied between 0.01 ha and 0.02 ha (Figure 3).

In each plot all trees $\geq$ 5 cm dbh (diameter at 1.3 m) were measured and identified. Voucher specimens were deposited at the Herbarium XAL, Instituto de Ecologia, Xalapa, Veracruz, Mexico. Canopy height (m) was measured with a Haga clinometer.

Density (individuals ha^{-1}) and basal area ($m^2.ha^{-1}$) among sites were compared by one-way ANOVA, and significantly different means were separated by a Tukey's test at P = 0.05.

Similarities based on tree species composition and abundance of each species among the study sites were determined using the Morisita index (SNEATH & SOKAL, 1973).

$$I_M = 2 \sum n_{1i} n_{2i} / (\lambda_1 + \lambda_2) N_1 + N_2$$

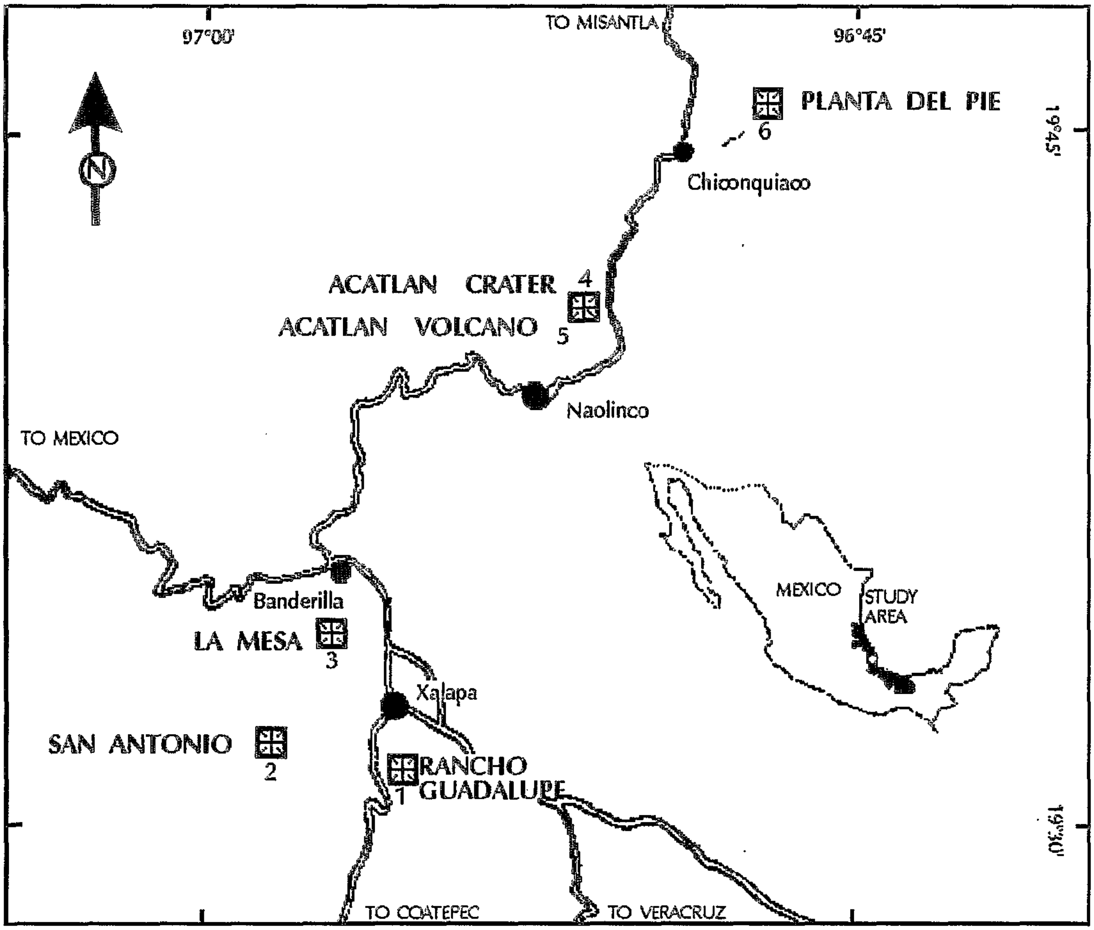

Figure 1
Map of the study area. The squares represent location of the study sites in central Veracruz, Mexico.

	Altitude m a.s.l	Precipitation mm	Mean T°C	Density ind/ha	Basal Area m^2/ha	Canopy Height (m)
1. Rancho Guadalupe	1250	1514	17,9	873	34,8	24,6
2. San Antonio	1400	1451	18,2	730	30,0	23,0
3. La mesa	1470	1451	18,2	745	25,1	23,0
4. Acatlàn crater	1840	1730	16,8	510	48,8	23,8
5. Acatlàn Volcano	1900	1730	16,8	1340	43,6	17,3
6. Planta del pie	2050	1806	14,2	645	60,6	25,5

Figure 2
Altitude (m a.s.l.), precipitation (mm), temperature (°C), density (individuals/ha), basal area (m^2 ha^{-1}), and canopy height (m) of the study sites in central Veracruz, Mexico.

Instead of using the number of individuals per species, the density of each species (n1i, n2i) was used. N is the total density, and is a measure of diversity devised by E. H. Simpson (Sneath & Sokal, 1973), estimated as:

$$n_{1i} (n_{1i} - 1)/N_1(N_1-1).$$

Temperate affinity index

An index of tree life-form temperate affinity was calculated. The temperate affinity index (TAI) was a transformation of the SIMPSON'S index:

$$TAI = \sum_{i=1}^{t} p_i^2 / \sum_{i=1}^{s} p_i^2$$

where: pi is the proportion of individuals density that species i contributes to the total density in the site, and t is the total number of temperate genera common to eastern deciduous forest in the United States and lower montane forests in central Veracruz, Mexico, and s is the total number of species in the sampled area.

Since site sampled plots number differ, less common tree species may have appeared on smaller sampled sites if sampled areas were larger in size. With this limitation in mind, TAI is used here as a first approximation to compare phytogeographical affinities among sites.

Results and discussions

Vegetation structure

Density of trees varied between 510 and 1340 individuals ha^{-1} (Figure 2); however, densities were not significantly different at all sites except site 5 which had the highest density ($P = 0.0001$). Basal area varied between 25.1 and 60.6 $m^2.ha^{-1}$ (Figure 2). The sites at lower altitudes (sites 1, 2 and 3) differed from the others in having smaller basal area per hectare. The largest basal area was recorded at the highest altitude, site 6 ($P < 0.05$). Mean canopy height varied between 17.3 and 25.5 m and the tallest trees were observed at site 6 (Figure 2).

In the temperate deciduous forests of the eastern United States, basal area of trees $\geq$ 10 cm dbh, roughly approximates 30 $m^2.ha^{-1}$ (HELD & WINSTEAD, 1975; GENTRY, 1988). The floristic composition of this forest includes temperate species that are common in some Mexican cloud forests. Mexican cloud forest sites with those temperate tree species seem to have a basal area close to 30 $m^2.ha^{-1}$ e.g., sites 1, 2 and 3, and the Biosphere Reserve El Cielo, Tamaulipas, where basal area was 31.5 $m^2.ha^{-1}$ (PUIG *et al.* 1987). In contrast, cloud forest sites with more neotropical tree species seem to present higher basal areas. In the Biosphere Reserve El Triunfo, Chiapas, basal area was 54 $m^2.ha^{-1}$ (WILLIAMS-LINERA, 1991). In Omiltemi, Guerrero, where temperate elements are less important than neotropical ones, the reported basal area was 49.8 $m^2.ha^{-1}$, but *Pinus ayacahuite* represented 14.8% of the total basal area (MEAVE *et al.*, 1992). In Costa Rica, basal areas were 39.7, 59.5, and 39.5 $m^2.ha^{-1}$ for moist, wet, and rain lower montane forests, respectively (HOLDRIDGE *et al.*, 1971).

Similarities among sites

According to the Morisita index (Figure 3), the largest similarity exists between sites 1, 2 and 3. The similarity between the two highest sites was relatively low (MI = 0.35) but they had the highest number of genera in common (eight). The Morisita index indicated that site 4 had the smallest similarity with the other sites (MI < 0.08 when compared to sites 1, 2, 3 and 6). The similarity between sites 4 (Acatlàn crater) and 5 (Acatlàn volcano) was also relatively low (MI = 0.39), but with five genera in common. The forest in the Acatlàn crater was the most different, apparently owing to aspect. This forest occupies the NW-facing slope inside the crater and thus it receives the least total insolation with respect to the other study sites.

Tree species composition

Tree species composition and families phytogeographical origin for each site are presented in the Appendix.

The TAI's were high for the six study sites, indicating that temperate tree species dominate these forests (Figure 4). The highest altitude sites, however, had lower values of TAI than the lower altitude sites.

	2. San Antonio	3. La Mesa	4. Acatlàn Crater	5. Acatlàn Volcano	6. Planta del Pie
1. Rancho Guadalupe	0,74	0,54	0,01	0,63	0,24
2. San Antonio		0,93	0,02	0,50	0,58
3. La Mesa			0,02	0,38	0,70
4. Acatlàn Crater				0,39	0,03
5. Acatlàn Volcano					0,35

Figure 3
Morisita index for pairs of study sites in central Veracruz, Mexico.

	TAI	Total N° Tree spp.	Temperate Genera	Sampled Area
1. Rancho Guadalupe	0,867	15	5	1700
2. San Antonio	0,982	13	4	2000
3. La Mesa	0,921	17	6	2000
4. Acatlàn crater	0,987	7	4	1000
5. Acatlàn Volcano	0,798	23	7	1000
6. Planta del pie	0,743	13	5	2000

Figure 4
Temperate affinity index (TAI), total number of genera, number of temperate genera, and sampled area for each study site in central Veracruz, Mexico.

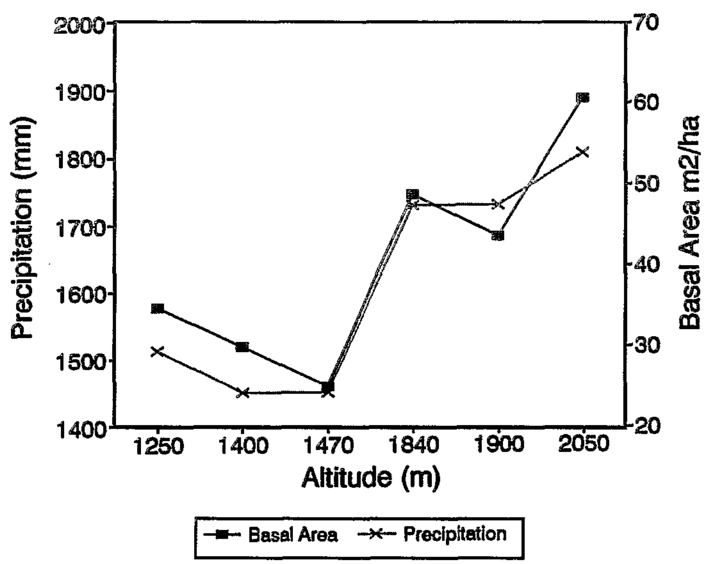

Figure 5
Variation in precipitation (mm) and basal area ($m^2.ha^{-1}$) along an altitudinal gradient in central Veracruz, Mexico.

Main species of a forest site were defined as those having a basal area representing 10% or more of the total. Because basal area is closely correlated with biomass, it is one of the most useful measures of species importance in community dynamics (TANNER, 1977). The study sites at the lowest altitudes (sites 1 and 2) had the same dominant species (*Carpinus caroliniana*, *Liquidambar macrophylla*, *Quercus germana*, and *Quercus xalapensis*). Site 3 shared three main species with sites 1 and 2. Site 4 has only one main species (*Ostrya virginiana*), and shares it only with site 5. Site 5 had three main species, but only shared one with sites 1, 2 and 3 (*Carpinus caroliniana*). At site 6, the only main species was *Quercus salicifolia*.

The two sites at higher altitudes (5 and 6) had three species in common which were also present at lower altitudes: *Clethra mexicana*, *Ilex tolucana*, and *Saurauia leucocarpa*. Other species were only recorded at the highest elevations, e.g. the temperate genus *Alnus*, and the tropical species *Cleyera theaeoides*, *Ternstroemia sylvatica*, and *Weinmannia intermedia*. The holartic species, *Liquidambar macrophylla* was absent from the study sites above 1800 m (sites 4, 5 and 6). *Ostrya virginiana* was absent from site 6 and 1; however, some individuals of *Ostrya virginiana* were found outside the sampling plots at site 1. *Carpinus caroliniana* was found neither at site 4 nor at site 6. Interestingly, a similar observation was made at El Triunfo, Chiapas, with *Liquidambar macrophylla* and *Carpinus caroliniana* being dominant tree species below an altitude of 1800 m, and tree species such as *Weinmannia pinnata*, *Ternstroemia tepezapote*, *Cleyera theaeoides*, and *Drymis granadensis* being dominant at the highest altitudes (WILLIAMS-LINERA 1991).

Variation in species composition with altitude has been observed in tropical montane forest, e.g., in the Andes (GENTRY, 1988), Monteverde, Costa Rica (LEE *et al.*, 1986), the Luquillo Mountains, Puerto Rico (WEAVER, 1991), and El Triunfo, Chiapas (WILLIAMS-LINERA, 1991). In neotropical forests there is a strong relationship between species richness and precipitation (GENTRY 1988). In a montane habitat in Puerto Rico there is evidence that greater rainfall and cloud cover may be the critical factors in the distribution of tree species (WEAVER, 1991).

I conclude that, in central Veracruz, tree stratum structure (density and basal area), tree species composition and their relative dominance vary with elevation. The sites located at lower altitudes are more similar among themselves in basal area (Figure 5) and tree species than sites at higher altitudes. Some holartic tree species were absent from sites at the highest altitudes, and some neotropical species were present only at these highest altitude sites. Most of the neotropical tree species were members of Andean-centered families (GENTRY, 1982). Representation of the latter group is highest in mountainous phytogeographic regions (GENTRY, 1982). Presence/absence of some temperate or tropical species at higher altitudes within the cloud forest of central Veracruz may be related to present higher precipitation, but also may result from historical events such as small or transient environmental changes (see SPRUGEL, 1991) as well as to geological time climatic changes (GRAHAM, 1976).

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