

Changes in Epiphyte Cover in Three Chronosequences in a Tropical Montane Cloud Forest in Mexico

Janette CORDOVA & Rafael F. DEL CASTILLO¹
CIIDIR Oaxaca, Instituto Politécnico Nacional,
Homos 1003, Oaxaca 71230, Mexico
¹Corresponding author

Abstract: Epiphyte cover at the lower portion of tree trunks was examined in three chronosequences with stands ca. 15, 45, 75 and > 90 years old, originally covered by tropical montane cloud forests (TMCFs), and in an adjacent primary forest in the southern state of Oaxaca, Mexico. Epiphytes were sampled at four equidistant levels from above the litter layer (0 cm) up to 160 cm of the tree trunk, using a 1 dm² sampling grid at each level. Twenty-four trees per successional stage and chronosequence were sampled. The method allowed for the detection of epiphytes in 99.3% of all the sampled trees. As the stand aged, total epiphyte cover increased following a sigmoidal pattern, with the highest rate of increase between 15 and 45 years after stand initiation. Moss, liverworts, and vascular plant cover increased while macro- and microlichen cover did not appear to be affected by the age of the stand. However, macrolichens were more abundant on the south side of trees. Abundance of mosses, liverworts, and vascular plants was positively correlated among each other. Microlichen cover decreased as the cover of mosses and vascular plants increased. Total epiphyte cover per unit of stem area tended to decrease with diameter of the host tree, a pattern also found in each of the first four seral stages studied. We conclude that microenvironmental changes associated with forest succession and epiphyte interactions are important in determining epiphyte abundance during secondary succession. Abundance and composition of epiphytes at the lower stem portion are properties that can be used to monitor the condition of the TMCFs.

KeyWords: conservation, lichens, liverworts, macrolichens, microlichens, mosses, orchids, succession, tropical montane cloud forest, vascular epiphytes

Introduction

Tropical montane cloud forests (TMCFs) are among the most threatened ecosystems in the world, yet they are little understood (HAMILTON *et al.* 1995; BRUIJNZEEL & VENEKLAAS 1998). A precise definition of these forests is difficult. However, they are characterized by persistent, frequent or seasonal cloud cover at the vegetation level, reduced tree size compared to lowland tropical moist forests, presence of sclerophyll leaves in many canopy tree species, and direct canopy interception of cloud water (HAMILTON *et al.* 1995). Epiphytes are well represented in both biomass and diversity (WOLF 1993; BRUIJNZEEL & PROCTOR 1995; HAMILTON *et al.* 1995), including liver-

worts (GRADSTEIN 1995), mosses (CHURCHILL *et al.* 1995), ferns (MERLIN & JUVICK 1995), lichens (SIPMAN 1995; SMITH 1995), and flowering plants (MEAVE *et al.* 1992). TMCFs have a great capacity to retain humidity, as fog interception by the canopy increases the water input by 5-20 or even 100 %, relative to that of ordinary rainfall (BRUIJNZEEL & PROCTOR 1995; CAVELIER *et al.* 1996). This capacity may explain the diversity and abundance of epiphytes, although possibly affected by vegetational disturbances. Changes in vegetation can lead to dramatic changes in the ecology and the hydrology of terrestrial ecosystems. Evapotranspiration, for instance, changes when factors such as the foliage area of the canopy, species composition, and plant density change (WARING & SCHLESINGER 1985; JACKSON *et al.* 2000). The conversion of primary to secondary forest implies important changes in forest cover, structure and function of the ecosystem, all of which greatly modify the microclimate. Therefore, it is likely that epiphytes respond to such changes. Indeed, research conducted in other forest types has revealed that epiphytes are very susceptible to microclimatic changes associated with disturbance, changes in vegetation, and succession (*e.g.* ESSEN *et al.* 1996; PECK & MCCUNE 1997). Because of their sensitivity to micro-environmental changes, the use of cryptogamic plants, many of which are epiphytes, have been proposed for forest evaluations (*e.g.* SMIRN 1995; KEDDY & DRUMMOND 1996).

The TMCFs of southern Mexico have, by unit area, the highest biodiversity in the country (RZEDOWSKI 1991). Nevertheless, they are also one of the most endangered forests (WILLIAMAS-LINERA 1992; JARDEL *et al.* 1993; ORTEGA & CASTILLO 1996); and, in many areas, they have been greatly disturbed (RZEDOWSKI 1978; ACOSTA CASTELLANOS 1997). Conversion of the original TMCFs to low-diversity pine (*Pinus* spp.) forests is one of the major trends detected for these ecosystems in southern Mexico (GONZÁLEZ-ESPINOSA *et al.* 1991, 1995). Associated with such changes, it has been recognized that pine dominated-canopy forests result in more open, exposed, drier, and warmer habitats than the original ones (GONZÁLEZ-ESPINOSA *et al.* 1995 and references therein). For the reasons stated above, epiphytes are one of the groups of plants expected to be most affected by such changes, but to our knowledge, no information is available about such changes.

To increase our understanding of the dynamics of TMCFs and to explore the possibility of using epiphytes for monitoring TMCFs, we document the changes in abundance and composition of major epiphyte groups (liverworts, mosses, microlichens, macrolichens, and vascular plants) along three chronosequences originally occupied by TMCFs, as well as in an adjacent near-pristine forest, in southern Mexico. We focus on the lower portion of the stem of the tree hosts, due to its easy access for TMCFs evaluation. To better understand the patterns of epiphyte colonization, we also examined the relationship between the abundance of the major epiphyte groups among themselves and with host tree diameter.

Materials and Methods

Study area

Fieldwork was undertaken in El Rincón region, ca. 70 km northeast of the city of Oaxaca, in the Sierra Juárez mountain range in the state of Oaxaca, Mexico. This region is characterized by steep topography, acidic soils, and elevations ranging from 500 to 2,700 m. The cloud forest belt occurs between 1,600 and 2,300 m, mostly on the windward side of the mountains. Part of the region has been converted to agricultural land, coffee plantations and secondary forests in different stages of development resulting from the abandonment of agricultural lands. Mean annual precipi-

precipitation recorded at the nearby meteorological station of Villa Alta (ca. 16 km from the study sites) is 1,719 mm year⁻¹, with a rainy season during summer and a dry season during winter. Mean annual temperature ranges between 20 and 22 °C (ANONYMOUS 1999). Fog is quite common and mostly derived from clouds formed over the Gulf of Mexico.

The southern portion of the region is occupied by a primary and near-pristine forest with little to non-human intervention with *Billia hypocaustanea*, *Cinnamomum zapatae*, *Oreopanax flaccidus*, *Quercus corrugata*, *Q. salicifolia*, *Q. sp.*, *Podocarpus matildae*, *Symplocos coccinea*, and *Temstroemia oocarpa* among the most conspicuous species. Mean diameter at breast height (dbh) of trees larger than 9 cm dbh was 35.3 ± 3.5 cm (mean ± 1 standard error). This site, El Jabali, was considered the latest successional stage in our study (stage 5, Fig. 1).

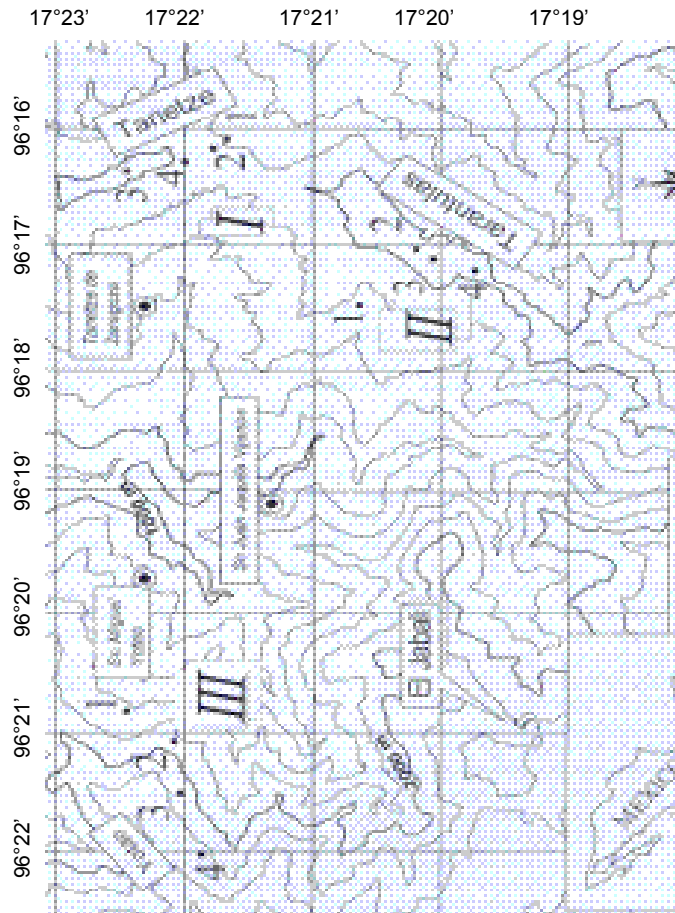


Fig. 1. Location of the three chronosequences studied Tanetze (I), Tarantulas (II), and Yotao (III), each with four seral stages (1-4), and El Jabali (stage 5), an area of primary forest, all located in the Sierra Juárez mountain range, Oaxaca, Mexico.

In addition, three chronosequences in the vicinity of El Jabali, each with four successional stages were selected (Fig. 1). Stage 1 was approximately 15-20 years old, based on the estimated age of the shade-intolerant *Pinus chiapensis*. This species requires heavy disturbances, such as fires or land clearings, for its successful establishment and does not become established in forest gaps (DEL CASTILLO 1996).

Stage 1 was characterized by the dominance of *Pinus chiapensis* and *Liquidambar macrophylla*. Other important elements were *Brunellia mexicana*, *Quercus sapotifolia*, and many shrubby species in the Asteraceae family. Some emergent trees, dominant in later successional stages, such as *Persea americana* were also found. The mean dbh of trees larger than 9 cm dbh was 13.9 ± 0.5 cm. Stage 2 was approximately 45 year-old, sharing many species with stage 1, but presenting a sharp decrease in Asteraceae and in the densities of *P. chiapensis* and *L. macrophylla*. The mean dbh of trees larger than 9 cm dbh was 19.7 ± 1.6. This stage had some elements typical of older forests, such as *Clethra kenoyeri*, *Phyllonoma laticuspis*, and *Rapanea jurgensenii*, commonly found in stage 3, which was approximately 75 years old. In stage 3, fewer and larger individuals of *P. chiapensis* were found. The mean dbh of trees larger than 9 cm dbh was 25.9 ± 2.2 cm. Typical elements found in stage 4 were *Ilex pringlei*, *Osmanthus americana*, *Cornus disciflora*, *Quetzalia occidentalis*, and *Weinmannia pinnata*, corresponding to a mature forest over 90 year-old. *Pinus chiapensis* and *L. macrophylla* were rare or absent in this stage. The mean dbh was 25.3 ± 2.4 cm. Due to the presence of families such as Actinidiaceae, Clethraceae, Chloranthaceae, Cunoniaceae, Ericaceae, Hammamelidaceae, Symplocaceae, Theaceae, and Winteraceae in the upper canopy layer, the old growth forests, and primary forest can be considered as an upper montane rain forests *sensu* WEBSTER (1995).

Field measurements and statistical analyses

In each successional stage, the epiphytes found on the first 160 cm height on the tree stems of 24 trees were sampled. Trees with a dbh greater than 9 cm were randomly chosen from an area of approximately 4 ha, excluding trees located within 15-20 m of the border with other stand types or trails. A total of 6 (stage 1), 13 (stage 2), 16 (stage 3), 19 (stage 4), and 9 (stage 5) families of host trees were sampled (see Appendix).

The epiphytes were sampled using a 10 x 10 cm grid placed on the stem at four height levels: 0-10, 50-60, 100-110 and 150-160 cm, with the 0 cm level located just above the surface of the litter layer. The exposition of the grids was assigned systematically in such a way that the epiphytes on the north side of the stem were sampled on the first tree; those on the south side were sampled on the second tree; those on the west side were sampled on the third tree, and so forth. The cover of mosses, liverworts, lichens, vascular plants, and microscopic epiphytes were recorded to the nearest 1 cm² with the aid of a hand lens and flashlight. Amorphous green layers on the cortex of trees were classified as microscopic epiphytes, as under a microscope, they appeared as masses of filaments, mostly protonema, algae and cyanobacteria. Specimens of each epiphyte found, and a sample of each host tree were collected for more precise taxonomic identification. The dbh of each host tree was also measured.

To investigate epiphyte changes in cover associated with the chronosequences, we used general linear models and the procedure GLM of SAS (SAS INSTITUTE 1990). The following factors were tested for: chronosequence, stand age, partitioned in its linear, quadratic and cubic components, chronosequence by stand age interactions, stem exposition, and dbh of the host tree. Chronosequence factor test for differences associated with the chronosequences studied independently of the age of the stand. The linear component of stand age tests for a linear increase (or decrease) in cover as the age of the stand increases. The quadratic and cubic components test for non-linear changes in cover associated with the age of the stand. The interactions test if changes associated with the age of the stand are conditioned by the chronosequences studied.

No relationship between epiphyte cover and the height of the sampling grid on the stem of the host tree was found, thus, epiphyte cover obtained at each sampling level was summed for the subsequent statistical analysis. Each host tree was considered as a sampling unit. Prior to analyses, the square root of epiphyte cover data was taken to increase the homogeneity of the variances. The abundance of each major epiphyte group per tree was correlated with the abundance of other epiphyte groups using Pearson product-moment correlations.

Results

Epiphytes at the lower portion of the trees (0-160 cm) were abundant in both the primary and secondary forests studied. Only one individual, a *Pinus chiapensis* tree in stage 1 of the Yotao chronosequence, that is 0.3 percent of the trees sampled, did not have epiphytes in the 4 dm² stem area sampled.

Total epiphyte cover at the lower portion of the trees increased significantly with age of the stand. Colonization of epiphytes through time follows a curvilinear pattern resembling a sigmoidal curve. From 0 to 15 years since the establishment of the secondary forest, colonization rate was slow, with the epiphyte cover reaching an average of 15 percent of the lower portion of the stem. The fastest rate of colonization occurred between 15 and 45 years. At the end of this period, epiphytes covered nearly 60 percent of the lower portion of the stem. After 45 years, colonization continued at a slower rate. Between 90 to 100 years after the establishment of the forest, epiphytes still did not reach the epiphyte cover observed in the primary forest, which was approximately 80 percent. Early colonization rate was slightly faster in Yotao chronosequence as shown by the significant linear by site and cubic by site interactions (table 1, Fig. 2A).

Table 1. Summary of general linear model analyses testing for chronosequence, age effects (linear, quadratic and cubic components), tree aspect, dbh of the host tree, and chronosequence by age interactions on total epiphyte, liverwort, moss, macro-, microlichen, and vascular plant cover at tree base along successional gradients in Sierra Juarez mountain range, Mexico; ns = not significant; * = $p \leq 0.05$; ** = $p \leq 0.01$; *** = $p \leq 0.001$; nest = not estimable.

Factor	Total epiphyte cover		Liverwort cover		Moss cover		Macro-lichen cover		Micro-lichen cover		Vascular plant cover		
	df	F	p	F	p	F	p	F	p	F	p	F	p
Site	2	0.9	ns	1.46	ns	0.18	***	2.26	ns	0.33	ns	0.24	ns
Age (linear)	1	56.26	***	19.2	***	5.92	*	0.49	ns	0.15	ns	12.35	***
Age (quadratic)	1	1.21	ns	3.66	*	0.03	ns	0.84	ns	1.12	ns	0.08	ns
Age (cubic)	1	20.21	***	4.67	*	2	ns	0.13	ns	0	ns	0	ns
Tree exposition	3	0.97	ns	1.71	ns	0.52	ns	4.03	**	0.48	ns	2.3	ns
Tree diameter	1	89.53	***	84.5	***	0.34	ns	2.51	ns	5.67	*	0.02	ns
Age (linear) vs.site	2	3.13	*	2.69	ns	0.03	ns	2.58	ns	0.24	ns	_____	nest
Age (quad.) vs.site	2	1	ns	0.48	ns	0.6	ns	2.9	ns	0.29	ns	0.78	ns
Age (cubic) vs.site	2	3.83	*	0.48	ns	2.38	ns	0.96	ns	0.01	ns	_____	nest

Liverworts had the highest variation in cover and a non-linear relationship with stand age. The rates of increase were highest between 15-45 years after abandonment (Fig. 2B, Table 1). Moss cover has a significant linear increase with stand age (Fig. 2C, Table 1), whereas macro- and microlichen cover did not present a statistically significant relationship (Fig. 3A-B, Table 1). Vascular plants were the less abundant and the less common group of epiphytes, and their cover increased linearly with the age of the stand (Fig. 3C, Table 1). Certain groups of vascular plants were only found in later successional stages. Ferns (*Polypodium* sp., Polypodiaceae) were the first and only group of vascular plants observed in stage 1. In stage 2, only ferns (polypodiaceae) and *Selaginella* were observed. Filmy ferns (Hymenophyllaceae) and

Lepanthes spp., a genus of micro-orchids, appeared in stages 4 and 5 while bromeliads were only detected in stage 4. The cover of microscopic epiphytes was not significant in any of the factors analyzed (Fig. 3D, analysis not shown).

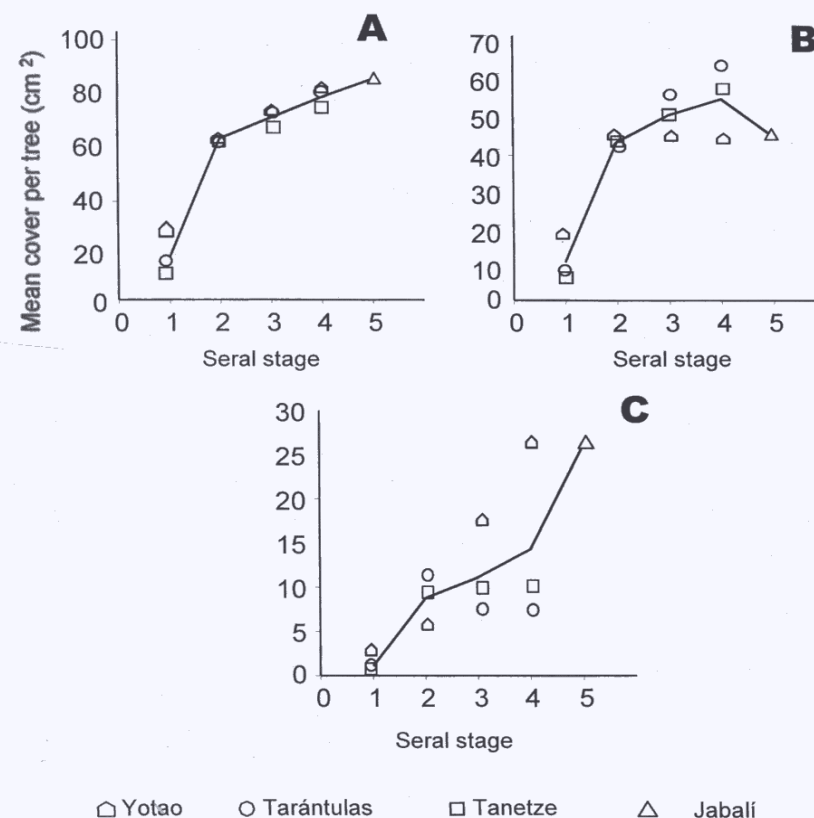


Fig. 2. Epiphyte cover per dm² at the lower portion of the host tree stem in three chronosequences (Tanetze, Tarántulas, and Yotao: stages 1-4), and in El Jabali (stage 5). Data are based on cover sampling of 4 dm² per tree. The line joins the mean epiphyte cover per successional stage of all the trees sampled in each seral stage. A. All epiphytes combined. B. Liverworts. C. Mosses.

Microlichens were more abundant on the S side and less abundant on the N side of trees (Table 1, Fig. 4). No other group of organisms was significantly affected by tree exposition. Epiphyte cover per stem unit area was negatively scaled with the dbh of the host tree. This relationship was also significant in liverworts and macrolichens (Table 1). Separate regression analysis performed on each seral stage between total epiphyte cover (square root transformed) and dbh revealed that such a negative relationship prevails in each seral stage except for the primary forest (Fig. 5).

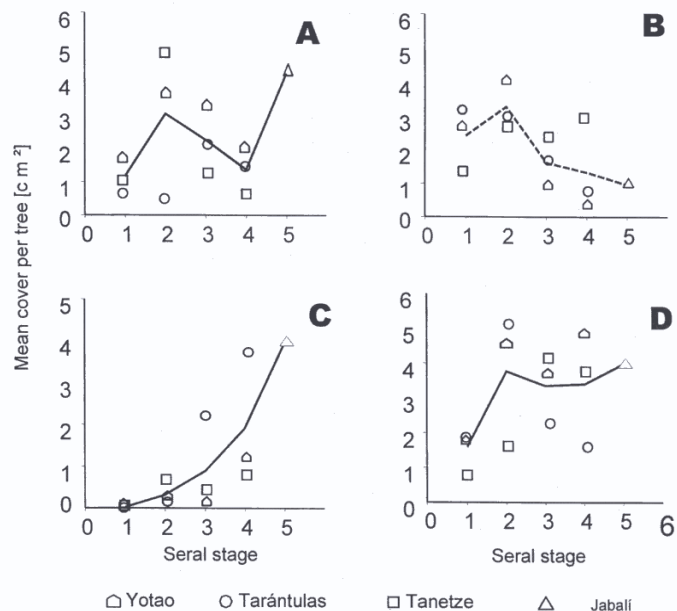


Fig. 3. Epiphyte cover per dm² at the lower portion of the host tree stem in three chronosequences (Tanetze, Tarántulas and Yotao: stages 1-4), and in El Jabali (stage 5). See Fig. 2 for further details. A. Macrolichens. B. Microlichens. C. Vascular plants. D. Microscopic epiphytes.

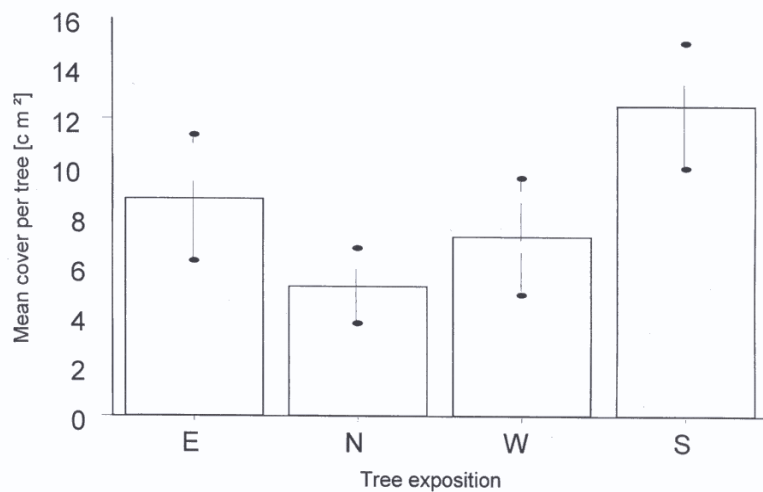


Fig. 4. Relationship between the microlichen cover per dm² (mean \pm 1 standard error) and tree exposition in a upper montane forest area, including a primary forest site and three chronosequences in the Sierra Juárez mountain range, Oaxaca, Mexico.

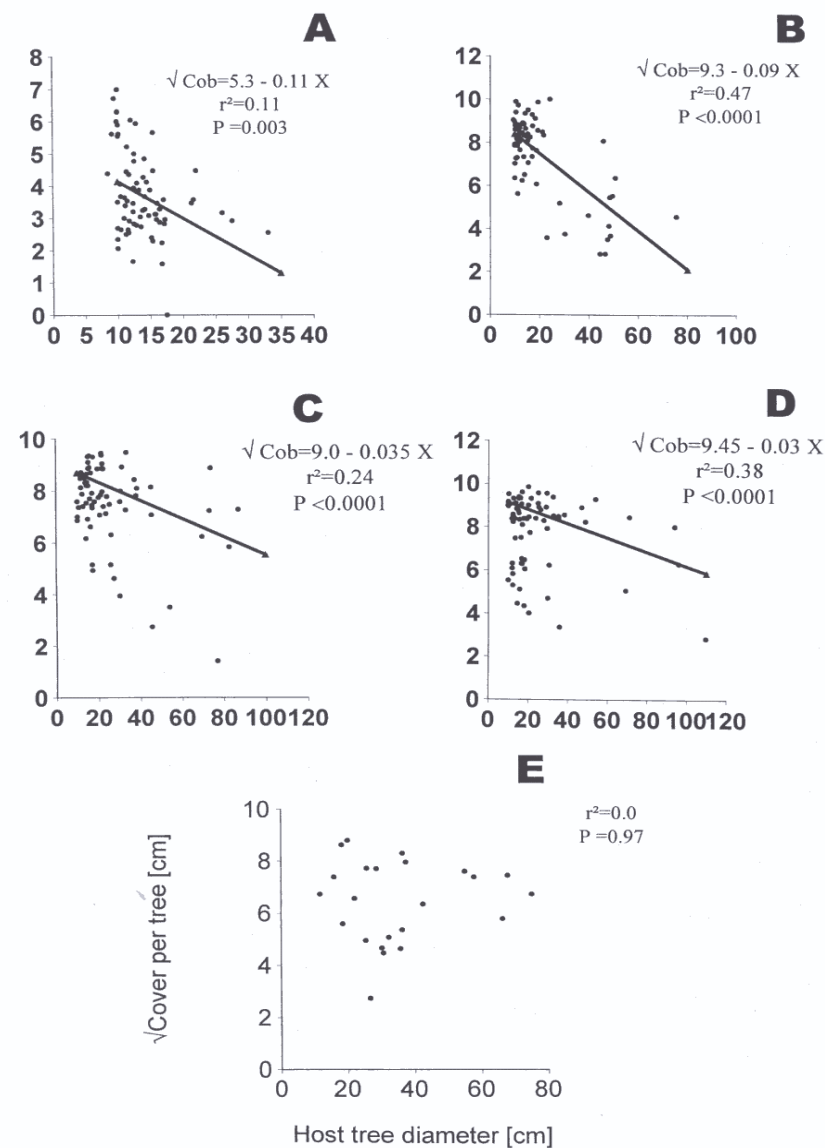


Fig. 5. Relationship between host tree diameter and epiphyte cover per dm². A. Incipient forest (ca. 15 years after abandonment). B. Young forest (ca. 45 years). C. Intermediate forest (ca. 75 years). D. Old-growth forest (> 90 years). E. Primary forest. All located in the Sierra Juárez mountain range, Oaxaca, Mexico.

In all successional stages, liverworts were by far the dominant group. This dominance increased with stand age, with the exception of the primary forest site, where liverwort dominance dropped slightly (Fig. 6). Mosses were the second most important group of epiphytes, followed by lichens. The relative cover of mosses and vascular plants increased continuously towards older successional stages. Macrolichens and microscopic epiphytes displayed an opposite trend, as they were proportionally more abundant in earlier successional stages. Microlichens also decreased slightly in cover with the age of the stand, except at stage 5 where relative cover increased (Fig. 6).

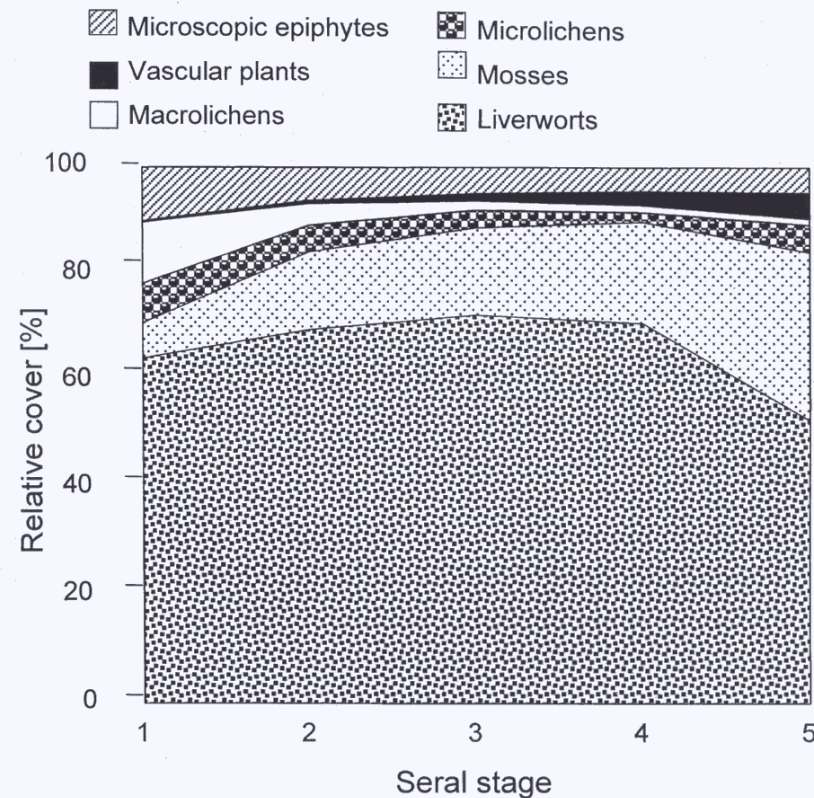


Fig. 6. Relative cover of major groups of epiphytes per seral stage at lower portion of the tree, based on data derived from three chronosequences in Sierra Juarez mountain range, Mexico, each with four seral stages (1-4), and in a nearby primary forest (stage 5).

When combining all data from the three chronosequences and the primary forest, cover of liverworts and vascular plants were positively correlated. Moss cover was positively correlated with that of liverworts, vascular plants, and microscopic epiphytes. Moss and vascular plant cover were negatively correlated with macrolichen cover, which in turn was positively correlated with that of microlichens. Microlichen cover was negatively correlated with microscopic epiphyte cover (Table 2).

Table 2. Pearson correlation coefficients and their significance, testing for associations in the abundance of major epiphyte groups per host tree in primary and secondary forest combined of Sierra Juarez mountain range, Mexico; ns = not significant; * = $p \leq 0.05$; ** = $p \leq 0.01$; *** = $p \leq 0.001$.

	Liverworts	Mosses	Macro lichens	Micro lichens	Vascular plants	Microscopic epiphytes
Liverworts	_____	0.147**	-0.038 ns	-0.016 ns	0.216***	-0.057 ns
Mosses		_____	-0.122*	-0.037 ns	0.204***	0.176***
Macrolichens			_____	0.136*	-0.117*	-0.057 ns
Microlichens				_____	0.067 ns	-0.113*
Vascular plants					_____	0.048 ns
Microscopic						_____

Discussion

The present study shows that abundance of epiphytes at the lower portion of the stem may change dramatically during secondary succession of TMCFs. However, the increase in abundance throughout the process of succession could be the consequence of at least three interacting factors: (1) colonization time, (2) micro-environmental changes during forest succession, and (3) biotic interactions involving inhibitory or facilitation processes (*sensu* CONNELL & SLATYER 1977), in which the first epiphytes established favor or inhibit the subsequent establishment of other epiphytes.

Time after disturbance has been an important factor in explaining the diversity of epiphytes in other systems (YEATON & GLADSTONE 1982; PHARO *et al.* 1999). Although not a rule, large trees are on average older than small trees, therefore, the lower levels of their stems are exposed for more time for colonization by epiphytes. Indeed, after disturbance, the first habitat to be colonized by bryophytes was the base of vascular plants in sand-pine scrub forest in Florida (EQUIHUA 1989). Nevertheless, the present study reveals that epiphyte cover per stem unit area tends to decrease as the diameter of the host tree increases even in old second-growth forests. Thus, it may be deduced that substrate availability and time of colonization are not the most important factors limiting the abundance of epiphytes at the lower portion of the stems, at least during the secondary succession of TMCFs.

The increase in epiphyte cover in older forests could be attributable in part to microclimatic variations associated with vegetational changes during succession. Greater canopy closure in primary tropical montane forests, compared with the canopy closure in secondary forests, results in increased humidity at lower levels in the forest by increasing fog catching ability and by decreasing direct sunlight exposure (BRUIJNZEEL & PROCTOR 1995). Old-growth forests also presents emergent young shade tolerant trees (BLANCO-MACÍAs 2001). The data obtained through this study indicates that these young trees, with smaller diameters, are the most suitable for epiphyte establishment. The presence of such trees and the more suitable microclimatic conditions of mature forests may help explain why older forests present a greater abundance of epiphytes. In a Neotropical montane forest in Costa Rica, shade tolerant woody plants were found to be the most adequate host for non-vascular epiphytes (ROMERO 1999).

If changes in humidity contribute to the differences in epiphyte cover observed in the chronosequences, it would be expected that those epiphytes more vulnerable to moisture deficit be the ones that have the higher rates of cover variation during forest succession. Sexual reproduction in bryophytes and ferns depend on a film of water on the undersurface of the gametophyte; lichens, on the other hand, are not known to depend on free water for their reproduction (BOLD *et. al.* 1980). Also, moisture availability is crucial for bryophyte development (BRUIJNZEEL & PROCTOR 1995). The higher sensitivity of bryophytes to water deficits may explain why moss and liverwort cover increased significantly with the successional stage. The common water requirements of bryophytes and ferns may explain the correlations detected in abundance between mosses, liverworts and vascular plants and their increase in abundance in older successional stages.

The fact that microlichens were more abundant on the south side of the trees also supports the idea that lichens are less affected by moisture deficits. The south side is expected to be the driest side of the trunk, as the Gulf of Mexico clouds, the most important source of humidity, come from the north. Other studies also support the idea that lichens are less drought-sensitive than are bryophytes. In a TMCF study in Hawaii, SMITH (1995) found that lichens dominated the driest montane forests, and their abundance decreased in more humid habitats. By contrast, bryophytes were more abundant in the humid montane rain forest. WOLF (1994) found that macro-lichens occur more abundantly in the exposed outer canopy than in the sheltered inner canopy of cloud forest trees.

The apparent lower water requirement of lichens may explain the negative correlation detected between lichens and bryophytes. Positive correlations between the biodiversity of bryophytes and that of vascular plants and negative correlations of these two groups with the biodiversity of lichens were obtained for a dry forest of Australia. Such results were explained by different moisture requirements between bryophytes and lichens (PHARO *et. al.* 1999). Alternatively, the negative correlation between lichens and other groups of epiphytes could reveal the existence of competition or inhibitory effects.

A facilitation process is another possible mechanism involved in the changes observed. Bryophytes are well known for trapping propagules and holding a substantial amount of water (PÓCS 1980). All of this may favor the establishment of certain groups of plants, as appear to be the case of *Polypodium* which grow well on top of bryophytes. By contrast, the micro-orchids, *Lepanthes*, usually establish directly on the cortex without any apparent layer of moss or liverworts (personal observation). Thus, the positive correlation between successional stage and epiphyte cover per unit area can be explained in some cases as the result of interactions between different types of epiphytes, and in other cases, by allochthonous processes such as microclimatic changes associated with forest succession.

Several factors may help explain why large trees have less epiphyte cover per unit of stem area at the lower portion of the stem. Epiphyte colonization rates occur probably at lower rates than the stem growth. Also, the substrate may become less stable as the tree grows in some species. For instance, in *P. chiapensis* the cortex may be shed by the attack of xylophagous insects. Moreover, stemflow at the base of the tree trunk may reach higher speeds in taller trees. Thus, the likelihood of epiphyte displacement by stemflow is expected to be greater in larger trees. In addition, the large amount of foliage of large trees may inhibit epiphyte growth by not allowing enough light to penetrate the canopy, resulting in insufficient light levels for epiphyte estab-

lishment. Indeed, epiphytes only exhibit positive growth when canopy closure was below a specific threshold level (e.g. ROMERO 1999). The cross-sectional area of sap wood in a tree stem is closely correlated with the amount of foliage (W ARING & SCHLESINGER 1985).

The replacement of primary or late successional forest dominated by hardwoods, by early successional forests, dominated by pine, is a common occurrence in the tropical montane forests of southern Mexico (GONZALEZ-ESPINOSA *et. al.* 1995). Such forest conversion results in decreased epiphyte abundance and diversity. The results of this study show that young forests harbor approximately 25 percent of the total epiphyte cover found in primary forests. A secondary forest will take more than 100 years to reach the level of epiphyte abundance found in a primary forest. Moreover, certain groups of plants such as orchids and bromeliads were only detected in later successional stages. *Lepanthes* orchids were particularly abundant in the later successional stages of the chronosequences of Tarantulas and Tanetze; this area has been reported to have the highest diversity of this genus (SALAZAR-CHÁVEZ & SOTO ARENAS 1996). Epiphyte reduction by forest conversion may, in turn, affect ecosystem processes in which epiphytes are involved, such as nutrient cycling (COXSON 1991; HAMILTON *et. al.* 1995; CLARK *et. al.* 1998), and hydrological process (W ARING & SCHLESINGER 1985). Also, conversion to pine forests resulting in drier and warmer micro-climates suggests that fire propensity is higher in these types of forests, and thus the survival of epiphytic plants is endangered. EQUIHUA (1989) found that fires in sand pine scrub destroy most of the epiphyte substrate.

Given the fast and severe degradation of TMCF in Mexico, one of the big challenges is to preserve remnant forests, restore altered forests, and harvest managed forests in a sustainable manner. The present study provides evidence that the abundance and composition of epiphytes at the lower portion of the stem are properties that can be used to monitor the condition of the TMCF, given the great sensitivity of this group of plants to vegetation changes. Bryophytes, and liverworts in particular, are among the best candidates for monitoring purposes as they are both abundant and sensible to forest changes.

Acknowledgements

We thank Raúl Rivera García for his invaluable field assistance, cartographic and editorial work. Onil Banerjee provided editorial help and s. Acosta for his help with tree identification. Two reviewers "offered useful comments and suggestions. We appreciate the support of the Cordova family, Alfredo Espinosa, and COFAA. This research project was funded by grants from The Darwin Initiative for the Survival of Species (United Kingdom), through A. Newton and R. F. del Castillo, and by CONACyT, Sistema de Investigación Benito Juárez and Instituto Politécnico Nacional through R. F. del Castillo.

References

- ACOSTA CASIELLANOS, S. (1997). Afinidades fitogeográficas del bosque mesófilo de montaña de la zona de Pluma Hidalgo, Oaxaca, México. *Polibotánica* 6: 25-30.
- ANONYMOUS (1999). *Anuario Estadístico del Estado de Oaxaca*. Instituto Nacional de Geografía e Informática, Aguascalientes, Ags. México.
- BLANCO MACIAS, A. (2001). *Estudio de la Suscesión Secundaria en el Bosque Mesófilo de El Rincón, Sierra Norte Oaxaca*. Bachelór thesis, Universidad Nacional Autónoma de México, Iztacala, Mexico.
- BOLD, H. C., ALEXOPOULOS, C.J. & DELEVORYAS, T. (1980). *Morphology of Plantr and Fungi*. 4d1 Ed. Harper & Row, New York.

- BRUIJNZEEL, L. A. & PROCTOR, J. (1995). Hydrology and biogeochemistry of tropical montane cloud forest: What do we really know? *In*: HAMILTON, L. S., JUVICK, J. O. & SCATENA, F. N. (eds). *Tropical Montane Forest*: 38-78. Springer, New York.
- BRUIJNZEEL, L. A. & VENEKLAAS, E. J. (1998). Oimatic conditions and tropical montane forest productivity: the fog has not lifted yet. *Emlogy* 79: 3-9.
- CAVELIER, J, SOLIS, D. & JARAMILLO, M. A. (1996). Fog interception in montane forest across the Central Cordillera of Panama. *Journal of Tropical Ecology* 12: 357-369. ; CHURCHILL, S. P., GRIFFIN, A. & LEWIS, M. (1995). Moss diversity of tropical Andes. *In*: Churchill, S. P., Balslev, H., Forero, E. & Luteyn, J. L. (eds). *Biodiversity and Conservation of Neotropical Montane Forest*: 335-346. The New York Botanical Garden, New York.
- CLARK, K. L., NADKARNI, N. M. & GHORZ, H. L. (1998). Growth net production, litter decomposition, and net nitrogen accumulation by epiphytic bryophytes in a tropical montane forest. *Biotropica* 30: 12-23.
- CONNELL, J. H. & SLATYER, R. O. (1977). Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist* 111: 1119-1144.
- COXSON, D. S. (1991). Nutrient release from epiphytic bryophytes in tropical montane rain forest (Guadeloupe). *Canadian Journal of Botany* 69: 2122-2129.
- DEL CASTILLO, R. F. (1996). Aspectos autoecológicos de *Pinus chiapensis*. *In*: *Memorias del 2do. Coloquio Regional de Investigación, Ciencias Exactas y Naturales*: 63-68. Universidad Autónoma del Estado de México, Toluca, Estado de México.
- EQUIHUA, C. (1989). *Bryophyte Succession After Fire in a Florida Sand-Pine Scrub*. M.Sc. Thesis, University of Florida, Gainesville, Florida.
- ESSEN, P.-A., RENHORN, K. E. & PETIERSSON, R. B. (1996). Epiphytic lichen biomass in managed and old-growth boreal forest: effect of branch quality. *Ecological Applications* 6: 228-238.
- FIELD, T. S. & DAWSON, T. E. (1998). Water sources used by *Didymopanax Pittieri* at different life stages in a tropical cloud forest. *Ecology* 79: 1448-1452.
- GONZALEZ-ESPINOSA, M., QUINTANA-ASCENCIO, P. F., RAMIREZ-MARCIAL, N. & GAYTÁN GUZMÁN, P. (1991). Secondary succession in disturbed *Pinus-Quercus* forests in the highlands of Chiapas, México. *Journal of Vegetation Science* 2: 351-360.
- GONZALEZ-ESPINOSA, M., OCHOA-GAONA, S., RAMIREZ-MARCIAL, N. & QUINTANA-ASCENCIO, P. F. (1995). Current land use trends and conservation of old growth forest habitats in the highlands of Chiapas, Mexico. *In*: Wilson, M. H. & Sader, S. A. (eds). *Conservation of Neotropical Migratory Birds in Mexico*: 190-198. Maine Agricultural and Forest Experiment Station Miscellaneous Publication 727, Orono, ME.
- GRADSTEIN, S. R. (1995). Diversity of Hepaticae and Anthocerotae in montane forest of the tropical Andes. *In*: Churchill, S. P., Balslev, H., Forero, E. & Luteyn, J. L. (eds). *Biodiversity and Conservation of Neotropical Montane Forest*: 321-334. The New York Botanical Garden, New York.
- HAMILTON, L. S., JUVICK, J. O. & SCATENA, F. N. (1995). *Tropical Montane Cloud Forest* [Ecological Studies 110]. Springer, New York.
- JACKSON, R. B., SCHENK, H. J., JOBBAGY, E. G., CANADELL, J., COLELLO, G. D., DICKINSON, R. E., FIELD, C. B., FRIEDLINGSTON, P., HEIMANN, M. & HIBBARD, K. (2000). Below-ground consequences of vegetation change and their treatment in models. *Ecological Applications* 10: 470-483.
- JARDEL, E., SANTIAGO, A. L. & MUÑOZ, M. (1993). El bosque mesófilo de montaña de la Sierra de Manandán. *Tiempos de Ciencia (Mexico)* 30: 20-28.
- KEDDY, P. A. & DRUMMOND, C. G. (1996). Ecological properties for the evaluations, management, and restoration of temperate deciduous forest ecosystems. *Ecological Applications* 6: 748-762.
- MEAVE, J., SOTO, M. A., CALVO, I. L. M., PAZ, H. H. & VALENCIA, A. S. (1992). Análisis sin ecológico del bosque mesófilo de montaña de Omiltemi, Guerrero. *Boletín de la Sociedad Botánica de México* 52: 31-77.
- MERLIN, M. D. & JUVICK, J. O. (1995). Montane cloud forest in the tropical Pacific: some aspects of their floristics, biogeography, ecology, and conservation. *In*: Hamilton, L. S., Juvick, J. O. & Scatena, F. N. (eds). *Tropical Montane Cloud Forest* [Ecological Studies 110]: 234-253. Springer, New York.
- ORTEGA, E. S. & CASTILLO, C. G. (1996). El bosque mesófilo de montaña y su importancia forestal. *Ciencias (Mexico)* 43: 32-39.
- PECK, J., & McCUNE, B. (1997). Remnant trees and canopy lichen communities in western Oregon: a retrospective approach. *Ecological Applications* 7: 1181-1187.
- PHARO, E. J., BEATHE, A. J. & BINNS, D. (1999). Vascular plant diversity as a surrogate for bryophyte and lichen diversity. *Conservation Biology* 13: 282-292.
- POCS, T. (1980). The epiphytic biomass and its effect on the water balance of two rain forest types in the Uluguru mountains (Tanzania, east Africa). *Acta Botanica Academiae Scientiarum Hungaricae* 26: 143-167.
- ROMERO, C. (1999). Reduced-impact logging effects on commercial non-vascular pendant epiphyte biomass in a tropical montane forest in Costa Rica. *Forest Ecology and Management* 118: 117-125.
- RZEDOWSKI, J. (1978). *La Vegetación de México*. Editorial Limusa, Mexico.
- RZEDOWSKI, J. (1991). Diversidad y orígenes de la flora fanerogámica de México. *Acta Botánica Mexicana* 14: 3-21.
- SALAZAR-CHÁVEZ, G. A. & SOTO ARENAS, M. A. (1996). El género *Lepanthes* SW en México. *Orquidea* 14: 1-231.
- SAS INSTITUTE (1990). *SAS/STAT User's guide, Version 6*. 4th ed. SAS Institute Inc., Cary, NC.
- SCHUSTER, R. M. (1988). Ecology, reproductive biology and dispersal of hepaticae in the tropics. *Journal of the Hattori Botanical Laboratory* 64: 237-269.
- SIPMAN, H. J. M. (1995). Preliminary review of the lichen biodiversity of the Colombian Montane forests. *In*: Churchill, S. P., Balslev, H., Forero, E. & Luteyn, J. L. (eds). *Biodiversity and Conservation of Neotropical Montane Forest*: 313-320. The New York Botanical Garden, New York.
- SMITH, C. W. (1995). Lichens as indicators of cloud forest in Hawaii. *In*: HAMILTON, L. S., JUVICK, J. O. & SCATENA, F. N. (eds). *Tropical Montane Cloud Forests* [Ecological Studies 110]: 309-314. Springer, New York.
- YEATON, R. I. & GLADSTONE, D. E. (1982). The pattern of colonization of epiphytes on calabash trees (*Crescentia alata* HBK) in Guanacaste Province, Costa Rica. *Biotropica* 14: 137-140.
- WARING, R. H. & SCHLESINGER, W. H. (1985). *Forest Ecosystems Concepts and Management*. Academic Press, Orlando, Florida.
- WEBSTER, G. L. (1995). The panorama of neotropical cloud forests. *In*: Churchill, S. P., Balslev, H., Forero, E. & Luteyn, J. L. (eds). *Biodiversity and Conservation of Neotropical Montane Forest*: 53-77. The New York Botanical Garden, New York.
- WILUAMS-LINERA, G. (1992). Ecología del paisaje y el bosque mesófilo en el centro de Veracruz. *Ciencia y Desarrollo (Mexico)* 105: 133-138.
- WOLF, J. H. D. (1993). Diversity patterns and biomass of epiphytic bryophytes and lichens along altitudinal gradient in northern Andes. *Annals of the Missouri Botanical Garden* 80: 928-960.
- WOLF, J. H. D. (1994). Factors controlling the distribution of vascular and non-vascular epiphytes in the Northern Andes. *Vegetation* 112: 15-28.

Appendix. Host trees sampled for epiphytes by taxonomic category and seral stage (stages 1-4) in three chronosequences and in an adjacent area of primary forest (stage 5) in Sierra Juarez Mountain range, Oaxaca, Mexico.

Family	Genus	Species	Stage				
			1	2	3	4	5
Actinidiaceae	<i>Saurauia</i>	sp.					1
Aquifoliaceae	<i>Ilex</i>	<i>pringlei</i>			3	2	
Araliaceae	<i>Dendropanax</i>	sp.			1	2	
Araliaceae	<i>Oreopanax</i>	<i>xalapensis</i>				2	
Araliaceae	<i>Oreopanax</i>	<i>flaccidum</i>					1
Betulaceae	<i>Alnus</i>	<i>acuminata</i>		1			
Brunelliaceae	<i>Brunellia</i>	<i>mexicana</i>	5				
Caprifoliaceae	<i>Viburnum</i>	<i>acutifolium</i>			1		
Caprifoliaceae	<i>Viburnum</i>	<i>discolor</i>				2	
Celastraceae	<i>Quetzalia</i>	<i>occidentalis</i>			2	3	
Clethraceae	<i>Clethra</i>	sp.		3	6	5	
Clethraceae	<i>Clethra</i>	<i>integerrima</i>		6			
Clethraceae	<i>Clethra</i>	<i>kenoyeri</i>			1	1	
Cornaceae	<i>Cornus</i>	<i>disciflora</i>		2			
Cunoniaceae	<i>Weinmannia</i>	<i>pinnata</i>		3	4	4	
Chloranthaceae	<i>Hedyosmum</i>	<i>mexicanum</i>	1	2			
Ericaceae	Unidentified			2		1	
Ericaceae	<i>Gaultheria</i>	<i>acuminata</i>		1			
Ericaceae	<i>Bejaria</i>	<i>mexicana</i>		1		1	
Ericaceae	<i>Lyonia</i>	<i>squamulosa</i>		1			
Ericaceae	<i>Vaccinium</i>	sp.			1		
Ericaceae	<i>Vaccinium</i>	<i>leucanthum</i>			1		
Euphorbiaceae	<i>Alchornea</i>	<i>latifolia</i>			3	1	
Fagaceae	<i>Quercus</i>	sp.		5	6	6	
Fagaceae	<i>Quercus</i>	<i>sapotifolia</i>		1			
Fagaceae	<i>Quercus</i>	<i>salicifolia</i>				1	1
Fagaceae	<i>Quercus</i>	<i>laurina</i>				1	1
Fagaceae	<i>Quercus</i>	<i>corrugata</i>					1
Guttiferae	<i>Vismia</i>	<i>camparaguey</i>		1			
Hamamelidaceae	<i>Liquidambar</i>	<i>macrophylla</i>	18	7	6	5	
Hippocastanaceae	<i>Billia</i>	<i>hippocastanum</i>				2	
Lauraceae	<i>Beilschmiedia</i>	<i>ovalis</i>			1		1
Lauraceae	<i>Persea</i>	sp.		10	6		1
Lauraceae	<i>Persea</i>	<i>americana</i>				2	
Lauraceae	<i>Persea</i>	<i>liebmannii</i>				3	
Lauraceae	<i>Ocotea</i>	<i>helicterifolia</i>				5	2
Lauraceae	<i>Cinnamomum</i>	<i>zapatae</i>					1
Magnoliaceae	<i>Magnolia</i>	<i>dealbata</i>	1	5	3	1	
Melastomataceae	<i>Miconia</i>	sp.		2			
Myricaceae	<i>Myrica</i>	<i>mexicana</i>			3		
Myrsinaceae	<i>Rapanea</i>	sp.		3			
Myrsinaceae	<i>Rapanea</i>	<i>jurgensenii</i>			3	2	
Myrsinaceae	<i>Rapanea</i>	<i>myricoides</i>			1		
Myrtaceae	unidentified					1	
Phyllonomaceae	<i>Phyllonoma</i>	<i>laticuspis</i>			1		
Pinaceae	<i>Pinus</i>	<i>chiapensis</i>	45	13	8	4	
Pinaceae	<i>Pinus</i>	<i>patula</i>			1		
Pinaceae	<i>Pinus</i>	<i>pseudostrobus</i>					3
Podocarpaceae	<i>Podocarpus</i>	<i>matudai</i>					1
Rutaceae	<i>Zanthoxylum</i>	<i>melanostictum</i>				1	
Symplocaceae	<i>Symplocos</i>	sp.					2
Symplocaceae	<i>Symplocos</i>	<i>coccinea</i>					1
Theaceae	<i>Ternstroemia</i>	<i>mutis</i>					2
Theaceae	<i>Ternstroemia</i>	<i>oocarpa</i>				3	1
Theaceae	<i>Ternstroemia</i>	sp.		3	2		
Theaceae	Unidentified	sp.					3
Theaceae	<i>Freziera</i>	sp.			1	3	
Theaceae	<i>Cleyera</i>	sp.				1	

Family	Genus	Species	Stage				
			1	2	3	4	5
Ticodendraceae	<i>Ticodendron</i>	<i>incognitum</i>					2
Winteraceae	<i>Drimys</i>	<i>granadensis</i> var. <i>mexicana</i>					2
Unidentified				1	6	3	1