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## Secondary succession in disturbed *Pinus-Quercus* forests in the highlands of Chiapas, Mexico

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**Abstract.** We present floristic and structural data on seral plant communities (Old-Field, Grassland, Shrubland, and Early Successional, Mid-Successional, and Mature Forest) resulting from the current land use pattern in the *Pinus-Quercus* forests in the highlands of Chiapas, Mexico. The number of species ranged from 24 in the Old-Field stage up to 100 in the Mature Forest, and the shrub layer was richest in all the forested stands. An almost complete floristic replacement exists between the open and the forested communities. *Quercus* and *Pinus* dominate the canopy of old-growth stands, but their recruitment does not occur or is very low in the shade. Vigorous seedlings and saplings of these species are found only in the open seral stages or in forest gaps. Demographic and phytosociological data are used to indicate the successional role of dominant species in the forested stages. Some implications of the regional land use patterns for conservation and succession are discussed.

**Keywords:** Chronosequence; Evergreen broad-leaved forest; Forest conservation; Montane rain forest; Regeneration; Tropical highlands; Vegetation structure.

**Identification and Nomenclature:** Rzedowski & Rzedowski (1979, 1985); Smith (1981); Standley & Williams (1976) and older works cited therein. Plants were identified and voucher specimens deposited at the Herbario-Hortorio of the Centro de Botánica, Colegio de Postgraduados, Chapingo, México.

### Introduction

Forest disturbance by logging, grazing, or farming starts or maintains a local revegetation process with changes in the original floristic composition and the age structure of the persistent species. At the landscape level, the complexity of the resulting successional sere depends on the overlapping of different land use patterns and practices through time and space (Keever 1950). On a regional scale, habitat utilization for forest and agricultural production fragments the primary landscape,

affecting the natural regeneration of some of the species in and from the remnant patches (Gómez-Pompa, Vázquez-Yáñez & Guevara 1972).

Understanding vegetation changes provoked by land use is essential for the application of management practices involving natural regeneration (Ewel 1979; Miles 1987). The effect of human activities in driving successional chronosequences has, so far, been overlooked by plant ecologists who have been mostly interested in those natural processes accounting for species replacement and community organization through time (e.g. Drury & Nisbet 1973; Connell & Slatyer 1977; Pickett, Collins & Armesto 1987). However, detailed accounts of successional seres incorporating the effects of regional land use patterns may provide information on less known aspects such as: the ability of exotic species to invade, the modification of the natural mechanisms of species replacement, the alteration of their demographic structure and successional role. In this connection, we may point to some of the limitations of current ecological theory for vegetation management.

In the highlands of Chiapas (1500-2700 m), southern Mexico, a complex vegetation mosaic has resulted from traditional hillside milpa agriculture and unplanned extensive logging for commercial purposes. A few decades ago the region was mostly covered by pine, oak, and pine-oak forests (seasonal formations), and evergreen cloud forests (Miranda 1952; Breedlove 1981). The high density of the inhabitant Mayan groups (Parra-Vázquez & Mera-Ovando 1989), and their unfavorable labor and economic relationships with the regional and national economy have forced them to modify their traditional slash and burn agricultural system (Alemán-Santillán 1989). The current landscape includes extensive young secondary forests, permanently cleared grazing and cultivated areas, and only small old-growth forest stands on the highest and/or steepest slopes (Wagner 1962).

We present an account of floristics and vegetation

structure of representative seral communities related to mesic pine-oak forests of the highlands of Chiapas. Density estimates and size-class distributions of living and dead individuals are used to determine the successional role of dominant and subdominant species. The results are pertinent to understanding forest dynamics in other high tropical regions with similar land use patterns in Central and South America.

### Study sites

Two sites (Ejido Chilil and Rancho Merced-Bazom; 5 km apart), of similar climate, elevation, soil type, topography, and vegetation mosaic were studied. The sites are located in the municipality of Huixtán (16°45' N, 92°30' W; 2300-2400 m) in the central part of the highlands of Chiapas, Mexico. The regional climate is temperate subhumid (García 1988), with a mean annual temperature of 13-14 °C, and 1100 - 1200 mm of mean annual rainfall (> 80% of the rainfall occurs mainly in May-October; data from 15-year records at the Chilil meteorological station). Nocturnal freezing temperatures may be frequent, particularly in non-forested areas, from December through March; freezing temperatures do not occur at the forest floor level in closed stands (Breedlove 1981; M. González-Espinosa, pers. observ.). The soils are dark brown, clayey loams, moderately deep (30 - 50 cm), and derived from Cretaceous calcareous rocks (Mera-Ovando 1989).

For centuries slash and burn agriculture in the region has maintained the spatial and temporal co-occurrence of all the successional stages following milpa abandonment (Collier 1975). Therefore, the chronosequence approach to the study of succession (Daubenmire 1968) was followed based on the assumption that the selected stands belong to the same successional sere and differ mostly because of their age. We propose the following stands as representative of secondary succession in those areas of the highlands of Chiapas where the more traditional agricultural systems are practised:

a. Old-Field. Fallow 3-4 years after the last milpa cultivation; grazed by sheep.

b. Grassland. Grazed by sheep. We do not know precisely when the last milpa cultivation occurred; this successional stage may remain stable for an indefinite time if moderately grazed.

c. Shrubland. Grazed by sheep and with at least three vegetation layers.

d. Early Successional Forest. The most frequent mean age of pines is 20-25 yr (counts of annual rings on cores). Dominant trees form a canopy of 80-90% cover at a height of 10-15 m. A few small epiphytes occur on

the largest branches. Some fuelwood and/or small poles are occasionally collected.

e. Mid-Successional Forest. Mean age of the oldest pines is 40-45 yr. The tallest trees form a canopy of 70-80% cover at a height of 20-25 m. Bromeliads, orchids, and epiphytic ferns cover most of the large branches. Some fuelwood, small poles, and occasionally large logs and epiphytes are collected.

f. Mature Forest. The oldest pines have a mean age of 80-100 yr. There is an open canopy at 35-45 m, and a more continuous understory tree layer at 8-12 m. A heavy cover by diverse epiphytes is typical of this forest. Fuelwood, poles, and some logs are regularly collected. A wind storm swept the site early in 1982 creating gaps in the canopy (M. Martínez-Icó, pers. comm.). We only sampled the large mature patches in the site (ca. 8 ha) where no recent severe disturbance provoked by natural or human causes was evident. We have not found an older pine-oak forest stand in the highlands of Chiapas.

### Materials and Methods

#### *Vegetation sampling*

Standard vegetation measurement methods (Mueller-Dombois & Ellenberg 1974) were used to estimate density, dominance, and frequency for each species (exclusive of epiphytes) in each layer:

a. Prostrate herbs in open stands: point-intercept method (2000 sampling points at intervals of 10 cm along 100 2-m sampling lines, set on 10 independent and randomly located groups).

b. Erect and prostrate 'herbs' (0-49 cm height) in closed stands (included lianas, vines, and seedlings and young shrubs and trees): quadrat method (30 independent and randomly located quadrats or subsamples, 10.0 m × 0.2 m each; sampling units were divided into 10 subquadrats of 1.0 m × 0.2 m for frequency estimates). Each plant rooted inside the quadrat was counted and its cover (maximum length × width of its foliage) was measured. Seedlings of tree and shrub species in the Shrubland were sampled using 100 quadrats (2 m × 1 m each).

c. 'Shrubs' (50-299 cm height, including saplings): quadrat method (25-30 independent and randomly located quadrats or subsamples, 10.0 m × 2.0 m each; sampling units were divided into 10 subquadrats of 2.0 m × 1.0 m for frequency estimates). Individuals rooted inside the quadrat were counted and their cover (maximum length × width of foliage) and height were measured.

d. Small 'trees' (>300 cm height and <15 cm DBH,

diameter at breast height, including some large shrubs): point-centered quadrat method (90-200 sampling points; 360-800 individuals). Living and dead individuals were included; identification of the latter was based on external and inner bark characteristics. The age of pines was estimated from tree growth rings in cores obtained at DBH. Rainfall and temperature seasonality suggest yearly growth rings.

e. Large trees (>15 cm DBH): point-centered quadrat method (90-200 sampling points; 360-800 individuals). Similar to above.

f. Additional samples of 90 (Early Successional), 200 (Mid-Successional), and 150 (Mature Forest) dead trees from throughout the stands were obtained for a more reliable estimate of their relative abundance.

### Analysis

Evaluation of the successional status of dominant and subdominant species was based on absolute density and dominance estimates, and on tree population size structures.  $\chi^2$  heterogeneity tests were used to compare the relative contribution of each species to the total number of living vs. dead trees (Zar 1984). The size-class distribution of living vs. dead plants was compared with two-sample, two-tailed Kolmogorov-Smirnov tests (Zar 1984). The significance of absolute density differences among stands was evaluated with the subsamples (Kruskal-Wallis & Dunn tests; Zar 1984; but see Hurlbert 1984). Calculations were performed with the Statgraphics software.

## Results

### Floristic composition and structure

#### Old-Field

Only one prostrate vegetation layer was recorded. Dominant species included both annuals and perennials (Table 1), and only 49% of the ground was covered with vegetation (Table 2). One third of the species was found only in this community. A few exotic species were recorded (Table 1). No seedlings of any shrub or tree species were found in this stand.

#### Grassland

Only one prostrate layer was recorded (Table 2), and the ground was mostly covered by vegetation or litter (Table 1). About one third of the species was restricted to this stand, and a considerable number (66%) was also found in the Shrubland. The perennials *Dichondra sericea* and *Oxalis corniculata* also occurred in some of the forested stands. Some seedlings of the shrubs

**Table 1.** Importance value (%) of species in the prostrate herbaceous layer of the Abandoned Old-Field (OLF), Grassland (GRA), and Shrubland (SHR) successional stands. (A) = annual, (P) = perennial, \* = exotic species, + = importance value < 1.0%.

Species <sup>1</sup>	OLF	GRA	SHR
Herbaceous composites			
<i>Dyssodia papposa</i> (A)	24.5		
<i>Stevia ovata</i> (P)			2.0
<i>Tagetes filifolia</i> (A)		5.3	+
Asteraceae 7	3.7		
Grasses			
<i>Aegopogon cenchrroides</i> (P)	9.0	4.3	9.4
<i>Axonopus affinis</i> (P)		4.9	
<i>Bromus carinatus</i> (A)*	1.9		
<i>Eragrostis</i> sp. (A)	8.7	4.9	1.6
<i>Panicum</i> sp. (P)		1.8	10.0
<i>Paspalum jaliscanum</i> (P)	+	10.6	6.1
<i>Paspalum minus</i> (P)	3.3	2.6	22.8
<i>Pennisetum clandestinum</i> (P)*	+	2.1	
<i>Poa annua</i> (A)*	+	1.5	
<i>Setaria geniculata</i> (P)	13.6	3.4	1.3
<i>Sporobolus indicus</i> (P)	3.0	17.5	1.3
<i>Vulpia bromoides</i> (A)	1.1	9.0	2.9
Other herbs and forbs			
<i>Alchemilla aphanoides</i> (P)	1.9	+	+
<i>Cuphea aequipetala</i> (P)	4.4		
<i>Dichondra sericea</i> (P)	2.3	1.1	+
<i>Houstonia serpyllacea</i> (P)	6.3	15.7	16.5
<i>Trifolium amabile</i> (P)	12.3	6.9	11.2
<i>Viola</i> sp. (P)	1.7	4.4	8.3
Relative cover (%)			
Bare ground <sup>2</sup>	40.8	2.2	4.3
Litter <sup>2</sup>	10.4	16.3	35.8

<sup>1</sup> Other species with importance value <1.0 in any of the stands were *Cirsium* sp. (P), *Galinsoga quadriradiata* (A), *Jaegeria hirta* (A), *Spilanthes oppositifolia* (P), *Stevia serrata* (P), *Taraxacum officinale* (P)\*, *Aristida* sp. (A), *Muhlenbergia vaginata* (A), *Paspalum* sp. (P), *Trinichloa stipoides* (P), *Zeugites americana* var. *mexicana* (P), *Cologania broussonetii* (P), *Cyperus* sp. (P), *Euphorbia* sp. (A), *Micropleura renifolia* (P), *Oxalis corniculata* (P), *Plantago australis* ssp. *hirtella* (P), *Stachys* sp. (P), *Baccharis vaccinioides*, *Cleyera theaeoides*, *Rubus pringlei*, *Asteraceae* 1 (*Verbesina* sp.?), 3 *Asteraceae*, 4 *Poaceae*, 1 *Liliaceae*, and 1 species of unknown family.

<sup>2</sup>Absolute values.

*Baccharis vaccinioides* were recorded. A few exotic species were recorded (Table 1).

#### Shrubland

49 species were present (Tables 1-3). Only seven species in the prostrate layer were relatively abundant (> 5%). Vegetation covered > 60%. The sparse erect layer included a few seedlings of tree species, and the two abundant but slender perennial composites *Stevia ovata* and *S. serrata* (Tables 3, 4). The dominant shrubs were *Pteridium aquilinum* and *Baccharis vaccinioides*.

**Table 2.** Summary of vegetation structure data in the successional stands. *N* = No. of species; AD = Absolute density (ind./m<sup>2</sup>); AC = Absolute cover (cm<sup>2</sup>/m<sup>2</sup>).

	<i>N</i>	AD	AC		<i>N</i>	AD	AC
OLD-FIELD				MID-SUCCESSIONAL FOREST			
Herbs	24		49	Herbaceous layer			
GRASSLAND				Herbs	26	24.5	741
Herbs	28			Vines & lianas	4	2.3	109
Seedlings of shrubs & trees	2			Ferns & allies	5	2.0	659
Total	30		82 <sup>1</sup>	Seedlings of shrubs	27	9.5	874
SHRUBLAND				Seedlings of trees	10	4.2	365
Herbaceous layer				Total	72	42.4	2748
Herbs	32			Shrubby layer			
Seedlings of shrubs & trees (< 5 cm)	3			Ferns	2	0.1	230
Total	35		60 <sup>1</sup>	Shrubs	24	0.7	1578
Seedlings of shrubs & trees (5-50 cm) <sup>2</sup>	11	0.4		Juveniles of trees	14	0.6	2193
Shrubby layer				Total	40	1.3	4001
Herbs	2	0.9	208	Small trees/large shrubs			
Ferns	1	0.4	25	Large shrubs <sup>4</sup>	9	112	334
Shrubs	5	0.3	40	Understory & canopy trees <sup>4</sup>	18	1636	10251
Juveniles of tree species	6	0.1	7	Total <sup>4</sup>	27	1748	10585
Total	14	1.6	280	Large trees			
Total number of species <sup>3</sup>	49 <sup>3</sup>			Large understory trees <sup>4</sup>	5	31	736
EARLY SUCCESSIONAL FOREST				Large canopy trees <sup>4</sup>	7	1122	28904
Herbaceous layer				Total <sup>4</sup>	12	1153	29640
Herbs	19	7.2	236	Total number of species	86 <sup>3</sup>		
Vines & lianas	6	2.0	66	MATURE FOREST			
Ferns & allies	5	1.1	216	Herbaceous layer			
Seedlings of shrubs	20	6.3	457	Herbs	21	11.9	77
Seedlings of trees	9	9.0	222	Vines & lianas	7	2.6	34
Total	59	25.6	1197	Ferns	10	6.3	254
Shrubby layer				Seedlings of shrubs	25	3.0	33
Ferns	1	0.1	127	Seedlings of trees	12	11.7	53
Shrubs	24	0.9	2630	Total	75	35.5	451
Juveniles of trees	15	0.7	2648	Shrubby layer			
Total	40	1.7	5405	Ferns	8	0.2	1079
Small trees/large shrubs				Shrubs	31	1.0	3109
Shrub species <sup>4</sup>	14	1220	4523	Juveniles of trees	13	2.3	7329
Understory & canopy trees <sup>4</sup>	19	7312	59130	Total	52	3.5	11517
Total <sup>4</sup>	33	8532	63653	Small trees/large shrubs			
Total number of species	76 <sup>3</sup>			Large shrubs <sup>4</sup>	9	298	905
				Understory & canopy trees <sup>4</sup>	12	3540	14568
				Total <sup>4</sup>	21	3838	15473
				Large trees			
				Large understory trees <sup>4</sup>	13	144	3499
				Large canopy trees <sup>4</sup>	7	470	22051
				Total <sup>4</sup>	20	614	25551
				Total number of species	100 <sup>3</sup>		

<sup>1</sup>Percent ground cover; <sup>2</sup>Data obtained with the quadrat method; see Materials and Methods for sampling details; <sup>3</sup>Total number of species may exceed their sum in the component sinusiae due to their occurrence in several of them; <sup>4</sup>AD ind./ha and AC cm/ha (sum of DBH's).

Vigorous saplings of pines and oaks were also recorded (most of the latter had resprouted from stumps).

#### Early Successional Forest

76 species were found in this stand (Tables 2-4). Only seven species were abundant in the erect herbaceous layer (Table 4), and most of the species (> 85%) were not found in the Old-Field, Grassland, or Shrubland. One half of them were represented by seedlings of shrubs and trees of old-growth forests. Two thirds of the species in the shrub layer were rare (Table 3), and a few were only recorded in this stand. A dense canopy 10-12

m high (rarely exceeding 15 m) dominated by pines and oaks was recorded (Table 3).

#### Mid-Successional Forest

A total of 86 plant species were recorded (Tables 2-4). The herbaceous layer was dominated by *Zeugites americana* var. *mexicana*, *Adiantum andicola*, *Rapanea juergensenii*, and *Hydrocotyle umbellata* (Table 4). More than 50% of the species in this layer were rare. Ca. 30% of the species were not found in the open stands or in the Early Successional Forest. Seedlings and juveniles of shrubs and trees accounted for the largest proportion

**Table 3.** Importance value (%) of species in the shrubby (SLA; 50-299 cm height), small trees and large shrubs (SMT >300 cm height and <15 cm d.b.h) and canopy layer (LAT >15 cm DBH) in the Shrubland (SHR), Early Successional Forest (ESF), Mid-Successional Forest (MSF), and Mature Forest (MAF) stands. (E) Early, (I) intermediate, and (L) late successional species. + = importance value <1.0%. 50 species not attaining an importance value > 3.0 in any type have been omitted. Full table available on request.

Species	SHR	ESF		MSF			MAF		
	SLA	SLA	SMT	SLA	SMT	LAT	SLA	SMT	LAT
<b>Ferns</b>									
<i>Dryopteris parallelogramma</i> (L)				3.2					
<i>Pteridium aquilinum</i> (E)	16.7	3.4		2.1			+		
<b>Shrubs</b>									
<i>Baccharis vaccinioides</i> (E)	17.1		+						
<i>Cestrum anagyris</i> (I)		3.9	+	2.8	1.0		1.4	+	
<i>Eupatorium ligustrinum</i> (E)		+	4.5		+		+		
<i>Litsea glaucescens</i> (E)		4.5	+	+	1.3				+
<i>Miconia</i> aff. <i>hemenostigma</i> (L)							4.5	1.5	
<i>Rubus</i> spp. <sup>1</sup> (E)	6.3	2.4		2.4			1.9		
<i>Salvia karwinskit</i> (I)		3.0	+	6.2					
<i>Solanum nigricans</i> (I)		7.2		2.8			3.1		
<i>Stevia ovata</i> <sup>2</sup> (E)	45.1								
<i>Stevia serrata</i> <sup>2</sup> (E)	12.8								
<i>Verbesina</i> sp.							3.0	3.2	
<i>Viburnum</i> aff. <i>elatum</i> (E)		14.7	+	7.9			1.4		
<i>Viburnum jucundum</i> ssp. <i>jucundum</i> (I)		3.4	2.6	5.2	2.0		5.1	+	
<b>Understory trees</b>									
<i>Cleyera theaeoides</i> (L)		+	1.4	1.9	4.3		1.6	6.3	8.9
<i>Magnolia sharpi</i> (L)							+	3.1	+
<i>Myrica cerifera</i> (E)		2.8	8.7	2.0	5.8				
<i>Oreopanax xalapensis</i> (L)		3.7	3.9	12.2	5.3		23.4	16.3	
<i>Prunus serotina</i> ssp. <i>capuli</i> (E)		9.8	5.6	3.0	3.8				
<i>Rapanea juergense</i> (L)		16.9	2.8	12.1	13.4		13.3	44.4	
<i>Rhamnus</i> sp. (I)		+	5.3	2.7	2.4		5.1	5.0	
<i>Symplocos limoncillo</i> (I)		1.8	3.5	5.5	5.8		3.0	+	
<i>Ternstroemia pringlei</i> (L)		+	+	1.7			12.2	8.7	
<b>Canopy trees</b>									
<i>Pinus oocarpa</i> (E)	+		7.0		4.7	15.7			3.0
<i>Pinus montezumae</i> (E)			+		+	3.3			+
<i>Pinus oaxacana</i> (E)	1.0 <sup>3</sup>		2.9		3.5	18.2			4.0
<i>Pinus pseudostrabus</i> (E)			1.1		3.2	16.9			3.2
<i>Quercus crassifolia</i> (E)	1.9	+	9.2		2.7	6.0		1.1	33.3
<i>Quercus laurina</i> (I)	+	4.3	24.0	3.8	30.3	27.2	1.8	2.3	31.4
<i>Quercus rugosa</i> (E)		1.2	7.4	+	5.7	9.6			2.7

<sup>1</sup>Includes *Rubus adenotrichus*, *R. corufolius*, and *R. sapidus*; <sup>2</sup>Not truly shrub species, but herbaceous perennials; <sup>3</sup>Includes a few *P. montezumae* and *P. pseudostrabus*.

of the total number of species in this layer. More than 50% of the species recorded in the shrub layer were rare (Table 3). A few saplings of tree species which are frequent in late successional stages were recorded. The understory tree layer (mostly 10-12 m high, and rarely >15 m high) was more diverse and less dense than the canopy of the Early Successional Forest (Table 3). A few shrubs attained sizes sufficient to be included in this layer. The upper canopy tree layer (mostly >20 m high, and rarely >25 m high) was dominated by pines and oaks (Table 3).

**Mature Forest**

100 species were recorded in this diverse and struc-

turally complex seral stand (Table 2). In general, all the layers in this forest had more species than in the other forested stands (Table 2). However, the herbaceous layer (mostly perennials) had a lower density and a much lower cover. More than two thirds of the species were rare. A conspicuous feature of this stand was its relatively high number of herbaceous ferns (Table 4). Vines and lianas were well represented. More than one third of the species in this layer were found in this stand only. Seedlings and juveniles of shrub and tree species (including shrubby ferns) accounted for no less than 45 out of 75 species. The shrub layer included three abundant species (Table 3), and >75% of the species were rare. In addition to most of the ferns, a number of shrubs

**Table 4.** Importance value (%) of species in the herbaceous layer of the Shrubland (SHR), Early Successional Forest (ESF), Mid-Successional Forest (MSF), and Mature Forest (MAF) stands. (A) = Annual, (P) = perennial, + = importance value < 1.0%. 92 species not attaining an importance value > 3.0 in any type have been omitted. Full table available on request.

Species	ESF	MSF	MAF
<b>Herbs</b>			
<i>Commelina erecta</i> var. <i>angustifolia</i> (P)	+	3.5	
<i>Hydrocotyle umbellata</i> (P)	1.4	5.8	4.8
<i>Smilacina flexuosa</i> (P)	4.1	4.0	3.2
<i>Zeugites americana</i> var. <i>mexicana</i> (P)	9.8	17.6	5.1
Species 24	4.0	1.8	+
<b>Vines and lianas</b>			
<i>Smilax</i> spp. <sup>1</sup>	5.7	3.9	4.4
<b>Ferns</b>			
<i>Adiantum andicola</i>	6.9	7.7	+
<i>Polypodium plebeium</i>			4.6
<i>Polypodium plesiosorum</i>	+	+	22.5
<b>Seedlings of shrub and tree species</b>			
<i>Fuchsia</i> spp. <sup>2</sup>	4.3	3.2	+
<i>Oreopanax xalapensis</i>	6.9	3.0	4.7
<i>Rapanea juergensenii</i>	5.7	6.2	14.6
<i>Rhamnus</i> sp.	11.3	1.1	+
<i>Rubus</i> spp. <sup>3</sup>	7.2	1.9	+
<i>Solanum nigricans</i>	4.9	4.3	+
<i>Viburnum</i> aff. <i>elatum</i>	4.7	4.7	+
<i>Asteraceae</i> 1 ( <i>Verbesina</i> sp. ?)	1.9	4.7	1.1

<sup>1</sup>*Smilax jalapensis* and *S.* aff. *mollis*; <sup>2</sup>*Fuchsia enclandra* and *F. microphylla*; <sup>3</sup>*Rubus adenotrichus*, *R. coriifolius*, and *R. sapidus*.

and trees were recorded in this stand only.

The understory tree layer (rarely >15 m high) was dominated by *Rapanea juergensenii*, *Oreopanax xalapensis*, *Ternstroemia pringlei*, *Cleyera theaeoides*, and *Rhamnus* sp. (Table 3). With the exception of a few *Pinus ayacahuite* saplings, no other pine species were represented. An open canopy layer (35-40 m high, and sometimes reaching 45 m) was dominated by *Quercus crassifolia* and *Q. laurina* (Table 3).

#### Density and size-class distribution of dominant species

The density of *Senecio barba-johannis* was similar among forested stands ( $H = 0.7$ ,  $P > 0.05$ ,  $N = 75$ ), but its size range decreased with successional age (Fig. 1). *Solanum nigricans* had higher densities in the Early and Mature Forests ( $H = 15.8$ ,  $P < 0.001$ ,  $N = 75$ ), and most of the plants were small. *Viburnum* aff. *elatum* had a broader size range and higher density in the Early Successional Forest than in the other stands ( $H = 16.4$ ,  $P < 0.001$ ,  $N = 75$ ). *Viburnum jucundum* ssp. *jucundum* was more abundant in the Mature Forest ( $H = 24.5$ ,  $P < 0.001$ ,  $N = 75$ ), where most (>80%) of the individuals

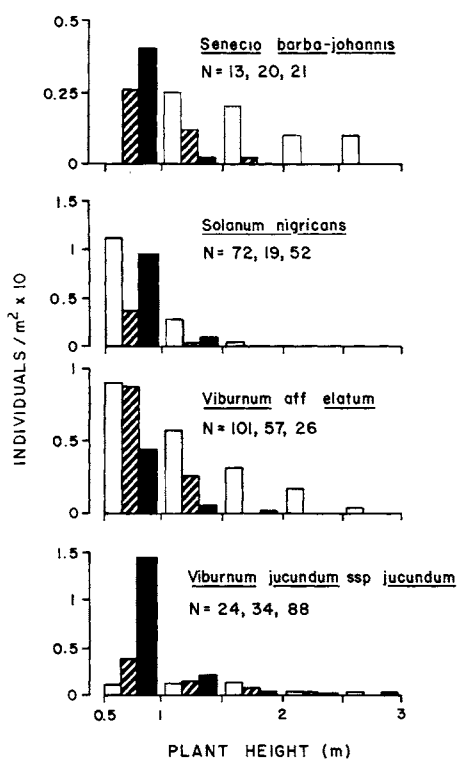
**Table 5.** Absolute density (AD, individuals/ha) of dead individuals of canopy and understory tree species in Early Successional Forest (ESF), Mid-Successional Forest (MSF), and Mature Forest (MF); results of  $\chi^2$  tests (null hypothesis of equal contribution of each species to the total number of dead and alive individuals).

Species	ESF		MSF		MF	
	AD	$\chi^2$	AD	$\chi^2$	AD	$\chi^2$
<i>Alnus acuminata</i> <sup>1</sup>	0		4 <sup>5</sup>	15 3***	1	
<i>Baccharis vaccinioides</i>	50 <sup>5</sup>	447 9***	3		0	
<i>Eupatorium ligustrinum</i>	10	2.8NS	0		0	
<i>Eupatorium mauetianum</i>	15 <sup>5</sup>	69.9***	8	3 4NS	0	
<i>Myrica cerifera</i>	45	3 2NS	15 <sup>5</sup>	10 7**	0	
<i>Oreopanax xalapensis</i>	10	1 8NS	0		2	
<i>Pinus</i> spp. <sup>2</sup>	80 <sup>5</sup>	253 3***	62 <sup>5</sup>	9 2**	8 <sup>5</sup>	48.4***
<i>Pinus oocarpa</i>	15	0 8NS	44 <sup>5</sup>	28 7***	12 <sup>5</sup>	238.7***
<i>Prunus serotina</i> <sup>3</sup>	0		0		10 <sup>5</sup>	201.0***
<i>Quercus crassifolia</i>	25	1.4NS	13 <sup>5</sup>	5 3*	8	1.7NS
<i>Quercus laurina</i>	45 <sup>6</sup>	13 2***	29 <sup>6</sup>	9 0**	21 <sup>5</sup>	39 6***
<i>Quercus rugosa</i>	5 <sup>6</sup>	17 8***	4 <sup>6</sup>	5 0*	4	
<i>Rapanea juergensenii</i>	5	3 4NS	0		8 <sup>6</sup>	22 9***
<i>Rhamnus</i> sp.	10 <sup>6</sup>	4 0*	2		6	0.9 NS
<i>Symplocos limoncillo</i>	10	0 9NS	0		1	
<i>Viburnum jucundum</i> <sup>4</sup>	35 <sup>5</sup>	40 4***	0		0	
Total No. dead ind /ha <sup>7</sup>	360		188		91	

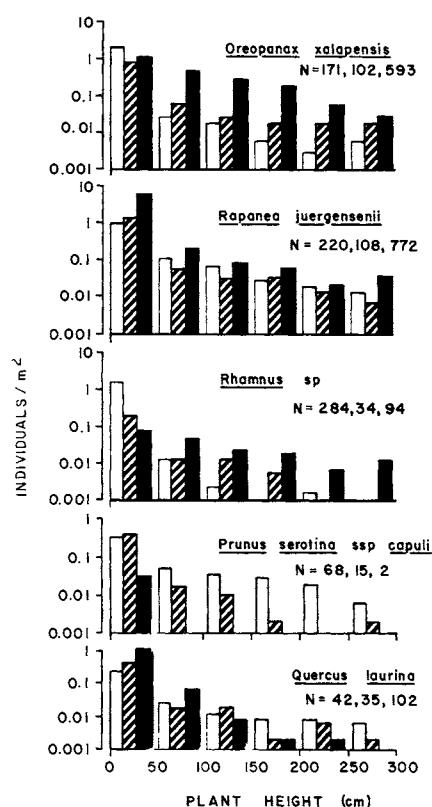
<sup>1</sup> ssp. *arguta*; <sup>2</sup>Dead individuals of *Pinus montezumae*, *P. oaxacana* and *P. pseudostrabus* could not be distinguished in the field; <sup>3</sup> ssp. *capuli*; <sup>4</sup> ssp. *jucundum*; <sup>5</sup> Higher relative contribution to total number of dead individuals in the stand; <sup>6</sup> Lower relative contribution to total number of dead individuals in the stand; <sup>7</sup> Other species contributing to this total were *Arbutus xalapensis*, *Cleyera theaeoides*, *Eupatorium* aff. *sordidum*, *Garrya laurifolia*, *Litsea glaucescens*, *Magnolia sharpi*, *Miconia* aff. *hemenostigma*, *Ternstroemia pringlei*, and *Verbesina* sp. NS =  $P > 0.05$ , \* =  $P < 0.05$ , \*\* =  $P < 0.01$ , \*\*\* =  $P < 0.001$ .

were small. Some dead plants of this species were only recorded in the Early Successional Forest, a lower number than expected given its relative abundance in the stand (Table 5). A few living *Baccharis vaccinioides* were recorded in the Early Successional Forest, where this species contributed a disproportionately high number of dead plants (Table 5).

Seedlings of *Oreopanax xalapensis* were less abundant in the Mid-Successional than in the Early Successional Forest ( $H = 7.0$ ,  $P = 0.03$ ,  $N = 85$ ), and its saplings were remarkably more abundant in the Mature Forest than in the other stands ( $H = 44.8$ ,  $P < 0.001$ ,  $N = 75$ ; Fig. 2). A higher number of seedlings and saplings of *Rapanea juergensenii* were found in the Mature Forest (seedlings:  $H = 40.7$ ,  $P < 0.001$ ,  $N = 85$ ; saplings:  $H = 18.7$ ,  $P < 0.001$ ,  $N = 75$ ; Fig. 2). Seedlings of *Rhamnus* sp. were more abundant in Early Successional Forest ( $H = 54.1$ ,  $P < 0.001$ ,  $N = 85$ ), but its saplings showed the highest abundance in the Mature Forest ( $H = 27.4$ ,  $P < 0.001$ ,  $N = 75$ ; Fig. 2). Saplings of *Prunus serotina* ssp. *capuli* become very rare as the forest ages ( $H = 14.7$ ,  $P < 0.001$ ,  $N = 50$ ; Fig. 2). The number of *Quercus laurina* seedlings increased with successional age ( $H = 23.6$ ,  $P$



**Fig. 1.** Size distribution of dominant shrub species in Early Successional (open bars), Mid-Successional (hatched), and Mature Forest (solid) stands. Plant height-classes at 0.5 m intervals; individuals with height < 0.5 m are not included (see Table 4). N = sample size in Early, Mid-Successional, and Mature Forest stands, respectively.



**Fig. 2.** Size distribution of seedlings (< 50 cm) and saplings (51- 300 cm) of dominant understory tree species in Early Successional (open bars), Mid-Successional (hatched), and Mature Forest (solid) stands. N = sample size in Early, Mid-Successional, and Mature Forest stands, respectively.

< 0.001,  $N = 85$ ), its saplings were similarly abundant among the forested stands (Fig. 2), and the number of young oaks (mostly resprouted stumps) was lower in the Shrubland ( $H = 17.5$ ,  $P < 0.001$ ,  $N = 100$ ; Table 3).

Significant differences among paired size-class distributions were found for *Myrica cerifera*, *Oreopanax xalapensis*, *Rapanea juergensenii*, and *Rhamnus* sp. (all  $D > 0.8$ ,  $P < 0.001$ ; 13 size-classes of 2 cm DBH each; Fig. 3). *O. xalapensis*, *R. juergensenii* and *Rhamnus* sp. had modes biased towards the smallest size-classes in the Mature Forest; *M. cerifera* increased its mode in the Mid-Successional stand, where more than expected dead individuals were recorded (Table 5). The size-class distribution of *Cleyera theaeoides* was not different between the Mid-Successional and Mature Forest ( $D = 0.5$ ,  $P > 0.05$ ; 17 size-classes), but both differed from the Early Successional Forest (both  $D > 0.6$ ,  $P < 0.05$ ).

The size-class distributions of *Pinus* spp., *P. oocarpa*, *Quercus crassifolia*, and *Q. laurina* were different among all successional forest stands (all  $D > 0.9$ ,  $P < 0.001$ , 45 DBH size-classes of 3 cm each). All these species tend to decrease their numbers, and to increase their size

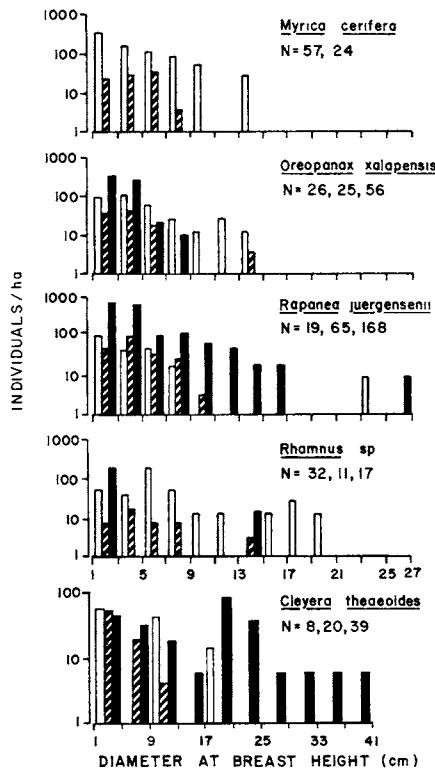
mode and size-class range in older stands (Fig. 4). Differences between the size-class distribution of living and dead individuals of *Pinus oocarpa* and *Pinus* spp. were found among all the forested stands ( $D$  ranged between 0.9 and 1.7,  $P < 0.01$ ). In the Early Successional Forest *P. oocarpa* died proportionally to its relative abundance, but in a higher proportion in the Mid-Successional and Mature Forest (Table 5). A higher than expected mortality of *Q. crassifolia* occurred in the Mid-Successional Forest. The number of dead *Q. laurina* trees in the Early and Mid-Successional Forests was lower than their relative abundance in the stands; the reverse occurred in the Mature Forest (Table 5).

## Discussion

### Vegetation structure and successional trends

The successional sequence derived from the land use pattern in the highlands of Chiapas shows a gradual increase in the total number of species. An almost

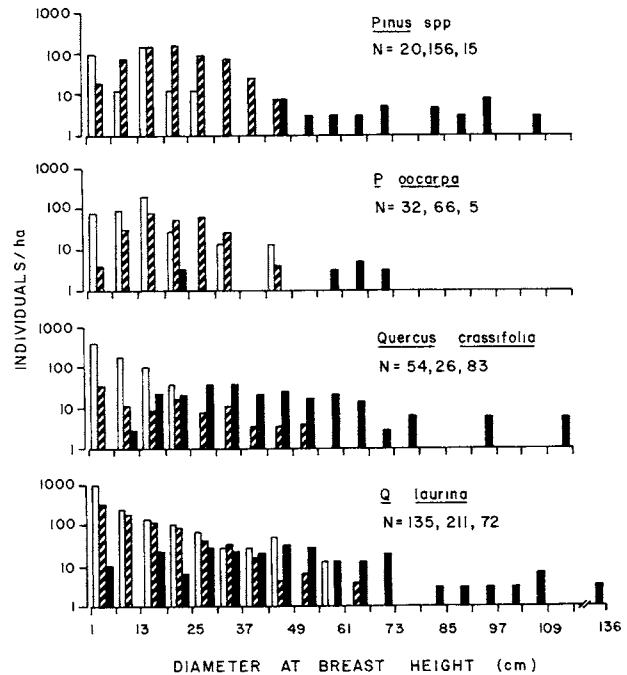




**Fig. 3.** Adult size distribution of dominant understory tree species in Early Successional (open bars), Mid-Successional (hatched), and Mature Forest (solid) stands. N = sample size in Early, Mid-Successional, and Mature Forest stands, respectively.

complete floristic and structural change occurs between the open and the early forested stage ('relay floristics'; Egler 1954). The replacement of a herbaceous community by a multilayered vegetation (three synusiae) may occur within 15-20 years; the development of a floristic composition typical of an old-growth forest may occur in 60-80 years. In our study, the continuing floristic replacement through the years is mostly accounted for by the recruitment of shrubs, with few further additions to the composition of the tree canopies.

The increase in species number and synusiae with successional age coincides with theory and many empirical studies of forest succession (West, Shugart & Botkin 1981). In the studied old-growth forest, the large number of species may also be the result of disturbances (Sousa 1984), such as those caused by infrequent selective logging and occasional windstorms. We have observed in the nearby mature primary forest at the Cerro Huitepec Reserve that occasional but severe windstorms may maintain an open canopy. This appears to be analo-



**Fig. 4.** Sapling and adult size distribution of dominant canopy tree species in Early Successional (open bars), Mid-Successional (hatched), and Mature Forest (solid) stands. N = sample size in Early, Mid-Successional, and Mature Forest stands, respectively.

gous to other forested areas where periodic disturbance prevents the development of steady-state stands (e.g. Veblen, Schlegel & Escobar 1980; Veblen 1985).

#### *Successional status of dominant species*

Plant indicators reliably related to particular seral stages and environmental conditions have long been recognized as a useful tool for vegetation management (Clements 1920). We propose a successional role for dominant and subdominant species in the pine-oak forests of the highlands of Chiapas (Table 3).

Early successional species include shrubs and trees which are major elements in shrublands, young secondary forests, and large gaps in old-growth stands. Their abundance decreases with the age of the stand, and their seedlings and juveniles are absent or have very low numbers under a closed forest canopy. Most of these species were found to have viable seed banks in forested stands (Ramírez-Marcial 1989).

Pines and oaks are characteristic components of mountain forests in southern Mexico and Guatemala (Steyermark 1950; Rzedowski 1978; Veblen 1978). The results of this work indicate that the regeneration of pines occurs only in exposed sites and may be favored by the current land use pattern. Cohorts of vigorous saplings are often found 5-8 yr after the last milpa, which may eventually be part of the canopy in mid-successional stands. Notwithstanding that most of their regeneration occurs in open stands, the occurrence of oak seedlings and saplings in the shade suggests that they are more tolerant than pines in the forests studied. Quintana-Ascencio (1989) found higher survivorship and growth of experimentally transplanted *Quercus crispipilis* (which coexists with *Q. crassifolia* and *Q. rugosa* in lower and/or drier sites) seedlings and saplings in the Shrubland stand than in forested communities.

Among the forested stands, the highest herb cover (mostly perennials) was found in the Mid-Successional Forest, possibly as a result of the higher heterogeneity of the light environment on its forest floor (Quintana-Ascencio 1989). Several shrubs and trees are ubiquitous in forested stands (Tables 3, 4), and are proposed here as intermediate successional as they do not occur in early open stands or in deep shade in old-growth forests (Table 3). A clearer picture arises for *Quercus laurina*. The mode of its diametrical classes (for individuals >3 m height; Figs. 3 and 4) moves towards larger values in old-growth stands, as its seedlings and saplings tend to become more abundant there. More numerous young plants may result from reproduction of a large number of adults in the old-growth forest. However, during self-thinning saplings may be differently predisposed to die, which may result from their increasing maintenance cost as they grow, which enhances their sensitivity to environmental changes (Waring 1987).

The most conspicuous feature of the understory layers in late seral stands is the extensive cover by ferns (including two arborescent species) which are not found in young secondary forests. Several shrub and tree species were only found in the Mature Forest, or had their abundance and size peaks there. The leaves of all these species are within the Raunkiaer mesophyll leaf-size class (2025-18 225 mm<sup>2</sup>; Shimwell 1971). Most of these species belong to genera typical of the more mesic evergreen broad-leaved forests in the subtropical and temperate zones (Klötzli 1988).

#### *Human impact on forest vegetation*

Human intervention may alter community development patterns. In the highlands of Chiapas, as in other Neotropical regions, the farming and logging activities of local people are diminishing the diversity and struc-

ture of the remnant secondary forests. Parra-Vázquez & Mera-Ovando (1989) documented a drastic deforestation caused by the creation of grazing lands in this region over the last 20 yr. Heavy grazing arrests the development of forested communities because of seedling removal and trampling (Quintana-Ascencio 1989). The occasional reduction of the grazing stocking rate may promote the rapid establishment and growth of some woody species, which in turn may facilitate the regeneration of other intermediate or late successional shrubs and trees. Light browsing of saplings and resprouts in shrublands may not permanently affect the ability of the oaks to continue in the sere (Quintana-Ascencio 1989).

Selective logging of pines in mature stands changes the light and temperature environment at the forest floor and may favor the establishment and growth of both pines and oaks (Glitzenstein, Harcombe & Streng 1986; Collins & Good 1987). However, the effects of natural self-thinning and interspecific competition are further enhanced by local preference for oak fuelwood and occasional fire. This human intervention may explain the increasing dominance by pines in the remnant secondary forests, as has also been suggested for other parts of the world where *Pinus* and *Quercus* meet (Klötzli 1975; Veblen 1978).

In the highlands of Chiapas the recent forest fragmentation and habitat modifications in the remaining patches are limiting conditions for many understory shrubs and trees. Particularly affected are those species with low tolerance to freezing temperatures and high insolation. These groups are the most diverse synusia of the forest flora in old-growth stands. The current trend towards more extensive dry pine forests will not prevent the local extinction of many mesic species.

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