

## Patterns in the vertical structure of the tropical lowland rain forest of Los Tuxtlas, Mexico

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### Abstract

The vertical structure of one hectare of tropical rain forest was studied at Los Tuxtlas, State of Veracruz, Mexico. The structure was analysed at various scales of analysis, using different methodologies e.g. profile diagrams (0.1 ha) and vertical structure diagrams (1 ha). All profile diagrams suggested presence of stratification to some extent. However, simultaneous evaluation of several adjacent profile diagrams showed that the use of one profile diagram only can be very misleading: gaps or layers apparent in a diagram did usually not reflect gaps or layers that could be recognized in the field.

Structure diagrams of abundance, basal area and crown cover showed that this forest community is not stratified, with the exception of an understorey layer below 7.5 m dominated by palms. The vertical structure was described using arbitrarily chosen height intervals. From the forest floor to the canopy top basal area, percentage of deciduous species (and individuals), and percentage of compound-leaved species (and individuals), increased, but total number of individuals and number of species decreased. Leaf sizes tended to decrease in the same direction, and crown cover was approximately evenly distributed. Species from different families dominated different parts along the vertical plane. It is concluded that the vertical structure of tropical rain forest can best be described as a complex gradient, involving many community features. Stratification can best be emphasized as a special case of such a gradient.

Nomenclature is given in Appendix 1 of Bongers *et al.* (1988).

### Introduction

The question whether tropical rain forest vegetation is stratified or not has been a topic of discussion for several decades (e.g. Richards 1952, 1983; Schulz 1960; Leigh 1975; Hallé *et al.* 1978; Lescure 1978; Rollet 1978; Bourgeron 1983; Whitmore 1984; and many others). Generalisation is difficult because concepts and criteria differ widely among studies.

Several reasons might account for this difficulty:

1. Evidence presented is anecdotal and interpretation subjective in most cases. Spatio-temporal variation in - and complexity of structure of tropical rain forest vegetation is high at the scales we were able to include, so that statistically and ecologically sound proof for hypotheses concerning vegetation structure is hard, if not impossible to obtain.
2. Methodology applied for the study of vertical

structure varies widely. The best known qualitative method is the profile diagram (Davis & Richards 1933, 1934; Hallé *et al.* 1978; Richards 1952, 1983), a more or less realistic drawing of a small strip of forest. Such a diagram should demonstrate the main structural features of the vegetation. A commonly used quantitative approach is the construction of vertical structure diagrams, in which the vertical distribution of one or several structure parameters is summarized for the whole plot. The particular patterns found should reflect the vegetation structure of the community (e.g. Grubb *et al.* 1963; Pajmans 1970; Holdridge *et al.* 1971; Uhl & Murphy 1981). The choice of method implies necessarily a choice for a scale which is typically very small (e.g. 0.04–0.08 ha) for a profile diagram, but large (usually >0.5 ha) for a structure diagram.

3. Variation exists in the emphasis put on different aspects of vertical structure. Bourgeron (1983) mentions three phenomena which are considered frequently: stratification of species, stratification of individuals, and stratification of leaf mass. Several others could be added e.g. stratification of physiological - (leaf types, ramification patterns) or function (photosynthetic properties, water balance) characteristics of the vegetation.

4. Even when applying equal concepts, methodology and criteria, stratification can be very different within or among forests. As Richard (1983) pointed out, a clear stratification can usually be found when relative dominance of one or very few species is high, while in mixed forests this is not the case. Locally, stratification may be found in one or several stages of the forest growth cycle and will thus depend on the proportion of gap, building- and mature phases (Whitmore 1984). Which particular strip of forest is chosen for a profile diagram will thus strongly influence the results.

Three questions emerge from the considerations mentioned above. What is the effect of scale of analysis upon the kind of conclusions that can be drawn with respect to stratification? Are patterns in different vegetation parameters related to each other? Is stratification an invariable property of the community or is the recognition of strata only a simplification enabling a clearer discussion of vertical vegetation structure?

In this paper we intend to address these questions using data from a detailed field study carried out in the tropical rain forest reserve of Los Tuxtlas, Mexico.

### Study site and field methods

The tropical rain forest under study is situated at the base of the Los Tuxtlas mountain range. Location, climate and soil are described in Bongers *et al.* (1988). A one hectare study plot without signs of recent human disturbance was chosen in a relatively mature part of the forest. The dynamics, general structure, composition and diversity of the vegetation on the plot have been described elsewhere (Bongers *et al.* 1988). Although it is the northernmost neotropical rain forest, Bongers *et al.* (1988) found the Los Tuxtlas forest to be comparable in many features to other lowland rain forests around the world. Important differences include the relatively low species richness, and the slow forest turnover.

All individual plants with a diameter at breast height (*DBH*) of at least 1.0 cm were mapped and identified, and the following measurements were taken: *DBH*, height (*H*), lowest ramification height (*LRH*), lowest crown limit (*LCL*), largest crown diameter (*D*<sub>1</sub>) and the diameter perpendicular to it (*D*<sub>2</sub>). Height measurements were done with a marked pole up to 5 m, and with a Suunto clinometer for higher trees. Crown cover was calculated according to the formula of an ellipse:

$$C = 0.25 \cdot D_1 \cdot D_2 \cdot \pi \quad (1)$$

Plants with a *DBH* < 1 cm, which were over 0.5 m high were also identified and counted per 10×10 m quadrat. Schematical profile diagrams were constructed with the aid of a computer program, using the field measurements as input. In the profile diagrams (Fig. 1) several structural features of the vegetation and individual trees are shown: variation in canopy height, in tree density, in size and shape of tree crowns, in height of lowest ramification and in bole diameters. Below the diagrams the density of individuals with a *DBH* ≥ 1 cm and a height < 7.5 m

is shown. The position of the tree crowns and boles is above the rooting point of the tree, but due to inclination or asymmetrical tree crowns some of these might have somewhat different positions in the forest. For the same reason, the circumference of the crowns indicates where foliage might be found and gives an estimate for the size of the crown, but it gives no information on actual foliage density or possible gaps within a crown. Also epiphytes and vines are left out, although it is known that especially the latter can have large crowns. Leaf sizes were determined by measuring the area of 20 randomly sampled mature leaves of one mature individual. Three diversity indices were calculated for 8 m layers. The Shannon-Wiener index  $H$ , the Simpson index  $C$  and the Equitability index  $E$  were calculated according to the formulas:

$$H = - \sum p_i {}^2\text{LOG } p_i \quad (2)$$

where  $p_i = n_i/N$ ;  $n_i$  = number of individuals of species  $i$ ;  $N$  = total number of individuals.

$$C = \sum p_i^2 \quad (3)$$

$$E = H/H_{\text{max}}, \text{ where } H_{\text{max}} = {}^2\text{LOG } S, S = \text{number of species} \quad (4)$$

## Results

### *Small-scale patterns: profile diagrams*

The small scale variation in vegetation structure is high in the horizontal-as well as in the vertical plane, as shown in the profile diagrams (Fig. 1). In many parts of the transects canopy openings as well as middle storey-and understorey openings are shown. The canopy openings in the profiles suggest that the forest at those locations contains canopy gaps, as a result of the fall of a tree or a large branch. The gaps at lower heights in the forest suggest that the vegetation is stratified locally. However, many apparent openings in fact are artifacts caused by the small width (10 m) of the transects. Trees in adjacent transects fill up the apparent gaps. Clear examples of such seeming canopy openings are found in transect 6 at 10–30 m along the transect, and transect 8 at

40–70 m and 90–100 m. These ‘gaps’ are filled with crowns of trees rooting just outside the transects in neighbouring ones, as is shown clearly by the vertical projections of the crowns of the higher trees in Fig. 2. An apparent middle storey opening is found in transect 5 at 20–40 m along the transect. This opening, suggesting stratifications, is filled with crowns from trees rooting in transects 4 and 6.

Not all openings in the diagram can be invalidated this way. Some of them are really existing openings. These gaps can be attributed to 1. exclusion effects by large, densely leaved crowns of canopy trees producing a deep shade (e.g. transect 7 at 40–70 m along the transect; transect 6 at 30–50 m; Fig. 2, compare A and B), and 2. a synchronized growth as a result of a gap phase regeneration (e.g. transect 7 at 0–20 m along the transect; transect 6 at 70–100 m). The influence of other factors (e.g. topography, the presence of a small runnel) can be important too but here no data are available to indicate and locate these effects precisely. Probably various factors interfere to produce a complex vegetation structure.

Discrete A, B or C layers, at fixed heights, do not exist in this forest. Layers, if present, occur at variable heights. An example is transect 6: from 20 to about 50 m along the transect a layer is present at 10–15 m above ground level and another one at about 30 m above ground level. From 70–100 m layers occur at a height of 18–20 m and below 7.5 m. Although stratification of individuals seems to occur at some locations, this is mostly due to a subjective interpretation of the vertical distribution of the tree crowns. The distribution of crowns along the vertical plane in the forest is continuous rather than discontinuous.

Figures 1 and 2 show the spatial distribution of *Nectandra ambigens* and *Pseudolmedia oxyphyllaria*, while Fig. 1 includes information on the palm species *Astrocaryum mexicanum* as well. These three species form the matrix of the community, as they account for 39% of the total community cover (Bongers *et al.* 1988). Figures 1 and 2 show the relative dominance of these three species at different heights in the canopy. The density of individuals between 1.3 and 7.5 m in height (Fig. 1) varies from 15 to 51 per 10 by 10 m plot in the four transects

presented here. Palms mostly account for over 50% of the individuals. The mean density of *Astrocaryum mexicanum* per 10 by 10 m plot is 7.6. Only 6 out of 40 plots have 4 or less individuals. This species characterizes the understorey below 8 m, considering that an average individual of this palm species covers about 9 m<sup>2</sup>.

### Large-scale patterns: vertical structure diagrams

A vertical structure diagram is defined here as a graph of a structure parameter showing its distribution along a number of arbitrarily defined height intervals. The construction of these diagrams presents some problems that have to be discussed first. The

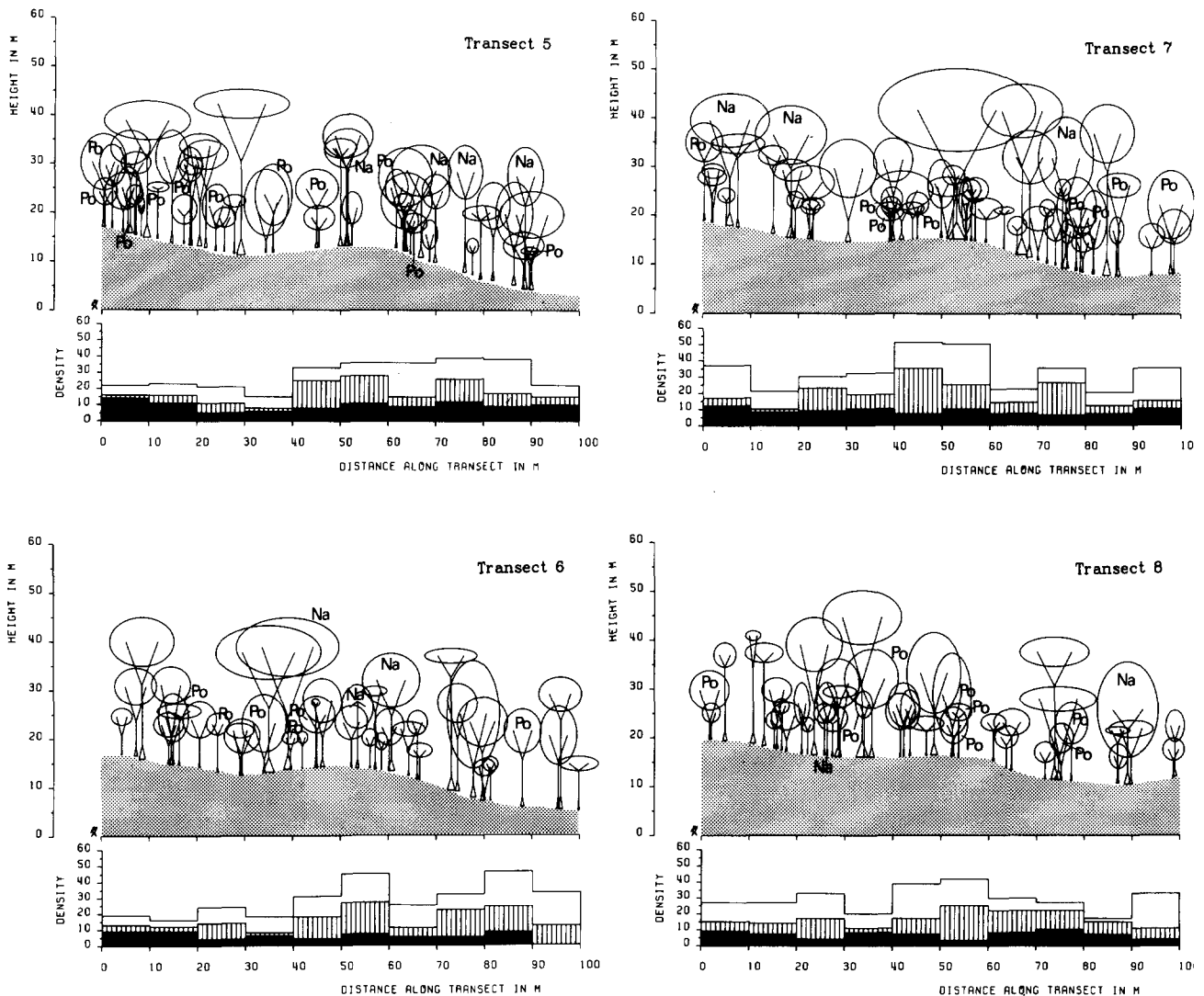


Fig. 1. Profile diagrams of four transects (transects 5, 6, 7, 8) of 100 × 10 m in the Los Tuxtlas rain forest. Only trees ≥ 7.5 m high are drawn. Indicated are soil level, tree height, crown depth, crown diameter, lowest ramification height and DBH. Species indicated in the diagrams are *Pseudolmedia oxyphyllaria* (Po), and *Nectandra ambigens* (Na). Below the profile diagrams the density of *Astrocaryum mexicanum* (black), other palms (shaded), and trees and shrubs (individuals between 1.3 and 7.5 m high) is given for 10 × 10 m plots.

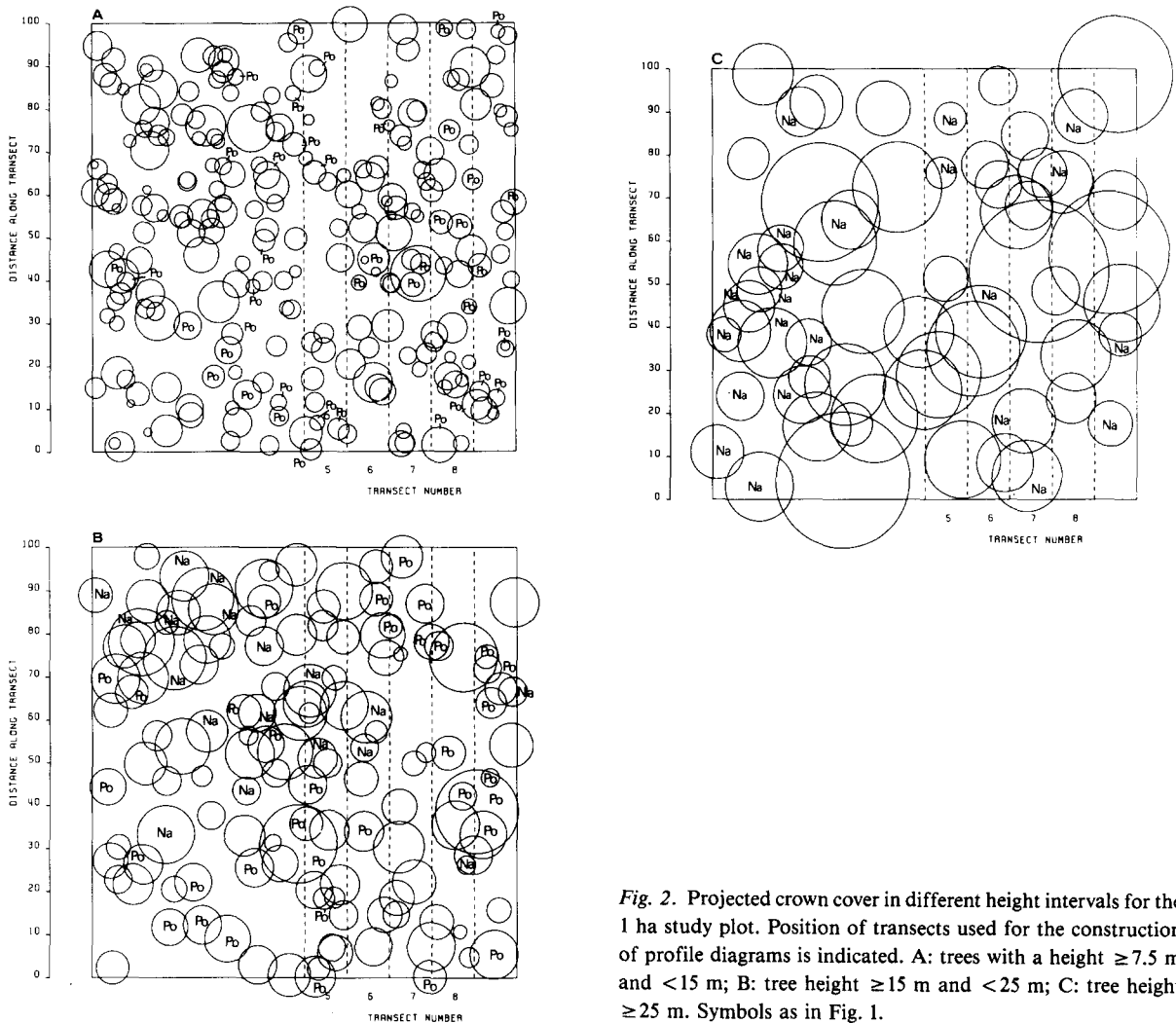


Fig. 2. Projected crown cover in different height intervals for the 1 ha study plot. Position of transects used for the construction of profile diagrams is indicated. A: trees with a height  $\geq 7.5$  m and  $< 15$  m; B: tree height  $\geq 15$  m and  $< 25$  m; C: tree height  $\geq 25$  m. Symbols as in Fig. 1.

height intervals should be large enough to eliminate small, insignificant irregularities, but small enough to show possible existing patterns in sufficient detail. Also, the possibility exists that the choice of the width of the intervals itself could significantly influence the result. Figure 3 shows the cumulative percentage of the number of trees that surpass a given height, as well as the cover and basal area presented by these individuals. If discrete strata at fixed heights exist in either of these parameters, this would be indicated by abrupt changes in the slopes of the curves. The slope of the curves in Fig. 3 change gradually however, with a relative breakpoint around a height of about 8 m, indicating a relatively high density and low basal area below this height. Be-

cause of the relative continuity of the curves, any division in equidistant intervals of at most 8 m should adequately describe the patterns involved, but more (smaller) intervals are possible if convenient.

#### *Density, cover and basal area*

The fact that the curves in Fig. 3 are continuous does not mean that the parameters are evenly distributed along the vertical plane. This would be the case only if the curve slopes were constant, which they are not in this case. Figure 4 shows that 75% of all individuals are 6 m or shorter. The basal area shows a reversed pattern, with 50% of all the basal area con-

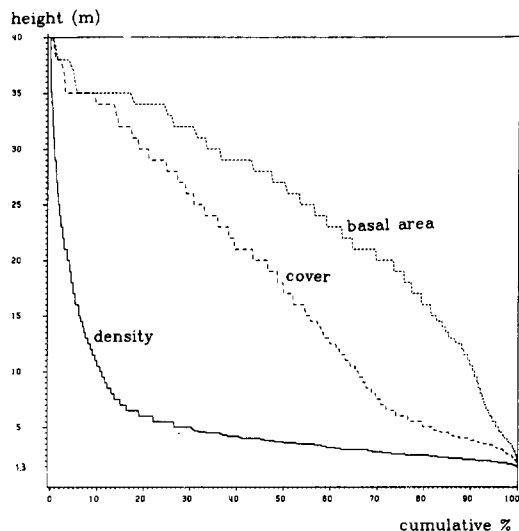


Fig. 3. Cumulative distribution of the number of individuals, basal area and cover along the vertical axis in the Los Tuxtlas forest. Indicated are percentages found above a certain height.

centrated in the 46 (1.5%) trees that are higher than 26 m, while the 2843 (95%) individuals below 19 m account for only 25% of the total basal area. The vertical distribution of vegetation cover shows another pattern. Here, as well as in the density distribu-

tion, a distinct layer dominated by a few but very abundant palm species (*Astrocaryum mexicanum*, *Chamaedorea schiedeana*, *C. tepejilote*, and *Bactris trychophylla*) is present below 7 m. Below this height, 2528 individuals (85%) make up 30% of the total cover, while above this height the cover is markedly evenly distributed. It has to be noted however, that in this calculation cover from lianas and epiphytes (which is concentrated above  $\pm 20$  m) is not included and that consequently cover in the higher intervals may be considerably higher.

#### *Deciduousness, compound leaves, and leaf size*

Arbitrary height intervals of 8 m (total tree height) were used to investigate vertical patterns in several physiological characteristics (Fig. 5). Patterns do not change substantially when other class limits are used. The percentage deciduousness increases with height, both on a species and on an abundance basis (Fig. 5A). The percentage deciduousness is probably less in the lower height classes than indicated in the figure. This results from equally counting all deciduous species here, although species can be facultative-

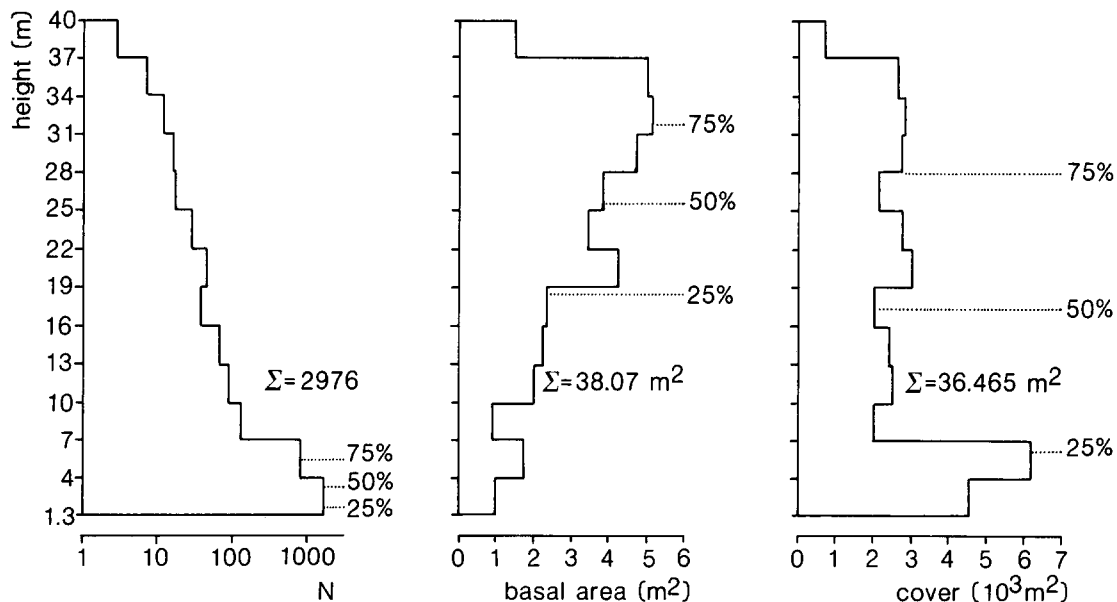


Fig. 4. Vertical distribution of density, basal area and cover. Only trees, shrubs and palms with a  $DBH \geq 1$  cm are used. The height class interval is 3 m, with the upper limit included in each class.

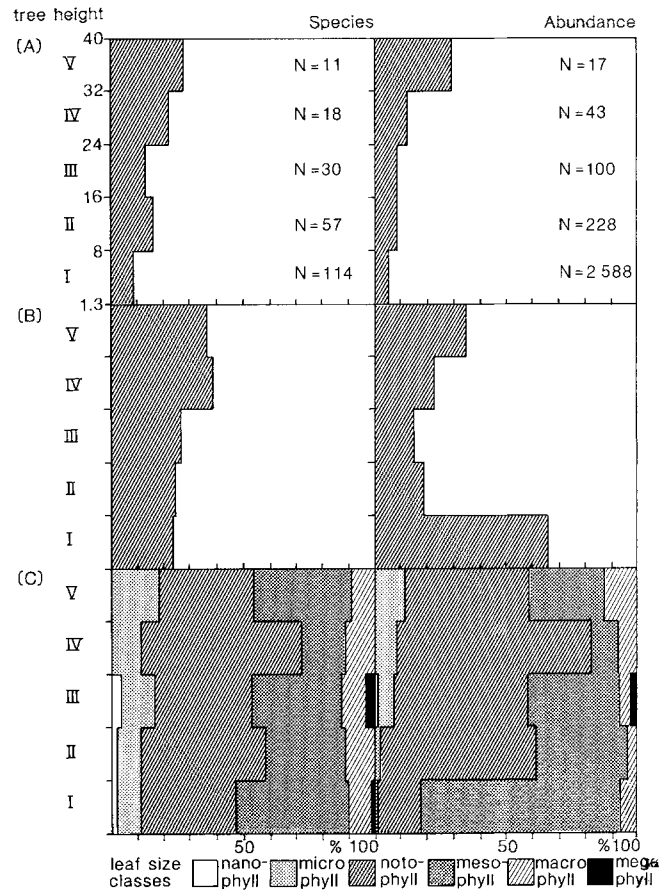


Fig. 5. Deciduousness, compound-leaved species and leaf sizes from understory to canopy. Only trees, shrubs and palms with a  $DBH \geq 1$  cm are included. Height interval 8 m, upper limit included. (A) % deciduous (shaded), (B) % compound (shaded), (C) leaf size classes. Left: weighted for number of species. Right: weighted for number of individuals.

ly deciduous, like *Poulsenia armata* and *Brosimum alicastrum*. Usually such species are deciduous only as far as canopy individuals are concerned. The percentage compound-leaved species, is fairly constant from 0–24 m ( $\pm 25\%$ ) but rises above this limit ( $\pm 38\%$ , Fig. 5B). The leaves of the palms found in Los Tuxtlas are considered to be functionally compound in this study. Due to the strong dominance of palms, the proportion of compound-leaved individuals is very high in the lowest height interval.

With respect to leaf size (size classes according to Raunkiaer as modified by Webb 1959) no general tendency can be found (Fig. 5c). Notophylls are predominant in height class IV, while in the understory (height class I) on an abundance basis, the mesophyllous palms again determine the pattern.

Microphylls are slightly more abundant higher in the canopy. Givnish (1984) proposed the use of one measure for leaf size, the effective leaf size, which is indicated by his index of leaf width:  $W = \sum P_i W_i$ , where  $W_i$  is the characteristic width of leaves in the Raunkiaer-Webb category of leaf area, and  $P_i$  is the proportion of species falling into that class. The characteristic leaf width for each category is defined as the square root of three quarters of the geometric mean of the upper and lower bounds of leaf area for that category. Calculation of this leaf width separately for 8 m height intervals gives (from height class I to V) 77.0, 68.8, 75.2, 67.8 and 69.8 mm respectively. However, leaf size has been taken to be constant for a species in this calculation, although it might vary considerably between different light-en-

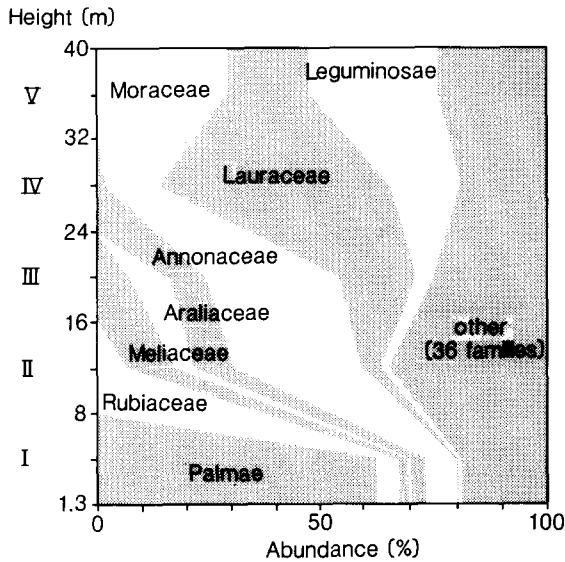


Fig. 6. The importance of some families from understory to canopy. Only trees, shrubs and palms with a  $DBH \geq 1$  cm are considered. Height class interval 8 m, upper limit included.

vironments (shade leaves being larger than sun leaves), and between juvenile and mature individuals (leaves of juveniles being larger). This might cause actual leaf size to be smaller towards the upper canopy than indicated by Fig. 5C. This suggests a gradual

but weak decrease in leaf size moving from understory to canopy.

*Floristics and diversity*

The importance of some families in 8 m height intervals is shown in Fig. 6. In the lowest height class palms are very abundant (62% of all individuals), while in the canopy classes (IV and V) Lauraceae are most important. Only three families (Lauraceae, Leguminosae and Moraceae) account for more than 50% of all individuals in the third, fourth and fifth height class (51.0, 78.9 and 75.9% respectively).

The vertical variation in several components of species richness and diversity is shown in Fig. 7. Open bars in the left side cumulatively add dark bars (from top to bottom), and represent the total number of species which in the recent past must have passed through that height interval. Thus the lowest open bar represents the total number of tree, shrub and palm species at least 0.5 m high found in the 1 ha plot. There is a strong decrease in species richness with increasing height (Fig. 7a). Almost 50% of all species do not surpass 8 m and only 24 species (15%) surpass 24 m. The diversity indices (Fig. 7b) show

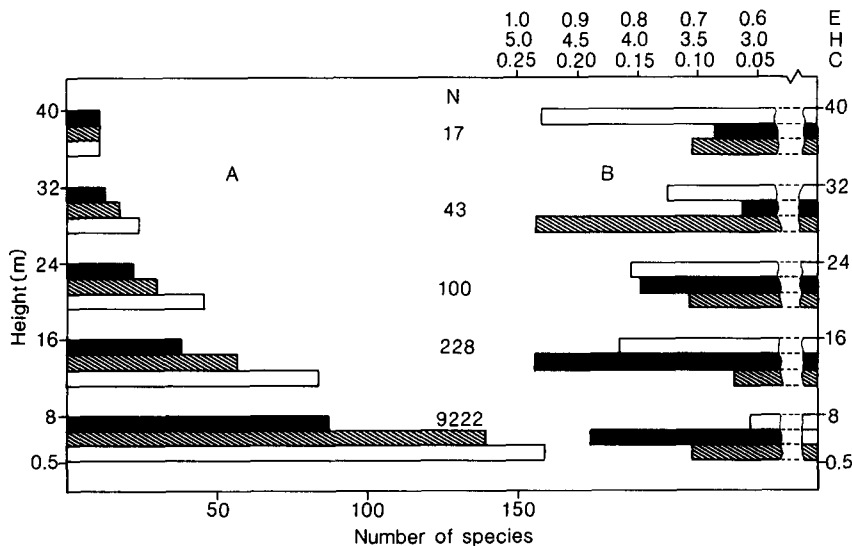


Fig. 7. Species diversity components from understory to canopy. Only trees, shrubs and palms, with a height  $\geq 0.5$  m are considered. Height class interval 8 m. A: dark bars indicate species which reach, but do not surpass the height class, hatched bars give the total number of species in the class, open bars are cumulative (from top to bottom) dark bars. B: Hatched bars give Simpson index (C), dark bars Shannon-Wiener index (H), and open bars Equitability index (E).



peaks in different height classes. The Simpson index  $C$  peaks in the 24–32 m class, the Shannon-Wiener index  $H$  in the 8–16 m class and the Equitability index  $E$  in the 32–40 m class.  $C$  peaks when  $H$  is lowest, and the other way around, as could be expected. A high value of  $C$  combined with a relatively low species richness gives a low  $H$  value: in class 24–32 m one out of 18 species (*Nectandar ambigens*) accounts for 20 out of 43 individuals. A low value of  $C$  (class 8–16 m) together with a relatively high species richness gives a high  $H$  value. Both indices are not completely opposite however. This is shown in the other three classes where the value of  $C$  is the same but the value of  $H$  differs.

Both  $H$  and  $C$  are sensitive to the number of species in the sample. As shown in Fig. 7A species richness decreases strongly with an increase in height.  $E$  is a diversity measure standardized for total number of species. Therefore it is more appropriate for the comparison of evenness or dominance between different height intervals. The value of  $E$  is highest in the highest class (32–40 m). This class shows the most equal distribution of individuals over species (11 species with together 17 individuals while 3 is the maximum number of individuals per species, again for *Nectandra ambigens*). The lowest class shows the lowest value of  $E$ ; 3 species of palms, out of 159 species, account for 4414 out of 9222 individuals.

## Discussion

Pattern in vegetation structure is a four-dimensional phenomenon. It can be studied at different scales, in space as well as in time. This paper is restricted to the spatial aspect of rain forest vegetation structure. Although all major phases of the forest growth cycle are included in the plot (gap phase 2.9%, building phase 13.6% and mature phase 83.5%), the forest plot under study is relatively undisturbed, when compared to other plots in the same forest or to other forests (Bongers *et al.* 1988). The results presented are thus mainly characteristic for the mature phase of the forest growth cycle. The small-scale profile diagram is thought to be a detailed, and more or less realistic representation of vegetation structure. The question is how representative such a diagram is. It

may be drawn from a strip of forest in a specific developmental phase, i.e. gap, building or mature phase. It needs to be narrow, to avoid that the diagram becomes too crowded to allow proper evaluation. But a narrow plot can suggest patterns (e.g. stratification) which in the field do not exist: empty spaces in the diagrams are in reality filled by trees rooting outside the plot. Furthermore, considerable differences can exist between adjacent profile diagrams in many features, indicating that patterns apparent from a single profile diagram cannot be generalized. Both effects were demonstrated clearly for the Los Tuxtlas forest (Figs. 1 and 2). However, if adjacent profile diagrams are evaluated simultaneously, small scale variation can be interpreted, although interpretation remains subjective. If local stratification is defined as the concentration of tree crowns or the occurrence of unoccupied space around a certain height, or a combination of both, in some parts of the profile diagrams stratification might be observed. This local stratification could be interpreted in some cases as the possible result of synchronized growth (gap-phase regeneration) or exclusion of small individuals by large canopy trees with densely leaved crowns (Alexandre 1983). In most cases however, no possible cause-effect relations could be detected. Also, height of strata seems to vary locally, suggesting that small scale local stratification is subject to strong temporal variation, and that the heights at which strata occur cannot be regarded as a stable community characteristic in the Los Tuxtlas forest.

Moving from the scale of one profile diagram to the simultaneous interpretation of several adjacent diagrams, logically the next step is the analysis of structural features of a large plot. Drawings of individual trees become impossible, and even if they were possible, uninterpretable. At this scale, structure diagrams are needed instead. The advantage of these diagrams is that small scale local differences are averaged out, and patterns characteristic of the community as a whole emerge. Many details and patterns which can be recognized locally are lost however.

The structure diagrams of density, basal area and crown cover (Figs. 4 and 5) of the Los Tuxtlas forest show that community stratification is absent, at

least over the same height range (above 7.5 m) as was covered by the profile diagrams. The only real layer which could be demonstrated to be present was a palm-dominated layer in the understorey below 7–8 m. Above that height, changes do occur in the variables mentioned above, but these are gradual rather than abrupt, which indicates the absence of strata at fixed heights in the vegetation.

The analysis of patterns in the vertical structure of rain forest vegetation is mostly concerned with distribution of individuals along the vertical axis. However, structure in its broad sense is also concerned with the spatial arrangement of physiognomical, taxonomic, morphological and functional characteristics of the elements building the vegetation. In the Los Tuxtlas rain forest, it was found (Fig. 6) that the percentage of deciduous species (and individuals) and the percentage of compound-leaved species (and individuals if understorey palms are excluded from consideration) increased towards the upper canopy, while leaf size tended to decrease. These changes in physiognomical characteristics while moving upward through the forest canopy may be adaptations to the considerable changes which occur in the microclimate (increasing temperature, vapour pressure deficit, light availability, Chiariello 1984). This is consistent with variation in these characters on a geographical scale; with increasing dryness, the proportion of deciduous species increases (Chabot & Hicks 1982), the proportion of compound-leaved species increases (Givnish 1978), and leaf size decreases (Dolph & Dilcher 1980; Givnish 1984; Webb 1968).

The profile diagrams (Fig. 2) showed that different species can reach different maximum heights (e.g. *Astrocaryum mexicanum* up to 7.5 m, *Pseudolmedia oxyphyllaria* up to 24 m, and *Nectandra ambigua* up to 30 m). Figure 7A showed that very few species reach the highest interval. Species richness increases with decreasing height. Almost half of the species do not reach beyond 8 m. This indicates that, for general usage, it is valid to speak of upper canopy, subcanopy and understorey species. The vertical distribution of families (Fig. 6) showed that species belonging to certain families are more successful as upper canopy species (e.g. Leguminosae, Lauraceae)

while other families are more successful in the understorey (Palmae, Annonaceae). Physiognomical characteristics (Fig. 5) show tendencies that could indicate adaptations to specific micro-environmental conditions along the vertical gradient in the forest. These results suggest a partitioning of habitats along the vertical gradient among species.

In summary, moving through various scales of analysis (change in methodology), different kinds of stratification appear (change in concepts), and different decision rules to delimit strata are required (change in criteria). It becomes clear then, that evaluations of patterns in vertical structure at different scales are complementary rather than mutually exclusive. The vertical structure of tropical rain forest can be described as a complex gradient involving many structural features. Stratification is only a special case of such a gradient. A description of a particular tropical rain forest would become complicated if terms like 'upper canopy' or 'understorey' were to be avoided. They are useful in order to convey all sorts of information about them. It has to be realized however that the significance of these terms is always relative, and that they can best be emphasized as endpoints, or parts of a structural gradient rather than as a reference to distinct strata.

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