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Population Structure of the Dominant Palm Species in the Understory of a Mexican Lowland Rain Forest

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Abstract Population structure was analyzed for five of the most common species of palms, *Astrocaryum mexicanum*, *Bactris tricophylla*, *Chamaedorea oblongata*, *C. tepejilote* and *Geonoma oxycarpa* in a Mexican lowland rain forest. Height and cover of palms with a height > 1.5 m were measured in three 600 m^2 plots. The most common species in terms of density were *C. tepejilote* and *A. mexicanum*. The highest accumulated cover corresponded to *A. mexicanum*.Taller palms of *C. tepejilote* showed higher cover. Almost all palm species had the same architectural model (Corner) and *B. tricophylla* had the Tomlinson model. Richness of palm species was low compared to other tropical forests although the understory palms in this community represent more than 50 % of all the individuals of the understory vegetation at Los Tuxtlas. The genus *Chamaedorea* was the most diversified (5 species) while the other genera had only one species.

Key words: Mexico / Neotropics / palms / population structure / species diversity / rain forest

Few studies have been carried out on the diversity and structure of the palm components within tropical forest communities, although palms usually occur in high numbers in mixed tropical forests. Palm species are very diverse in some lowland rain forests like in Sunda Shelf and New Guinea and of Central and South America (Uhl & Dransfield,1987). Palms may also occur in large stands of single species and dominate the vegetation. For example, *Nypa fruticans* in Borneo and Sumatra (Uhl & Dransfiled, 1987), *Raphia taedigera* in Costa Rica and Caribbean plains (Myers *et al.*, 1985), *Copernicia alba* in South America (Uhl & Dransfiled, 1987) are some of the most striking examples. However, the population structure and patterns of distribution have been rarely studied and poorly quantified (Piñero *et al.*, 1977; Kahn & de Castro, 1985).

A study of the palm flora of Los Tuxtlas natural reserve in Southeast Mexico describes 10 species (Ibarra-Manríquez, 1988). Biogeographically, this area is very important because it represents the northernmost limit of lowland rain forest in the Neotropics (Dirzo & Miranda, 1991). Community structure studies at Los Tuxtlas have shown that palms are a very important component of the vegetation (Piñero *et al.*, 1977; Bongers *et al.*, 1988) and in some patches of the forest, palms constituted more than 50 % of all understory trees with a girth breast height of > 3.3 cm (Oyama, 1984; Oyama *et al.*, in prep.). In this report, population structure and relationships between cover with height are presented for the five most common palm species of Los Tuxtlas.

MATERIALS AND METHODS

This study was conducted at the Estación de Biología Tropical Los Tuxtlas in Southest Mexico. The vegetation of this 700 ha reserve is classified as lowland rain forest (Miranda & Hernández-X., 1963). Detailed description of this area can be found in Lot-Helgueras (1976) and Ibarra-Manríquez and Sinaca-Colín (1987).

Palms with a height > 1.5 m were tagged and mapped in three plots of 600 m^2 (30 x 20 m). Height and cover were recorded for all palms. Height was measured directly. Cover was estimated from the largest crown diameter (D_1) and the diameter perpendicular to D_1 according to the formula of a circle.

The population structure of the species was assessed using 0.50 m height-classes in order to compare all species. Differences in cover among height-classes were assessed with a non-parametric analysis of variance (Kruskal-Wallis-test) (Zar, 1974) for each species.

Architectural models of palms were characterized following the models proposed by Hallé et al. (1978) based on a set of morphorogical characters that includes the life-span of meristems and the degree and type of differentiation of vegetative meristems.

RESULTS

Density, cover, architecture model and maximum height for the five species of palms are presented in Table 1. *Chamaedorea tepejilote* (0.1 / m^2) had the highest density followed by *Astrocaryum mexicanum* (0.06 / m^2),*C. oblongata* (0.02 / m^2), *Bactris tricophylla* (0.01 / m^2) and *Geonoma* oxycarpa (0.001 / m^2). *Astrocaryum mexicanum* had the highest cover followed by *C. tepejilote*, *B. tricophylla*, *C. oblongata* and *G. oxycarpa* (Table 1).

All the palms were located in the understory layer of the vegetation (below 8 m) with some plants of *A. mexicanum* reaching the maximum height (7.6 m). The population structure of *A. mexicanum*, *C. tepejilote* and *C. oblongata* was characterized by a high number of plants in the smallest categories of height followed by a continuous decrement in numbers in

Table 1. Architecture model, density, cover, basal area and maximum height of the five most common species of palms at Los Tuxtlas.

Species	Model	Density (#/1800 m^2)	Cover (m^2)	Height (m)
Astrocaryum mexicanum	Corner	115	1244.25	7.6
Chamaedorea tepejilote	Corner	173	331.73	5.8
Chamaedorea oblongata	Corner	34	28.3	5.0
Bactris tricophylla	Tomlinson	18	62.34	5.0
Geonoma oxycarpa	Corner	2	6.32	2.0

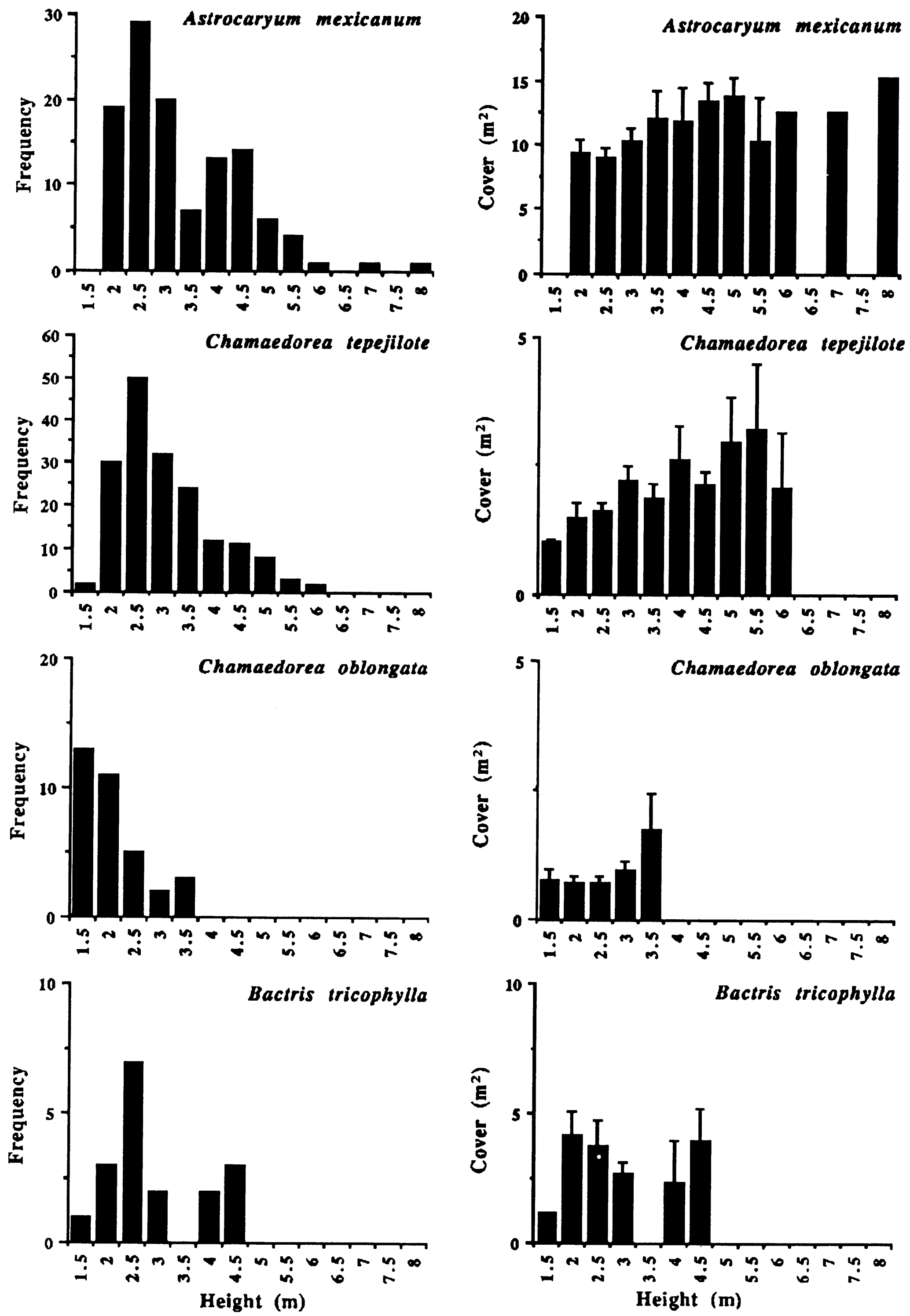

Fig. 1. Population structure and relationships between height and cover for four palm species at Los Tuxtlas forest. Means ± S.E. are presented for cover. *Geonoma oxycarpa* data were excluded due to low sample size.

higher height-classes (Fig. 1). The population structure of *B. tricophylla* and *G. oxycarpa* were not well represented due to the low number of plants recorded in the sampling plots.

Cover varied significantly among height-classes only in *C. tepejilote* (H=16.7; $P < 0.05$) with a tendency for cover to be large in the largest heigh-classes (Fig. 1).

DISCUSSION

Few studies exist on the structure of palm vegetation in tropical communities. Population structure of some species and diversity of the palm flora has been found to vary geographically (Uhl & Dransfiled, 1987) and locally in relation to environmental factors (Kahn & de Castro, 1985). Thirty-two species of palms were differentiated under different hydromorphic conditions with few species dominating different zones in Central Amazonia (Kahn & de Castro, 1985). Los Tuxtlas forest is not so diverse in its palm flora although the whole number of individuals is comparable to that of other tropical communities. We found 342 individuals (> 1.5 m) in 1800 m^2 (or 1900/ha). If we include the smaller individuals of all palms species at los Tuxtlas, the density will be, at least double or more. For *C. tepejilote* only, more than 750 plants (including juveniles and immature palms) have been recorded in the same area (Oyama, 1987; Oyama, 1990; Oyama *et al.*, in prep.). *Chamaedorea tepejilote* and *A. mexicanum* were the most common species followed by *C. oblongata*, *B. tricophylla* and *G. oxycarpa*. Only two individuals of *G. oxycarpa* were found in the 1800 m^2 sampled. Although the presence of many rare species coexisting with a few dominant plant species is a very common feature of tropical communities (Clark, 1986; Whitmore, 1988), there is no clear explanation to this phenomena. Hypotheses relating genetic drift (Fedorov, 1966), habitat specialization (Ashton, 1969), biological interactions (Janzen, 1970; Connell, 1971) and the pattern of natural regeneration of forest (Denslow 1987) have been proposed.

Ten palm species have been described for Los Tuxtlas (Ibarra-Manríquez, 1988) but only five were included in the present study because we only measured palms higher than 1.5 m. *Reinhardtia gracilis* and *Chamaedorea ernesti-augustii* are two other very common but small palm species at Los Tuxtlas (A. Mendoza and S. Bullock, pers. coms.). Palm species differed in several aspects. For example, *A. mexicanum*, *B. tricophylla* and *G. oxycarpa* are monoecious while *Chamaedorea* spp. are dioecious. Flowering time is also different among species; *A. mexicanum*, *B. tricophylla* and *C. oblongata* flower in the dry-season (March-May) but *C. tepejilote* and *G. oxycarpa* from September or later (Ibarra-Manríquez, 1988).

The great differentiation of some genera and the monospecificity of others is still one of the enigmas in tropical communities. The genus *Chamaedorea* is represented by five species at Los Tuxtlas but other genera had only one species. There was not any apparent correlation to an environmental or biological factor for *Chamaedorea* species. Kahn and De Castro (1985) reported ecological differentiation of species by occupying different soil conditions, and in a well-drained soils they found 11 species of *Bactris* and six species of *Geonoma* in 7200 m^2 plot. In a more extensive study, Dransfield (1984) found 111 species belonging to 20 genera in 52864 ha in Sarawak although palms did not dominate the vegetation within this locality. Geographically, a great diversity of palms may be found in very different regions. For example, the Chocó region of Colombia and parts of the island of Borneo may be singled out as being extraordinarily rich in palms (Uhl & Dransfield, 1987). Los Tuxtlas forest, being a locality close to the northern limit of the distribution of the tropical rain forest in

Continental America (Dirzo & Miranda, 1991) may represent a marginal region of palm distribution in which low diversity is found due to historical factors and speciational processes, but with a high density of few species by the occupancy and expansion of local ecological niches.

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K. OYAMA, R. DIRZO, G. IBARRA-MANRIQUEZ　メキシコ低地多雨林内の優占的なヤシ類の集団構造

メキシコの低地多雨林 (Los Tuxtlas) において，最も一般的な5種のヤシ類—*Astrocaryum mexicanum, Bactris tricophylla, Chamaedorea oblongata, C. tepejilote* と *Geonema oxycarpa* —について集団構成の分析がなされた。ヤシ類で 1.5 m 以上の高さの個体とそのカバーが 600 m^2 コドラート3個について測定された。密度の高い種は *C. tepejilote* と *A. mexicanum* であった。カバー面積が最も広いのは *A. mexicanum* であった。*Chamaedorea tepejilote* が最も密度の高いヤシであったが，カバー面積も大きかった。ほとんどすべてのヤシの種のアーキテクチャーは Corner モデルを示したが，*B. tricophylla* は Tomlinson モデルであった。Los Tuxtlas の林内植生の，個体の 50% 以上がヤシ類で占められているが，ヤシの種類数は他の熱帯森林に比較するとすくない。*Chamaedorea* 属は最も多くて5種あったが，他の属はそれぞれ1種しかなかった。