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Establecimiento y Sobrevivencia de Plantulas de Especies Arboreas en un Bosque Tropical Deciduo de Baja Diversidad, Dominado por una sola Especie

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RESUMEN

1. La típica gran diversidad de los bosques tropicales de tierras bajas es contradicha por ejemplos de bosques dominados por una sola especie arbórea del dosel (dejando de lado sitios de sucesión temprana o suelos inundables). Varios factores y mecanismos han sido propuestos como importantes en el mantenimiento de poblaciones de árboles tropicales con altas densidades (y por ende, bosques de baja diversidad). Para uno de tales casos, la composición florística y la estructura fueron examinadas considerando el componente leñoso con al menos un DAP de 2.5 cm. A su vez, la hipótesis de que los patrones de establecimiento y sobrevivencia difieren entre las especies, explicando la discontinuidad entre bosques dominados por una sola especie y bosques mixtos, fue puesta a prueba.

2. En la vertiente Pacífica de México, Celaenodendron mexicanum Standley (Euphorbiaceae) forma tales bosques de dominancia concentrada y se halla restringida a ellos. Este bosque de Celaenodendron (CF) se presenta en parajes discontinuos que varían en tamaño desde <0.1 a >1000 ha, inmersos en un bosque mixto rico en especies (MF). Las propiedades de los suelos en los primeros 20 cm de profundidad de ambos tipos de bosque fueron comparados considerando sus características físicas, la concentración de nutrientes, así como sus efectos sobre la germinación y establecimiento de varias especies leñosas. También, se llevaron a cabo experimentos sobre sobrevivencia de semillas y plántulas, en varios sitios con CF y MF adyacentes, de especies comunes del MF, así como de Celaenodendron mexicanum.

3. El bosque de Celaenodendron mexicanum fue significativamente menos diverso que el bosque mixto, con más de un cincuenta por ciento de individuos conespecíficos (DAP > 10 cm). Sin embargo, las especies subsidiarias en CF fueron también aquellas características del MF. Celaenodendron mexicanum fue la única especie exclusiva de sus parajes. De tal modo, la composición florística sugiere que la presencia de una sola especie,

Celaenodendron mexicanum, distingue estos parajes de dominancia concentrada y las especies subsidiarias son también asociadas comunes en los parajes adyacentes de alta diversidad.

4. Bosques tropicales maduros de tierras bajas con baja diversidad de especies arbóreas han sido considerados, a menudo, como el resultado de la restricción a condiciones edáficas particularmente desfavorables. Sin embargo, en el presente caso factores topográficos y edáficos no explican la discontinuidad de los tipos de bosques establecidos. Los patrones de germinación y sobrevivencia de plántulas (a cuatro meses de edad) de

Celaenodendron mexicanum y ocho especies comunes del MF no fueron diferentes cuando crecieron sobre suelo proveniente de CF o de MF. Además, la germinación exitosa y con el correspondiente establecimiento de plántulas de la especie más común del MF (Caesalpinia eriostachys), en ambos tipos de bosque, señala que su baja densidad en CF no es debida a alguna simple restricción fisiológica en estos estadios tempranos de desarrollo.

5. No hubo evidencia de efectos de mecanismos compensatorios actuando en estos tempranos estadios y no hay razón para dudar que la dominancia de Celaenodendron mexicanum continuará a través de subsecuentes generaciones. La sobrevivencia de semillas postdispersadas de Celaenodendron mexicanum hasta el estadio de plántulas de un año de edad (1.3%) fue mayor que aquella de dos especies comunes del MF species (0.0%) y no muy diferente que la de la especie más importante del MF (Caesalpinia eriostachys, 2.3%). En CF las clases de tamaño menores (DAP < 10 cm), cuyos individuos pueden estar representando las cohortes más recientes que ingresaron a la población, también Celaenodendron mexicanum fue la especie dominante. Esto sugiere que CF es persistente y un paraje con menos dominancia y menores individuos de Celaenodendron mexicanum representa una fase intermedia de MF cambiando a CF. En este paraje, a pesar de la mayor lluvia de semillas de las especies del MF, la sobrevivencia de las semillas postdispersadas y de las plántulas fue similar a la observada en los parajes con individuos mayores y con mayor dominancia de

Celaenodendron mexicanum.

6. Los datos no apoyan la idea de la existencia de un mecanismo de escape frente a los depredadores mediante defensas químicas o fructificación en masa en intervalos interanuales largos e impredecibles o la ausencia de depredadores. Invertebrados, presumiblemente hormigas, tan bien como vertebrados fueron removedores (depredadores) importantes de semillas post-dispersión. Además, los roedores fueron aparentemente depredadores de las plántulas de Celaenodendron mexicanum. La remoción (depredación) de semillas de tres especies comunes del MF y de Celaenodendron mexicanum, no fue diferente entre tipos de bosque aunque hubo grandes diferencias entre especies.

7. La dominancia de Celaenodendron mexicanum y la pobre representación de otras especies en CF, podría estar relacionada a diferentes intensidades de los procesos de mortalidad. Los experimentos mostraron que la mortalidad al año de edad no fue diferente entre los tipos de bosques para Celaenodendron mexicanum y especies del MF. Así, el contraste existente en diversidad de los parajes no puede realmente ser atribuido a una sobrevivencia diferente de las semillas post-dispersión y de las plántulas. Sin embargo, diferencias en el grado de gregarismo de estas especies debe resultar en una gran heterogeneidad espacial en las densidades de semillas. De tal modo que, aún con similar sobrevivencia es probable que el reclutamiento de nuevos individuos a la población difiera en espacio y entre especies.

SUMMARY

1. The typical high diversity of lowland tropical forests is remarkably contradicted by examples of forest dominated by a single species of canopy tree (disregarding early successional sites or waterlogged soils). Several factors and mechanisms have been proposed as important in maintaining high-density populations of tropical trees (and hence, low-diversity forests). For one such case, structure and floristic composition was examined in the woody component with DBH \geq 2.5 cm, and the hypothesis was tested that patterns of differential species establishment and survivorship account for the discontinuity of the established forest types.
2. On the Pacific slope of México, Celaenodendron mexicanum Standley (Euphorbiaceae) forms monodominant forests and it is essentially restricted to these. This monodominant forest (CF) occurs as discontinuous patches ranging in size from <0.1 to >1000 ha, within species-rich mixed forest (MF). Soil properties at depths up to 20 cm of both forest types were compared regarding their physical and nutrient status, and their effects on germination and establishment of several species. Also, experiments were conducted on seed and seedling survivorship at several sites in adjacent CF and MF using common species of MF, as well as Celaenodendron mexicanum.
3. The Celaenodendron mexicanum forest was significantly less diverse than mixed forest, with more than fifty percent of individuals conspecific (DBH \geq 10 cm). However, the subsidiary species in CF were also those characteristic of MF. Celaenodendron mexicanum itself was the only species exclusive to its patches. Thus, the floristic composition supports the view that the distinction of these monodominant stands depends on the presence of a single species, Celaenodendron mexicanum, and the subsidiary species are also common associates in adjacent high diversity stands.
4. Mature tropical lowland forests with low diversity of tree

species often have been considered as the result of restriction to particular difficult soil conditions. However, topographic and edaphic factors did not account for the discontinuity of the established forest types. Soil from CF did not result in patterns of germination and seedling survivorship (to four months) different from MF soil for Celaenodendron mexicanum and eight common species of MF. Moreover, the most common species of the MF (Caesalpinia eriostachys), successfully germinated and established in both forest types, demonstrating that its low density in CF is not due to some simple physiological restriction on this early stage.

5. There was no evidence for an effect of compensatory mechanisms in these early stages, and there is no reason to doubt that Celaenodendron mexicanum's dominance will continue through subsequent generations. The survivorship of postdispersal seeds to year-old seedling of Celaenodendron mexicanum (1.3%) was higher than those of two common MF species (0.0%) and not much different than that for the most important species of MF (Caesalpinia eriostachys, 2.3%). In CF the smaller size classes (DBH < 10 cm), whose individuals may represent more recently recruited cohorts, also were dominated by Celaenodendron mexicanum. This suggests that CF is persistent and a stand (CF3) with less dominance and smaller individuals of Celaenodendron mexicanum is an intermediate phase of MF changing into CF. In this stand, in spite of greater seed rain from MF species, survivorship of postdispersal seeds and seedling were similar to mature CF.

6. The data do not support the existence of a mechanism of escape from predators by chemical defenses or mast fruiting at long intervals or absence of predators. Invertebrates, presumably ants, as well as vertebrates were important seed removers (predators). Rodents also were predators of Celaenodendron mexicanum seedlings. Among three common species of MF and Celaenodendron mexicanum there were no differences in seed removal (predation) between forest types, although there were

large differences between species.

7. The dominance of Celaenodendron mexicanum, and the poor representation of other species in CF, might be related to different intensities of mortality processes. Experiments showed that mortality to age one year did not differ between forest types for Celaenodendron mexicanum and MF species. Thus, existing contrasts in stand diversity cannot be readily attributed to differential survivorship of post-dispersal seeds and seedlings. However, differences in the degree of gregariousness of these species must result in a great spatial heterogeneity in the densities of seeds. Even with similar survivorship, then, it is probable that recruitment will differ in space.

INTRODUCCION

Los bosques tropicales son unas de las comunidades vegetales más diversas del mundo. Por ello, mucho del esfuerzo en investigación ha sido orientado a explicar por qué hay tantas especies coexistiendo en pequeñas áreas? (Grubb, 1977; Connell, 1978; Hubbell, 1979; Huston, 1979; Tilman, 1980). Sin embargo, también hay casos de bosques maduros sobre suelos de buen drenaje que están dominados por una sola especie, los cuales colindan con bosques de gran diversidad. Estas especies están representadas por un 50-100% de los individuos del dosel y presentan regeneración abundante.

Ejemplos de tales especies han sido mencionadas para Asia y Africa, como tan bien para América, cubriendo desde pequeñas áreas a miles de hectáreas (ver Richards, 1952; Whitmore, 1975; Connell & Lowman, 1989; Hart et al, 1989). Aparentemente, la dominancia a través de todo su rango es típico de estas especies. Estas especies merecen atención por representar sus poblaciones una extraordinaria contradicción de la estructura poblacional típica de las especies arbóreas en los bosques tropicales (baja densidad de individuos pero distribuidos en pequeños agregados. A su vez, los bosques dominados por una sola especie pueden ser útiles por su analogía con los monocultivos establecidos por el hombre (Janzen, 1977). Sin embargo, en la mayoría de los dasos, datos sobre la autoecología de estas especies son todavía muy pocos. Igualmente, la existencia de estudios experimentales sobre los factores que pueden estar determinando su dominancia son muy escasos.

Estudios comparativos entre especies pueden ayudarnos a entender las dinámicas de estos bosques en términos de poblaciones arbóreas (Clark, 1986; Clark & Clark, 1992). Claramente, para ello es necesario contar con información cuantitativa sobre la regeneración de las especies del dosel. Las diferencias entre especies en cuanto los procesos dinámicos,

tales como crecimiento y regeneración, pueden estar determinando las diferencias en estructura poblacional así como en composición florística de los bosques a una escala local (Botkin et al., 1972; Swaine, 1989). Whitmore (1975) enfatizó que para entender los procesos que afectan la regeneración de los árboles del dosel, mucha más atención debería ser dirigida a los estadios de semilla/plántula y pequeños juveniles. En un estudio reciente, los resultados de hacer extrapolaciones de tasas de mortalidad y crecimiento en seis especies no pioneras del bosque tropical lluvioso sugieren fuertemente que, la mayoría de los sucesos determinantes de cuales juveniles van a llegar a exponer su copa en el dosel se presentan antes de que los árboles tengan cuatro centímetros de diámetro (Clark & Clark, 1992).

Los bosques que crecen en climas estacionalmente secos, los cuales representan el 42% de todos los bosques tropicales, han sido comparativamente poco estudiados (Murphy and Lugo, 1986). En recientes revisiones de bosques dominados por una sola especie (Connell & Lowman, 1989; Hart et al., 1989), han sido dejados de lado aquéllos que se hallan en regiones con una prologada sequía anual. Si bien, el número de especies arbóreas es generalmente menor en los trópicos secos, sin embargo los bosques con dominancia concentrada en una sola especie no son correspondientemente más comunes. En realidad, cuando la precipitación es menor a los 1600 mm no se manifiesta ninguna tendencia en diversidad (Gentry, 1988; en preparación). Ejemplos de bosques tropicales secos dominados por una sola especie han sido mencionados por varios autores (Montoya-Maquín, 1966; Swaine & Hall, 1981; Gentry, en preparación), siendo algunos ejemplos muy conspicuos por su contraste con un bosque adyacente más diverso. En otros casos, la apariencia de tales bosques puede estarse haciendo borrosa o su extensión reduciéndose por el uso extensivo de las zonas de trópico seco estacional para agricultura, pasturas y extracción de carbón, entre otros.

In this thesis, a study of the dynamics of a low-diversity forest was carried out with a population approach, giving special

emphasis to early stages of the life cycle: seeds and seedlings. The focal species was Celaenodendron mexicanum Standley (Euphorbiaceae), which dominates discontinuous patches of deciduous forest near the southwestern coast of México, a tropical region with highly seasonal rains.

La presente tesis está organizada en tres manuscritos independientes. En el Capítulo I, la historia natural de C. mexicanum es descrita y la estructura y composición florística de sus agregados poblacionales son comparadas con la del bosque que los rodea. El caso de Celaenodendron mexicanum es analizado en el contexto de otros bosques tropicales dominados por una sola especie y se discuten varias de las hipótesis sobre la existencia de ellos.

Notoriamente, mucha de la información existente sobre estas especies dominantes tanto de bosques secos como húmedos es descriptiva o incluso de tipo anecdótica. De tal modo, la mayoría de los posibles factores determinantes de su condición de dominantes no han sido puestos a prueba experimentalmente. En los Capítulos II y III, se describen experimentos que ponen a prueba algunas de estas hipótesis. Por ejemplo, explicaciones de la abundancia local y de los agregados poblacionales tan nítidamente demarcados de tales especies dominantes se han centrado generalmente en las relaciones planta-suelo. Así, en el Capítulo II, las propiedades del suelo de bosques dominados por Celaenodendron mexicanum son comparadas con aquéllas de los suelos del bosque mixto adyacente. También, son presentados experimentos sobre los efectos de los suelos sobre la germinación y establecimiento de varias especies. Una explicación alternativa es que la dominancia es debida a la excepcionalmente baja mortalidad de los individuos de estas especies, comparada a la de la mayoría de las otras, como un resultado de la saciación de depredadores (Boucher, 1981) o de la defensa química (Janzen, 1974) frente a la depredación, herbivoría o patógenos. En el Capítulo III, presento experimentos que evalúan la hipótesis de que el contraste en diversidad puede estar derivando de

diferencias en la sobrevivencia de las especies en los estadios de semillas post-dispersadas y plántulas hasta el año de vida. Finalmente, se presentan algunos comentarios finales.

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MONOSPECIFIC DOMINANCE OF A TROPICAL DECIDUOUS FOREST IN MEXICO

Abstract. The typical diversity of lowland tropical forests is contradicted by examples of forest dominated by a single species of canopy tree (disregarding early successional sites or waterlogged soils). On the Pacific slope of México, Celaenodendron mexicanum Standley (Euphorbiaceae) forms such forests. Natural history study shows that this species is dioecious, wind-pollinated, autochorous, deciduous but drought-resistant, slow-growing, VA mycorrhizal, rich in secondary metabolites, and has both specialist parasites and generalist predators.

Monodominant forests of Celaenodendron mexicanum (CF) occur as discontinuous patches ranging in size from <0.1 to >1000 ha. Celaenodendron mexicanum is essentially absent outside of these patches, which are surrounded by forest with a high diversity of tree species (mixed forest, MF). Five samples, three from CF and two from MF, were compared regarding structure and floristics in the woody component with DBH \geq 2.5 cm.

The percentage of canopy trees with DBH \geq 10 cm attributable to the most common species was high in two CF samples (63% Celaenodendron mexicanum) compared with MF samples (19% Caesalpinia eriostachys Benth.). Diversity was correspondingly low in these two CF samples relative to MF samples (Inverse of Simpson's Index = 4 and 13, respectively; Exponential Shannon-Wiener index = 6 and 16). The third sample of CF had an intermediate value for dominance (35%) and diversity indices similar to MF samples (7 and 12). Discriminant analysis showed three groups with floristic richness as the principal distinguishing attribute. The structural characteristics of overall density and basal area did not differentiate monodominant and mixed samples. The trees and lianas occurring in CF were also found in MF; Celaenodendron mexicanum itself was the only species exclusive to its monodominant patches. Celaenodendron mexicanum also dominates the smaller size classes (DBH < 10 cm) in all three CF samples. These individuals may represent recruitment and suggest that CF is persistent, and that CF3 is an intermediate phase of MF changing into CF.

INTRODUCTION

Lowland tropical wet forest is typically characterized by its great floristic diversity in small plots (Richards, 1952; Whitmore, 1975; Gentry, 1982). Conspecific canopy trees are commonly aggregated (Hubbell, 1979; Hubbell & Foster, 1987), but not to the extreme of dominating the forest canopy. In contrast, forests may be nearly monospecific or comprise a specialized flora in conditions of exaggerated disturbance (e.g. Cavanillesia platanifolia (Bonpl.) Kunth (Budowski, 1970), or on permanently water-logged soil (e.g. Pterocarpus officinalis Jacq., Janzen, 1978; Raphia spp., Letouzey, 1978; Myers, 1984). However, there are also some cases of mature forests on well-drained soils that are dominated by single species with between 50-100% of the canopy individuals, covering small areas or thousands of hectares (Hart, Hart & Murphy, 1989). Examples have been reported in Asia and Africa as well as in the Americas (Davis & Richards, 1933, 1934; Eggeling, 1947; Richards, 1952; Montoya-Maguín, 1966; Letouzey, 1968; Janzen, 1974; Whitmore, 1975; Connell, 1978; Swaine & Hall, 1981; Hart et al., 1989; Connell & Lowman, 1989; Hart, 1990). Such stands are found on a variety of substrates and in diverse rainfall regimes.

Monodominant forests actually contain many other species, and are found in immediate juxtaposition to diverse forests. The accompanying species typically are also present in the adjacent higher-diversity stands. Apparently, dominance is typical of the principal species throughout their ranges (e.g. Gilbertiodendron dewevrei (De Wild.) Léonard in Central Africa, Hart et al. 1989; Cynometra alexandri C.H.Wright in East Africa, Eggeling 1947), but data on their autecology are especially scarce. The abundance of saplings suggests the principal species is persistent and capable of maintaining its dominance in subsequent generations, but quantitative data are few and most of the descriptions regarding smaller size classes or regeneration processes have been based on anecdotal evidence. These forests merit attention as extraordinary deviations from typical tropical forest

structure, and as natural analogs of monocultures established by man (Janzen, 1977).

Regions with prolonged annual drought have been disregarded in recent reviews of monodominant forests (Connell & Lowman, 1989; Hart et al., 1989). The number of tree species is generally lower in the dry tropics, but monodominant forests are not correspondingly more common. In fact, no trend in diversity is apparent as precipitation decreases below 1600 mm (Gentry, 1988; in prep.). No general dominance-diversity pattern has been suggested, perhaps reflecting the variety of driving factors—drought, fire, hurricanes, megafauna, humans—and the importance of history. However, examples of monodominance are conspicuous by comparison with adjacent more diverse forest.

In the tropical Pacific region of México, with highly seasonal rains, there are deciduous forests dominated by an arborescent Euphorbiaceae, Celaenodendron mexicanum Standl. This species is distributed in dense discontinuous, uneven-sized patches, some of which exceed 1000 ha. Celaenodendron mexicanum is essentially absent outside of these patches which are distinctive for their homogeneous canopy and sparse understory. The patches are found immersed in deciduous forest of exceptionally high diversity, and with a dense understory. Quantitative studies of the vegetation have not encountered Celaenodendron mexicanum in the pattern typical of other species, of single individuals or sparse aggregations (Lott, Bullock & Solís-Magallanes, 1987).

Although the species has been mentioned in regional floristic studies (Nelson, 1899; Ferris, 1927; Rzedowski & McVaugh, 1966; Rzedowski, 1978; Lott et al., 1987), the forests it forms have not been studied, nor have they appeared on regional maps (e.g. Díaz, 1969; Dirección General del Inventario Nacional Forestal, 1970). In vegetation descriptions, Celaenodendron mexicanum was first mentioned as a principal component in a few coastal areas of tropical semi-deciduous forest (Rzedowski & McVaugh, 1966). This vegetation type is

distinct from deciduous forest in structure and floristics and at low elevations is generally restricted to major drainage channels (Lott et al., 1987). Many species in this vegetation are deciduous for only a few weeks as is Celaenodendron mexicanum on dry hillsides sites, although the mechanisms are quite distinct (Bullock & Solís-Magallanes, unpub. data). The superficial phenological similarity may have contributed to errors in mapping forest types. Some maps show the area between Manzanillo and Puerto Vallarta as occupied mostly by semi-deciduous forest (Rzedowski & McVaugh, 1966; Díaz, 1969; Flores et al., 1971; Rzedowski, 1978). In fact, the vast majority of the region below 500 m is occupied by deciduous forest, as indicated on the map of the Dirección General del Inventario Nacional Forestal (1970). The lack of previous recognition of monodominant forests of Celaenodendron mexicanum reflects inaccessibility of the larger, purer forests. Moreover, it is likely that many patches have disappeared, because deforestation has been intensive throughout most of the species' range.

In this report, we describe the natural history of Celaenodendron mexicanum and compare the structure and floristics of its patches with the surrounding forest. We discuss this case in the context of other monodominant tropical forests, and the hypotheses for their existence.

STUDY AREA

The research was done on the property or in the vicinity of the Estación de Biología Chamela, situated in the state of Jalisco (México), at about 125 km NW of Manzanillo and at about 2 km from the Pacific coast (19°30' N, 105°03' W). The climate is warm and seasonally dry. The mean annual temperature is 24.9°C (Bullock, 1986). The mean annual precipitation is 707 mm (1977-1991), of which 80% falls between July and October. There are occasional hurricanes. The region comprises low hills and plains between the Pacific Ocean and the Sierra Cacoma. The elevations within the station range from 30 to 550 m. The soil's

are young, generally shallow, and have a low content of organic matter and mineral nutrients (Maass, Jordan & Sarukhán, 1988).

Tropical deciduous forest is the predominant vegetation, except on deep soils along (temporary) water courses (Lott et al., 1987; nomenclature of Rzedowski, 1978; equivalent to Seasonal Deciduous Forest of Beard, 1955; Short Deciduous Forest of Miranda and Hernández-Xolocotzi, 1963). This vegetation type is common on the Pacific slope of Mesoamérica, with some extensions as far north as Sonora (México), and as far south as Guanacaste (Costa Rica), and with many analogues in the Caribbean Basin and South America (Gentry, in prep.). In the study area, 233 tree species have been recorded, distributed in 55 families; Euphorbiaceae is the second family in number of tree species (Lott, in press). The flora is also rich in life forms, with an outstanding diversity and abundance of climbing plants (Bullock, 1990; Lott, in press), and abundance of epiphytes (Lott et al., 1987), compared to typical descriptions of deciduous forest (Rzedowski, 1978; Gentry, in prep.). Also, the diversity of woody species is exceptionally high (Lott et al., 1987; Gentry, in prep.). The most outstanding physiognomic feature of this vegetation, is the almost completely loss of leaves for several months each year (Bullock & Solís-Magallanes, 1990; Medina, in prep.). Grasses are rare, and fire is absent.

VEGETATION STUDY METHODS

This study is based on five samples, each consisting of six transects of 100 m². These correspond to the typical high diversity or "mixed" forest at Chamela (MF1 and MF2), and to three forests with Celaenodendron mexicanum dominant in the canopy (CF1, CF2, CF3). All samples are from deciduous, hillside stands.

The data for mixed forest were based on 2 m by 50 m transects reported in Lott et al. (1987). Our MF1 and MF2 comprise data from their Set 1 and Set 2, but are limited to the first six of the original ten transects from each, so that the

area was equal to our samples. These transects were not contiguous (see Lott et al., 1987, for details).

The stands referred to as CF1, CF2 and CF3 were sampled by us in summer 1989. Each of these corresponds to a discrete patch in which we established six adjacent transects of 4 m by 25 m. The transects were necessarily contiguous, given the small area of these patches; respectively, 0.50, 0.11 and 0.06 ha. Although smaller than typical patches, these particular forests were sampled because they were the only ones readily accessible, and could be used in subsequent experimental studies, being protected from outside disturbance. Outside of the station there were patches of similar and much larger size.

Within each transect we measured all stems with diameter at 1.3 m height (DBH) ≥ 2.5 cm, and rooted within the transect. For inclined stems, height was measured as distance along the stem. For plants which branched below 1.3 m, only stems meeting the criterion were measured, and basal area was calculated for the plant based on the sum of areas of these stems.

Taxonomic identification usually was made in the field; in doubtful cases material was collected for determination in the local herbarium or by specialists. Nomenclature follows Lott (in press). A total of 150 taxa were recorded; 21 were not identified to species in the CF samples (11.6% of the individuals). Voucher specimens of Celaenodendron mexicanum from our plots are deposited in the following herbaria: MEXU, EBCH, IEB, USNM, CAS, CORD.

The transect data were used to calculate Curtis' Importance value (CVI, Mueller-Dombois & Ellenberg, 1974) for each species in each sample. Floristic richness was expressed as the number of species present. Also, we calculated two indices of diversity, combining floristic richness and abundance per species. The Inverse of Simpson's Index ($ISI = 1/\sum_{i=1}^s p_i^2$) is more sensitive to changes in abundance of the more important species (Peet, 1974), and is thus a measure of the relative concentration of dominance (Whittaker, 1965; 1972). The Exponential Shannon-Wiener index

($ESW = e^{H'}$, where $H' = -\sum_{i=1}^s p_i \ln p_i$) is more sensitive to changes in the number of rare species, and is thus more subject to sample bias.

The samples (each consisting of six transects) were compared regarding the floristic and structural data expressed on a standard area basis (100 m² and ha respectively). One-way analysis of variance (ANOVA) were developed, using the Bonferroni method to adjust the nominal significance level to 0.05 (dividing by the number of ANOVAs being performed, $0.05/18 = 0.0028$). The minimum differences for the simultaneous tests were calculated by the Tukey method (Montgomery, 1984). Descriptive statistics and the univariate tests provided the basic information on the distribution of the variables and helped identify some differences among groups. Discriminant analysis was used in an interpretive manner to determine the degree of separation of the samples and to identify the variables contributing most to this separation. This method permits the optimal separation among predefined groups. Applications and limitations of discriminant analysis in ecological studies are clearly discussed by Williams (1983) and James & McCulloch (1990). The SAS program (SAS Institute, 1985) was used, with the direct method, not step-by-step.

NATURAL HISTORY OF CELAENODENDRON MEXICANUM

Celaenodendron is a monotypic genus (Euphorbiaceae, subfamily Oldfieldioideae, tribe Hyaenancheae, subtribe Paivaesusinae; Webster, 1975), described by Standley (1927), and found only in the region from Mazatlán (23°14' N) to south of Manzanillo (19°N) along México's Pacific coast. In Jalisco, it is found only at low elevations and only within 10 km of the coast, in discontinuous and typically well-delimited patches of variable size (<0.1 ha to >1000 ha, Fig. 1.1a, b). In these, it is by far the most abundant species, and in all cases dominates the forest canopy. These patches differ from mixed forest in having an open understory, notably poor in or devoid of very small diameter

woody plants and of herbaceous vegetation. Leaves of Celaenodendron mexicanum decompose very slowly and a thick litter persists throughout the year (in the dry and wet seasons, respectively, 4.5 ± 0.1 and 2.8 ± 0.1 cm thick). In contrast, the litter of adjacent mixed forest is thin and more seasonal, almost there is not in the wet season (2.0 ± 0.1 and 0.4 ± 0.1 cm in the dry and wet seasons). In the dry season, the foliage of Celaenodendron mexicanum acquires a reddish hue and persists until after almost all other species are leafless. Although these leaves may cease to be functional long before they fall, the trees are without leaves for a relatively short period, and flush with the first summer rains, simultaneous with flowering (Fig. 1.2). The flowers are dioecious and the wind-pollinated (Bullock, in prep.).

The ovary is trilobulate; each locule bears two ovules, but matures at most one seed. Maturation occurs after eight to ten months. The mature fruit (3 cm dia.) is explosive. Mean seed dry mass is 80.8 ± 0.9 mg and the endosperm is oily. Germination is hypogeous and the eophylls are simple, in contrast to the normally trifoliolate leaves. Apparently there is no innate dormancy, and germination occurs rapidly in moist conditions at normal temperatures (Rincón & Huante, 1988; Martijena, unpub. data). The seeds lose viability when stored for one year at local ambient temperature and humidity.

The trees form vesicular-arbuscular mycorrhizae (Gavito & Martijena, unpub. data). These do not have the typical arbuscules of temperate broadleaf species but rather highly ramified intracellular hyphae, coincident with the observations of Alexander (1989) in other tropical trees.

Predispersal predation by parrots is sometimes conspicuous, but no insects have been detected inside the seeds before or after their dispersal. Rodents eat the dispersed seeds. The most abundant rodent in the area, Liomys pictus pictus (Heteromyidae) (Ceballos, 1990), eats the seeds even in the presence of oatmeal (Martijena & Bullock, unpub. data). The leaves are typically

damaged, apparently by psyllids. One case was observed of herbivory by lepidopteran larvae (Lasiocampidae). Attine ants were only once observed cutting the leaves; these were later rejected from the nest, which suggest they are unsuitable for the ants' fungus. A phloem-boring beetle (Pseudothysanoes thomasi Wood: Scolytidae) is known only from Celaenodendron mexicanum (Equihua Martínez & Atkinson, 1986). Relationships with predators and parasites, or other plants, may be affected by secondary metabolites: leaves and twigs of Celaenodendron mexicanum are rich in terpenes and flavonoids (Castañeda et al., 1992).

Compared to the average for trees and shrubs at Chamela, the trifoliolate leaves are smaller (18.5 cm² vs 124.1-15.7 cm²) and more coriaceous (96.5 g m⁻² vs 87.0-22.0 g m⁻², n=15 species, Castellanos et al., 1989). The bark is smooth and green or grayish green and exfoliates in plates of irregular shape, leaving darker marks. The tree, which is commonly called "guayabillo borcelano" (Jalisco) or "palo prieto" (Sinaloa), has a straight trunk that can reach 25 m height; small buttresses develop occasionally. The wood has a specific gravity of 0.94, higher than 72% of Chamela trees (Barajas-Morales, 1987). This density and our observations and measurements on rings suggest the trees are slow-growing. The wood is esteemed for its strength and durability, and is used locally for posts, construction timber and furniture. Presently, stands of Celaenodendron mexicanum are being cut, without knowing if these will regenerate.

RESULTS

Dominance and Diversity

The CVI values (sum of Relative Density, Relative Frequency and Relative Basal Area, which has a maximum of 300) for Celaenodendron mexicanum in CF1 and CF2 were four times greater than for the most important species in MF samples, Caesalpinia eriostachys Benth. (Table 1.1). In CF3, the CVI of Celaenodendron mexicanum was half that of both CF1 and CF2, but was double that

of Caesalpinia eriostachys in MF samples (Table 1.1). The ranked abundance curves showed greater differences between the most abundant and other species in all three CF samples than in MF1 and MF2 (Fig. 1.3). These curves also emphasize differences in the number of uncommon species: fewest in CF1 and CF2, more in CF3 and most in MF samples.

In CF1 and CF2, Celaenodendron mexicanum accounted for about 50% of all individuals and 60% of the basal area (Table 1.1, Fig. 1.4); in CF3 the figures were 31% and 32% for individuals and basal area, respectively. It was the most common species in all size classes, representing 100 % (CF1 and CF2) of all individuals in the largest DBH class, and 36% (CF1) and 46% (CF2) in the smallest class (Fig. 1.4). In CF3, Celaenodendron mexicanum was well represented in the smallest size class (34% of all individuals), but there were few large Celaenodendron mexicanum, and none larger than 30 cm DBH (Fig. 1.4). Thus, the CF3 canopy was formed mostly by all the other species.

In contrast, Caesalpinia eriostachys represented on average 3% of the individuals in MF samples. The species was least common in small size classes, and only exceeded 50% in the largest DBH class in MF2 and MF1 (Fig. 1.4). However, Caesalpinia eriostachys accounted for 21% of the total "basal area" in MF1 and MF2 due to a few large individuals; (the old trunks are hollow, formed of a ring of cylinders).

The dominance of Celaenodendron mexicanum, as percentage of stems, in CF1 and CF2 is correlated with low diversity as measured by ISI ($r=-0.86$, $p<.0001$, $n=30$). CF3 showed an intermediate value of ISI, differing only from MF2 (Table 1.2). However, according to the ESW index and floristic richness, CF1 and CF2 were less diverse than both MF samples and CF3, which were similar (Table 1.2). The contrast of the indices showed, again, that CF1 and CF2 had both a less equal distribution of individuals among species, and also a less diverse flora.

Considering only individuals of large size (DBH ≥ 10 cm), the number of species did not differ between forest types (Table

1.2). Thus, the canopy of CF samples had a species richness similar to MF samples, although each species was represented by few individuals. Among smaller individuals ($2.5 \text{ cm} \leq \text{DBH} < 10 \text{ cm}$), CF1 and CF2 presented the smallest number of species, although CF2 did not differ significantly from CF3 and MF1 (Table 1.2). This suggests that floristic poverty in CF1 and CF2, relative to the other samples, was principally at the level of small individuals.

Regarding the species richness of lianas, the CF samples presented the lowest values, but CF2 did not differ significantly from the MF samples (Table 1.2).

Floristic relations

Table 1.3 presents the common species and their densities in CF and MF samples. The criterion for common species was at least ten individuals in one of the samples and at least one individual in another. Eleven species met this criterion: four in CF1 and CF2, five in CF3 and ten in MF samples. The most notable elements shared among samples and stand types were species of Lonchocarpus and Guapira cf. macrocarpa Miranda. Although the complete absence in CF samples of other common species of MF samples was also notable, only one species occurred in the former which was not in any of the original 20 transects of Lott et al. (1987) in deciduous forest: Celaenodendron mexicanum itself.

Structural characteristics

The proportional distribution of individuals among DBH classes differs strikingly between samples (Fig. 1.4). In MF1, MF2 and CF3 about 50% of the individuals were 2.5 to 5 cm DBH, but in CF1 and CF2 this size class represented only 33% (d.f.=1,25, $P < 0.0001$). However, most of the understory elements did not reach the minimum size for the survey technique and thus were not sampled. In contrast, the 10 to 20 cm DBH class was better represented in all CF (22%) than in MF samples (9.3%) (d.f.=1,25, $P < 0.0001$).

Regarding the density of stems and basal area (total or by DBH class), there were few significant differences and no clear pattern, except the density of lianas that was lower in CF samples (Table 1.4). The overall average total basal area was $28.8 \text{ m}^2 \text{ ha}^{-1} \pm 2.4$.

Discriminant Analysis

Four variables were used in the discriminant analysis: number of species among all individuals (DBH \geq 2.5 cm, lianas and trees), number of species with large individuals (DBH \geq 10 cm), density of lianas (DBH \geq 2.5 cm) and density of small individuals (DBH $<$ 10 cm). Other variables were discarded due to lack of normality, correlation between variables or inequality of the dispersion matrices according to Box's M test. The predefined groups were the five samples. The assignment of prior probabilities according to the different areal extent of the forest types did not modify the results.

According to the value of Wilks' lambda, of the four functions obtained, only two were significant; the parameters of these two functions are given in Table 1.5. The other functions did not contribute substantially to separating the samples. The first function explained 60% of the total variance. In Fig. 1.5, where the horizontal axis represents this function, one can observe that it permitted a good discrimination between CF1 and CF2 from the other samples. This function, according to the standardized coefficients, was dominated by the variable species richness (Table 1.5). Observations with high values for the first function were those with greater species richness (MF1, MF2 and CF3).

In the second function, which explained 37% of the variance, the highest standardized coefficients corresponded to three variables: density of small individuals, density of lianas, and again, species richness (Table 1.5). This last variable had a negative standardized coefficient although it was positively correlated with the discriminant function. This contradiction was

due to the high correlation of species richness and the number of small individuals. Because correlations affect the signs and magnitudes of the individual coefficients, the importance of these variables cannot be assessed. Thus, the second function represented the variation between samples in the density of lianas. In this regard there was no great difference between CF1 and CF2 from MF samples (Fig. 1.5). The only points separated by their low density of lianas corresponded to CF3.

Both functions correctly classified only 77% of the observations. This low percentage reflects the similarity of some samples in the dominant variable in one or the other function. However, the five samples were clearly arranged in three groups, with only 14% error in classification of the transects into these groups: CF1 and CF2 samples together, CF3 alone and MF1 with MF2 in a third group.

DISCUSSION

Adjacent mixed and monodominant stands in tropical forests typically share a common flora (Hart et al., 1989), as in the case of Celaenodendron mexicanum. The apparent absence in CF samples of some common species of MF must be due in part to random and historical factors, as occurs among MF samples (Lott et al., 1987). We also recognize that the shorter, wider and contiguous transects in CF forests decreased the probability of encountering species present at low densities. However, the rate of species accumulation is clearly lower in the monodominant forests. We would expect larger samples to show that some species are more rarified than others, because regeneration of particular species is often affected by neighborhood composition (e.g. Enright, 1982).

The overall degree of dominance in our CF samples is comparable to other examples from tropical lowlands (Fig. 1.6). Dominance is greater in larger size classes, and more than 60% of the trees in the largest class belong to one species. Notably, in Celaenodendron mexicanum and Gilbertiodendron deweyrei, the

figure exceeds 90% in the largest class. However, all the examples available for Fig. 1.6, except Celaenodendron mexicanum, are from wet forest. Other monodominants in highly seasonal forests are Talbotiella gentii Hutch & Greenway, endemic to Ghana (Swaine & Hall, 1981), and Quercus oleoides Cham. & Schlecht in Central América and México (Montoya Maguín, 1966). On the Pacific slope of México, Cordia eleagnoides DC. (Boraginaceae) occasionally forms dense and extensive aggregations (Pennington & Sarukhán, 1968). Similar to Celaenodendron mexicanum, Cordia eleagnoides is associated with both deciduous and semi-deciduous forest. It is wind-pollinated and wind-dispersed, and has dense heartwood. However, its recruitment is highly sporadic (van Groenendael, Bullock & Pérez Jiménez, in press), its growth in juvenile or coppice conditions is rapid, and it is often common but not dominant. These characteristics suggest a very different dynamics than in Celaenodendron mexicanum.

Although trees under 5 cm DBH have not often been sampled, abundant regeneration has been reported in Cynometra alexandri in Uganda (Eggeling, 1947) and in Gilbertiodendron dewevrei in Zaire (Hart et al., 1989), extending to invasion of adjacent mixed forests. Celaenodendron mexicanum also dominates among the small individuals. Since these may represent younger trees, it is probable that the population is persistent, not representing a seral stage. In turn, the presence of small Celaenodendron mexicanum in CF3, many below the crowns of other species, suggests that Celaenodendron mexicanum not only tolerates its own shade but also can recruit in more diverse forests. The CF3 can be interpreted as a transitional site of MF changing progressively into CF. The gradual character of the process of replacement of MF trees by Celaenodendron mexicanum could explain the higher diversity of CF3 compared to the other two CF samples.

Possible mechanisms which determine and maintain the dominance of one canopy tree species in lowland tropical forests have been reviewed recently, again with the focus on wet or very wet forests on well-drained soils (Hart et al., 1989; Connell &

Lowman, 1989; Hart, 1990). The oldest explanation turns on the capacity of one species, more than others in the area, to tolerate unfavorable soils, e.g. Shorea curtisii Dyer ex King in Asia (Whitmore, 1975) and Eperua falcata Aubl. in South America (Davis & Richards, 1934). However, other species dominate forests on soils with diverse nutrient status, e.g. Talbotiella gentii (Swaine & Hall, 1981) and Gilbertiodendron dewevrei (Hart et al., 1989). Moreover, this explanation is weak in the typical cases of monodominant forests with floras which include many species also common in the surrounding diverse forests, as between CF and MF.

One related hypothesis supposes that ectomycorrhizal (ECM) associations are the dominant factor (Janos, 1980; Alexander, 1989). Possible examples are Gilbertiodendron dewevrei and Julberpardia seretii (De Wild.) Troupin in equatorial Africa (Swaine & Hall, 1981). Most tree species form vesicular-arbuscular mycorrhizae (VAM) with fungi that occupy a wide taxonomic range of hosts; thus, a high diversity of trees does not decrease inoculation of seedlings. Endomycorrhizal fungus species, however, are highly host-specific, so their preemption of soil space should be unfavorable to most VAM tree seedlings. Also, ECM may have physiological advantages in situations with low or intermittent nutrient supply (Harley & Smith, 1983), as in the dry tropics, which would further favor dominance by ECM trees. However, Högberg (unpub.) found that in African dry forests ECM species are sparse compared to more abundant populations of VAM tree species, such as monodominant Talbotiella gentii. Celaenodendron mexicanum also forms VAM, as do many species in the adjacent diverse forests (Gavito pers. com.). Whether its peculiar morphology reflects host specificity is unknown.

Extremely high escape from predators and herbivores, or predator satiation, may influence dominance in some cases (Janzen, 1974; 1981). Experiments with Quercus oleoides suggest that satiation of seed predators can explain the maintenance but not the establishment of dominance (Boucher, 1981). Satiation of

the generalist seed predators of Celaenodendron mexicanum has not been studied but seems unlikely because of the prolonged exposure to predators. The seed crop is exposed to parrots for eight months before dispersal, which occurs several months before germination is possible. However, dispersal is fairly synchronous and overlaps the community maximum of seed fall, so the possibility of satiation occurring cannot be excluded. For Gilbertiodendron dewevrei, seed and seedling mortality is actually higher than for a common species in adjacent mixed forest; apparently lower mortality in larger size classes is more important in determining dominance (Hart et al., 1989). In the case of Dryobalanops aromatica Gaertn. in Malaya, more frequent reproduction and greater persistence of seedlings than in other species may maintain its dominance (Whitmore, 1975: 191).

Another interpretation of monodominance is successional (Connell, 1978; Hart, 1990), as the result of sequential replacement by one species which is the most resistant to stress, or the best competitor in the pool of shade-tolerant species. The development of such dominant populations, that characteristically have slow-growth and poor seed dispersal, usually is impeded or diverted by disturbance. This climax thesis suggests that tropical forests with high species diversity represent mid-successional stages and monodominant stands, which appear to be increasing in range (such as Gilbertiodendron dewevrei), are remnant populations after ancient, large-scale disturbance or climatic change. However, it is not clear what life history traits of a species, other than shade-tolerant seedlings and long life span, render it the competitive dominant. Also, this scenario raises doubts about the absence of very similar species, present as subdominants, or a progression of stands with reduced numbers of shade-tolerant species, each one occupying a large proportion of the canopy. Moreover, actual historical information is lacking. Presumed age structure (i.e. size) in different species support several scenarios of recent stand history, including progressive recruitment or synchronous mass

establishment. These contrasts occur in single species, such as Dryobalanops aromatica (Whitmore, 1975). In Celaenodendron mexicanum, with individuals showing climax features, forests are at least multi-age. In dry forest, inexorable progression to a monodominant climax must confront extreme stresses, such as hurricanes and multi-annual drought in the region occupied by Celaenodendron mexicanum. However, the relative resistance of this species is suggested by the phenology data (Fig. 1.2a) and the rarity of branch and treefalls.

The mechanisms outlined above are not exclusive alternatives, and none is universal. Their realistic plurality stimulates a broader conception of forest dynamics (Mueller-Dombois, 1990). Attempts to evaluate these ideas draw attention to diverse lines of evidence, and to the need for studies of broader geographic and ecological scope, long-term or historical observation, and experiments on critical processes like recruitment.

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TABLE 1.1. Species with highest importance values and their percentage dominance (means and standard errors from six transects of 100 m²; individuals with DBH \geq 2.5 cm).

Sample	Species	CVI	(%) Individuals		(%) Basal Area	
			\bar{X}	\pm s.e.	\bar{X}	\pm s.e
MF2	<u>Caesalpinia eriostachys</u> Benth.	29	3.3	0.8	20.2	7.1
MF1	<u>Caesalpinia eriostachys</u> Benth.	33	3.3	0.9	21.5	13.0
CF3	<u>Celaenodendron mexicanum</u> Standl.	67	31.8	4.4	30.8	6.5
CF2	<u>Celaenodendron mexicanum</u> Standl.	132	56.5	6.0	68.4	4.6
CF1	<u>Celaenodendron mexicanum</u> Standl.	119	48.7	6.5	61.5	8.4

TABLE 1.2. Floristic diversity (means and standard errors from six transects of 100 m²; ticked vertical bars indicate values which are not significantly different at adjusted P=0.05).

Sample	Diversity indices				Floristic richness (spp n#/100 m ²)							
	ISI		ESW		DBH _{≥2.5}		<10.0		≥10.0		Lianas	
	\bar{x}	s.e.	\bar{x}	s.e.	\bar{x}	s.e.	\bar{x}	s.e.	\bar{x}	s.e.	\bar{x}	s.e.
MF2	15.0	1.4	10.2	0.9	24.7	0.8	22.5	0.5	4.2	0.8	3.0	0.5
MF1	10.8	1.6	14.2	1.3	19.5	1.4	15.7	1.4	4.8	1.0	3.0	0.8
CF3	7.5	1.0	12.0	1.3	20.0	1.6	17.3	1.8	6.2	0.6	0.5	0.2
CF2	3.4	0.9	6.0	1.7	12.3	2.1	10.2	2.0	4.0	0.6	1.5	0.6
CF1	3.8	0.6	5.9	0.9	10.2	1.1	8.5	0.8	3.7	0.6	0.3	0.2

TABLE 1.3. The most common species and their respective densities (no./600 m²).

	CF1	CF2	CF3	MF1	MF2	
CF	<u>Celaenodendron mexicanum</u> Standl.	75	122	103	--	--
	<u>Lonchocarpus</u> spp.	21	4	29	14	55
	<u>Guapira cf. macrocarpa</u> Miranda	4	13	4	9	6
	<u>Cordia alliodora</u> (Ruiz & Pav) Oken	2	--	2	10	8
	<u>Caesalpinia eriostachys</u> Benth.	--	--	5	8	11
MF	<u>Croton pseudonivcus</u> Lundell	--	--	--	27	19
	<u>Croton</u> sp.	--	--	--	16	11
	<u>Serjania brachycarpa</u> Rose	--	--	--	11	12
	<u>Apoplansia paniculata</u> Presl.	--	--	--	7	10
	<u>Thouinia paucidentata</u> Radlk.	--	--	--	2	22
	<u>Caesalpinia pulcherrima</u> (L.) Sw.	--	--	--	1	11

TABLE 1.4. Structural characteristics (ticked vertical bars indicate means which are not significantly different at P=0.05).

Density (no./ha)	DBH \geq 2.5		<10.0		\geq 10.0		\geq 30.0		Lianas	
	\bar{X}	s.e.	\bar{X}	s.e.	\bar{X}	s.e.	\bar{X}	s.e.	\bar{X}	s.e.
MF2	5233	449	4767	400	433	78	17	18	583	100
MF1	3883	393	3217	353	667	88	33	23	533	157
CF3	5583	363	4500	450	1083	125	50	24	50	24
CF2	3650	292	2550	201	1100	126	33	23	183	77
CF1	2583	203	1833	166	750	68	33	23	50	37
Basal Area (m ² /ha)										
MF2	21.8	2.3	10.3	0.8	11.5	2.0	1.2	1.3	1.39	0.81
MF1	30.4	3.0	6.9	0.8	23.4	3.4	7.3	5.7	0.80	0.35
CF3	34.1	2.8	10.8	1.7	23.3	4.4	5.4	2.9	0.03	0.02
CF2	33.0	4.3	7.2	0.3	25.8	4.1	2.9	2.1	0.47	0.23
CF1	24.8	2.5	5.3	0.9	19.4	2.2	3.3	2.3	0.10	0.07

TABLE 1.5. Discriminant functions: their statistics and variables, Variable 1: number of species among all individuals (lianas and trees, $DBH \geq 2.5cm$); variable 2: number of species with large individuals ($DBH \geq 10cm$); variable 3: density of lianas ($DBH \geq 2.5cm$); variable 4: density of small individuals ($DBH < 10cm$).

	Function 1	Function 2
Canonical Correlation	0.88	0.83
Eigenvalue	3.60	2.23
(%) Variance	59.57	36.92
Standardized Coefficients		
Variable 1	0.88	0.62
Variable 2	-0.33	-0.12
Variable 3	0.03	0.91
Variable 4	0.26	-1.19

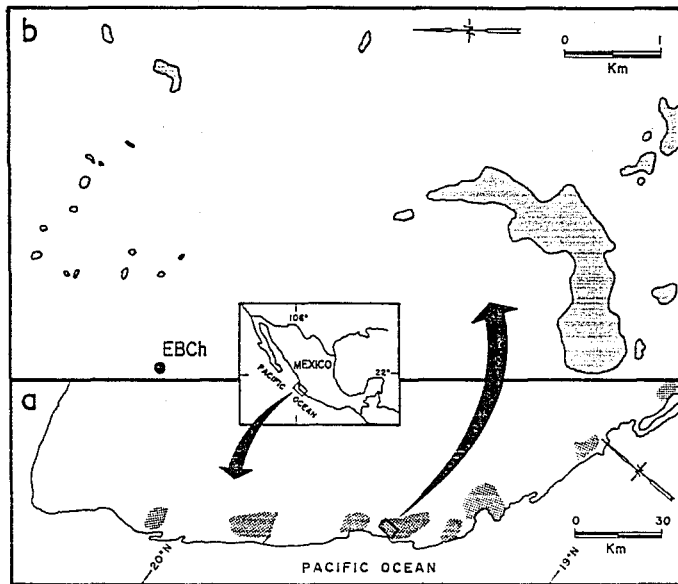


Fig. 1.1. a. Location of the study site and regional distribution of herbarium records and visual reports of *Celaenodendron mexicanum* Standl. b. Local distribution of *Celaenodendron mexicanum*-dominated forest near Chamela, based on aerial photographs and ground study.

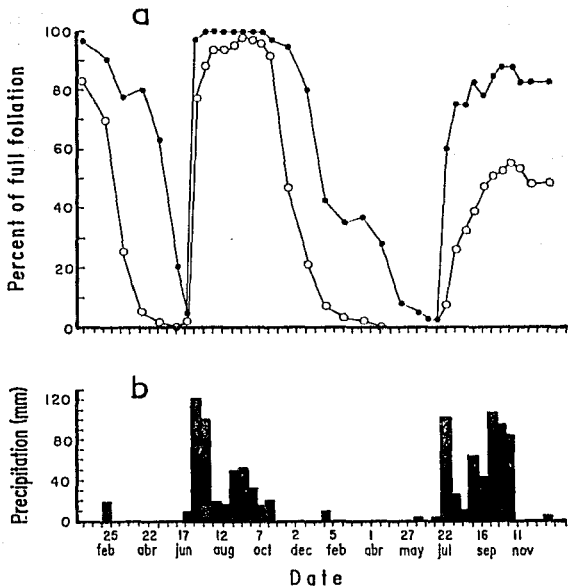


Fig. 1.2. a. Phenology of Celaenodendron mexicanum Standl. (solid circles) and other species (open circles). b. Precipitation at Chamela.

Notes: Phenological data are for 1985-1986, based on visual observation of ten trees (Bullock & Solís-Magallanes, unpub. data). The leaf presence curve for other species is the mean of ten individuals of each of ten tree and liana species common in high-diversity forest (Caesalpinia eriostachys Benth., Cordia alliodora (Ruiz & Pav.) Oken, Cordia elaeagnoides D.C., Croton sp., Croton pseudoniveus Lundell, Guapira cf. macrocarpa Miranda, Lonchocarpus constrictus Pittier, Lonchocarpus lanceolatus Benth., Serjania brachycarpa Rose, Trichilia trifolia L.). Precipitation data are for the same 1985-1986 period.

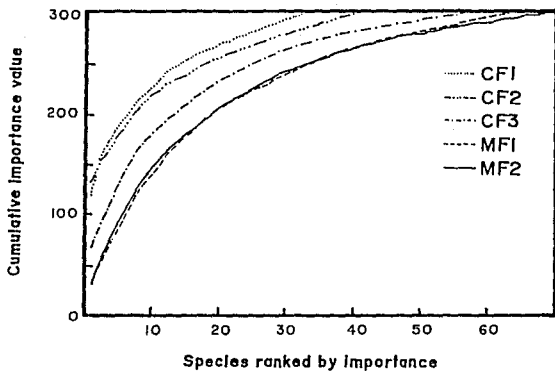


Fig. 1.3. Dominance-diversity curves: cumulative Curtis' Importance Value for species ranked by importance.

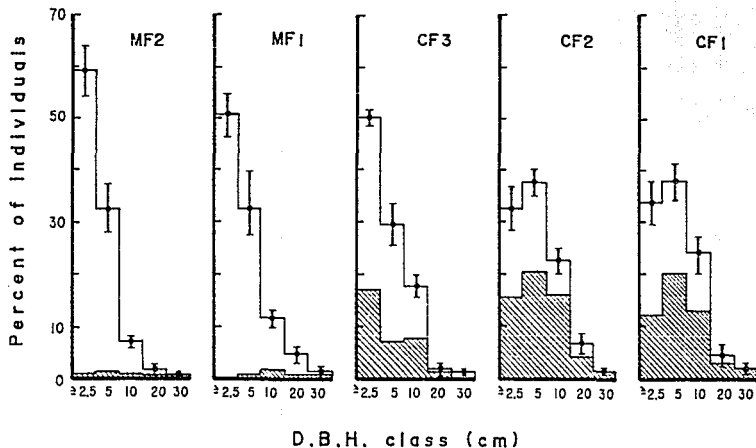


Fig. 1.4. Size structure and dominance: percentage of all individuals plants with $DBH \geq 2.5$ cm in each size class, separating the dominant species (diagonal lines) from all others. The percentage of the dominant within each size class is noted below. The "dominant" was Caesalpinia eriostachys Benth. in MF samples and Celaenodendron mexicanum Standl. in the other samples.

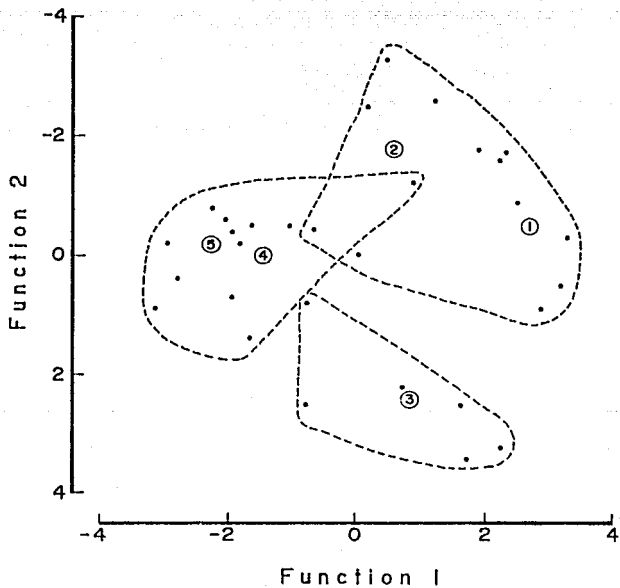


Fig. 1.5. Discriminant function scores for the samples. "o" centroids, 1: MF1, 2: MF2, 3: CF3, 4: CF2, 5: CF1.

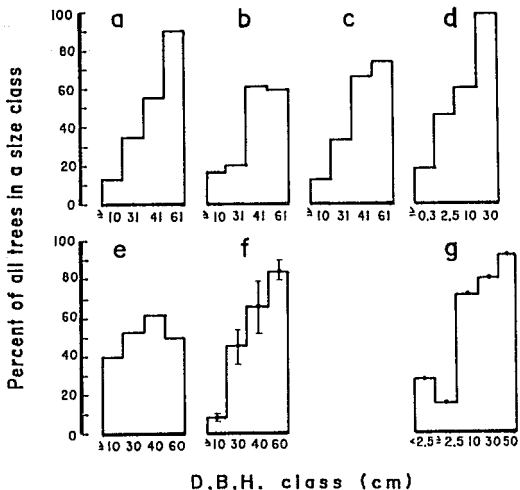


Fig. 1.6. Percentage of the dominant species among stems in each size class, for several monodominant lowland tropical forests. Mean and standard error are shown if available; plot size and number are noted below, with sources. a. *Mora excelsa* Benth. b. *Mora gonggrippii* (Kleinhoonte) Sandwith. c. *Eperua falcata* Aubl. d. *Celaenodendron mexicanum* Standl. e. *Tetraberlinia tubmaniana* J.Léonard. f. *Cynometra alexandri* C.H.Wright. g. *Gilbertiodendron dewevrei* (De Wild.) León. Regeneration is common in all these examples, although sampling has extended below 2.5 cm DBH in only two cases: *Celaenodendron mexicanum* (height ≥ 130 cm) and *Gilbertiodendron dewevrei* (height ≥ 50 cm).

Notes: a, b and c are each from one 1.49 ha plot in Guyana (Davis & Richards, 1934); d is from two plots of 625 m² each in México (this paper); e is from one 0.55 ha plot in Liberia (Voorhoeve, 1964); f is from two plots of 1.42 ha each in Uganda (Eggeling, 1947); g is from 24 plots of 625 m² each for stems with DBH ≥ 10 cm, and from 12 plots of 25 m² each for smaller stems in Zaïre (Hart, 1990). Examples from islands are excluded (e.g. *Mora excelsa* Benth. in Trinidad; Gunther, 1942; Beard, 1946), because the absence of herbivores or competitors may promote monodominance (Janzen, 1974).

SOIL PROPERTIES, GERMINATION AND SEEDLING ESTABLISHMENT IN SOILS
FROM MONODOMINANT AND HIGH-DIVERSITY TROPICAL DECIDUOUS FORESTS

Abstract. Low diversity of tree species in mature tropical lowland forests often has been attributed to poor soil conditions. This idea has not been tested exhaustively in monodominant stands in which the subsidiary species are also those characteristic of adjacent high-diversity stands. For one such case, I examined soil properties, and conducted experiments to assess soil effects on germination and establishment of several species. Celaenodendron mexicanum Standley (Euphorbiaceae) dominates, and is virtually restricted to, discontinuous patches (CF) within high-diversity forest (MF) in southwestern México; the subsidiary species in CF also occur in MF. CF was found occupying flatlands as well as hillsides of all aspects, and slope gradients of hillside CF were typical of the region.

There were no significant differences between CF and adjacent MF for soil texture or most of the nutrients tested. The effects of soils from CF and MF on seedling establishment was tested with greenhouse experiments with Celaenodendron mexicanum and three common species of MF (Recchia mexicana Moc. & Sesse, Caesalpinia eriostachys Benth. and Cordia alliodora (Ruiz & Pav.) Oken). The percentages of germination did not show differences between soils from CF and MF. Similarly, seedling survivorship to four months in the species tested was independent of soil source. Seedling height at this time was not significantly different between soils from CF or MF for MF species. Seedlings of Celaenodendron mexicanum reached greater heights on CF soil from two sites but not from a third. Field experiments were conducted with Caesalpinia eriostachys, the most common species in MF, to evaluate its establishment in both CF and MF. Successful germination and establishment in both forest types demonstrated that its low density in CF is not due to some simple physiological restriction on new seedlings.

Thus, topographic and edaphic factors apparently do not determine the distribution of CF. Moreover, the experiments demonstrate that soil characteristics at depths up to 20 cm do not result in patterns of differential species establishment which might account for the discontinuity of the established forest types.

INTRODUCTION

Spatial distributions of plants are frequently determined by edaphic factors (Krukkeberg, 1969), but experimental studies related to this are concentrated in the temperate region. It has long been emphasized that the edaphic factor is important in the tropics (Davis & Richards, 1933, 1934; Richards, 1952; Ashton, 1964; Webb, 1968, 1969), although the important factors are not necessarily the same in all regions, or as those operating in the temperate zone. Spatial differences in soils have been reported that correspond to differences in dominance-types (Bunyavejchewin, 1983, 1985) or even in floristic richness of forests (Davis & Richards, 1934; Ashton, 1977; Huston, 1980).

Tropical forests dominated by one or a few species have been considered to result from edaphic conditions unfavorable for plant growth (Davis & Richards, 1934; Richards, 1952; Hartshorn, 1988), such as poor nutrient status, presence of some minerals in toxic concentrations, and temporary or permanent flooding. The dominant species is confined to such sites, where the soil conditions probably exclude many potential competitors. In the neotropics, particular cases of such forests on impoverished soils, disregarding flooded soils, have reinforced the interpretation that extremely low fertility leads to low diversity of canopy trees (Hart, 1990). However, Huston (1980) found a negative correlation between soil nutrient availability and tree species richness of forty-six Costa Rican forest sites, supporting the interpretation that, excluding extremely deficient sites, the lowest species richness occurs under rich growth conditions (Huston, 1979). Similar observations were reported by Ashton (1964) for Malaysian rain forests and by Hall & Swaine (1976) in Ghana.

Distributions limited by edaphic factors are mentioned in the literature for several trees that dominate the stands where they occur: Eusideroxylon zwageri T. & B. on pure or loamy sand (Richards, 1952), Mora gonggrijpii Kleinh. on reddish and heavy clay (Budowski, 1966), Julbernardia seretii (De Wild.) Troupin on

shallow soils (Hart, Hart & Murphy, 1989), Eperua falcata Aubl. on white sand (Davis & Richards, 1934), Shorea curtissii Dyer King on hill crests and Dryobalanops aromatica Gaertn. in Malaya (Whitmore, 1975: 191). In the last case, the author considered that this species maintained dominance by more frequent reproduction and greater persistence of seedlings than in other species, though its general restriction to sedimentary rocks must have been significant. However, the possible factors have not been tested experimentally in any case.

It is now apparent that some other monodominant tropical forests are not restricted to extremely poor soils, but that they develop under more benign and varied conditions (Hart, 1990). Forests dominated by Mora excelsa Benth., Cynometra alexandri C.H. Wright, Talbotiella gentii Hutch & Greenway, Eusideroxylon zwageri T. & B. and Gilbertiodendron dewevrei (De Wild.) have been reported on a wide variety of substrates (Beard, 1946; Eggeling, 1947; Swaine & Hall, 1981; Hart et al., 1989).

In the present study, the nutrient contents and texture of soils of a monodominant forest were compared with those of adjacent mixed forest in a seasonally dry tropical region, and germination and establishment of several species were evaluated experimentally in soils from both forests.

On the southern coast of the state of Jalisco, México, there are deciduous forests dominated by a single species, Celaenodendron mexicanum Standl. (Euphorbiaceae). The Celaenodendron mexicanum forests (CF) appear from low-level aerial inspection to occur on low hills of all aspects in juxtaposition with mixed forests (MF). The latter has exceptionally high diversity for its precipitation (Lott, Bullock & Solís-Magallanes, 1987; Gentry, in prep.). A floristic and structural description of CF was given by Martijena & Bullock (submitted), together with observations on the natural history of Celaenodendron mexicanum. CF apparently occurs no more than 10 km inland.

Based on the differences in vegetation structure and

floristic composition between the forests this investigation was focused on two questions:

Are soils from CF with high dominance different from MF soils and/or do they represent a distinct environment in terms of seedling establishment?

Do soils from CF with less dominance and smaller Celaenodendron mexicanum trees differ from soils from MF or high-dominance CF, in nutrient status and/or in terms of seedling establishment?

EXPERIMENTAL DESIGN AND METHODS

Study area

The research sites were in or near the Estación de Biología Chamela (19°30'N, 105°03'W) in Jalisco, México. This is close to the Pacific coast, about 125 km NW of Manzanillo, at elevations below 150 m. The climate is warm, with a mean annual temperature of 24.9 C (Bullock, 1986). The most important feature of this ecosystem is the marked rainfall seasonality. The mean annual precipitation is 707 mm (1977-1991), of which 80% falls between July and October, and there are occasional hurricanes (Bullock, 1986). The region comprises low hills and plains between the Pacific Ocean and the Sierra Cacoma. Previous descriptions of MF soils showed that they are young, with structure poorly developed (Entisols, USDA), generally shallow, and have low organic matter and mineral nutrient contents (García-Oliva, Maass & Martínez, 1992).

Soil Analysis

Four sites were selected with adjacent CF and MF. (In the present study, the sites denoted MF1 and MF2 do not correspond to the names used in Martijena & Bullock, submitted.) Previous floristic and structural analysis of the CF showed that Celaenodendron mexicanum in CF3 had less dominance in percentage of individuals than in CF1 and CF2 (35% versus an average of 63%). In the latter two, floristic richness was less, while CF3

was similar to mixed forest (11 and 21 tree species/100 m² respectively). It was suggested that CF3 is an intermediate phase of MF changing into CF (see Martijena & Bullock, submitted).

Because rainfall seasonality is the most important factor which influences the structure and dynamics of tropical dry ecosystems (Murphy & Lugo, 1986), soil sampling was repeated on four dates in order to represent the variation within and between dry and wet seasons, as well as transition periods. The sampling dates were 9-11 July 1989, 14-15 November 1989, 7 September 1990 and 17 May 1992. Each time, ten soil samples were taken in each one of the four sites (five in CF and five in MF), for a total of 40 samples. Each soil sample was a composite sample of five that were taken within a radius of 1.5 m, to a depth of 10 (or 20) cm. This depth was chosen because it is below the immediate influence of leachates from the litter yet within the root zone of established seedlings. The samples were air-dried in complete shade and then passed through a 1.68 mm sieve. Although this mesh was slightly smaller than the standard 2 mm, both sizes were compared for the May 1992 samples and no differences were found in values of organic carbon content and texture (MANOVA, $df=3, 42$; $P=0.9$). Chemical analysis were conducted on soil samples from the first three dates in the Laboratorio de Análisis Químicos, Centro de Ecología (U.N.A.M., Mexico city) and from the fourth date in the Laboratorio de Ecología Terrestre (C.I.C.E.S.E., Ensenada).

Soil texture was determined following the Bouyoucos procedure with the hydrometer method, and using the classification of the U.S.D.A. (Gee & Bauder, 1982). Soil pH was measured by a potentiometer after suspension of 1 g soil in 2.5 ml water. The concentration of organic carbon was determined with the method of Walkley & Black (Nelson & Sommers, 1982). It is reported and organic matter is not, avoiding the problems associated with estimating the content of the latter in soil. (For more details of estimation limitations see Nelson & Sommers, 1982). Determinations of total P and total N were made

colorimetrically (Technicon Instruments Corporation, 1977a, 1977b, 1978). Concentration of extractable PO₄ was also estimated with a colorimetric method (Spectronic 21, wavelength 640 nm), after extraction with Melich II. Atomic absorption spectrometry was used for exchangeable cations (Perkin-Elmer, 1976). Extractions for Fe, Mn, Zn and Cu were made with DTPA (Lindsay & Norvell, 1969); Ca, Mg, K and Na were extracted with ammonium acetate (Schollenber & Simon, 1945). Not all nutrients were analyzed for each of the dates. The presence of other elements such as cobalt, molybdenum, cadmium, chromium, nickel and arsenic was not detected in the soil samples by the methods used.

Establishment assays

Greenhouse experiments were conducted to test the effect of properties of soils from CF and MF on the establishment of four species. The species were Celaenodendron mexicanum and three of the most typical species of MF (Lott et al., 1987): Recchia mexicana Moc. & Sesse. (Simaroubaceae), Caesalpinia eriostachys Benth. (Leguminosae: Caesalpinoideae), Cordia alliodora (Ruiz & Pav.) Oken (Boraginaceae). Moreover, assays with other common MF species were performed, but no replications regarding forest type were possible due to technical limitations. These species were Casearia corymbosa HBK. (Flacourtiaceae), Piptadenia constricta (Micheli) Macbr. (Leguminosae: Mimosoideae), Lysiloma microphyllum Benth. (Leguminosae: Mimosoideae), and Cochlospermum vitifolium (Willd.) Spreng. (Cochlospermaceae). The experimental design is summarized in Table 2.1.

The assays were done at Chamela during the wet seasons of 1989 and 1990, in a shade structure (plastic screen) just outside the forest. The soil was collected prior to each experiment from three or fewer of the sites where soil properties were studied. The soils were air-dried in complete shade and passed through a 1.68 mm sieve before potting. The containers for these experiments were black plastic bags, 7.8 cm diameter and 34 cm tall, with perforation at the bottom for drainage. A fixed number

of fresh seeds was sown in each container, determined for each species according seed size. The position of the containers was randomized initially, and again periodically during the experiments. When rains did not occur, the containers were watered enough to keep the soils damp.

In four species, the experiments evaluated germination, survivorship, and growth during four months. Sowing dates were as follows: Celaenodendron mexicanum, 19 August 1989; Casearia corymbosa, 5 September 1989; Caesalpinia eriostachys, 6 June 1990; Recchia mexicana, 27 August 1990. After germination was recorded, only one seedling was left to grow in each container. Seedling survivorship and height were recorded periodically. In all cases, harvester (Attine) ants eventually attacked the seedlings; each experiment was considered to have ended at the census prior to such attack.

In the other four species (Cordia alliodora, Piptadenia constricta, Lysiloma microphyllum and Cochlospermum vitifolium), only germination was evaluated. The experiments were initiated on 29 August 1990, and all seedlings were discarded when they emerged.

At three sites (1, 2 and 3), an experiment was performed to test whether the establishment of species other than Celaenodendron mexicanum was possible on the natural forest floor. Seeds of Caesalpinia eriostachys were arranged in five units in each one of the CF and MF (30 units total). Each unit (625 cm²) was delimited by a half-buried plastic ring that stood out 0.5 cm, and was covered by a wire cage (1.25 cm mesh; 25 x 25 x 10 cm) which prevented potential removal by animals of the twelve seeds. The experiment was initiated in March 1990 (as part of a study of seed removal; Martijena, unpubl.). The units were inspected weekly and the number of seedlings recorded until no more appeared (6 July).

Statistical analysis

Standard parametric methods were used in the statistical

analyses; variation is reported as standard error. Data in percent or proportions of soil elements (mg kg^{-1}) were subjected to arcsine transformation before analysis to reduce heteroscedasticity among treatments and to eliminate dependence of treatment variances on treatment means (Zar, 1984). Data on pH, which were in logarithmic form, and height data, which displayed none of these problems, were not transformed.

Most of the nutrient data were analyzed by MANOVAs. Nutrients are often correlated in the soil and substantial information may be lost when correlations among variables are ignored. (For a complete review of analyses, see Hair, Anderson & Tatham, 1987, and James & McCulloch, 1990.) In different models the variables were divided into groups such that the variance-covariance matrices were homogeneous. In the performance of this analysis the SAS program (SAS Institute Inc., 1985) was used. ANOVAs were used to analyze height data for Celaenodendron mexicanum, Caesalpinia eriostachys and Casearia corymbosa, germination data for these species and for Recchia mexicana and Cordia alliodora, and data from the experiments on establishment of Caesalpinia eriostachys seedlings in the forests.

The general procedure consisted in making a preselected set of comparisons between combinations of means. Planned contrasts have the advantage that separate answers to separate biological questions are provided. Unlike most multiple post-hoc comparisons, per-comparison error rates are obtained, so the comparisons are more robust (Day & Quinn, 1989). Three contrasts (Table 2.2) were of interest according to the questions mentioned above. The F statistic was used in all univariate tests, and Pillai's Trace and Wilks' Lambda in the multivariate tests.

Ideally, planned comparisons should be orthogonal and test completely separate hypotheses (Sokal & Rohlf, 1981). Unfortunately, the third contrast (Table 2.2) was not orthogonal although it was relevant and interesting in the context of this study, and its results could be related in some way with the other hypotheses. Thus, to be conservative in the experiment-wise

type I error rate, the nominal significance levels for all three contrasts were adjusted using the Bonferroni method (dividing by the number of tests being performed; $0.05/3=0.0166$) (Sokal & Rohlf, 1981). The contrast analyses were carried out with the SYSTAT Program (Wilkinson, 1988).

The germination data for Piptadenia constricta, Lysiloma microphyllum, Cochlospermum vitifolium, and survivorship data for the others species were arranged in contingency tables and analyzed with the G statistic (Zar, 1984: 71). Height data of Recchia mexicana seedlings had unequal sample sizes, but they were analyzed by an ANOVA modified for proportional replication (Zar, 1984: 215), and no contrast was made.

RESULTS

Soil properties

For the samples from the dry-wet transition (July 1989), the contrast for sites 1, 2 and 4 with Mn, K, total N, Fe and Cu indicated a significant forest type effect (Table 2.3; $df=5, 44$; $P=0.004$). The relevance of total N here was suggested by its significant value in univariate analyses ($P<0.0006$). Total N content was higher in CF samples than in MF samples. However, there was no difference between soils from CF3 and MF3. In turn, CF3 soil was different from those of the other CF in the contents of Mn, K, total N, Fe and Cu in combination ($df=5, 44$; $P=0.005$), and Zn, PO_4 , Ca, Na, Mg in combination ($df=5, 44$; $P=0.00002$). These results may be due to significantly higher content of Cu, and lower Ca in the CF3 samples, as indicated by univariate analysis (ANOVA, $P<0.002$).

Organic carbon content did not differ between forests in the dry season (May) or at the dry-wet transition (July) (Table 2.3; $df=1, 64$; all $P>0.4$). In contrast, in samples for the wet season (September) and wet-dry transition (November), when organic matter from litterfall probably was being incorporated into the soil, the samples from CF1, CF2 and CF4 had more organic carbon ($df=1, 64$; $P<0.0004$). The quantities were almost twice as large

as the corresponding values from MF (average quotient of CF/MF: $1.7 \pm .2$, $n=18$). At the same time, organic carbon content in soils from CF3 and MF3 were similar ($df=1$, 64 ; $P>0.1$).

In the wet-season sample (September) also, soils from CF at sites 1, 2 and 4 were different from MF in the contents of Mn, K, total N, Fe in combination ($df=5$, 44 ; $P=0.0001$). Again, the difference might be largely a function of total N content, as suggested by univariate analysis (ANOVA, $P<0.00001$). In the September sample Cu was not detectable in either forest type by the methods used. In the wet-dry season transition sample (November) there were no differences in the nutrient contents of forest soils. In both September and November, the soil from CF3 was similar to those from the others CF and from MF3.

In spite of these seasonal changes, soil pH did not change with the seasons (Table 2.3; $df=48$; $P=0.08$) and was similar between each CF and its adjacent MF ($df=1$, 48 ; $P>0.3$). All values were very close to neutral pH ($6.87 \pm .05$, $n=48$).

Soil texture was not different between forests; all soils were classified as sandy-loam. The percentages of soil particles ranged from 52 to 79% for sands, 11 to 30% for silts, and 8 to 20% for clays.

In short, the major differences are between seasons rather than between forest types. The levels of almost all the elements measured in the soils changes between the dry and wet seasons (Table 2.4). In general, the mean values are larger in the dry-wet transition when the decomposition process starts with the first rains, and smaller when the vegetation is growing (wet period). This pattern is present in both CF and MF. This fluctuation was expected and agrees with the seasonality of precipitation.

Germination

Germination percentages for Celaenodendron mexicanum, Recchia mexicana, Caesalpinia eriostachys and Cordia alliodora did not differ significantly between soils from CF and from MF

(Table 2.5). Concordant with these results were those from the assays of the others species, which were performed on soils from only one site.

Lysiloma microphyllum and Casearia corymbosa presented the highest values of germination percentage ($87\% \pm 3.8$ and $71.4\% \pm 9.2$, respectively). Celaenodendron mexicanum had a lower average germination, near that of Caesalpinia eriostachys ($47.8\% \pm 2.4$ and $58.3\% \pm 2.9$, respectively). The other species showed even lower percentages: Cordia alliodora, $28.9\% \pm 3.4$; Recchia mexicana, $14.8\% \pm 1.8$; Cochlospermum vitifolium, $5.2\% \pm 0.5$; and Piptadenia constricta, $3.8\% \pm 0.7$.

Seedling survivorship

There were no differences in seedling survivorship of Celaenodendron mexicanum, Recchia mexicana and Caesalpinia eriostachys growing on soils from CF or MF to ages of about four months (Table 2.6). Casearia corymbosa did not show differences between seedlings growing on soils from both forest types of site two.

Although Celaenodendron mexicanum had the highest average of seedling survivorship ($97.9\% \pm 2.4$), Casearia corymbosa and Caesalpinia eriostachys were also very successful ($91.7\% \pm 8.3$ and $91.0\% \pm 7.4$, respectively). In contrast, Recchia mexicana showed a much lower survivorship ($77.6\% \pm 10$). Survivorship of Caesalpinia eriostachys evaluated to about age one year (393 days) was the same as at four months. Data for Celaenodendron mexicanum, Recchia mexicana and Casearia corymbosa did not extend to one year.

Seedling growth

Only Celaenodendron mexicanum showed differences in seedling height depending on which forest and site the soil was from (Table 2.7; $df=1, 65$; $P<0.015$). Celaenodendron mexicanum seedlings reached greater heights on soil from MF1 and MF2 ($12 \text{ cm} \pm 0.4$, $n=24$) than on soils from CF1 and CF2 ($10.1 \text{ cm} \pm 0.8$,

n=23). Seedlings growing on CF3 soil were significantly taller than seedlings on soils from the other CF (df=1, 65; P=0.000047). Heights of Celaenodendron mexicanum seedlings on CF3 soils were similar to those on MF3 soils (13.8 cm \pm 0.5, n=24).

Establishment in situ

The field experiments with Caesalpinia eriostachys seeds showed germination was as successful in CF as in neighboring MF (Table 2.8; df=1, 24; P>0.08). At sites 1 and 2 an average of 83.3% of the seeds became seedlings (s.e.=4.11, n=20). Germination was also similar between CF3 and MF3 (69.2% \pm 7.5; df=1, 24; P=0.8). The lower value in CF3 was significantly different from the other CF sites (df=1, 24; P=0.006). In these in situ experiments germination was greater than in the greenhouse. This was probably due to poorer drainage in the greenhouse containers. However, in all cases mortality was independent of soil origin, and of forest type.

DISCUSSION

The levels of some nutrients are different between CF and MF, but not in all sites and the differences are not concordant among dates. Moreover, the differences are less than the range between the seasons (Table 2.4). The results of physical and chemical analysis of the soils do not support the idea that Celaenodendron mexicanum establishes on soils different from those where MF develops. Values reported for MF in a previous work (García-Oliva et al., 1992) lie within the range estimated for the sites studied in the present paper. As indicated by other authors (Maass, Jordan & Sarukhán, 1988), the soil on hillsides at Chamela has low fertility. Availability of surfaces for cation exchange is low, as shown by the low clay content (14 to 23%) and the low estimated concentration of organic matter (less than 5%). Thus, low retention capacity may account for the notorious decrease in most of the cations (e.g. Ca, Na, Mg, Mn, K) in the wet season (Table 2.4). However, these conditions are not

striking compared to "white sand soils" (Davis & Richards, 1934; Jordan & Herrera, 1981), and typical stands at Chamela are among the most diverse in neotropical dry forests.

Furthermore, in contrast to sites with unfavorable soil (e.g. mangroves, swamp forests) that may have few species in common with adjacent rich sites, the species that are found as mature trees with Celaenodendron mexicanum are also found in the surrounding MF (Martijena & Bullock, submitted). However, nothing is known about the natural dynamics of these species or their representation as saplings in the understory of MF or CF.

Other examples of monodominant forests abutting mixed forest without distinct changes in soil conditions and with most of the species occurring in both forest types include Pocillocauron pauciflorum (Guttiferae) in India (Kadambi, 1942) and Gilbertiodendron dewevrei in Zaïre (Hart et al., 1989). In the case of Shorea curtissii Dyer ex King in Malaya, the content of major nutrients is similar, but there are differences in water relations, resulting from topographic and soil factors, which determine the sites it occupies (Whitmore, 1975).

Some species of MF at Chamela may be largely restricted to particular topographic conditions, e.g. Opuntia excelsa Sánchez-Mejorada on ridgetops (Bullock et al., pers. com.). Many species are restricted to deep soils in arroyos, presumably because they are intolerant of the water stress typical of hillside sites (Lott et al., 1987). However, the presence or absence of Celaenodendron mexicanum is not limited by topography. Its forests occur in arroyos as well as on hillsides with convex slopes and on all aspects. The microsites occupied are also undistinctive: slope gradients immediately adjacent to Celaenodendron mexicanum trees in four CF are not different from the slopes of random points in MF ($df=1, 145; P=0.15; \text{range } 2.5^\circ \text{ to } 29^\circ$). Moreover, measurements of soil moisture in the first 10 cm during the dry season in one CF and its adjacent MF show microsites conditions are similar for seedlings (Fig. 2.1).

This apparent similarity corresponds to the results of

experiments on establishment in several species. Seeds of common MF species can germinate and establish seedlings in similar percentages in soils of CF and MF, shown by Recchia mexicana and Caesalpinia eriostachys. The experiments with seeds of Celaenodendron mexicanum show that they are able to germinate and establish in soil from MF. The only difference found between its seedlings growing in CF or MF soil was in height (unfortunately, no information is available on total or root biomass). These results reflect some differences between sites, but not between forest types. Thus the distribution of Celaenodendron mexicanum, and of the other species tested, does not appear to be limited by soil characteristics at depths up to 20 cm.

The occurrence, in some cases, of ectomycorrhizal associations in monodominant forests has suggested that dominant tree species may have an enhanced ability to replace and exclude many other species (Connell & Lowman, 1989). Quercus oleoides Cham. & Schlecht is a monodominant mutualistic with ectomycorrhizal fungi and its distribution is correlated with poor soils. However, the particular soil conditions differ among sites (Pennington & Sarukhán, 1968), and in Costa Rica most of subsidiary species found in Quercus oleoides patches are also found in adjacent mixed forest (Boucher, 1981). In the case of Celaenodendron mexicanum, it is known that an endomycorrhizal association is formed (Gavito & Martijena, unpublished) and that spores of endomycorrhizal fungi are also common in MF soil (Gavito, pers. com.). Endomycorrhizal relations may be pertinent to the mineral nutrition of the major canopy species, but their impact on dominance is unclear because they occur in both forest types and have low specificity. According to Janos (1982), the dependence of neotropical trees on the same few endomycorrhizal fungi species limits their ability to exclude one another competitively.

Assertion of dominance by a single species in an old-growth forest may be possible due to a greater tolerance of other stresses such as shade. In Chamela, most of the MF species and

Celaenodendron mexicanum are deciduous. Leaf fall in MF occurs during the first several months of the dry season but in CF the leaves are kept until late in the dry season (Martijena & Bullock, submitted: Fig. 1.2). Although the canopy of Celaenodendron mexicanum is fairly dense and is present most of the year, the shade it casts is somewhat less than that of the surrounding MF (Fig. 2.2). This is because MF has a dense understory with many climbing plants, which contrasts strongly with the open understory of CF. Thus, light intensity on the forest floor probably does not prevent the establishment of species other than Celaenodendron mexicanum in its forests. This is reflected by the high percentage of establishment from the seeds of Caesalpinia eriostachys sown in CF.

Clearly, more remains to be investigated about the ecological behavior of this species to account for its achieving or maintaining dominance. Such as aspects of seasonality of photosynthesis, tolerance of climatic variability, growth and survival between the seedling and sapling stages, adult longevity, and effects of predators and parasites. The longer-term behavior of juveniles of other species in Celaenodendron mexicanum forest also merits attention. However, certain hypothesized mechanisms for explaining these monodominant stands can be discarded. Specifically, there is no evidence for differential species establishment determined by soil properties, nor are there unfavorable changes in other physical conditions related to the discontinuity in forest composition or to differences in dominance of Celaenodendron mexicanum in its stands.

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TABLE 2.1. Summary of experimental designs and analysis (G: greenhouse, F: forest, CF: Celaenodendron forest, MF: Mixed forest; n: the number of units in each forest)

Assays	Sites								n
	1		2		3		4		
	CF	MF	CF	MF	CF	MF	CF	MF	
Soil Analysis	X	X	X	X	X	X	X	X	5
<u>Celaenodendron mexicanum</u> (G)	X	X	X	X	X	X			12
<u>Reecchia mexicana</u> (G)	X	X	X	X					25
<u>Caesalpinia eriostachys</u> (G)	X	X	X	X					25
<u>Caesalpinia eriostachys</u> (F)	X	X	X	X	X	X			5
<u>Cordia alliodora</u> (G)	X	X	X	X					5
<u>Casearia corymbosa</u> (G)			X	X					7
<u>Piptadenia constricta</u> (G)			X	X					1
<u>Lysiloma microphyllum</u> (G)			X	X					1
<u>Cochlospermum vitifolium</u> (G)			X	X					1

TABLE 2.2. Hypotheses and planned comparisons

Hypotheses	Contrast	Treatments							
		CF	MF	CF	MF	CF	MF	CF	MF
$\frac{CF1+CF2+CF4}{3} = \frac{MF1+MF2+MF4}{3}$	1	1	-1	1	-1	0	0	1	-1
CF3=MF3	2	0	0	0	0	1	-1	0	0
$\frac{CF1+CF2+CF4}{3} \neq CF3$	3	1	0	1	0	-3	0	1	0

TABLE 2.3. Contrasts of soil characteristics from CF and MF at four sites: pH, organic carbon (O.C.) and extractable nutrients. Data are in the original scale (\pm standard error): Zn, PO₄, Ca, Na, Mg, Mn, K, total nitrogen (T.N.), Fe, Cu and total phosphorus (T.P.; mg kg⁻¹); pH (log) and O.C. (%).

Model	Contrast 1	Contrast 2	Contrast 3
<u>Dry season:</u>	<u>May</u>		
O.C.	2.4 \pm 0.4 = 2.3 \pm 0.3	2.5 \pm 0.5 = 2.3 \pm 0.4	2.4 \pm 0.4 = 2.0 \pm 0.5
<u>Dry-wet transition:</u>	<u>July</u>		
O.C.	0.7 \pm 0.1 = 0.8 \pm 0.1	0.6 \pm 0.1 = 0.5 \pm 0.1	0.7 \pm 0.1 = 0.6 \pm 0.1
Zn, PO ₄ Ca, Na, Mg	CF1,2,4 = MF1,2,4	CF3 = MF3	CF1,2,4 \neq CF3*
Mn, K, T.N., Fe, Cu	CF1,2,4 \neq MF1,2,4*	CF3 = MF3	CF1,2,4 \neq CF3*
pH	6.8 \pm 0.2 = 6.7 \pm 0.2	6.5 \pm 0.3 = 6.4 \pm 0.3	6.8 \pm 0.2 = 6.5 \pm 0.3
<u>Wet season:</u>	<u>September</u>		
O.C.	2.7 \pm 0.3 > 1.7 \pm 0.1*	2.1 \pm 0.1 = 2.1 \pm 0.1	2.7 \pm 0.3 = 2.1 \pm 0.1
Zn, PO ₄ Ca, Na, Mg	CF1,2,4 = MF1,2,4	CF3 = MF3	CF1,2,4 = CF3
Mn, K, T.N., Fe, Cu	CF1,2,4 = MF1,2,4	CF3 = MF3	CF1,2,4 = CF3
pH	7.0 \pm 0.1 = 7.1 \pm 0.1	7.1 \pm 0.1 = 6.5 \pm 0.3	7.0 \pm 0.1 = 7.1 \pm 0.1
T.P.	240 \pm 20 = 432 \pm 112	131 \pm 18 = 118 \pm 6	240 \pm 20 = 131 \pm 18
<u>Wet-dry transition:</u>	<u>November</u>		
O.C.	2.4 \pm 0.4 > 1.5 \pm 0.3*	2.4 \pm 0.4 = 2.4 \pm 0.4	2.4 \pm 0.4 = 2.4 \pm 0.4
Zn, PO ₄ Ca, Na, Mg	CF1,2,4 = MF1,2,4	CF3 = MF3	CF1,2,4 = CF3
Mn, K, T.N., Fe, Cu	CF1,2,4 = MF1,2,4	CF3 = MF3	CF1,2,4 = CF3
pH	7.0 \pm 0.1 = 7.0 \pm 0.1	6.8 \pm 0.2 = 6.7 \pm 0.1	7.0 \pm 0.1 = 6.8 \pm 0.2
T.P.	2043 \pm 155 = 1956 \pm 233	1866 \pm 211 = 2665 \pm 396	2043 \pm 155 = 1860 \pm 211

(*) significant at P<0.005

TABLE 2.4. Seasonal values for soil characteristics (\pm standard error; abbreviations and units as in TABLE 2.3).

Property	Dry season	Dry-Wet	Wet season	Wet-Dry season
O.C.	2.33 \pm 0.25	0.76 \pm 0.04	CF:2.39 \pm 0.37 MF:1.51 \pm 0.26	CF:2.67 \pm 0.34 MF:1.69 \pm 0.14
Zn		9.8 \pm 0.5	1.6 \pm 0.2	4.9 \pm 0.5
PO ₄		12.0 \pm 1.0	10.2 \pm 1.5	13.0 \pm 1.1
Ca		4714 \pm 348	83 \pm 8	519 \pm 50
Na		1479 \pm 34	2.0 \pm 0.1	64.0 \pm 3.1
Mg		1303 \pm 115	16 \pm 2	142 \pm 8
Mn		CF:314 \pm 40 MF:329 \pm 46	CF:20 \pm 4 MF:20 \pm 6	68 \pm 4
K		CF:1075 \pm 84 MF:826 \pm 125	CF:11 \pm 1 MF:8 \pm 1	49 \pm 3
T.N.		CF:1899 \pm 274 MF:1248 \pm 223	CF:2738 \pm 430 MF:1751 \pm 115	220 \pm 37
Fe		CF:59.8 \pm 9.7 MF:53.1 \pm 6.9	CF:11.8 \pm 2.0 MF:13.5 \pm 2.9	48.7 \pm 2.0
Cu		CF:3.2 \pm 0.6 MF:1.9 \pm 0.4	(*)	3.8 \pm 0.2
pH		6.8 \pm 0.1	7.0 \pm 0.1	7.0 \pm 0.1
T.P.			2006 \pm 108	283 \pm 48

(*) Not detectable by the method used.

TABLE 2.5. Contrasts of germination percentages (\pm standard error).

Species	Contrast	on soils from
<u>Celaenodendron mexicanum</u>	$50.0 \pm 4.4 = 40.4 \pm 4.1$	CF1,2 = MF1,2
	$47.5 \pm 6.7 = 58.3 \pm 3.8$	CF3 = MF3
	$50.0 \pm 4.4 = 47.5 \pm 6.7$	CF1,2 = CF3
<u>Becchia mexicana</u>	$11.7 \pm 2.2 = 17.9 \pm 2.8$	CF1,2 = MF1,2
<u>Caesalpinia eriostachys</u>	$60.0 \pm 3.7 = 56.7 \pm 4.4$	CF1,2 = MF1,2
<u>Cordia alliodora</u>	$27.3 \pm 0.5 = 30.5 \pm 5.1$	CF1,2 = MF1,2
<u>Casearia corymbosa</u>	$54.3 \pm 5.4 = 88.6 \pm 6.4$	CF2 = MF2
<u>Piptadenia constricta</u>	3.3 = 4.3	CF2 = MF2
<u>Lysiloma microphyllum</u>	89.7 = 84.3	CF2 = MF2
<u>Cochlospermum vitifolium</u>	5.3 = 4.7	CF2 = MF2

TABLE 2.6. Comparisons of survival percentages.

Species	Comparison	on soils from
<u>Celaenodendron mexicanum</u>	91.7 = 100.0	CF1 = MF1
	100.0 = 100.0	CF2 = MF2
	100.0 = 100.0	CF3 = MF3
<u>Reechia mexicana</u>	53.8 = 92.3	CF1 = MF1
	81.8 = 82.4	CF2 = MF2
<u>Caesalpinia eriostachys</u>	96.0 = 96.0	CF1 = MF1
	100.0 = 72.0	CF2 = MF2
<u>Casearia corymbosa</u>	83.3 = 100.0	CF2 = MF2

TABLE 2.7. Contrasts of seedling heights (cm, \pm standard error).

Species	Contrast	on soils from
<u>Celaenodendron mexicanum</u>	$10.1 \pm 0.8 \neq 12.6 \pm 0.5^*$	CF1,2 = MF1,2
	$14.0 \pm 0.8 = 13.7 \pm 0.6$	CF3 = MF3
	$10.1 \pm 0.8 \neq 14.0 \pm 0.8^*$	CF1,2 = CF3
<u>Recchia mexicana</u>	$16.2 \pm 1.4 = 17.7 \pm 0.7$	CF1,2 = MF1,2
<u>Caesalpinia eriostachys</u>	$12.4 \pm 0.4 = 11.2 \pm 0.6$	CF1,2 = MF1,2
<u>Casearia corymbosa</u>	$12.7 \pm 1.0 = 10.7 \pm 1.2$	CF2 = MF2

(*) significant at $P < 0.015$

TABLE 2.8. Contrasts of establishment of Caesalpinia eriostachys in the forests (\pm standard error).

Contrast	on soils from
$90.8 \pm 3.8 = 75.8 \pm 6.9$	CF1,2 = MF1,2
$61.7 \pm 7.6 = 76.7 \pm 13.9$	CF3 = MF3
$90.8 \pm 3.8 = 61.7 \pm 7.6$	CF1,2 = CF3

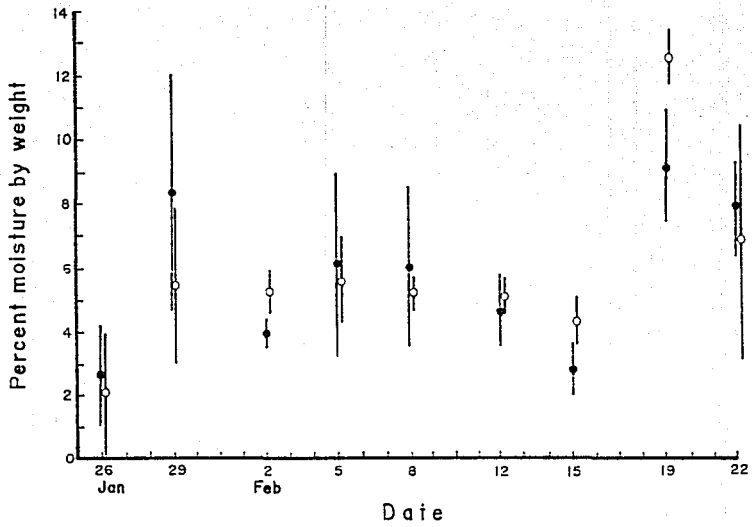


Fig. 2.1. Gravimetric measurements of soil moisture in a *Celaenodendron mexicanum* forest (solid circles) and its adjacent mixed forest (open circles) in the dry season (26 Jan. to 22 Feb. 1990); mean \pm standard error.

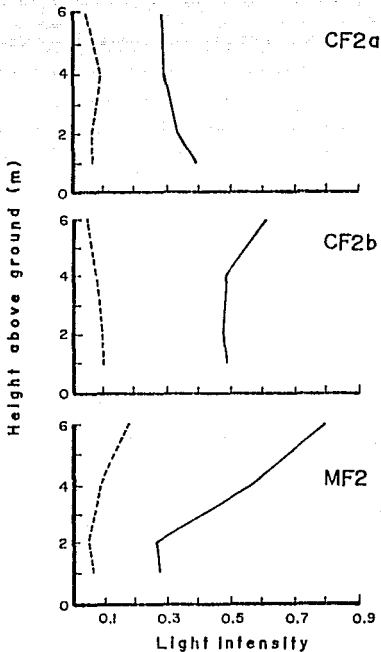


Fig. 2.2. Light intensity in a Celaenodendron mexicanum forest (at two points, CF2a and CF2b) and in adjacent mixed forest (MF2) in the wet season (broken line) and in the dry season (solid line); light is in arbitrary units from hemispherical photography.

SEED AND SEEDLING SURVIVAL OF FOUR TREE SPECIES IN ADJACENT
SPECIES-RICH AND MONODOMINANT TROPICAL FORESTS

Abstract. We tested the hypothesis that survivorship of postdispersal seeds and seedlings differs between species of high-diversity stands and one species that occurs only as high-density populations; contrasting patterns of mortality in mixed and monodominant stands were expected. Celaenodendron mexicanum Standley (Euphorbiaceae) dominates the canopy and understory in discontinuous patches (CF) within species-rich forest (MF) in southwestern México. Experiments were conducted on seed and seedling mortality (removal or predation, and in situ mortality) at several sites in adjacent CF and MF using common species of MF, Casearia corymbosa, Trichilia trifolia, and Caesalpinia eriostachys, as well as Celaenodendron mexicanum.

1. Mortalities did not differ in Casearia corymbosa and Trichilia trifolia between CF and MF. Their early losses were 100%; no seedlings were established. Post-dispersal seed predation accounted for 37% to 100% of the mortality in Casearia corymbosa, and 42% in Trichilia trifolia; the remainder failed to germinate.

2. In the other two species, early losses were large but not total. Survivorship varied between sites, but there were no significant differences corresponding to forest type.

3. Celaenodendron mexicanum suffered large losses in the stages before seedling establishment. Some 87% of its seeds were removed, and another 7% did not germinate. Before the cotyledons were exposed, predation reduced the remainder, but this mortality differed greatly between sites (2-100%). Although only 2% of the seeds produced seedlings in situ, subsequent survivorship to age one year was high (51%).

4. Caesalpinia eriostachys, the most common species of MF, had low initial mortality: 47% due to seed removal and failure to germinate. However, the first-year survivorship of seedlings was only 5%. As a result, the survivorship to one-year-old plants was not much different for Caesalpinia eriostachys (2.3%) and Celaenodendron mexicanum (1.2%).

5. Invertebrates, presumably ants, as well as vertebrates were important seed predators (removers), although the impact of each varied between species and sites. Rodents were apparently the vertebrate predators of Celaenodendron mexicanum seeds and seedlings.

6. Mortality patterns were similar in mature CF and in a stand with less dominance and smaller individuals of Celaenodendron mexicanum.

7. Differences of mortality between species were notable, but were not associated with forest types. However, differences in the degree of gregariousness within these species probably cause the quantities of seeds produced by each to differ greatly between established forest types. Thus, even with similar survivorship, recruitment may differ in space.

INTRODUCTION

Natural enemies of seeds and seedlings may be a significant force in maintaining the low density of conspecific trees in tropical forests, and thus in maintaining high local species diversity (Janzen, 1970; Connell, 1971). The Janzen-Connell model predicted survival only at greater distances from the parent because of the aggregation and attacks of host-specific predators, herbivores and/or pathogens. With recruitment probability lowered near conspecific adults, the probability of non-conspecific establishment in these sites increases (Clark & Clark, 1984). However, some tropical tree species typically or locally occur at extraordinarily high densities, forming low-diversity or monodominant stands with abundant recruitment, although these stands may be immersed in high-diversity forests.

Examples of such species were early emphasized by Richards (1952; see also Whitmore, 1975) and in recent years interest has reappeared in those which are not specialists of early succession or water-logged soils (see Janzen 1974, 1977; Swaine & Hall, 1981; Connell & Lowman, 1989; Hart et al., 1989; Hart, 1990; Martijena & Bullock, submitted). Explanations of their local abundance and sharply delimited patches have focused less on seed and seedling mortality and more on plant-soil relations, such as soil fertility (Janzen, 1974; Huston, 1980; Hartshorn, 1988), and mycorrhizae (Connell & Lowman, 1989; Högberg, unpub.). However, these have been rejected in some cases (e.g. Swaine & Hall, 1981; Martijena, in preparation).

Alternatively, the existence of some such populations has been interpreted in terms of levels of mortality from predation, herbivory or disease, that are low relative to other species in some defined spatial context. The mechanisms may be predator satiation by mast fruiting (Janzen, 1971), or absence of enemies (Janzen, 1970, 1974). Boucher (1981) found that where Quercus oleoides (Fagaceae) has already achieved high density, satiation of predators by abundant acorn production enables the species to maintain recruitment. However, if its density falls to the level

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typical of tropical trees, it will go locally extinct. Absence of specialist (Janzen, 1970) or generalist mammalian seed predators or herbivores may also change recruitment patterns, and allow trees to develop high-density populations (Janzen, 1972; Dirzo & Miranda, 1991).

Given the heterogeneity of intra-population density on a local scale (Hubbell, 1979; Hubbell & Foster, 1987), it is of interest whether survivorship is similarly heterogeneous, even without consideration of predator satiation. In some cases of monodominance the problem can be simplified to a contrast between stand types. Goldberg (1985) found the effects of predation differed between stands and between species of monodominant and mixed subtropical forests. Similarly, experiments with various mangrove species showed that levels of predation on seeds were correlated with conspecific dominance, but the sign of the correlation differed between species (Smith, 1987).

We have studied these contrasts in Celaenodendron mexicanum Standley (Euphorbiaceae) in southwestern México. This species occurs in patches (CF) where more than fifty percent of the trees are conspecific, although these patches are surrounded by high-diversity mixed forest (MF). Celaenodendron mexicanum attains densities far greater than is usual for even the most common species of MF (means of 1661 vs 158 trees ha⁻¹), and is essentially absent outside of CF. On the other hand, species of MF are poorly represented in CF, although present. Also, floristic and structural analysis showed that there is variation in Celaenodendron mexicanum dominance and in the proportional distribution of individual among DBH classes between CF stands (Martijena & Bullock, submitted).

Field experiments with post-dispersal seeds of Celaenodendron mexicanum and three species of MF were conducted in both types of forest, CF and MF, to evaluate the hypothesis that the contrast in diversity may derive from differential survivorship in the stages of post-dispersal seeds and seedlings to age one year. We also introduced a factor of "predator type"

in the experiments, intended to distinguish seed removal by vertebrates and invertebrates. This was because leaf-cutter (Attine) ants at our site are known to collect seeds, including those of the most common canopy tree in mixed forest, Caesalpinia eriostachys (Leguminosae).

Based on the differences in vegetation structure and floristic composition between the forests, and considering both types of enemies and the mortality specific to each stage, the investigation was focused on answering the following questions:

Does survivorship of each species differ between CF with high dominance and MF, in the stages of post-dispersal seeds and seedlings to age one year?

Does survivorship at a given stage of each species differ between the CF with less dominance and MF or high-dominance CF?

Does the percentage of losses in the stage of post-dispersal seed change when invertebrates are the only predators?

EXPERIMENTAL DESIGN AND METHODS

Site, climate and vegetation

The research sites were in or near the Estación de Biología Chamela property (19°30'N, 105°03'W) in Jalisco, México. This is close to the Pacific coast, about 125 km NW of Manzanillo. The climate is warm and seasonally dry. The mean annual temperature is 24.9°C. The mean annual precipitation is 707 mm (1977-1991), of which 80% falls between July and October (Bullock, 1986).

Tropical deciduous forest is the predominant vegetation, except on deep soils along (temporary) water courses (Lott et al., 1987). The trees and lianas are exceptionally diverse for the site's precipitation (Gentry, in prep.). A vegetation description of CF was given by Martijena & Bullock (submitted); it has a limited latitudinal range and apparently occurs no more than 10 km inland.

Four sites with adjacent CF and MF were chosen. At these same sites, soils have been analyzed and evaluated for establishment of several species (Martijena, in prep.). Floristic

and structural analysis showed that in CF3 Celaenodendron mexicanum had less dominance than in CF1 and CF2 (35% vs an average of 63%). In the latter two, individuals of all size classes were present, but there were proportionally more large trees. In CF3 about 50% of the individuals had trunk diameter <5 cm (Martijena & Bullock, submitted). It was suggested that CF3 is a intermediate phase of MF changing into CF (Martijena & Bullock, submitted). CF4 presents the same characteristics as CF1 and CF2.

The species studied were Celaenodendron mexicanum, and three of the most common species of MF (Lott, Bullock & Solís-Magallanes, 1987): Casearia corymbosa HBK. (Flacourtiaceae), Trichilia trifolia palmeri (C. DC.) Pennington (Meliaceae), Caesalpinia eriostachys Benthham (Leguminosae: Caesalpinioideae).

Characteristics of Celaenodendron mexicanum

Celaenodendron mexicanum is dioecious, and is not known to present mast cycles of fruiting. Fruit maturation occurs eight to ten months after flowering. There are at most three seeds per fruit; the seeds are light brown with a mean dry mass of 80.8 mg and oily endosperm. The maximum observed distance of seed dispersal from the explosive fruits is eight meters, with the greatest abundance at four meters. There is no innate dormancy, and germination (hypogeous) occurs rapidly in moist conditions at normal temperatures (Rincón & Huante, 1988; Martijena, unpublished data). The seeds lose viability when stored for one year at local ambient temperature and humidity (Martijena, unpublished data). On the forest floor at the beginning of the dispersal period, 10% of the seeds show a dark coloration; these increase in frequency to 78% at the start of the rainy season. These seeds are empty or have low germination compared to those with light coloration (0 to 17% vs more than 50%).

Predispersal predation by parrots is sometimes conspicuous. No insects have been detected inside the seeds before or after their dispersal, when fruits taken from trees or seeds from the forest floor were kept under observation. The most abundant

rodent in the area Liomys pictus pictus (Heteromyidae) (Ceballos, 1990), readily eats the seeds (Martijena & Bullock, unpubl. data).

The leaves are typically damaged, apparently by psyllids. One case was observed of herbivory by lepidopteran larvae (Lasiocampidae). Attine ants were only once observed cutting the leaves; these were later rejected from the nest, which suggests they are unsuitable for the ants' fungus. Relations with predators and parasites, or other plants, may be affected by secondary metabolites: leaves and twigs of Celaenodendron mexicanum are rich in terpenes and flavonoids (Castañeda et al., 1992).

Experimental assays

Experiments were designed to evaluate losses by removal, germination failure and seedling mortality, in both types of forest. The experiments and the forests where they were done are shown in the Table 3.1.

To evaluate seed predation (removal), a known number of seeds was placed simultaneously in CF and adjacent MF at one or more sites according to seed availability. Seeds were collected in the station, and selected for those in an apparently healthy state. Casearia corymbosa seeds were cleaned of the fleshy aril to avoid attack by fungi until the assay was established. Starting dates of experiments were as follows: Celaenodendron mexicanum, 9 June 1989; Casearia corymbosa, 16 September 1989; Trichilia trifolia and Caesalpinia eriostachys, 9 March 1990.

Seeds of each species were arranged in units of 625 cm², delimited by a half-buried ring of plastic that stood out of the ground 0.5 cm. Twelve seeds were placed inside, according to the average density of Celaenodendron mexicanum seeds in CF (192 seeds m⁻²). Because Casearia corymbosa seeds were scarce, there were only ten seeds per unit, and only six units. Removal of seeds by invertebrates was evaluated in each species except Caesalpinia eriostachys. In the same CF and MF, similar units to

those described before were installed but were covered by a cage (1.25 cm wire mesh; 25 x 25 x 10 cm), fixed by stakes which prevented removal of the seeds by vertebrates. The enclosure design allowed access by small-to-medium-size insects, but prevented herbivory by mammals and large insects. The protected and unprotected units of each pair were not far from each other minimizing the effects of animal territoriality or foraging area. Because removal of Caesalpinia eriostachys seeds by ants was already known, and the seeds were too large to pass through the mesh, only five uncovered units were set up. Ten units in each forest were used for Trichilia trifolia and Celaenodendron mexicanum. All units were inspected weekly or biweekly and the number of seeds and seedlings was recorded until no more seedlings appeared. We use the term "visit" in reference to any week in which any seeds were removed from a given unit. When no more removal occurred the seeds that did not germinate were analyzed with tetrazolium to determine viability.

Mortality in Celaenodendron mexicanum in the transition between seedlings with closed and exposed cotyledons was evaluated with another experiment, which started on 9 August 1989. Again there were unprotected units (seeds exposed to removal by vertebrates and invertebrates) and caged units excluding vertebrates. However, the experiment was done protecting all seeds from removal by burying them and coating the ring with a sticky resin. The units were inspected weekly, and when germination started, the resin was removed. Numbers of germinated seeds and seedlings were registered until no more seedlings appeared. Then, the cages of the protected units were removed and all seedlings were left completely exposed. At that time, only four seedlings were left to grow in each unit; their survivorship was recorded monthly to age one year. When there was mortality, we looked for evidence of the causes.

To evaluate Celaenodendron mexicanum seedling survivorship independent of differences in the seed and germination phases, we used transplanted seedlings. A cohort of 48 seedlings was

germinated in a shadehouse, in individual black plastic bags with soils from CF2 or MF2. The seedlings were transplanted in September 1990 to CF2 and MF2, burying the containers with the bottoms open. In each forest the seedlings were arranged in six units with four seedlings each. Half of the units were covered by cages (mesh 1.25 cm; 25 x 25 x 30 cm) which excluded vertebrates. Survivorship was recorded to one year. Also, during the two years of experimentation, the natural appearance and mortality of Celaenodendron mexicanum seedlings was registered in three permanent plots (25 x 25 m; in CF1, CF2 and CF3).

Caesalpinia eriostachys seedlings from seeds surviving the removal experiment (described before), and others from a study done at the same time and sites (as part of the soil study), were censused periodically for survivorship to age one year.

Statistical analysis

Standard parametric methods were used in the statistical analyses; variation is reported as standard error. All data (percentage per unit) were subjected to arcsine transformation before analysis to reduce heteroscedasticity among treatments and to eliminate dependence of treatment variances on treatment means (Zar, 1984).

The general procedure consisted in making a preselected set of comparisons between combinations of means. Planned contrasts have the advantage that separate answers to separate biological questions are provided. Unlike most multiple comparisons, per-comparison error rates are obtained, so the comparisons are more robust (Day & Quinn, 1989). Four contrasts (Table 3.2) were of interest according to the questions mentioned above. The F statistic was used in all tests.

Ideally, planned comparisons should be orthogonal and test completely separate hypotheses (Sokal & Rohlf, 1981). Unfortunately, the third contrast was not orthogonal although it was relevant and interesting in the context of this study, and its results could be interrelated in some way with the other

hypotheses. Thus, to be conservative in the experiment-wise type I error rate, the nominal significance levels for all three contrasts were adjusted using the Bonferroni method (dividing by the number of tests being performed; $0.05/3=0.0166$) (Sokal & Rohlf, 1981). The contrast analyses were carried out with the SYSTAT program (Wilkinson, 1988).

RESULTS

Survivorship of post-dispersal seeds

Casearia corymbosa. This species had the greatest variation in the percentage of seed removal, from 0 to 100% (Table 3.3). In both forest types, exclosures significantly reduced removal of the seeds. When free of exclosures, removal was significantly more intense in CF2 than MF2. These results suggest that invertebrates were not important in removing these seeds, and that the difference between CF2 and MF2 reflected the spatial pattern vertebrate activity. Removal by invertebrates was not different between the forest types. At the end of the second week, seeds that had not been removed were already covered by fungus and none germinated in either forest.

Trichilia trifolia. Regardless of the degree of protection of the seeds, 26 to 65% of them were removed, indicating removal by invertebrates (Table 3.3). Also, there were no differences between the units in CF and MF. In CF3 removal was greater, and also faster, than in the other CF (Table 3.3): in 65% of the units with or without exclosures, all the seeds were removed in one to three visits (Fig. 3.1). At the other two sites, only 15% of the units had all seeds removed, and 80% of the units had four or fewer seeds removed in three or fewer visits. These results suggest there were differences in the spatial distribution of removers, and differences in their behavior between sites. At site 3 invertebrates seemed to be important because removal was similar between open and caged units.

After 13 weeks, when the wet season had started, unremoved seeds had not germinated. Almost all these seeds were empty and a

few had no living tissue. Thus, as in Casearia corymbosa, there were no survivors among Trichilia trifolia seeds (Table 3.4). Caesalpinia eriostachys.- There was no difference in removal of these seeds between forest types (Table 3.3). On average $47.2\% \pm 7.1$ of the seeds were removed. Although the seeds were exposed during 13 weeks, not one seed was taken in 27% of the units without enclosure (Fig. 3.2). All seeds were removed in only 20% of the units. The number of visits to a given unit was three at most. The percent of remaining seeds that germinated was similar among the forests. On average, $46.7\% \pm 6.5$ of the initial seeds escaped removal and germinated (Table 3.4).

Celaenodendron mexicanum.- These seeds were removed as much in CF as in MF, and there was no difference between units with and without enclosure (Table 3.3). On average, after exposure for eight weeks, $89.7\% \pm 2.4$ of the seeds had been removed. However, they were removed in different ways, in both CF and MF, depending on the presence or absence of enclosures, i.e. on which animals were involved. All twelve seeds were removed in a single visit in 22% of the open units, and in one to three visits in 82% (Fig. 3.3). On the other hand, in the units that prevented vertebrate predation, only 32% of the units had all the seeds removed in two or three visits, and there was no case in which all twelve seeds were taken in one visit. Moreover, in 15% of the enclosure units half of the seeds or less was removed in as many as four visits. Apparently, these different patterns indicated faster removal by vertebrates from the open units. Vertebrate predation was evident from rodent tooth marks on pieces of seeds, which were similar to the pieces left by a captive mouse in feeding tests (Martijena & Bullock, unpublished data).

Among the unremoved seeds there was substantial failure to germinate in all units ($68.7\% \pm 10.6$). Thus, survivorship of the initial twelve seeds was low ($3.2\% \pm 0.2$), although similar between forests and independent of the kind of predators (Table 3.4). The seeds which failed to germinate were empty or without living tissue.

Survivorship in the seed-seedling transition

When Caesalpinia eriostachys seeds started to germinate, they quickly exposed their cotyledons and no mortality was appreciated in the transition.

Germinating seeds of Celaenodendron mexicanum delayed several days before the cotyledons became exposed, and only 79.1% \pm 3.6 achieved this. There were no general differences between units with or without enclosure. However, in CF1 and MF2, mortality was greater among germinating seeds that were exposed to all animals than with vertebrates excluded (Table 3.5), reaching 100% in MF2. Again, these differences may reflect the spatial pattern of vertebrate distribution, regardless of forest type. In almost all cases, the epicotyl was cut and dropped in situ, uneaten, and with tooth marks on the cut end.

Survivorship of seedlings to age one year

Only 4.6% \pm 1.5 of Caesalpinia eriostachys seedlings survived to age one year in all forests (Table 3.6). Mortality was as high in MF as in CF.

In contrast, Celaenodendron mexicanum seedlings had lower mortality which did not differ between CF and MF (Table 3.6). On average, 51.4% \pm 6.0 of the seedlings that had germinated in the forests and 91.7% \pm 3.7 of transplanted seedlings survived to age one year. Greater survivorship of transplanted seedlings may have been due to the presence of their containers, or better initial development in shadehouse conditions.

Natural seedling establishment of Celaenodendron mexicanum

From July 1989 to July 1991 few established seedlings attributable to natural processes were found. In 1989, 29 recently emerged seedlings were observed in the permanent plot of CF2 and 14 in CF3. In the following year, only 28% of these were still alive in CF2 and 64% in CF3. Over the same time interval, seedling survival in the experiments was 30% (CF2) and 68% (CF3). Thus, early survivorship was not affected by experimental

treatments or the aggregation into units. Moreover, the size of seedlings from experimental and natural processes at 7 to 12 months of age was similar in both forests (8.0 ± 0.2 cm and 8.3 ± 0.3 cm respectively).

The high natural seedling survivorship in CF3 is especially interesting because relatively few trees there have seed crops, many being of small size. Early in the 1990 wet season, 50 seedlings were observed in CF3, and 46% of them survived to the next summer. At the same time only one seedling was detected in CF2 and it did not survive. No seedlings were seen in the CF1 plot, although seed dispersal and seedling establishment occurred elsewhere in the CF1 stand. Falling debris has been shown to be a strong source of juvenile mortality in moist/wet forests (Hartshorn, 1972; Vandermeer, 1977; Clark & Clark, 1989). However, no evidence of seedlings dying as result of litterfall was found in any of the experimentally or naturally established plants in either forest type.

DISCUSSION

We had suggested that differences in survivorship in post-dispersal seeds and seedlings may account for the existence of these forest stands contrasting in diversity. This was not the case. The experiments showed no higher mortality in the early stages for MF species in CF, and similarly Celaenodendron mexicanum was not freer of mortality in CF than in MF. This result also applies to comparisons with the "transitional" CF3 stand. The idea that species forming monotonous stands are relatively free of predation (Janzen, 1974) does not apply to Celaenodendron mexicanum. A similar conclusion may apply for Gilbertiodendron dewevrei, which forms extensive monodominant stands in central Africa (Hart et al., 1989). Also, the seeds of Celaenodendron mexicanum are not remarkably toxic, and as in the case of Quercus oleoides the predators are generalists.

Seed predation (removal) was important for all the species (Fig. 3.4). Variations in predation rate were more conspicuous

between species (26% to 94%) than between sites. All the species tested are common as adults, and the species with the highest predation is that which forms monodominant stands. This suggests that overall seed predation rates are uninformative about adult populations, as is amply shown by the overlapping predation rates of rare and abundant trees elsewhere (e.g. Janzen, 1975; Boucher, 1981; De Steven & Putz, 1984; Howe et al., 1985).

The importance of invertebrate predation was shown by similar removal of seeds from protected and unprotected units in the case of Trichilia trifolia and Celaenodendron mexicanum. The animals involved were presumably ants. Apparently, rodents also removed Celaenodendron mexicanum seeds. The evidence suggests they must be considered as predators, not dispersers, of Celaenodendron mexicanum. Vertebrates were the major removal agent in the case of Casearia corymbosa seeds (the absence of the fleshy aril is presumably natural after dispersal for this species, whatever its effect on ground-foraging animals).

The second most important cause of mortality for these three species was failure of the seeds to germinate. Together with predation, this resulted in no establishment of Casearia corymbosa or Trichilia trifolia seedlings in any forest (Fig. 3.4 and Table 3.7). Some seeds of Celaenodendron mexicanum also failed to germinate, and predation on the young seedlings was observed.

In contrast, Caesalpinia eriostachys showed exceptionally low predation of seeds, and the lowest losses during germination. The probability of its seeds becoming seedlings was the highest among these species, 0.47 (Table 3.7), while Celaenodendron mexicanum seeds had a probability of only 0.02. However, survivorship of Caesalpinia eriostachys seedlings during their first year was 0.05, one order of magnitude less than in the previous stage. In this early establishment phase, Celaenodendron mexicanum seedlings increased in survivorship by the same amount. Thus, the probability of a post-dispersal seed becoming a year-old seedling was not much different between these two species.

Because of fluctuations in the physical environment, predation, fruit crops and other factors, seedling populations and their survival rates vary through the years. Thus, data from one year can lead to incorrect interpretations when they are considered typical. We also recognize that doing the experiments in two different years may be responsible for the apparent difference in mortality pattern between these two species. However, it is notable that the results were independent of forest type in both years.

Although Celaenodendron mexicanum does not have the lowest early mortality, the local density of seeds over which the probabilities occur may differ greatly. In consequence, net seedling recruitment may differ greatly among species. We suggest that in CF, where the combined seed crops of many Celaenodendron mexicanum is high, the number of the surviving seedlings is more than sufficient to maintain the population. Even across the boundary between the forest types where the density of Celaenodendron mexicanum seeds is lower, recruitment can occur in CF and invasively in MF despite high losses. Experiments that involved placing seeds in mixed forest where Celaenodendron mexicanum does not occur demonstrated that in spite of high losses, seedlings could establish. The apparently long life and slow growth of this species may facilitate its eventual dominance from a seedling pool accumulated during a few years. Equal losses in common species of MF that do not form aggregates should result in a significantly lower number of seedlings, and poor or null recruitment in CF, as in the extreme cases of Casuarina corymbosa and Trichillia trifolia.

Some alternative explanations that might account for such a pattern of abundance and restricted distribution on a local scale have been rejected in the case of Celaenodendron mexicanum. Apparently, topographic factors such as aspect and slope do not determine its local distribution. Specialization on poor soils was examined in another study (Martijena, in prep.), but there were no significant differences between CF and adjacent MF for

most of the nutrients tested. Greenhouse experiments do not show better establishment of MF species or Celaenodendron mexicanum on soils from either forest type. Field experiments with Caesalpinia eriostachys showed successful germination and establishment in both forest types, further emphasizing the lack of restriction on early stages. The presence of common species of MF in the canopy of CF suggests that they are not physiologically intolerant of the soils on which Celaenodendron mexicanum grows. Also, Celaenodendron mexicanum forms a mycorrhizal association (Gavito & Martijena, unpublished), but the relation is endomycorrhizal, and thus probably not specific.

It remains unknown whether the trend of increased survivorship with increasing age is maintained by Celaenodendron mexicanum across all ages, or at least through juvenile stages, and if other species differ in their patterns of adult mortality. There is circumstantial evidence that Celaenodendron mexicanum is relatively drought tolerant. After a severe drought (1985-1986), there were many standing dead trees of various species in MF, while only the smallest branches of Celaenodendron mexicanum were affected. However, the reality of these apparent advantages need to be confirmed in the long-term studies, and their physiological bases need to be identified.

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TABLE 3.1. Summary of experimental designs to evaluate losses as (1) seeds, (2) germinated seeds and seedlings to one year old (CF: Celaenodendron forest; MF: Mixed forest; open: seeds exposed to action of vertebrates and invertebrates; excl: seeds with exclosure exposed only to invertebrates)

Assays	Species	Sites				Condition
		1		2		
		CF	MF	CF	MF	
(1)(2)	<u>Casearia corymbosa</u>			X	X	open/excl
(1)(2)	<u>Trichilia trifolia</u>	X	X	X	X	open/excl
(1)(2)	<u>Caesalpinia eriostachys</u>	X	X	X	X	open
(1)	<u>Celaenodendron mexicanum</u>	X	X	X	X	open/excl
(2)	<u>Celaenodendron mexicanum</u>	X	X	X	X	open/excl

TABLE 3.2. Hypotheses and planned comparisons

Contrast	Hypotheses
1	$\frac{CF1+CF2+CF4}{3} = \frac{MF1+MF2+MF3}{3}$
2	$CF3 = MF3$
3	$\frac{CF1+CF2+CF4}{3} = CF3$
4	open = enclosure

TABLE 3.3. Seed predation (removal) (mean% \pm s.e.)

Species	Contrast	Ho	Condition
<u>Casearia corymbosa</u>	100 \pm 0 > 37 \pm 20*	CF2 = MF2	open
	7 \pm 8 = 0 \pm 0	CF2 = MF2	exclosure
	100 \pm 0 > 7 \pm 8*	Open = Excl	CF2
	37 \pm 20 > 0 \pm 0*	Open = Excl	MF2
<u>Trichilia trifolia</u>	26 \pm 8 = 26 \pm 8	CF1,2 = MF1,2	open-excl
	66 \pm 15 = 78 \pm 12	CF3 = MF3	open-excl
	26 \pm 8 < 66 \pm 15*	CF1,2 = CF3	open-excl
	48 \pm 8 = 34 \pm 8	Open = Excl	CF-MF
<u>Caesalpinia eriostachys</u>	33 \pm 11 = 50 \pm 13	CF1,2 = MF1,2	open
	43 \pm 22 = 73 \pm 19	CF3 = MF3	open
	33 \pm 11 = 43 \pm 22	CF1,2 = CF3	open
<u>Celaenodendron mexicanum</u>	90 \pm 4 = 88 \pm 5	CF1,2,4 = MF1,2,4	open-excl
	90 \pm 9 = 95 \pm 4	CF3 = MF3	open-excl
	90 \pm 4 = 90 \pm 9	CF1,2,4 = CF3	open-excl
	94 \pm 3 = 85 \pm 4	Open = Excl	CF-MF

(*) significant at P<.0166

TABLE 3.4. Seed survivorship (mean \pm s.e.)

Species	Contrast	Ho	Condition
<u>Casuarina corymbosa</u>	0 \pm 0 = 0 \pm 0	CF2=MF2	open-excl
	0 \pm 0 = 0 \pm 0	Open=Excl	CF2-MF2
<u>Trichilia trifolia</u>	0 \pm 0 = 0 \pm 0	CF1,2=MF1,2	open-excl
	0 \pm 0 = 0 \pm 0	CF3=MF3	open-excl
	0 \pm 0 = 0 \pm 0	CF1,2=CF3	open-excl
	0 \pm 0 = 0 \pm 0	Open=Excl	CF-MF
<u>Caesalpinia cristatachys</u>	60.0 \pm 10.4 = 63.1 \pm 10.4	CF1,2=MF1,2	open
	46.7 \pm 18.8 = 25.0 \pm 17.7	CF3=MF3	open
	60.0 \pm 10.4 = 46.7 \pm 18.8	CF1,2=CF3	open
<u>Celaenodendron mexicanum</u>	4.4 \pm 2.1 = 1.4 \pm 0.8	CF1,2=MF1,2	open-excl
	5.0 \pm 5.3 = 3.3 \pm 3.5	CF3=MF3	open-excl
	4.4 \pm 2.1 = 5.0 \pm 5.3	CF1,2=CF3	open-excl
	2.5 \pm 1.2 = 4.0 \pm 1.8	Open=Excl	CF-MF

TABLE 3.5. Predation on germinated seeds (mean% \pm s.e.)

Species	Contrast	Ho	Condition
<u>Caesalpinia eriostachys</u>	0 \pm 0 = 0 \pm 0	CF1,2=MF1,2	open
	0 \pm 0 = 0 \pm 0	CF3=MF3	open
	0 \pm 0 = 0 \pm 0	CF1,2=CF3	open
<u>Celaenodendron mexicanum</u>	22.9 \pm 7 = 31.4 \pm 10	CF1,2=MF1,2	open-excl
	27.1 \pm 5 = 13.8 \pm 8	CF3=MF3	open-excl
	22.9 \pm 7 = 27.1 \pm 5	CF1,2=CF3	open-excl
	50.5 \pm 19 > 6.7 \pm 7*	Open=Excl	CF1
	100.0 \pm 0 > 9.6 \pm 7*	Open=Excl	MF2
	20.2 \pm 5 = 12.5 \pm 2	Open=Excl	CF2,3-MF1,3

(*) significant at P<.0166

TABLE 3.6. Seedling survivorship to age one year (mean% \pm s.e.)

Species	Contrast	Ilo	Condition
<u>Caesalpinia criostachys</u>	7.0 \pm 2.6 = 1.0 \pm 1.1	CF1,2=MF1,2	open
	7.5 \pm 6.8 = 3.3 \pm 3.7	CF3=MF3	open
	7.0 \pm 2.6 = 7.5 \pm 6.8	CF1,2=CF3	open
<u>Celaenodendron mexicanum</u> (seedlings germinated in the forests)	33.4 \pm 10.6 = 54.9 \pm 12.3	CF1,2=MF1,2	open
	67.9 \pm 12.6 = 64.0 \pm 5.2	CF3=MF3	open
<u>Celaenodendron mexicanum</u> (transplanted seedlings)	33.4 \pm 10.6 = 67.9 \pm 12.6	CF1,2=CF3	open
	91.7 \pm 5.8 = 91.7 \pm 5.8	CF2=MF2	open-excl
	83.3 \pm 5.8 = 100.0 \pm 2.2	Open=Excl	CF2-MF2

TABLE 3.7. Stage transition probabilities (survivorship) of the four species in CF and MF combined

Species	Seed-seedling	seedling-1st year	Seed-1st year
<u>Casearia corymbosa</u>	0.00	---	0.00
<u>Trichilia trifolia</u>	0.00	---	0.00
<u>Caesalpinia criostachys</u>	0.47	0.05	0.02
<u>Celaenodendron mexicanum</u>	0.02	0.51	0.01

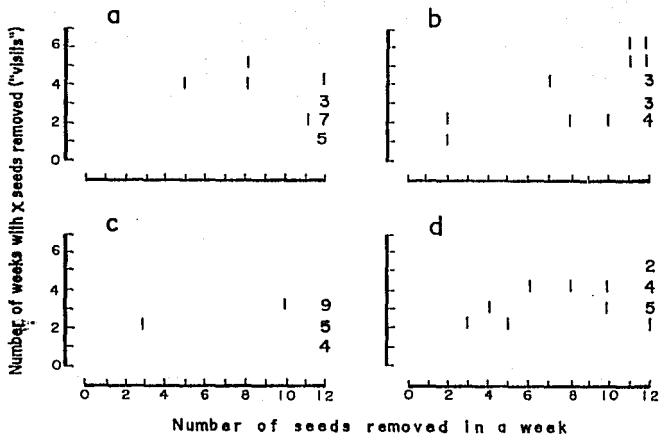


Fig. 3.1. Removal of *Trichillia trifolia* seeds related to the number of visits (weeks with at least one seed removed) in a. open units in CF and MF of sites 1 and 2; b. units with enclosure at the same sites; c. open units in CF3; d. units with enclosure in MF3.

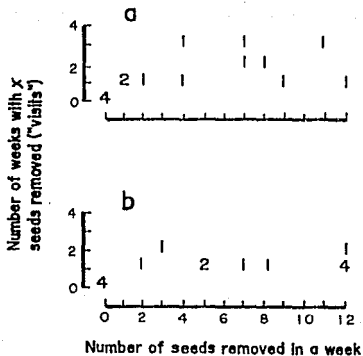


Fig. 3.2. Removal of Caesalpinia eriostachys seeds related to the number of visits in a. CF of sites 1 and 2 together; b. MF of the same sites (all the units were without enclosure).

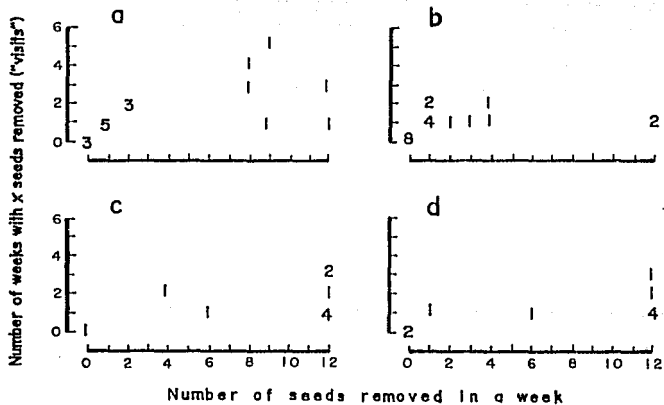
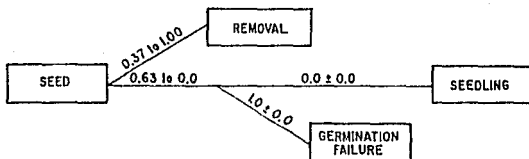


Fig. 3.3. Removal of Celaenodendron mexicanum seeds related to the number of visits in a. open units in CF and MF of sites 1, 2 and 4 together; b. units with enclosure at the same sites; c. open units in CF3; d. units with enclosure in MF3.

a)



b)

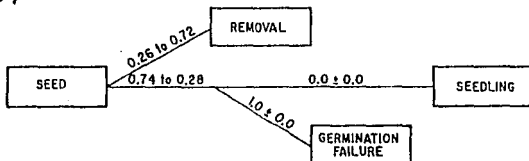
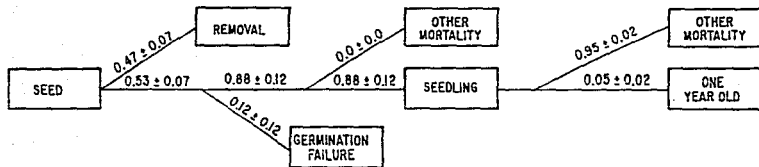
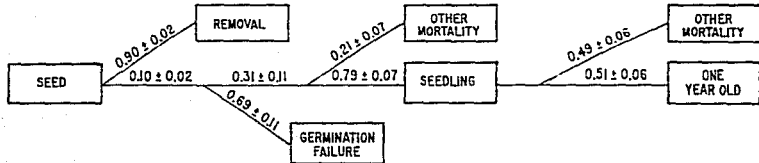


Fig. 3.4. Flow chart of each species showing probabilities of mortality and of transition between stages. More than one probability is given on path segments where significant differences were found in the planned contrasts. Other values are means. a. *Caesaria corymbosa*; b. *Trichilia trifolia*; c. *Caesalpinia eriostachys*; d. *Celaenodendron mexicanum*

c)



d)



COMENTARIOS FINALES

Varios posibles mecanismos han sido propuestos para promover y/o mantener la dominancia por parte de una especie arbórea del dosel en bosques tropicales de tierras bajas sobre suelos sin problemas de drenaje. Ellos no representan alternativas exclusivas y ninguno es universal. Los intentos de evaluar estas hipótesis en casos particulares han dirigido la atención sobre diversos tipos de evidencia y sobre la necesidad de estudios en un ámbito ecológico y geográfico amplio, datos que cubran largos períodos y experimentos.

En el presente caso, ciertos mecanismos propuestos para explicar la existencia de parajes dominados por una sola especie pueden ser descartados. Específicamente, no hay evidencia de diferencias en el establecimiento de las especies determinadas por las propiedades del suelo, o por algún otro factor no medido que pudiera relacionarse con la discontinuidad en composición que ambos bosques representan. Las atractivas ideas de Janzen (1970) sobre escape de la depredación a través de adaptaciones, tales como semillas químicamente tóxicas o la saciación de los depredadores de semillas (ej. por fructificación en masa en intervalos impredecibles y a largo plazo) no han sido puestas a prueba exhaustivamente; sin embargo, no hay indicios que lleven a suponer que ellas sean aplicables a Celaenodendron mexicanum. Apparently, las semillas no son tóxicas, siendo comidas por un mamífero generalista y la reproducción es anual, si bien puede ser muy variable. Además, como en el caso de Gilbertiodendron deweyrei, Celaenodendron mexicanum tiene pérdidas relativamente grandes en el estadio de semilla post-dispersión por la acción de depredadores.

Otra interpretación de la dominancia concentrada en una sola especie es sucesional (Connell, 1978; Hart, 1990), explicada como el resultado de un reemplazo secuencial por parte de una especie, la cual es la más resistente al estrés, o la mejor competidora del conjunto de especies tolerantes a la sombra. Esta hipótesis

del clim ax sugiere que los bosques tropicales con gran diversidad de especies representan estados intermedios en la sucesi3n y que los parajes dominados por una sola especie, los cuales parecen estar incrementando su distribuci3n (tales como Gilbertiodendron deweyrei), son poblaciones que han sido limitadas o reducidas espacialmente por disturbios de gran escala o cambios clim aticos. Sin embargo, no ha sido definido que otro rasgo de la historia de vida de estas especies, adem as de pl ntulas tolerantes a la sombra y esperanzas de vida larga, la convierten en la dominante competitivamente. Esta interpretaci3n contradice la noci3n de que  reas de gran diversidad pueden representar refugios en el caso de grandes cambios ambientales. Sin embargo, a n no se cuenta con informaci3n hist3rica que pudiera documentar que tales parajes de dominancia concentrada son antiguos o muy viejos. La dendrocronolog a a n no ha tomado parte en estos estudios. De hecho, estructuras de edades estimadas (por ej. usando el tama o) de estas especies dominantes, sugieren diversos escenarios de la historia reciente de estos parajes, desde regeneraci3n progresiva a establecimiento sincr3nico en masa. Estos sugeridos patrones tan contrastantes se presentan para una misma especie, como sucede con Dryobalanops aromatica (Whitmore, 1975). Celaenodendron mexicanum muestra varias caracter sticas asociadas a especies clim aticas y sus poblaciones presentan individuos de diferentes edades sino de todas las edades posibles.

En el caso de Dryobalanops aromatica en Malasia, un proceso de reproducci3n m s frecuente y una mayor persistencia de las pl ntulas que en las otras especies puede estar manteniendo su dominancia (Whitmore, 1975: 191). En cambio, Celaenodendron mexicanum, en el paso de semilla dispersada a pl ntulas de un a o de vida no mostr3 una mayor probabilidad de sobrevivencia que la m s com n de las especies del bosque mixto (MF). Sin embargo, las densidades locales de semillas, sobre las cuales las probabilidades estimadas se aplican, deben estar difiriendo grandemente. En consecuencia, el ingreso neto de nuevas pl ntulas a la poblaci3n puede ser muy diferente entre las especies.

Así, se propone que en los parajes de Celaenodendron mexicanum (CF), donde la producción combinada de semillas de muchos individuos es alta, el número de plántulas sobrevivientes es suficiente para mantener la población. Incluso, aún en la zona de contacto entre ambos tipos de bosques, donde la densidad de semillas de Celaenodendron mexicanum es más baja, el reclutamiento de nuevos individuos de esta especie puede darse en CF e invadir el MF, a pesar de sus altas pérdidas. Por el contrario, similares pérdidas sufridas por las especies comunes del MF, las cuales no forman agregaciones densas y por ende muestran una menor densidad de semillas, deben resultar en un número significativamente menor de plántulas y en un pobre o nulo establecimiento en CF. Las grandes variaciones interanuales de factores climáticos, producción de frutos y también de las poblaciones de depredadores pueden ser comunes, por lo que el ingreso de nuevos individuos a la población puede darse irregularmente o de una manera discontinua. El banco de semillas, después del período de germinación y antes del nuevo período de fructificación y dispersión, queda totalmente vacío. Tal que, las cohortes de semillas no se superponen en el suelo. Sin embargo, para un organismo de larga vida y con lento crecimiento como Celaenodendron mexicanum, la variación temporal en el reclutamiento de plántulas puede no ser de importancia a largo plazo para la dinámica de la población, o al menos para el mantenimiento de la dominancia. Una vez un individuo se establece y ocupa el espacio, puede por un largo período de tiempo impedir la entrada de otros individuos o especies. En el largo plazo, el banco de juveniles de diferentes edades acumulados puede proveer los individuos que ingresan a las clases adultas. Esta tipo de banco también puede facilitar la eventual dominancia al invadir el MF.

No se cuenta con datos sobre si la tendencia de una mayor sobrevivencia a mayores edades es mantenida en el caso de Celaenodendron mexicanum a través de todas las edades, o al menos en todos los estadios de los juveniles, ni tampoco sobre si las

otras especies tienen diferentes patrones de mortalidad de adultos. En los bosques tropicales secos, las especies vegetales deben enfrentarse a estreses extremos, tales como huracanes y multi-anales sequías. Sin embargo, la relativa resistencia de Celaenodendron mexicanum es sugerida por los datos fenológicos y por evidencia circunstancial. Después de una severa sequía (1985-1986), hubo muchos árboles muertos en pie de diferentes especies en el MF, mientras solamente las ramas más pequeñas de Celaenodendron mexicanum fueron afectadas. Correspondiéndose con eso, ramas y troncos caídos son extremadamente raros en CF y en cambio, muy comunes en el MF.

Sin embargo, la existencia de aparentes ventajas a largo plazo necesita aún ser confirmada y sus bases fisiológicas identificadas. A su vez, tampoco se conoce por qué Celaenodendron mexicanum se presenta en agregaciones poblacionales discontinuas y solamente cerca de la costa, es decir por qué no se ha extendido y cubierto más (o todos) los sitios ocupados por MF? Factores topográficos no limitan fuertemente la distribución de CF, pero su abundancia relativa y su desempeño en diversas situaciones aún no ha sido cuantificado. Desafortunadamente, puede ser difícil ahora debido a la extracción y deforestación extensivas. La limitación a la zona cercana a la costa es también interesante y podría estar relacionada a condiciones menos severas en la estación seca (la presencia de neblina y de brisa marina), las cuales podrían permitir una más larga estación de crecimiento.

Claramente, el comportamiento en el largo plazo de los juveniles de las otras especies en los parajes de Celaenodendron mexicanum y en el bosque mixto, también merecen atención. Más necesita ser investigado acerca del comportamiento ecológico de esta especie dominante, cubriendo aspectos de estacionalidad de la fotosíntesis, tolerancia a la variación climática, crecimiento y sobrevivencia durante los estadios de juveniles y pre-reproductivos, así como longevidad de adultos. Dadas las características mostradas en este estudio, la cuestión de la

longevidad y persistencia tiene especial importancia. A fin de contar con una aproximación sobre la longevidad de adultos, las tasas de crecimiento pueden ser comparadas con los tamaños los árboles de mayor tamaño. El estudio de la anatomía del leño sugiere que el ancho de los anillos de crecimiento anual es del orden de 0.5 mm. Así, la edad mínima aproximada para el 1.7% de los árboles, los cuales exceden los 30 cm de DAP, sería de 292 años.

Finalmente, las posibilidades de que CF sea autolimitante (Horn, 1975) o incluso sujeta a colapso (Mueller-Dombois, 1988) no ha sido estudiada y por lo tanto no puede ser excluida. Por otro lado, parece que la existencia de CF no es un fenómeno azaroso (Hubbell, 1979) ya que la dominancia por una sola especie es una característica consistente de las poblaciones de Celaenodendron mexicanum. La interpretación general de CF es aún el sujeto de importantes cuestiones, las cuales necesitan ser investigadas en escalas grandes de tiempo y espacio.

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