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ESTRUCTURA, DIVERSIDAD Y MORTALIDAD DEL COMPONENTE ARBOREO EN UN MOSAICO AMBIENTAL DE CHAMELA, MEXICO

TESIS

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ABSTRACT

Relief and soil features have been recognized as significant ecological determinants of the spatial vegetation patterns. The objective of this dissertation focuses on thorough analysis of the spatial patterns of the structure and dynamics of the tree communities of a tropical deciduous forest. The patterns depicted were further related to morpho-pedological and soil constraint variations.

This study enhances three topics, which have been poorly documented for this type of forests, namely: 1) spatial variation patterns of the tree component and relief and soil features at a mesoscale level (from hundreds to thousands of hectares); 2) the description and analysis of tree mortality and its implications on forest dynamics; 3) the relationship between tree communities, morpho-pedological land units and soil features. The study was conducted at the Chamela Biological Station in Jalisco, Mexico. The area was dissected into 14 morpho-pedologic land units. Climatic conditions (temperature and precipitation) among units did not vary substantially. The dissertation comprises six chapters. Chapter I (introduction) and chapter VI (Discussion) provide a general overview. The results are presented in four independent, but complementary, parts.

The first part of results deals with the analysis of relief and soil to distinguish core differences among soil features related to water constrains, nutrients, drainage and physical space for rooting system development. Data were obtained from 46 sampling sites within the 14 morpho-pedologic land units. Four groups were distinguished as a result of a thorough data analysis of morpho-pedological land units. Four soil constrain classes were defined based upon key relief and soil features. The classes were assessed in order to ponder their properties for limiting or favoring plant development.

The second part reports the results of the study on living tree component of the forest. Trees with a DBH ≥ 5 cm were considered only. The tree sampling was made through 21 plots of 0.24 Ha, distributed only in six morpho-pedologic land units. From the data analysis it was found large variations between structure and diversity among land units. However, the most conspicuous difference occurs among dominant species.

The third part investigates the relationship between relief and soil features and the alive tree component. Data of relief and soils were pulled into a matrix so-called "environmental matrix"; whereas data on the tree component were organized into two matrices, one with structural characteristics and the other with species composition. All data contained in the matrices were analyzed through simple correlation and canonical correspondence analysis (CCA). No significant correlation was found between arboreal structure and relief and soil features. In contrast, half of the dominant tree species showed significant correlation with the same features. The CCA from species-environment, through a Monte Carlo test, showed a significant relation with both first axis and all canonical axes ($F=5.122$, $p<0.005$; $F=2.795$, $p<0.005$, respectively). Elevation was significantly correlated with the first canonical axis ($r=0.80$; $p<0.05$) and exchangeable bases in the soils were correlated with the second axis ($r=0.64$; $p<0.05$). The total variation explained by these two axes was of 30%.

The fourth part deals with the analysis of the dead tree component of the forest studied. Data on dead trees were gathered from the same 21 plots previously mentioned in the second part. Dead trunks with a DBH ≥ 5 cm were sampled. Six subsequent sampling efforts were conducted. The first so-called "initial record" was taken in 1995 and provided a complete arboreal necromass inventory. The next sampling efforts took place at the end of rainy and dry seasons in 1995, 1996 and 1997. These last five sampling efforts were called as "seasonal records". In order to study relationships among arboreal necromass, living tree component, relief and soil features, data were integrated into a matrix so-called "mortality matrix". Arboreal necromass was best related to the structure of the living tree component, whereas no relationship was found with relief and soil features, either independently or as a land unit.

Furthermore, a descriptive analysis was performed in order to provide additional data to document trend patterns. These patterns were also compared to literature describing in comparable ecosystems.

In brief, this study showed that the relief and soil mosaic depicted at the Chamela Biological Station explains up to some extent current spatial patterns of the tree dominant species. An added value foreseen from this dissertation focuses on the integrated analysis of relief, soil and tree component attributes. This depicts the current landscape complexity of the study area. Therefore this dissertation suggests that previous and future ecosystem patterns and processes surveyed ought to be framed within this landscape complexity. In addition, the results provide practical applications for sound land use planning efforts on this type of ecosystems.

RESUMEN

El relieve y el suelo se han reconocido entre los determinantes ecológicos de los patrones espaciales de la vegetación. Por ello, su análisis ha sido importante al tratar de reconocer y entender las diferencias entre las comunidades vegetales establecidas en ambientes heterogéneos. El objetivo general de la tesis fue analizar los patrones espaciales de la estructura y dinámica de la comunidad arbórea de un bosque tropical deciduo y establecer su relación con variaciones morfo-pedológicas y de condiciones limitantes en el suelo.

La relevancia de este trabajo reside en tres aspectos escasamente documentados para este tipo de bosques: 1) el estudio de la variación en los patrones del componente arbóreo y factores del relieve y el suelo desde una dimensión espacial de mesoescala (cientos de hectáreas a decenas de kilómetros cuadrados); 2) la descripción y el análisis de la mortalidad de los árboles y sus implicaciones en la dinámica del bosque; 3) el análisis de la relación de los patrones de la comunidad de árboles y las variaciones morfo-pedológicas y del suelo. El estudio se realizó en la Estación de Biología de Chamela, en Jalisco, México. En dicha área se han delimitado 14 unidades morfo-pedológicas, entre las cuales el clima cálido húmedo y la precipitación son homogéneos. La tesis se integra de seis capítulos. El capítulo I (Antecedentes) y el capítulo 6 (Discusión) contienen aspectos generales. Los resultados se presentaron en cuatro capítulos independientes, pero temáticamente complementarios.

La primer parte analizó un grupo de características del relieve y el suelo, para definir las principales diferencias en las condiciones y recursos limitantes del suelo en el área de la Estación. Las características analizadas se relacionaron con limitantes en la oferta de agua, los nutrientes, el drenaje del agua y el espacio para el desarrollo de las raíces. La información provino de 46 sitios de muestreo ubicados en las 14 unidades morfo-pedológicas. El análisis de la información permitió clasificar dichas unidades en cuatro grupos que definen las categorías de mayor contraste de limitantes en el suelo.

Una segunda etapa, consistió en el análisis de la estructura y la composición de especies del componente arbóreo vivo del bosque tropical deciduo. Los diferentes atributos estimados provinieron de árboles vivos con diámetro a la altura del pecho (DAP) $\geq$ 5 cm, que fueron muestreados en 21 parcelas de 0.24 ha, distribuidas en seis de las 14 unidades morfo-pedológicas. El análisis del componente arbóreo de las seis unidades morfo-pedológicas mostró que diferentes atributos estructurales y de diversidad varían entre las unidades, pero el principal distintivo se presentó entre las especies que dominan el dosel.

La tercera etapa examinó la relación entre aspectos del relieve y suelo con el componente arbóreo vivo. Para tal fin la información del relieve y el suelo de la primer parte se integró en una matriz designada como "matriz ambiental". De igual manera, la información del componente arbóreo de la segunda parte se integró en dos matrices, una con datos de estructura y otra con la composición de especies. La información de las matrices sobre el componente arbóreo fueron relacionadas con la "matriz ambiental" mediante análisis de correlación simple y análisis de correspondencia canónica (ACC). Se encontró que la mayoría de las especies que son dominantes en el dosel se correlacionaron significativamente con factores del relieve y el suelo, pero esto no ocurrió con las características estructurales. El ACC efectuado con las especies y la matriz ambiental, de acuerdo a las pruebas de Monte Carlo, mostró una relación significativa para el primer eje y para el conjunto de ejes canónicos ($F=5.122$, $p<0.005$; $F=2.795$, $p<0.005$, respectively). Esto indicó que la relación entre las especies y las variables ambientales fue

altamente significativa. La elevación se correlacionó significativamente con el primer eje canónico ($r= 0.80$; $p<0.05$) y las bases intercambiables con el segundo eje ($r=0.64$; $p<0.05$). Ambos ejes explicaron un 30% de la varianza registrada en la composición de especies arbóreas del dosel.

En la parte cuatro se estudió el componente arbóreo muerto del BTD de Chamela. La información de los árboles muertos provino de las mismas 21 parcelas en que se estudió el componente arbóreo vivo. En dichas parcelas se muestrearon todos los troncos con DAP ≥ 5 cm. El componente arbóreo muerto se integró de un registro inicial efectuado a principios de lluvias de 1995 y cinco registros estacionales realizados a fines de la época de lluvias y secas de 1995, 1996 y 1997. Con el propósito de analizar el componente arbóreo muerto inicial y sus registros estacionales se organizó una "matriz de mortalidad", la cual se relacionó con la matriz "ambiental". Se encontró que la estructura de la necromasa arbórea presenta notables variaciones espaciales, las cuales mantuvieron una relación más estrecha con la biomasa arbórea, que con los factores del relieve y el suelo.

Adicionalmente a los resultados antes señalados, cada parte presentó información que describe los patrones del mosaico de relieve y suelos y del componente arbóreo, así como sus principales tendencias de variación. Dichos patrones fueron comparados con lo que la literatura reporta para otros bosques afines.

En resumen, se puede enfatizar que la Estación de Biología de Chamela no sólo mantiene una alta diversidad biológica, sino que también alberga un mosaico de relieve y suelos. Dicho mosaico tuvo una contribución parcial para explicar los patrones de variación en las especies dominantes del dosel del BTD. Un aporte adicional de este trabajo es que ofrece un panorama general de la complejidad del paisaje derivado de la integración de los patrones de variación del componente arbóreo y factores del relieve y el suelo. El reconocimiento de tal complejidad puede ser una referencia para interpretar los alcances de los patrones y procesos documentados en estudios anteriores y para delinear estudios futuros en los que el espacio y su heterogeneidad sean componentes de análisis intrínseco. Por último, se discuten algunas alternativas donde los resultados derivados de este trabajo pueden ser de utilidad práctica para la planeación del uso y manejo de los recursos en este tipo de bosques.

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CAPÍTULO I
ANTECEDENTES GENERALES

INTRODUCCIÓN

Los bosques tropicales son altamente diversos en especies arbóreas y, aunque la apariencia fisonómica de su dosel tiende a ser homogénea (Forman y Godron 1986), las comunidades vegetales que los integran son estructuralmente variables en el espacio y dinámicas en el tiempo (Condit 1996, Chazdon 1996, Newberry *et al.* 1999). La caracterización y el análisis de la diversidad y la complejidad estructural de las comunidades arbóreas han sido el propósito de gran parte de la investigación ecológica realizada en dichos ecosistemas (Hubbell y Foster 1986, Hubbell 1998, Leigh 1990, Ashton 1992, Phillips *et al.* 1994, Bullock *et al.* 1995, Condit *et al.* 1995, Richards 1996, Newberry *et al.* 1999, Hubbell *et al.* 1999, Peres 1999).

Tradicionalmente, el estudio de la estructura, la composición de especies, la diversidad, la mortalidad y la dinámica de las comunidades arbóreas de los bosques tropicales se ha realizado en extensiones menores de 10 ha y, principalmente, en bosques tropicales lluviosos. Otro esfuerzo importante para el estudio de dichas comunidades es el que se ha realizado en un conjunto de parcelas permanentes de "gran" tamaño (16-50 ha; Condit *et al.* 1995, Hubbell 1998). A través de estos trabajos ha sido posible analizar el papel de diferentes factores ecológicos que influyen y se relacionan con los patrones del componente arbóreo, tales como las interacciones bióticas, la disponibilidad de recursos como la luz, los nutrientes del suelo, el relieve y los disturbios (Brokaw 1982, Putz 1983, Campbell 1994, Lieberman *et al.* 1985, Oliveira-Filho *et al.* 1998, Newberry *et al.* 1999). Estos estudios han generado información ecológica sumamente valiosa, no obstante, gran parte de ella tiene limitaciones para ofrecer una mejor comprensión de los patrones y procesos que ocurren en el componente arbóreo a un nivel de mesoescala (> 1^0-10^2 km^2; Delcourt y Delcourt 1988, Campbell 1994, Chazdon 1996, Ricklefs 2000) o a un nivel regional (> 10^2 km^2).

Al nivel de mesoescala, se ha documentado la importancia ecológica de las variaciones climáticas, geomorfológicas, de relieve, de suelo y de disturbio para determinar variaciones en el tipo de vegetación y en la distribución y abundancia de especies de plantas; así como en la estructura y dinámica natural de sus comunidades. Dicha interacción se basa en el reconocimiento de que en un paisaje convergen porciones de terreno con diferente aptitud para proveer condiciones y recursos claves para el establecimiento y desarrollo de las plantas (Carmean 1975, Breimer et al. 1986, Etchevers 1999, Herrick 2000). Por ello, el medio físico puede ser un determinante ecológico de los patrones de la vegetación en los bosques tropicales (Clark *et al.* 1995, Tuomisto *et al.*1995, Chazdon 1996, Condit 1996).

El análisis de la relación de factores del medio físico con la estructura y la diversidad, más allá del nivel local, junto con el interés por probar algunas hipótesis teóricas (Grubb 1977, Connell 1978, Huston 1980, Hubbell y Foster 1986), ha motivado numerosos estudios en los bosques del Neotrópico, de Asia y de África (Cleef *et al.* 1982, van Kekem 1986, van Reuler 1986, Gentry 1988, Salo y Räsänen 1989, Hommel 1990, Duncan 1992, Coughenour y Ellis 1993, Gentry y Ortiz 1993, Poorter *et al.* 1994, Duivenvoorden y Lips 1995, Richards 1996, Siebe *et al.* 1995, Tuomisto *et al.* 1995, Clark *et al.* 1995, 1996, Sollins 1998, Webb y Fa'aumu 1999, Pyke *et al.* 2001, Villers-Ruíz *et al.* 2003). Como resultado, se ha llegado ha reconocer la importancia del drenaje, la oferta de agua y nutrientes del suelo y la posición en el relieve para explicar las variaciones en la estructura y la diversidad de las comunidades de diversos grupos de plantas, o en la distribución y abundancia de algunas especies particulares. Sin embargo, los estudios para relacionar los nutrientes del suelo y la diversidad han dado resultados controversiales o poco contundentes (Huston 1980, Gentry 1988, Clinebell *et al.* 1995, Trejo 1998, Salas 2002). Al tratar de entender la manera en que opera la relación entre factores del relieve y el suelo con la vegetación de los boques tropicales, se ha hecho evidente la influencia del sitio particular de estudio, la escala de trabajo, el diseño de muestreo, la obtención y el tipo de información considerada, así como de la interpretación o las herramientas de análisis empleadas. En el caso del suelo, por ejemplo, además de su variabilidad espacio-temporal inherente, la información sobre algunas de sus propiedades físicas o químicas es dependiente del tipo de análisis de laboratorio realizados (Sollins 1998).

Una de las aproximaciones para analizar la complejidad ambiental en los bosques tropicales corresponde al enfoque morfo-pedológico. Este enfoque parte de reconocer que el relieve y el suelo no son estructural, ni funcionalmente, independientes (Geissert y Rossignol 1987, Gerrard 1992). Por lo anterior, se ha insistido en vincular al relieve y el suelo, y adoptarlos como referencias de heterogeneidad ambiental cuando se pretende analizar la vegetación, siendo que comúnmente la variación de ambos factores es compatible con los mosaicos estructurales de algunas comunidades o grupos de plantas (Coughenour y Ellis 1993, Gentry y Ortiz 1993, Clark *et al.* 1995, Siebe *et al.* 1995). Sin embargo, la incorporación de información cuantitativa del relieve y el suelo a los estudios de vegetación en los bosques tropicales continúa siendo un reto (Chazdon 1996. Condit 1996, Sollins 1998).

El reconocimiento del vínculo de los factores del relieve y el suelo con unidades morfo-pedológicas, puede ser la base para caracterizar y analizar los patrones y la dinámica de las especies, las comunidades y los tipos de vegetación en los bosques tropicales (Chazdon 1996, Condit 1996, Sollins 1998, Ricklefs 2000). Lo cual constituye una visión congruente con la concepción tradicionalmente adoptada en la ecología del paisaje, donde *a priori* se supone que los factores del relieve y el suelo, junto con los organismos interactúan de manera integral, pero que determinados patrones y procesos muestran mayor relevancia en dimensiones espaciales particulares (Farina 1995, Wiens 1995, Zonneveld 1995, Perry 1996). Por ello, el estudio de la complejidad de la vegetación en los bosques tropicales con una aproximación paisajística, requiere de la adopción de metodologías, herramientas y supuestos de trabajo alternativos a los que son seguidos con otros enfoques para analizar árboles individuales, comunidades o ecosistemas en localidades específicas. Por ejemplo, en el enfoque de paisaje toda la información proveniente de puntos (parcelas de muestreo, individuos o estructuras individuales) es parte de un espacio previamente caracterizado, y por tanto puede ser representada en unidades areales (Velázquez *et al.* 2003). Por lo que para conservar tal referencia espacial se recurre al uso de cartografía y a la expresión de los resultados en mapas (Breimer *et al.* 1986, Tricart y KiewietdeJonge 1992, Alexander y Millington 2000), cuya generación y análisis puede realizarse mediante el uso de sistemas de información geográfica (Chazdon 1996, Wellens *et al.* 2002). Además, debido a que los inventarios y las caracterizaciones de los factores del relieve, del suelo y del componente biológico conforman bases de datos múltiples, se recomienda el uso de técnicas multivariadas para facilitar su manejo y análisis (Kent y Coker 1992, Greig-Smith 1995, Jogman *et al.* 1995).

A diferencia del conocimiento ecológico que se tiene para los bosques tropicales de ambientes más húmedos, el conocimiento sobre los patrones y procesos ecológicos que ocurren en los bosques tropicales estacionalmente secos es más limitado (Murphy y Lugo 1986, Hytteborn y Skarpe 1992, Bullock *et al.* 1995). Aunque se ha planteado que estos bosques tienden a ser menos diversos que los bosques más húmedos, ha habido un amplio reconocimiento de que en algunos casos su diversidad de plantas leñosas puede ser equivalente, o incluso mayor (Gentry 1988, Trejo 1998). Fisonómicamente su dosel aparenta ser un continuo, aunque en realidad presenta diferencias florísticas y estructurales recurrentes (Murphy y Lugo 1986, Mooney *et al.* 1995, Gillespie *et al.* 2000). Ambientalmente, se ha documentado que los bosques tropicales estacionalmente secos se establecen en condiciones variables de geomorfología, litología y suelos (Holdridge 1967, Trejo 1996, Villers-Ruíz *et al.* 2003). Asimismo, entre los múltiples aspectos de interés para conocer más acerca de éstos bosques destaca la inquietud por establecer que relación ecológica mantiene la heterogeneidad en factores del relieve y el suelo con los patrones paisajísticos de la vegetación. Resolver dicha inquietud puede generar conocimiento básico para entender los patrones y procesos naturales que ocurren en ellos y que puede ser útil para planear su mejor uso, conservación y restauración (Campbell 1994, Tuomisto *et al.*1995, Chazdon 1996, Condit 1996, Cook 1998, Halffter 1998, Sollins 1998, Peres 1999). Esto último constituye una necesidad, al considerar que este tipo de bosques se encuentran entre los más dañados del mundo y que están sujetos a notables transformaciones antrópicas (Murphy y Lugo 1986, Janzen 1990).

En México, los bosques tropicales estacionalmente secos comúnmente se han denominado como selvas bajas caducifolias (Miranda y Hernández X. 1963) o bosques tropicales caducifolios (BTC; Rzedowski 1986). Así, considerando que ésta última designación ha sido ampliamente difundida a través de la obra "Vegetación de México" (del Dr. J. Rzedowski), se adoptó para su uso en esta tesis, y en su traducción al inglés se referirá como "Tropical Deciduous Forests".

Los BTCs ocupan aproximadamente 7% del territorio nacional (Palacio-Prieto *et al.* 2000). Sin embargo, entre las limitadas excepciones, este tipo de bosques se han conservan en buen estado en algunas áreas extensas como la Reserva de la Biosfera Chamela-Cuixmala (A. Miranda com. personal), o en regiones como la porción sureste de la cuenca del río Tepalcatepec, en Michoacán (Mendoza *et al.* 2003). En tanto que en gran parte de las regiones del país los BTCs han experimentado acelerados procesos de amenaza y transformación (Robichaux y Yetman 2001, Trejo y Dirzo 2000, Velázquez *et al.* 2002). Asimismo, en muy pocas regiones se ha fomentado la investigación biológica en niveles comparables con el área de la Estación de Biología de Chamela. Este sitio cuenta con numerosos trabajos sobre flora, vegetación, fauna y procesos ecosistémicos (por ejemplo, Lott *et al.* 1987, Martínez-Yrízar *et al.* 1992, Ceballos 1995, Bullock 2000, Maass *et al.* 2002), producto de casi tres décadas de intenso trabajo, lo que ha valido ser reconocido entre los sitios más estudiados del país (Noguera *et al.* 2002).

En Chamela, al igual que en otros sitios con BTC, la mayor parte de los estudios con plantas leñosas se han centrado en escalas locales (Martijena 1993, Balvanera 1999, Kelly *et al.* 2001, Segura *et al.* 2003), en tanto que las aproximaciones de mesoescala y regionales siguen siendo escasas. En algunas partes del país se cuenta con estudios de mesoescala o a nivel regional que han consistido en la elaboración de cartografía general y descripciones de la cobertura de los BTCs, su florística, su fisonomía y su estructura (Rzedowski 1986, Lorence y García-Mendoza 1989, Lott 1993, Trejo 1998, Pérez-García *et al.* 2001, Pérez-García 2002, Salas 2002, Villers-Ruiz *et al.* 2003). Sin embargo, en general aún se conoce poco sobre la relación de los mosaicos geomorfológicos y del suelo con los patrones del componente arbóreo de los BTCs, desde la perspectiva integradora de la ecología del paisaje. Esto no sólo restringe la disponibilidad de información básica para la investigación acerca de los procesos que subyacen a dichos patrones, sino que también dificulta contar con información que sustente el manejo de los recursos y que sea congruente con escalas apropiadas para la toma de decisiones. Es en este contexto que la tesis trata de contribuir aportando información sobre el papel de factores del relieve y el suelo para explicar los patrones estructurales, de mortalidad y dinámica del componente arbóreo a un nivel de mesoescala en el BTC de Chamela.

OBJETIVOS E HIPÓTESIS DE TRABAJO

La estructura y la diversidad de las comunidades arbóreas es producto de procesos históricos y ecológicos determinados espacial y temporalmente por múltiples factores. La figura I.1 muestra el modelo adoptado en este trabajo acerca de la relación entre la geomorfología, el suelo e indirectamente el efecto o la relación de ambos, sobre los factores de disturbio (que son factores clave a nivel de mesoescala). Con base en dicho modelo se plantearon los ojetivos y las hipótesis de trabajo que sirvieron de guía para el desarrollo de este estudio. Cabe señalar, que por el restringido estado de conocimiento que se tiene sobre la dinámica de este tipo de ecosistemas y el tipo de información existente sobre el sitio de estudio al iniciar el trabajo, en cada capítulo fue necesario responder una serie de preguntas descriptivas básicas.

Objetivo general

El objetivo general de la tesis fue analizar la relación entre el componente arbóreo (estructura, composición y mortalidad) del bosque tropical caducifolio (BTC) de la Estación de Biología de Chamela y el mosaico debido a las variaciones morfo-pedológicas y a un conjunto de limitantes en el suelo (características del relieve y el suelo que inducen contrastes en condiciones y recursos que son claves para el establecimiento y desarrollo de las plantas).

Objetivos particulares

1) Identificar las características del relieve y el suelo que determinan los principales contrastes en condiciones limitantes en el suelo, a fin de establecer su ocurrencia en el área de la Estación de Chamela y sus posibles implicaciones en los patrones de la vegetación de BTC.

2) Analizar la estructura y la composición del componente arbóreo del BTC de Chamela y relacionar las variaciones del dosel con el mosaico morfo-pedológico y de contrastes en las condiciones limitantes en el suelo.

3) Caracterizar al componente arbóreo muerto del BTC y determinar la correspondencia de sus de sus variaciones con el mosaico morfo-pedológico y de contrastes en condiciones limitantes en el suelo.

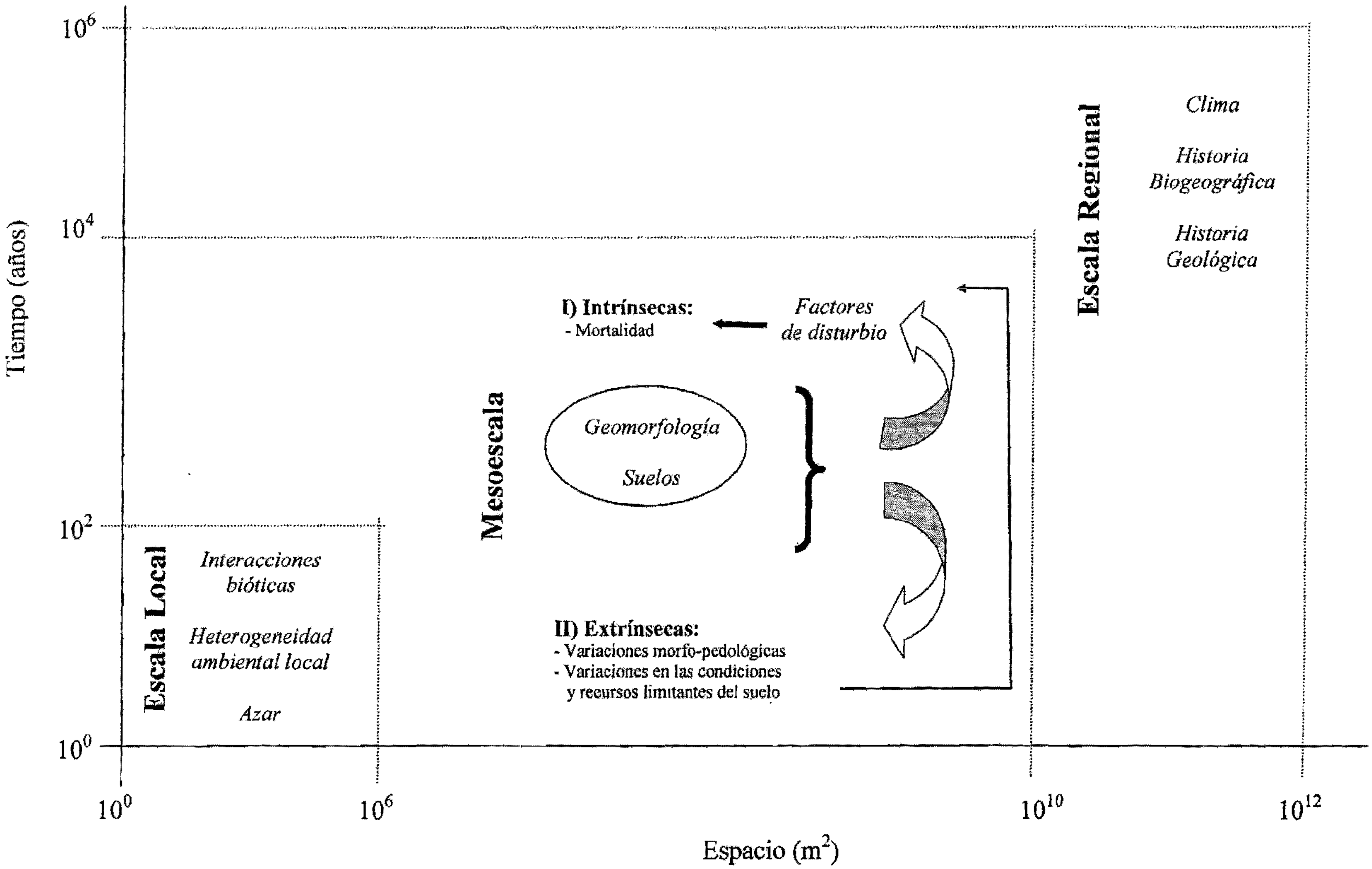

Figura I.1. Factores que influyen en la estructura, la diversidad y la dinámica de las comunidades (cursivas), pero que tienen distinto nivel de relevancia en diferentes dimensiones espacio-temporales. Las unidades señaladas en los ejes de la gráfica sólo ilustran órdenes de magnitud en el sentido espacial y temporal.

Hipótesis de trabajo

1) Las características del relieve y el suelo de la Estación de Chamela inducen diferencias espaciales en condiciones y recursos del suelo claves para las plantas; por lo tanto, el paisaje se integra de un mosaico de unidades de terreno con distintas condiciones limitantes en el suelo.

2) Los patrones del componente árboreo del BTC de la Estación Biológica de Chamela están estrechamente relacionado con el mosaico morfo-pedológico y el de contrastes en las condiciones limitantes en el suelo. De manera que, distintas unidades morfo-pedológicas o diferencias en las condiciones limitantes en el suelo (factores relacionados con el drenaje, la erosión y la disponibilidad de agua, nutrientes y espacio para las raíces) se relacionan y contribuyen a explicar las variaciones espaciales en la estructura, la diversidad y la composición de especies.

3) Las diferentes unidades morfo-pedológicas o de condiciones limitantes en el suelo se relacionan con variaciones en la ocurrencia e intensidad de disturbios como el estrés hídrico y el viento; por ello, se espera que la mortalidad y la dinámica del componente arbóreo en dichas unidades de terreno reflejen y permiten estimar el efecto espacialmente diferencial de los disturbios.

ÁREA DE ESTUDIO

El estudio se efectuó en la Estación de Biología de Chamela de la UNAM, en Jalisco, México (Fig. I.2). La Estación de Chamela se localiza cerca de la costa del Océano Pacífico (19°30′-19°31′ N, y 105°00′-105°05′ O). El clima regional es cálido sub-húmedo con lluvias en verano (Aw_0i; Tabla I.1), considerado entre los más secos de los cálido húmedos (García 1988). La temperatura media anual es de 24.6°C. La precipitación promedio anual se estima en 788 mm, aunque oscila entre 453 y 1,392 mm; asimismo, se reporta que cerca del 80% de la precipitación cae entre julio y octubre, lo que induce una marcada estacionalidad (Bullock 1986, Maass *et al.* 2002). En la época de lluvias, entre cuatro y seis tormentas ciclónicas intensas son responsables de casi un 50% de la precipitación total anual, y usualmente son acompañadas de fuertes vientos (García-Oliva *et al.* 1995).

En el área de la Estación (1,600 ha) fueron delimitadas 14 unidades morfo-pedológicas (Cotler *et al.* 2002; Fig. I.2); tal delimitación se basó en criterios litológicos, formas del relieve, tipos de suelo, disectación de cauces y las evidencias de algunos procesos morfodinámicos como la erosión (Verstappen 1983, Geissert y Rossignol 1987; Tabla I.2). En tres de las 14 unidades (valles aluviales y piesdemonte), se presenta vegetación de bosque tropical subcaducifolio (Rzedowski 1986), que es equivalente a la denominada selva mediana subcaducifolia (Miranda y Hernández X. 1963); mientras que, en las 11 unidades restantes se presenta bosque tropical caducifolio (BTC; Rzedowski 1986). Este trabajo, se centró en analizar los patrones estructurales, la composición de especies y la dinámica del componente arbóreo del BTC, sólo este tipo de vegetación se consideró debido a que es predominante en la región circundante al sitio de estudio, y más allá, a un nivel regional (cerca del 13% del estado de Jalisco) y nacional (7%; Palacio-Prieto *et al.* 2000).

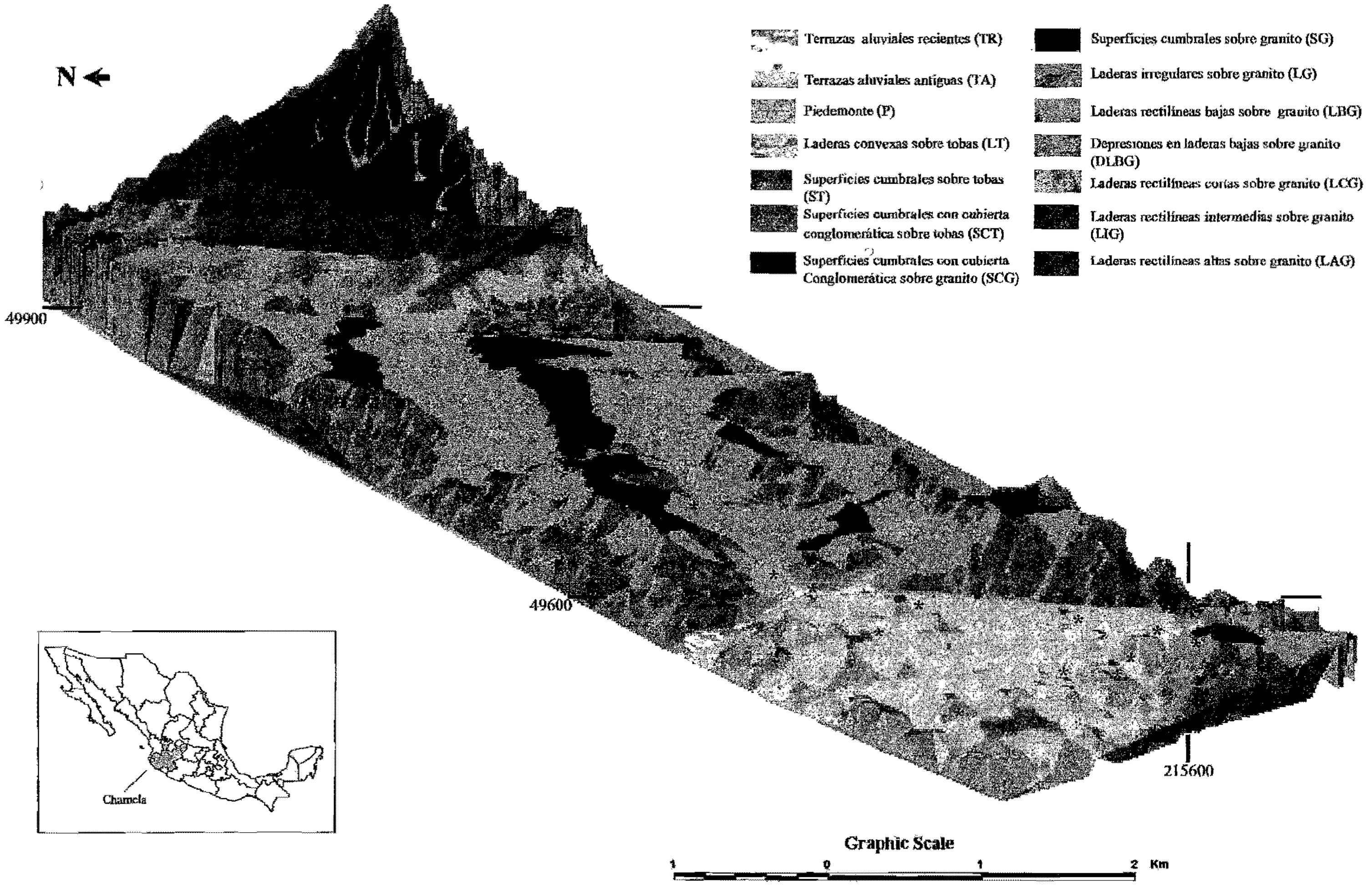

Figura I.2. Mapa morfo-pedológico tridimensional de la Estación de Biología de Chamela, Mexico. Las abreviaturas de las unidades son usadas para identificarlas a través de todo el texto. Los asteriscos (*) indican la ubicación de los 46 perfiles de suelo analizados. El factor de exageración vertical fue de tres y el color gris del borde es producto de una deformación técnica (proyección UTM, Zona 14, Datum Nad 27, Espheroid Clarke 1886, Grid 1000m).

Tabla I.1. Características climáticas de la región donde se localiza la Estación de Biología de Chamela.

CONDICIÓN CLIMÁTICA	CARACTERÍSTICAS GENERALES
Temperatura	La temperatura media anual es de 24.6°C (1978-2000), con un promedio mensual máximo de 30°C (± 3°C) y un mínimo de 19.5°C (± 6.8°C). Los valores máximos se registran entre Junio y Septiembre cuando hay mayor humedad atmosférica (García-Oliva *et al.* 2002).
Precipitación	La precipitación promedio es de 788 mm (1977-2000). En 23 años de registro, García-Oliva *et al.* (2002) han observado recurrentes variaciones interanuales. En 1985, ocurrió una precipitación mínima de 453 mm y en 1992 una máxima de 1392. La precipitación total anual es determinada principalmente por la incidencia de tormentas ciclónicas.
Patrón de lluvias	El patrón de precipitación es marcadamente estacional. Las lluvias se concentran entre los meses de junio-julio a octubre (Bullock 1986), las variaciones "regulares" son influenciadas por los vientos alisios y los ciclones tropicales del Pacífico, pero también son afectadas por los fenómenos climáticos de "El Niño" (ENSO) y "La Niña" (Hernández *et al.* 2001). Los vientos alisios explican el patrón de lluvias de junio a agosto (inicio de lluvias), mientras que las tormentas ciclónicas ejercen su mayor influencia entre septiembre y octubre. El patrón de precipitación consiste de 51 eventos en promedio (1983-1990); los cuales son, en su mayoría, de poca duración (el 57% son < 1.5 horas) y cantidad (el 62% son eventos de lluvia < 8 mm). Los eventos de baja precipitación se relacionan con lluvias convectivas. Tan sólo alrededor de 6 eventos de precipitación explican el 50% de la lluvia anual, y estos se asocian con los ciclones o las tormentas tropicales (García-Oliva *et al.* 1995 y 2002).
Tormentas ciclónicas y otros fenómenos climáticos	Chamela se encuentra en la región de la costa del océano Pacífico con menor probabilidad de incidencia de ciclones (Manzanillo a Puerto Vallarta), sin embargo, recibe su efecto a través de las tormentas ciclónicas (García-Oliva *et al.* 2002). También allí el ENSO induce un incremento en las lluvias de invierno y una disminución en la lluvia entre los meses de junio a agosto, mientras que "La Niña" induce un aumento de la precipitación en los meses de verano (Hernández *et al.* 2001). En general, estos fenómenos no sólo influyen de manera importante los volúmenes anuales de precipitación, sino en su patrón de distribución.
Viento	El patrón de circulación del viento en la región de Chamela es producto de distintos fenómenos climáticos de mayor escala, (los monzones, los vientos alisios, las tormentas ciclónicas y los fenómenos de "El ENSO" y "La Niña"). Asociado a dichos fenómenos se registran diferencias en la dirección y la magnitud del viento a lo largo del año. De manera local, el relieve y las diferencias en altitud operan como superficies de fricción y pueden regular el flujo del viento, disminuyendo su rapidez o generando turbulencia (García-Oliva *et al.* 1991). Dentro de la Estación, algunos sitios están más expuestos al viento (p.e. laderas altas del cerro "Maderas" y las crestas de los lomeríos sobre granito, tobas y conglomerados); mientras que en otros (como los cauces de arroyos y los interfluvios entre los lomeríos), las condiciones del relieve pueden ser suficientes para atenuar o dar protección contra el efecto del viento de la brisa marina, de los vientos alisios y de las tormentas ciclónicas durante la estación de lluvias (Bullock 1986). Durante el "invierno" (noviembre-marzo), en la costa de Jalisco dominan vientos secos que provienen del Oeste (con dirección al Este) y corresponden al anticiclón del pacífico Nororiental. Durante la estación de secas, los vientos no son dominados por la circulación global (Bullock 1986) y durante el verano dominan los vientos húmedos del Este (alisios) producidos por el anticiclón Bermudas-Azores. En esta época del año, el patrón de lluvias determina claramente el patrón del viento. Los promedios mensuales de velocidad del viento son mayores entre marzo y junio (Bullock 1986, Camou 2001). La velocidad del viento predominante es de 1m/s (3.6 km/hr). Los vientos de mayor intensidad se registran entre abril y mayo, y a principios de la época de lluvias (2 y 3 m/s).
Estrés hídrico	El estrés hídrico se ha relacionado con la ausencia de precipitación, la alta radiación neta y las condiciones del sustrato. El efecto de estas condiciones puede tener su mayor intensidad a mediados y fines de la época de secas (abril-junio), cuando pueden inducir condiciones de mayor déficit hídrico en las plantas, en relación a lo que ocurre cuando el recurso agua es disponible (julio-diciembre; Burgos 1999, Huante *et al.* 2002). En el verano hay sequías ("canícula") durante los meses de agosto y septiembre (Bullock 1986), estas pueden generar un incremento en el déficit hídrico debido a la alta demanda evaporativa; aunque en caso de no presentarse, el balance entre la evapo-transpiración potencial y la real es moderado (Burgos 1999). Al término de la época de lluvias el estrés hídrico puede atenuarse por la baja radiación en invierno y, de haber, por la precipitación invernal (Bullock 1986).

Tabla I.2. Características generales de las 14 unidades morfo-pedológicas de Chamela de acuerdo a lo reportado por Cotler *et al.* (2002). En los casos donde hubo una condición de altitud o pendiente segunda en importancia dentro de una misma unidad, esto se indicó poniéndola entre paréntesis.

Unidades Morfo-pedológicas	Tipos de Suelo (FAO 1998)	Litología	Altitud (m s.n.m.)	Pendiente (°)	Densidad del drenaje (km/km^2)	Área (km^2)	Formas del Relieve
Laderas rectilíneas cortas sobre granito (LCG)	Regosol esquelético	Granitos	180-520	35-45	7.5-8.5	1.018	Lomeríos altos
Laderas rectilíneas altas sobre granito (LAG)	Luvisol crómico	Granitos	280 - 450	20 - 45	7 - 7.5	1.467	
Laderas rectilíneas intermedias sobre granito (LIG)	Luvisol crómico	Granitos	240 – 280	8 - 20	6 - 6.5	1.506	
Laderas rectilíneas bajas sobre granito (LBG)	Luvisol ródico	Granitos	200 - 240	4 - 12	5.5	0.836	
Depresiones en laderas rectilíneas sobre granito (DLBG)	Regosol estagni-epiesquelético y estagni-eútrico	Granitos	235 - 240	≤ 5	0	0.0137	
Laderas convexas sobre tobas (LT)	Regosol epiesquelético y Cambisol mólico	Tobas	90 - 120	4 - 12	8 - 13	2.15	Lomeríos bajos
Superficies cumbrales sobre tobas (ST)	Regosol epiesquelético, Cambisol mólico y Luvisol crómico	Tobas	110 - 130	≤ 5	0	0.0405	
Superficies cumbrales con cubierta conglomerática sobre tobas (SCT)	Regosol epiesquelético	Conglomerados	110 - 115	≤ 2	0	0.047	
Superficies cumbrales sobre granito (SG)	Luvisol crómico	Granitos	140 – 150 (170 – 200)	4 - 8	0	0.14	Lomeríos intermedios
Superficies cumbrales con cubierta conglomerática sobre granito (SCG)	Regosol epiesquelético y Faeozem estagni-epiesquelético	Conglomerados	100 - 170 (135 – 200)	2 - 8 (8 - 20)	0	1.014	
Laderas irregulares sobre granito (LG)	Regosol luvi-esquelético	Granitos	130 - 170	12 - 20	8	7.48	
Piedemonte (P)	Faeozem háplico	Sedimentos coluviales	80 - 90	4 - 12	0	0.177	
Terrazas aluviales antiguas (TA)	Fluvisol eútrico	Sedimentos aluviales	80 - 85	≤ 2	0	0.044	Valles
Terrazas aluviales recientes (TR)	Regosol Endoesquelético	Sedimentos aluviales	80 - 85	≤ 2	0	0.023	

DISEÑO DE MUESTREO

Suelos y relieve

El estudio tomó como referencia inicial las 14 unidades de terreno representadas en el mapa morfo-pedológico (1:5,000) de la Estación de Biología de Chamela (Fig. I.2). La caracterización de las unidades se basó en información proveniente de 46 sitios de muestreo, ubicados entre uno y seis en las distintas unidades, de acuerdo a la heterogeneidad de las mismas. En cada sitio se obtuvo información de las características del suelo de cuando menos un perfil "tipo" (representativo), cada perfil fue descrito en campo y simultáneamente se le tomaron muestras de suelo por horizonte para su posterior análisis en laboratorio.

Debido a que el propósito inicial de este estudio fue analizar la estructura, la diversidad, la mortalidad y la dinámica del componente arbóreo del BTC, en relación con el mosaico morfo-pedológico, las parcelas de vegetación se distribuyeron en seis unidades morfo-pedológicas contrastantes (Figs. I.2; I.3a). Las unidades morfo-pedológicas seleccionadas tuvieron vegetación de BTC como atributo común, pero contrastaron al considerar la combinación de los criterios de geomorfología, relieve y suelos. El tipo de vegetación fue un primer criterio para excluir a tres unidades (terrazas aluviales recientes y antiguas, y piesdemonte). Las unidades de las depresiones (DLBG) y las superficies cumbrales con cubierta conglomerática sobre tobas (SCT) no fueron incluidas, debido a que su extensión no era suficiente (alrededor de 1 ha) para establecer las parcelas. Tampoco se incluyeron las laderas convexas sobre tobas (LT), las laderas irregulares sobre granito (LG) y las laderas rectilíneas cortas sobre granito (LCG), porque el establecimiento de parcelas en dichas unidades obligaba a considerar los criterios de exposición (norte, sur, este, oeste), de tipo de ladera (rectilínea, quebrada, cóncava o convexa) y de niveles de pendiente (moderadamente inclinada, fuertemente inclinada o abrupta); lo que implicaba un mayor número de parcelas para cubrir todas las combinaciones posibles derivadas de los criterios antes señalados.

Las seis unidades morfo-pedológicas (con su respectiva designación en inglés) que fueron consideradas para el estudio del componente arbóreo fueron las siguientes: (1) Superficies de erosión sobre granito (SG [*Summit areas over granites*; SAG]), (2) Superficies de erosión sobre tobas (ST [*Summit areas over tuffs*; SAT]), (3) Superficies de erosión con cubierta conglomerática sobre granito (SCG [*Summit areas with a conglomerate cover on granites*; SACG]), (4) Laderas rectilíneas bajas sobre granito (LBG [Low *rectilinear slopes over granites*; LSG]), (5) Laderas rectilíneas intermedias sobre granito (LIG [*Intermediate rectilinear slopes over granite*; ISG]), y (6) Laderas rectilíneas altas sobre granito (LAG [*High rectilinear slopes over granite*; HSG]).

Componente arbóreo vivo y muerto

El componente arbóreo se describió a partir del información proveniente de 21 parcelas de vegetación de 30 x 80 m (0.24 ha; Fig. I.3b), mismas que fueron distribuidas entre las seis unidades morfo-pedológicas antes señaladas. Para ubicar las parcelas en las unidades de interés primero se seleccionaron sitios potenciales sobre la cartografía, y ya en el campo, se trató de establecer las parcelas en sitios con similitud en la profundidad del suelo, el afloramiento de rocas, la altitud y la pendiente. En lo posible, las parcelas se ubicaron en

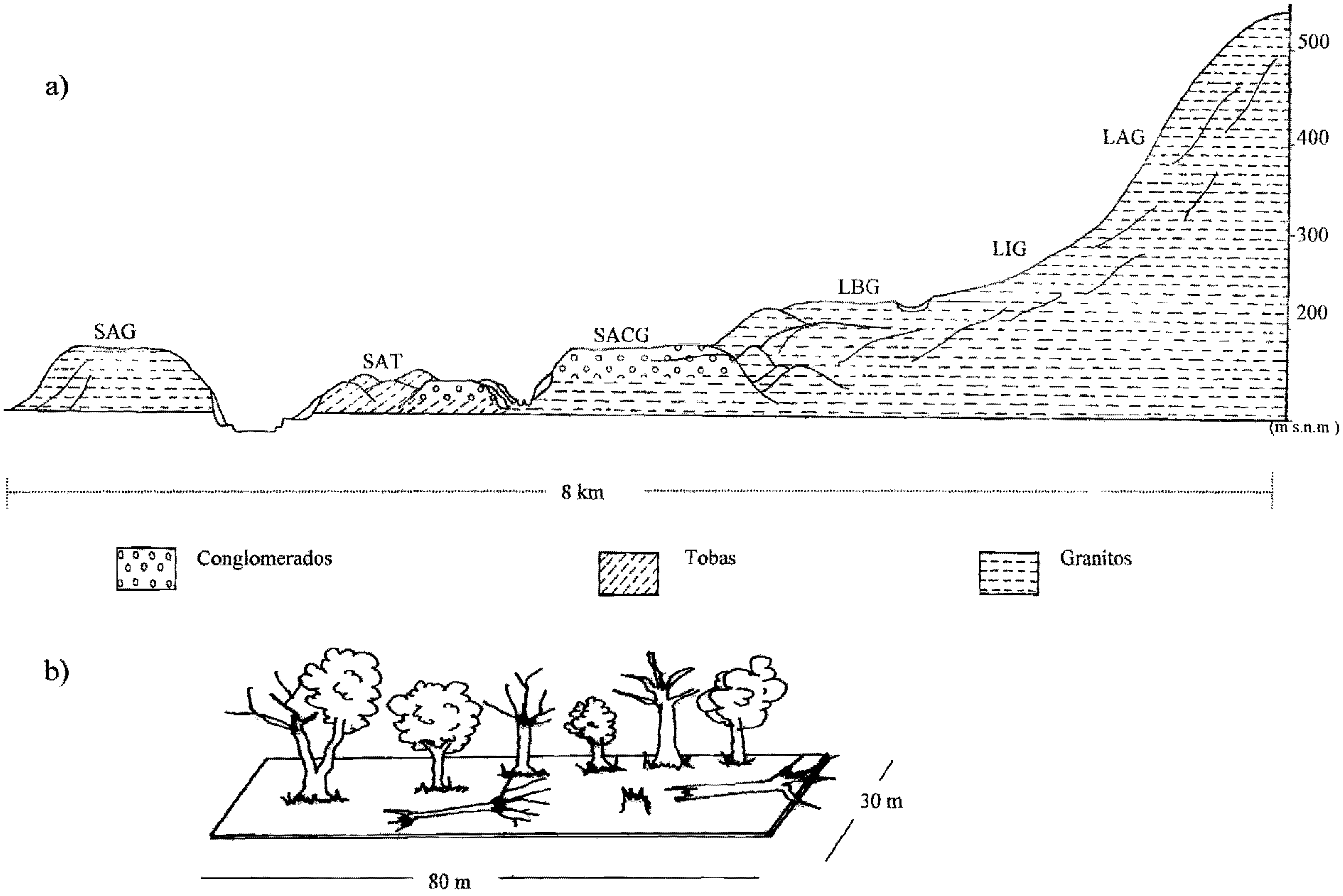

Figura I.3. a) Transecto idealizado de las seis unidades morfo-pedológicas donde se analizó la estructura, composición y dinámica del componente arbóreo en la Estación de Chamela. b) Esquema de una parcela utilizada para la cuantificación de los árboles vivos y muertos (0.24 ha).

geoformas independientes (crestas y laderas) y distantes unas de otras.

Debido a que para los bosques tropicales se carece de una metodología ampliamente discutida para analizar los patrones de mortalidad arbórea en el paisaje, en este trabajo se adecuaron algunas sugerencias metodológicas propuestas por Lorimer (1985) para el análisis regional de la historia del disturbio de un bosque. Por ejemplo, el uso de parcelas de >1000 m^2 distribuidas dentro de unidades de paisaje previamente delimitadas, y la inclusión del registro de evidencias directas e indirectas de la perturbación (estado de descomposición de los troncos muertos). Con base en lo anterior, se decidió que las parcelas de vegetación tuvieran una superficie de 0.24 ha. La forma rectangular se adoptó con la idea de incluir lo más ampliamente posible el efecto de la variabilidad micro-espacial.

El número de parcelas fue limitado porque dado su carácter de "parcelas permanentes" su establecimiento implicaba un mayor esfuerzo. Sin embargo, fue necesario establecerlas como parcelas permanentes porque uno de los objetivos de la tesis fue el análisis de la dinámica del bosque, lo cual implicaba hacer un monitoreo temporal. Las parcelas fueron georeferenciadas y se subdividieron en una retícula de 10 X 10 m. En cada parcela se registró información sobre el relieve y se realizó un perfil de suelo, en cuyas muestras se realizaron análisis físicos y químicos en laboratorio.

Debido a que los árboles del estrato arbóreo superior (dosel) son un componente estructural y funcionalmente clave en este tipo de bosques (Murphy y Lugo 1986, Martínez-Yrízar *et al.* 1992), pero también por razones logísticas, teniendo en cuenta la alta densidad de individuos y la alta diversidad de especies, el estudio se planteó para analizar solamente los árboles del dosel. En cada parcela se caracterizó y cuantificó al componente arbóreo con diámetro a la altura del pecho (1.3 m; DAP) ≥ 5 cm. Dicho DAP se adoptó con base en un muestreo preliminar, efectuado con el propósito de encontrar un criterio para excluir a los arbustos e individuos juveniles que no formaban parte del dosel. A cada árbol se le midió el DAP, se le tomó una muestra para su determinación taxonómica y se le colocó una etiqueta metálica para posteriormente hacer el monitoreo temporal.

El inventario y la caracterización del componente arbóreo muerto y de los nuevos reclutas se efectuó en las parcelas permanentes y, para ambos componentes se mantuvo el mismo criterio de DAP que se uso para caracterizar el componente arbóreo vivo. El componente arbóreo muerto "inicial", correspondió al registro de los árboles muertos efectuado al inicio del estudio (antes de la época de lluvias de 1995) y este incluyó toda la necromasa arbórea existente en las parcelas que cumplía el criterio de DAP. En las cinco estaciones climáticas siguientes, se efectuó un registro de la mortalidad arbórea, el cual se designó como componente arbóreo muerto estacionalmente. Específicamente, dichos monitoreos se efectuaron consecutivamente a fines de las lluvias de 1995, 1996 y 1997 (diciembre) y a fines de las secas de 1996 y 1997 (junio). Los monitoreos estacionales consistieron en cotejar la sobrevivencia de los árboles originalmente etiquetados.

Teniendo en cuenta el criterio de diámetro adoptado (≥ 5 cm), se reconoce que los resultados y conclusiones derivadas de este trabajo refieren a la fracción de la comunidad arbórea analizada y no a todas las plantas leñosas u formas de vida que integran la vegetación del BTC de Chamela.

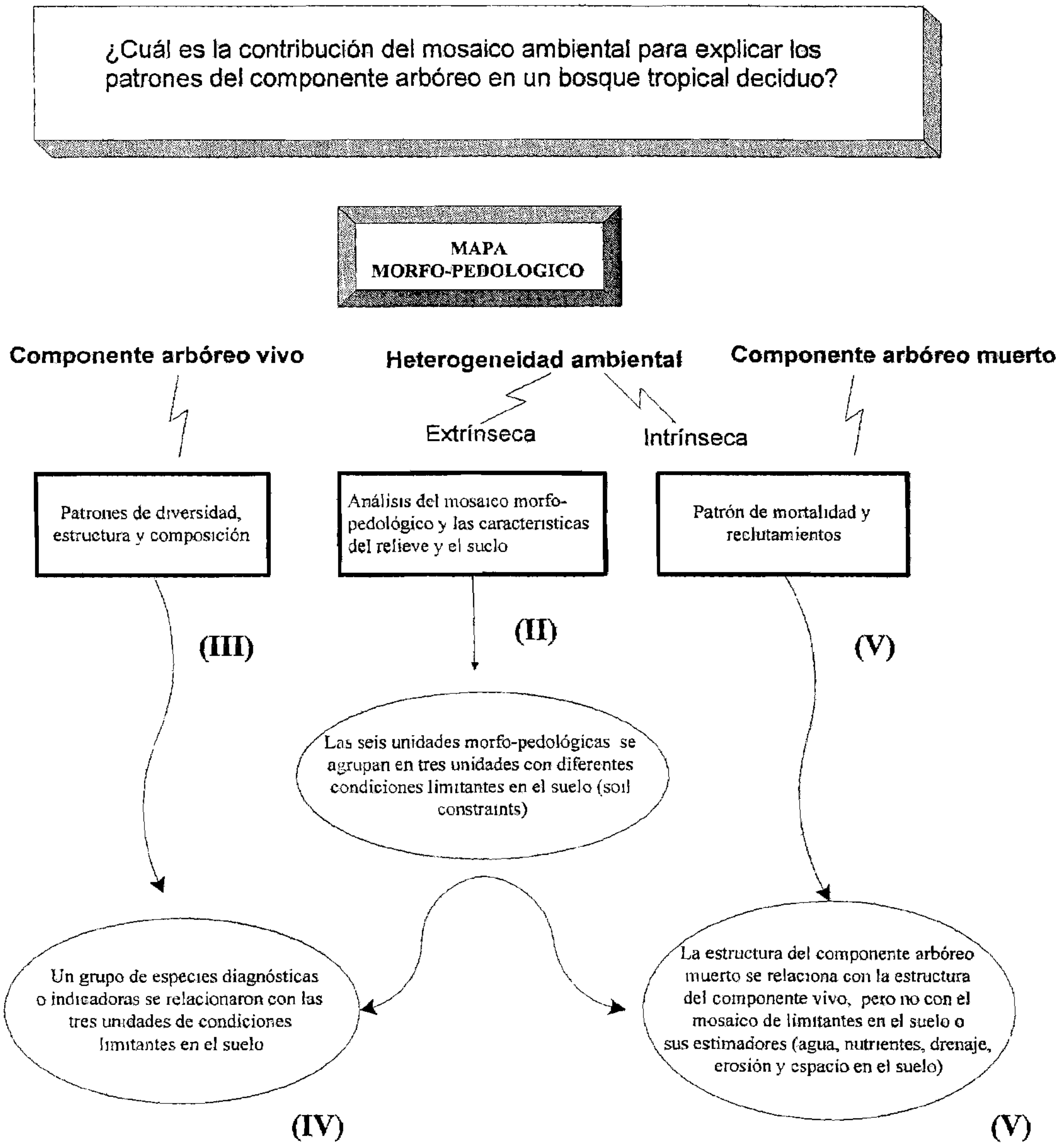

Figura I.4. Resumen gráfico de la estructura de la tesis, el contenido general de los diferentes capítulos y la relación que mantienen entre sí. Los números romanos indican el número de capítulo donde se analiza el tema indicado.

ESTRUCTURA DE LA TESIS

Los principales resultados de la tesis están contenidos en los cuatro capítulos siguientes (Fig. I.4). Debido que cada uno de esos capítulos responde a temas y preguntas relativamente independientes, los resultados fueron presentados en un formato convencional para su publicación y en idioma inglés. El Capítulo II analiza e integra las características del relieve y el suelo de las 14 unidades morfoedafológicas de la Estación de Chamela y, con base en ellas, define cuatro clases de limitantes en el suelo ("soil constraints"). Estas clases muestran dónde se encuentran los principales contrastes en condiciones y recursos limitantes en el suelo y los factores que los definen (relieve y suelo).

El Capítulo III describe y analiza la estructura y la organización de la diversidad de la comunidad arbórea del dosel, de acuerdo al diseño original de muestreo, basado en seis unidades morfo-pedológicas. El Capítulo IV, explora la relación de factores del relieve y el suelo con el patrón de organización del componente arbóreo del BTC, teniendo en cuenta la agrupación de sus correspondientes unidades morfo-pedológicas en tres clases de contraste en condiciones limitantes en el suelo; para ello, integró información de los dos capítulos anteriores. El Capítulo V consistió en la descripción y el análisis de la estructura de la necromasa arbórea y del patrón de mortalidad de los árboles del dosel. Así como de las implicaciones ecológicas de las diferentes condiciones de muerte de los árboles para la regeneración y en análisis del balance entre los reclutamientos y la mortalidad.

La discusión general de la tesis (Capítulo VI) resume las principales contribuciones del estudio, se plantean algunas dudas sobre el tema analizado que aún siguen latentes, y hace un análisis de las limitantes del trabajo. También enfatiza la importancia de este estudio como un generador de información y una experiencia que puede servir de base para otros trabajos de investigación, relacionados principalmente con la comunidad de plantas arbóreas y diferentes modelos de variación en el medio físico, en la región de Chamela o en ecosistemas afines. Adicionalmente, analiza brevemente algunas implicaciones de este estudio para la conservación y el manejo de especies de árboles de este tipo de bosque.

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CAPÍTULO II

SOIL CONSTRAINTS AND LAND CLASSIFICATION IN A TROPICAL DRY ECOSYSTEM AT CHAMELA, MEXICO

ABSTRACT

Soil and relief information was analyzed to define spatial differences in soil constraints at Chamela, Mexico. The information was taken from of 46 sampling sites, which were representative of 14 morpho-pedological land units. Based on relief and soil features, and through multivariate analyses, the sites were classified into groups. Qualitative and quantitative analyses of indicators concerning erodability, space for roots, water and nutrient availability showed a large heterogeneity in the soil conditions and resources. The integration of results through a land classification and soil indicators analysis helped us to distinguish areas belonging to four classes of soil constraints. The area with very few constraints was small and mostly concentrated on alluvial terraces and nearby piedmonts. However, differences from few to many soil constraints prevailed in the hills. Those spatial differences were represented on a soil constraints map. In places where very few soil constraints were noticed, a subdeciduous forest was developed, whereas a deciduous forest was presented elsewhere. We considered that a map on land classification and soil constraints might constitute a reference for ecological research and practical uses.

KEY WORDS: *Relief, soil, morpho-pedological land units, land classification.*

INTRODUCTION

The physical factors are critical for understanding ecosystem patterns and processes. Climate, relief and soil control productivity, distribution and diversity of plant communities to an important extent (Tilman 1982, Kozlowski *et al.* 1991). An understanding of heterogeneity in the relief and soils is important for recognition and analysis of plant community patterns in tropical forests (Huston 1980, van der Hammen 1984, Breimer *et al.* 1986, Kalliola *et al.* 1993, Clark *et al.* 1995, Duivenvoorden & Lips 1995, Villers-Ruíz *et al.* 2003). Small differences in water, drainage, nutrients, air and space for root development can be ecologically important because they underlie spatial contrasts in plant development (Carmean 1975, Tilman 1982, Grime 1994). So, these characteristics and others physical, chemical or biological properties have been proposed as indicators of the soil quality (Karlen *et al.* 1997, Etchevers 1999).

The soil quality is a basic integrative idea in soil science, and it refers to the potential of a given soil to support plant growth and the natural ecosystem function without inducing environmental degradation (Karlen et al. 1997, Etchevers 1999, Herrick 2000, Astier-Calderón et al. 2002). The use of soil quality concept is still keeping a wide discussion in soil science Karlen et al. 1997, Etchevers 1999, NRCS 2001). However, assessing the soil quality is not a goal in itself; the purpose is to understand, protect and improve long-term agricultural productivity, water quality, and habitats of all organisms including people (Doran & Jones 1996, NRCS 2001). The soil quality cannot be measured directly, so many soil characteristics are used as indicators to asses it. Indicators of soil quality can be assessed by qualitative or quantitative techniques. Here "soil constraints" term was used linked to the idea that spatial differences in soil quality simultaneously determine spatial differences in soil constraints for the plants.

To date, many studies in tropical deciduous forests (TDF) have been focused on the availability and variability of specific resources, such as water and nutrients (Ben-Shahar 1990, Campo 1995, Jaramillo & Sanford 1995, Oliveira-Filho *et al.* 1998, Salas 2002). Plant size and leaf phenology strongly reflect physical conditions that prevail in these ecosystems (Reich & Borchert 1984, Borchert 1994, Holbrook *et al.* 1995, Jaramillo & Stanford 1995, Eamus 1999, Bullock 2002). Even structure and composition differences at the landscape level have been related to lithology, relief and soils (Coughenour & Ellis 1993, Sampaio 1995, Villers-Ruíz *et al.* 2003). Although, climate, landforms, lithology and soils are highly variable (Trejo 1995), their implications for soil resources and physical conditions in different landscape locations have been poorly analyzed.

The ecosystem at Chamela is well known in many topics (Noguera *et al.* 2002). Here, the literature on a system of micro-basins has reported that relief consists of low and steep hills on granite and that soil depth is shallow, sandy-loams with poor structure and less than 5% of organic matter (Solís 1993, Galicia *et al.* 1999, Maass *et al.* 2002). However, outside this system, other different lithology, geomorphology and soil types have been recognized (Cotler *et al.* 2002). This study presents a survey on relief and soil features and soil constraints at the Chamela landscape. Soil constraints were represented in a spatially explicit model, which showed the prevailing environmental mosaic and provides a basis for understanding the biotic patterns.

METHODS

Sampling and soil characterization

A total of 46 sampling sites were examined (Appendix I). These sites were distributed in the space considering all 14 different morpho-pedological land units defined previously by Cotler *et al.* (2002) at the Chamela Biological Station were included. To select sites with representative soil profiles, we previously augered along transects on each land unit following the different land forms. At each sampling site we dug a pit to expose the soil profile. One sampling site was enough to describe homogeneous units, but we chose up to six to describe heterogeneous units. The altitude, slope gradient and orientation were recorded at each site.

The profiles were systematically described in the field, according to Siebe *et al.* (1996). For each soil horizon we recorded thickness, stoniness, color, structure, bulk density, aggregate stability and root density. Chemical and physical analyses were performed on air-dried and sieved soil (< 2 mm). Texture was determined by the Bouyoucos method (van Reeuwijk 1992). The organic matter was determined by wet oxidation with K_2CrO_7 and colorimetric determination of the reduced ions of Cr^{3+} (Schlichting *et al.* 1995). Total nitrogen was extracted by H_2SO_4 digestion and determined by the Kjeldahl method (van Reeuwijk 1992); ammonium in the extracts was determined colorimetrically. The total phosphorus was extracted by acid digestion and determined colorimetrically (Schlichting *et al.*

1995), and available phosphorus was extracted with the Bray I method (van Reeuwijk 1992). Cation-exchange capacity was determined by extraction with ammonium acetate at pH 7 (van Reeuwijk 1992).

Physiological soil depth, where roots have the potential to penetrate and develop, was estimated based on horizon type and stoniness (Siebe *et al.* 1996). The amount of clay, organic matter, total nitrogen, total and available phosphorus and exchangeable bases (Ca^{++}, Mg^{++}, K^{+} Na^{+}) were estimates from all horizons until the physiological soil depth of each profile and corrected by bulk densities. So, each variable was a "weighted average" at the physiological depth and expressed in units of mass per m^2 of soil.

Other soil features that could indicate key conditions and important resources for vegetation were also evaluated (Breimer et al. 1986, Siebe et al. 1996, Karlen et al. 1997, Etchevers 1999). These features included erodability, drainage, potential space for root development, available water holding capacity (AWC), water content at field capacity (FC) and nutrient supply. Soil erodability was evaluated in surface horizons by the factor "K" in the universal soil loss equation (Wischmeier et al. 1971, adapted by Siebe et al. 1996). The drainage classes were assigned in each site as described in the "Soil Survey Manual" (USDA 1993). Available water holding capacity (AWC) and water content at field capacity (FC) were determined from reference tables, based on texture, organic matter content and bulk density (Krahmer et al. 1995, Siebe et al. 1996). Both of them were calculated as sums of each horizon to one meter or until Cw horizon.

Data analyses

The data were arranged in a matrix of 46 rows (sampling sites) and 17 columns with relief and soil variables (altitude, slope gradient, orientation, physiological depth, solum depth, stoniness, clay content, AWC, FC, organic matter, total nitrogen, total and available phosphorus, exchangeable base bases [Ca^{++}, Mg^{++}, K^{+} and Na^{+}]).

In order to classify the sites, relief and soil variables were standardized to mean = 0 and variance = 1. The dendrogram was created by the average linkage method by using Euclidian distance (Jongman *et al.* 1995). The same matrix was used to perform a principal component analysis (PCA) to arrange the plots.

The assessment of soil constraints classes was a qualitative analysis of some soil quality indicators and consisted of relative comparisons and its graphical presentation by the "amoeba-approach" (Brink Ten *et al.* 1991, Astier *et al.* unpublished). Each indicator of key conditions and resources for the plants (erosion, drainage, stoniness, space for roots, water and nutrients) was represented in the "amoeba graphic" as a mean value of groups of sampling sites obtained by classification. The prior land unit classification and the present assessment of soil constraints were integrated to depict the current relief-soil mosaic at Chamela. This mosaic was represented spatially in a map by reclassifying morpho-pedological land units according to soil constraint classes, through the use of a Geographical Information System (Arcview 3.2). To provide a better visualization of major relief-soil pattern, a digital elevation model was constructed from contour lines at 10-m intervals.

RESULTS

Relief and soil features

The most important differences identified regarding relief and soil properties at Chamela were related to three elevational belts, and their corresponding major landforms (high, intermediate and low hills, and valleys). The lower belt (< 100 m) included sites on antique and recent alluvial terraces (AT and RT land units) and piedmonts (P unit), where the slope gradient was less than two degrees. The second belt (ranging from 100-200 m) grouped sites on low and intermediate hills (slopes on tuffs [ST], summit areas on tuffs [SAT], summit areas on granite [SAG], summit areas with conglomerates on granite [SACG], summit areas with conglomerates on tuffs [SACT] and uneven slopes on granite [USG] land units), characterized by slopes with various gradients and summit areas with varied lithology and soils. The third belt comprised sites above 200 m, on the high hill ("Cerro Maderas") with long slopes (low, intermediate and high rectilinear slopes on granite units [LSG, ISG and HSG]) and associated depressions (DSG unit), as well as short slopes on granite (SSG unit).

Land unit classification

Three main groups from the dendrogram were identified around 90 in Euclidian distance (Fig. II.1). The main group I (after named as A), included six sites on terraces (antique alluvial terraces [AT] and recent alluvial terraces [RT]), piedmonts (P), summit areas on tuffs (SAT) and uneven slopes on granite (USG). At a lower level of Euclidian distance (53), within main group II, three additional groups could be further recognized (B, C and D). Group B included 11 sites belonging to smooth-slope units in the high hill (low and intermediate rectilinear slopes [LSG and ISG]), and their depressions (DSG). Group C comprised 16 sites in the intermediate belt, which were on slopes and summits on erosion-planation surfaces (summit areas on tuffs [ST], uneven slopes on granite [USG], summit areas with conglomerates on granite [SACG], summit areas with conglomerates on tuffs [SACT] and summit areas on granite [SAG]). The smallest and most heterogeneous group was D, which included only four sites from the intermediate belt, representing three morpho-pedological land units (summit areas on granite [SAG], summit areas with conglomerates on granite [SACG] and uneven slopes on granite [USG]). The main group III (or E) had the largest linkage distance in the dendrogram and grouped eight sites within the high altitude belt, on steep slopes on granite (high and short slopes on granite [HSG and SSG]).

The ordination of the sampling sites along two main axes generated through principal component analysis (PCA; Fig. II.2) showed an overall good approximation with the main groups in the dendrogram (Fig II.1). The sites belonging to the main group II were located in the centre of the ordination axes. The sites of the group B were distinguished from sites grouped as C and D, but these were intermixed. The first three principal components explained 65% of total variance, of which 35.2% corresponded to the first component (Table II.1). The largest factors loading on the first component were physiological depth, AWC, total nitrogen and exchangeable bases, while slope and altitude were the most strongly correlated factors with the second component, and stoniness with the third component.

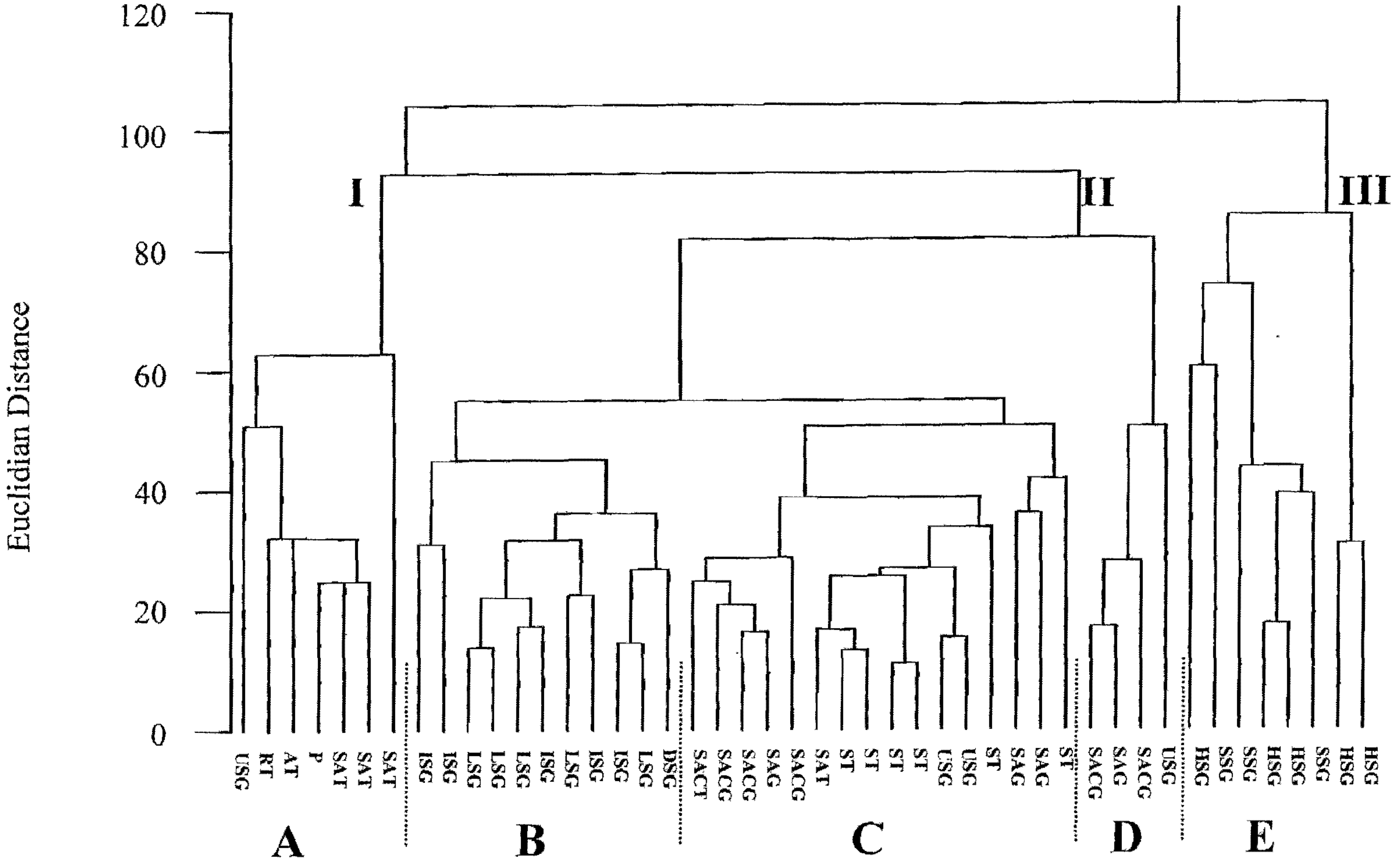


Figure II.1. Dendrogram obtained from the classification of 46 sampling sites at Chamela.

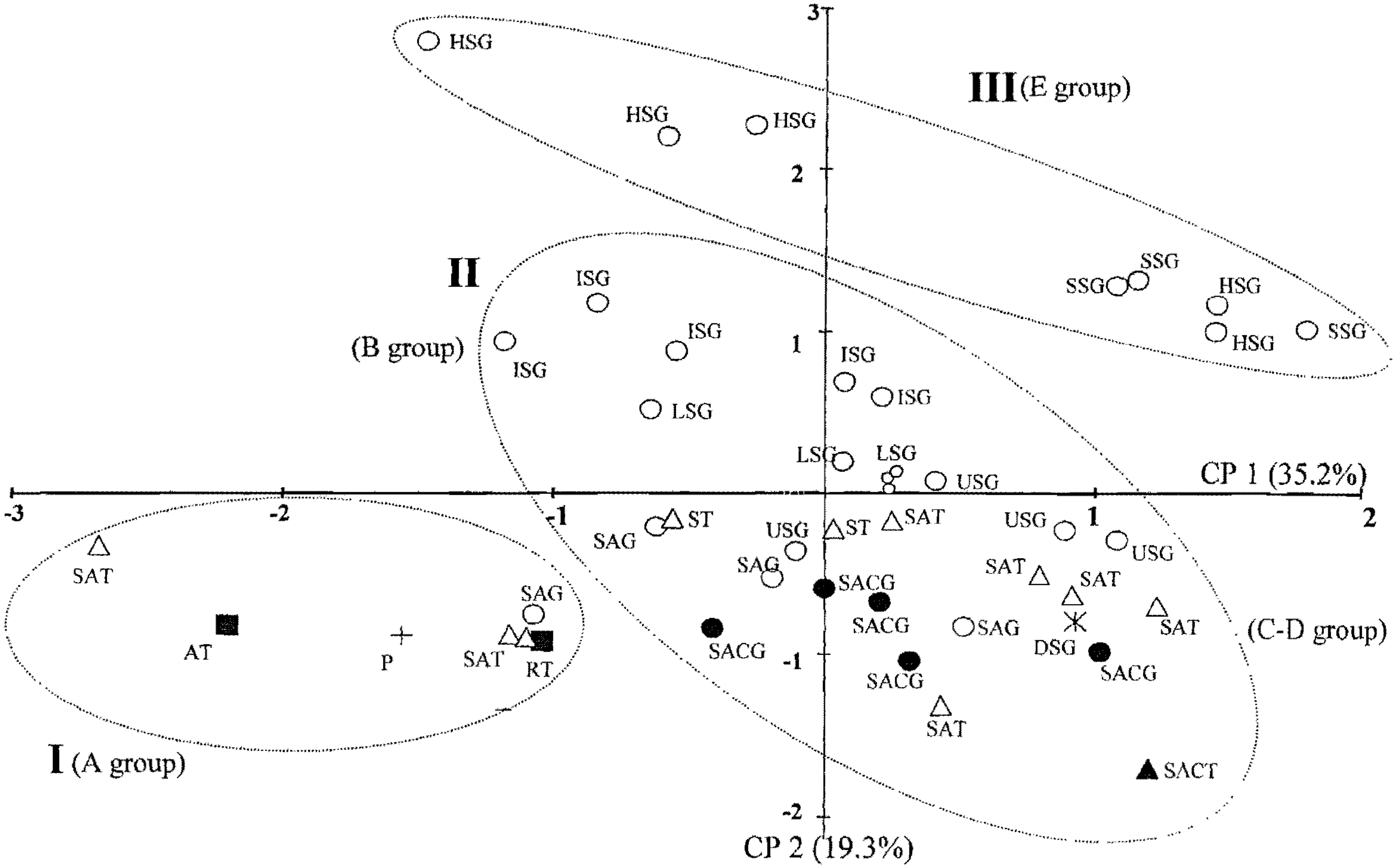


Figure II.2. PCA ordination of the 46 sampling sites on the two leading principal axes based on 18 relief and soil variables. These two axes explained 54.5% of the variance. Sites belonging to each morpho-pedological land unit are identified in the ordination space by the different symbols, while polygons delimit the three main branches of the dendrogram (I, II and III).

Table II.1. Summary table of the PCA based on 46 sampling sites.

Principal Component	Eigenvalue	Explained Variance (%)	Cumulative Percentage	Factors loading
I	7.75	35.2	35.2	Depth soil Field water capacity Total nitrogen Exchangeable bases
II	4.24	19.3	54.6	Slope Elevation
II	2.07	9.4	63.9	Stoniness

Soil constraints assessment

The soil and relief characteristics showed that different morpho-pedological unit groups share some trends in their indicators of conditions and resources (Table II.2, Figs. II.1 and 2). Across all groups the soils presented a small erodability factor, good drainage, good root penetration and large organic matter content, mainly in the surface horizon. However, important differences among groups were also distinguished. The most evident contrast in soil constraints was detected in the group A.

Except for the land unit in depression (DSG), sampling sites in B group were less heterogeneous in the soil constraints indicators analyzed and their physiological depth, AWC and FC were larger than those in groups C, D and E. The soil in sites of the group E ranged from deep moderate to deep, and AWC, FC and total phosphorus tended to be larger than at sites with a shallow soil. Therefore, this was one of the most heterogeneous groups considering soil depth, AWC, FC, organic matter content, total and available phosphorus and exchangeable bases. In the field, sites within this group showed litter and soil transport and accumulation only at low portions of steepest slopes, but usually the estimation of erodability was small.

The sites belonging to groups C and D were more heterogeneous in terms of lithology (granite, tuff and conglomerates) and landform (summits and slopes). These sites had a variable nutrient supply; although in general sites in summit areas with conglomerates (SACG and SACT had the smallest content of clay, organic matter, total nitrogen, total and available phosphorus, and exchangeable bases. In addition, soils at these sites are shallow, stoniness and have very little available water (AWC and FC); these characteristics, along with the nearby plots location on ordination space carry us to consider them as a single group (C-D).

Due to the soil heterogeneity of the groups, a hierarchical trend of constraints among them was observed (Fig. II.3). The extremes correspond to A sites (very few constraints), and C-D sites (with the largest number of soil constraints factors, for example: soil depth, AWC and FC), while the group E was intermediate. Thus, the relative hierarchy by four soil constraints classes was designated to distinguish the principal differences on landscape: Class 1, with very few soil constraints typified to group A. Class 2, with few soil constraints was used for group B. Class 3, with some soil constraints, for group E, and Class 4, with many constraints, marked to the group C-D (Table II.3).

The map of soil constraints land units shows a physical mosaic within the Chamela Biological Station (Fig. II.4); where favourable conditions are depicted by very few soil constraints, which were restricted in the space, among a particularly complex mosaic of more constraints (few, some and many soil constraints classes).

DISCUSSION

The quantitative analyses through landscapes continue being a challenge for tropical forest studies (Sollins 1998) and the soil quality and constraints assessment has rarely been exhibited as a basis to suppose spatial differences on the tropical vegetation. This study integrated the relations between landforms and soils, on quantitative and qualitative bases, at the Chamela

Table II.2. Qualitative and quantitative criteria to assess classes of soil constraints. The assessment included several indicators of conditions and resources important to plant development, which represent the prevailing condition in each group's plots and refer to the criteria by Siebe *et al.* (1996)[a] and Pagel *et al.* (1982)[b], the latter specifically referring to tropical soils. * Extreme data compared to the group's remaining sites; >h indicates a high heterogeneity.

Condition/ Resource	Indicator	Group A	Group B	Group C	Group D	Group E
Erosion	Erodability[a] (K Factor)	Very low-low	Very low-low	Very low	Low	Very low-low
	Slope[a]	Almost flat-slightly inclined	Almost flat – slightly inclined	Almost flat – slightly inclined	Almost flat – slightly inclined	Pronounced, steep slopes
	Drainage[a]	Good-Very Good	Good (* Scarce)	Good	Good	Good
Space for root development	Physiological depth[a] (cm)	Moderate-Deep 65.8 ± 23.3	Moderate 57.2 ± 16.5 (*18)	Shallow (h) 31.0 ± 20.8	Moderate 48.0 ± 11.5	Shallow (>h) 36.9 ± 30.1
	Root penetration[a]	Very good	Moderate-Very good	Very good	Very good	Very good
	Stoniness[a] (L/m^2)	73.0 ± 9.4	114 ± 63 (190)	206 ± 135	339 ± 154	175 ± 161
Water in soil	aWC[a] (L/m^2)	Moderate 92 ± 24	Low 71 ± 15 (35)	Very low 41 ± 21	Very low-(low) 49 ± 7	Low (>h) 54 ± 39
	FC[a] (L/m^2)	Moderate (>h) 270 ± 70	Low 209 ± 43 (97)	Very low 110 ± 51	Low 145 ± 10	Low (>h) 158 ± 123
Nutrients	Organic matter[a] (Kg/m^2)	High- Very High 11.8 ± 4.8	High 11.1 ± 3.0 (5.1)	Medium-High 9.4 ± 5.3	Medium High-High 8.1 ± 1.8	Medium High-Very High (>h) 11.7 ± 10.2
	Total nitrogen[a] (kg/m^2)	0.9 ± 0.4	0.6 ± 0.2 (0.2)	0.5 ± 0.2	0.5 ± 0.1	0.6 ± 0.4
	Total phosphorus[b] (g/m^2)	Moderate (326.7 ± 99)	Scarce (73.0 ± 32.2)	Scarce (68.1 ± 47.2)	Scarce (159.2 ± 220.5; > h)	Scarce (62.8 ± 50.7)
	Available phosphorus (g/m^2)	3.4 ± 3.7	1.1 ± 0.3 (0.13)	1.9 ± 1.6	1.7 ± 1.4	0.6 ± 0.6
	Exchangeable bases[b] (cq/m^2)	Moderate-High 87.2 ± 30.3	Moderate 37.1 ± 26.9 (8.2)	Moderate 34.8 ± 24.3	Moderate 37.0 ± 16.0	Moderate-(Regular) 30.2 ± 18.6

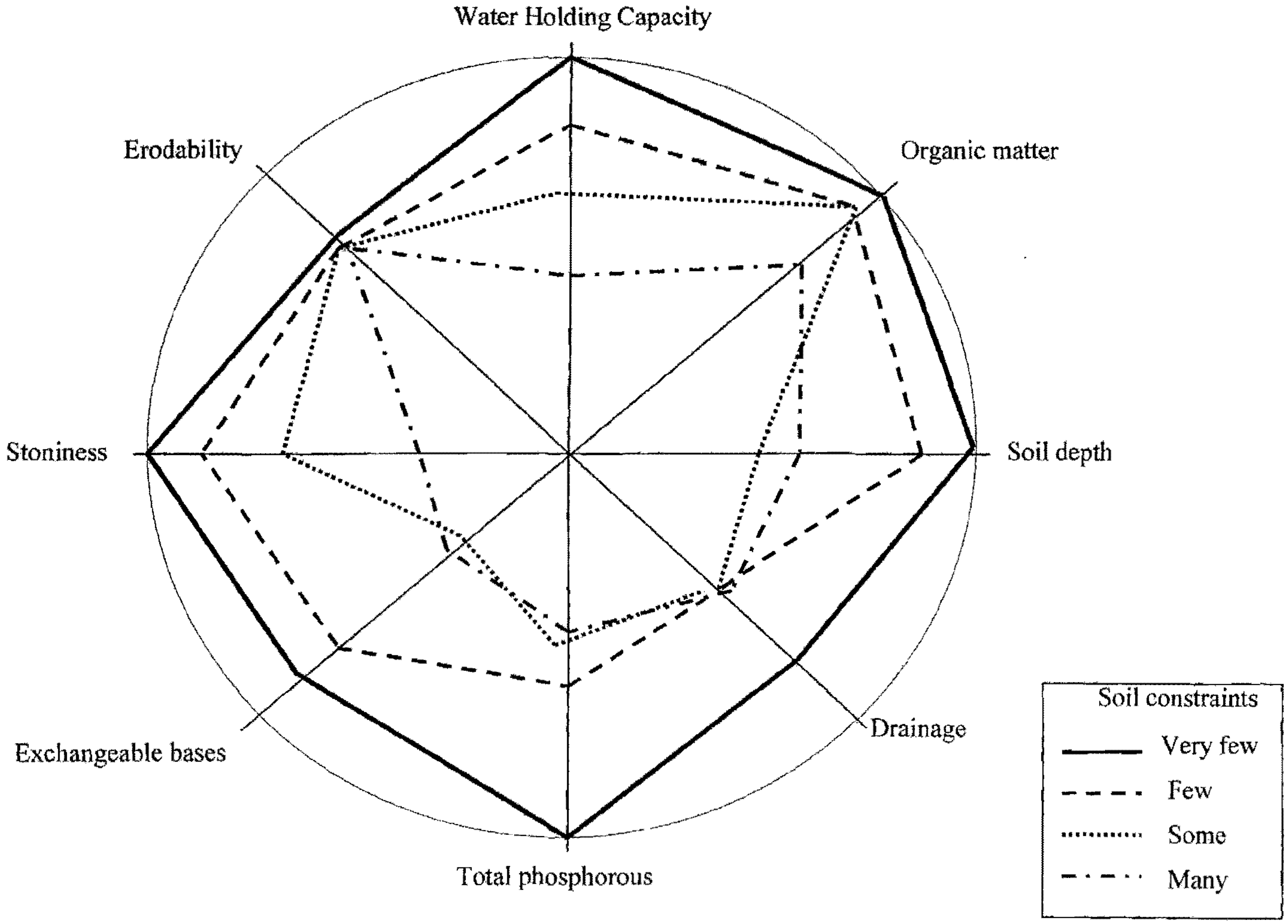
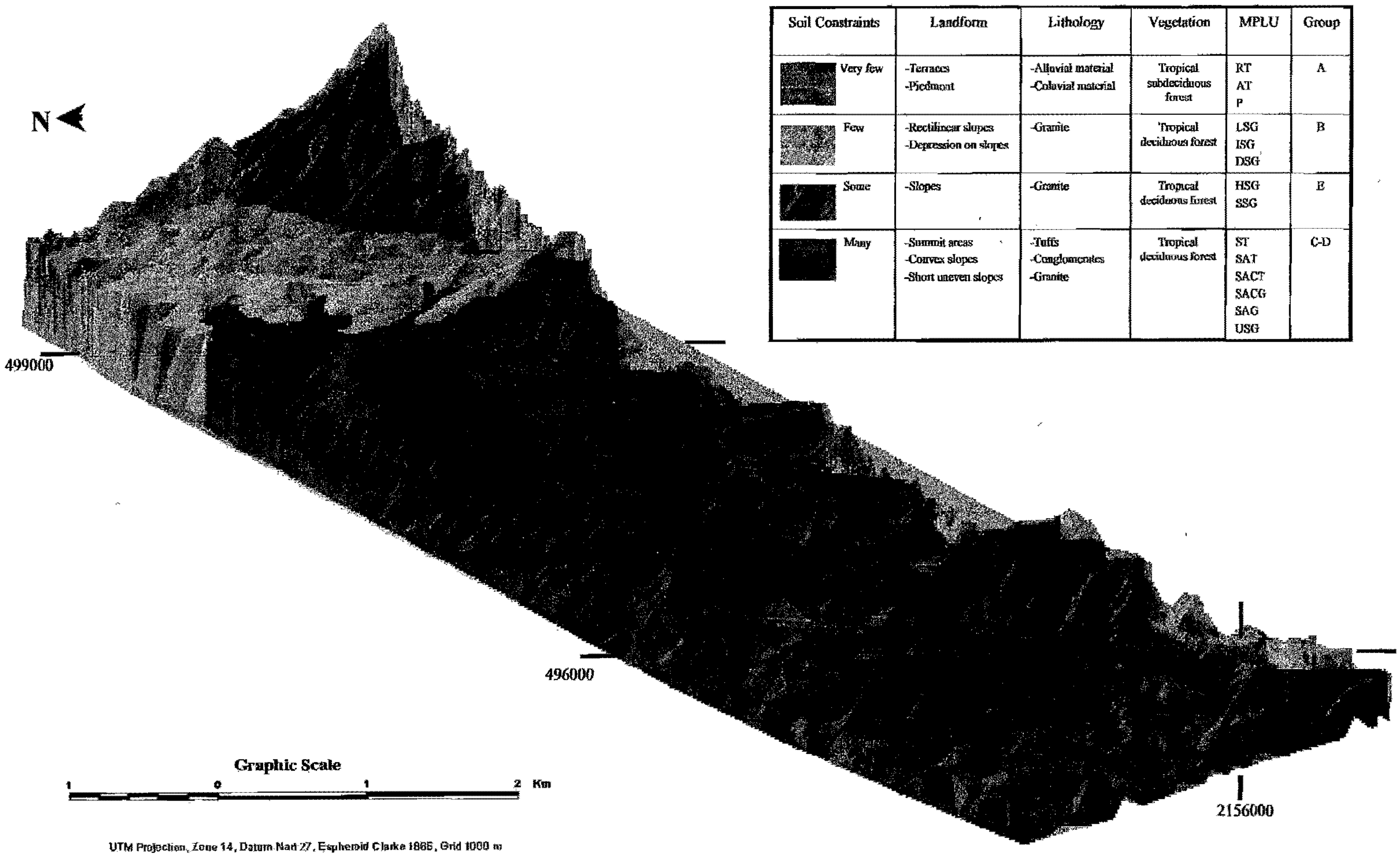


Figure II.3. Integral qualitative assessment of soil constraints classes. Each different geometric figure (like an "amoeba") represents a specific soil constraint class. The continuous bold line refers to group of sites with very few soil constrains and the broken lines represent the relative position in soil constraints of other groups. The values of "amoeba" axes were rough, but were related with mean values for each group of sampling sites; except for stoniness, external values in each indicator were larger and refer to less soil constraints.

Table II.3. Relationship among the main landforms, morpho-pedological land units, groups defined by their soil and relief features through exploratory statistical analyses and their respective assessment by soil constraints classes. The four classes of soil constraints have a relative hierarchy: class 1 having the least soil constraints and class 4 having the most.

Landforms	Morpho-Pedological Land Units	Altitudinal Belts	Classification Analysis	Principal Component Analysis	Soil Constraints Assessment (Classes)
Valley	AT RT	< 100 m	A	I	1. Very few
Intermediate Hills	P SACG USG	100-200 m	C	II	4. Many
	SAG SACG USG		D		
Lower Hills	ST SAT SACT		C		
High Hills	LSG DLG ISG	> 200 m	B		2. Few
	HSG SSG		E	III	3. Some



Soil Constraints	Landform	Lithology	Vegetation	MPLU	Group
▓ Very few	-Terraces -Piedmont	-Alluvial material -Coluvial material	Tropical subdeciduous forest	RT AT P	A
▒ Few	-Rectilinear slopes -Depression on slopes	-Granite	Tropical deciduous forest	LSG ISG DSG	B
▓ Some	-Slopes	-Granite	Tropical deciduous forest	HSG SSG	E
■ Many	-Summit areas -Convex slopes -Short uneven slopes	-Tuffs -Conglomerates -Granite	Tropical deciduous forest	ST SAT SACT SACG SAG USG	C-D

Figure II.4. Three dimensional soil constraints map of the Biological Station of Chamela. MPLU= morpho-pedological land units, abbreviations are those used throughout the text. Vertical exaggeration factor is 3, and the grey colour in borders should not be considered, as it is due to a normal technical deformation.

landscape, and we could show where the most important variations in relief, soil characteristics and soil constraints were located. The relationship between that environmental variations and the tree community patterns (structure and species distribution) go to be showed in two subsequent chapters.

The original morpho-pedological map (Cotler *et al.* 2002) summarizes some of the most important relief and soil variations. However, the map failed to depict significant patterns among the 14 units regarding soil constraints indicators. Our analysis shows that, only four classes (shown as groups of land units in Fig. II.3) were distinguishable based on the relief and soil quality indicators. The elevation, slope steepness, soil depth, available water holding capacity, total phosphorus and exchangeable bases were depicted as those features that best organize the variation among 46 sites as well as among soil constraints land units.

The assessment of soil constraints indicators allowed us to distinguish a rank from very few to many soil constraints classes. This is especially relevant since soil features such as supply and availability of water and nutrients are crucial in a tropical deciduous forest (Wright 1992, Borchert 1994, Jaramillo & Sanford 1995, Sampaio 1995, Eamus 1999, Maass *et al.* 2002). At Chamela, it is already known that areas with few soil constraints maintain a subdeciduous forest (group A), while on the other three classes of soil constraints (2-4) support a deciduous forest (Lott *et al.* 1987, Durán *et al.* 2002).

In group A (class with very few soil constraints), alluvial terraces and piedmonts are the most distinctive land units (TA, TR and P), with respect to its vegetation (subdeciduous forest). Trees with a near-perennial phenology, and the greatest height and stem diameters characterize this forest type. Among the species best depicting that vegetation are *Thouinidium decandrum* Humb. & Bompl., *Trichillia trifolia* L. subsp. *palmeri* (C. DC.) Pennington, and *Capparis verrucosa* Jacq. (Lott *et al.* 1987). So, phenology and species composition suggested that relief and soil conditions could supply to physiological demands of vegetation and species restricted to these areas (Eamus 1999). However, there were sampling sites belonging to group A on ridges, with good nutrient status and soils with moderate to high deep, which were covered by a deciduous forest, like the other remaining groups of land units. The vegetation differences in group A might be attributed to sites on ridges having neither concentrated runoff and nor receive additional water supply through morning fog, as occurs in alluvial terraces and it nearest piedmonts (Tricart & KiewietdeJonge 1992, Maass *et al.* 2002). In addition, they could be receiving more radiation due to crest location (Galicia *et al.* 1999).

Soil constraints, even when promoting small spatial variations in key resources, may be ecologically important within a specific kind of vegetation, through its influence on spatial differences in vegetation development, its dynamics and, eventually, affecting biodiversity and some ecosystem processes (Carmean 1975, Tilman 1982, Ben-Shahar 1990, Coughenour & Ellis 1993, Brown *et al.* 1994, Oliveira-Filho *et al.* 1998, Etchevers 1999, Galicia *et al.* 1999, Vose & Maass 1999). The analyses of the soil constraints mosaic and its potential implications on vegetation are, therefore, needed to understand the features that influence ecological patterns and processes at the landscape level, which in turn represent a basis for understanding and planning natural resources management and its conservation (Breimer *et al.* 1986, Geissert & Rossignol 1987, Tricart & KiewietdeJonge 1992, Oliveira-Filho *et al.* 1998, Herrick 2000).

The map of soil constraints at Chamela may be a useful tool that depicts spatial projections of an environmental mosaic (Fig. II.4). The four major soil constraints land units identified here summarize environmental differences in the landscape.

The present report defines that relief and soil at Chamela, providing a different assessment of soil resources which can later be related to vegetation and floristic patterns (Chapter IV). Together with natural vegetation patterns, it will be useful for ecological research studies for decision-making in management (Breimer *et al.* 1986, Brown *et al.* 1994, Agbenin & Tiessen 1995, van der Zee & Zonneveld 2001). Thus, soil constraints indicators will be used to monitor long-term changes in the natural vegetation cover and to evaluate different management strategies, such as the silvo-pastoral system practiced in the surrounding areas to the Chamela Biological Station (Maass *et al.* 1988, Astier *et al.* 2002). Also, the soil constraints map may be regarded as a reference to improve sustainability practices for productive systems or other uses alternatives, through identifying geomorphological land units (landforms-lithology) and their soils properties related to infiltration, water availability, erodability and nutrients. Besides, the soil constraints mosaic should be useful to model hydrological responses to climatic change (Vose & Maass 1999), rather than to assume that soil depth or water holding capacity are homogeneous; because the hydrological dynamic in a system will be modified by soil moisture storage capacity and its drainage. Therefore, we will know different hydrological responses to climatic change in the complex territory and to model their spatial location.

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CAPÍTULO III

TREE STRUCTURE AND DIVERSITY PATTERNS IN A TROPICAL DECIDUOUS LANDSCAPE AT CHAMELA, MEXICO

ABSTRACT

Structure and tree species diversity were described and analysed in a tropical deciduous forest at Chamela, Mexico. Twenty one 0.24-ha plots (totalling 5.04 ha) were studied and trees with DBH $\geq$ 5 cm were sampled. The plots were distributed among six morpho-pedological land units. Average tree density was 1,386 individuals per ha^{-1}, basal area was equal to 15.9 m^2 ha^{-1}, average height was 6.8 m and total richness was 148 species, 102 genera and 43 families. Many variations were found close to overall or average estimates of the tree component among plots and six land units. The species composition was diverse and low similarity index values were obtained between all pairs of plots (< 0.2). Dominance was shared by a relatively small group of species, among which *Caesalpinia eriostachys* Benth. had the largest importance value (12.8%); however, not even this species was present in all six land units, indicating a strong spatial segregation. In contrast, most species were classified as rare due to their limited distributions among plots and morpho-pedological units as well as their low abundance. According to the principal component analyses structure and diversity were not related to their corresponding morpho-pedological land unit; nevertheless, the ordination of plots based on dominant species showed two groups related to different lithology (granite and non-granite). The approach used in this study allowed us to identify dominance/rarity patterns in the forest canopy on the landscape at Chamela.

KEY WORDS: *Species composition, dominance, rarity, land units, structural heterogeneity.*

INTRODUCTION

Studies on structure and tree diversity in tropical forests are very common. The majority of them refer to local scale and mostly centred upon tropical humid forests. Also, many of these studies lack an integration of the morpho-pedological mosaic to describe and analyze the structural, compositional and diversity patterns. Without a reference on the environmental complexity at the landscape, however, it is difficult to locate vegetation plots and give a spatial perspective for results obtained (Campbell 1994, Chazdon 1996, Ricklefs 2000).

Despite the apparent homogeneous physiognomy of tropical forest (Rzedowski 1986, Menaut *et al.* 1995), the canopies constitute a complex arrangement of tree species (Condit 1996). Traditionally, botanists and phytogeographers have documented the existence of heterogeneous canopies in tropical forests (Van der Hammen & Ruiz 1984, Gentry 1988, Gentry & Ortiz 1993, Duivenvoorden & Lips 1995, Richards 1996). Vegetation studies of the tropical deciduous forest (TDF) usually focus upon moisture gradients (Coughenour & Ellis 1993, Trejo 1998, Villers-Ruíz *et al.* 2003), but geomorphological heterogeneity has also been recognized as important through ecological studies where a landscape approach was used (Van Devender *et al.* 2000, Pérez-García 2002). This approach could help to describe structure, species composition and diversity patterns on landscapes. It also may suggest places where spatial variations in the forest canopy or habitat preferences for species could be found. This kind of information may also provide criteria for exploring ecological processes, bases for diversity conservation action and an adequate management of particular species (Hubbell & Foster 1992, Campbell 1994).

The purpose of this study was to describe and analyze tree component patterns of a TDF at Chamela, Jalisco, Mexico. We posed two questions: Is tree diversity organised according to the mosaic of different morpho-pedological land units?, How does the distribution, abundance, dominance and rarity of species vary across the landscape?

METHODS

Tree community characterization

The tree canopy component was measured in 21 plots of 0.24 ha (30 X 80 m). The plots were distributed among six morpho-pedological land units: 1) SAG: Summit areas over granite (n=3), 2) SAT: Summit areas over tuffs (n=4), 3) SACG: Summit areas with conglomerate cover on granite (n=3), 4) LSG: Low rectilinear slopes over granite (n=4), 5) ISG: Intermediate rectilinear slopes over granite (n=4), and 6) HSG: High rectilinear slopes over granite (n=3). These morpho-pedological land units were chosen among a total of 14 land units defined on the Chamela Station (Cotler *et al.* 2002), based on a vegetation cover of TDF and a different combination of lithology, relief and soil types (see Chapter II).

Previous studies at Chamela were based on diameter at breast high (DBH) ≥ 3 cm, without a distinction among trees, shrubs and sapling individuals (Lott *et al.* 1987, Gentry 1988, Martínez-Yrízar *et al.* 1992). However, this study was only concerned with describe the canopy trees (DBH ≥ 5 cm). The diametric criterion adopted was a result of a preliminary analysis in small plots (10 X 10 m). It consisted of comparing the vertical location of canopy for each individual tree and its DBH at 1.3 m of high. Results suggested a high probability that individuals with DBH ≥ 5 cm belong to canopy strata. In plots, all trees were counted and for multi-stem trees each one of its individual trunks was numbered. For each trunk the DBH was measured. Density referred exclusively to individual trees, while for distribution analysis of diameters all individual trunks were taken into account. The taxonomic identity of each tree was determined to species level. Reliability of taxonomic determination was achieved by carefully comparing the collected specimens among themselves and with vouchers deposited at the Chamela Station herbarium. Canopy height was measured with an optical range finder (Ranging Inc. model 620), along two 80 m parallel transects in each plot, recording on two transects 82 point readings at 2 m intervals.

Data analyses

To explore if structure parameters were different among land units, Kruskal-Wallis comparisons (Zar 1984) were used to test for density, basal area, multi-stem individuals, and number of families, genera and species. When the null hypothesis was rejected, Tukey test was performed to recognize significant differences between pairs of land units.

In order to assess the completeness of landscape tree diversity representation, cumulative species-area curves were elaborated through a non-parametric model, Chao 1 (Colwell 2000) which is an estimator of species richness based on abundance data (Moreno 2001). In all cases, cumulative frequency was the mean value of 50 iterations with three or four increments for each morpho-pedological land unit and 21 for the entire study. Statistical differences between observed and estimated richness species data were analyzed by chi-square test (Siegel & Castellan 1995).

To describe relative species dominance within the tree community, rank abundance diagrams were constructed. The resultant curves were based upon the proportional abundance of species in a plot on a log scale against rank from most to least abundant (Magurran 1990). A fitting of tendency line was described by the "Abundance Curve Calculator" program (Danoff-Burg 2003). Diversity was described as species richness by Shannon (base e) and Simpson indices (Magurran 1990). Diversity index were compared among land units by a Kruskal-Wallis test. A comparison between plots on granite and non-granite materials (tuffs and conglomerates) was made with a Mann-Withney test (Zar 1984), our null hypothesis was that diversity is analogous among land units and parental materials, respectively.

β diversity was assessed between pairs of plots using the quantitative versions of Sørensen (CN) and Morisita-Horn (C_{MH}) similarity indices, considering species abundance according to the following formulae (Magurran 1990):

$$CN = \frac{2\,jN}{(aN + bN)}$$

Where jN = sum of the lowest abundance values of the species shared between two plots, aN = total number of individuals in plot A, and bN = total number of individuals in plot B.

$$C_{MH} = \frac{2\,\Sigma(an_i\ bn_i)}{(da + db)\ aN * bN}$$

Where an_i and bn_i = number of individuals of the i-th species in sites A and B; aN and bN = total number of individuals in sites A and B, respectively; $da = an_i^2 / aN^2$; $db = bn_i^2 / bN^2$.

Differences in shared species between pair plots with very low (0.25), low > 0.25–0.50), moderate (> 0.50–0.75) and high (> 0.75) similarities were compared with a Kruskal-Wallis test.

Species, genera and family dominance were determined by plot, by morpho-pedological land unit and for all plots as percent "Importance Value" (Kent & Coker 1992):

$$\%\ \text{Importance Value (Dominance)} = \frac{\text{relative density (\%)} + \text{relative basal area (\%)}}{2}$$

Species were classified into eight rarity categories analogous to those described by Rabinowitz (19819) and Rabinowitz *et al.* (1988), by adapting the criteria for habitat specificity, geographical range and population size to the Chamela Station area. Species which were encountered in ≤ 3 morpho-pedological land units were specific to habitat or narrow, whereas those species occurring in ≥ 4 land units were tabulated as widely habitat or generalist. The "geographical range" criterion was replaced by one of spatial distribution, based on the number of plots occupied by a given entity; species were considered to have a restricted distribution when they were present in ≤ 4, or ≤ 12 plots, depending on whether they had been classified as having narrow or wide habitat. The population size was defined in terms of the midpoint in tree abundance for all species (range = 0.2 - 85 trees ha^{-1}), being half-way between the highest and lowest values in the set of data. Thus, a population was considered to be small-sized if its abundance was 43 trees ha^{-1}. Accordingly, cell I included to the most common species at Chamela (i.e., non rare) and species in cell V only tended to be common, whereas species in cell VIII represents cases of extreme rarity (Table III.1) and species in cell VII just tended to be rare. Species which could occur in other cells gave us non-clear tendency about common or rare condition.

The plots were ordered according to differences in structure and dominant tree species, by Principal Component Analysis (PCA; Jongman *et al.* 1995). For PCAs, three matrices of variables were used: (a) a matrix with 15 structural variables per plot (number of trees and of stems, mean DBH and its standard deviation, total basal area, mean height and its standard deviation, number of multi-stemmed trees and its proportion, summed dominance of the five most important species in the entire sample, Shannon and Simpson indices, species, genera, and family richness); (b) a matrix of structural variables along with the abundances of ten dominant species per plot (63 species); (c) a matrix of the abundances of ten most dominant species.

RESULTS

Structure and diversity

In 21 plots, a total of 6,984 trees with DBH ≥ 5 cm was recorded, which is equivalent to a density of 1,386 trees ha^{-1}. Basal area was 15.9 m^2 ha^{-1} and a total of 79.94 m^2 for all plots. The structural attributes of tree canopy in a TDF at Chamela were heterogeneous (Fig. III.1). Plots with lowest and highest density had 804 and 2,117 individual trees ha^{-1}, respectively. Plots on summit areas on granite (SAG) showed the highest tree density; nevertheless, its basal area was less than other land units with less tree density such as summit areas (SAT and SACG) and slopes (LSG). However, according to the Kruskal-Wallis tests abundance among the six land units (or between land units grouped by granite and no-granite), showed non-significant differences ($p<0.05$). Basal area in intermediate slopes (ISG) was significantly different from that of high slopes (HSG; $Q=1.688$, $p<0.05$) and of summit areas on conglomerates (SACG, $Q=1.76$, $p<0.05$), but was similar to other land units. Basal area differences in intermediate slopes (ISG) could be related to its greater percentage in multi-stem individuals or a higher frequency in two diameter categories (15 – 24 cm and 25 - 34 cm).

The Kruskal-Wallis test showed that multi-stemmed trees percentage was not different among six land units, but according a Mann-Withney test it was significantly different between land units on granite and non-granite ($U=94$, $p<0.05$). In plots on granite the average of multi-stemmed trees was 12.5%, but in plots on tuffs (SAT) and conglomerates (SACG) this trait occurred in about 22% of tree individuals. Although canopy height reached

Table III.1. Criteria followed to classify species by rarity categories in the Chamela TDF. Categories were defined by habitat specificity (morpho-pedological land units*), spatial distribution (number of plots**), and population size. Cells I and VIII correspond to extremes, they grouped common and extremely rare species, respectively.

	Habitat specificity (Distribution in morpho-pedological land units)			
	Wide (≥ 4 *)		Narrow (≤ 3 *)	
Population size / Spatial distribution	Broad (> 12**)	Restricted (≤ 12 **)	Broad (> 4 **)	Restricted (≤ 4 **)
Large population (> 43 individuals ha^{-1})	I **Common species**	II	III	IV
Small population (≤ 43 individuals ha^{-1})	V	VI	VII	**VIII** **Rare species**

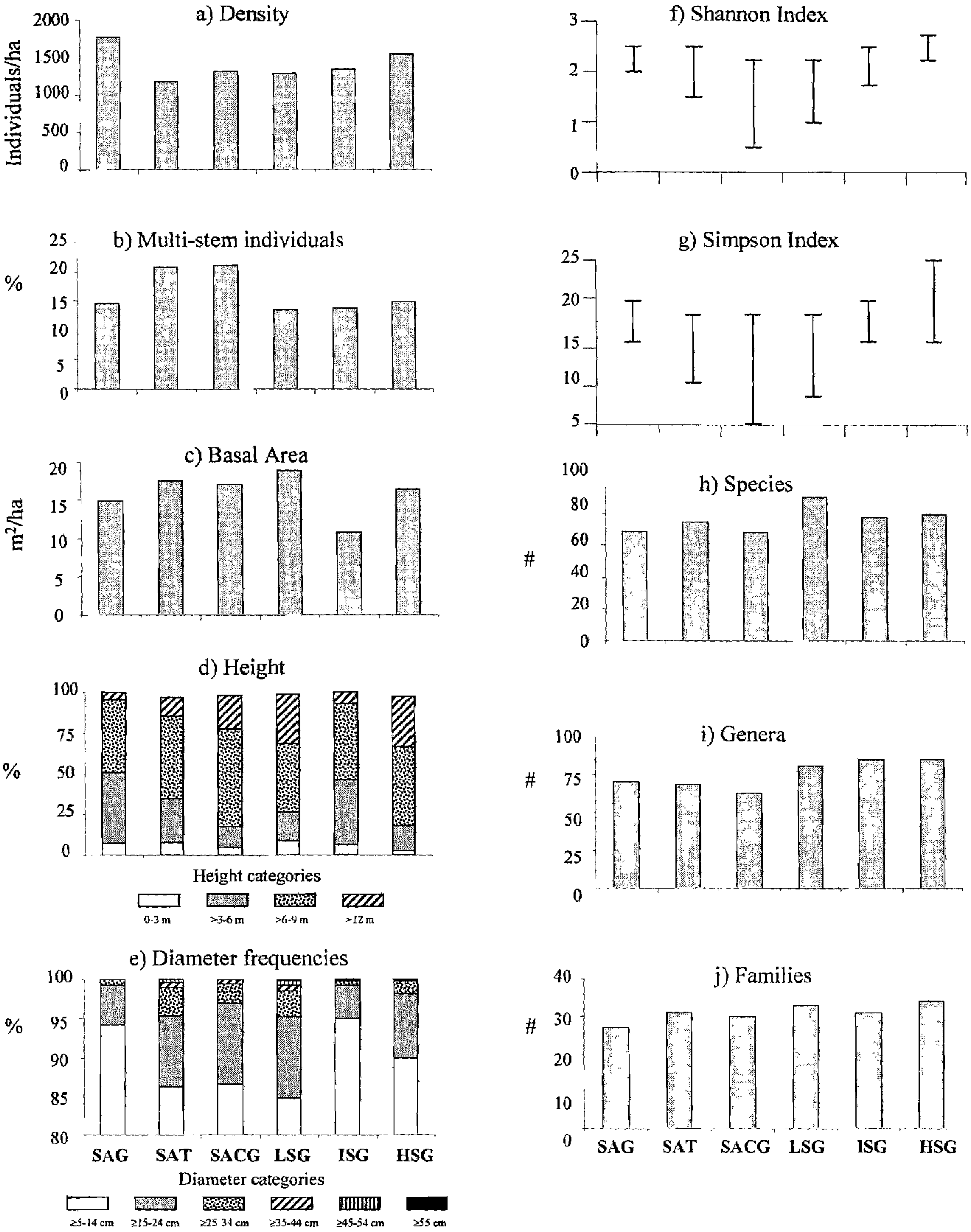

Figure III.1. Structure of the tree component in the Chamela TDF, for each morpho-pedological land unit (SAG, SAT and SACG are summited areas over granite, tuffs and conglomerates, respectively, while LSG, ISG and HSG are low, intermediate and high slopes over granite).

a maximum value of 17 m, over 61% of the 1,800 readings were between 5 and 9 m, and 4% of them were ≤ 2 m. Canopy height had a mean of 6.8 m (± 2.56 standard deviation), but it was highly variable among plots. However, a comparison of the variation coefficients on canopy height among land units showed no significant differences (χ^2 =2.21, D.F= 5, $p< 0.05$).

According to diameter categories, trunks with ≤14 cm DBH made up 90% of the total and contributed to approximately 52% of total basal area. Although stem diameters up to 72 cm were recorded, density of stems ≥ 35 cm was low (contribution to basal area was 9.8%). Summit land units (SAT, SACG) and low slopes (LSG) showed a similar percentage of frequencies between ≥ 5 - 14 (around 85%) and ≥ 15 - 24 (near 10%) diameter categories; whereas in other summit and slopes land units on granite (SAG, ISG and HSG) the thinnest trunks were more common. Nevertheless, no significant differences were found among land units, when comparing both diametric classes of frequencies ≥ 5 - 14 ($\chi2$ = 1.065; DF=5; $P<0.05$) and ≥ 15 - 24 ($\chi2$ = 4.46; DF=5; $P<0.05$.)

In this study, 42 families, 102 genera and 148 species were found (Appendix II). Families, genera and species richness, as well as Shannon and Simpson diversity index, were not statistically different among land units according to the Kruskal-Wallis test ($p<0.05$). Furthermore, only in high slopes on granite (HSG) there was a tendency toward highest diversity index (Fig. III.1). Mean Shannon index was 3.08 (range 2.30 - 3.47) and mean Simpson index was 14.8 (range 5.2 - 24.3). According a Mann-Whitney test both diversity index did not differ significantly (Shannon index: $U = 0.57$, $p<0.05$; Simpson index: $U = 0.59$, $p<0.05$). Families with the largest number of genera and species were Leguminosae, Euphorbiaceae and Rubiaceae (Fig. III.2 a, b). The three most diverse genera were *Lonchocarpus*, *Bursera* and *Caesalpinia*, together with 22 species (28%; Fig.III.2c). Ratios of families/genera (1:2.4), families/species (1:3.5), and genera/species (1:1.4), indicate that generic richness is relatively large in the Chamela TDF canopy.

A few families, genera and species were well represented in the canopy, whereas most components in all these categories contributed little, more than richness, to community structure (Figs. III.3 a, b, c). While only ten families comprised 77.6% of all individual trees, the other 32 families comprised only 22.4% of abundance. Leguminosae accounted for 35.4% of all individuals. Ten genera accounted for 53.2% individuals while the remaining 46.8% corresponded to 92 additional genera. An analogous tendency occurred among species: 40% of individuals belonged to ten species and the remaining 60% correspond to 138 species. The proportions were similar when Importance Value was considered, except for ten dominant genera, which accounted for 70%.

The relationships between number of species and its number of individuals clearly showed that many of species had few individuals (Fig. III.4a). A similar tendency appeared in the dominance-diversity curve for Chamela TDF (Fig. III.4b). This dominance-diversity curve proved a significant fit to the theoretical log normal model (χ^2 = 18.45, $p<0.048$). The comparison among Chamela curve and curves of other tropical forests showed that Chamela was more closed to the tropical wet forest in Manaus, Brazil, than to a Costa Rican TDF, though two both fitted also to log normal model. Additionally, clear differences appeared among the Chamela curve and others belonging to temperate forest fitted to normal and geometrical series.

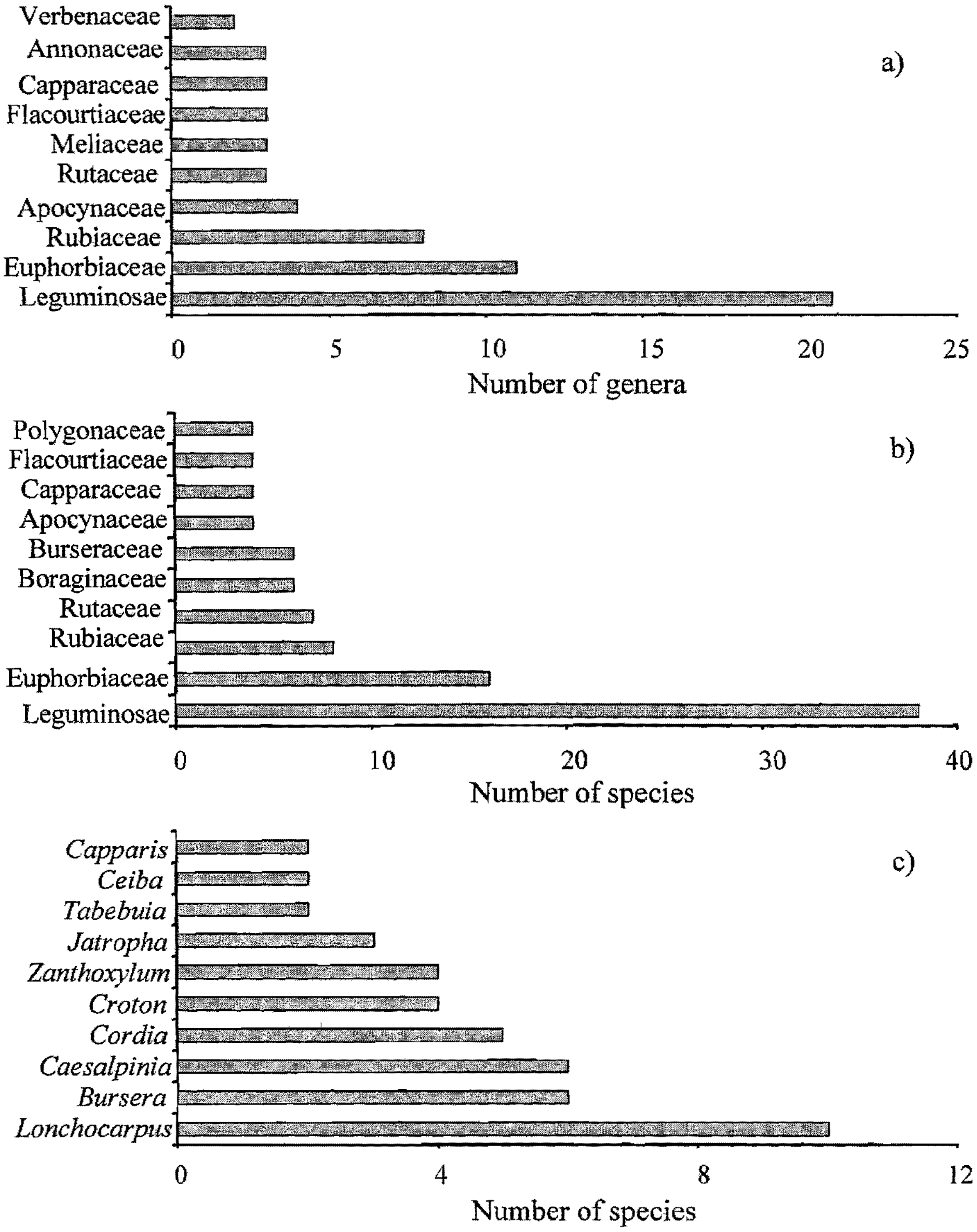

Figure III.2. a) Distribution of genera among the most important families. Leguminosae, Euphorbiaceae, Rubiaceae, and Apocynaceae include 42.4% of the 102 recorded genera. b) Distribution of species among families. Leguminosae, Euphorbiaceae, Rubiaceae, Rutaceae, Boraginaceae, and Burseraceae contain 54.3% of the 148 recorded species. c) Distribution of species among genera; *Lonchocarpus*, *Bursera*, *Caesalpinia*, *Cordia*, *Croton*, and *Zanthoxylum* made up 25.5% of the 148 recorded species.

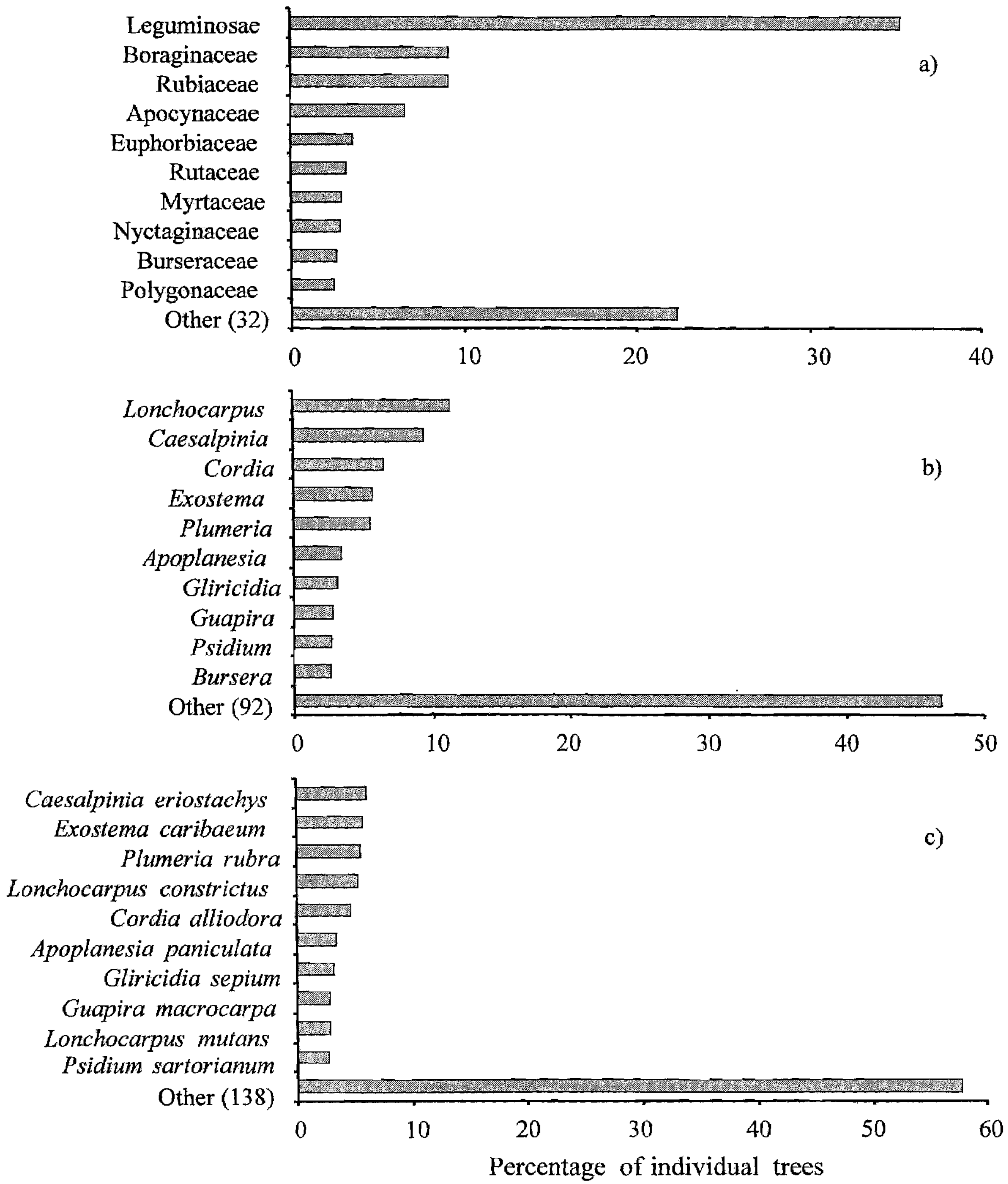

Figure III.3. Percentages of individual trees by: a) Family, b) Genera, c) Species.

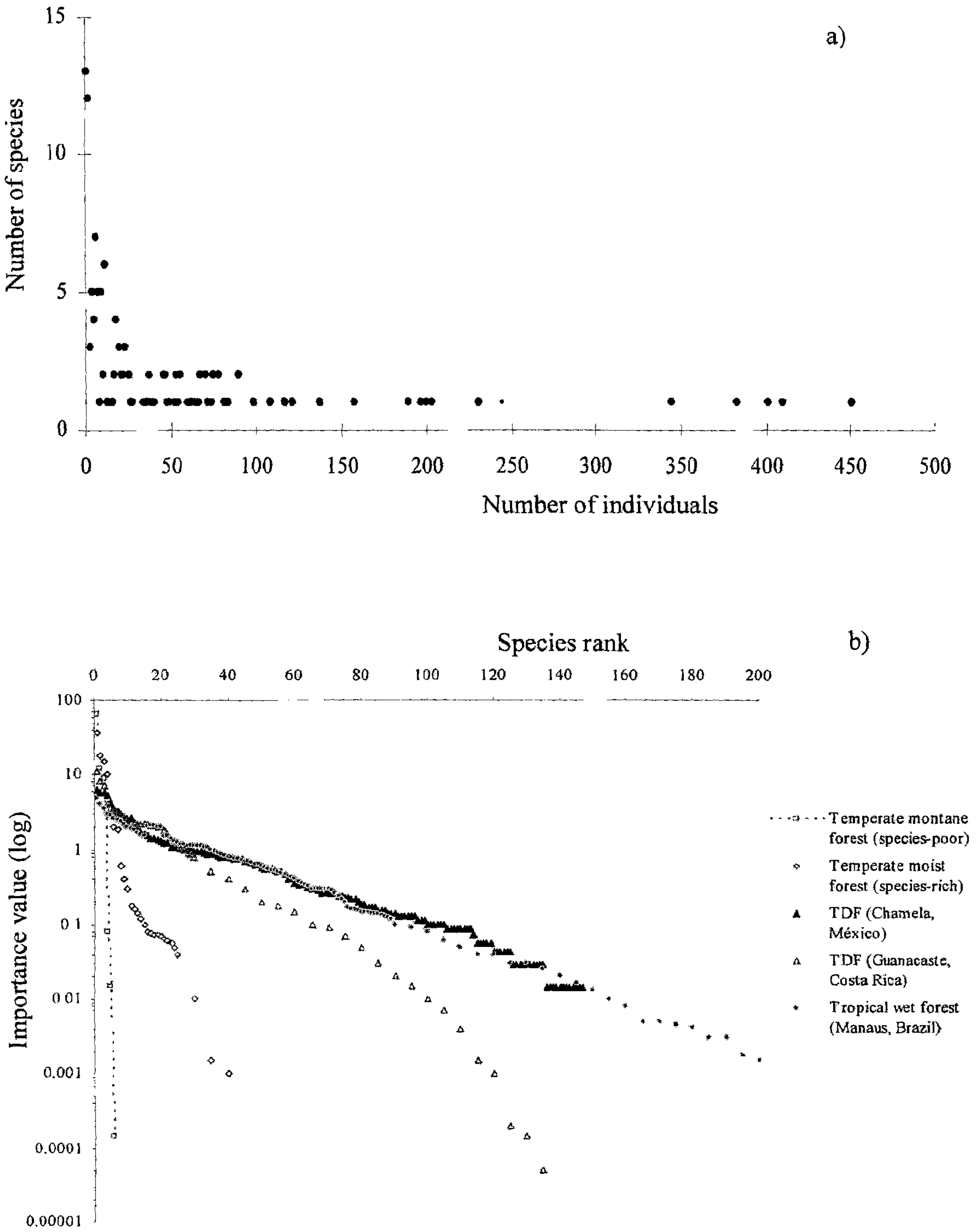

Figure III. 4. Abundance of species: a) Relation between number of species and individuals for TDF at Chamela, b) Comparison of the dominance-diversity curve of Chamela and others in tropical and temperate forests reported by Hubbell (1976).

The species-area curves for all plots showed that a large proportion of tree species diversity of the Chamela TDF was included in this study (Fig. III.5 a). However, based on the Chao 1 richness estimator, we could see more tree species may be included still, because significant differences between observed and estimated species richness ($\chi^2 = 35.75$, $p<0.05$) resulted from a chi-square test for total sample. The adjusted curves for each land unit showed similar trends (Fig. III.5 b); different slopes suggested that there are differences, albeit moderate, in their total diversity. Also, the chi-square test showed that observed species in summit areas on tuffs and conglomerates (SAT and SACG; $\chi^2 = 7.98$, $\chi^2 = 11.08$, respectively) and on slopes on granite (LSG and HSG; $\chi^2 = 18.31$, $\chi^2 = 11.45$, respectively) were significantly different from estimated richness obtained by Chao 1 ($p<0.05$). In summit areas and intermediate slopes on granite, the differences between observed and estimated species richness were not significant (SAG and ISG; $\chi^2 = 2.66$, $\chi^2 = 3.13$, respectively).

Spatial organisation

The species composition and dominance varied spatially. Dominant species were not distributed uniformly in land units and they did not contribute to the same abundance when they were presents (Fig. III.6). The Importance Value range of the ten dominant species in each land units varied from 58.2% to 85.9%. None of the species was found to be the most dominant in all land units.

A group of six species was classified as common canopy species at Chamela TDF, which represented 4.1% of all species, but contained 30% of all individuals (Table III.2). In contrast, 68 species (46.3%) were classified as extremely rare. Rare species had low densities (≤ 43 trees ha^{-1}) and narrow distribution on plots (< 4) and land units (≤ 3). Twelve species were represented by one individual in the entire sample. Similarly, most families and genera were rare, having restricted distribution and low abundance.

A large variation was observed in the spatial organization of different species. Although *Caesalpinia eriostachys* Benth. was the most important species (12.8% of dominance), for example, it was unevenly distributed at the landscape, completely lacking in intermediate slopes (ISG), and scarce in summit areas on granite (SAG; Fig. III.2). A similar pattern was found for other dominant species such as *Apoplanesia paniculata* Presl., *Cordia elaeagnoides* D.C., and *Caesalpinia coriaria* (Jacq.) Willd. In contrast, *Psidium sartorianum* (Berg.) Ndzu., *Plumeria rubra* L., *Lonchocarpus constrictus* Pitt., and *Cordia alliodora* (Ruiz &Pav.) Oken occurred in all land units, but they were extremely variables in importance values.

The tree species composition at Chamela varied between sites, producing a large species turnover (β diversity) among plots. Similarity values ≤ 0.2 for both Sørensen and Morisita-Horn index prevailed at around 40 % of paired-plot comparisons (Fig. III.7). Large species overlaps between plots were not always matched by large similarities, considering that only a few species were shared and their frequency differed significantly between similarity classes ($p < 0.05$).

PCA based on all structural attributes showed that plots located on the right half of PC I axis had the stems of greater diameter and height (Fig. III.8a). Plots located on the upper

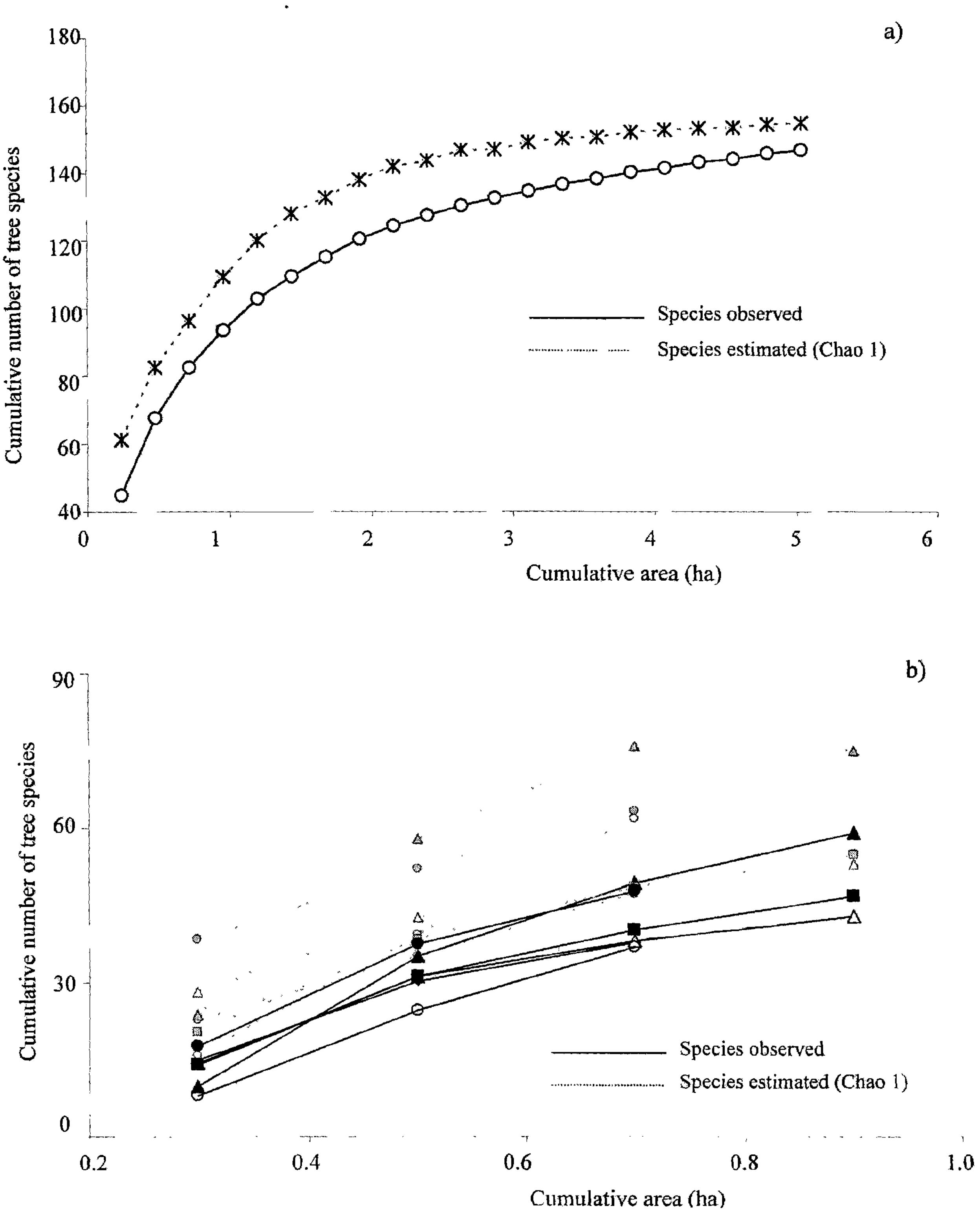

Figure III.5. Species.area relationship for: a) all 21 plots grouped; and b) plots grouped by morpho-pedological land unit (◆ = SAG, Δ = SAT, ○ = SACG, ▲= LSG, ■ = ISG, and ● = HSG).

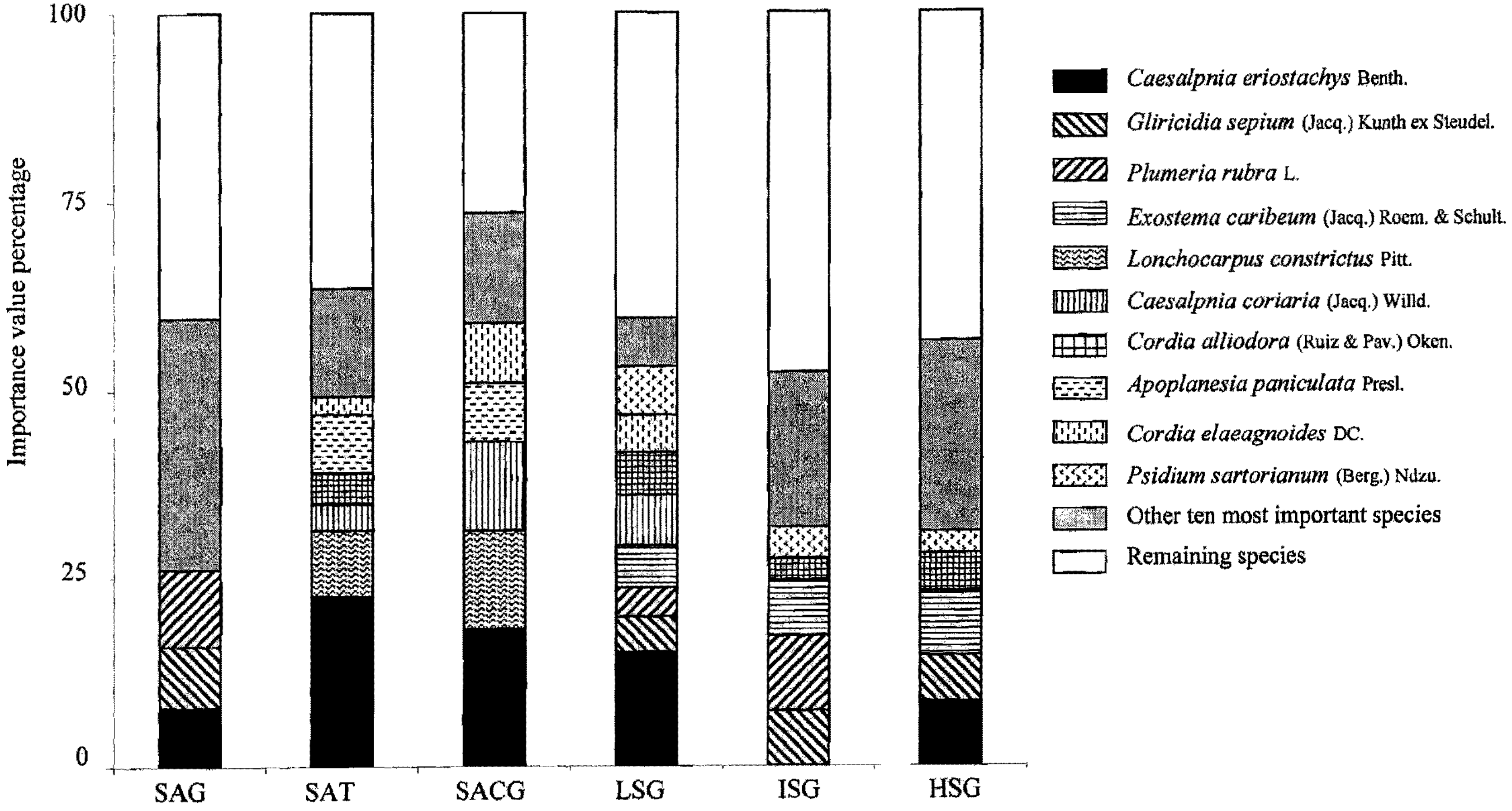

Figure III.6. Ten dominant species in all 21 plots (specific shadow). Bars signal the importance value contribution of ten dominant species in each morpho-pedological land unit.

Table III.2. Classification of species by rarity categories, cells I and VIII correspond to extremes, containing common and extremely rare species, respectively. In each category, S is equal to percentage of species (their absolute number in parentheses), P is equal to percentage of individuals in each category and BA is equal to percentage of basal area.

		Habitat specificity (Distribution in morpho-pedological land units)			
		Wide (≥ 4)		Narrow (≤ 3)	
Population size	Spatial distribution among plots	Broad (> 12)	Restricted (≤ 12)	Broad (> 4)	Restricted (≤ 4)
Large population (> 43 individuals ha^{-1})		**I** S = 4.1 % (6) P = 30.3 % BA = 34.4 %	II S = 0.7 % (1) P = 3.6 % BA = 2.2 %	III S = 0.0 % (0) P = 0.0 % BA = 0.0 %	IV S = 0.0 % (0) P = 0.0 % BA = 0.0 %
Small population (≤ 43 individuals ha^{-1})		V S = 12.9 % (19) P = 24.5 % BA = 18.3 %	VI S = 21.1 % (31) P = 20.5 % BA = 21.4 %	VII S = 15.0 % (22) P = 10.9 % BA = 15.8 %	**VIII** S = 46.3 % (68) P = 9.8 % BA = 8.0 %

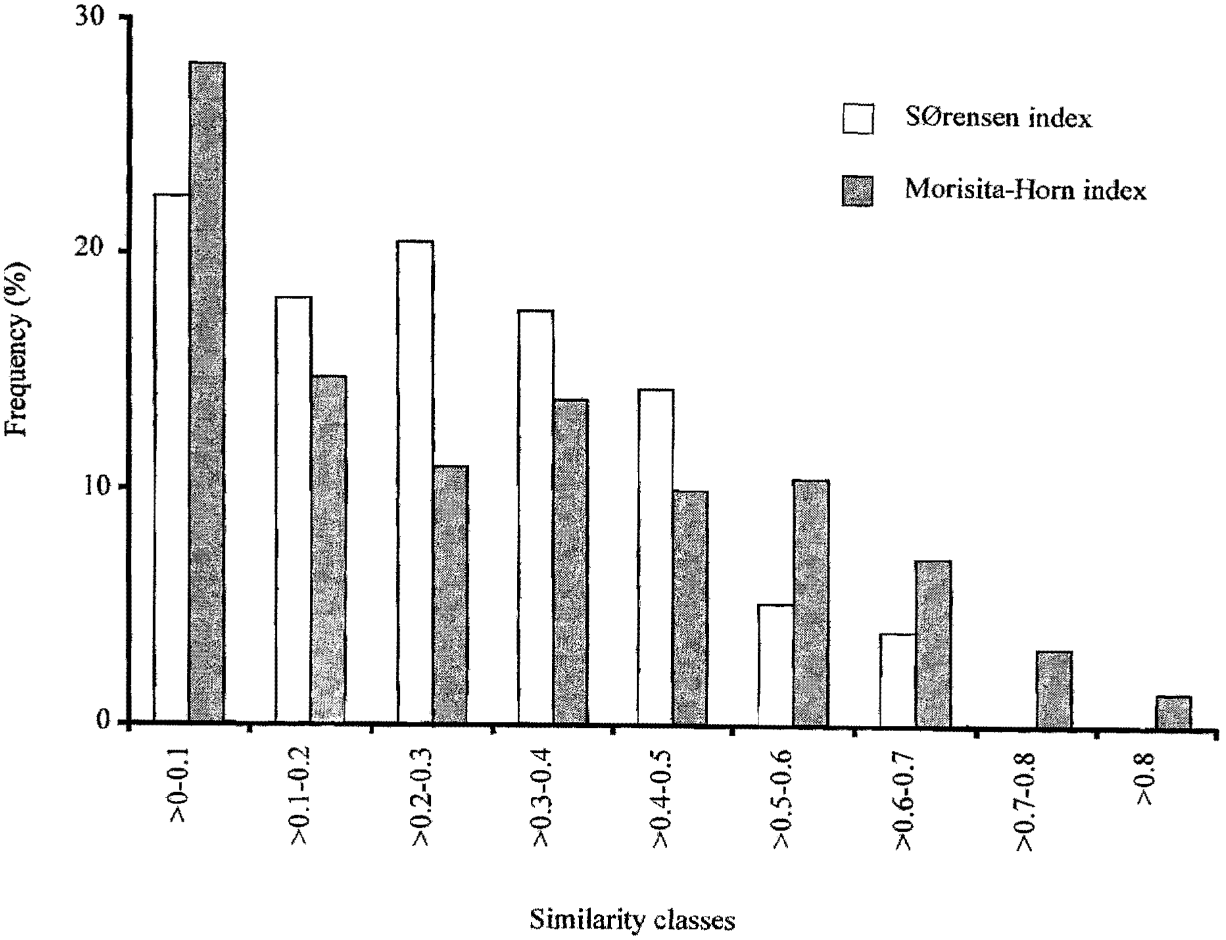

Figure III.7. Distribution of frequencies of similarity classes, among all possible pair plots.

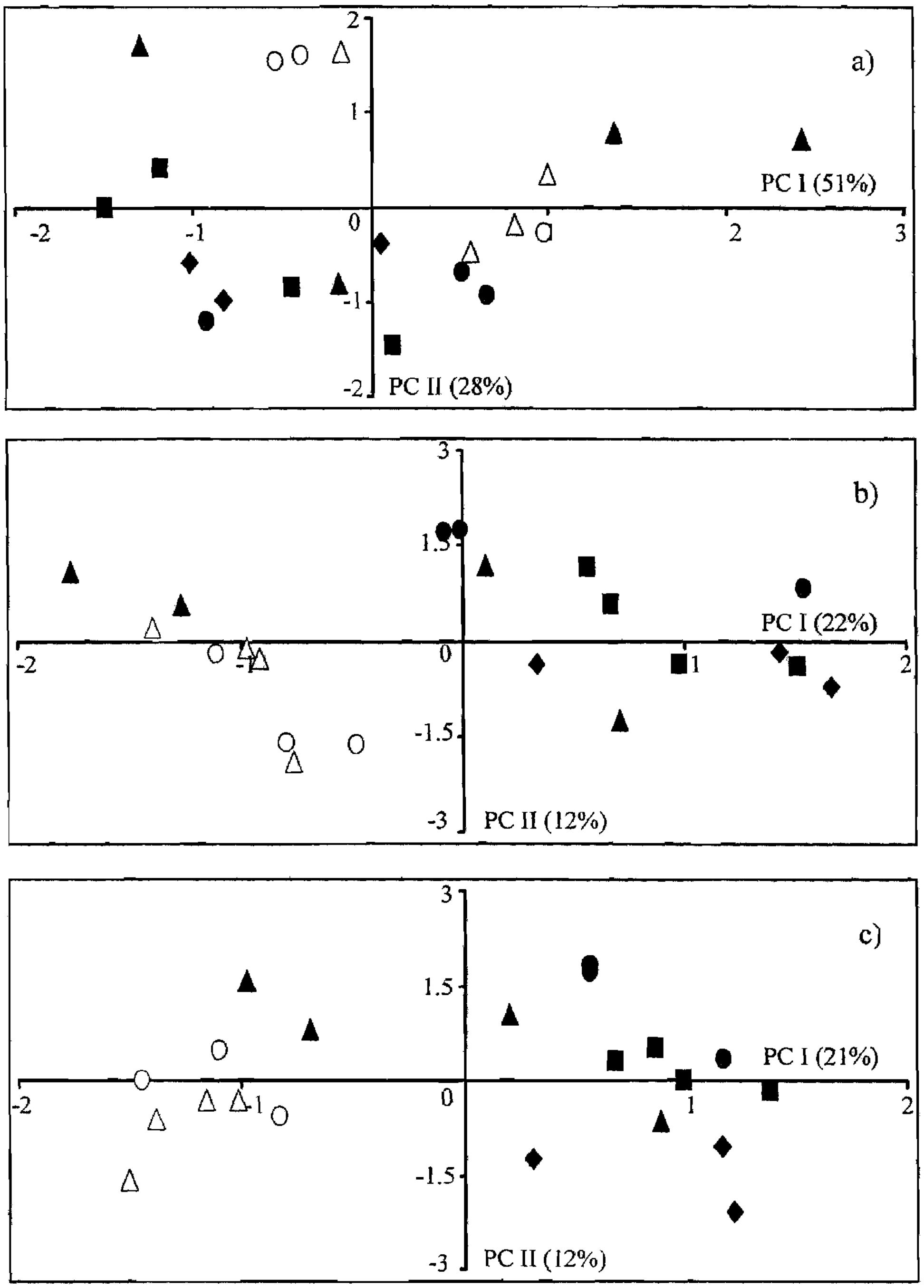

Figure III.8. PCA ordination of the 21 study plots, based on matrices of: a) 16 structural variables; b) 79 variables: 16 structural and 63 corresponding to the abundances of the ten dominant species in each plot; and c) the abundance of 63 species, comprising the 10 most important species in each plot. The percentages next to the axes show the explained variance by each principal component. Symbols for the different morpho-pedological land units: ♦ = SAG, Δ= SAT, ○= SACG, ▲= LSG, ■ = ISG, and ● = HSG.

part of PC II axis had large dominance values for the five most important species, and they were the least dense and diverse. The two first principal components accounted for 79% of total variance. The second PCA, based on structure and abundance of the ten species most dominant in each plot, produced a different ordination and a much lower proportion of variance explained by the first two principal components (34%). In this case, most plots tended to be grouped by lithology (Fig. III.8b), with plots on tuffs and conglomerates located along the left portion (negative) of PC I axis, whereas those on granite were grouped in the right (positive) half. Along PC II axis, the most diverse plots were located on the positive part, regardless of morpho-pedological land unit. In the third PCA, which did not consider general structure but was based only on the ten most dominant species per plot (63 species), variance explained by PC I plus PC II axes was 32%, and plot ordination was generally similar to the previous PCA. Here, plots were again separated by lithology and those sharing morpho-pedological land units tended to be closer to each other (Fig. III.8c).

DISCUSSION

Structural organization

The structure of the TDF at Chamela was similar to other forests of the same kind: tree density was moderately-high, < 10 cm DBH prevails, < 10 m height was common and moderate multi-stem individuals were observed (Murphy & Lugo 1986a, Murphy y Lugo 1986b, Sampaio 1995, Killen *et al.* 1998, Trejo 1998, Martínez-Yrízar *et al.* 2000, Salas 2002). In addition, the organization of different taxonomic categories suggested similarity with a fundamental pattern among Mexican and others Neotropical TDFs (Gentry 1995). However, slight or major differences with other studies may be attributed to differences in sampling procedures, especially the minimum DBH used to include trees (≥ 1 cm, ≥ 2.5 cm or ≥ 10 cm), as well as the inclusion of other woody components such as climbers, shrubs and cacti. This may, partially explain, why the density and basal area values reported by Lott *et al.* (1987), Gentry (1988) and Martínez-Yrízar *et al.* (1992) for Chamela´s TDF are larger than ours. Human disturbance may also induce considerable structural differences among forests (González & Zak 1996, Parthasarathy & Karthikeyan 1997, Sampaio 1995, Gillespie *et al.* 2000), but the examined sites at Chamela are well-preserved. Important structural and floristic differences occurred when Chamela´s canopy was compared with the mixed deciduous forest in Thailand or the dry forest in Africa (Menaut *et al.* 1995, Rundel & Boonpragob 1995), where the tallest trees and lowest density occur.

The 148 tree species recorded in this study exceed figures reported for analogous forests (Murphy y Lugo 1986b, Menaut et al. 1995, González & Zak 1996, Killeen et al. 1998, Parthasarathy & Karthikeyan 1997, Oliveira-Filho et al. 1998, Vázquez & Givnish 1998, Gillespie et al. 2000). Similarly to species, families and genera richness was large. Canopy trees recorded here accounted for 34.4% of the total 125 vascular plant families reported for Chamela (Lott 1993). Families and genera richness fell within the rank reported by Trejo & Dirzo (2002) for woody plants in 20 Mexican TDFs, and resembled the family richness reported at Los Colorados (N Colombia), Coloso (Venezuela), 38 localities in the Brazilian caatinga (Sampaio 1995) and seven sites in Central America (Gillespie et al. 2000). The dominance of Leguminosae and Euphorbiaceae was consistent with findings in other Mexican and Neotropical TDFs (Gentry 1995, Killeen *et al.* 1998, Sampaio 1995, Trejo 1998, Gillespie *et al.* 2000, Martínez-Yrízar *et al.* 2000, Pérez-García 2002), but not in Paleotropical ones where Combretaceae, Dipterocarpaceae, Ebenaceae, Lythraceae and Verbenaceae are dominant (Menaut *et al.* 1995, Rundel & Boonpragob 1995, Sussman & Rakotozafy 1994, Parthasarathy & Karthikeyan 1997, Richards 1996). Rubiaceae, Rutaceae and Boraginaceae were important in Chamela such as in other Mexican TDFs (Trejo 1998, Salas 2002); the former two also prevailed in India (Parthasarathy & Karthikeyan 1997), while Rubiaceae dominated in the eastern-central area in the Caribbean island of St. Lucia (González & Zak 1996) and in some sites in Central America (Gillespie *et al.* 2000).

Out of the 555 genera reported in Chamela's flora (Lott 1993), an important percentage corresponded to arboreal life form and we registered 102 genera. Genera richness was similar to that of woody plants at Caleta, Michoacán (Trejo 1998), and for the Brazilian caatinga (Sampaio 1995). In contrast to families, genera and species do not show patterns of shared dominance with other TDFs in the Neotropics (Gentry 1995, Trejo 1998). In Chamela, the exclusively arboreal genera *Lonchocarpus* and *Bursera*, together with *Croton* (shrubs or small trees), were the most specious. Also *Caesalpinia,* a genus with a large geographical range and which makes an important contribution to structure of similar forests (Lott & Atkinson 2002), was noticeable for its abundance. In contrast, *Tabebuia, Casearia* and *Trichilia,* three widely distributed genera in Neotropical TDFs (Gentry 1995, Gillespie *et al.* 2000), were restricted and not dominant at Chamela. The 148 species represented 65% of the total 227 arboreal species recognized by Lott & Atkinson (2002).

Caesalpinia eriostachys, the dominant species was not important in some morpho-pedological land units or was completely absent. *C. eriostachys* was also common in TDFs nearest to coast in Oaxaca (Trejo 1998, Salas 2002). In contrast, some species like *Bernardia mexicana* Mc Vaugh, *Ceiba aesculifolia* (HBK.) Britt. & Baker, *Esenbeckia berlandieri* Baill. subsp. *acapulcensis* (Rose) Kaastra and *Tabebuia impetiginosa* (Mart. Ex DC.) Standley, which are relatively abundant in other Mexican regions where TDF is prevailing (Trejo 1998, Salas 2002), were rather rare at our Chamela study plots.

Species-area curves were never levelled in less than one hectare in the different land units analyzed at Chamela. But the opposite trend in comparable and even smaller areas resulted in other tropical dry forests with fewer species in Puerto Rico (Murphy y Lugo 1986b), India (Parthasarathy & Karthikeyan 1997) and Bolivia (Killeen *et al.* 1998). The species accumulation for the total area studied (5.04 ha) showed the best tree species representation at Chamela, but the Chao 1 model predicted that additional species could be included. In agreement with result and considering the morpho-pedologic mosaic, the common rare species, and the floristic checklist (Lott 1993), it is expected an increase that the number of species will increase with the number of new land units.

Dominance

The canopy at Chamela is typically diverse in tree species, even though a relatively small group of species was recognized as dominant. A log normal series provided the best model for adjusting the dominance-diversity curve; its pattern reaffirmed that dominance is shared by a small number of species with larger abundance (Magurran 1990). The log normal series was a good fitting to diversity-abundance curve for the TDF at Chamela, like as two other curves of tropical forests reported by Hubbell (1979). When those curves were qualitatively compared, the Chamela TDF appeared more closed to a Brazilian tropical wet forest than to a Costa Rican TDF. This tendency could be explained because the Chamela TDF has been recognized as a highly diverse forest in tree species, comparable to high diverse tropical humid forests (Gentry 1988).

According to the existence of a relief and soil mosaic at Chamela (Chapter II), the group of dominant species differed among plots and morpho-pedological land units. Only few dominant species, such as *Caesalpinia eriostachys* and *Cordia alliodora* (Ruiz & Pav.) Oken., were apparently indifferent to habitat variations. While species closely related, such as *Caesalpinia coriaria* (Jacq.) Willd. and *Cordia elaeagnoides,* showed a restricted dominance in few land units (SAT and SACG).

Many authors have attempted to explain why few species may dominate local plant communities in tropical forests, citing to natural disturbance, past damage, drainage, substrate, micorrhizae and management, as key factors (Dittus 1985, Duncan 1992, Hart *et al.* 1989, Campbell 1994, Richards 1996, Oliveira-Filho *et al.* 1998). Generally, other non-mutually exclusive hypotheses have been put forward, most relevant here being dispersal and regeneration success (Hubbell 1979, Harper 1981), habitat specificity (Whittaker 1972) and resource heterogeneity (Tilman 1982, Wiens 1995).

In Chamela an extreme condition of local dominance is exemplified by *Piranhea mexicana* (also reported as *Celaenodendron mexicanum*; Lott 1993, Martijena & Bullock 1994), and *Cordia elaeagnoides* DC. (Groenendael *et al.* 1996, Rosas 2000), but only *C. elaeagnoides* was included in this study. An attempt to understand local processes involved with monodominance of *P. mexicana* was made by Martijena & Bullock (1994), whose results demonstrated the difficult in explaining the monodominance pattern. Further studies of these patterns, on long-term and in especially wider geographical areas, are needed.

The general dominance pattern in Chamela is common with other Mexican TDFs (Salas 2002, Trejo & Dirzo 2002) and other Neotropical forests (Murphy & Lugo 1986b, Killeen *et al.* 1998, Oliveira-Filho *et al.* 1998); thus, dominant species have been suggested as sufficient to summarize differences between localities (Hall 1977, Ashton & Hall 1992, Greig-Smith 1996).

Rarity

In contrast to the few species dominant in the tree community of Chamela was the prevalence of rarity. Most families, genera and species were rare, and although their contribution to density and basal area were relatively small, rare species determined the large richness of the different taxonomic categories. Almost 47% of tree species were extremely rare. This proportion is larger than that reported for the moist forests at Barro Colorado (Hubbell & Foster 1989) and Coromandel, India (Parthasarathy & Karthikeyan 1997).

Although rarity of species may result from sampling criteria (Greig-Smith 1996, Ricklefs 2000, Kelly *et al.* 2001), the phenomenon of rarity in tropical forests seems to be more common than recognized thus far (Hubbell & Foster 1989, Campbell 1994, Parthasarathy & Karthikeyan 1997, Pitman *et al.* 1999, Ricklefs 2000). Rarity is a scale-dependent phenomenon and is consequently relative to the specific time and space frames where a community is analyzed (Harper 1981, Rabinowitz 1981, Ricklefs 2000). Thus, in contrast to more local or wide studies in Chamela (Lott *et al.* 1987, Balvanera *et al.* 2002, Segura *et al.* 2003), the present work contributes to identify rare species based on sampling across land units.

Our results indicate that the assessment of rarity could have been substantially different if a smaller number of such units had been examined or if other criteria had been adopted (such as the study by Kelly *et al.* (2001), who based their judgement on abundances only). For example, our dominant species *Apoplanesia paniculata* Presl., *Exostema caribaeum* (Jacq.) Roem. & Schult., *Lonchocarpus constrictus* Pitt., *Plumeria rubra* L., *Psidium sartorianum* (Berg.) Ndzu., and *Caesalpinia eriostachys*, all had low abundances or were even absent from certain land units.

As with dominance, rarity has also been explained by several hypotheses that are not mutually exclusive: habitat specificity, mass effect, limiting regeneration conditions (seed dispersal and seedling and sapling survival), and immigration (Grubb 1977, Hubbell 1979, Harper 1981, Rabinowitz 1981, Shmida & Wilson 1985, Rabinowitz *et al.* 1988, Hubbell & Foster 1989). However, habitat preference and specialization for regeneration only partially explain rarity among tree species at Barro Colorado (Grubb 1977, Hubbell & Foster 1989).

The "mass effect", strongly related to the "source-sink" phenomenon, suggested that local dispersal processes may promote establishment of species in sites where they cannot be self-maintaining (Shmida & Wilson 1985, Hanski 1998). This may explain why some species such as *Lippia mcvaughii* Mold. and *Piranhea mexicana* regenerate at sites where adult individuals are absent (Martijena & Bullock 1994, Durán *et al.* 2002). That process may also serve to maintain species such as *Trichilia trifolia* L. subsp. *palmeri* (C. DC.) Pennington, *Pterocarpus* sp. and *Capparis verrucosa* Jacq. in the TDF canopy at low densities, when they are common in adjacent semideciduous forests (Lott *et al.* 1987). This local diversity maintaining phenomenon has been pointed out as typical of metapopulational dynamics (Hanski 1998, 1999). The "mass effect" also operates at regional and biogeographical scales (Shmida & Wilson 1985). Thus, over long time periods, propagules immigration of species which are abundant in nearby regions, such as *Alstonia longifolia* (A. DC.) in Manantlán (Vázquez G. & Givnish 1998), may be acting to support these species at Chamela even though their densities are low enough to qualify as rare.

Rarity due to limitation on regeneration, which may be infrequent or erratic at times, seems to affect some tree species in the Chamela TDF. This may be the case with *Cordia elaeagnoides*, a relatively abundant species with annual massive seeding, but lacking a broad distribution or abundant regeneration (Rosas 2000). Scarcity of *C. elaeagnoides* seedlings and saplings has been attributed to the pulses in the recruitment of this species, in a scale of decades, in well-lit environments that only appear in the canopy after catastrophic disturbances (Groenendael *et al.* 1996), such as category 5 hurricanes, although they are not frequent enough in Chamela to be considered recurrent (García-Oliva *et al.* 2002).

In an attempt to explain the maintenance of rarity on tropical canopies, Hubbell (1998) proposed a "unified" theory, based on dispersal limitation, though the "niche assembly" theory is not rejected. The unified theory predicts that dispersal limitation and the probability of replacement for new immigration could help to maintain a great number of rare species by means of a continuous increment in the variance of relative abundance of species (such as occurred in Barro Colorado forest). However, as he signalled, the greatest challenge is reach a balance between empirical evidence and theoretical models.

Low frequencies of rare species within a sample make it difficult to analyze the diversity patterns in a community, so these taxa are commonly excluded from data sets before carrying out classification and ordination analyses of vegetation (e.g. Green & Young 1993, Greig-Smith 1996, Jongman *et al.* 1995). Unfortunately, satisfactory techniques for analyzing rarity are lacking (Ricklefs 2000). Considering that rare species represent a key component in the large tree diversity in the Chamela TDF, it is obvious that understanding their patterns and overall ecological relationships will be basic for their conservation. We suggest that an analysis centred on rare species, from a phytogeographical perspective and at a larger spatial scale than that used for the present analysis, would improve our understanding of rarity in Chamela.

Spatial organization

Remarkable local abundance of widely distributed species strongly suggests habitat preferences. Similar tendency was recognised in the micro-basins at Chamela (Balvanera 1999, Segura *et al.* 2003), also in other forests such as Barro Colorado (Panama; Hubbell & Foster 1989), Beza Mahafaly (Madagascar; Sussman & Rakotozafy 1994), the Amazonian (Gentry & Ortíz 1993, Campbell 1994, Tuomisto *et al.* 1995) and La Selva (Costa Rica; Clark *et al.* 1995).

The dominant component was clearly differentiated between granite and non-granite lithology. An analogous tendency of effect of specific parent materials could be observed in data on Oaxaca TDFs (Pérez-García 2002, Salas (2002). Also, Trejo (1998) recognized that different lithology could explain the diversity differences among 20 Mexican TDFs. Villers-Ruíz *et al.* (2003) reported also that lithology was significantly related to species assembly of dry vegetation. Likewise, TDFs in Central America and the Brazilian caatinga occurs in a mosaic of lithologies (Sampaio 1995, Gillespie *et al.* 2000) which may influence the distribution of dominant species.

Similarity of species composition was significantly higher only among closed plots within a same land unit ($p < 0.05$). Its result could be comparable with other experiences where a greater similarity occurred between TDFs of nearby localities, although distance showed to be only a partially explanatory variable (Balvanera *et al.* 2002, Trejo & Dirzo 2002).

Considering the structural and floristic heterogeneity in the Chamela TDF, we suggest prudence with the "representative samples", since single sample must reflect strong local particularities. So, it is useful mean values plus standard deviations and ranges, in order to describe structure and species composition, because they will provide idea on variability before make a generalization over an area. Obviously, heterogeneous tropical forests are difficult to describe if complete information on their environmental mosaic is lacking (Campbell 1994, Chazdon 1996, Greig-Smith 1996, Ricklefs 2000). Far from to recognize of tree community variations along local elevational gradients, homogeneity should not be taken for granted the TDF canopy at Chamela. Most differences on structure, species diversity, dominance, rarity, as was documented in this chapter, form a heterogeneous mosaic of tree communities along the landscape. Implications both theoretical and practical ought to take into account because the best decision for conservation and management in a particular site or species cannot be applied in all area.

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CAPÍTULO IV

RELATIONSHIP BETWEEN TREE PATTERNS AND THE ENVIRONMENTAL MOSAIC IN A TROPICAL DECIDUOUS FOREST AT CHAMELA, MEXICO

ABSTRACT

We conducted a landscape analysis of the structure and tree diversity in a tropical deciduous forest (TDF) at Chamela, Mexico. The purpose was to examine the relationship between tree community attributes and a relief and soil mosaic. Structure and species diversity was recorded in 21 plots (30 x 80 m) along six morpho-pedological land units. Previously, based in relief and soil factors these land units were classified into three soil constraints classes (few, some and many). In each plot, we had a record on elevation, slope, soil depth, available water holding capacity and nutrients content, and other record on measures of trees with DBH ≥ 5 cm and their taxonomic identity. The diversity estimates were significantly correlated with relief and soil nutrient attributes ($p< 0.05$), but poor correlation occurred with structural attributes. A Two Way Indicator Species Analysis (TWINSPAN) showed that a relatively small group of species, referred to as "indicator" (31), had a strong spatial segregation. The abundance of "indicator" species was according to the three soil constraints classes. This pattern was confirmed by a Canonical Correspondence Analysis (CCA). The plots were ordinated on axes as a continuum, although we may distinguish their segregation by the three soil constraints classes. CCA indicated that elevation, available water holding capacity and exchangeable bases were features which significantly explained the variance in the arboreal dominant species (29%). However, no significant difference with structure was found among the soil contraints land units.

KEY WORDS: *Tree diversity, spatial diversity organization, relief, soil constraints.*

INTRODUCTION

Tropical deciduous forests (TDF) host a large diversity of tree species, whose spatial organisation presents complex patterns (Murphy & Lugo 1986, Gentry 1995). Mechanisms and factors which explain and maintain the high tree diversity and its patterns are among the topics widely studied in these forests. Local studies have emphasized the importance of topographic gradients in order to explain diversity or structural spatial differences in the plant communities (Oliveira-Filho *et al.* 1994, Galicia *et al.* 1999, Balvanera *et al.* 2002), while regional approaches have shown the climatic control (Gentry 1988, Coughenour & Ellis 1993, Gillespie *et al.* 2000, Trejo & Dirzo 2002). At the mesoscale level, TDFs studies on woody plants have shown the importance of lithology, geomorphology, elevation and soil to explain diversity and structural patterns (Coughenour & Ellis 1993, De Wolf 1998, Pérez-García 2002, Salas 2002). Those environmental factors also have shown to be ecologically important in more humid tropical forests (Duivenvoorden & Lips 1995, Siebe *et al.* 1995, Clark *et al.* 1995, Sollins 1998).

There is a generally accepted idea that tree patterns in TDFs are regulated by water availability and by topography and soil aspects related to the water resource (Murphy & Lugo 1986). Other factors such as soil nutrients, space in the soil, stoniness, drainage or erodability also help to explain why spatial differences in structure, diversity and distribution of particular species could be occurring. However, until now it has been a challenge to prove the relation between the plant patterns and soil characteristics (Gonzalez & Zak 1996, De Wolf 1998, Sollins 1998), thus more case studies are necessary to designate the ecological meaning of the soil to explain vegetation patterns at the TDFs landscapes.

Relief in the Chamela region is characterized by small hills and slopes with different steepness (Cotler *et al.* 2002). The Chamela Biological Station is known as an ecosystem in which TDF is develop on a lithology of granite and Entisol soil type (characterized by its poor structure, stoniness, sandyness and with low available water holding capacity; Solís 1993, Galicia *et al.* 1999). However, recently Cotler *et al.* (2002) documented that area includes a relief and soil mosaic where TDF occurs at least in 11 morpho-pedological land units. Based on this knowledge, we showed that those land units could be categorized in at least three classes of soil constraints (few, some and many constraints; see Chapter II).

The canopy of the Chamela TDF is spatially heterogeneous in its structure, species composition and diversity (Chapter III). This chapter, therefore, serve up to prove that structure and diversity in the tree community are related with the environmental mosaic defined by relief and soil features and soil constraints conditions.

METHODS

Characterization of environmental mosaic and tree community

Relief and soil features and tree community patterns were studied in 21 plots (30 x 80 m). Plots were located on six morpho-pedological land units previously mapped (Cotler *et al.* 2002), and classified into three soil constraints classes (Chapter II). Ten of the plots belong to land units with many soil constraints (Summit areas over granite, tuffs and conglomerates [SAG, SAT and SACG, respectively]), three plots belong to land unit with some soil constraints (High slopes over granite [HSG]) and eight plots belong to land units where there are few soil constraints (Low and Intermediate slope over granite [LSG and ISG, respectively]). These morpho-pedological land units were chosen among a total of 14 defined on the Biological Station of Chamela (Cotler *et al.* 2002), because they present the cover of TDF and have differences in the combination of relief, soil and lithology (see Chapter II). Lithology, relief and soils characteristic of each land unit are summarized in Table IV.1.

Relief and soil information for 21 plots were obtained from field and laboratory analyses. At each site, information on altitude, slope and exposure was recorded and a soil profile was dug. Soil profiles were systematically described *in situ*, by recording thickness, stoniness, colour, structure, bulk density, aggregate stability and root density. Technical details to obtain soil information are described in Siebe *et al.* (1996) and in Chapter II. Site information was organized in an matrix named as "environmental matrix", it contained variables related to relief (elevation and slope), water (available water holding capacity and stoniness) and nutrient soil conditions (C:N ratio, exchangeable bases, total and available phosphorous).

A general characterization of the tree community structure and diversity is summarized

Table IV.1. Soil features on six land units at Chamela. The secondary condition in elevation and slope in two units is mentioned in parentheses. Other numbers in parentheses refer to standard deviation values. * Available water holding capacity and Carbon:Nitrogen ratio.

Soil constraints	Many			Few		Some
Major landforms	Low hills	Intermediate hills		High hill		
Morpho-pedological land units	Summit areas	Summit areas	Summit areas	Low slopes	Intermediate slopes	High slopes
Lithology	Tuffs	Granite	Conglomerates	Granite	Granite	Granite
Elevation (m)	110 - 130	140 – 150 (170 – 200)	100 - 170 (135 – 200)	200 - 240	240 - 280	280 - 450
Slope (°)	≤ 5	4 - 8	2 - 8 (8 - 20)	4 - 12	8 - 20	20 - 45
Type (FAO 1998)	Mollic Cambisol, Episqueletic Regosol and Cromic Luvisol	Cromic Luvisol	Episqueletic Regosol and Stagni- Episqueletic Phaeozem	Rhodic Luvisol	Cromic Luvisol	Cromic Luvisol
Depth (cm)	29.0 (13.7)	66.5 (16.3)	22.5 (3.5)	50.0 (10.7)	73.3 (18.0)	61.0 (38.0)
Water* (L/m^2)	32.7 (13.1)	69.7 (27.3)	40.3 (10.7)	64.7 (5.1)	84.1 (21.8)	82.4 (46.4)
C:N ratio*	13.1 (2.1)	10.5 (0.1)	12.8 (1.6)	11.5 (4.1)	11.6 (0.2)	8.9 (4.7)
Total phosphorus (g/m^2)	59.4 (23.2)	68.4 (43.5)	31.6 (11.6)	62.2 (10.1)	100.6 (46.6)	76.7 (60.2)
Exchangeable bases (eq/m^2)	37.9 (13.4)	25.7 (6.5)	37.6 (24.4)	29.6 (11.8)	29.8 (8.4)	41.1 (22.7)

in Table IV.2. This information belonged to trees with DBH ≥ 5 cm in the 21 plots (more methodological details are described in Chapter III). The data on tree community by plot were organized on three matrices: "structural matrix", "total species matrix" and "indicator species matrix". The structural matrix included 11 variables per plot (number of trees, mean DBH and its standard deviation, total basal area, height variation coefficient, number of multi-stemmed trees, added importance values of the five most important species, Shannon and Simpson indices, species, and family richness). The species matrix included the total species in all samples (148). The indicator species matrix was derived by using a "Two Ways Indicator Species Analysis" (TWINSPAN; Jongman *et al.* 1995) from the total species found in the 21 plots. For TWINSPAN, a scale of importance of each species was developed to be used in the process of making a dichotomized ordination, therefore six importance value classes were designated (Class 1= species is not present, Class 2 = importance value >0 to 2.5%, Class 3 = > 2.5 to 5%, Class 4 = >5 to 10%, Class 5 = >10 to 20%, and Class 6 = >20%). The "indicator" species group was defined by presence grade (exclusive or nearly exclusive distribution) and by presence value (importance value class). TWINSPAN allowed the identification of the species known as "indicators" and showed a separation of plots by groups.

Data analyses

In order to detect bivariate relationships among the structure, diversity and species composition, and specific relief and soil variables, non-parametric Spearman rank correlations were performed at 95 and 99% confidence levels (Zar 1984).

To determine the tree community-environment patterns, groups of variables contained in a pair of matrices of both kinds were analysed simultaneously through some "Canonical Correspondence Analysis" (CCA; ter Braak & Smilauer 1998). Two CCAs using different combinations of species (total species and "indicator" species derived from TWINSPAN analysis) and environmental variables were carried out in order to reduce redundancy and to eliminate variables. The principal results were derived from the CCA based on 31 "indicator" species and three environmental variables, which mixed non-correlated variables related to relief (elevation), water (available water holding capacity) and nutrient (exchangeable bases, C:N ratio or phosphorus). A CCA with the structural and environmental matrices was also conducted. In each case, the statistical significance between species and the whole set of environmental variables was evaluated by Monte-Carlo test (199 permutations). Species or structural variables, plots and environmental variables were simultaneously plotted in the CCA ordination diagrams.

RESULTS

Diversity estimates were significantly correlated with both relief and some nutrients, while species richness was only correlated with nutrient variables. Nonetheless, structural attributes had a poor correlation with the relief and soil variables (Table IV.3).

On the other hand, the abundance of at least 25 species was significantly correlated with several relief, water or nutrient variables (Table IV.4). The highest correlation values

Table IV.2. Structure and diversity of the tree canopy component for the total sample and for the different land units. Mean values (± 1 SD) were estimated according to the number of plots in each land unit (three or four).

				Soil contraints	Many			Few		Some
				Major landforms	Low Hills	Intermediate Hills		High Hills		
				Morpho-pedological land units	Summit areas on granite	Summit areas on tuffs	Summit areas on conglomerates	Low slopes on granite	Intermediate on granite	High slopes on granite
		Total	Mean	Range						
STRUCTURE	Density (ind. ha^{-1})	--	1386 (347)	804 – 2117	1772 (92)	1163 (250)	1307 (111)	1297 (512)	1347 (204)	1543 (499)
	DBH (cm)	--	9.4 (1.3)	5 - 72	8.5 (3.6)	10.1 (6.6)	9.9 (5.3)	10.3 (6.5)	8.2 (3.6)	9.3 (4.6)
	Basal area (m^2 ha^{-1})	--	15.9 (5.3)	6.7 - 27.6	14.8 (4.2)	17.6 (3.5)	17.1 (3.8)	18.8 (8.9)	10.7 (4.4)	16.4 (2.6)
	Canopy height (m)	--	6.8 (2.0)	0 - 17	5.7 (1.8)	6.6 (2.3)	7.6 (2.3)	7.4 (1.8)	6.0 (1.8)	7.9 (1.9)
	Multiple-stemmed trees (%)	--	17.2 (6.7)	2 - 10	14.7 (0.4)	22.4 (10.8)	21.6 (7.9)	14.9 (5.7)	13.8 (0.7)	15.8 (6.3)
DIVERSITY	Shannon Index (ln)	--	3.08 (0.33)	2.30 - 3.47	3.17 (0.11)	3.08 (0.28)	2.69 (0.52)	2.98 (0.34)	3.19 (0.27)	3.33 (0.16)
	Simpson Index	--	14.80 (5.12)	5.2 - 24.3	16.3 (2.9)	13.8 (4.7)	9.7 (6.5)	12.4 (4.2)	17.0 (3.8)	20.0 (4.9)
	Number of species	148	44 (9)	30 - 58	45 (2)	46 (11)	38 (11)	45 (12)	43 (9)	48 (3)
	Number of genera	102	36 (7)	22 - 51	37 (0)	36 (9)	30 (11)	34 (5)	40 (10)	40 (2)
	Number of families	42	22 (4)	16 - 28	20 (2)	24 (5)	20 (6)	21 (4)	23 (4)	25 (2)

Table IV.3. Spearman correlation coefficients. Relations between the structure and diversity attributes and the relief and soil features. Significance level is showed by asterisks (* = $p < 0.05$, ** = $p < 0.001$).

		Relief		Water			Nutrients			
		Elevation (m above sea level)	Slope (°)	Depth (cm)	Clays (g/m^2)	Available water holding capacity (L/m^2)	Organic mater (kg/m^2)	Total nitrogen (kg/m^2)	Total phosphorus (g/m^2)	Exchangeable cations (eq/m^2)
STRUCTURE	Trees (#)	0.19	0.23	0.02	0.21	0.05	-0.11	0.14	-0.09	-0.03
	Basal area (m^2 ha^{-1})	-0.21	-0.11	-0.08	-0.04	0.03	0.27	0.29	0.05	0.38
	Canopy height (m)	0.10	-0.03	0.11	0.08	0.24	0.19	0.26	0.13	0.48*
	Multiple-stemmed trees (%)	-0.32	0.02	-0.25	-0.29	-0.25	-0.46*	-0.24	-0.20	-0.12
DIVERSITY	Species (#)	0.016	0.52	0.29	0.23	0.30	0.52*	0.69**	0.50*	0.53*
	Shannon index	0.34	0.65*	0.52*	0.49*	0.47*	0.46*	0.63**	0.54*	0.46*
	Simpson index	0.38	0.72**	0.57**	0.51*	0.50*	0.45*	0.59**	0.54*	0.43

Table IV.4. Spearman correlation coefficients for bivariate relationship between abundance of some dominant species with relief and soil features. Asterisks showed the significance level (* = $p < 0.05$, ** = $p < 0.001$).

	Relief		Water			Nutrients							
	Elevation (m above sea level)	Slope (°)	Depth (cm)	Clays (g/m2)	Available water holding capacity L/m2)	Organic mater (kg/m2)	Total nitrogen (kg/m2)	Total phosphorus (g/m2)	Available phosphorus (mg/m2)	Exchangeable cations (eq/m2)	Calcium (eq/m2)	Potasium (eq/m2)	Sodium (eq/m2)
Apoplanesia paniculata Presl.	-0.80**	-0.49	-0.52*	-0.51*	-0.47*	0.10	-0.12	-0.23	0.45*	0.17	0.30	-0.31	-0.35
Bourreria purpusii Brandegee	0.36	0.26	0.23	0.18	0.11	-0.11	0.06	0.10	-0.58**	-0.45*	-0.48*	0.04	0.07
Caesalpinia coriaria (Jacq.) Willd.	-0.57**	-0.51*	-0.50*	-0.40	-0.38	0.02	-0.08	-0.33	0.31	0.15	0.30	-0.32	-0.11
Caesalpinia eriostachys Benth.	-0.51*	-0.40	-0.47*	-0.54*	-0.37	0.05	-0.23	-0.29	0.17	-0.01	0.13	-0.46*	-0.23
Caesalpinia sclerocarpa Standl.	-0.34	-0.28	-0.28	-0.18	-0.15	0.06	0.13	-0.14	0.43	0.44*	0.52*	0.07	0.13
Casearia tremula (Griseb.) Wright	-0.52*	-0.40	-0.26	-0.28	-0.14	0.10	-0.06	-0.06	0.12	0.04	0.15	-0. 14	-0.13
Coccoloba sp.	0.82**	0.75**	0.38	0.18	0.37	-0.11	-0.00	0.27	-0.34	-0.10	-0.18	0.22	0.29
Comocladia engleriana Loes	-0.57**	0.43	0.29	0.34	0.22	-0.20	-0.04	0.01	-0.27	-0.21	-0.37	0.13	0.11
Cochlospermum vitifolium (Willd.) Spreng	0.23	0.30	0.45*	0.29	0.44*	-0.08	0.05	0.30	-0.21	-0.06	-0.15	0.17	0.30
Cordia alliodora (Ruiz & Pav.) Oken.	0.13	0.24	0.23	0.37	0.23	0.49*	0.64**	0.29	0.21	0.50*	0.52*	0.35	0.32
Cordia elaeagnoides DC.	0.44*	-0.53*	-0.57**	-0.54*	-0.33	-0.08	-0.40	-0.44*	0.35	0.05	0.18	-0.41	-0.48*

… continued

	Elevation (m above sea level)	Slope (°)	Depth (cm)	Clays (g/m2)	Available water holding capacity (L/m2)	Organic mater (Kg/m2)	Total nitrogen (Kg/m2)	Total phosphorus (g/m2)	Available phosphorus (mg/m2)	Exchangeable cations (eq/m2)	Calcium (eq/m2)	Potasium (eq/m2)	Sodium (eq/m2)
Exostema caribaeum (Jacq) Roem & Schult	0.79**	0.55**	0.55**	0.55*	0.48*	-0.06	0.26	0.30	-0.48*	-0.06	-0.15	0.50*	0.47
Forchameria pallida Liebm	-0.35	-0.27	-0.26	-0.16	-0.30	0.49*	0.17	-0.11	0.31	0.25	0.33	-0.06	-0.32
Gliricidia sepium (Jacq) Kunth ex Steudel	0.60*	0.27	0.54*	0.39	0.49*	-0.05	-0.02	0.30	-0.63**	-0.33	-0.42	0.21	0.28
Guapira macrocarpa Miranda	0.46*	-0.84**	0.30	0.19	0.23	0.20	0.22	0.19	-0.08	0.11	-0.04	0.17	0.27
Hauya elegans DC.	0.66**	0.66**	0.36	0.29	0.35	0.03	0.25	0.28	0.02	0.13	0.02	0.33	0.30
Helietta lottiae Chiang	0.22	0.13	0.10	0.11	-0.00	-0.14	-0.18	-0.18	-0.51*	-0.37	-0.41	-0.11	-0.10
Heliocarpus pallidus Rose	-0.76**	0.00	-0.36	-0.28	-0.37	0.28	0.14	0.01	0.49*	0.24	0.33	-0.36	-0.07
Lonchocarpus constrictus Pitt	-0.61**	-0.30	-0.38	-0.29	-0.28	0.09	0.18	-0.13	0.70**	0.50*	0.58**	-0.04	-0.11
Lonchocarpus minor Sousa	-0.72**	-0.12	-0.52*	-0.37	-0.60**	0.22	0.09	-0.20	0.58**	0 30	0.35	-0.18	-0.40
Luhea candida (DC) Mart	0.46*	0.47*	0.48	0.53	0.56**	-0.08	0.20	0.28	0.13	0.33	0.19	0.53*	0.52*
Pitirocarpa constricta (Micheli) Macbr	0.80**	0.70**	0.45*	0.53*	0.41	-0.04	0.28	0.21	-0.21	0.10	-0.04	0.48	0.32
Plumeria rubra L.	0.20	0.01	0.33	0.23	0.26	-0.13	-0.01	0.19	-0.52*	-0.36	-0.46*	0.10	0.13
Psidium sartorianum (Berg.) Ndzu	0.46*	0.11	0.23	0.38	0.26	0.10	0.15	0.08	-0.32	0.02	0.00	0.27	0.20
Rhandia turberi S Wats	-0.49*	-0.66**	-0.42	-0.35	-0.18	-0.26	-0.39	-0.34	0.13	-0 14	-0.01	-0.34	-0 29

occurred between species and relief. Positive correlations were found between elevation and abundance of *Coccoloba* sp., *Exostema caribaeum* (Jacq.) Roem. & Schult. and *Pitirocarpa constricta (Micheli)* Macbr., while negative correlations occurred with *Apoplanesia paniculata Presl., Heliocarpus pallidus* Rose and *Lonchocarpus minor* Sousa. *Gliricidia sepium* (Jacq.) Kunth ex Steudel., *E. caribaeum* and *P. constricta* were positively correlated with soil depth and water availability, and an opposite relation occurred with *A. paniculata, Cordia elaeagnoides* DC. and *L. minor* Sousa. Finally, *Lonchocarpus constrictus* Pitt. and *Cordia alliodora* (Ruiz & Pav.) Oken. showed positive correlations with some nutrients, while *Bourreria purpusii* Brandegee and *Plumeria rubra* L. were related negatively with them.

A group of 31 "indicator" species was identified through TWINSPAN classification. The majority of those species corresponds to species which were significantly correlated by bivariate correlations and were part of the five most dominant species in each plot (Chapter III; Table IV.5). Based on its presence grade and presence value, various species showed affinity by the different soil constraints classes. *Gliricidia sepium* [Jacq.] Kunth ex Steudel., *Exostema caribeum* [Jacq.] Roem. & Schult. and *Plumeria rubra* L. were compatible with the class with few soil constraints. *Cordia alliodora* [Ruiz & Pav.] Oken. and *Guapira macrocarpa* Miranda were compatible with the class with some soil constraints. The class with many soil constraints showed affinity with *Caesalpinia eriostachys* Benth., *C. coriaria* [Jacq.] Willd. and *Apoplanesia paniculata* Presl.

TWINSPAN classification based on total species showed a tendency to segregate plots into at least three groups; the first grouped sites which belonged to intermediate slopes (ISG) and one site on low slopes (LSG), all of them identified with few soil constraints (Table IV.5). The second group was defined with two sites of high slopes (HSG) and, the third group of plots distinguished by many soil constraints located in summit areas (SAT and SACG). Only the first and second classification levels were considered to reduce error of plot classification because the eigenvalues were relatively low (< 0.35; Fig. IV.1).

The results of the CCA are displayed on ordination diagrams (Fig. IV.2). Plots with a high value of a species appear to be close to the point for that species on the CCA diagram, while the arrows represent each relief or soil factor and they are plotted pointing in the direction in which variables were influenced community species variation. CCA based on total species showed an analogous pattern of plot and species ordination with CCA based only upon 31 "indicator" species (Fig. IV.2a, b). In the last CCA, plots tended to be segregated by groups throughout the first canonical axis. The groups correspond to land units of the three soil constrains classes. Plots of the class with many soil constraints were positioned on the negative extreme of the first canonical axis, plots of the class with few soil constraints were located at space amid, and plots with some soil constraints were placed on the positive extreme.

Among CCAs the strength of relations was indicated by higher values for both species-environment correlations (Table IV. 6), but only the eigenvalues of two respective first axes indicated a good dispersion of the species along those axes (λ=0.51 for total species and λ=0.50 for "indicator" species). Although similar eigenvalues were obtained, the variance explained in the CCA based on total species was smaller than variance obtained with CCA based on 31 "indicator" species. In the last CCA, the variance accounting for the two first

Table IV.5. Indicator species (bold) designated by Twinspan analysis, in relation to soil constraints classes (F=few, S= some and M=many). For code of abbreviations for morpho-pedological land units refer to the methods section.

INDICATOR SPECIES	MORPHO-PEDOLOGICAL LAND UNITS (SOIL CONSTAINTS CLASS)																					GROUPS	IMPORTANCE VALUE	SOIL CONSTRAINTS
	SAG (M)	ISG (F)	ISG (F)	SAG (M)	SAG (M)	ISG (F)	HSG (S)	ISG (F)	LSG (F)	LSG (F)	HSG (S)	HSG (S)	LSG (F)	LSG (F)	SACG (M)	SACG (M)	SAT (M)	SAT (M)	SAT (M)	SAT (M)	SACG (M)			
Luehea candida (DC.) Mart.	–	–	–	1	–	1	–	1	1	1	1	3	1	–	1	–	–	–	–	–	–	00000		
Tabebuia chrysantha (Jacq.) Nicholson	–	–	–	1	–	1	1	1	–	1	3	1	–	2	–	–	–	–	–	–	–	00000		
Schoepfia sp.	–	–	–	–	–	1	1	–	–	1	–	1	–	1	–	–	–	–	–	–	–	00000		
Lonchocarpus mutans Sousa	**3**	–	1	**2**	**2**	1	**2**	1	1	1	**2**	**2**	1	–	–	–	**1**	**1**	–	**2**	–	00001	1.93	Some-Many
Colubrina triflora Brongn.	–	–	–	–	–	–	1	1	1	1	1	1	–	–	1	–	–	–	–	–	–	00001		
Karwinskia latifolia Standl.	–	–	–	–	–	1	1	–	–	–	–	1	–	1	–	–	–	–	–	–	–	00001		
Tabebuia impetiginosa (Mart.) Standl.	1	–	–	–	–	–	–	–	–	–	1	2	–	–	–	–	–	–	–	–	–	000100		
Croton niveus Lundell	–	1	–	–	–	–	–	–	–	3	–	–	–	–	–	–	–	–	–	–	–	000101		
Lonchocarpusguatemalensis Benth.	–	–	–	–	–	–	–	–	–	1	2	1	–	–	–	–	–	–	–	–	–	000101		
Piptadenia constricta (Micheli) Macbr.	–	1	–	2	1	1	**2**	1	1	1	**3**	**3**	1	–	–	–	–	1	–	–	–	000110	1.44	Some
Bauhinia ungulata L.	–	1	–	–	–	–	–	2	1	1	2	1	–	–	–	–	–	–	–	–	–	000110		
Hauya elegans DC.	–	–	–	–	–	–	2	4	–	–	1	3	–	–	–	–	–	–	–	–	–	000111		
Gliricidia sepium (Jacq.) Kunth ex Steudel.	4	**3**	**5**	3	3	**3**	3	**3**	**3**	**1**	3	2	**2**	**1**	1	–	–	–	–	–	–	001000	4.80	Few
Exostema caribaeum (Jacq. Roem. & Schult.	1	**3**	**2**	2	1	**4**	4	**2**	**3**	**4**	3	2	**1**	–	–	–	–	–	–	1	–	001001	4.00	Few
Coccoloba sp.	–	1	–	–	1	3	**2**	1	2	–	**3**	**3**	–	–	–	–	–	–	–	–	–	001001	1.49	Some
Colubrina heteroneura (Griseb.) Standl.	–	1	–	1	–	–	1	1	3	1	1	2	–	–	–	–	–	–	–	–	–	001001		
Comocladia engleriana Loes	–	**2**	**3**	1	3	**2**	2	**1**	–	**1**	2	1	–	–	–	–	–	–	–	–	–	001001	1.60	Few
Sideroxylon stenospermum (Standl.) Pennington	1	–	**2**	2	1	**1**	2	**3**	**2**	**1**	1	2	–	–	–	–	–	–	–	–	–	001001	1.21	Few
Plumeria rubra L.	3	**4**	**5**	4	4	**3**	2	**3**	**4**	**2**	–	–	–	–	1	–	1	–	–	–	1	001010	5.12	Few
Cochlospermum vitifolium (Willd.) Spreng.	1	1	–	3	4	1	–	1	1	–	–	1	–	–	1	–	–	–	–	–	–	001010		
Esenbeckia nesiotica Standl.	1	–	2	2	1	3	2	1	–	1	1	–	–	–	–	–	–	–	–	–	–	001010		
Helietta lottiae Chiang.	**3**	1	–	**3**	**1**	2	2	–	–	–	–	–	1	–	–	–	–	–	–	–	–	001010	1.14	(Many)
Machaonia acuminata Humb. & Bonpl.	–	3	–	2	3	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	001011		
Zanthoxylum caribaeum Lam. vel. aff.	1	1	–	–	1	–	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	001011		
Thevetia ovata (Cav.) A. DC.	–	1	–	–	1	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	001011		
Bursera fagaroides (HBK.) Engl.	–	2	1	1	1	2	1	–	–	–	–	–	–	–	–	–	–	–	–	–	1	001011		
Croton alamosanus Rose	–	1	1	–	–	–	1	1	1	–	–	–	1	–	–	–	–	–	–	–	–	001011		
Lysiloma microphyllum Benth.	–	**4**	**3**	2	1	–	–	**1**	**3**	**1**	1	–	**1**	–	–	–	1	–	–	–	1	001100	1.58	Few
Diphysa occidentalis Rose	–	1	1	–	–	1	–	–	1	1	–	–	–	–	–	–	–	–	–	–	1	001100		
Bourreria purpusii Brandegee	1	**3**	**2**	2	2	**3**	3	**3**	**2**	**2**	–	–	1	–	–	–	1	–	1	1	–	001100	2.16	Few
Diospyros aequoris Standl.	1	2	–	1	1	3	1	1	1	–	–	–	1	1	–	–	–	1	–	–	–	001100		
Dalbergia sp.	–	2	–	1	1	2	1	1	2	–	1	1	–	1	1	–	–	1	–	1	–	001100		
Bursera excelsa (HBK.) Engl.	–	–	–	1	2	–	–	1	1	1	–	–	–	1	–	–	–	–	–	–	–	001100		
Bursera instabilis McVaugh & Rzed.	–	–	1	2	3	–	–	1	1	1	–	1	–	–	–	–	1	1	–	1	–	001101		
Allenanthus hondurensis Standl.	1	–	–	1	1	–	–	–	1	–	–	–	–	–	–	–	–	–	–	1	–	001101		
Bursera heterestes Bullock	2	–	–	2	1	–	–	1	1	1	–	–	–	–	–	–	–	–	–	–	2	001101		
Haematoxylum brasiletto Karst.	1	–	–	–	2	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	001101		
Lonchocarpus magallanesii Sousa	2	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	001101		
Adelia oaxacana (Muell. Arg.) Hemsl.	1	–	1	1	1	2	2	–	–	–	–	–	–	–	1	–	–	–	–	–	–	00111		
Brongniartia sp. nov.	1	–	–	1	1	1	1	–	1	–	–	–	–	–	–	–	–	–	–	1	–	00111		
Guapira macrocarpa Miranda	**1**	1	1	**2**	**1**	2	**4**	2	2	–	**3**	**2**	1	**1**	**2**	–	**1**	**2**	–	**3**	**1**	010	2.29	Some-Many
Lonchocarpus eriocarinalis Micheli.	**2**	–	–	**2**	**2**	1	1	1	–	2	1	–	–	–	–	–	**1**	**2**	–	**2**	**1**	010	1.03	Many
Guettarda elliptica Sw.	1	1	–	1	1	1	1	1	1	1	1	1	–	–	–	–	–	1	–	1	1	010		
Samyda mexicana Rose	1	1	2	1	2	1	1	1	1	1	–	1	1	–	1	–	1	1	–	1	–	0110		
Bursera arborea (Rose) Riley	1	1	1	1	1	2	1	2	2	1	1	1	1	–	1	1	1	1	1	–	–	0110		
Caesalpinia platyloba S. Wats.	1	–	1	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	0110		
Psidium sartorianum (Berg.) Ndzu.	–	**4**	**3**	2	–	**2**	2	–	**3**	**3**	2	2	**3**	**2**	1	–	1	1	–	1	–	011100	2.86	Few
Alstonia longifolia (A. DC.)	1	2	–	–	1	–	1	1	1	1	–	1	2	1	1	1	–	–	–	–	–	011100		
Hintonia latiflora Sessé & Moc. ex DC. Bullock	1	2	–	–	–	–	–	1	2	1	1	–	1	1	–	1	1	1	–	–	–	011100		
Malpighia ovata Rose	–	–	–	1	–	1	1	1	1	1	1	1	1	1	1	1	1	–	–	–	–	011100		
Ficus cotinifolia HBK.	–	–	–	–	–	–	–	2	–	–	1	–	–	1	1	–	–	–	–	–	–	011100		

… continued

INDICATOR SPECIES	MORPHO-PEDOLOGICAL LAND UNITS (SOIL CONSTAINTS CLASS)																					GROUPS	IMPORTANCE VALUE	SOIL CONSTRAINTS
	SAG (M)	ISG (F)	ISG (F)	SAG (M)	SAG (M)	ISG (F)	HSG (S)	ISG (F)	LSG (F)	LSG (F)	HSG (S)	HSG (S)	LSG (F)	LSG (F)	SACG (M)	SACG (M)	SAT (M)	SAT (M)	SAT (M)	SAT (M)	SACG (M)			
Chloroleucon mangense (Jacq.) Britton & Rose	1	**2**	**2**	1	–	–	1	**3**	**2**	**2**	1	–	**2**	–	2	1	1	1	1	2	1	011101	1.65	Few
Ipomoea wolcottiana Rose	**3**	1	1	**2**	**1**	1	1	1	2	1	–	1	1	–	**2**	–	**1**	**1**	**1**	**3**	**2**	011101	1.54	Many
Erytrhroxylum rotundifolium [illegible]	–	2	–	1	1	1	1	1	1	1	1	–	2	1	–	1	1	1	–	1	–	011101		
Leucaena lanceolata S. Wats	–	–	1	1	–	–	–	–	1	–	–	–	–	–	–	–	–	1	–	1	–	011101		
Erythroxylum mexicanum HBK.	–	1	–	1	–	1	–	–	1	2	1	1	1	1	1	1	–	1	–	–	1	01111		
Amphipterygium adstringens [illegible]	–	–	–	**2**	**2**	–	–	2	1	–	–	–	–	–	**1**	–	**2**	–	**1**	**1**	**2**	1000	0.79	Many
Caesalpinia caladenia Standl.	1	–	–	1	1	–	–	1	–	–	–	–	–	–	–	–	1	–	2	–	–	1001		
Esenbeckia berlandieri Baill.	–	–	–	–	–	–	1	–	–	1	1	–	–	–	–	–	1	1	–	–	–	1001		
Lonchocarpus cochleatus Pitt.	–	–	–	–	–	–	–	–	–	1	1	–	–	–	–	–	–	1	1	–	–	1001		
sp. 1	–	1	–	–	1	1	1	1	1	1	1	–	1	1	1	–	1	1	1	1	1	10100		
Erythrina lanata Rose	–	–	–	–	1	–	–	1	2	1	–	–	–	1	1	–	1	–	1	1	1	10100		
Cordia alliodora (Ruiz & Pav.) Oken.	**1**	1	–	**2**	–	–	**2**	1	2	3	**3**	**3**	3	3	**2**	–	**3**	**3**	–	**3**	–	10101	2.96	Some-Many
Croton pseudoniveus Lundell	–	–	–	–	–	–	–	1	1	1	2	1	1	2	1	–	1	1	–	1	–	10101		
Capparis indica (L.) Fawc. & Rendle	–	–	–	–	–	–	–	–	–	–	2	1	1	1	–	–	1	1	–	–	–	10101		
Randia thurberi S. Wats	1	1	1	1	1	–	–	–	1	1	–	–	1	1	2	1	–	1	2	–	1	1011		
Jatropha chamelensis Pérez-Jiménez	1	–	1	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	1011		
Casearia tremula (Griseb.) Wright	1	–	–	1	–	–	–	1	2	1	–	–	1	1	2	1	1	1	2	1	1	110000		
Lonchocarpus sp.	1	–	–	–	1	–	1	–	–	1	1	–	–	1	1	1	1	1	1	1	–	110000		
Lonchocarpus constrictus Pitt.	**1**	–	1	**1**	**1**	–	1	1	–	2	1	1	1	2	**3**	**5**	**3**	**4**	**2**	**2**	**1**	110001	3.99	Many
Caesalpinia sclerocarpa Standl.	–	–	–	–	–	–	–	–	–	2	1	1	**3**	**1**	**2**	**3**	**2**	**1**	–	**2**	**2**	110001	1.67	Many
Caesalpinia eriostachys Benth.	**4**	–	–	–	**1**	–	2	–	–	–	3	2	**5**	**5**	**5**	**3**	**4**	**5**	**5**	**4**	**5**	11001	12.08	Many
Jacquinia pungens A. Gray	–	–	–	–	–	–	–	1	–	1	1	–	1	1	**2**	**2**	**1**	**2**	–	**2**	**1**	11001	0.86	Many
Forchhammeria pallida Liebm.	–	–	1	–	–	–	–	–	–	–	1	–	1	2	–	1	1	2	–	1	–	11001		
Acacia cochliacantha Humb. & Bonpl.	–	–	2	–	–	–	–	–	–	1	–	–	–	–	–	2	–	–	–	–	4	11010		
Jacaratia mexicana A. DC.	–	–	–	–	–	–	–	1	–	–	1	–	–	–	**1**	**2**	**2**	**2**	–	**1**	–	11010	0.57	Many
Jatropha malacophylla Standl.	–	–	1	–	–	–	–	–	1	–	–	–	–	–	1	1	1	–	2	1	1	11010		
Ceiba grandifolia Rose	1	–	–	–	1	–	1	–	–	–	–	–	–	–	–	–	1	1	1	1	1	11010		
Cnidosculus spinosus Lundell	1	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	1	2	–	–	–	11011		
Recchia mexicana Moc. & Sesse	–	–	–	–	–	–	–	–	–	–	–	–	1	3	1	–	–	–	–	–	–	111000		
Cordia sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	3	–	–	–	–	–	111000		
Cordia elaeagnoides DC.	–	–	–	–	–	–	–	–	–	–	–	–	**2**	**3**	**4**	**4**	–	**3**	**2**	–	**1**	111001	2.27	Many
Pithecellobium unguis-cati (L.) Mart.	–	–	–	–	–	–	–	–	–	–	–	–	1	1	–	1	1	–	–	–	1	111010		
Trichilia trifolia (C. DC.) Pennington	–	–	–	–	–	–	–	–	–	1	–	–	–	2	–	1	–	1	–	1	–	111011		
Caesalpinia coriaria (Jacq.) Willd	–	–	–	–	–	–	–	–	–	3	–	–	**2**	**2**	**2**	**1**	**1**	**2**	**2**	**3**	**5**	111011	3.44	Many
Apoplanesia paniculata Presl.	**2**	–	–	–	–	–	–	–	–	–	–	–	1	1	**3**	**4**	**3**	**2**	**4**	**3**	**2**	111011	3.02	Many
Ruprechtia fusca Fern.	1	–	–	–	–	–	–	–	–	–	–	–	1	1	2	1	2	1	1	1	1	111011		
Casearia corymbosa HBK.	–	–	–	–	–	–	–	–	–	–	–	–	1	–	1	1	1	1	–	–	1	111011		
Achatocarpus gracilis H. Walt.	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	1	–	1	–	1	1	111011		
Chlorophora tinctoria L. Gaud.	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	1	1	1	–	1	–	111011		
Lippia mcvaughii Mold.	–	–	–	–	–	–	–	–	–	–	–	–	1	1	–	–	1	–	1	1	–	111011		
Thouinia paucidentata Radlk.	–	–	–	–	–	–	–	1	–	–	–	–	**2**	–	**1**	–	**2**	**2**	–	**1**	–	11110	0.46	(Many)
Ruprechtia pallida Standl.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	2	–	–	11110		
Caesalpinia pulcherrima (L.) Sw.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	–	1	1	–	111110		
Heliocarpus pallidus Rose	**1**	–	–	–	–	–	–	–	–	–	–	–	–	–	**2**	–	**3**	**1**	**4**	**3**	–	111110	1.55	Many
Lonchocarpus minor Sousa	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	**2**	**1**	**1**	**3**	–	111110	0.65	Many
Jatropha standleyi Steyerm.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	**3**	–	**1**	**2**	–	111110	0.51	(Many)
Coccoloba liebmannii Lindau	–	–	1	–	–	–	–	–	–	–	–	–	–	–	1	–	1	2	1	1	1	111110		
Spondias purpurea L.	**1**	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	**2**	**1**	**2**	**2**	**1**	111110	0.50	Many
Gyrocarpus jatrophifolius Domin.	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	1	1-		111111		
	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1			
	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	1	1	1	1	1			
	0	1	1	1	1	1	1	1	1								0	0	0	0	1			
		0	0	1	1	1	1	1	1															
				0	0	0	0	1	1															

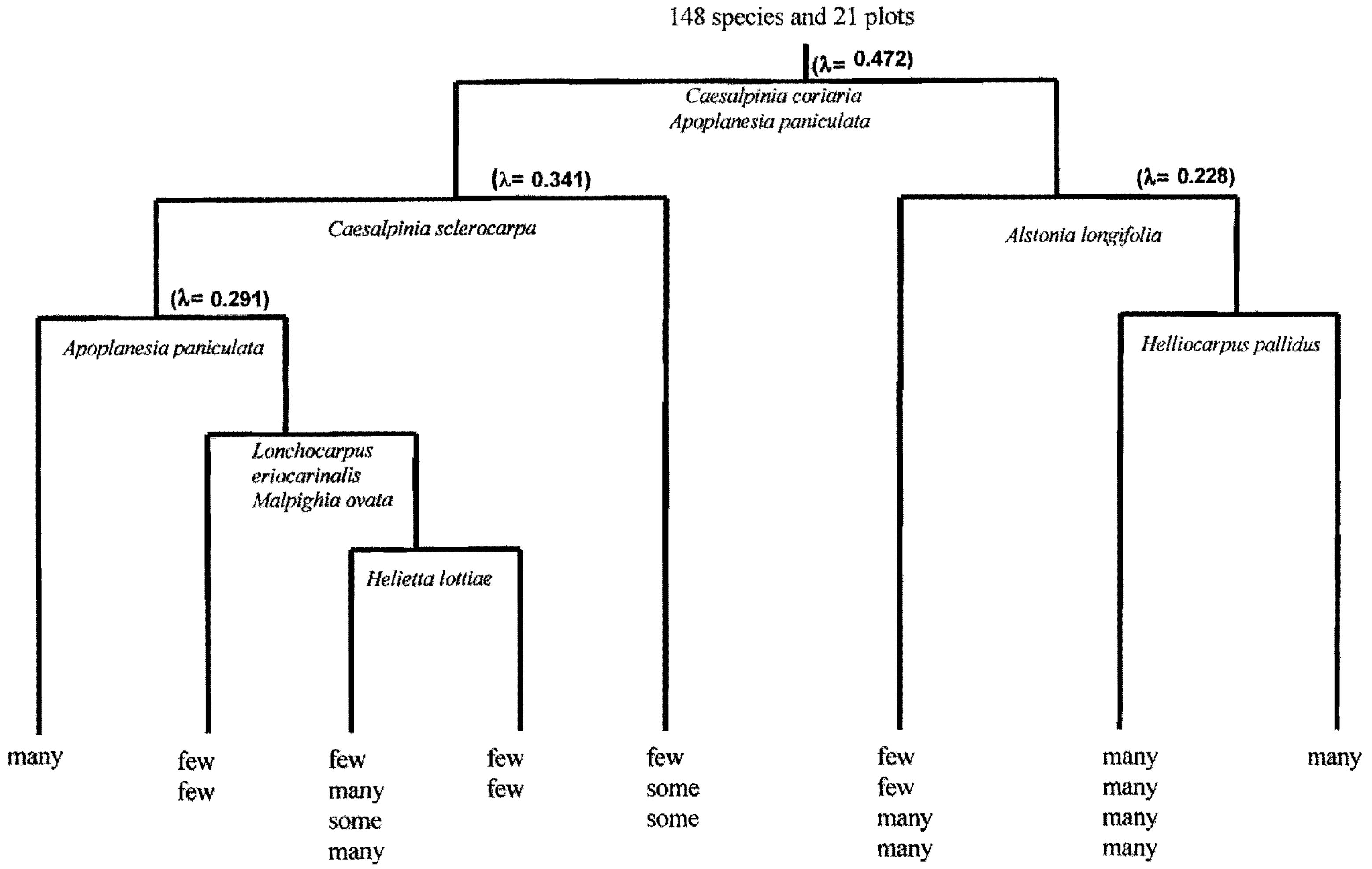

Figure IV.1. Plots classification with a two ways indicator species analysis (TWINSPAN). Words below dendrogram branches indicate plots and the corresponding soil constraints class. Indicator species which separate groups are specified in each division.

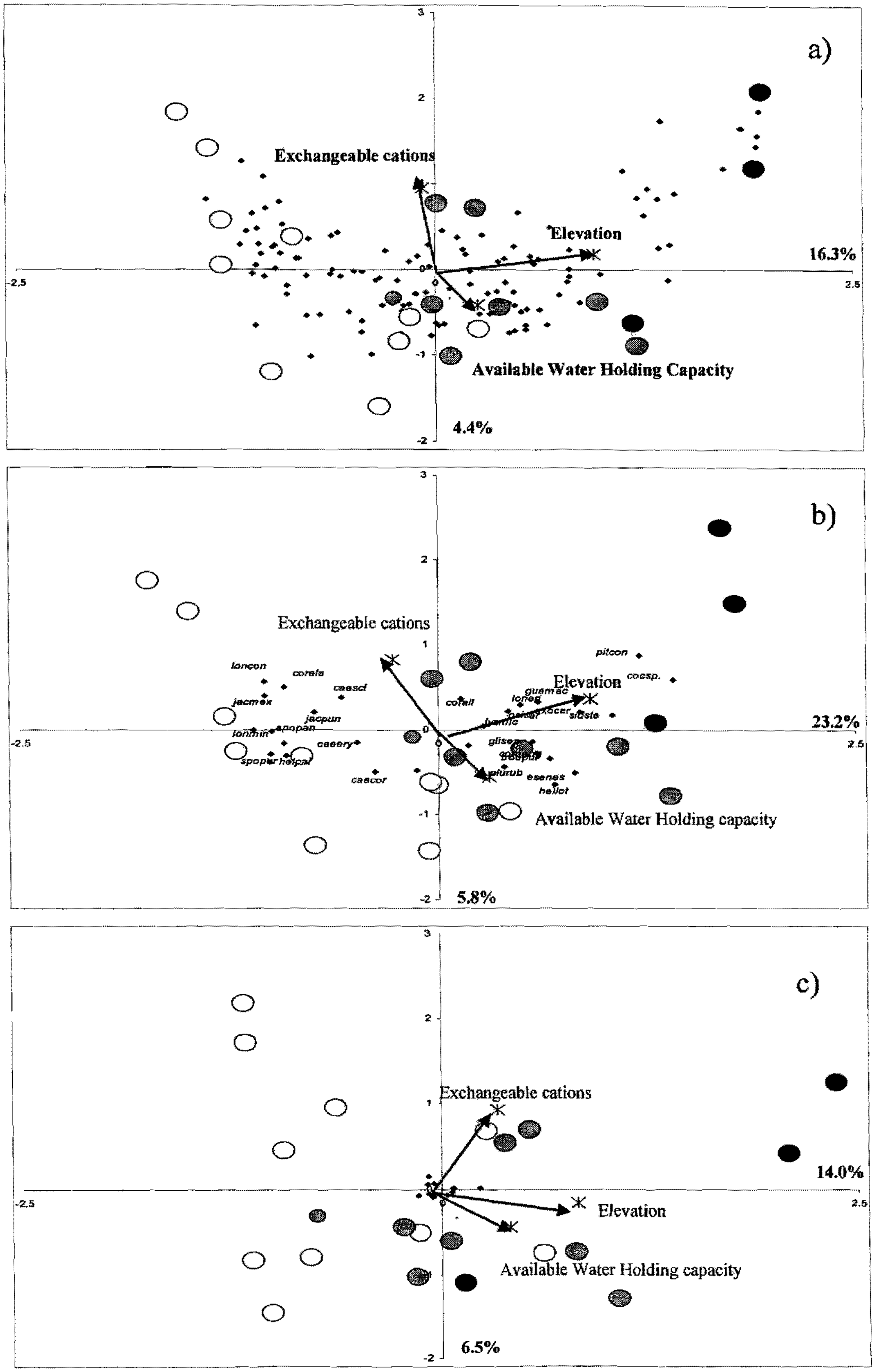

Figure IV.2. Canonical correspondence analyses triplots for a) total species-environment, b) indicator species-environment and c) structure-environment. Diamonds in a) and b) correspond to species, while in c) distinguish structural features. The arrows and asterisks show environmental variables. Circles represent plots, white colour is for many soil constraints, grey for few constraints and black identified to plots with some constraints.

Table IV.6. Summary of canonical correspondence analysis (CCA) for 31 species in 21 plots in a TDF at Chamela.

Main matrix	Second matrix	Species-Environment Correlations			Eigenvalues			% Cumulative explained variance			Total inertia
		Axis 1	Axis 2	Axis 3	λ_1	λ_2	λ_3	Axis 1	Axis 2	Axis 3	
Species composition (148)	Site variables (3)	0.93	0.80	0.79	0.51	0.20	0.11	16.3	22.7	26.0	3.14
Species composition (31)	Site variables (3)	0.87	0.73	0.63	0.50	0.13	0.09	23.2	29.0	33.0	2.16
Structure attributes (11)	Site variables (3)	0.71	0.38	0.31	0.01	0.005	0.001	14	20.5	21.5	0.073

axes was 29%. Elevation was significantly correlated with the first canonical axis ($r = 0.80$; $p<0.05$) and exchangeable bases were correlated with the second axis ($r=0.64$; $p<0.05$). The Monte Carlo tests carried out for the first canonical axis was statistically significant ($F=5.122$, $p<0.005$), such as occur with the significance of all canonical axes ($F=2.795$, $p<0.005$). These results showed a significant relation between the species and environmental explanatory variables.

The CCA done with the structural matrix showed a weak relationship between structural attributes and environmental variables (Fig. IV.2c). Others additional CCAs based on indicator species matrix, in which C:N or phosphorous were included as nutrient variables in the environmental matrix, showed that the available water holding capacity was the variable of secondary importance after elevation. In those analyses, plots distribution tendencies, species, and explained variance percentages were nearly comparable with the result obtained by using exchangeable bases in the environmental matrix, which are shown in Figure IV.2b.

DISCUSSION

TDF at Chamela exhibits a large heterogeneity in structure, composition and diversity in the tree communities, in addition to a complex environmental mosaic. Results suggested that elevation and some soil characteristics explain spatial differences in the arboreal dominant component.

Despite the controversy on relationships between soil nutrients and species richness (Huston 1980, Tilman 1982, Gentry 1988), we found that species richness and other diversity indices were positively correlated with physical variables (soil nutrients, available water holding capacity and slope). However, correlations did not occur between structure and relief and soil factors, which were relatively consistent with results for one Caribbean dry forest (Gonzalez & Zak 1996).

At least 25 dominant species exhibited significant bivariate relationships with relief and soil characteristics, suggesting that the presence of some species might be conditioned by relief and soil features. Significant correlations provided us an approximation to recognize the importance of relief and soils, which was reaffirmed by the CCA test. Also some species proved to be more abundant in specific environmental conditions; however, we are aware that significant correlations are difficult to explain, in an ecological sense, as well the lack of correlation (Sollins 1998). Although there were attempts to understand the processes to establish and develop in particular tree species (Martijena 1993, Huante 1996), still other studies are necessary.

Based on species composition, TWINSPAN analysis separated plots by lithology (granite and non-granite), as did the principal component analysis showed in Chapter III. These lithology differences in Chamela tended to be associated with soil constraints classes. Also, lithology was shown as a key factor in explaining the differences in species composition in other Mexican TDFs (Pérez-García 2002) and dry vegetation in the Baja California Peninsula (Villers-Ruíz *et al.* 2003). TWINSPAN allowed for the detection of "indicator" species, which in accordance with soil constraints classes, were dominant in the canopy, and a large portion of them were well-correlated with relief and soil variables.

Based on "indicator" species, results of the CCA showed that the most dominant species summarized an important portion of variance on canopy. This suggested that the distribution of dominant species could not be at random. CCA results showed that a fraction of the variance in the species composition at the Chamela TDF could be explained by elevation, available water holding capacity and exchangeable bases (29%). Spatial heterogeneity of species composition on TDF landscapes and the importance of elevation, topography or lithology have been previously reported (De Wolf 1998, Killeen *et al.* 1998, Vázquez & Givnish 1998, Villers-Ruíz *et al.* 2003). As expected at the mesoscale level (Perry 1994), relatively few environmental factors explained differences in the tree community.

Species and plots were distributed in a continuum on ordination diagrams, which suggest that a gradual transition in tree species is occurring rather than discrete contrasts. The percentage of explained variance in the CCA based on "species" and "environmental" matrices were relatively low, but it should not be interpreted ecologically as non-significant (ter Braak & Smilauer 1998). Similar or lower percentages have been obtained from CCA in other tropical forests (Oliveira-Filho *et al.* 1994, Duivenvoorden & Lips 1995, De Wolf 1998, Trejo 1998, Villers-Ruíz *et al.* 2003), but the most important issue of these analyses is their value to identify those factors which explain the complex patterns in tropical plant communities.

Elevation was the variable most correlated with the first canonical axis. Although elevation rank in TDF is shorter than other humid tropical forests (Gentry 1988), elevation should be taken into account to analyze differences in structure and composition, because elevation even at ten or hundred of meters may promote important differences or gradients in humidity, nutrients and micro-weather conditions (Coughenour & Ellis 1993, Sussman & Rakotozafy 1994, Mooney *et al.* 1995, Sampaio 1995, De Wolf 1998, Killeen *et al.* 1998, Oliveira-Filho *et al.* 1998, Vázquez & Givnish 1998).

At the local level, in the micro-basins system at Chamela elevation has been clearly associated with structural and compositional differences (Galicia *et al.* 1999, Segura *et al.* 2003). In regional studies, Salas (2002) and Villers-Ruíz *et al.* (2003) found that elevation influenced floristic variations; at a macro-regional level, however, elevation does not explain floristic differences in 20 Mexican TDFs (Trejo 1998). At Chamela, elevation was more significant than other specific soil variables, which may be related with the two most different levels distinguished; one, related with hills on tuffs and conglomerates located between 110-200 m above sea level, and two, an important landform on granite was above 300-500 m (cerro "Maderas"). Elevation rank at Chamela seems to be ecologically important because it integrated many other conditions associated to elevation steps, especially differences in soil constraints (Chapter II). It is possible that other micro-weather conditions could be related to elevation, but landforms and exposition slope neither do nor suggest that an environmental gradient like as reported for the micro-basins system (Galicia *et al.* 1999) occurs along 100 to 540 m elevation at the Chamela Biological Station.

Available water in soil has been considered among the most important limiting factor for plant development in TDF (Mooney *et al.* 1995). However, a CCA showed that exchangeable bases were the best explanatory variable, more than available water holding capacity, it results is according to suggestion that nutrients increase in importance when species are tolerant or can adapt to hydric stress (Murphy & Lugo 1986, Borchert 1994, Eamus 1999). However, when phosphorous or C:N ratio were used to represent the nutrient variable, available water holding capacity was more important in explaining variance in the dominant species composition among plots. A possible reason for this result is that those nutrients present continuous fluctuation and pulses in the soil system or are limitless in these ecosystems (Campo 1995, Jaramillo & Sanford 1995).

The partial explanation resultant (29%) suggests the need to explore other explanatory variables of the variance in dominant species composition found along the landscape. Disturbance has been highlighted among factors which influence differences in diversity and the distribution and abundance of tree species (González & Zak 1996). So, in an attempt to explain spatial differences in composition we tried to explore through tree mortality, assuming that tree mortality will be an indicator of disturbance (Chapter V). Other factors beyond the scope of this study which are deemed significant for spatial variance among woody plant in TDF forests are biotic interactions, demographic mechanisms, and biogeographic processes (Trejo 1998, Kelly & Bowler 2002, Lott & Atkinson 2002).

In this study, the plots ordination based on structural variables was not in agreement with the soil constraints land units, and lacked of correlations with relief and soil features. Plots and structure attributes exhibited a middle position between two first canonical axes. Besides, a low percentage of variance explained and a lower eigenvalues for the canonical axes were resulted. This result was according to the lowest bivariate correlation among relief, soil and structural variables. However, our results contrast with the relations found among structural attributes and elevation gradient, slope, and water content in the micro-basins system a Chamela (Galicia *et al.* 1999, Segura *et al.* 2003) and in other Mexican TDFs (Salas 2002). These differences could be attributed to the elevation gradient, being that those examples have a lower boundary to humid tropical forest, while in our plots, such extreme transition never occurred. Thus, the environmental mosaic at Chamela could present at least two scales: local and mesoscale levels. Local level reflects the small topographic gradients and the other level is related with lithology, elevation and soil constraints variations.

This study was a first attempt to understand an overall relation between the TDF tree community and the relief and soil mosaic across the landscape at Chamela. Here, some ideas about the ways as tree species and relief and soil features may be related were provided. Like other studies on tropical forests (Oliveira-Filho *et al.* 1994, Duivenvoorden & Lips 1995, De Wolf 1998, Trejo 1998, Villers-Ruiz *et al.* 2003), we conclude that the relief and soil mosaic is important to explain diversity and compositional differences in tree canopy, yet only partially explain it.

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CAPÍTULO V

TREE MORTALITY PATTERNS IN A MEXICAN TROPICAL DECIDUOUS FOREST AND THEIR IMPLICATIONS ON ITS CANOPY NATURAL DYNAMICS

ABSTRACT

The purpose of this study was to characterise tree mortality patterns in the tropical deciduous forest at Chamela, Mexico, to relate them to relief and soil mosaic, and to analyse their implications for forest dynamics. The study was conducted on 21 permanent plots (0.24 ha) distributed among six morpho-pedological land units. In July 1995, we recorded the stock of dead trunks ≥ 5 cm DBH on each plot, either dead or partially dead trees ("initial record"). Five seasonal evaluations of tree mortality ("seasonal records") and of new tree living recruitment into the ≥ 5 cm DBH were carried out at the end of the three rainy seasons (December 1995, 1996, 1997), as well as two dry seasons (June 1996, 1997). We recognized five death conditions: (I) standing dead, (II) fallen dead, (III) standing dead, sprouting at base, (IV) fallen dead, sprouting at base, (V) individuals with both dead and living trunks. The initial record of dead woody component represented 32% of all trunks ≥ 5 cm DBH on the plots, a 2:1 live to dead trunks ratio. 79% of the initial record occurred as standing dead trunks, these were randomly distributed within plots and only a 30% of them were clearly associated with canopy gaps.

The standing death condition was higher in the seasonal records of dead trees (95%). Nearly 70% of the initial record and 60% of the seasonal records did not have any potential to resprout based on a total lack of living tissues, suggesting that both resprouting and establishment from seeds are important processes in this forest. Mortality was higher during the rainy seasons than in the dry seasons and treefall direction corresponds to wet season winds. There was no evident equilibrium between the quantity of dead trees and living new recruited trees, or between the most prominent species dying and recruiting. Plots were ordinated by a principal component analysis based on a matrix with variables of the initial and seasonal records of dead trees. Plots location on the ordination space was not related to their corresponding morpho-pedological unit and soil constraints land unit. Correlations between the two first canonical components with relief and soil features were not significant. However, the principal component axes were well correlated with structural attributes of the living tree component (canopy height and frequency of multi-stem trees). The dynamic of the canopy at the tropical deciduous forest at Chamela is complex and differ from the gap dynamic widely described for tropical humid forests since a higher percentage of trunks die and remain standing.

KEY WORDS: *Tree death, recruitment, natural forest dynamics, Chamela Mexico.*

INTRODUCTION

Tree mortality in a forest is an ecologically important phenomenon, because it releases resources and growing space (Franklin *et al.* 1987) and helps maintain to micro-environmental conditions (Putz 1983, Hagan & Grove 1999). Thus, tree mortality may promote the persistence of a regeneration mosaic (Grubb 1977, Whitmore 1978, Brokaw 1982, Clark

1990). As a collective phenomenon on the forest, the tree mortality is expressed by the amount of tree necromass, conditions or type of death among individuals, and their distributions in space and time (Lorimer 1985, Foster & Boose 1995). At the landscape level, mortality patterns are presumably affected by the environmental mosaic promote by geomorphology (lithology, relief and morpho-dynamic processes) and soil heterogeneity as well as by the extent and intensity of disturbance effects (e.g. pests, herbivore, droughts, landslides, wind, fires or flooding; Shugart 1984, Rykiel 1985, Turner 1987, Michener *et al.* 1998).

Studies on tree mortality patterns and natural dynamics in tropical forests have been mostly performed in humid forests and focused at local levels (Putz 1983, Hubbell & Foster 1986, Popma *et al.* 1988, Kapos *et al.* 1990, Samper 1992, Denslow & Hartshorn 1994, Martínez-Ramos 1994, Condit *et al.* 1995). However, there is a striking lack of information on tree mortality and natural dynamics for tropical deciduous forests (TDF; Gerhardt & Hytteborn 1992, Josse 1994, Mooney *et al.* 1995, Harmon *et al.* 1996, Segura *et al.* 2003). The gap dynamic model developed for humid tropical forests (Whitmore 1978, Brokaw 1982, Putz 1983, Hubbell & Foster 1986, Poorter *et al.* 1994, Gale & Barfod 1999) might not be applicable to TDFs, owing to the marked seasonality of the regions where they thrive and because the particular structural, phenological and physiological attributes in their tree communities (Murphy & Lugo 1986a, Bullock & Solís-Magallanes 1990).

The lack of understanding of tree mortality patterns and natural dynamics is a serious problem, considering the large extent of these ecosystems in the intertropical regions of all continents and their critical conservation status (Murphy & Lugo 1986a, Janzen 1990, Mooney *et al.* 1995, Trejo & Dirzo 2000, Velazquez *et al.* 2002). Detailed information on both phenomena is necessary because it can provide bases for a better management through recognized the natural processes in a forest (Harmon *et al.* 1986, Spies *et al.* 1988, Bakker *et al.* 1996).

Although the TDF at Chamela is among the best investigated sites in Mexico (Noguera *et al.* 2002), we have still a poor idea about tree mortality and natural forest dynamics (Durán *et al.* 2002, Maass *et al.* 2002b, Segura *et al.* 2003). Since Chamela is located near the Pacific coast, the rainy season is regularly accompanied by winds of cyclonic storms (Bullock 1986, García-Oliva *et al.* 1995). During these climatic events, wind can uproot or break trees, such as commonly occurs in other tropical forests (Dittus 1985, López-Portillo *et al.* 1990, van Bloem *et al.* 2003). In the four to eight month long dry season, water stress increases while net radiation remains high (Maass *et al.* 2002a). Consequently, internal water reserves in trees can be crucial to trees survival until the following rainy season (Schulze *et al.* 1988, García-Oliva *et al.* 2002). It is therefore likely that during the dry season standing could be a common form of trees to die, while during the rainy season trees can die fallen. Both water stress and wind effects may be extended in time or exacerbated in space by the influence of microclimate, lithology, topography and soil features (Turner 1987, Michener *et al.* 1998, Arriaga 2000). Based on these arguments, morpho-pedological land units may be significant determinants of spatial variation in the tree mortality patterns. Furthermore, tree necromass patterns are likely related to the spatial differences in the soil constraints at Chamela (Chapter II).

The purpose of this study was to document tree mortality patterns in the TDF at Chamela, Mexico, and to analyse them in relation to the relief and soil mosaic, and its different morpho-pedological and soil constraints land units. Mortality and recruitment patterns in the dry and rainy seasons were also investigated for the purpose of examining their implications for forest dynamic.

METHODS

Sampling methods

In 1995, 21 permanent plots (0.24 ha; 30 X 80 m) were established on six morpho-pedological land units in the Chamela Biological Station: 1) Summit areas over granite (SAG), 2) Summit areas over tuffs (SAT), 3) Summit areas with a conglomerate cover on granite (SACG), 4) Low rectilinear slopes over granite (LSG), 5) Intermediate rectilinear slopes over granite (ISG), 6) High rectilinear slopes over granite (HSG). The relief and soil features in each land unit were known and these land units correspond to three categories of "soil constraints" derived from multivariate analysis (Chapter II): few (LSG and ISG), some (HSG) and many (SAG, SAT and SACG). Selection criteria of these land units considered that they represented different combinations of geoform and soil type at the Chamela Station.

In each plot, we recorded living and dead trunks with DBH (1.3 m high) ≥ 5 cm. Dead trunks were recorded at the beginning of the rainy season in July 1995, which represented the mortality accumulated over an unknown period. These are named as "initial dead trees record" in this study. The evaluations of mortality continued during five subsequent seasons through the monitoring of trees originally tagged as live in all 21-plots. Monitoring was performed at the end of the rainy seasons in December of 1995, 1996 and 1997, as well as at the end of the dry seasons in June of 1996 and 1997. Dead trunks data originated by this seasonal monitoring was named as "seasonal records". A careful examination of individual trees with dead trunks both for the initial and seasonal records allowed us to distinguish three different kinds: 1) the whole tree was dead, which was confirmed by the lack of living cambium at the base of the trunk or along the root system; 2) the main trunk was dead but the tree had already resprouted at its base; 3) the tree had at least one dead and one live trunk. In some cases when there were doubts about the condition of an individual tree, confirmation of its assigned status was obtained throughout subsequent monitoring.

We measured DBH of all dead trunks in both completely or partially dead trees (considering that the latter expression is legitimate for modular organisms; Harper 1977). In all cases, we determined whether the death of trunks had produced a canopy gap, referred it as an open space at least 12 m^2 (radius = 2 m) projected in relation the crown position. A distinction was made between standing and fallen dead trunks. For the latter, the fallen direction was also recorded. Each dead trunk was assigned to one of four rank decomposition categories (Table V.1). In each plot, all records of dead trunks were mapped in Cartesian coordinates, based on a 10 x 10 m grid. During the seasonal evaluations of dead trees, all live recruitments trees which newly enter to the DBH ≥ 5 cm class were recorded and tagged, their DBH measured, and their identity noted.

Table V.1. The decomposition categories assigned to dead trunks.

Decomposition categories	Description
A	Trunk without sprouts, with a complete bark and fine branches (diameter ≤ 3 cm). The bark did not show evidence of decomposition.
B	Trunk with bark, but without sprouts or fine branches (diameter ≤ 3 cm). The bark did not show evidence of decomposition.
C	Trunk with only portions of bark, and without sprouts and fine branches (diameter ≤ 3 cm). The trunk showed evidence of incipient decomposition.
D	Trunk with traces of bark. The trunk showed only principal branches (direct elongations) and generalized decomposition.

Data analysis

The trunk fall direction data were analysed using statistics for circular distributions (Batchelet 1981). Mean angles were determined with F-tests and $\chi 2$ circular tests were performed to determine whether significant differences occurred.

An exponential function was used to calculate the annual mortality rate (Sheil *et al.* 1995):

$$r = (C_t / C_0)^{1/t} - 1$$

where r= annual mortality rate, t=time in yr since first sampling, C_t=population size after t yr , C_0=initial population size. "Turnover" measured as the stand half-life of the initial population (Körning & Balslev 1994) was calculated as:

$$t½ = \ln(0.5) / \ln(1-r)$$

A single trunk diameter frequency distribution, including both live and dead trunks, was obtained for all plots by using four diameter classes, with 5 cm intervals, and a further class which included all trunks with DBH > 25 cm clumped. This frequency distribution enabled us to compare the largest probability of death among size classes.

The spatial distributions of dead trunks in each plot were analysed through simulations produced by Ripley's L function for several distance ranges; this allowed testing the null hypothesis of a random spatial distribution of dead trunks within the plots (Haase 1995).

In order to determine if the necromass content and mortality dynamics were related to morpho-pedological land units, we performed two multivariate analyses (Jongman *et al.* 1995), a principal component analysis (PCA) and a canonical correspondence analysis (CCA). For that purpose, a "mortality" matrix was organized with nine variables. Three of the variables belonged to the initial record of dead trees: its total basal area, number of trunks in condition I and II (see Fig. V.1), and number of dead trunks with resprouts and multiple-stemmed trees (conditions III, IV and V). The remaining six variables belonged of seasonal records (total basal area, number of trunks in condition I and II, number of trunks with resprouting and multiple-stemmed trees, numbers of trees dead in dry season, numbers of trees dead in wet season, and the percentage of annual mortality).

Other "environmental" matrix included six variables: elevation, stoniness, water holding capacity, C:N ratio, phosphorous, and exchangeable bases. Prior to performing the PCA we checked the "mortality" matrix, extreme values and lack of multicolinearity within correlation matrices. To establish relationships between PCA axes defined by mortality variables and relief, soil and structural characteristics, simple linear correlations were performed. CCA simultaneously analysed "mortality" and "environmental" matrices (ter Braak & Smilauer 1998), and included a statistical significance analysis of the relation between the mortality and environmental variables by Monte Carlo permutation tests.

Also, differences in density and basal area of the initial and seasonal records among three classes of soil constraints were tested by analysis of variance. In order to test climatic influence on seasonal mortality record, a correlation analysis was performed with the

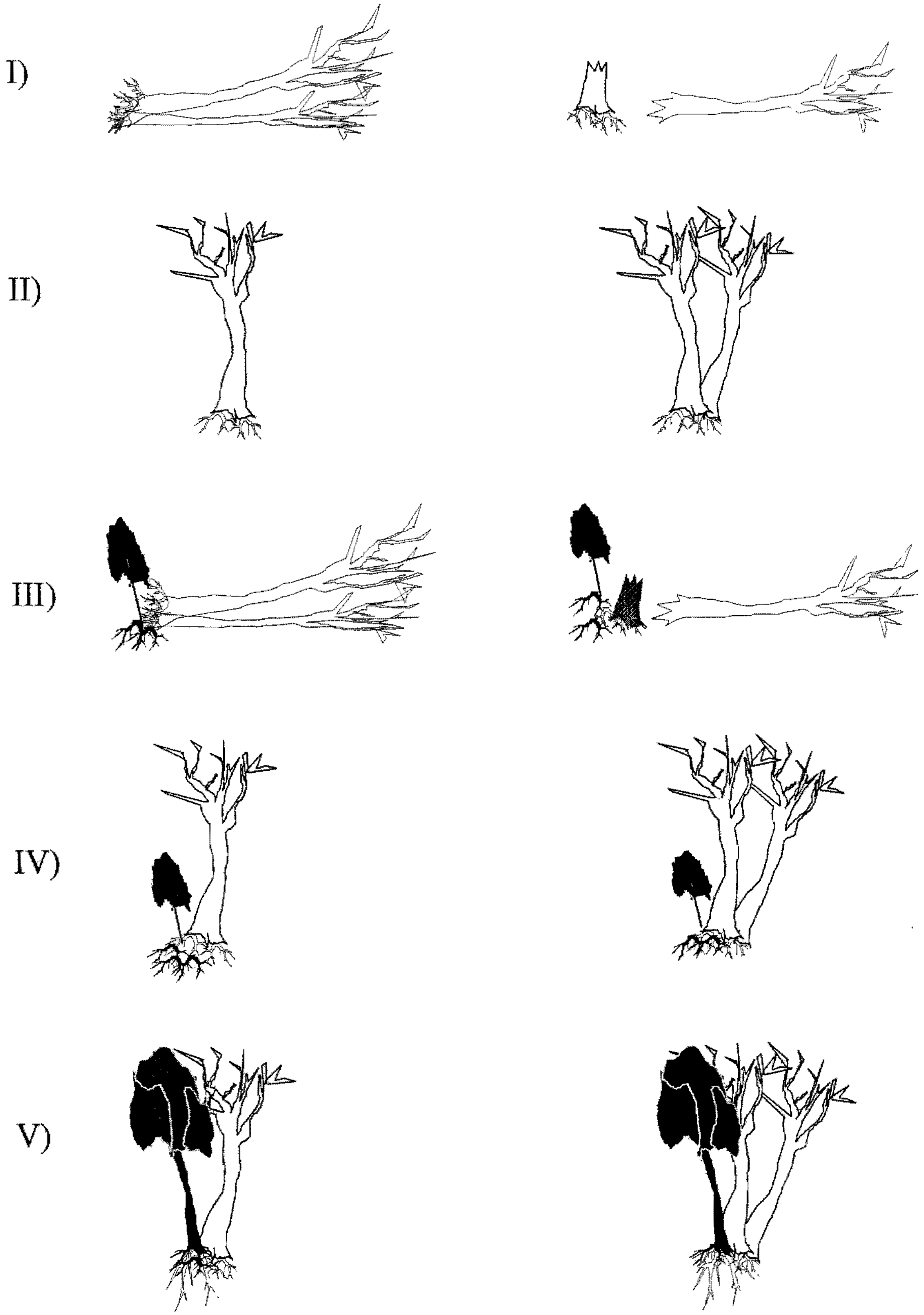

Figure V.1. Five death conditions in the tree community at the Chamela TDF. The I and II conditions correspond to dead trees, and III, IV and V conditions represent living trees with necromass in their trunks.

respective precipitation records in rainy and dry seasons which occurred during the analyzed period.

RESULTS

General patterns

Density of the initial record of dead trees was 647 dead trees ha^{-1}, and its basal area was 7.46 m^2 ha^{-1}. This represented approximately 32.5% of the total trunks (live and dead) with DBH $\geq$ 5 cm in all plots, and a similar percentage with respect to basal area (live and dead). In the seasonal records, overall 432 tree individuals with trunks DBH $\geq$ 5 cm were found dead. Thus, the mean annual rate of death was 2.5% and this represented 1.5% of their living basal area. Percentual rank of the initial record, as a proportion of the live tree component, was variable among plots and fluctuated between 32 to 55%. A narrower rank was obtained for seasonal records of dead trees in relation to live trees (4.5 to 7.6 %).

Most dead trunks in the initial record were in an advanced state of decomposition: 74% of them were assigned to the C and D decomposition categories (without bark and fine branches, and with clear wood decomposition). In contrast, a large part of seasonally records contained dead trees in a status of early decomposition (92%; A-decomposition category). With the exception of one individual tree of *Lonchocarpus mutans* (Sousa), which was found dead after having been seen with a severe fungal infection, neither other trees died during the study period showed damage apparently caused by other trees or by pathogens. However, some of the trees seemed to have lost vigour sometime before the date when their death was noted. For these, an advanced decomposition in their trunks was noted (8%; B-D categories).

Based on an analysis of the condition of the dead trunks (standing or fallen and presence or absence of living tissues), we classified them according to five death conditions (Fig. V.1): (I) fallen dead trees, uprooted or snapped below a height of 1.3 m; (II) standing dead trees; (III) trees with fallen dead trunks with resprouts or showing living cambium at the base and/or subterranean portions; (IV) trees with standing dead trunks with resprouts or showing living cambium at the base and/or subterranean portions; and (V) trees with dead fallen and/or standing trunks which also have live trunks with DBH $\geq$ 5 cm. Only the conditions I and II included fully-dead trees. For the initial record, standing dead trees prevailed (II; 47.7%); this condition, together with the other two characterised by the presence of standing dead trunks (IV and V), made up for nearly 70% (Fig. V.2a). These three death conditions also prevailed for the seasonal record, where they accounted for almost 95% of all dead trees (Fig. V.2b). Condition I was second most important for the initial record of dead trees (30%), and jointly with condition III (also fallen trunks), accounted for approximately 32% of dead trees and its basal area. In the seasonal records, condition I and III had a considerably lower contribution (3.5 and 1.5%, respectively).

Diameter frequency distribution indicates that the tree necromass and the living mass were better represented by trunks with a DBH < 10 cm in both initial (71%) and seasonal (80%) records (Fig. V.3). The proportion of dead trunks, as a fraction of the live trunks, was more or less constant among 5 to 20 cm, while a lower proportion was recorded in seasonally dead trunks with a DBH > 20 cm. Canopy gaps were formed by 30% of dead trees of both

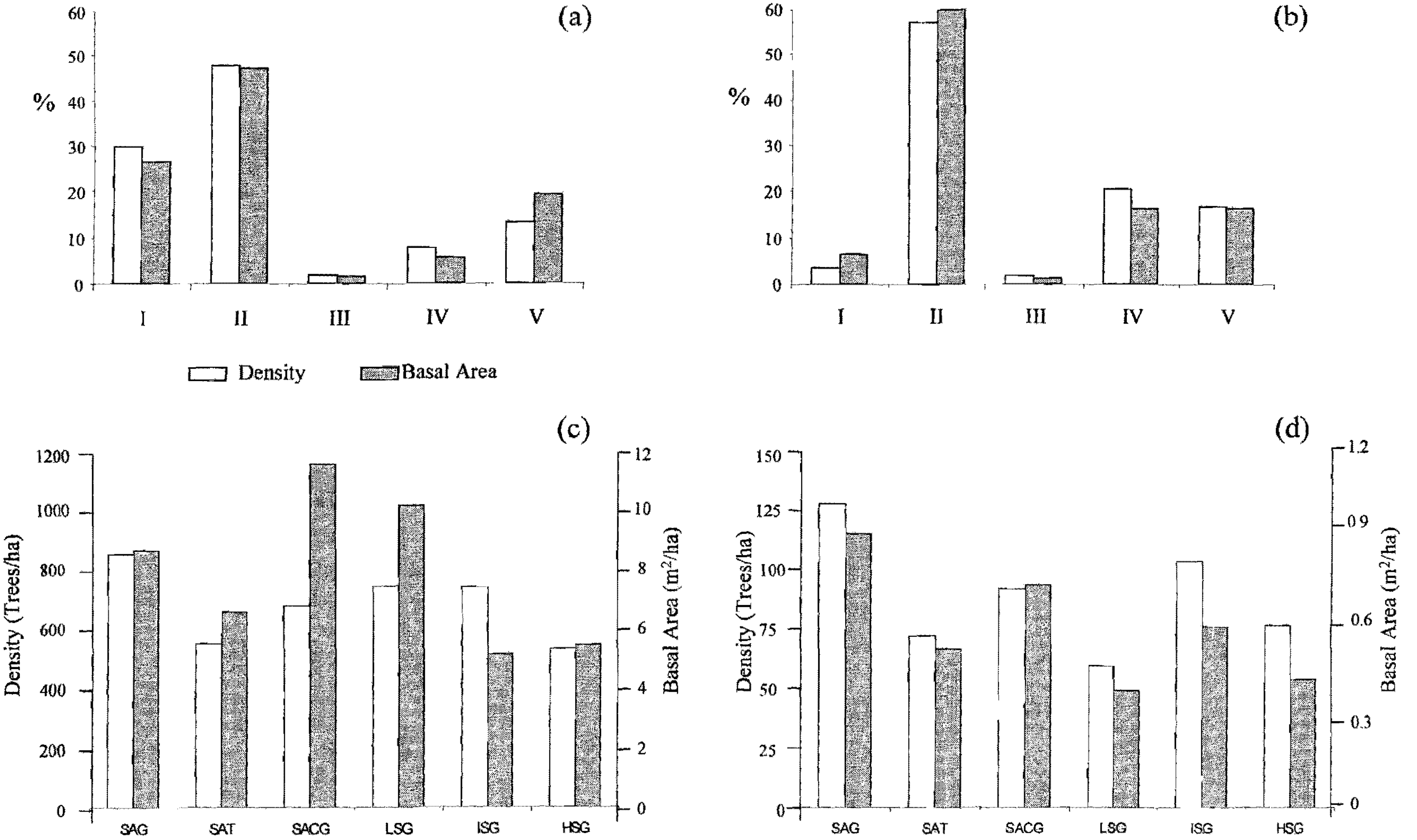

Figure V.2. Density and basal area for each of five mortality conditions in the initial dead component (a), and the seasonal dead component (b). Below, density and basal area are showed by each morpho-pedological land unit in the initial dead component (c), and the seasonal dead component (d). Roman numbers below (a) and (b) indicate different mortality conditions in which appeared the tree necromass (see Results section). Abbreviators below (c) and (d) correspond to different morpho-pedological land units (see Sampling methods section).

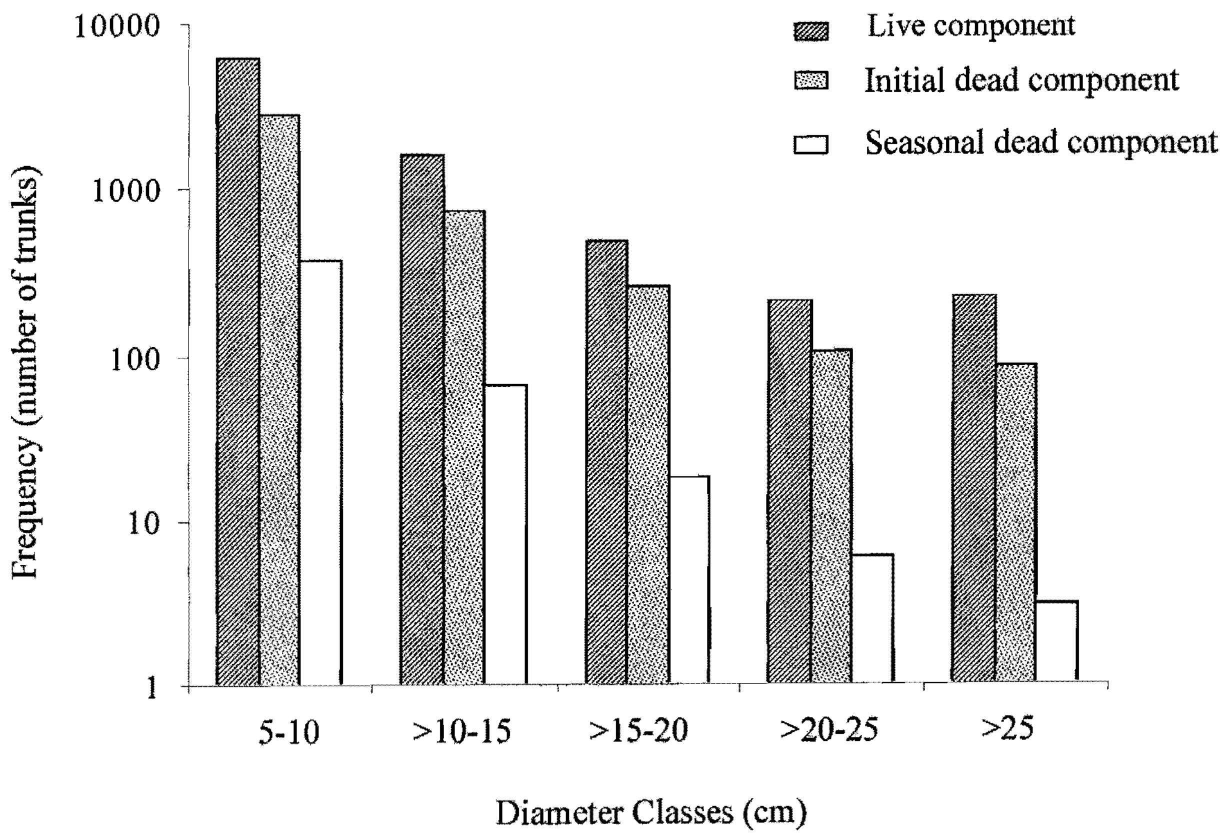

Figure V.3. The frequency distribution of live and dead trunks by diameter class.

the initial and seasonal records, but gaps generally had a very diffuse shape.

The crowns of fallen dead trunks in the initial and seasonal records were oriented in several directions (Fig. V.4), but a large majority of them were within the range 225 - 20° (passing through North azimuth). Mean vector and its standard deviation for 1,211 fallen trunks (21 plots) in the initial record were 313° ± 87.2 and for 27 fallen trunks recorded during the five seasons were 317° ± 64.3. In both cases, the trend for a Northwest orientation was significant according to a Rayleigh uniformity test ($p < 0.05$). An F-test showed that differences between mean angles of fall direction in the initial and seasonal records was not significant ($F=0.04$, $p > 0.84$). However, mean angles of fallen direction differed significantly between land units that belonged to few (328° ± 112°) and many (296° ± 76°) soil constrains conditions ($F=12.91$, $p < 0.05$).

A significantly larger mean mortality occurred during the rainy season than the dry season ($t\text{-test} = 4.81$, $p < 0.05$). All seasonally dead trees (N=432) were not compensated with new living recruitments (N = 75; Table V.2). Species identification in the initial record was difficult due to advanced decomposition state in the majority of the trunks. 80 species were identified in the seasonal record. The new recruitment belonged to 37 species, most of which were common or even present as dominant species in the seasonally dead records and in the living component (147 species; Table V.2). Through seasonal records, some species with a major number of individuals in the tree living component recorded more than five dead individuals (26 species), however, the relation between abundance of live and dead trees was not significant ($R^2 \leq 0.3$, $p < 0.05$). At least three species with more than 100 living individuals: *Adelia oaxacana* (Muell. Arg.) Hemsl., *Bourreria* cf. *purpusii* (Brandegee) and *Lonchocarpus mutans* showed less than five dead individuals, while nearly 28% of living individuals of *Achatocharpus gracilis* (H. Walt), *Lonchocarpus* sp. and *Thouninia paucidentata* (Radlk.; 18, 32 and 38 individuals, respectively) were dead.

In the seasonal records, species with and without sprouts (total death) and more than 10 dead ndividuals were different. Species with total dead individuals (condition I and II) were *Exostema caribaeum* (Jacq.) Roem. & Schult., *Guapira* cf. *macrocarpa* (Miranda), *Hellieta lottiae* (Chiang) and *Plumeria rubra* (L.); while *Apoplanesia paniculata* (Presl.), *Caesalpinia eriostachys* (Benth.), *Gliricidia sepium* (Jacq.) Kunth ex Steudel. and *Thouinia paucidentata* presented dead trunks with sprouts, living cambium at the base and/or also have living trunks with DBH ≥ 5 cm.

The mean annual mortality rate for the tree community was 2.1% and its half-life estimate in the tree canopy community was 33 years. However, the mean annual mortality rate was variable when it was estimated by each diametric classes (2.4 - 0.5%) given an average equal to 1.6%, based on this value the half-life estimates in the tree canopy increased to 44 years.

A non-significant correlation ($p > 0.05$) was obtained between the seasonal tree dead records and the respective seasonal precipitation.

Spatial variations

The fit of Ripley's L function to the data of distance between dead trunks showed that trunks

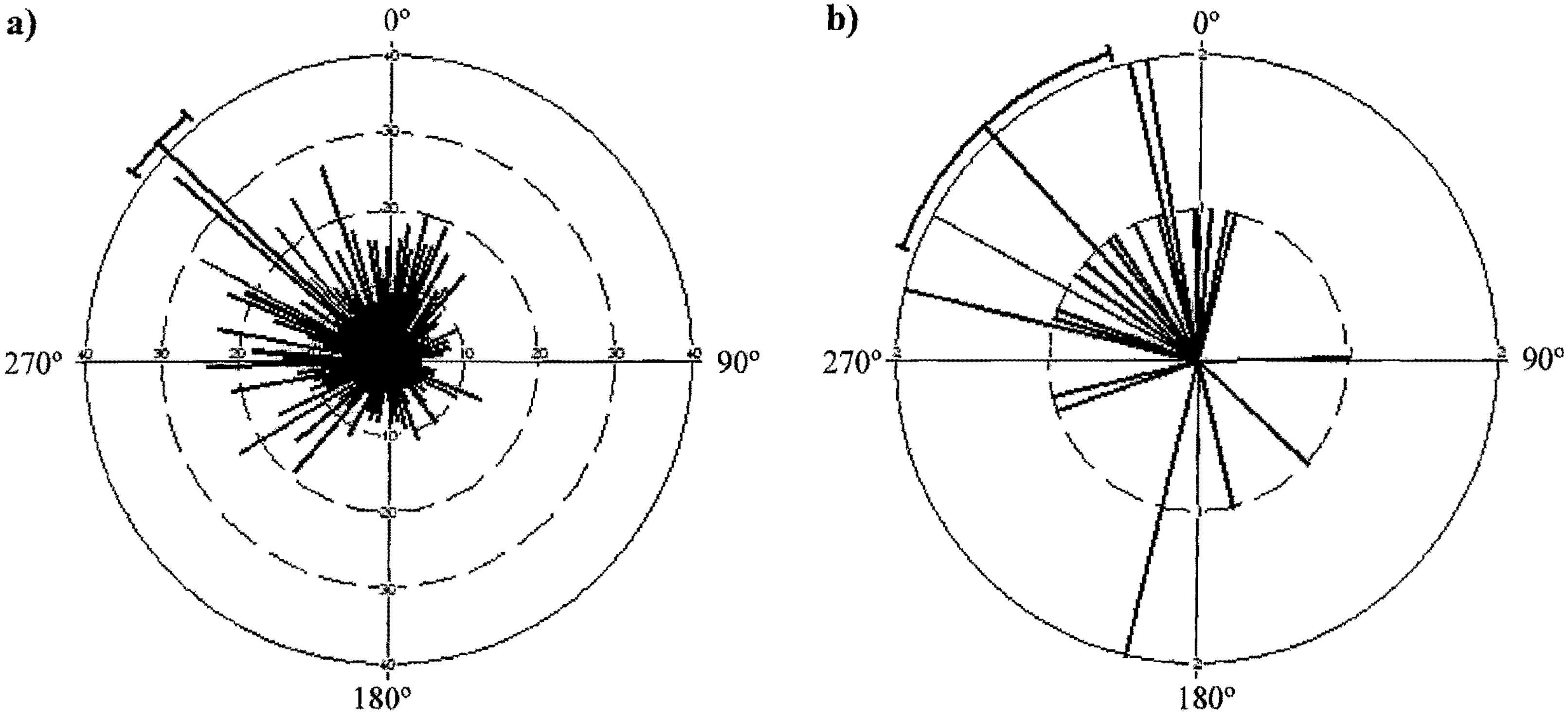

Figure V.4. Fall direction distributions of dead trees on the initial (a) and the seasonal (b) records. The length of the bars shows the number of views in each direction. The longest bar belongs to mean vector and its circular standard deviation.

Table V.2. General comparisons among alive trees (1995), dead trees (initial and seasonal) and new recruitments with DBH ≥ 5 cm, based on frequency, basal area and dominant species. In the initial dead component, taxonomic identity was not determined because trunks decomposition was advanced. *Period 2.5 years; five climatic seasonal periods.

	Alive	Dead (Initial)	Dead (Seasonal)*	Recruitments*
Total Trees (#)	6,874	3,221	432	75
Basal Area (m^2)	76.65	36.76	2.87	0.16
Species (#)	147	----	80	37

	Species	Tree Frequency	Species	Tree Frequency	Species	Tree Frequency
More Abundant Species	*Caesalpinia eriostachys*	429	*Exostema caribaeum*	35	*Apoplanesia paniculata*	11
	Exostema caribaeum	393	*Plumeria rubra*	33	*Exostema caribaeum*	8
	Lonchocarpus constrictus	368	*Hellieta lottiae*	24	*Lonchocarpus constrictus*	5
	Plumeria rubra	347	*Apoplanesia paniculata*	19	*Heliocarpus pallidus*	4
	Cordia alliodora	299	*Cordia alliodora*	19	*Lonchocarpus eriocarinalis*	3
	Percentage Sum	27	Percentage Sum	30	Percentage Sum	41

were randomly distributed ($p < 0.05$) within all plots, and this result was maintained when different distance ranges among trunks were considered.

Initial and seasonal records of dead trees were variable within and among morpho-pedological land units, both in terms of density and basal area (Fig. V.2 c and d) as well as in the death conditions.

According to the PCA with both initial and seasonal dead tree records, plots were segregatedby frequency of dead trunks, but not according to their location in morpho-pedological land units (Fig. V.5). The first two PCA axes explained ca. 63% of the total variance, and the variables with the largest weight on the first axis were basal area and number of dead trunks without resprouts in the seasonal records (condition I and II). On the second axis, the largest weight corresponded to the number of dead trunks during the rainy season, which had resprouts in their bases or others living trunks (conditions III-V). Although the second axis seemed separated soil constraint classes, neither relief nor soil features were well-correlated with the axes, suggesting a very weak influence of substrate heterogeneity on mortality patterns. The living tree component also affects the PCA: the first axis was significantly correlated ($p < 0.01$) with the number of living trees and canopy height, whereas the second axis had a significant correlation with the number of living multi stemmed trees.

CCA triplot and its global permutations test to judge non-relation between mortality and environmental variables, both first and trace (all) canonical axes (eigenvalue = 0.066, F-ratio = 4.89, p = 0.42 and eigenvalue = 0.072, F-ratio = 0.92, p = 0.45, respectively).

DISCUSSION

Dead tree component at Chamela

Tree mortality patterns observed in the TDF of Chamela seemed to share many characteristics with an Ecuadorian dry forest (Josse 1997). However, it differed substantially from those mortality patterns reported for similar forests in Puerto Rico (Murphy & Lugo 1986b) or others with frequently recurrent fires, hurricanes or other catastrophic disturbances (López-Portillo *et al.* 1990, Menaut *et al.* 1995, Lugo & Scatena 1996, van Bloem *et al.* 2003), where major disturbances promote massive mortality. We recorded substantial but possibly continuous tree mortality (2.1% y^{-1}). Dead trees were an important structural component of the Chamela landscape; we found a near 1:2 ratio between dead and living trunks. In a previous study, Segura *et al.* (2003) recognized a similar ratio along a topographic gradient within a small watershed. However, its pattern differed in Puerto Rico´s TDF, where the ratio was 0.08:1 and the basal area for dead trees represented a very small contribution (Murphy y Lugo 1986b). Comparisons are limited by the lack of sufficient studies in similar ecosystems. Methodological restrictions are also important to note, such as the minimum DBH criterion used for sampling "trees".

Although dead trees were almost proportionally distributed across our DBH classes, the dead individuals may have been underestimated because only trunks with DBH ≥ 5 cm were considered. Thinner trunks represent an important component of coarse woody debris (Harmon *et al.* 1986, Murphy y Lugo 1986b, Uhl & Kauffman 1990, Maass *et al.* 2002b) and

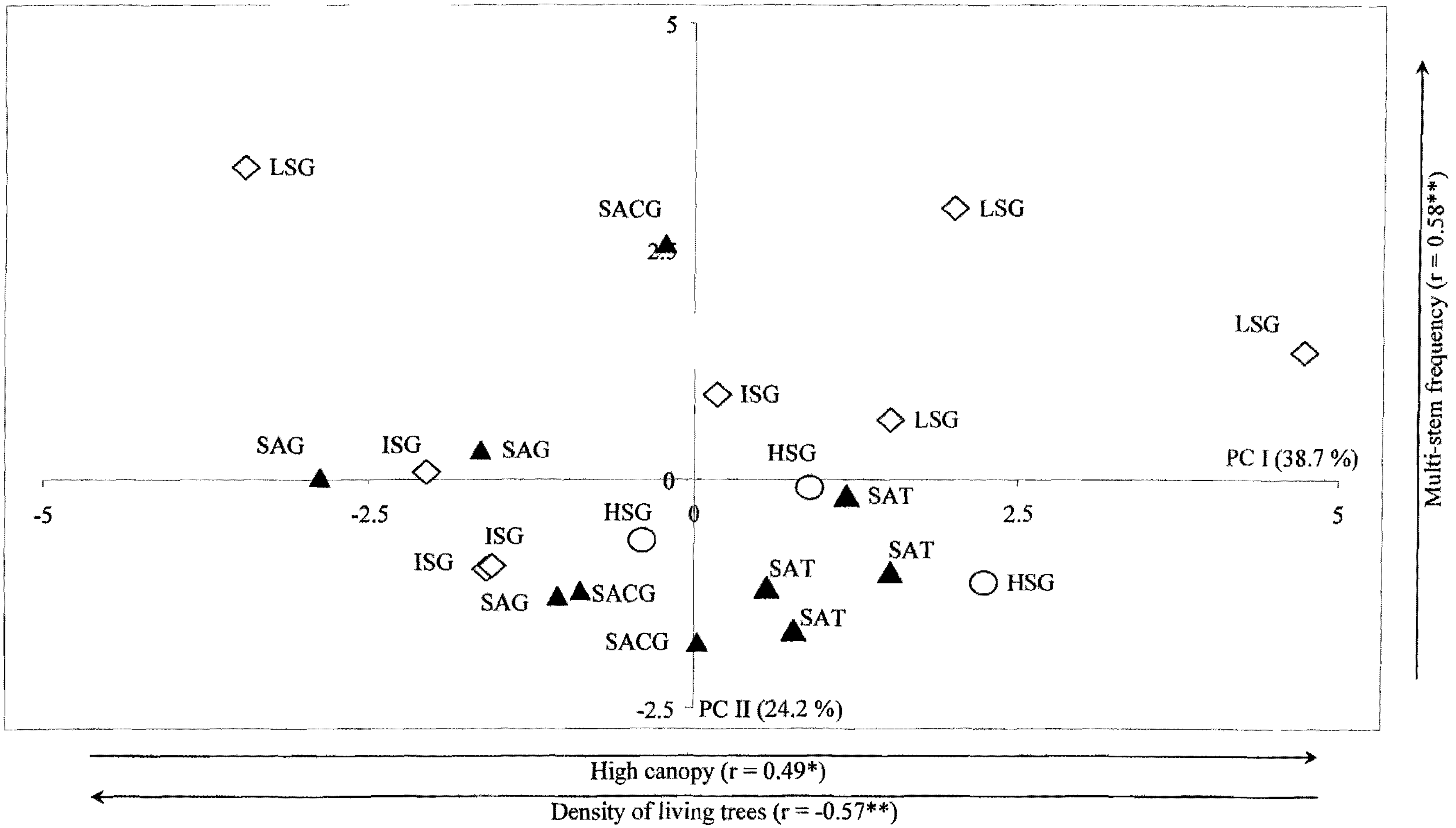

Figure V.5. Ordination of 21 study plots based on a Principal Component Analysis with nine uncorrelated mortality variables. Percentages next to the axes indicate the variance explained by each principal component. Significant correlations between the first two components and structural characteristics of the living tree component (* = $p < 0.05$, ** = $p < 0.01$) are indicated. Symbols for the different soil constraints conditions: ◇= few, O = some, and ▲ = many. Capital letters next to symbols indicate the morpho-pedological land units.

are very important in the living component at Chamela (Bullock 1990, Martínez-Yrízar *et al.* 1992) and other dry forests in Mexico (Trejo 1998). In agreement with reports for other similar or moister tropical forests (Murphy y Lugo 1986b, Rankin-de-Merona *et al.* 1990, Josse 1994, Taylor *et al.* 1996), the largest number of deaths at Chamela occurred among trunks with DBH < 10 cm. However, in contrast to other forests (Lieberman *et al.* 1985, King 1986, Körning & Balslev 1994), no relationship became apparent between DBH and death condition.

The lack of balance between tree mortality and new living recruitments through seasonal surveys in Chamela, together with the apparently slow decomposition of trunks (which may last for several years, or possibly decades), suggests that the necromass is actively accumulating at the landscape. This imbalance has been recognized by Josse (1994) in other dry forests. A similar imbalance has also been reported for other tropical forests where new recruits grow and increase the tree biomass, but not compensate for losses by death (Rankin-de-Merona *et al.* 1990, Condit *et al.* 1995, Taylor *et al.* 1996, Laurence *et al.* 1997, Hubbell *et al.* 1999). This result supports the previous finding of a dead wood net accumulation in the Chamela by Maass *et al.* (2002b).

The annual mortality rate by diameter class showed a differential susceptibility to die, 1.6% was the mean annual mortality rate among diameters which indicates a canopy turnover of 44 years. However, a turnover of about 33 years based on the general annual mortality rate (2.1%) may be more realistic, because the first diameter category (DBH >5-9.9 cm) contributed to 80% of seasonal mortality and constitutes 72% of living tree component. For the first diameter category, the annual mortality rate calculated was lower than two comparable periods analyzed by Josse (1997) in an Ecuadorian dry forest (3.4 and 3.7%). This difference could be explained because the Ecuadorian forest is secondary. The TDF at Chamela has a lower mean turnover (47.3 years) than the value reported for most other dynamic forests (Putz 1983, Lieberman *et al.* 1985, Hubbell & Foster 1990, Körning & Balslev 1994). However, the differences in susceptibility to die among diameter classes, together with our conclusion about turnover time must be taken with caution because the short observation period may fail to detect processes that take place over larger intervals (Shugart 1984, Phillips 1996).

The large variation in wood decomposition rates observed in this study is also common in many broadleaved forests (Harmon *et al.* 1986, López-Portillo *et al.* 1990, Harmon *et al.* 1996, Yin 1999), modifying the idea that decomposition is typically a fast process in tropical forests (Lang & Knight 1983). We only observed rapid wood decomposition in softwood species such as *Plumeria rubra*, *Jacaratia mexicana* (A. DC.) and *Ipomoea wolcottiana* (Rose), as well as some *Bursera* species. Except for *P. rubra*, none of these species were dominant in the canopy as living trees. The knowledgement of wood decomposition has helped in reconstructing disturbance history in temperate forests, including synchronous mortality events (Lorimer 1985, Spies *et al.* 1988, Harmon *et al.* 1986, Foster & Boose 1995). However, at Chamela such reconstruction is probably not feasible because of the high diversity in the tree community (Durán *et al.* 2002) and the large variation in specific wood density (Barajas-Morales 1987), which results in highly variable decomposition rates.

Tree mortality conditions

We simultaneously recorded the death of genets and ramets, although these have different ecological, physiological and population implications (Harper 1977, Silvertown & Lovett-Doust 1992). We used five death conditions to represent an extension to other categories usually recognised in tropical forests: fallen dead (uprooted or snapped) and standing dead (Putz 1983, Clark 1990, Rankin-de-Merona *et al.* 1990, Denslow & Hartshorn 1994, Körning & Balslev 1994, Gale & Barfod 1999). Our additional two conditions were based on the recognition that some trees may be composed of both living and dead trunks (biomass and necromass), and that some trees with completely dead trunks may soon sprout new stems from their bases. These are common conditions in other TDFs (Murphy & Lugo 1986, López-Portillo *et al.* 1990, Harmon *et al.* 1996, Sampaio *et al.* 1993). Thus, the death of trunks to ground level, without death of the genet, is a mechanism of tree necromass supply that is not unique to Chamela.

Standing necromass (conditions II, IV and V) prevailed, in both the initial and seasonal dead tree records, which is a common pattern in other tropical and temperate forests worldwide (Lieberman *et al.* 1985, van Schaik & Mirmanto 1985, Rankin-de-Merona *et al.* 1990, Strasberg *et al.* 1995, Bretz & Dobbertin 1996, Lertzman *et al.* 1996, Asner & Goldstein 1997). Moreover, fallen dead trunks were considerably less frequent in the seasonal records than in the initial record (5.6 and 31.5%, respectively). It is probably that some of the fallen trunks in the seasonal records initially died standing, but the decomposition process weakened their support systems and caused their fallen.

The opening of canopy gaps due to falling trees is not common at Chamela. The few existing canopy gaps tend to be small, perhaps because most dead trees had DBH<10 cm. Since the DBH of trunks is proportional to its height and crown area (Bullock 2000) and these, in turn, influence the opening of the canopy (Popma *et al.* 1988), the rather small trunks DBH at Chamela avoid opening large gaps as occurs in tropical rain forests (Brokaw 1982, Denslow & Hartshorn 1994, Martínez-Ramos 1994). Perhaps for this reason, a comparison of the understorey structure and species composition in gaps and below undisturbed forest canopy failed to show differences (Allen *et al.* 1998).

Tree mortality patterns and environmental mosaic

Although the phenomenon of tree mortality is complex, and it is difficult to point out a direct causes of death of an individual tree or its parts. It is known that senescence, weakness, and disturbance will act as determining factors to die (Shugart 1984, Franklin *et al.* 1987, Pederson 1998, Gale & Barfod 1999). The standing death of trees had been attributed to water stress (Gale & Barfod 1999) while the falling of dead trunks is typically attributed to wind and storms (King 1986, Arriaga 2000). Accordingly, we proposed seasonal monitoring to explore the influences of two sources of environmental stress, which are frequent at the Chamela region (Hernández *et al.* 2001, García-Oliva *et al.* 2002): (1) water stress, associated to the long dry season; and (2) intense winds associated to tropical storms and rare hurricanes during the rainy season.

Water is the major limiting resource in seasonal tropical ecosystems such as Chamela (Murphy & Lugo 1986, Bullock & Solís-Magallanes 1990, Borchert 1994, Mooney *et al.* 1995, Maass *et al.* 2002a, van Bloem *et al.* 2003). Water stress is expected during the dry season because of the scant or null precipitation and a high net radiation. Also there is a large fluctuation in annual precipitation among years and even grought spells within a single wet season (Bullock 1986, Maass *et al.* 2002a, García-Oliva *et al.* 1995). Water stress through embolisis (or cavitation) induces death in tree structures such as branches, crowns, trunks, or even the whole individual tree (Dittus 1985, Murphy & Lugo 1986, Leighton & Wirawan 1986, Condit *et al.* 1995, Harmon *et al.* 1996, Pederson 1998, Bullock 2000).

We found that standing death was the common condition in both dry and rainy seasons. This result was unexpected because we supposed standing death trees had been related to water stress, but that condition prevailed during the rainy season. We know that the trees have a high tolerance to water stress through morphological, physiological and phenological mechanisms (Borchert 1994, Holbrook *et al.* 1995, Eamus 1999). However, there are thresholds beyond which death occurs. Thus, death cannot appear until after the dry season. Because of this delay, death could be a manifestation of events in previous seasons, derived from a progressive weakening process or from continuous limitation of the capacity of an individual to store photosynthates for subsequent seasons (Lott *et al.* 1987, Pederson 1998). The delayed effect of water stress will increase with the severe pruning of living leaves and branches by wind during the rainy season (Nelson *et al.* 1994, van Bloem *et al.* 2003).

Windthrow seems to be a secondary cause of mortality because only 5.4% of seasonal records were comprised of trunks that died by falling. This result may be explained by the fact that some trees have high wood density and stability nodules that confer resistance to be broken or uprooted (Barajas-Morales 1987). A minor quantity of fallen dead trees has been recorded in other places of America and Indian Ocean (Putz 1983, King 1986, Strasberg *et al.* 1995, Asner & Goldstein 1997, Gale & Barfod 1999), where strong wind associated to storms cause less windthrow to the trees. Also, it is possible that the effect of the wind might be minimized by the short canopy height (mean 6.8 m).

The prevailing direction of fall in both initial and seasonal records was Northwest. This direction is apparently related to the predominant wind direction during the rainy season (García-Oliva *et al.* 2002) and with the general storm tracks from Southeast to Northwest (Hernández *et al.* 2001). A significantly ($p<0.05$) larger proportion of fallen trunks was observed in the three morpho-pedological land units on summit areas on granite, tuffs and conglomerates (SAG, SAT and SACG), which are the closest to the sea, exposed to winds and where many soil constraints prevail (e.g. shallow soils). In contrast, we recorded the lowest fallen tree frequency in high slopes on granite (HSG; with most sloping and high elevation), where we expected that trees would be more likely to die by falling. Nevertheless, the PCA showed that the amount of dead trunks and its mortality condition was independent of the landforms, this has also been reported for other forests (Kapos *et al.* 1990, Samper 1992, Körning & Balslev 1994, Poorter *et al.* 1994, Gale & Barfod 1999, Arriaga 2000). Though, a small topographic gradient analyzed at Chamela was clearly related to differences in necromass amount and its condition (Segura *et al.* 2003).

Endogenous factor to the forest system might be influencing tree mortality at Chamela.

Thus, random distribution of dead trunks in the plots, which is not consistent with contagious or aggregate factors, will suggest to us that intra or interspecific competitive interactions occur (Kenkel 1988). These lead to the expectation of a larger mortality in plots with a higher tree density, as was reported. Also, significant correlations ($p<0.05$) between PCA axes and the alive tree component lead us to assume that the structure of the dead tree component is strongly related to structural attributes of the living component.

In addition, we found that the seasonal records and death conditions (standing or fallen) were not related to seasonal precipitation quantity or to the soil properties related to water availability (such as clay content, soil depth, and estimates of water holding capacity and field capacity). However, mean frequencies and basal area of standing dead trunks (both initial and seasonal records) were significantly different ($p<0.05$) among the land units and its corresponding three classes of soil constraint. Much of the variability in tree mortality remains to be explained; other factors or other spatial and temporal scales beyond the scope of this study will contribute greatly to explain tree mortality in Chamela.

Implications of mortality patterns for forest dynamics

The death of trees has an ecological importance in a forest through its influence on regeneration (Harmon *et al.* 1986, Franklin *et al.* 1987, Clark 1990, Martínez-Ramos 1994). Although natural dynamics at Chamela and other TDFs is still poorly understood (Murphy & Lugo 1986, Gerhardt & Hytteborn 1992, Mooney *et al.* 1995), we recognized that constant death and regeneration is taking place. Thus, the five mortality conditions found in Chamela seemingly differ in their impact on soil as well as on canopy and understorey plants in their neighbourhood (Putz 1983, King 1986, Gale & Barfod 1999).

In TDFs, resprouting is a well-known mechanism for natural regeneration (Murphy & Lugo 1986, Gerhardt & Hytteborn 1992, Sampaio *et al.* 1993). Resprouting refers to cases in which death does not involve the whole tree, so necromass is provided to the ecosystem without losing the particular genomics presence in the community. This phenomenon has been especially recognized as a natural mechanism for forest recovery after fires and hurricanes to perturb on some tropical forests (Ewel 1980, Murphy y Lugo 1986, López-Portillo *et al.* 1990, Harmon *et al.* 1996, Arriaga 2000, van Bloem *et al.* 2003). Taking into account the proportion of dead trunks that were resprouting at their base (9.4% in the initial record, and 20% in seasonal records), it is recognized that resprouting acts as a regeneration mechanism at Chamela. Resprouting is frequent in some species such as *Gliricidia sepium*, *Caesalpinia eriostachys* and *C. coriaria* (Jacq.) Willd. Also, it was common among some remnant trees that were present in fields burned for agriculture and cattle pastures, beyond the borders of the Chamela Station (Miller & Kauffman 1998, J. M. Maass personal communication).

The ecological implications of resprouting are diverse. Resprouts have a high root:shoot ratio, so there is a greater advantage over regeneration by seeds, avoiding critical stages of a plant's life cycle such as seed germination and seedling establishment (Harper

1977, Martínez-Ramos 1994). Nonetheless, seed regeneration occurs at Chamela and the highly diverse seedling bank was not restricted to open sites or partially closed canopies (Durán *et al.* 2002, E. Durán personal observation). Huante (1996) found at Chamela that species such as *Gliricidia sepium*, *Heliocarpus pallidus* (Rose.), *Plumeria rubra* e *Ipomoea wolcotiana* had seedlings and saplings with strong preferences for open sites, and that most seedlings display shade tolerance or are adapted to considerable microclimatic variability. Until now, however, studies on seed regeneration are scarce. This mechanism has been reported as key in a TDF in Ghana (Lieberman & Li 1992), where seedlings are shade-tolerant and survival to pre-adult stages in the dry season is determined by root density and soil water availability.

At Chamela, as in other TDFs, several ecological questions about the role of tree mortality in the maintenance of diversity and in natural forest dynamics remain unanswered (Hytteborn & Skarpe 1992, Mooney *et al.* 1995). Because long-term phenomena such as ENSO, droughts or hurricanes may promote mortality and recruitment pulses, as well as cause significant variations in growth and other demographic adjustments in tree populations (Leighton & Wirawan 1986, Hubbell & Foster 1990, López-Portillo *et al.* 1990, Condit *et al.* 1995, Groenendael *et al.* 1996, Phillips 1996). Hence, studies on cumulative and current mortality and recruitment in many permanent plots on a variety of substrates, like the present one, will be of the utmost importance to understanding forest dynamics.

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CAPÍTULO VI
DISCUSIÓN GENERAL

APROXIMACIÓN DE ESTUDIO

Esta tesis constituye el primer acercamiento a la descripción y análisis de los patrones del componente arbóreo a nivel de mesoescala en el bosque tropical caducifolio (BTC) de Chamela, México. El enfoque de ecología del paisaje que se adoptó en este estudio, implicó considerar al espacio como uno de los componentes del paisaje y *a priori* asumir que no es homogéneo (Farina 1995, Wiens 1995). Sobre esta base se definieron unidades de terreno, producto de la interacción del relieve, la geomorfología y el suelo, como la base para el análisis de la vegetación (Geissert y Rossignol 1987, Zonneveld 1989, Cotler *et al.* 2002). La premisa de este enfoque es que los patrones y procesos ecológicos son modificados espacialmente por la existencia de mosaicos constituidos por unidades de terreno cuya naturaleza es producto de la interacción entre el medio abiótico y biótico (Wiens 1995).

Este enfoque se ha usado para el análisis de patrones de la vegetación en ecosistemas tropicales, aunque los estudios de caso son relativamente limitados, sobre todo tratándose de proyectos de tesis (Hommel 1987, Duivenvoorden y Lips 1995, Verweij 1995, Pérez-García 2002). Esta situación que se puede atribuir, en parte, a que los estudios de ecología del paisaje abordan múltiples aspectos, lo que implica resolver limitaciones logísticas para llevarlos a cabo. Sin embargo, los resultados generados con este tipo de aproximaciones han permitido documentar una parte importante de la complejidad que caracteriza a los paisajes de los bosques tropicales que se han analizado.

Entre los ecosistemas tropicales estacionales de México y del mundo, Chamela es reconocido como uno de los sitios donde se cuenta con más estudios ecológicos sobre la flora, la fauna y los procesos ecosistémicos (Martínez-Yrízar *et al.* 1990, Lott 1993, García y Ceballos 1994, Campo 1995, García-Oliva *et al.* 2002, Maass *et al.* 2002a, Maass *et al.* 2002b, Noguera *et al.* 2002). En el caso de los árboles, la literatura abarca estudios locales sobre la morfología, la fenología, la fisiología, la autoecología y la influencia de árboles individuales sobre su entorno inmediato; los cuales comúnmente se han enfocado a especies particulares del BTC o a algunos grupos funcionales o taxómicos (Bullock y Solís-Magallanes 1987, Martijena 1993, Groenendael *et al.* 1996, Huante 1996, Martijena y Bullock 1994, Bullock 2000, Galicia 2001, Kelly *et al.* 2001, Parra-Tabla y Bullock 2003). Por otra parte, se cuenta con descripciones generales de la diversidad de las plantas leñosas dentro de la Estación de Biología de Chamela (Lott *et al.* 1987, Durán *et al.* 2002). Asimismo, existen trabajos sumamente detallados sobre la estructura y la composición del componente arbóreo, y sus posibles factores determinantes que se han venido realizando en el gradiente topográfico-altitudinal del sistema de "microcuencas experimentales" (Martínez-Yrízar *et al.* 1992, Balvanera 1999, Galicia *et al.* 1999, Sarukhán *et al.* 2000, Kelly y Bowler 2002, Segura *et al.* 2003). El sistema de las microcuencas alberga gran parte de la notable diversidad arbórea del BTC y de las variaciones espaciales que caracterizan la región. Sin embargo, se trata de una condición peculiar donde, en decenas de metros, ocurre la transición de BTC a un bosque más húmedo y semideciduo, lo que explica en parte la gran riqueza florística y las marcadas variaciones estructurales encontradas.

El medio físico en la Estación de Chamela ha sido ampliamente analizado, particularmente en lo que se refiere al régimen climático (Bullock 1986, García-Oliva *et al.*

2002), los suelos y el relieve, especialmente en el sistema de microcuencas (Solís 1993, Campo 1995, Galicia *et al.* 1999, Maass *et al.* 2002a).

Los diferentes estudios ecológicos señalados, son producto de más de 20 años de intenso esfuerzo de investigación y han contribuido notablemente a la comprensión de los patrones y procesos que tienen lugar en Chamela. No obstante, los estudios que responden a preguntas ecológicas casi no han considerado la heterogeneidad del relieve y el suelo que se presenta en toda el área de la Estación y en su región circundante. Un primer reconocimiento general de los contrastes en las geoformas fue considerado por Lott *et al.* (1987) en su diseño de muestreo de la vegetación leñosa ("upland 1", "upland 2", "arroyo"). Pero no fue sino hasta el estudio de Cotler *et al.* (2002) que se identificaron de manera explícita las principales variaciones litológicas, geomorfológicas y de suelos en el área. De esta manera el trabajo que aquí se presenta pudo contar con una referencia espacial del mosaico morfo-pedológico para analizar el componente arbóreo.

Este estudio, acorde al enfoque de paisaje con que fue desarrollado, se distingue de otros trabajos que analizan la comunidad arbórea del BTC, porque se basó en el reconocimiento y el análisis de unidades de terreno cartografiadas (unidades morfo-pédológicas); así como en el análisis integral de características del relieve, el suelo y el componente arbóreo (estructura, composición, diversidad, mortalidad y reclutamiento). Específicamente, el estudio de los patrones del componente arbóreo basado en unidades de terreno y el análisis espacio-temporal de los patrones de mortalidad arbórea, son aspectos que hasta ahora no se han documentados de manera amplia en la zona de estudio o en otras áreas con ecosistemas similares.

PRINCIPALES RESULTADOS Y CONCLUSIONES

El propósito central de la tesis fue conocer la contribución del mosaico ambiental relacionado con factores del relieve y el suelo, para explicar la organización espacial de la diversidad arbórea del BTC de la Estación de Chamela. El trabajo intentó responder las siguientes preguntas: ¿Cuáles son los principales contrastes en el mosaico ambiental de Chamela?, ¿Los cambios espaciales en la estructura y la composición de especies arbóreas del BTC son acordes con las variaciones de dicho mosaico y los factores de relieve y del suelo que lo determinan?, ¿La necromasa y la mortalidad arbórea incrementan las diferencias ambientales entre las unidades de terreno (morfopedológicas y de contrastes en limitantes en el suelo)?

Responder la primera pregunta implicó integrar una base de datos sobre el relieve y el suelo de las 14 unidades morfo-pedológicas, previamente delimitadas en la Estación. Con dicha base se efectuó una clasificación y evaluación de las condiciones del suelo, lo que condujo a definir cuatro condiciones de contrastes en limitantes en el suelo (Capítulo II). La unidad con "muy pocas" limitantes en el suelo coincidió con las áreas donde se desarrolla el bosque tropical semideciduo (valles aluviales y pies de monte), mientras que las tres unidades restantes que corresponden a superficies cumbrales, lomeríos y laderas (con "pocas", "algunas" y "muchas" limitantes en el suelo) presentaron vegetación de BTC.

Para reconocer si la estructura y la composición de especies arbóreas del BTC mostraban correspondencia con las unidades de condiciones limitantes en el suelo, fue necesario contar con una descripción y análisis de la estructura, composición y diversidad del componente arbóreo (Capítulo III). Dicho análisis se efectuó usando parcelas de vegetación que se establecieron, de acuerdo al diseño original, en seis unidades morfo-pedológicas con vegetación de BTC donde se reconocieron claras diferencias en cuanto a la litología, relieve y suelos. Se encontró que el componente arbóreo es estructuralmente variable dentro y entre las unidades morfo-pedológicas; asimismo, que se integra de diferentes asociaciones de especies. La mayoría de las especies fueron raras, mientras que un grupo relativamente reducido dominó el dosel. Con la información de los Capítulos II y III, fue posible relacionar la estructura y la composición de especies con el relieve y el suelo de las tres unidades con distinto nivel de limitantes en el suelo (Capítulo IV). La diversidad, más que la estructura, se relacionó significativamente con algunas características del relieve y el suelo, la tendencia registrada fue hacia una mayor diversidad de especies, al incrementar la concentración de nutrientes. Las especies dominantes se correlacionaron significativamente con características del relieve y el suelo, particularmente la elevación y los nutrientes. Un grupo de especies dominantes destacó como el atributo del dosel que mostró cambios significativos en relación con las diferencias en litología y en las limitantes en el suelo.

La posibilidad de que la necromasa arbórea acentuará las diferencias entre las unidades morfo-pedológicas o de limitantes en el suelo fue explorada en el Capítulo V. En él se caracterizó la necromasa arbórea presente al inicio del estudio (1995) y la mortalidad estacional de los árboles durante el periodo 1995-1997. También se analizó la mortalidad arbórea con relación a las unidades de condiciones limitantes en el suelo. Los resultados mostraron que la necromasa arbórea es un componente estructural clave en el BTC de Chamela, con una relación 2:1 entre biomasa y necromasa. Sin embargo, las variaciones espaciales de la necromasa arbórea no se relacionaron significativamente con las unidades de contraste en las limitantes del suelo, o con características del relieve o el suelo. En cambio, una relación estrecha fue encontrada entre la estructura de ambos componentes vivo y muerto. También se encontró que gran parte de los árboles muertos correspondieron con las especies que dominan en el dosel.

Las principales conclusiones del trabajo son las siguientes. (1) El área de la Estación de Chamela presenta un complejo mosaico ambiental que puede referirse en cuando menos tres modelos: one, de diferencias litológicas gruesas; dos, por unidades morfopedológicas; tres, por contrastes en cuanto a limitantes en el suelo. (2) El tipo de vegetación menos representado (bosque tropical semideciduo) caracteriza los sitios con muy pocas limitantes en el suelo. El resto del área, con diferente grado de limitantes en el suelo, presentó vegetación de BTC. (3) El grupo de especies que dominan el dosel del BTC constituye un distintivo que varía acorde con las diferencias en litología y con factores del relieve y el suelo que inducen limitantes en el suelo. (4) Una alta proporción de las especies fueron raras, lo que dificultó caracterizar sus patrones de distribución, a la escala en que se realizó el estudio. (5) La necromasa arbórea es un componente estructural importante del BTC que libera recursos (espacio, luz, nutrientes) e influye en las condiciones ambientales. No obstante, la necromasa arbórea no parece adicionarse como una fuente de variación ambiental acorde con las unidades de terreno delimitadas previamente. (6) Por último, en relación a la hipótesis originalmente planteada ambiental, se mostró que éste contribuye parcialmente a explicar los patrones de dominancia del componente arbóreo vivo en el BTC de Chamela.

Derivados de los resultados destaca el reconocimiento de la existencia de diferentes modelos de variación ambiental (unidades morfo-pedológicas, diferencias litológicas y contrastea en limitantes en el suelo) que pueder servir de referencia para analizar los patrones en el componente biológico. Un valor adicional de este trabajo es que ofrece un panorama general de la complejidad del paisaje derivado de la integración de los patrones de variación del componente arbóreo y factores del relieve y el suelo.

IMPLICACIONES PARA OTROS ESTUDIOS

La descripción de los patrones del componente arbóreo del BTC de Chamela, junto con el análisis de las relaciones que mantienen con otros componentes del entorno (relieve y suelos), son esenciales porque generan bases para otros estudios sobre la autoecología de algunas especies, la sinecología, la exploración de hipótesis teóricas y la experimentación (Harper 1982, Kent y Coker 1992, Jongman *et al.* 1995). Asimismo, a partir del reconocimiento de diferentes modelos de variación ambiental se cuenta con un marco de referencia que, de acuerdo a los propósitos de estudio, podría ayudar al diseño de muestreo, la selección de variables y la escala de análisis en estudios relacionados con las siguientes líneas de investigación:

Patrones de la vegetación y el mosaico ambiental

Una primera sugerencia es que previo al estudio de la relación entre el medio físico y las lantas debe haber un reconocimiento explícito de que dicha relación es multiescalar (Zonneveld 1989, Coughenour y Ellis 1993; Fig. VI.1). Por ello, la dimensión de éste, y prácticamente cualquier otro estudio, corresponderá sólo a un fragmento del espacio en que dicha interacción ocurre. En consecuencia, los resultados constituyen una visión parcial de un fenómeno que es notablemente más complejo, tan sólo en su dimensión espacial (Farina 1995, Sollins 1998). Sin embargo, una una mejor comprensión de dicha relación se lograría de complementar los resultados con información generada a escalas mayores y de menor detalle, en el mismo tipo de ecosistema y con analogía en la metodología y las variables de análisis.

En el contexto regional, ocurren cambios estructurales en el BTC y en el tipo de vegetación asociada con otras fuentes de variación ambiental que no se encuentran en la Estación de Biología (Durán *et al.* 2002, S. Bullock com. personal). Dichas variaciones se relacionan con la distancia a la costa, y con diferencias altitudinales y geomorfológicas; así como con variaciones litológicas, climáticas y de manejo. Por ello, una visión general del mosaico ambiental y de sus coberturas, podría generarse al efectuar una regionalización y caracterización de los BTC, con quienes ecológica o biogeográficamente interactúa el BTC de Chamela. Como un requerimiento mínimo se debería contar con una visión general de toda el área de conservación (Reservas de la Biosfera Chamela-Cuixmala y la Unidad Experimental de Zootecnia de la Universidad de Guadalajara; aproximadamente suman 12,600 ha) así como de las unidades naturales en que tales reservas están inmersas (cuencas del arroyo de Chamela

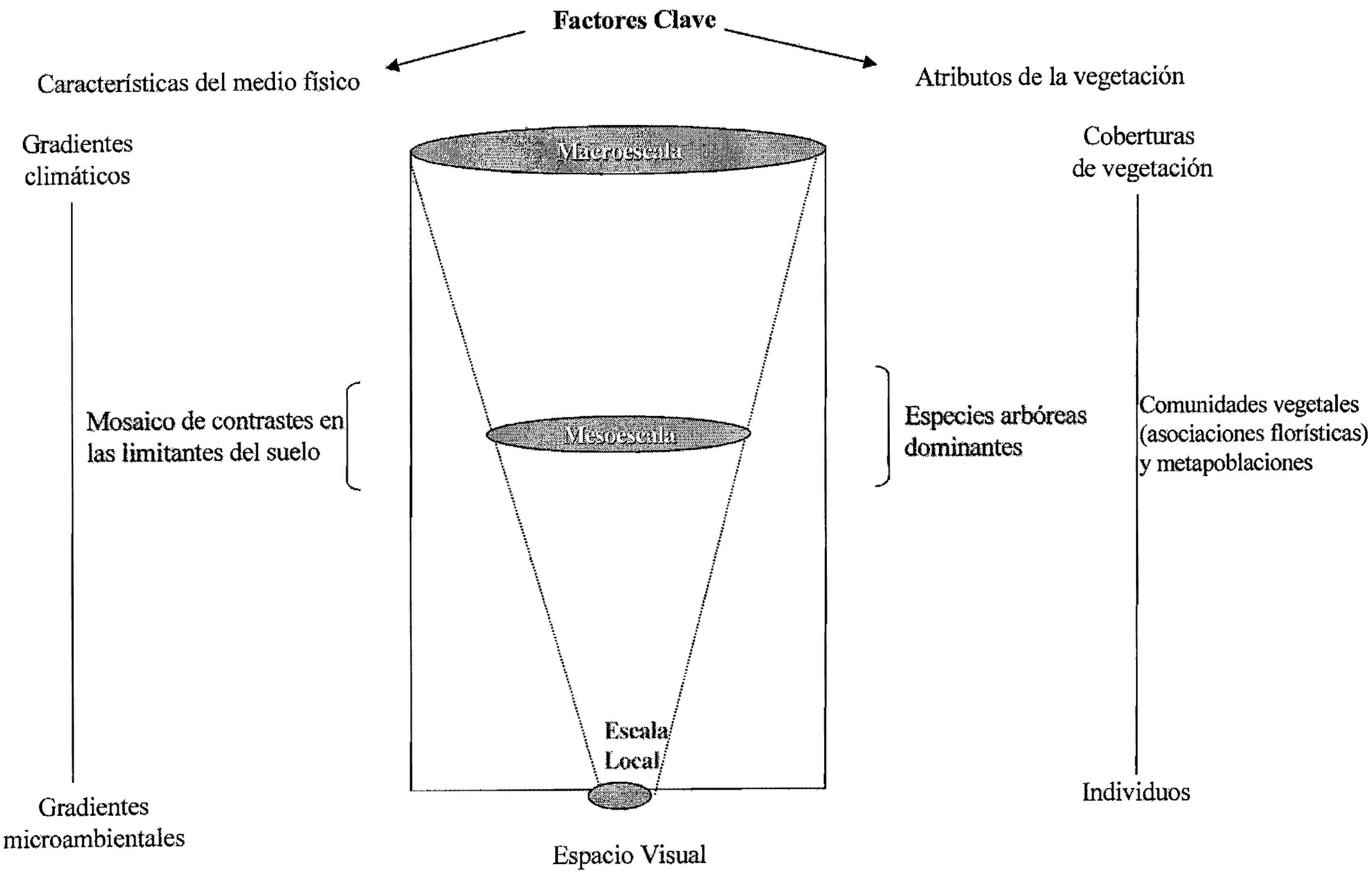

Figura VI.1. La relación planta-medio físico ocurre a todas las dimensiones espaciales posibles. Diferentes niveles de observación permiten reconocer patrones acerca de dicha relación que son producto o que tienen relación con factores claves propios de cada dimensión espacial.

y del río Cuixmala). Esto permitiría conocer si la relación medio físico-vegetación documentada para la Estación de Biología es general, al incorporar rangos de elevación más amplios y variaciones climáticas.

Otra alternativa es analizar si especies afines a condiciones particulares del relieve o el suelo dentro de la Estación, responden de manera análoga en otros sitios dentro y fuera de la zona de conservación. Para ello, se podrían delimitar *a priori* "hábitats potenciales" (contrastes en limitantes en el suelo) y realizar un reconocimiento de las especies. Por ejemplo, se espera que *Piptadenia constricta* y *Coccoloba* sp., tengan afinidad por sitios con suelos moderadamente profundos y que pertenezca a la unidad de terreno de "algunas" limitantes en el suelo y donde la elevación supere los 300 m.

A un nivel local, sería deseable examinar la estructura del dosel y su relación con el relieve y el suelo al interior de las diferentes unidades de limitantes en el suelo. Esto, debido a que los gradientes topográfico-altitudinales (decenas de metros) de Chamela pueden inducir notables cambios estructurales en el BTC, e incluso transiciones de vegetación decidua a semidecidua, como se ha mostrado en el sistema de "microcuencas experimentales" (Balvanera 1999, Galicia *et al.* 1999, Maass *et al.* 2002a, Segura *et al.* 2003). Por lo tanto, el muestreo debe considerar la estructura jerárquica del terreno al interior de las unidades de contraste en limitantes en el suelo; así como tener en cuenta que la mayoría de las laderas no presentan el gradiente extremo de humedad y de vegetación reconocido en las cuencas.

Una sugerencia práctica para el estudio del componente arbóreo vivo, es el uso de unidades de muestreo de tamaño menor al usado en este trabajo (0.24 ha; por ejemplo transectos o relevés). Esto permitiría contar con un mayor número de parcelas, y con ello, una mejor representación de la variabilidad del dosel. Hasta ahora, el uso del parcelas de 0.1 ha "tipo Gentry", que consiste en el establecimiento de 10 transectos de 50 X 2 m distribuídos al azar, ha sido ampliamente adoptado para estudios en BTC (Gentry 1988, Lott *et al.* 1987, Trejo 1998, Gillespie *et al.* 2000, Salas 2002). Sin embargo, debería tenerse en cuenta que dicha propuesta se generó como parte de los métodos para realizar inventarios de diversidad a fin de reconocer áreas prioritarias para la conservación en poco tiempo ("Rapid Assessment Program"; Parker *et al.* 1993), pero no necesariamente puede ser el tamaño y la forma idóneos cuando se pretende analizar la estructura u otros patrones y procesos ecológicos como la mortalidad o la dinámica del dosel.

El tamaño de parcela es un criterio clave que depende del objetivo de estudio, y que se define al iniciar un estudio (Palmer *et al.* 2000). El tipo de parcela y su tamaño no sólo puede limitar la posibilidad de comparar los resultados, sino también porque puede inducir la sub o sobreestimación de algunos atributos de la vegetación (Mueller-Dombois y Ellenber 1974, Kent y Coker 1992). Distintos criterios del tamaño y forma de la parcela se han adoptado para caracterizar la estructura de la comunidad arbórea del BTC de Chamela, por ejemplo cuadros de 10 X 10 m fueron usados por Balvanera *et al.* (2002), cuadros de 30 x 80 m se están usando para los estudios de vegetación y funcionamiento del ecosistema en las microcuencas (Sarukhán *et al.* 2000, Segura *et al.* 2003) y transectos por Lott *et al.* (1987) y Balvanera (1999). Por lo anterior, as aún necesario evaluar las ventajas y limitaciones de las distintas unidades de muestreo adoptadas para los estudios sobre diversidad y estructura, análogos a lo que reporta De Wolf (1998) para un bosque seco en Senegal.

También es importante considerar que para este tipo de bosques la literatura carece de propuestas metodológicas estándares para el muestreo de vegetación, particularmente en aproximaciones de mesoescala o regionales, a diferencia de lo que se presenta para los bosques templados (Lorimer 1985). Teniendo en cuenta como son los mosaicos ambientales donde comúnmente se desarrollan los BTC (Trejo 1998), y de acuerdo con Sollins (1998) considero que más que muestreos aleatorios, se deberían efectuar muestreos estratificados dirigidos o al azar, partiendo del reconocimiento de unidades de terreno definidas por su geomorfología, suelo, vegetación y manejo. Ejemplos de estas aproximaciones lo constituyen por una parte las parcelas permanentes del proyecto de las microcuencas de Chamela donde el gradiente fue subdividido por pisos altitudinales, y exposición de las laderas (Galicia *et al.* 1999). A nivel de mesoescala, el trabajo de Pérez-García (2002) en un BTC de Oaxaca, muestra como a partir del reconocimiento de geoformas y de diferencias en el desarrollo del suelo se establecieron parcelas para reconocer claras variaciones florísticas.

En otro sentido, el análisis de la estructura poblacional de especies de árboles en las microcuencas experimentales ha llevado a la conclusión de que fluctuaciones en el reclutamiento determinan la coexistencia de especies congenéricas (*Bursera, Caesalpinia, Cordia, Jatropha* y *Tabebuia*; Kelly *et al.* 2001, Kelly y Bowler 2002). De acuerdo al análisis de la estructura y la composición de la comunidad arbórea realizado en esta tesis (Capítulo III), se sabe que la presencia ("coexistencia") y la abundancia de los géneros considerados por Kelly *et al.* (2001) a nivel de toda el área de la Estación (1600 ha), fue diferente de lo reportado para las microcuencas. En otras unidades morfoedafológicas los pares o grupos de especies congenéricas fueron "comunes" o "raros" (*sensu* Kelly *et al.* 2001), o su relación de abundancia fue inversa a lo que en dicho estudio se reporta para las microcuencas. Esta situación lleva a cuestionar la aseveración de que la coexistencia de especies congenéricas está regulada únicamente por un reclutamiento diferencial en el tiempo, como Kelly y Bowler (2002) sostienen. Considerando que la dinámica natural de las poblaciones podría ser regulada desde un nivel metapoblacional (Hanski 1999), cabe preguntar ¿de qué manera la coexistencia determinada por pulsos en el reclutamiento puede estar influenciada espacialmente por mosaicos ambientales (relieve y suelos) como el de Chamela?, ¿hasta donde los procesos de "poza-fuente", en cuanto a la dispersión de propágulos (Shmida y Wilson 1986), no podrían contribuir a regular la coexistencia de las especies congenéricas o funcionalmente análogas? Para responder estos cuestionamientos es necesario reconocer los diferentes modelos de variación ambiental que se presentan en el área de la Estación Chamela y patrones espaciales de las especies de acuerdo a dichos modelos.

Otra reflexión en cuanto a las implicaciones que este trabajo puede tener para estudios futuros, es el reconocimiento de que además de los árboles, otros grupos taxonómicos y otras formas de vida pueden ser indicadores ecológicos de la heterogeneidad del relieve, el suelo u otros fatores del medio físico. Entre los grupos y las formas de vida que en otros ecosistemas se ha encontrado que responden de manera diferencial a la oferta de agua, los nutrientes, la aireación, el drenaje o el espacio en el suelo para el desarrollo de raíces, se encuentran especies de los grupos de pteridofitas y palmas, y de las familias Melastomataceae y Cactaceae, así como algunos arbustos, hierbas, trepadoras y epífitas (Tuomisto y Ruokolainen 1993, Clark *et al.*1995, González y Zak 1996, Pérez-García 2002, Salas 2002). En ecosistemas como el de Chamela, el tipo de vegetación y su fenología pueden ser indicadores de los contrastes ambientales en las unidades de terreno (por ejemplo bosque tropical subcaducifolio, bosque tropical caducifolio y enclaves xerofíticos), así como de la presencia y la abundancia de cactáceas (*Pachycereus*, *Stenocereus* y *Opuntia*), u otras especies que mantienen afinidad por condiciones ambientales específicas como *Heliocarpus pallidus* o *Apoplanesia paniculata* (Huante 1996, Trejo 1998, Pérez-García 2002).

Patrones de mortalidad y dinámica del dosel

Este trabajo caracterizó la necromasa arbórea "inicial" (comienzo del estudio), así como la mortalidad y los reclutamientos estacionales en el dosel del BTC por casi tres años. Originalmente se pensó que la necromasa arbórea inicial y estacional podría ser un estimador indirecto de la incidencia de los disturbios y que su variación estaría acorde con las unidades de terreno o las variables del relieve y el suelo. Asimismo, que al relacionar la diversidad arbórea con "unidades de terreno categorizadas por niveles de disturbio" se podría probar la hipótesis del disturbio intermedio (Connell 1978). Nuestros resultados mostraron que no existe una relación entre las variables del relieve y el suelo y la mortalidad arbórea, como tampoco ocurrió una mayor diversidad cuando la frecuencia de los individuos muertos o su área basal fueron intermedias, como lo prevee la hipótesis de Connell (1978). Por ahora, la limitada información con que se cuenta, no permite rechazar o aceptar dichas hipótesis. En relación a lo anterior, persisten dos preguntas relevantes: 1) ¿La necromasa arbórea es el mejor estimador del disturbio? y 2) ¿Los sitios analizados representan todo o la mayor parte del gradiente de disturbio?

Acerca del primer cuestionamiento, en un futuro se debería considerar la necromasa de otras formas de vida o la abundancia de algunas especies reconocidas como indicadoras de perturbación. En relación al segundo cuestionamiento, el estudio de la mortalidad se debería ampliar en el área de conservación con el fin de tener una mejor representación de la dinámica que presenta el BTC, para ello se sugiere usar otras parcelas permanentes del igual tamaño al aquí presentado (0.24 ha). Asimismo, se deberían incluir otras localidades de la región mediante el uso de parcelas no permanentes de menor superficie (0.12 ha).

Otras parcelas permanentes deberían permitan amplíar el gradiente de distancia a la costa e incluirs unidades geomorfológicas sobre caliza (cerca del faro en Cuixmala), y de sitios con apariencia más xérica (presencia de cactáceas). Esto con fin de tener una mejor representación del gradiente de perturbación. Las parcelas permanentes ayudarían a conocer, espacial y temporal, el fenómeno de la mortalidad y la dinámica del dosel; mientras que las parcelas no permanentes permitirían documentar cómo es la relación biomasa/necromasa arbórea del BTC en sitios con diferente intensidad de disturbio natural o antrópico. Aunque el análisis del disturbio antrópico no fue uno de los objetivos de este trabajo, este aspecto se debe analizar porque en la región los estados secundarios o alterados de BTC son comunes, producto del abandono de tierras que fueron utilizadas con fines agrícolas o ganaderos (Maass *et al.* 1995). En este sentido, Gillespie *et al.* (2000) ejemplifica como analizar la intensidad del pastoreo y su impacto en la diversidad de plantas leñosas.

Una mayor mortalidad de troncos se registró en las categorías de menor diámetro y entre algunas especies dominantes en el dosel, lo que sugiere que ocurre mortalidad compensatoria (Connell *et al.* 1984), es decir, que los individuos de las especies y las tallas más comunes tienen mayor probabilidad de morir. Aunque esto aparentemente descarta la ocurrencia de un patrón de mortalidad aleatoria (Hubbell y Foster 1986), antes de adoptar un modelo teórico para el BTC de Chamela, es necesario realizar estudios orientados a la prueba de diferente hipótesis y al análisis de la ocurrencia de dichos fenómenos.

Este trabajo se basó en la premisa de que el estrés hídrico y el viento de las tormentas ciclónicas, junto con la relación espacial que éstos mantienen con variaciones en el terreno (geomorfología y suelos), son los que rigen la mortalidad de los árboles. Por ello, sería deseable analizar los registros de mortalidad con información de los factores microclimáticos relacionados con el estrés hídrico (dinámica temporal de la precipitación, temperatura máximas/mínimas) y con la incidencia del viento (cantidad de precipitación, intensidad de las tormentas). Sin embargo, en este estudio sólo se analizó la relación de la mortalidad estacional con datos de la precipitación mensual debido a que no existe información disponible sobre variables climáticas de interés para este trabajo. Por lo anterior, una continuación del estudio de la mortalidad y la dinámica, se debe mantener una coordinación con otros grupos de investigación, a fin de integrar bases de datos sobre los fenómenos climáticos recurrentes anualmente y los que inciden en el largo plazo.

Finalmente, el reconocimiento de la alta proporción de la necromasa arbórea, en relación a la biomasa, sugiere que además de su implicaciones ecológicas en los ciclos de nutrientes (Martínez-Yrízar *et al.* 1990, Maass *et al.* 2002b) y en la regeneración de las plantas, la necromasa podría contribuir a promover la diversidad de la microfauna (observación personal) como se ha documentado para bosques templados (Harmon *et al.* 1986 Franklin *et al.* 1987). Por lo anterior, se propone el uso de las parcelas de este estudio y la información sobre la biomasa/necromasa para analizar la diversidad y la preferencia de hábitat de algunos grupos de la microfauna (como insectos y pequeños mamíferos y reptiles).

IMPLICACIONES PARA EL MANEJO Y LA CONSERVACIÓN

Los BTC se han señalado como uno de los ecosistemas tropicales que están en mayor riesgo de transformación en el mundo (Murphy y Lugo 1986, Janzen 1990). En México, de los 159,209 Km^2 de selva baja caducifolia que había en 1993, cerca del 15% (23,329 km^2) cambió por la actividad humana a coberturas para el año 2000; siendo Jalisco, uno de los estados donde de manera importante ocurrió la transformación (Velázquez *et al.* 2002). Específicamente en la región de Chamela, fuera de las áreas de conservación se aprecia una creciente deforestación del BTC para usos agrícolas y pecuarios (Maass 1995, A. Miranda com. personal). Aunque debido a las condiciones del relieve, el suelo y el clima, la transformación anárquica de la vegetación natural a agricultura de temporal y pastoreo extensivo genera muy bajos rendimientos.

La continua deforestación ha ocasionado una creciente fragmentación en el entorno del área de conservación en Chamela y, con ello, una inminente pérdida de biodiversidad (o la extinción local de especies); así como la ocurrencia de problemas de erosión y posibles alteraciones en el balance hídrico regional. Esta situación ocurre al margen de la creciente generación de conocimiento producto de la investigación en las zonas de reserva, especialmente en la Estación de Chamela (Noguera *et al.* 2002); por ello, urge expandir los productos, la información y las experiencias de la investigación hacia los responsables de efectuar o decidir el uso del suelo y el manejo de los recursos naturales fuera de la reserva y en otras regiones con características similares. No obstante, dicha transferencia debe ser acorde a las necesidades de los usuarios y encaminada a adoptar políticas regionales sobre el uso de estos ecosistemas. En este sentido, el ejercicio de definir unidades de terreno y hacer su caracterización, como se realizó en este trabajo, es relevante porque propone un modelo acerca del mosaico de relieve y suelos en el área (Zonneveld 1989, Tricart y KiewietdeJonge 1992). Asimismo, el reconocer diferentes limitantes en el suelo entre las unidades de terreno permite identificar sitios con diferente aptitud del terreno para sostener el desarrollo de la vegetación natural. Un análisis regional de la transformación de las coberturas naturales y el estado de la fragmentación del paisaje, en apego al reconocimiento previo de unidades de terreno con diferente aptitud de uso y susceptibilidad a los cambios, podría orientar acciones específicas o negociaciones locales que permitan promover usos más adecuados del terreno, la conservación o la restauración de distintas localidades de la región.

Los resultados de la composición de especies muestran que el BTC casi no presenta especies maderables con valor comercial en el mercado formal, como caoba, cedro, rosa morada, primavera o parota. En cambio presenta algunas especies de árboles con demanda local para la construcción de casas, entre las que destacan por su alta abundancia y por la calidad de su madera el barsino o cuerámo y el guayabillo borcelano (*Cordia elaeagnoides* D.C. y *Piranhea mexicana* (Standl.) A. Radcliffe-Sm., respectivamente), mapilla *Tabebuia chrysanta* y *Tabebuia impetiginosa.* La extracción de *C. elaeagnoides* se realiza de manera autorizada bajo el rubro de "aprovechamiento de otras tropicales" (comunicación personal en la delegación SEMARNAT-INIFAP, en Tomatlán, Jalisco). Debido a la falta de información, los permisos de aprovechamiento se otorgan con base en estudios técnicos que "aseguran" el uso racional del recurso y su regeneración. Esto último, basado tan sólo en el supuesto de distribución homogénea de la especie y regeneración natural por árboles padres, con turnos mínimos de 10 años, tratándose de una especie tropical. El notable desconocimiento de la ecología de la especie propicia que la supervisión de la extracción, por parte de las autoridades del ramo, sea limitada. Localmente también se realizan extracciones no autorizadas de *C. elaeagnoides,* y aunque aparentemente son de "baja" intensidad", éstas son recurrentes, por lo que ejercen una fuerte presión por éste recursos.

Como resultado de este estudio sabemos que *C. elaeagnoides* se presenta en densidades relativamente altas, que su distribución no es generalizada y, que preferentemente se encontró en sitios sobre tobas y conglomerados, donde existen muchas limitantes en el suelo (Capítulo III). Su abundancia se correlacionó negativamente con la profundidad del suelo, la concentración de arcillas y la disponibilidad de fósforo (Capítulo IV).

La información generada en la tesis sobre la distribución, el estado de la población y las condiciones que caracterizan su hábitat, junto con observaciones *in situ* de su regeneración en sitios abiertos, y su aparente preferencia por sitios perturbados donde la luz no es un recurso limitante, junto con los antecedentes de otros estudios (Huante 1996, Groenendael *et al.* 1996, Galicia 1999, Rosas 2000), puede servir de plataforma para planear el uso y manejo sustentable de este recurso. Debido a que esta especie no sólo es susceptible de regenerarse de manera natural, sino que acorde a su ecología, representa una opción para reforestar o restaurar áreas alteradas o para producir postes y madera a niveles semicomerciales.

No obstante la importancia del barsino y el guayabillo borcelano, el mayor potencial de uso de los árboles del BTC de Chamela no es maderable. Tradicionalmente, numerosas especies arbóreas se usan localmente con distintos propósitos (Yetman *et al.* 2000, Bye *et al.* 2002, Rendón 2003) por ejemplo: *Amphipterygium adstringens* (Schlecht.) Schiede (cuachalalate) tienen un uso medicinal, *Croton alamosanus* Rose (vara blanca) en su estado juvenil se extrae como soporte o "tutor" en los cultivos de jitomate, *Gliricidia sepium* sirve como cerco vivo y forraje, *Plumeria rubra* L.(cascalosúchil) es ornamental, *Psidium sartorianum* (Berg.) Ndzu. (arrayán) tiene frutos comestibles y con ellos se elaboran dulces.

De acuerdo a los resultados del presente trabajo, sabemos que la mayoría de las especies dominantes en el dosel no tienen una distribución generalizada y su abundancia podría relacionarse con ciertos rangos de elevación o con características específicas del suelo (Tabla VI.1). Asimismo, que varias de estas especies mueren y se reclutan con mayor frecuencia y otras pueden rebrotar. Esta información a las necesidades de manejo de plantas en los bosques tropicales, el cual de acuerdo a Hubbell y Foster (1992) debe realizarse sobre la base de entender y reconocer dónde y cómo se encuentran de manera natural las poblaciones de las especies de interés, su mortalidad y el reclutamiento de sus individuos jóvenes, así como los factores ambientales con los que se relacionan. De acuerdo a lo anterior, este trabajo indudablemente proveé de información ecológica sobre las especies arbóreas que sería útil considerar al pretender su manejo.

Por otra parte, en relación al uso de la leña del BTC, se sabe que aparentemente los pobladores cercanos a la costa no hacen un uso recurrente de ella, pero que su uso es más frecuente en los poblados más alejados de la zona costera y de las vías primarias de comunicación. Debido a que el uso de leña puede implicar extraer grandes cantidades de necromasa, es probable que la relación 2:1 de la biomasa:necromasa, que de manera natural se encontró en el BTC de la Estación de Chamela (Capítulo V), se modifique en bosques donde se extrae dicho producto. Este tipo de manejo de recursos puede tener implicaciones ecológicas, porque reduce el aporte de nutrientes y materia orgánica que de manera contínua proveé la necromasa arbórea (Maass *et al.* 2002b), asi como por su relación con fauna del suelo. Sin embargo, hasta ahora no se cuenta con una estimación de los niveles de extracción para inferir sus niveles de impacto ecológico.

En cuanto a la designación de sitios prioritarios para la conservación, más allá de enfatizar la importancia de los valles aluviales y sus piesdemonte colindantes, los resultados (gran diversidad local y baja similitud entre la mayoría de las parcelas, así como la escasa abundancia de la mayoría de las especies) justifican la conservación del área de la Estación de Biología de Chamela y sus alrededores. Finalmente, también cabe enfatizar que la Estación de Biología no sólo mantiene una alta diversidad biológica, sino que también alberga un mosaico de hábitats que *per se* tiene valor de conservación, porque puede servir para estudios futuros sobre el suelo, la geomorfología, la geología, la tectónica del sitio y el clima regional. Por ello, es importante concientizar a los académicos, conservacionistas y tomadores de decisiones de

Tabla VI. 1. Especies de importancia por su uso local en la región de Chamela. Abundancia y tendencias en su distribución de acuerdo a las tres clases de limitantes en el suelo.

		Limitantes en el Suelo					
		Muchas (10 parcelas)		Algunas (3 parcelas)		Pocas (8 parcelas)	
Especies	Individuos Totales (5.04 ha)	Árboles/ha	Distribución (# parcelas)	Árboles/ha	Distribución (# parcelas)	Árboles/ha	Distribución (# parcelas)
Amphipterygium adstringens (Schlecht.) Schiede	64	22	7	0	0	6	2
Caesalpinia eriostachys Benth.	429	123	9	44	3	53	2
Cordia elaeagnoides DC.	96	30	5	0	0	13	2
Croton alamosanus Rose	12	0	0	1	1	6	5
Psidium sartorianum (Berg.) Ndzu.	172	3	5	36	3	73	7
Spondias purpurea L.	21	9	7	0	0	0	0

que además de los organismos, el mosaico ambiental es un legado de la historia geológica y biogeográfica del sitio, de manera que su estudio permitirá entender los mecanismos mediante los cuales se estructura y evoluciona el componente físico de un paisaje (Sollins 1998), así como la biota asociada a éste. Además de que es ampliamente reconocido que la conservación del hábitat es clave para la conservación estructural y funcional de cualquier ecosistema (Hansen y Rotella 1999). Dada la continua transformación del BTC, las zonas de conservación, como la Reserva de la Biósfera de Chamela-Cuixmala acrecentarán su importancia no sólo como fuentes de información, sino también como modelos para la planeación del uso y manejo de los recursos, para la conservación y la restauración de este tipo de ecosistemas. Por ello, es necesario contar con información desde distintas perspectivas y tener en cuenta que los ecosistemas son complejos y multi-escalares.

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APÉNDICES

APÉNDICE I.

Perfiles de suelo analizados para definir los principales contrastes en cuanto a las limitantes en el suelo, en área de la Estación de Biología de Chamela, Jalisco, México (Cap. II). UMP es la abreviatura de las unidades morfo-pedológicas que son definidas en la figura I.1 de la sección introductoria de la tesis. La localización de los perfiles se indica respecto a las principales rutas de acceso a la zona de investigación, parajes localmente conocidos y la ubicación de las parcelas permanentes para el estudio del componente arbóreo vivo y muerto (Caps. III-V)

#	Perfil	Litología	UME	Geoforma y elevación (msnm)	Localización	Profundidad (cm)	Horizontes	Raíces	Textura (%)			Piedras	Densidad Aparente (g/ml)	pH (CaCl$_2$)	Materia orgánica (%)
									Arcilla	Arena	Limo				
1	U	Granito	LCG	Laderas cortas (210)	A 800 m al este del cruce del lindero sur y el camino al "Rincón de Ixtán"	0 - 4/6	Ah1	MA	20.8	65.2	14.0	60	1.0	5.9	7.2
						4/6 - 25	Ah2	MA	22.8	63.2	14.0	50	1.2	4.9	6.3
						25 - 42	(B)Cw	Me	26.8	63.2	10.0	70	1.3	4.4	0.2
						42 - 70	Cw	B	24.8	69.2	6.0	95	1.4	4.5	0.2
2	BB	Granito	LCG	Laderas cortas (190)	Por el araje denomindo "Rincón de Ixtán"	0 -4	Ah1	MA	28	56	16	5	(1.05)	5.7	5.4
						4-10	Ah2	A	28	62	10	10	(1.25)	5.0	2.4
						10-30	AB	Me	34	52	14	15	1.4	4.4	1.2
						>30	Cw	N	--	--	--	100	--	--	--
3	Z1	Granito	LCG	Laderas cortas (310)	Por el lindero sur, un km al Este del cruce del lindero el camino al "Rincón de Ixtán"	0 - 2	Ah1	EA	20.8	71.2	8.0	30	1.2	6.0	11.0
						2 - 7	Ah2	MA	22.8	69.2	8.0	50	1.2	6.0	7.7
						7 - 21	AC	A	30.8	57.2	12.0	90	1.2	5.8	3.2
						21 - 52	Cw	MB	28.8	63.2	8.0	95	1.3	4.7	1.5
4	E1	Granito	LAG	Ladera alta (410)	Parcela E1, por el lindero sur al subir desde el paraje "La Cascalotera"	0-4	Ah	EA	28.6	53.1	18.3	5	1.2	6.5	8.7
						4-30	Ae	EA	25.6	57.1	17.3	5	1.2	6.2	3.4
						30-44	AB	A	33.6	53.1	13.3	10	1.4	5.8	1.3
						44-80	Btw1	Me	35.6	49.1	15.3	2	1.4	5.5	1.4
						80-90	Btw2	Me	43.6	43.1	13.3	1	1.6	5.4	0.8
5	E3	Granito	LAG	Ladera alta (370)	Parcela E3, por el lindero sur a un Km subiendo por el "Rincón de Ixtan"	0-3	Ah1	EA	24.2	61. 6	14.3	3	1.2	6.8	8.4
						3-8	Ah2	EA	16.3	66.6	17.3	35	1.2	6.6	7.8
						8-18	A(B)	MA	16.2	68. 6	15.3	50	1.2	6.2	4.6
						18-27/30	(B)Cw	A	22.2	62. 6	15.3	70	1.2	5.8	2.8
						27/30-40	Cw	N	14.2	78. 6	7.3	99	--	5.4	1.9

#	Perfil	Litología	UME	Geoforma y elevación (msnm)	Localización	Profundidad (cm)	Horizontes	Raíces	Textura (%)			Piedras	Densidad Aparente (g/ml)	pH (CaCl$_2$)	Materia orgánica (%)
									Arcilla	Arena	Limo				
6	E4	Granito	LAG	Ladera alta (450)	Parcela E4, un km al noreste del paraje "La Cerrillosa"	0-3	Ah1	EA	24.9	54.6	20.6	2	1.2	7.4	8.3
						3-23	Ah2	MA	25.6	53. 2	21.3	5	1.4	6.5	8.6
						23-44	Btw	A	29.6	49. 2	213	5	1.2	6.2	2.1
						44-86	BCw	Me	25.6	53. 2	21.3	80	1.4	6.0	1.4
						86-	Cw	N	17.6	73. 2	9.20	>80	--	6.3	1.0
7	CC	Granito	LAG	Ladera alta (430)	Parcela E2, 1,000 al noreste del paraje "La Cerrillosa"	0-5	Ah	MA	20	62	18	3	(0.87)	6.4	5.9
						5-27/30	Ae	MA	36	38	26	3	(1.06)	5.1	1.4
						27/30-70/75	Bt	Me	52	30	18	6	(1.19)	4.8	0.8
						70/75-80	Cw	N	32	58	10	90	1.35	5.3	0.6
8	Q	Granito	LAG	Ladera alta (540)	A 3 m del lindero sur en la cresta del Cerro Maderas	0 - 4	Ah1	EA	20.8	70.0	9.2	5	1.2	6.9	7.6
						4 – 9	Ah2	EA	20.8	70.0	9.2	20	1.2	6.9	5.9
						9 - 20	AC1	MA	28.8	62.0	9.2	70	1.3	6.2	3.4
						20 - 30	AC2	A	24.0	62.0	14.0	85	1.3	6.0	2.1
						30 - 57	Cw	Me	34.8	53.2	10.0	90	1.4	5.4	0.7
9	C1	Granito	LIG	Ladera media (290)	Parcela C1, a 200 m el este del paraje "La Cerrillosa"	0-3	Ah1	EA	23.4	55.3	21.3	2	<1.0	6.6	7.6
						3-9	Ah2	MA	21. 4	59.3	19.3	7	1.2	6.1	4.5
						9-25	AB	A	27.4	51.3	21.3	5	1.2	4.8	1.6
						25-44	Btw1	A	30.2	47.3	22. 6	2	1.2	4.4	1.4
						44-70	Btw2	B	35.4	43.4	21.2	1	1.2	4.1	0.7
						70-78	BC	MB	31.4	45.6	23.3	2	1.4	4.1	0.7
10	C2	Granito	LIG	Ladera media (330)	Parcela C2, 400 al noreste del paraje "La Cascalotera"	0-3	Ah1	EA	21.4	49.3	29.3	1	1.2	6.9	9.7
						3-15	Ah2	EA	23.4	45.3	31.3	5	1.4	6.2	3.6
						15-27	AB	Me	29.4	43.3	27.3	1	1.4	5.3	1.7
						27-57	Btw1	Me	31.4	41.3	27.3	10	1.2	4.8	1.1
						57-80	Btw2	Me	33.4	41.3	25.3	15	1.2	5.0	0.6
						80-94	BCw	B	25.4	49.3	25.3	50	1.4	4.8	0.6
						94-100	Cw	N	25.4	51.3	23.3	--	--	4.8	0.5
11	C3	Granito	LIG	Ladera media (310)	Cuadro C3, a 500 m al Este por el camino de "La Cascalotera al cerro "Maderas"	0-2	Ah1	EA	18.2	61.6	20.3	5	1.2	6.3	9.3
						2-15	Ah2	MA	26.2	56.6	17.3	15	1	5.6	2.6
						15-27	A(B)	A	26.2	52.6	21.3	40	1.2	5.1	1.6
						27-60/70	B(Cw)	Me	30.2	54.6	15.3	35	1.2	4.7	1.0
						60/70-74	Cw	N	10.2	78.6	11.3	99	--	4.7	0.5

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#	Perfil	Litología	UME	Geoforma y elevación (msnm)	Localización	Profundidad (cm)	Horizontes	Raíces	Textura (%)			Piedras	Densidad Aparente (g/ml)	pH ($CaCl_2$)	Materia orgánica (%)
									Arcilla	Arena	Limo				
12	C4	Granito	LIG	Ladera media (310)	Parcela C4, 100 al Sureste del cuadro C1, subiendo por la misma ladera	0-3	Ah1	EA	18.2	68.6	13.3	1	1.2	6.8	5.9
						3-20	Ah2	EA	18.2	66.6	15.3	7	1.4	6.3	2.5
						20-32	Btw1	MA	24.2	58.6	17.3	10	1.2	5.4	1.1
						32-54	Btw2	A	30.2	54.6	15.3	25	1.2	5.0	1.0
						54-59/63	BCw	MB	22.0	63	15	50	1.2	5.0	0.7
						59/63-70	Cw	MB	18.0	69	13	98	--	5.0	0.6
13	B	Granito	LBG	Ladera intermedia (290)	Por el camino antiguo a la Huerta, 500 m al este del paraje "La Cerrillosa"	Ah	0-8	EA	32.8	49.2	18	3	(1.05)	6.2	4.4
						AB	8-15	EA	38.8	39.2	22	5	(1.13)	5.8	2.3
						Btw1	15-22	MA	50.8	29.2	20	15	1.2	5.1	0.3
						Btw2	22-50	A	52.8	33.2	14	25	1.3	4.6	1.1
						Cw	50-81	B	25.8	60.2	14	--	1.4	4.2	0.5
14	D1	Granito	LBG	Ladera baja (220)	Parcela D1, a 200 m al Oeste del paraje "La Cascalotera"	0-4	Ah1	EA	22.2	55.3	22.6	10	1.2	5.9	4.6
						4-15	Ah2	MA	26.2	49.3	24.6	7	1.0	6.3	2.0
						15-30	(A)B	A	32.2	44.3	23.6	10	1.4	5.7	1.2
						30-46/55	Btw	M	40.2	41.3	18.6	10	1.4	5	1.3
						46/55-60	BCw	B	26.2	59.3	14.6	65	--	5.1	0.6
15	D3	Granito	LBG	Ladera baja (230)	Parcela D3, por el lindero Norte a 200 m al Oeste del paraje "La Cerrillosa"	0-2	Ah1	EA	18.2	63.8	18	3	1.2	7.0	6.0
						2-8	Ah2	MA	24.2	55.8	20	10	1.4	6.4	3.4
						8-18	(A)B	A	26.2	51.8	22	10	1.3	6.1	1.9
						18-33/43	Btw1	Me	24.2	55.8	20	10	1.6	5.8	1.5
						33/43-60	Btw2	B	32.2	53.8	14	10	1.6	5.2	1.2
16	D4	Granito	LBG	Ladera baja (230)	Parcela D4, por lindero Norte 50 m al este de la parcela D3	0-3	Ah1	EA	20.2	58.6	21.3	3	1.2	6.6	13.3
						3-17	Ah2	MA	24.2	56.6	19.3	5	1.4	6.5	3.1
						17-25	AB	Me	30.2	52.6	17.3	5	1.4	6.4	1.7
						25-44	Btw1	B	26.2	56.6	17.3	2	1.4	6.4	1.4
						44-57	Btw2	B	22.2	54.6	23.3	5	1.4-1.6	6.7	1.2
17	D5	Granito	LBG	Ladera baja (220)	Parcela D5, por el lindero Norte en la ladera baja del cerro Maderas al Oeste del paraje "La Cerrillosa"	0-4	Ah1	EA	16.2	64.6	19.3	15	1.2	6.8	6.7
						4-17	Ah2	EA	22.2	58.6	19.3	10	1.2	5.7	3.2
						17-30	AB	Me	24.2	58.6	17.3	20	1.2	4.9	1.0
						30-40/50	Btw	Me	30.2	55.6	14.3	15	1.4	4.8	1.0
						40/50-63	BC	B	32.2	56.6	11.3	80	1.2	4.7	0.7

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#	Perfil	Litología	UME	Geoforma y elevación (msnm)	Localización	Profundidad (cm)	Horizontes	Raíces	Textura (%)			Piedras	Densidad Aparente (g/ml)	pH ($CaCl_2$)	Materia orgánica (%)
									Arcilla	Arena	Limo				
18	DD	Granito	LBG	Ladera baja (225)	Parcela D2, a 500 m al Norte del paraje "La Cascalotera"	0-4/7	Ah	EA	28	58	14	2	(0.9)	5.8	5.3
						4/7-20	Ae	A	34	50	16	15	(1.08)	5.5	2.4
						20-33	Bt	M	54	34	12	15	(1.25)	4.7	0.6
						33-52	Cw	N	60	26	14	15	1.35	4.2	0.6
19	C	Material de Arrastre	DLG	Depresión en laderas (220)	Cerca de lindero Norte, a 100m al Este del paraje "La Cascalotera"	0 - 4	Ah1	EA	32.8	39.2	28.0	2	(1.06)	4.5	8.4
						4 - 18	Ah2	EA	36.8	29.2	34.0	25	1.0	4.1	1.5
						18 - 40	AC	A	34.8	58.2	7.0	70	1.2	6.2	0.5
						40 - 60	2Cr	MB	36.8	51.2	12.0	5	1.4	6.5	0.2
20	B1	Tobas	ST	Cresta (100)	Parcela B1, cerca del metro 1,400 de la vereda Ardilla	0-4	Ah_1	EA	28.9	33.1	38	5	1.2	7.2	15.6
						4-9	Ah_2	EA	30.9	31.1	38	7	1.4	7.0	7.8
						9-24	A(B)	B	32.9	37.1	30	30	1.4	6.3	3.4
						24-44	(B)Cw	B	28.9	41.1	30	60	1.2	5.8	1.5
						44-60	Cw	--	--	--	--	99	--	5.4	--
21	B2	Tobas	ST	Cresta (110)	Parcela B2, cerca del metro 800 de la vereda tejón	0-4	Ah_1	EA	31.4	44.6	24	5	1.2	7.0	14.5
						4-10	Ah_2	EA	33.4	40.6	26	15	1.2	6.8	8.6
						10-20	AB	MA	27.4	42.6	30	70	1.2	6.6	3.7
						20-34	(B)Cw	Me	23.4	50.6	26	80	1.2	6.2	1.8
						34-45	Cw	MB	--	--	--	99	--	6.2	1.8
22	B3	Tobas	ST	Cresta (110)	Parcela B3, cerca del metro 2,300 de la vereda tejón	0-3	Ah_1	EA	22.9	49.1	28	50	1.2	7.1	10.1
						3-13/17	A(B)	EA	28.9	43.1	28	40	1.4	6.1	3.7
						13/17-35	(B)Cw	Me	26.9	45.1	28	85	1.2	5.3	1.6
						35-43	Cw	N	24.9	47.1	28	90	--	5.1	1.2
23	B4	Tobas	ST	Cresta (110)	Parcela B4, cerca del metro 2,300 de la vereda Tejón	0-3	Ah_1	EA	22.9	48.6	28.6	2	1.2	7.2	14.8
						3-17	Ah_2	MA	28.9	44.6	26.6	2	1.4	6.3	5.9
						17-37	(B)Cw	MA	29.1	44.6	26.3	60	1.2	5.8	1.5
						37-50	2Cg	N	22.6	48.6	28.9	50	>1.6	5.1	0.9
24	M	Tobas	ST	Cresta (130)	Por la torre del metro 2,700 de la vereda Tejón	0-3	Ah_1	EA	30.8	49.2	20	15	(1.08)	6.9	11.6
						3-8	Ah_2	A	30.8	47.2	22	5	(1.21)	6.8	6.3
						8-32	A(B)	A	36.8	45.2	18	15	(1.21)	5.5	1.4
						32-49/56	Bw	Me	56.8	19.2	24	3	1.4	5.3	0.6
						49/56-73	Cw	B	26.8	59.2	14	85	1.4	5.3	0.6

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									Arcilla	Arena	Limo				
25	X	Tobas	ST	Cresta (141)	Por el metro 550 de la vereda Tejón	0-5	Ah	EA	30.8	47.2	22	2	(1.05)	6.2	10.2
						5-12	AB	A	34.8	37.2	28	5	(1.3)	6.1	4.6
						12-37	Bt	B	54.8	23.2	22	0	(1.45)	6.2	1.6
						37-54	BC	B	40.8	33.2	26	0	1.4	6.0	1.0
						54-64	Cw$_1$	B	30.8	55.2	14	0	1.3	5.9	0.5
						64-100	Cw$_2$	MB	22.8	65.2	12	0	1.3	6.2	0.1
26	V	Tobas	ST	Cresta (135)	Por el metro 1,250 de la vereda Ardilla	0-4	Ah	MA	24.8	59.2	16	2	1.0	5.5	11.2
						4-16	AC	MA	28.8	49.2	22	50	1.3	5.3	2.6
						16-34	Cw$_1$	B	38.8	37.2	24	40	1.4	4.9	1.6
						34-47	Cw$_2$	N	40.8	35.2	24	90	1.4	5.1	1.6
27	P	Tobas	LT	Cresta (110)	Por el metro 650 de la vereda Ardilla	0-3	Ah	EA	30	40	30	5	(0.92)	6.8	7.7
						3-16	AB	MA	40	32	28	2	(1.23)	5.5	5.1
						16-32	Bw	MA	36	34	30	5	1.4	6.2	1.7
						32-65	Cw	N	24	62	14	--	1.5	6.2	0.6
28	B5	Tobas	LT	Ladera (100)	Parcela B5, por el lindero Norte y el cruce con el arroyo Colorado	0-3	Ah$_1$	EA	30.2	26.6	43.3	5	1.2	7.2	10.7
						3-11	Ah$_2$	MA	30.2	26.6	43.3	5	1.4	7.2	5.9
						11-20	A(B)	A	26.1	30.6	43.3	5	1.4	6.7	1.6
						20-37	Bt	Me	26.2	32.6	41.3	2	1.4	6.4	0.9
						37-43/50	BC	B	22.2	44.6	33.3	60	1.4	6.4	0.4
						43/50-68	Cw	MB	14.2	58.6	27.3	70	1.0	6.5	0.6
29	W	Tobas	LT	Ladera alta (110)	Por el metro 1,500 de la vereda Tejón	0-3	Ah	EA	38.8	41.2	20	25	1.0	6.8	13.4
						3-14	AC	MA	34.8	45.2	20	35	(1.17)	6.8	3.7
						14-50	Cw	B	38.8	45.2	16	70	1.4	6.0	1.4
30	N	Conglomerados	SCT	Cresta (110)	A 50 m de la vereda Tejón	0-3	Ah1	EA	24.8	61.2	14	5	(0.9)	7.1	6.8
						3-7/13	Ah2	MA	22.8	65.2	12	50	(0.9)	7.5	5.0
						7/13-10/17	AC	MA	26.8	61.2	12	85	(1.05)	7.0	1.3
						10/17-40	2BC	Me	32.8	53.2	14	2	(1.32)	7.1	0.6
						40-71	3Cwg	N	20.8	73.2	6	--	1.5	6.4	0.3

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									Arcilla	Arena	Limo				
31	A2	Granito	SG	Cresta (180)	Parcela A2, en la cresta de la cuenca 1, pasando el cuadro alto-alto	0-3	Ah1	EA	23.4	57.3	19.3	7	1.2	6.6	7.8
						3-21	Ah2	EA	21.4	59.3	19.3	15	1.2	5.8	2.4
						21-31	AB	A	29.5	57.3	13.2	10	1.4	5.4	1.1
						31-54	Btw	Me	39.4	45.3	15.3	10	1.4	4.4	1.2
						54-78	BCw	B	17.4	67.3	15.3	60	1.2	4.4	0.8
						78-89	Cw	N	11.4	71.3	17.3	95	--	4.6	0.4
32	A3	Granito	SG	Cresta (180)	Cuadro A3, 30 m al este de la torre de la vereda “La Calandria”	0-3	Ah1	A	14.2	68.6	17.3	5	1.2	6.5	6.2
						3-11	Ah2	EA	17.3	66.6	16.2	5	1.2	5.3	2.3
						11-28	AB	A	20.0	62.6	17.4	5	1.4	4.6	1.2
						28-37	BC	Me	22.2	64.6	13.3	30	1.2	4.5	1.0
						37-40	Cw	N	14.2	78.6	7.3	99	--	4.5	--
33	H	Granito	SG	Cresta (200)	Parcela A1, a 400 m del lindero Sur, donde inicia el cauce de la Cuenca 1	0-4	Ah1	EA	28.8	57.2	14	7	1.2	5.9	7.2
						4-15	Ah2	EA	28.8	57.2	14	15	1.3	5.8	3.7
						15-31	AB	MA	38.8	49.2	12	50	1.2	4.4	2.5
						31-55	Bt(w)	A	46.8	43.2	10	60	1.2	4.2	0.2
						55-76	Btw	A	34.8	43.2	22	70	1.2	4.1	0.2
						76-104	Cw	N	34.8	53.2	12	98	1.4	4.3	0.3
34	AA	Granito	SG	Cresta (150)	A 5 m de la biblioteca de la Estación	0-2	Ah		24.8	63.2	12.0		(1.42)	7.5	4.8
						2-10	Ah2		30.8	53.2	16.0		(1.34)	7.3	1.4
						10-32	AB		28.8	55.2	16.0		1.2	7.4	1.0
						32-64	B(C)		30.8	53.2	16.0		1.4	6.8	1.9
						64-100	Cw		49.8	35.2	15.0		1.5	5.7	0.0
35	E	Conglomerados	SCG	Cresta (190)	Por el cruce del camino antiguo a la Huerta y el camino al Rincón de Ixtán	0-4	Ah	EA	28.8	59.2	12	2	(1.2)	5.4	5.5
						4-23	AB	MA	32.8	49.2	18	50	(1.4)	4.8	2.5
						23-55	Btw	A	44.8	35.2	20	60	(1.2)	4.8	0.7
						55-80	BC	A	35.8	47.2	17	80	(1.4)	4.8	0.1
36	J	Conglomerados	SCG	Cresta (160)	Parcela F3, en la cresta Centro-Oeste entre los arroyos Hornitos y Cuastecomates	0-4	Ah	EA	30	56.0	14	1	(1.2)	7.0	7.2
						4-20	Ah(p)	EA	30	58.0	12	5	(1.4)	6.1	2.6
						20-30/42	ACw	A	30	54.0	16	75	(1.4)	5.5	1.6
						30/42-58	2Cwg	MB	26.8	55.2	18	3	(1.5)	5.6	0.6

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									Arcilla	Arena	Limo				
37	Z_3	Conglomerados	SCG	Cresta Ladera alta (150)	Cresta Centro-Oeste entre los arroyos Hornitos y Cuastecomates	0-3	Ah$_1$	EA	30	56.0	14	15	(1.2)	6.5	6.6
						3-8	Ah$_2$	MA	30	58.0	12	15	(1.4)	6.4	3.7
						8-28/35	ACw	A	30	54.0	16	20	(1.4)	5.5	1.8
						28/35-68	(A)Cw	B	26.8	55.2	18	80	(1.5)	5.6	1.4
38	F_1	Conglomerados	SCG	Cresta (160)	Parcela F1, en la cresta del lindero sur, a 500 al Este del cruce con el arroyo Colorado	0-3	Ah$_1$	EA	17.6	69.8	12.6	1	1.2	6.9	6.7
						3-22	Ah$_2$	EA	17.6	66.4	16.5	3	1.4	5.9	2.8
						22-38	A(C)	A	19.6	61.8	18.6	5	1.4	5.4	1.3
						38-50	Cw	B	15.6	67.8	16.6	20	1.2	5.3	0.6
						50-60	2Cwg	MB	33.6	49.8	16.6	--	1.6	4.9	0.6
39	F_2	Conglomerados	SCG	Cresta (190)	Parcela F2, en la cresta este del cerro entre el arroyo Cuastecomates y el paraje del "Rincón de Ixtán"	0-2	Ah$_1$	EA	16.9	71.6	11.6	1	1.2	5.6	7.5
						2-10/15	Ah$_2$	EA	20.2	62.6	17.3	5	1.2	4.7	2.2
						10/15-25	ACw	A	26.9	50.6	22. 6	60	1.4	4.7	1.4
						25-40/45	Cw	B	16.9	64.6	18.6	85	1.4	4.8	1.7
						40/45-61	2Cwg	B	44.9	34.6	20.6	--	1.6	5.8	0.8
40	T	Granito	LG	Ladera irregular (170)	A 500 m al Este del cruce del antiguo lindero Sur y el camino al "Rincón de Ixtán"	0 - 3	Ah	MA	20.8	65.2	14.0	2	1.1	6. 7	6.0
						3 - 20	AC	A	26.8	59.2	14.0	10	1.3	6.1	1.8
						20 - 59	Cw	B	24.8	63.2	12.0	50	1.4	5.8	1.2
41	FF	Granito	LG	Ladera irregular (150)	Al Oeste del cerro entre los arroyos Cuastecomates y Hornitos	0-1	Ah	MA	18.0	78.0	4.0	0	(1.01)	7.3	10.4
						1-10	AC	A	20.0	70.0	10.0	70	(1.25)	7.0	1.1
						10-90	Cw	N	20.0	72.0	8.0	75	1.35	6.8	0.0
42	Z	Granito	LG	Ladera irregular (130)	Cerca del metro 50 de vereda Tejón	0-5	Ah	EA	30.8	51.2	18.0	15	(1.14)	6.7	4.8
						5-22/29	Bw	A	30.8	55.2	14.0	30	(1.32)	5.8	1.9
						22/29-45	Cw	Me	38.8	49.2	12.0	70	1.4	5.2	1.1
43	Z2	Granito	LG	Ladera irregular (170)	Cerca del cruce entre el lindero Sur y el camino al "Rincón de Ixtán"	0-3	Ah1	EA	20.8	69.2	10.0	2	1.19	6.90	5.9
						3-13	Ah2	A	20.8	67.2	12.0	5	(1.2)	6.70	2.3
						13-31	AC	A	22.8	65.2	12.0	10	(1.2)	6.35	0.9
						31-52	Cw	B	18.8	71.2	10.0	50	1.54	5.95	0.5

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#	Perfil	Litología	UME	Geoforma y elevación (msnm)	Localización	Profundidad (cm)	Horizontes	Raíces	Textura (%)			Piedras	Densidad Aparente (g/ml)	pH ($CaCl_2$)	Materia orgánica (%)
									Arcilla	Arena	Limo				
44	EE	Material de Arrastre	P	Pie de monte (95)	Cerca del arroyo Hornitos donde cruza con el arroyo Colorado	0-7	Ah	MA	18	72	10	1	(1.00)	7.1	5.22
						7. - 28	AB	A	20	68	12	0	(1.20)	6.7	1.17
						28-46	BC1	Me	24	70	6	2	(1.27)	6.3	0.55
						46-67	BC2	MB	28	66	6	2	1.4	6.1	0.22
45	R	Material Aluvial	TA	Terrazas (85)	10 m al Este del cruce de los arroyos Hornitos y Colorado	0-1	Ah	EA	20.8	69.2	10.0	20	(1.1)	5.9	6.7
						1-14	AC	MA	22.8	65.2	12.0	2	(1.4)	5.9	3.1
						14-31	C1	A	20.8	69.2	10.0	4	1.4	5.9	1.4
						31-80	C2	A	28.8	63.2	8.0	10	1.4	6.1	1.0
46	S	Material Aluvial	TR	Terrazas (80)	Cerca del cruce entre el arroyo Colorado y el camino "Eje Central"	0 - 4	Ah	MA	20.0	74.0	6.0	5	(1.11)	5.3	10.5
						4 - 12	AC	MA	22.0	72.0	6.0	5	(1.20)	4.9	3.1
						12 - 53	Cw1	A	22.0	76.0	2.0	2	(1.31)	5.3	0.8
						53 - 80	Cw2	Me	20.0	80.0	0	40	1.4	5.6	0.0

APÉNDICE II.

Lista de especies y morfoespecies encontradas en las 21 parcelas estudiadas; se especifica el número de parcelas donde se encontró cada especie en el componente arbóreo vivo (a), en los árboles muertos registrados estacionalmelmente en el periodo analizado (b), y en los árboles reclutados estacionalmente (c). Las especies fueron identificadas por la Dra. Emily J. Lott (Universidad de Texas E.U.A.), con base en observaciones de campo y la revisión con colectas de herbario.

#	Especie	Familia	Clave*	Presencia entre (# parcelas):		
				a) el componente vivo	b) los muertos estacionalmente	c) los nuevos reclutas
1	*Acacia cochliacantha* Humb. & Bonpl. ex Willd.	Leguminosae	ACACOC	5	1	1
2	*Acacia* sp.	Leguminosae	ACA-SP	2	--	--
3	*Achatocarpus gracilis* H. Walt.	Achatocarpaceae	ACHGRA	6	2	--
4	*Adelia oaxacana* (Muell. Arg.) Hemsl.	Euphorbiaceae	ADEOAX	7	1	--
5	*Albizia occidentalis* Brandegee.	Leguminosae	ALBOCC	3	--	--
6	*Allenanthus hondurensis* Standl. var. *parvifolia* L. Wms.	Rubiaceae	ALLHON	5	1	--
7	*Alstonia longifolia* (A. DC.)	Apocynaceae	ALSLON	14	2	1
8	*Amphipterygium adstringens* (Schlecht.) Schiede.	Julianaceae	AMPADS	9	--	--
9	*Annona palmeri* Safford.	Annonaceae	ANNPAL	3	--	--
10	*Apoplanesia paniculata* Presl.	Leguminosae	APOPAN	11	4	3
11	*Bauhinia ungulata* L.	Leguminosae	BAUUNG	8	3	1
12	*Bernardia mexicana* (Hook. & Arn.) Muell. Arg.	Euphorbiaceae	BERMEX	1	1	--
13	*Bernardia spongiosa* McVaugh	Euphorbiaceae	BERSPO	1	--	--
14	*Bourreria* cf. *purpusii* Brandegee	Boraginaceae	BOUPUR	15	2	1
15	*Brongniartia* sp. nov. ined. O. Dorado	Leguminosae	BRO-SP	7	2	--
16	*Bursera arborea* (Rose) Riley.	Burseraceae	BURARB	20	--	--
17	*Bursera excelsa* (HBK.) Engl.	Burseraceae	BUREXC	5	--	--
18	*Bursera fagaroides* (HBK.) Engl.	Burseraceae	BURFAG	7	1	1
19	*Bursera heterestes* Bullock.	Burseraceae	BURHET	7	2	--
20	*Bursera instabilis* McVaugh & Rzed.	Burseraceae	BURINS	10	1	--
21	*Bursera* sp.	Burseraceae	BUR-SP	2	--	--
22	*Caesalpinia caladenia* Standl.	Leguminosae	CAECAL	6	1	--
23	*Caesalpinia coriaria* (Jacq.) Willd.	Leguminosae	CAECOR	11	2	--
24	*Caesalpinia eriostachys* Benth.	Leguminosae	CAEERI	15	5	1
25	*Caesalpinia platyloba* S. Wats.	Leguminosae	CAEPLA	3	--	--
26	*Caesalpinia pulcherrima* (L.) Sw.	Leguminosae	CAEPUL	4	--	1
27	*Caesalpinia sclerocarpa* Standl.	Leguminosae	CAESCL	13	--	--
28	*Calliandra emarginata* (Willd.) Benth.	Leguminosae	CALEMA	1	--	--
29	*Capparis indica* (L.) Fawc. & Rendle.	Capparaceae	CAPIND	7	--	--
30	*Capparis verrucosa* Jacq.	Capparaceae	CAPVER	2	--	--
31	*Casearia corymbosa* HBK.	Flacourtiaceae	CASCOR	8	4	1
32	*Casearia tremula* (Griseb.) Wright	Flacourtiaceae	CASTRE	15	2	--
33	*Ceiba aesculifolia* (HBK.) Britt. & Baker	Bombacaceae	CEIAES	2	--	--
34	*Ceiba grandifolia* Rose	Bombacaceae	CEIGRA	9	1	--
35	*Chiococca alba* (L.) Hitchc.	Rubiaceae	CHIALB	1	--	--
36	*Chloroleucon mangense* (Jacq.) Britton & Rose var. *leucospermum*	Leguminosae	CHLMAN	19	2	--
37	*Chlorophora tinctoria* L. Gaud.	Moraceae	CLHTIN	6	1	--
38	*Citharexylum hirtellum* Standl.	Verbenaceae	CITHIR	1	--	--
39	*Citharexylum standleyi* Mold. var. *mexicanum* Mold.	Verbenaceae	CITSTA	3	--	--
40	*Cnidosculus spinosus* Lundell.	Euphorbiaceae	CNISPI	4	--	1
41	*Coccoloba liebmannii* Lindau.	Polygonaceae	COCLIE	8	1	--
42	*Coccoloba* sp.	Polygonaceae	COC-SP	9	5	--
43	*Cochlospermum vitifolium* (Willd.) Spreng.	Cochlospermaceae	COCVIT	9	--	--
44	*Colubrina heteroneura* (Griseb.) Standl.	Rhamnaceae	COLHET	8	2	1
45	*Colubrina triflora* Brongn.	Rhamnaceae	COLTRI	7	--	--
46	*Comocladia engleriana* Loes.	Anacardiaceae	COMENG	10	3	--
47	*Conzatia multiflora* (B.L. Rob.) Standl.	Leguminosae	CONMUL	2	--	--
48	*Conzatia* sp.	Leguminosae	CON-SP	2	1	--

#	Especie	Familia	Clave*	Presencia entre (# parcelas):		
				a) el componente vivo	b) los muertos estacionalmente	c) los nuevos reclutas
49	*Cordia alliodora* (Ruiz & Pav.) Oken.	Boraginaceae	CORALL	17	9	2
50	*Cordia dentata* Poir.	Boraginaceae	CORDEN	3	1	--
51	*Cordia elaeagnoides* DC.	Boraginaceae	CORELA	8	2	1
52	*Cordia seleriana* Fern.	Boraginaceae	CORSEL	2	--	--
53	*Cordia* sp.	Boraginaceae	COR-SP	2	--	--
54	*Crescentia alata* HBK.	Bignoniacea	CREALA	1	1	--
55	*Croton alamosanus* Rose.	Euphorbiaceae	CROALA	6	1	--
56	*Croton niveus*	Euphorbiaceae	CRONIV	2	1	1
57	*Croton pseudoniveus* Lundell.	Euphorbiaceae	CROPSE	13	4	1
58	*Croton* sp.	Euphorbiaceae	CRO-SP	2	1	--
59	*Dalbergia* sp.	Leguminosae	DAL-SP	14	3	--
60	*Daphnopsis* sp.	Thymeleaceae	DAP-SP	1	--	--
61	*Diospyros aequoris* Standl.	Ebenaceae	DIOAEQ	11	3	--
62	*Diphysa occidentalis* Rose	Leguminosae	DIPOCC	6	1	--
63	*Erythrina lanata* Rose var. *occidentalis* (Standl.) Krukoff & Barneby	Leguminosae	ERYLAN	10	1	1
64	*Erythroxylum mexicanum* HBK.	Erythroxylaceae	ERYMEX	15	1	--
65	*Erytrhroxylum rotundifolium* Lunan sens. lat.	Erythroxylaceae	ERYROT	16	4	--
66	*Esenbeckia berlandieri* Baill. subsp. *acapulcensis* (Rose) Kaastra	Rutaceae	ESEBER	5	1	--
67	*Esenbeckia nesiotica* Standl.	Rutaceae	ESENES	9	2	--
68	*Eugenia rekoi* Standl.	Myrtaceae	EUGREK	2	--	--
69	*Exostema caribaeum* (Jacq.) Roem. & Schult.	Rubiaceae	EXOCAR	16	8	3
70	*Ficus cotinifolia* HBK.	Moraceae	FICCOT	4	--	--
71	*Forchhammeria pallida* Liebm.	Capparaceae	FORPAL	9	--	1
72	*Forestiera* cf. *rhamnifolia* Griseb.	Oleaceae	FORRHA	3	--	--
73	*Gliricidia sepium* (Jacq.) Kunth ex Steudel.	Leguminosae	GLISEP	17	7	--
74	*Guapira* cf. *macrocarpa* Miranda.	Nyctaginaceae	GUAMAC	20	6	2
75	*Guettarda elliptica* Sw.	Rubiaceae	GUEELL	16	7	--
76	*Gyrocarpus jatrophifolius* Domin.	Hernandiaceae	GYRJAT	4	--	--
77	*Haematoxylum brasiletto* Karst.	Leguminosae	HAEBRA	3	1	--
78	*Hauya elegans* DC.	Onagraceae	HAUELE	5	1	--
79	*Helietta lottiae* Chiang.	Rutaceae	HELLOT	7	3	--
80	*Heliocarpus pallidus* Rose.	Tiliaceae	HELPAL	6	4	1
81	*Hintonia latiflora* (Sessé & Moc. ex DC.) Bullock	Rubiaceae	HINLAT	12	1	--
82	*Hybanthus mexicanus* Ging.	Violaceae	HYBMEX	2	--	--
83	*Ipomoea wolcottiana* Rose.	Convolvulaceae	IPOWOL	18	5	--
84	*Jacaratia mexicana* A. DC.	Caricaceae	JACMEX	7	--	--
85	*Jacquinia pungens* A. Gray	Theophrastaceae	JACPUN	12	1	1
86	*Jatropha chamelensis* Pérez-Jiménez	Euphorbiaceae	JATCHA	3	--	--
87	*Jatropha malacophylla* Standl.	Euphorbiaceae	JATMAL	8	--	1
88	*Jatropha standleyi* Steyerm.	Euphorbiaceae	JATSTA	3	--	--
89	*Karwinskia latifolia* Standl.	Rhamnaceae	KARLAT	4	--	--
90	*Lagrezia monosperma* (Rose) Standl.	Amaranthaceae	LAGMON	3	--	2
91	*Leucaena lanceolata* S. Wats.	Leguminosae	LEULAN	5	1	--
92	*Lippia mcvaughii* Mold.	Verbenaceae	LIPMCV	5	3	--
93	*Lonchocarpus cochleatus* Pitt.	Leguminosae	LONCOC	4	--	--
94	*Lonchocarpus constrictus* Pitt.	Leguminosae	LONCON	20	2	3
95	*Lonchocarpus eriocarinalis* Micheli.	Leguminosae	LONERI	13	2	3
96	*Lonchocarpus guatemalensis* Benth.	Leguminosae	LONGUA	5	--	--
97	*Lonchocarpus magallanesii* Sousa.	Leguminosae	LONMAG	3	--	--
98	*Lonchocarpus minor* Sousa.	Leguminosae	LONMIN	5	2	2
99	*Lonchocarpus mutans* Sousa.	Leguminosae	LONMUT	16	3	2
100	*Lonchocarpus* sp. 1	Leguminosae	LON-SP1	3	5	--
101	*Lonchocarpus* sp. 2	Leguminosae	LON-SP2	2	--	--
102	*Lonchocarpus* sp. 3	Leguminosae	LON-SP3	13	--	--
103	*Luehea candida* (DC.) Mart.	Tiliaceae	LUECAN	11	3	--
104	*Lysiloma microphyllum* Benth.	Leguminosae	LYSMIC	13	3	1
105	*Machaonia acuminata* Humb. & Bonpl.	Rubiaceae	MACACU	4	2	--

#	Especie	Familia	Clave*	Presencia entre (# parcelas):		
				a) el componente vivo	b) los muertos estacionalmente	c) los nuevos reclutas
106	*Malpighia emiliae* W. R. Anderson.	Malphigiaceae	MALEMI	1	--	--
107	*Malpighia ovata* Rose.	Malphigiaceae	MALOVA	15	2	--
108	*Margaritaria nobilis* L.	Euphorbiaceae	MARNOB	1	--	--
109	*Mataiba spondioides* Standl.	Euphorbiaceae	MATSPO	1	--	--
110	*Morisonia americana* L.	Capparaceae	MORAME	2	--	--
111	*Ophellantha spinosa* Standl.	Euphorbiaceae	OPHSPI	1	--	--
112	*Ouratea mexicana* (Humb. & Bonpl.) Engl.	Ochnaceae	OURMEX	2	--	--
113	*Oxandra lanceolata* (Sw.) Baill.	Annonaceae	OXALAN	1	--	--
114	*Pedilanthus calcaratus* Schlecht.	Euphorbiaceae	PEDCAL	2	1	--
116	*Phyllanthus botryanthus* Muell. Arg.	Euphorbiaceae	PHYBOT	4	--	--
117	*Piptadenia constricta* (Micheli) Macbr.	Leguminosae	PIPCON	14	5	2
118	*Pithecellobium unguis-cati* (L.) Mart.	Leguminosae	PITUNG	5	1	--
119	*Plumeria rubra* L.	Apocynaceae	PLURUB	13	9	1
120	*Poeppigia procera* Presl.	Leguminosae	POEPRO	4	--	--
121	*Prockia crucis* P. Browne ex L.	Flacourtiaceae	PROCRU	2	--	--
122	*Psidium sartorianum* (Berg.) Ndzu.	Myrtaceae	PSISAR	16	4	2
123	*Psychotria microdon* (DC.) Urb.	Rubiaceae	PSYMIC	2	--	--
124	*Pterocarpus* sp.	Leguminosae	PTE-SP	1	--	--
125	*Randia thurberi* S. Wats.	Rubiaceae	RANTHU	15	4	1
126	*Recchia mexicana* Moc. & Sessé	Simaroubaceae	RECMEX	3	--	--
127	*Ruprechtia fusca* Fern.	Polygonaceae	RUPFUS	10	4	--
128	*Ruprechtia pallida* Standl.	Polygonaceae	RUPPAL	2	1	--
129	*Samyda mexicana* Rose	Flacourtiaceae	SAMMEX	18	4	1
130	*Sapium pedicellatum* Huber.	Euphorbiaceae	SAPPED	1	--	--
131	*Sapranthus violaceus* (Dunal) Safford.	Annonaceae	SAPVIO	1	--	--
132	*Sciadodendron excelsum* Griseb.	Araliaceae	SCIEXC	1	--	--
133	*Senna atomaria* (L.) I. & B.	Leguminosae	SENATO	1	--	--
134	*Schoepfia* sp.	Olacaceae	SHO-SP	5	--	--
135	*Sideroxylon stenospermum* (Standl.) Pennington	Sapotaceae	SIDSTE	12	1	--
136	*Spondias purpurea* L.	Anacardiaceae	SPOPUR	7	1	1
137	*Stemmadenia* cf. *grandiflora* (Jacq.) Miers	Apocynaceae	STEGRA	2	1	--
138	*Swietenia humilis* Zucc.	Bignoniaceae	SWIHUM	2	--	--
139	*Tabebuia chrysantha* (Jacq.) Nicholson	Bignoniaceae	TABCHR	10	--	--
140	*Tabebuia impetiginosa* (Mart.) Standl.	Bignoniaceae	TABIMP	4	1	--
141	*Thevetia ovata* (Cav.) A. DC.	Apocynaceae	THEOVA	5	--	--
142	*Thouinia paucidentata* Radlk	Sapindaceae	THOPAU	6	5	1
143	*Trichilia trifolia* L. subsp. *palmeri* (C. DC.) Pennington	Meliaceae	TRITRI	5	2	1
144	*Trichilia* sp.	Meliaceae	TRI-SP	3	--	--
145	*Zanthoxylum arborescens* Rose.	Rutaceae	ZANARB	2	--	--
146	*Zanthoxylum caribaeum* Lam. vel. aff.	Rutaceae	ZANCAR	5	1	--
147	*Zanthoxylum fagara* (L.) Sarg.	Rutaceae	ZANFAG	2	--	--
148	*Zanthoxylum* sp.	Rutaceae	ZAN-SP	1	--	--