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GRUPOS FUNCIONALES DE PLANTAS DE INTERÉS BIOGEOQUÍMICO EN UN ECOSISTEMA TROPICAL ESTACIONAL: EVALUACIÓN DE LOS PATRONES DE REABSORCIÓN DE NITRÓGENO Y FÓSFORO

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A Daniela

Por que nos cambió la vida con su sonrisa

A Carlos

Por que está conmigo

A mis papás

Por que sin ellos este proyecto no hubiera concluído

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RESUMEN

Los bosques tropicales caducifolios se caracterizan por presentar una gran diversidad de especies y se encuentran ampliamente distribuidos en México. A pesar de ello, no han sido estudiados extensivamente desde una perspectiva biogeoquímica. El estudio de procesos biogeoquímicos no ha sido abordado en grupos de especies a nivel de las características foliares ni de la reabsorción de nutrientes como el N y P, en general.

La determinación de grupos funcionales ha sido propuesta como una forma de simplificar el estudio del efecto de las especies en las propiedades de los ecosistemas y de los efectos del cambio global en las interacciones entre las especies. El concepto de grupos funcionales de plantas propone que las especies pueden agruparse de acuerdo con sus efectos comunes en los procesos del ecosistema o por su forma de respuesta a las perturbaciones o cambios. La reabsorción de N y P representa un proceso por medio de la cual las plantas minimizan la pérdida de nutrientes durante la senescencia foliar, es decir, es un importante proceso de conservación de los nutrientes. El estudio de las especies a nivel de grupos funcionales de índole biogeoquímica y la evaluación de la reabsorción como proceso y estrategia de las especies representan una nueva forma de abordar el estudio del ciclaje de los nutrientes en el bosque tropical caducifolio de Chamela.

La estructura de la tesis va de lo general a lo particular. Es decir, parte de un análisis general con 58 especies para determinar la presencia de grupos funcionales con un enfoque biogeoquímico basado en atributos foliares de los árboles. Posteriormente, se hace un análisis en 21 especies sobre el proceso ecofisiológico de la reabsorción de N y P para valorar el ámbito de variación y las posibles coincidencias entre ellas. Finalmente se evalúa la reabsorción a un nivel más fino de detalle con seis especies para establecer la relación entre la reabsorción (eficiencia y proficiencia) de N y P y la disponibilidad de nutrientes y agua.

Se evaluaron atributos foliares de interés biogeoquímico (el área foliar específica, las concentraciones de N, P, lignina y carbohidratos solubles) que se relacionan con la capacidad fotosintética y con la calidad química del follaje. La evaluación de dichos atributos se realizó en 58 especies de las más abundantes y frecuentes en el área de las cinco cuencas experimentales del proyecto de largo plazo "Estructura y dinámica de un ecosistema tropical estacional" en la Reserva de la Biósfera Chamela-Cuixmala. El análisis de grupos funcionales se realizó con un método de ordenación multivariado. Los resultados indicaron que no hay grupos funcionales

discretos, pero sí hay especies que comparten atributos foliares que pueden tener un impacto diferencial sobre algunos procesos ecosistémicos. El análisis de componentes principales mostró la concentración foliar de carbohidratos solubles, la concentración de N y la concentración de lignina explicaron un gran porcentaje de la variabilidad en las especies del bosque tropical caducifolio de Chamela (capítulo 2).

La evaluación de la reabsorción de N y P se realizó durante tres años consecutivos (1999, 2000 y 2001) en 21 especies de árboles de la misma localidad. Se evaluaron tanto la eficiencia como la proficiencia de reabsorción. Se comparó la reabsorción para conocer el ámbito de variación de este proceso entre diferentes grupos de especies con diferentes fenologías foliares: caducifolias de la época seca (incluyendo leguminosas y no leguminosas), caducifolias de lluvias y una especie subcaducifolia. Los resultados mostraron que la eficiencia de reabsorción (ER) varió ampliamente entre las especies (0-83%) al igual que la proficiencia de reabsorción (8-29 mg g^{-1} de N y 0.3-2.3 mg g^{-1} de P). En general la reabsorción fue baja en comparación con otros ecosistemas y es indicativa de que la cantidad de N y P que circula a través de la hojarasca es alta en este ecosistema. El análisis interanual mostró que la reabsorción promedio de N y P medida con los dos parámetros aumentó con la disminución en la disponibilidad de agua. El análisis de componentes principales con los parámetros de reabsorción mostró que la eficiencia de reabsorción de P junto con la concentración de P en las hojas senescentes fueron los atributos de mayor peso en la ordenación (Capítulo 3).

Por último, la reabsorción de N y P se evaluó a un nivel más fino de detalle con seis especies creciendo en sitios con condiciones contrastantes de disponibilidad de nutrientes en el suelo, durante tres años consecutivos. Los resultados mostraron que la ER de N y P estuvo controlada más por la disponibilidad de agua que por la disponibilidad de nutrientes en el suelo. Sin embargo, la proficiencia de reabsorción de P sí presentó una relación negativa tanto con la disponibilidad de P en el suelo como con la de agua (Capítulo 4).

En el último capítulo (Capítulo 5), se propone un modelo conceptual sintético que muestra como se distribuyen las especies del bosque tropical de Chamela en relación con las características foliares de interés biogeoquímico que se estudiaron junto con la reabsorción de N y P, mostrando el impacto potencial de las especies sobre procesos del ecosistema como la descomposición y la productividad. El trabajo aporta una importante base de datos de atributos foliares de interés biogeoquímico de especies de árboles adultos en condiciones de campo. Los resultados permiten plantear

preguntas de interés funcional a un nivel que no había sido explorado anteriormente (i.e. grupos de especies o especies individuales). Así mismo, la evaluación de la reabsorción por más de un año representa una de las pocas contribuciones con esta escala temporal, permite establecer que la variación interanual del proceso está relacionada con la disponibilidad del agua y ofrece una perspectiva más realista de la relevancia de la reabsorción en los ciclos de N y P de este ecosistema.

Capítulo 1

INTRODUCCIÓN GENERAL

Los grupos funcionales de plantas en el contexto de la biogeoquímica de Chamela

De acuerdo con Silver *et al.* (1996) la biodiversidad incluye tanto la riqueza de especies como la diversidad funcional. Ésta, se define a nivel del ecosistema como la gama de procesos que contribuyen a que los flujos de materia y energía a través del ecosistema se mantengan. Entre la diversidad de procesos funcionales están los biogeoquímicos como son la captura, la retención y la transferencia de nutrientes, otros aspectos de las plantas como la producción primaria neta o las rutas fotosintéticas, y procesos como la descomposición. El concepto de grupos funcionales propone que las especies pueden agruparse de acuerdo con respuestas comunes al ambiente o a efectos comunes en los procesos ecosistémicos (Díaz y Cabido 2001). Sin embargo, el conocimiento de la relación entre las características asociadas con las "respuestas" de las plantas a los factores ambientales tales como los recursos y los disturbios, y las características que determinan los "efectos" de las plantas en las funciones ecosistémicas como el ciclaje biogeoquímico, aún es incipiente (Lavorel y Garnier 2002). El impacto de los distintos grupos funcionales de plantas en los procesos biogeoquímicos se ha hecho evidente en estudios que han mostrado que las especies difieren en la asignación y forma de capturar y procesar sus recursos y en sus interacciones con otras especies. Por ello, los cambios en la composición de especies o en la diversidad pueden implicar que los cambios en las características funcionales de los organismos alteren los procesos del ecosistema (Chapin *et al.* 1996).

La disponibilidad de agua y de nutrientes intervienen en el control de la estructura y la dinámica del ecosistema, de tal forma que la introducción o la remoción de especies pueden alterar la disponibilidad de los recursos y afectar, por ejemplo, la calidad del mantillo para la descomposición y la temperatura y la humedad del suelo, que a su vez son factores que controlan los procesos de mineralización de los nutrientes (Chapin *et al.* 1997). Se ha propuesto que la clasificación de especies en grupos funcionales es una forma de simplificar el estudio del efecto de las especies en las propiedades de los ecosistemas y de los efectos del cambio global en las interacciones entre las especies (Vitousek y Hooper 1993). Sin embargo, no existe una

clasificación funcional universal, por lo que la clasificación depende del proceso o factor ambiental en cuestión (Lavorel 1997).

Los bosques tropicales caducifolios (tropical dry forests) representan más de 40% del área de bosque tropical del mundo (Murphy y Lugo 1995) y en México están ampliamente distribuidos (Rzedowski 1978). Son ecosistemas muy diversos con un alto número de endemismos (Gentry 1982) y aunque se han documentado desde el punto de vista florístico y estructural (Bullock y Solís-Magallanes 1990; Segura *et al.* 2003) Jaramillo y Sanford (1995) documentaron que los procesos del ciclaje de los nutrientes no han sido estudiados tan extensivamente como en los bosques húmedos. Actualmente, la discrepancia persiste y son muy pocos los estudios publicados sobre biogeoquímica (Turner *et al.* 2001; Franco *et al.* 2005). Los bosques tropicales caducifolios se caracterizan por desarrollarse en un ambiente con una alta estacionalidad en la precipitación y tienen un largo período seco dentro del ciclo anual durante el cual la mayoría de las plantas pierden sus hojas. La producción primaria de estos bosques es controlada principalmente por la cantidad y la distribución anual de la lluvia (Murphy y Lugo 1986).

El planteamiento de los grupos funcionales de plantas puede ser utilizado para simplificar el estudio de aspectos biogeoquímicos del ecosistema de Chamela, es decir, determinar grupos de especies que tengan efectos similares sobre procesos ecosistémicos importantes como el ciclaje de los nutrientes y la descomposición, entre otros. Para ello, la evaluación de atributos foliares, como el área foliar específica (AFE) y la composición química foliar (concentraciones de N y P, concentración de lignina y carbohidratos solubles) en algunas de las especies más abundantes y frecuentes del bosque tropical seco de Chamela permite una primera aproximación a la definición de grupos funcionales de árboles desde una perspectiva biogeoquímica. Con base en lo anterior, la primera pregunta de esta tesis es:

¿Se pueden determinar grupos funcionales de plantas en el bosque tropical caducifolio de Chamela con base en atributos foliares de interés biogeoquímico?

El ciclaje de los nutrientes y la eficiencia de reabsorción

En los bosques tropicales caducifolios como el de Chamela, diferentes minerales se acumulan en el suelo durante la época seca, probablemente por el descenso en la demanda de las plantas que cesan su crecimiento y por la pérdida de sus hojas. Dos de los minerales más importantes para el funcionamiento del ecosistema son el N y P

(Chapin 1980) y una gran parte de éstos se encuentra en formas orgánicas en las plantas, ya que éstas tienen una gran demanda de estos elementos para producir proteínas, transportadores energéticos, material genético y fosfolípidos (Chapin *et al*. 2002). Durante el período inicial de la senescencia foliar, que es el último estadio en el desarrollo ontogénico de las hojas, ocurre una redistribución de los nutrientes que implica principalmente la degradación de los cloroplastos y la exportación de N, P y otros nutrientes hacia otros órganos. El proceso de reabsorción de nutrientes foliares, que constituye un importante mecanismo de conservación de los nutrientes, incide directamente sobre el ciclaje a nivel del ecosistema. En la segunda fase de la senescencia, ocurre un proceso final de muerte celular una vez que la redistribución de nutrientes ha sido completada. Las hojas muertas constituirán la hojarasca y los nutrientes que no se van en la hojarasca son reabsorbidos y serán reutilizados posteriormente. Los que se van en la hojarasca entrarán al proceso de descomposición.

El crecimiento de las plantas en los ecosistemas terrestres está comúnmente limitado por la disponibilidad de N, aunque la limitación por disponibilidad de P también ocurre frecuentemente (Chapin 1980), particularmente en muchos bosques tropicales (Vitousek 1984). Por ello, la reabsorción de N y P de los tejidos senescentes puede tener importancia adaptativa, debido a que los nutrientes reabsorbidos quedan disponibles para ser utilizados posteriormente en la formación de semillas, en el crecimiento o para el almacenamiento, haciendo que las especies sean menos dependientes de los nutrientes del suelo (Aerts y Chapin 2000).

Un parámetro utilizado comúnmente para cuantificar la reabsorción de nutrientes es la eficiencia de reabsorción (Killingbeck y Costigan 1988). Este parámetro describe el porcentaje del almacén foliar del nutriente que es reabsorbido antes de la abscisión evaluado a partir del contenido de nutrientes por unidad de masa o de área foliar, en las hojas maduras y en las senescentes. Otro parámetro para cuantificar la reabsorción es la proficiencia de reabsorción, definida como el nivel al cual una planta reduce un elemento en sus hojas senescentes (Killingbeck 1996); las especies con alta proficiencia o capacidad de reabsorción muestran bajas concentraciones de nutrientes en las hojas senescentes. Ambos parámetros son atributos fundamentales del mismo proceso y son utilizados para evaluar la reabsorción de nutrientes (Killingbeck 1996).

Actualmente, el entendimiento de la reabsorción de nutrientes proviene de estudios que se han realizado únicamente durante un año (Lal, et al. 2001; Yuan, et al. 2005; Luyssaert, et al. 2005; Richardson, et al. 2005; Cárdenas y Campo 2007), lo que

implícitamente supone que la reabsorción medida una vez para un individuo o población dada es un dato representativo de la capacidad de reabsorción y que no varía (Killingbeck 1996). Esto puede ser cierto para algunas especies en algunos ambientes, pero no es universalmente verdadero. Se ha encontrado que las plantas pueden reabsorber diferentes cantidades de nutrientes (Killingbeck et al. 1990; May and Killingbeck 1992, Killingbeck 1993).

Con base en lo anterior, la siguientes preguntas de esta tesis son:

¿Qué tan eficientes son las especies de árboles de Chamela en la reabsorción de nutrientes, particularmente de N y P?; ¿Es posible identificar grupos de especies de árboles en relación a sus patrones de reabsorción? y ¿Cómo es la variación anual de la reabsorción en las especies?.

La concentración final de nutrientes en las hojas, así como la eficiencia de reabsorción, varían substancialmente entre las especies y también es determinada por condiciones ambientales externas (Pugnaire y Chapin 1993, Killingbeck 1996, Vitousek 1998, Aerts *et al*. 1999). Sin embargo, existe aún un debate sobre el papel que juegan los diferentes factores ambientales en la reabsorción. Se espera que las plantas que crecen en sitios con baja disponibilidad de nutrientes reabsorban más N y P que las especies que crecen en sitios más fértiles (Aerts y Chapin 2000). Sin embargo, la evidencia disponible hasta ahora no resuelve definitivamente si esta tendencia se sostiene o no (Aerts y Chapin 2000).

Bajo este contexto, se planteó realizar una evaluación para determinar la relación entre la eficiencia de reabsorción y la disponibilidad de nutrientes en el suelo, por lo que se estableció la tercera serie de preguntas de investigación:

¿Qué relación existe entre la reabsorción de N y P y la disponibilidad de nutrientes en el suelo? e igual que en el caso anterior se hizo la pregunta ¿Existen variaciones anuales importantes en la reabsorción de N y P?

Con base en lo expuesto anteriormente, el objetivo general de esta tesis fue:

Establecer la existencia de grupos funcionales de plantas con efectos similares en procesos biogeoquímicos del ecosistema con base en atributos foliares y en un atributo ecofisiológico, estimado a partir de atributos foliares, y determinar la relación entre la reabsorción de nutrientes y su disponibilidad en el suelo.

Los objetivos particulares fueron:

1. Establecer la presencia de grupos funcionales de árboles en el bosque tropical caducifolio de Chamela con base en características morfológicas y químicas foliares con implicaciones biogeoquímicas.

2. Determinar y comparar los patrones de reabsorción (eficiencia y proficiencia) de N y P foliar de 21 especies de árboles y su variabilidad anual.

3. Determinar y comparar la eficiencia y la proficiencia de reabsorción de N y P foliar y su variabilidad anual en seis especies de árboles, creciendo en sitios con condiciones contrastantes de disponibilidad de nutrientes en el suelo.

Estructura de la tesis

El manuscrito de esta tesis está formado de tres partes principales que van de lo general a lo particular, la presente introducción general, tres capítulos que describen los resultados de esta investigación y un capítulo final. En el Capítulo 2 se explora la existencia de grupos funcionales de especies de árboles del bosque tropical caducifolio que podrían tener efectos similares en procesos biogeoquímicos del ecosistema, con base en el análisis de atributos morfológicos y químicos foliares de 58 especies de árboles utilizando métodos multivariados de ordenación. En el Capítulo 3 se presentan los resultados de la evaluación de los patrones de reabsorción de N y P de 21 especies de árboles, se determina su variabilidad anual y se explora la posibilidad de agruparlas en función de sus patrones de reabsorción con métodos de ordenación. Los Capítulos 2 y 3 están redactados en formato de artículo para su publicación. En el Capítulo 4 se analizan los patrones de reabsorción de N y P en seis especies de árboles (dos leguminosas fijadoras de N y cuatro no leguminosas) en función de características contrastantes del ambiente y de la variabilidad anual de la precipitación. Este capítulo fue publicado en la revista "Trees, Structure and Function" en el mes de marzo del 2005. Por último, se presentan algunas consideraciones sobre el significado y la relevancia general del proyecto de tesis (Capítulo 5). La bibliografía citada en cada capítulo se presenta en conjunto al final del manuscrito.

PLANT FUNCTIONAL GROUPS IN A TROPICAL DRY FOREST:
EVALUATION OF BIOGEOCHEMICAL TRAITS

INTRODUCTION

Functional diversity is emerging as an aspect of crucial importance in determining ecosystem processes (Díaz & Cabido 2001). There is a growing consensus that the effects of diversity on ecosystem processes should be attributed to the functional traits of individual species and their interactions rather than to species number *per se* (Tilman 1999, Walker 1999, Chapin 2000).

Functional diversity is defined as the various ways leading to the maintenance of energy and material flows through an ecosystem (Vitousek & Hooper 1993; Silver *et al*. 1996). Examples of functional diversity in forest ecosystems are found in the fields of biogeochemical processes, primary productivity and carbon cycling. Most organisms contribute in some way to nutrient cycling, but some species or groups of species have a stronger influence than others as a result of their effects on ecosystem functions (Silver *et al*. 1996). Plant functional traits, whether plants are nitrogen-fixing legumes, warm-season bunchgrasses or rosette forbs, are strong drivers of ecosystem processes (Hooper & Vitousek 1999, Tilman 1999).

The concept of plant functional type was developed in order to group species according to their specific traits, their response to environmental variations or their effect on ecosystem functions (Lavorel *et al*. 1997; Díaz & Cabido 2001). The functional-type approach focuses on common solutions of many species to the same environmental challenges irrespective of their ancestry (Lavorel 1997). There is no universal classification of functional types. Rather, the classification depends on the aim of the study, its scale (from local to global), and the ecosystem process or environmental factor of interest (Gitay & Noble 1997,

 Lavorel 1997). Therefore, functional types are, like most categories used to simplify the natural world, arbitrary divisions of a relatively continuous trait space. Most of the literature on functional types refers to functional response types (groups of species with similar responses to a particular environmental factor such as resource availability, disturbance or CO_2 concentration; Gitay & Noble 1997, Lavorel *et al.* 1997). However, studies on the links between diversity and ecosystem functioning tend to focus on functional effect types (Díaz & Cabido 2001). Functional effect types are groups of plants that have similar effects on the dominant ecosystem processes, such as primary productivity, nutrient cycling and trophic transfer. Examples include nitrogen fixers, ecosystem ingeneers, nurse species and fire-promoting species.

The consideration of plant functional types in biogeochemical models may be a useful tool to simplify or to deepen in the analysis of those processes (Schimel *et al.* 1995). Grouping species by functional attributes is one way to address such questions. Based on a deductive approach, it is possible to propose a functional classification derived from *a priori* considerations (Gitay y Noble 1997). A primary mechanism underlying species effects on nutrient cycling likely involves among-species differences in litter quality and quantity (Wedin & Tilman 1990; Hobbie 1992). For example, it is well documented that physico-chemical features of leaf litter cause important interspecific variability in decomposition rates (Cornelissen 1996; Swift et al 1979). The impact of leaf quality on nutrient cycling is determined by biochemical constituents like soluble carbohydrates, lignin, and essential minerals (N, P, K), tightly related to leaf morphology. These are considered "soft traits" (Cornellisen *et al.* 2002) that are easy to measure for a large number of species and sites and are indirectly related to functional processes as nutrient conservation and decomposition. Numerous studies have related decomposition rate to chemical litter quality indices such as total N and lignin-to-N ratio (Melillo, 1982).

Nutrient cycling processes have been well documented for tropical moist forests (Vitousek & Sanford 1986), but little comprehensive information exists for tropical dry deciduous forest. In the tropical dry forest of Chamela, in Western México, some major pathways of nutrient cycling such as litter

production (Martínez-Yrízar & Sarukhan, 1990) and decomposition (Martínez-Yrízar 1995; Anaya *et al*. 2007) microbial biomass (González 1997), fine root turnover (Kummerow *et al*. 1990; García-Oliva & Tapia 2001) and phosphorus cycling pathway (Campo *et al*. 2001) have been documented. However, none of these studies have been carried out at the species level or considering functional groups.

The Chamela tropical dry forest flora has 1149 plant species from 125 families. From a functional perspective, we can recognize different ways in which species respond to environmental variables or may affect ecosystem processes. For example, preliminary data indicate that at least 54 species of legumes are potentially N fixers (V. Jaramillo pers. com.) and González (2001) reported that nodulation was confirmed in 9 legumes, including *Lonchoarpus eriocarinalis* Micheli. and *Piptadenia constricta* (Pers.) J.F. Macbr., which are among the most abundant species in the Chamela tropical dry forest. It is likely that N-fixing and non-fixing legumes have different implications for biogeochemical cycles in this ecosystem.

Most species in the Chamela forest are leafless for a period of 5-8 months during the dry season each year (Bullock & Solís-Magallanes 1990). Leaf-fall from these species represents a major input of organic matter and nutrients to the soil. In contrast, three species drop their leaves during the wet season (Fanjul & Barradas 1987). These species (*Coccoloba liebmannii* Lindau; *Forchammeria pallida* Liebm.; *Jacquinia pungens* (A. Gray.)) represent a group with contrasting water use characteristics (Fanjul & Barradas 1987; Janzen 1970). However, their basic nutrient-use related traits are still unknown. Among the dry-deciduous species, the Leguminosae is the most important family representing 15% of the total number of species (Lott 2002).

Although tropical forests are among the most diverse ecosystems in the world, it is possible to find patches of mature forest dominated by a single species immersed in the forest matrix. In the tropical dry forest of Chamela, the semievergreen *Piranhea mexicana* (Standl.) A. Radcliffe-Sm. establishes in patches of different sizes conforming monospecific stands within the species rich forest (Martijena 1994). If *P. mexicana* has differential functional

properties, the monodominant *P. mexicana* stands could be a potential priority for conservation (Walker 1999). Although species conservation is not the aim of this work, assessing the functional role of this species could contribute to the understanding of nutrient cycling in Chamela.

The objective of this study was to identify functional types of tree species of the Chamela tropical dry forest that may have similar effects on biogeochemical processes based on leaf morphological and chemical traits. Thus, according to the previous considerations, a first approach to the definition of tree functional types of biogeochemical interest in the tropical dry forest of Chamela should include species from the following groups: dry-deciduous species including N-fixing legumes, non-fixing legumes, and non-legumes, wet-season deciduous species, and the semievergreen *Piranhea mexicana*.

MATERIALS AND METHODS

Study site

The study was conducted at the Chamela Biological Station (Universidad Nacional Autónoma de México) located on the Pacific coast of Jalisco, Mexico (19°29′N, 105°01′W). The landscape is dominated by low hills with steep slopes (> 20°). Mean annual precipitation is 756 mm, mainly concentrated between July and November ranging between a minimum of 391 mm and a maximum of 1393 mm (data from 1977-2006; source http://www.ibiologia.unam.mx/ebchamela/). The dominant vegetation type is a highly diverse tropical deciduous forest. This is a dense forest, 4-15 m tall, with a well-developed understory of shrubs and a strongly seasonal phenology (Lott *et al*. 1987). With few exceptions, the species bear no leaves for several months during the dry season each year (Bullock & Solís-Magallanes 1990, Martínez-Yrízar & Sarukhán 1990). Live-above ground biomass ranges from 81 to 85 Mg/ha (Martínez-Yrízar *et al*. 1992), whereas below ground biomass ranges from 17 to 31 Mg/ha (Castellanos *et al*. 1991; Jaramillo *et al*. 2003). The main soil parent material is Cretaceous rhyolite (Campo *et al*. 2001). Soils are sandy clay-loams, poorly developed, classified in the USDA system as Typic Ustorthents and in the FAO system (1998) as Regosols (Cotler *et al.*

2002). Kaolinite is the dominant clay mineral (Campo *et al.* 2001) and the mean pH is 6.9 (García-Oliva *et al.* 1999).

Field methods

We chose 58 dominant tree species (Durán *et al*. 2002; Balvanera et al. submitted) representing 25 plant families (Table 1). The species were chosen from five groups based on their potential influence on biogeochemical cycles: 12 N-fixing legumes and 4 non N-fixing legumes (González 2001), 36 dry-seasons deciduous, 3 wet-season deciduous, and the semievergreen *Piranhea mexicana.* Fully expanded sun live leaves (10) without apparent herbivore damage, of at least two individuals of each species with comparable diameter at breast height (5-15 cm dbh) were collected in July 2000. Wet-season deciduous species leaves were collected in November 1999. All leaves were placed in plastic bags until processed in the field station laboratory. Measurements were performed the same day that leaves were collected.

Laboratory methods

Morphological traits were determined on fresh leaves. Blade configuration was classified as simple or compound leaves; leaf consistency as soft or coriaceous; and leaf hairiness and wax coating as present or absent. These traits were determined upon leaf visual inspection. Leaf phenology was classified as dry-season deciduous, wet-season deciduous or semievergreen. Single-side leaf surface area was measured with a Delta – T image analyzer (Windias software). Leaves were then oven-dried at 70°C for 48 h and weighed. Leaf mass per area (LMA, g m^{-2}) was obtained by dividing the dry weight by the leaf area. To determine foliar chemical traits (N and P, lignin and soluble carbohydrate concentrations) all leaves from each individual were pooled. Leaves were then ground in a Thomas Scientific mill to pass a 40-mesh screen. Total nitrogen and phosphorus were determined after acid digestion by a semi-Kjeldahl method (Stuart 1936) and samples were determined colorimetrically with an autoanalyzer (Bran-Luebbe Auto Analyzer III, Norderstedt, Germany; method No. 696-82W; Technicon Industrial System 1977). Lignin concentrations were determined by the acid-detergent fiber determination (Van

Soest 1963). Soluble carbohydrates were determined by the phenol-sulphuric method (Dubois *et al*. 1956), with dextrose as a standard.

Data analysis

Five continuous foliar traits, leaf mass per area (LMA) and the four chemical parameters, were analyzed by principal component analysis (PCA) in the 58 species. All analyses were performed with PC-ORD 4 (McCune & Mefford 1997). To determine the relationship among the foliar traits used in each PCA, Pearson's correlations were performed. Non-metric multidimensional scaling analyses (NMS, an ordination method suited to discontinuous data; McCune & Mefford, 1997) were performed for categorical variables (leaf phenology, morphology, consistency, hairiness and wax coating). The analysis did not produce interpretable results; therefore, they are not presented for the sake of brevity.

RESULTS

The mean LMA was 68.7 g m^{-2} and ranged between 21 g m^{-2} (*Psychotria microdon*, Rubiaceae) and 138 gm^{-2} (*Forchhameria pallida*, Capparaceae). Mean foliar N was 30.9 mg g^{-1} but ranged between 16 mg g^{-1} (*Jacquinia pungens*, Theophrastaceae) and 52 mg g^{-1} (*Guapira macrocarpa*, Nyctaginaceae). Mean foliar P was 2.0 mg g^{-1} and ranged between 0.9 mg g^{-1} (*Lonchocarpus sp.*, Leguminosae) and 3.9 mg g^{-1} (*Jacaratia mexicana*, Caricaceae). Mean lignin concentration was 16% and ranged between 3% (*Euphorbia tanquahuete*, Euphorbiaceae) and 33% (*Lonchocarpus eriocarinalis*, Leguminoseae). Mean soluble carbohydrate concentration was 4.5% and ranged between 0.4% (*Cordia alliodora*, Boraginaceae) and 14 % (*Sciadodendron excelsum*, Araliaceae) (Table 2).

Correlations among traits

Two significant (P<0.05) correlations between traits were evident (Table 3): LMA was negatively correlated with foliar N concentration (Fig. 1a) and lignin was negatively correlated with soluble carbohydrate concentrations (Fig. 1b).

PCA description

The first three axes of the PCA accounted for 80.8% of the variation in the data set (Table 4). The first axis was heavily weighted to soluble carbohydrates, lignin and leaf N concentrations; the second axis was related to LMA, leaf N and P concentrations, and the third axis was also heavily weighted towards LMA and leaf P concentrations.

Axis 1 explained 34.5% of total variation in the data set (43% of the explained variation by the first three axes). Higher scores along this axis indicated species with greater soluble carbohydrate concentrations and low lignin and leaf N concentrations (Fig. 1a). Axis 2 explained 31.4% of total variation. Increasing values along this axis indicated lower LMA (thinner leaves) and higher leaf N and P concentrations (Fig. 1a). Increasing values along Axis 3 indicated higher foliar P concentrations and LMA values (Fig. 1b).

Both figures showed a great dispersion of the data along the axes. There was not a clear grouping of species; however, some species tended to occupy specific areas of the ordination space. For example, the N-fixing legumes, along with some dry-deciduous species and the semievergreen *Piranhea,* showed low to intermediate soluble carbohydrate concentrations (axis 1), high to intermediate LMA (axis 2), and low to intermediate foliar P concentrations (axis 3) (Figs. 1a and b). The non N-fixing legumes, except for *Bahuinia*, were grouped together with the wet-deciduous species because of their high LMA and intermediate to high soluble carbohydrate concentrations (Fig. 1a).

DISCUSSION

Principal component analysis showed that soluble carbohydrates (SC), leaf N and lignin explain a high degree of the variability in these tropical dry forest species. Soluble carbohydrate concentration is an important determinant of initial mass loss rate and for C mineralization during decomposition (Reinestern *et al.* 1984). This foliar trait could determine litter decomposition rate at the species level; this is, the grater SC concentration, the faster the initial decomposition rate due to the high energy availability for microorganisms. High soluble carbohydrate and low lignin should promote leaf

decomposability, however low lignin was associated with low foliar N. This trait variation makes it difficult to predict the potential impact of foliar traits in decomposition. Results from the PCA suggest that more than a half of species, including the N-fixing legumes, some non-legumes and *Piranhea* that showed intermediate to low SC concentrations and intermediate to high lignin concentrations, could produce relatively recalcitrant litterfall.

Results from the PCA suggest that species share common traits like low SC concentration, high LMA and low foliar P concentration (most legumes, some dry-deciduous and *Piranhea*) could have similar effects on decomposition processes in the ecosystem, influencing organic matter residence time in the soil. Litterfall from these species would show low decomposition rates, delaying nutrient release to the soil. The low SC concentration in mature leaves could result in lower concentrations in senescent leaves, since some SC are resorbed prior to leaf fall (Chapin y Kedrowski 1983). The low concentration of available carbon would limit decomposer activity (Swift 1979) and the thick leaves (indicated by a high LMA), harder for breakdown, would further limit the initial stages of decomposition (Chapin *et al.* 2002). Together, these traits would increase organic matter residence time, and would reduce nutrient cycling rates. However, the ordination results suggest that other species which share common foliar traits, for example, the dry-deciduous species with low LMA (thin leaves easy to breake) and intermediate SC concentrations, suggest these species could promote faster decomposition and nutrient cycling rates.

Leaf mass per area (LMA, the inverse of specific leaf area) was very important in accounting for variation in the 58 species analysis. It has been shown to be highly correlated with photosynthetic capacity, growth, and productivity from the leaf to the ecosystem scale (Reich *et al.* 1997; Wright *et al.* 2004). The negative correlation between LMA and N foliar concentration in the species in Chamela is consistent with results reported by Reich *et al.* (1997) in their study with 280 plant species from six biomes ranging from tropical and temperate forests to alpine tundra and desert. It is also consistent with results of Wright *et al.* (2004) in their worldwide study with 2458 species from 176 sites. Both studies found a negative correlation among LMA, foliar N

concentration, and photosynthetic rate. Most of the tree species considered in my study with intermediate to high LMA values would probably have lower photosynthetic capacities, and lower relative growth rates (Reich *et al*. 1997) than the fewer species with lower LMA and higher leaf N concentrations (e.g. *Psychotria microdon, Pterocarpus orbiculatus*, and *Trichilia trifolia*). The relative growth rates of plant species in Chamela was assessed at the seedling stage by Huante *et al*. (1995). It could be expected that species with higher LMA and lower leaf N would show the slower growth rates in their study. This is consistent with *Piranhea*, which is a slow growing plant at the seedling level (Huante *et al.* 1995) with high LMA. However, *Trichilia trifolia* is a slow growth species (Huante *et al.* 1995), but with relatively low LMA; other species like the legumes *Lonchocarpus eriocarinalis* and *Caesalpinia sclerocarpa,* with high LMA, showed intermediate relative growth rates (Huante *et al.* 1995). These comparisons suggest that it is not straightforward to establish correlations between results obtained with seedlings and the foliar traits of mature individuals. The relevance of LMA as a foliar attribute defining species variation was evident in this study. Its strong correlation with other fundamental foliar variables makes it key to the understanding of terrestrial ecosystem functioning. This foliar trait is easy to measure in a great number of species and could be useful to establish broader scale patterns that allow formulating hypothesis on ecosystem functioning in other dry forests in Mexico.

Leaf P concentration (the third principal component of the PCA) was also very variable among species. This probably reflects the variability in soil P availability reported for Chamela (Campo *et al*. 2001; Rentería *et al*. 2005). Rentería *et al*. (2005) found that species growing in sites with high soil P availability showed greater foliar P concentrations than individuals from the same species growing in sites with lower soil P availability. Based on this evidence, they proposed that measurement of foliar P could allow deducing variations in soil P availability at the local level. Such a relationship in the context of the present study would suggest that most of the potentially N-fixing legume species, two non N-fixing legumes, and some dry-deciduous species would grow in sites with intermediate to low levels of soil P availability, while

most of the dry-deciduous and the wet-deciduous species, would grow in sites with high soil availability.

Mean N and P foliar concentrations in this study (3.1 and 0.2%, respectively) were similar to those reported by Jaramillo and Sanford (1995; 2.96 and 0.28% for N and P, respectively) for other sites in the Chamela forest. Likewise, mean foliar N and P were consistent with the range of variation reported in India (N = 0.86-4.1%, and P = 0.08-0.6%); but, are higher than those reported by Montes y Medina (1997) for tree species in Venezuela (N, 0.8-1.8% and P, 0.03-0.14%). Values for the Chamela species were similar to those reported by Reich *et al.* (1997) for broad-leaved woody deciduous species. The range of variation in foliar N concentration in the Chamela forest, including many compound-leaved species, was 16-52 mg g^{-1}, while Reich *et al.* (1997) reported a range of 9 to 41 mg g^{-1} in six biomes worldwide. More recently, Wright et al. (2004) reported leaf N to vary between 2 and 64 mg g^{-1}. These comparisons show that the variability found in the tropical dry forest of Chamela is in the same range of variation of that reported across biomes worldwide.

The use of general leaf trait relationships should enable the development of more accurate general models of vegetation productivity, distribution, and dynamics at scales and for regions not previously possible (Aber et al. 1996; Reich *et al.* 1997). The assessment of traits like LMA, relatively easy to measure and correlated to variables concenrning ecosystem functioning (Reich *et al.* 1997; Wright et al. 2004), provides a useful tool in this direction.

Table 1. The 58 study species listed in biogeochemical functional groups proposed *a priori* in the tropical dry forest, Chamela, Jalisco, Mexico. Abbreviations are used for species identity in further Tables and Figures. Name of the species follows Lott (2002) nomenclature.

Species	Abbreviation	Family or subfamily
Dry-Season Deciduous		
N-fixing legumes		
Albizia occidentalis Brandegee.	Albi	Mimosoideae
Apoplanesia paniculata Presl	Apop	Papilionoideae
Brongniartia sp nov. ined. O.	Bron	Papilionoideae
Chloroleucon mangense (Jacq.) Britton y Rose var. *leucospermum* (Brandegee) Barneby y Grimes [*Pithecellobium mangense* (Jacq.) MacBride; *P. leucospermum* T. Brandeg.].	Chlo	Mimosoideae
Erythrina lanata Rose subsp. *occidentalis* (Standl.) Krukoff y Barneby.	Eryt	Papilionoideae
Gliricidia sepium (Jacq.) Steudel.	Glir	Papilionoideae
Lonchocarpus eriocarinalis Micheli.	L. eri	Papilionoideae
Lonchocarpus magallanesii Sousa	L. mag	Papilionoideae
Lonchocarpus sp. 1	sp 1	Papilionoideae
Lonchocarpus sp. 2	sp 2	Papilionoideae
Lysiloma microphyllum Benth. [=*L. divaricatum* (Jacq.) Macbr.].	Lysi	Mimosoideae
Piptadenia constricta (Pers.) J.F. Macbr.	Pipt	Mimosoideae
Platymiscium lasciocarpum Sandw.	Plat	Papilionoideae
Pterocarpus orbiculatus DC. [=*P. amphymenium* DC.].	Pter	Papilionoideae

Non N-fixing legumes

Bahuinia ungulata L.	Bahu	Caesalpinoideae
Caesalpinia sclerocarpa Standl.	C. scl	Caesalpinoideae
Caesalpinia eriostachys Benth.	C. eri	Caesalpinoideae
Haematoxylum brasiletto Karst.	Haem	Caesalpinoideae

Non legumes

Adelia oaxacana (Muell. Arg.) Hemsl.	Adel	Euphorbiaceae
Amphypterigium adstringens (Schlecht.) Schiede.	Amph	Julianaceae
Bursera excelsa (Kunth) Engl. var. *acutidens* (Sprague y Riley) Mc Vaugh y Rzed.	B. exc	Burceraceae
Bursera instabilis Mc Vaugh y Rzed.	B. ins	Burceraceae
Capparis indica (L.) Fawc. y Rendle.	Capp	Capparaceae
Casearia corymbosa Kunth.	Case	Flacourtiaceae
Clorophora tinctoria (L.) Gaud.	Clor	Moraceae
Cnidosculus spinosus Lundell.	Cnid	Euphorbiaceae
Cochlospermum vitifolium (Willd.) Spreng.	Coch	Cochlospermaceae
Colubrina heteroneura (Griseb.) Standl.	Colu	Rhamnaceae
Comocladia engleriana Loes.	Como	Anacardiaceae
Cordia alliodora (Ruiz y Pav.) Oken.	Cord	Boraginaceae
Croton pseudoniveus Lundell.	Crot	Euphorbiaceae
Esenbeckia nesiotica Standl.	Esen	Rutaceae
Euphorbia tanquahuete Sessé y Moc.	Euph	Euphorbiaceae
Exostema caribeum (Jacq.) Roem. y Schult.	Exos	Rubiaceae
Guapira cf. *macrocarpa* Miranda.	Guap	Nyctaginaceae
Guettarda elliptica Sw. [= *G. macrosperma* Donn. Sm.].	Guet	Rubiaceae
Helietta lottiae Chiang	Helie	Rutaceae

Heliocarpus pallidus Rose [earlier reported as *H. occidentalis* Rose].	Helio	Tilaceae
Ipomoea wolcottiana Rose.	Ipom	Convolvulaceae
Jacaratia mexicana A. DC.	Jaca	Caricaceae
Jatropha chamelensis Pérez-Jiménez.	J. cha	Euphorbiaceae
Jatropha standleyii Steyerm.	J. sta	Euphorbiaceae
Luehea candida (DC.) Mart.	Lueh	Tilaceae
Plumeria rubra L.	Plum	Apocynaceae
Psychotria microdon (DC.) Urb.	Psyc	Rubiaceae
Ruprechtia fusca Fern. [=*R. standleyana* Cocucci]	Rupe	Polygonaceae
Samyda mexicana Rose.	Samy	Flacourtiaceae
Sciadodendron excelsum Griseb.	Scia	Araliaceae
Spondias purpurea L.	Spon	Anacardiaceae
Tabebuia chrysantha (Jacq.) Nicholson.	T. chr	Bignoniaceae
Tabebuia impetiginosa (Mart.) Standl. [=*T. palmeri* Rose].	T. imp	Bignoniaceae
Trichilia trifolia L. subsp. *palmeri* (C. DC.) Pennington.	Tric	Meliaceae
Tohuinia paucidentata Radlk.	Tohu	Sapindaceae
Urera caracasana (Jacq.) Griseb.	Urer	Urticaceae

Wet-season Deciduous

Coccoloba liebmannii Lindau.	Cocc	Polygonaceae
Forchhammeria pallida Liebm.	Forc	Capparaceae
Jacquinia pungens (A. Gray.)	Jacq	Theophrastaceae

Semievergreen

* *Piranhea mexicana* (Standl.) A. Radcliffe–Sm. [*Celaenodendron mexicanum* Standl.].	Pira	Euphorbiaceae

Table 2. Values for continuous and categorical leaf traits of 58 tree species of the tropical dry forest in Chamela, Jalisco, Mexico: leaf mass per area (LMA), foliar nitrogen concentration (N), foliar phosphorus concentration (P), lignin concentration (Lig), and soluble carbohydrate concentration (S. car), leaf phenology (Phe), leaf consistency (Con), leaf morphology (Mor), leaf hairiness (Hair), and wax coating (Wax).

	LMA	N	P	Lig	S. car	Phe[1]	Con[2]	Mor[3]	Hair*	Wax*
Sp	g m^{-2}	mg g^{-1}	mg g^{-1}	%	%					
Dry-season deciduous										
N-fixing legumes										
1 Albi	69.7	45.7	1.5	15.0	4.8	1	2	2	2	1
2 Apop	58.6	36.3	1.5	20.4	2.6	1	1	2	2	2
3 Bron	45.6	31.4	1.4	15.7	3.9	1	1	2	2	2
4 Chlo	89.1	49.9	1.2	16.7	3.1	1	1	2	2	2
5 Eryt	39.4	39.8	1.8	27.2	2.0	1	1	2	2	2
6 Glir	45.7	37.3	1.8	21.1	2.8	1	1	2	2	2
7 L.eri	73.7	31.8	1.7	33.4	3.1	1	2	2	2	1
8 L.mag	68.7	38.3	1.2	16.9	4.4	1	2	1	2	2
9 sp 1^y	64.8	35.6	0.9	17.2	4.2	1	1	2	2	2
10 sp 2^y	75.9	39.2	1.3	16.7	3.5	1	1	2	2	2
11 Lysi	MD	33.0	1.1	9.2	3.6	1	1	2	2	2
12 Pipt	78.6	37.3	1.9	24.9	1.6	1	1	2	2	2
13 Plat	72.6	35.3	1.3	16.4	4.3	1	2	1	2	2
14 Pter	24.7	39.1	1.4	17.6	3.9	1	1	2	2	2
Non N-fixing legumes										
15 Bahu	39.1	36.6	1.7	32.5	1.8	1	1	1	2	2
16 C.eri	135.1	27.6	1.1	7.3	4.9	1	1	2	2	2
17 C.scl	111.6	27.2	1.3	11.1	5.4	1	1	2	2	2
18 Haem	84.6	23.3	1.2	9.9	4.9	1	2	1	2	1
Non-Legumes										
19 Adel	64.2	22.7	1.6	15.5	6.3	1	1	1	1	2
20 Amph	64.5	24.2	1.6	16.2	6.5	1	1	1	2	2
21 B.exc	72.0	22.6	1.7	17.5	6.1	1	1	2	1	2
22 B.ins	53.4	25.0	1.0	22.2	4.7	1	2	1	2	1
23 Capp	85.6	38.1	2.3	10.2	2.2	1	2	1	2	1

	LMA	N	P	Lig.	S. car	Phe[1]	Con[2]	Mor[3]	Hair*	Wax*
24 Case	56.1	34.6	2.6	20.4	2.0	1	1	1	1	2
25 Clor	63.5	28.7	2.1	14.3	3.7	1	1	1	2	2
26 Cnid	42.5	38.9	3.4	3.8	6.6	1	1	1	1	2
27 Coch	40.3	34.7	2.6	8.5	7.6	1	1	1	2	2
28 Colu	47.0	29.6	2.0	17.5	1.8	1	1	1	2	2
29 Como	64.8	23.7	1.7	8.0	7.7	1	2	2	1	2
30 Cord	75.0	26.8	1.7	30.0	0.4	1	2	1	1	2
31 Crot	46.5	30.1	1.9	23.8	2.8	1	2	1	2	1
32 Esen	102.5	29.1	2.3	8.8	3.0	1	2	1	2	1
33 Euph	46.3	27.3	1.6	3.2	8.2	1	1	1	2	2
34 Exos	67.3	21.4	1.7	5.4	9.3	1	1	1	2	2
35 Guap	77.1	52.0	2.0	19.0	1.0	1	1	1	2	2
36 Guet	71.0	21.3	1.3	19.1	1.8	1	1	1	2	2
37 Helie	64.7	28.6	1.6	6.3	3.9	1	1	1	2	2
38 Helio	83.9	37.2	3.3	28.1	3.4	1	1	1	1	2
39 Ipom	48.5	41.1	1.8	28.1	1.6	1	1	1	2	2
40 Jaca	38.1	47.1	3.9	4.1	6.4	1	1	2	2	2
41 J.cha	53.2	26.5	3.1	7.5	4.2	1	1	1	1	2
42 J.sta	58.5	26.5	2.8	10.3	5.6	1	2	1	1	1
43 Lueh	46.3	24.9	1.1	13.1	5.5	1	1	1	1	2
44 Plum	53.8	35.2	1.7	20.3	7.3	1	1	1	2	2
45 Psyc	21.6	38.1	1.7	6.7	10.8	1	1	1	2	2
46 Rupr	103.4	24.7	2.1	17.1	1.2	1	2	1	1	1
47 Samy	92.0	20.0	1.3	26.0	2.3	1	1	1	2	2
48 Scia	46.7	30.2	3.0	14.0	13.8	1	1	1	2	2
49 Spon	46.8	29.3	2.3	9.5	5.1	1	1	1	2	2
50 T.chr	48.2	38.0	2.3	19.6	2.2	1	1	1	1	2
51 T.imp	59.4	33.1	1.9	26.6	5.0	1	1	1	2	2
52 Tohu	53.7	29.2	2.2	13.9	4.2	1	1	1	1	2
53 Tric	35.3	31.5	2.4	12.7	5.2	1	1	1	1	1
54 Urer	52.5	32.5	2.6	18.3	3.1	1	1	1	1	2
Wet-season deciduous										
55 Jacq	56.3	16.1	1.4	11.4	12.8	2	2	1	2	1
56 Cocc	102.9	18.4	1.4	16.8	3.4	2	2	1	1	2

	LMA	N	P	Lig.	S. car	Phe[1]	Con[2]	Mor[3]	Hair*	Wax*
57 Forc	138.3	22.9	1.5	9.8	6.5	2	2	1	2	1
Semievergreen										
58 Pira	86.2	23.8	2.3	20.2	1.6	1	2	1	2	1

[1] Dry season=1, Wet season=2; [2] Soft=1, Coriaceous=2; [3] Simple=1, Compound=2;

*Presence=1, Absence=2. MD= Missing Data. [Y]=Genus *Lonchocarpus*

Table 3. Correlation coefficients (r) between continuous traits used in PCA of 58 species of the tropical dry forest in Chamela, Jalisco, Mexico. Significant correlations (P<0.05) in bold.

	LMA	Leaf N	Leaf P	Lignin
LMA	0.1000			
Leaf N	**-0.3631**	0.1000		
Leaf P	-0.2967	0.2343	0.1000	
Lignin	-0.0329	0.1566	-0.1252	0.1000
S. carbohydrates	-0.1139	-0.2510	0.0510	**-0.5978**

Table 4. Loadings for five continuous traits in the first three principal components of the principal components analyses (PCA) for 58 tree species of the tropical dry forest in Chamela, Jalisco, Mexico. Variance (%) explained by each axis in parentheses. A coefficient whose absolute value is >0.33 is equivalent to a correlation with the axis at P < 0.05.

	Principal components		
Trait	**Axis 1**	**Axis 2**	**Axis 3**
Explained variation	(34.5)	(31.4)	(14.8)
LMA	0.197	**-0.593**	**0.538**
Leaf N	**-0.465**	**0.402**	-0.159
Leaf P	-0.084	**0.564**	**0.777**
Lignin	**-0.599**	-0.286	-0.086
S. carbohydrates	**0.615**	0.293	-0.271

a)

$y = -0.2245x + 4.3433$
$R^2 = 0.1071$

Log [N (mg g^{-1})]

Log [LMA (gm^{-2})]

b)

$y = -0.6158x + 2.9199$
$R^2 = 0.372$
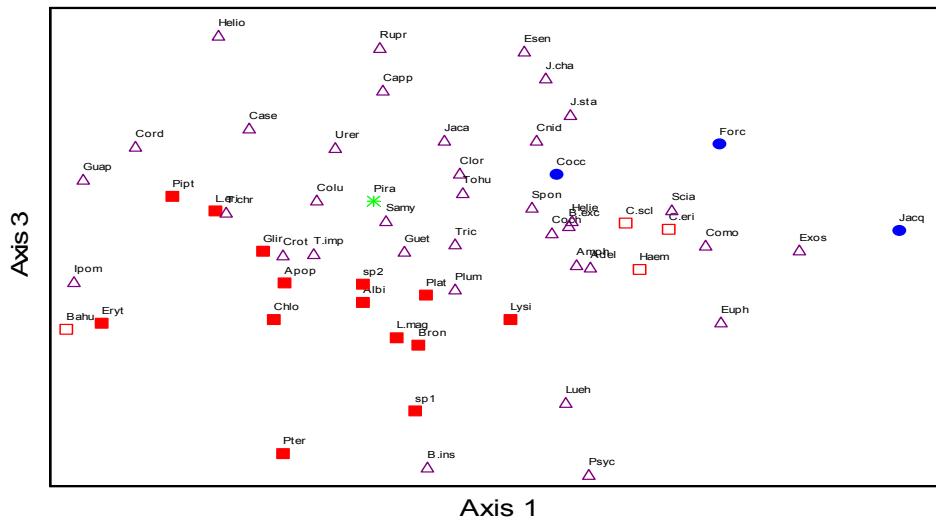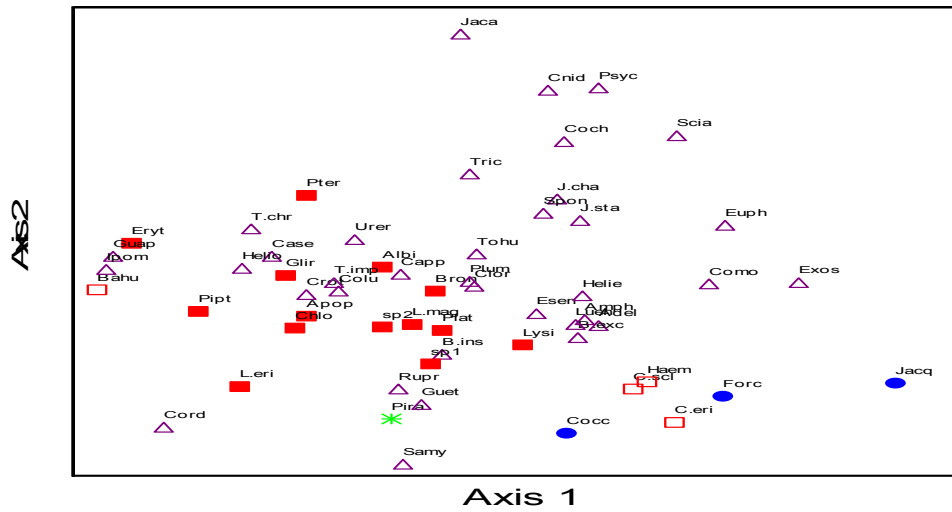
Log [C. Sol (%)]

Log [Lig (%)]
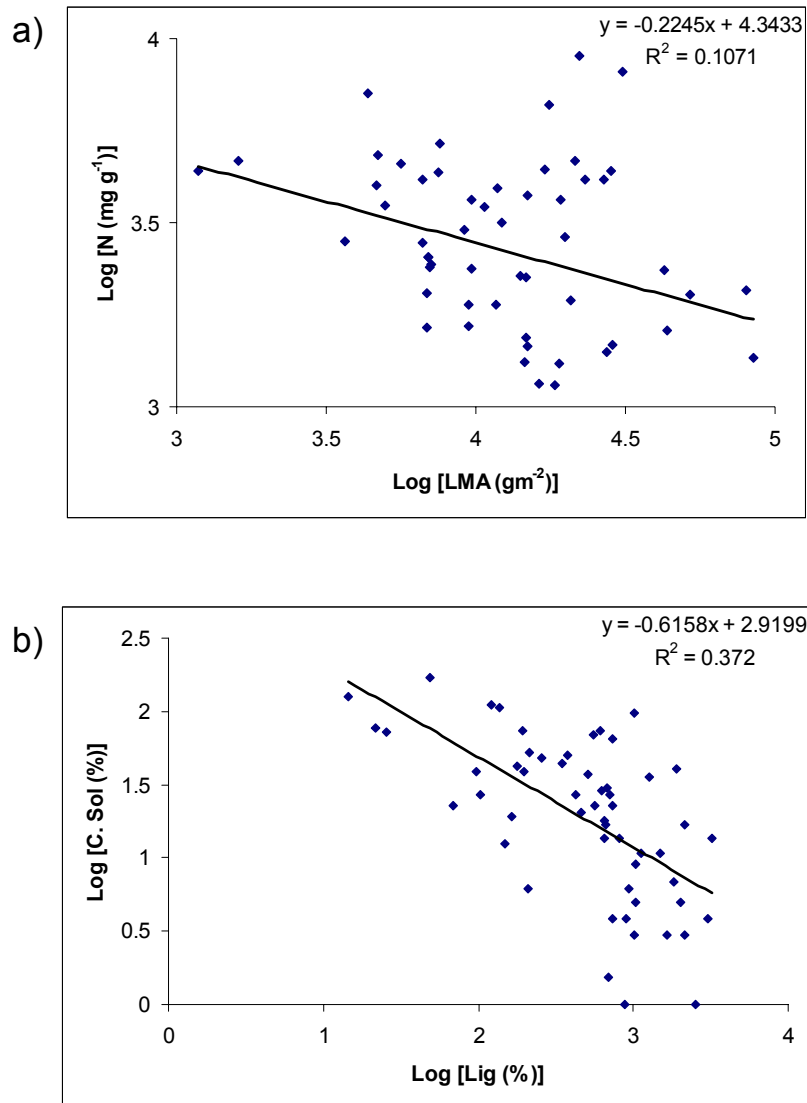
Figure 1. Relationships between a) Leaf mass per area and leaf N concentration; and b) lignin and soluble carbohydrates in 58 tree species of the tropical dry forest of Chamela, Jalisco, Mexico. All variables are $\log_n$-scaled. Both coefficients were significant in a linear regression ($P<0.001$).

A ordination results for five continuous traits of 58 species of the tropical dry forest in Chamela, Jalisco, Mexico. Axes 1, 2, and 3 explained 34.5, 31.4, and 14.8% of the variation, respectively. Symbols indicate the four groups that could potentially show different biogeochemical properties. Abbreviation of species names as in Table 1.

ASSESSMENT OF NITROGEN AND PHOSPHORUS RESORPTION IN 21 TREE SPECIES OF A MEXICAN TROPICAL DRY FOREST

INTRODUCTION

Nutrient resorption during senescence is an important physiological process for nutrient retention in terrestrial plants (Aerts 1996). Especially nitrogen and phosphorus are largely withdrawn from senescing leaves before abscission, and used for new growth or stored in vegetative tissue until the next growing season. Therefore, plants are less dependent on current nutrient uptake from the soil, which can have important ecological consequences in different aspects such as competition and plant fitness, among others.

Before leaves detach from the plant, on average about 50% of the N and P contained in mature leaves is resorbed and redirected towards growing parts or storage tissues (Aerts, 1996). Still, the proportion of nutrients withdrawn from leaves varies widely among species, since <5 to 80% of leaf N and 0-95% of leaf P may be resorbed (Aerts y Chapin 2000). The ability of a plant to resorb nutrients is termed resorption efficiency (RE) (Killingbeck 1996). Recently, Heerwaarden *et al*. (2003) proposed that current measures of nutrient RE may lead to substantial underestimation, suggesting that resorption is even more important for nutrient retention than previously thought.

Nutrient concentration in senesced leaves, known as resorption proficiency (Killingbeck 1996), is a parameter that describes the minimum level to which a nutrient is reduced during senescence. If woody plants reduce foliar N and P in senesced leaves to concentrations below 0.7% and 0.05%, respectively, nutrient resorption can be considered highly proficient and thus an effective nutrient conservation mechanism (Killingbeck 1996). Nutrients that are not resorbed determine the quality of litter and thus nutrient resorption indirectly influences soil nutrient cycling (Hobbie 1992). Resorption proficiency can be influenced by external factors such as nutrient availability (Aerts y Chapin 2000), soil moisture availability (Boerner 1985; Del Arco *et al*. 1991; Escudero *et al*. 1992; Pugnaire y Chapin 1993; Demars y Boerner 1997;

Rentería *et al*. 2005), as well as by internal factors like gradual leaf shedding (Milla *et al*. 2005) and N concentration in green leaves (Yuan *et al*. 2005). Results from a study with six tree species of the tropical dry forest of Chaemla were generally indicative of incomplete N and P resorption (Rentería *et al*. 2005) and suggested that water more than soil nutrient availability controls resorption in this ecosystem. Resorption proficiency is also a feature that varies intrinsically among species (Killingbeck, 1996; Richardson *et al*. 2005). For example, species harboring N-fixing bacteria have lower N resorption proficiency (higher N levels in senesced leaves) than non-symbiotic species (Killingbeck 1996).

Resorption proficiency is related to ecosystem functioning as it expresses the N and P available for decomposition after leaf shed. Therefore, resorption proficiency of vegetation is an important parameter to incorporate in the description of nutrient cycles at the ecosystem level.

The concept of plant functional type was developed in order to group species according to their specific traits, their response to environmental variations or their effect on ecosystem functions (Lavorel *et al*. 1997; Díaz y Cabido 2001). Plant species may exhibit differences in N and P resorption efficiency and proficiency, thus allowing the possibility to group species with differential effects on nutrient cycling.

The aim of this study was to quantify N and P resorption efficiency and proficiency in tree species of a tropical dry forest to asses the relationship between resorption measures and precipitation, and also to determine the extent to which tropical dry forest species may be grouped based on their nutrient resorption patterns. The study of broader range of species would allow better estimates of resorption of nutrient cycling in this forest.

MATERIALS AND METHODS

The study was conducted at the Chamela Biological Station (Universidad Nacional Autónoma de México), a 3200 ha nature reserve located on the Pacific coast of Jalisco, Mexico (19°29′N, 105°01′W). Mean annual precipitation is 736 mm (1983-2004; García-Oliva pers. com.) concentrated between July and November. The dominant vegetation type is a highly diverse tropical dry forest. This is a dense forest, 4-15 m tall, with a well-developed shrub understory and a strongly seasonal phenology (Lott *et al*. 1987). With few exceptions, the species have no leaves for several months during the dry season each year (Bullock y Solís-Magallanes 1990, Martínez-Yrízar y Sarukhán 1990). Lott (1985) reports 758 plant species from 107 families for the

Station, with Leguminosae as the most important family with 15% of the species. Weathering of the main parent material, rhyolite, results in weakly developed sandy-clay-loam soils (García-Oliva 1992) classified in the USDA system as Typic Ustorthents.

Nutrient resorption efficiency (RE) and proficiency were assessed in 21 dominant tree species (Balvanera *et al*. submitted) representing 15 plant families (Table 1). The species belong to groups differing in leaf phenology: 17 dry-season deciduous species (5 legumes and 12 non-legumes), three wet-season deciduous species (*Coccoloba liebmannii*, *Forchhammeria pallida*, *Jacquinia pungens*, and the semievergreen *Piranhea mexicana*, which forms monospecific patches within the forest.

The study was conducted during the 1999, 2000, and 2001 growing seasons. Total annual precipitation was 1131, 545, and 440 mm, respectively. Field work consisted of collecting both mature and senesced leaves from 3-8 mature individuals of each species with comparable diameter at breast height (5-10 cm dbh). Fully expanded sun green leaves (5-15) were collected from each individual tree one month after the beginning of the rainy season (July-August). Attached senescent leaves (5-15) (yellow and ready to drop) were collected at the onset of the dry season. Because leaf abscission does not occur simultaneously in all species, senescent leaves were collected between November and January each year. Leaves (mature and senescent) of wet-deciduous species were collected only in 1999 and 2000 in January and July in both years. Because of the high variation in the timing of leaf-fall, senescent leaves of nine species could not be collected in 1999, and those of *Gliricidia sepium*, in 2001. Except for two species *Tabebuia chrysantha* and *T. impetiginosa,* the species will be referred to hereafter by their generic name.

Single-side surface area of all leaves without the petiole was measured with a Delta –T Image Analyzer, oven dried at 70°C for 48 h and weighed. The compound leaves were measured whole with all the foliols attached to the raquis. All leaves from each individual tree were pooled after measurement. Leaf mass per area (LMA g m^{-2}) was obtained by dividing the dry weight by the leaf area. Mature and senescent leaves were ground in a Thomas Scientific mill to pass a 40-mesh screen. Total N and P were determined after acid digestion by a semi-Kjeldahl method. Samples were determined colorimetrically with an autoanalyzer (Bran-Luebbe Auto Analyzer III, Norderstedt, Germany; method No. 696-82W; Technicon Industrial System 1977). To estimate resorption efficiency on a leaf area basis, element concentration was first converted to foliar content by multiplying LMA by concentration (mg g^{-1}) to yield content per unit area. Resorption efficiency (%) was calculated as the content of mature leaves minus

that of senescent leaves, divided by the content of mature leaves (Kilingbeck y Costigan 1988). N and P concentrations in senescent leaves, expressed as percentages, were used as a measure of resorption proficiency (Killingbeck 1996).

Principal component analyses were used to explore the relationship among the different measures of nutrient resorption and to explore how the species may group regarding both N and P resorption efficiency and proficiency and leaf N and P concentrations. Average values of the three study years for the resorption measures were used in the PCA. The analyses were performed in PC-ORD, Multivariate Analysis of Ecological Data, Version 2.0 (McCune y Mefford 1997). A one-way analysis of variance was performed to examine annual variation of variables for each individual species.

RESULTS

LMA

LMA of mature leaves (all years pooled) ranged from 35.5 ± 1.6 to 163.9 ± 21.8 g m^{-2} (Table 2). LMA of senescent leaves was higher than in mature leaves in nearly all species (47.6 ± 2.7 to 153.4 ± 6.1), with a mean increase of 34%. LMA of both mature and senescent leaves showed inter-annual variations (P<0.05, data not shown).

Foliar N and P concentrations

Foliar N and P concentrations of mature leaves during the whole study period ranged from 16.6 to 52 mg g^{-1} and from 0.8 to 4.1 mg g^{-1}, respectively (Figs. 1 and 2). Mean N and P concentrations (species pooled) were significantly different among sampling years (P = 0.0003). The mean highest N concentration (33.6 mg g^{-1}) was found in the dry 2001, while the mean highest P concentration (2.4 mg g^{-1}) was found in the wet 1999. At the individual species-level, foliar N concentrations were significantly different among sampling years in eight species, with the higher values occurring in the dry 2000 and 2001 (Fig. 1). The legumes *Bahuinia, Erythrina, Piptadenia* and *Gliricidia*, and the non-legumes *Guapira, Ipomoea* and *T. chrysantha*, showed consistently high foliar N concentrations during the three years of study (Fig. 1). Foliar P concentrations were significantly different (P < 0.05) among sampling years in 13 of the 21 species, with the highest values generally occurring in the wet 1999, except for *Lonchocarpus* and *Piptadenia* (Fig. 2).

With few exceptions, mean foliar N:P mass ratios were significantly higher (P < 0.001) in the 2000 and 2001 dry years than in the 1999 wet year (Table 3). Low N:P values (below 14) occurred in 11 of the 21 species in the wet year (Table 3); these species showed higher ratios in the dry years. Wet-deciduous species showed low N:P ratios.

Senescent-leaf nutrient concentrations varied from 7.6 to 28.6 mg g^{-1} (N), and from 0.3 to 2.3 mg g^{-1} (P) (Tables 4 and 5). N and P concentrations in senescent leaves were 42% and 48% lower than in mature leaves, respectively. There was no clear pattern in the inter-annual differences in N concentrations of senescent leaves (Table 4), but mean P concentrations were higher (P = 0.005) in the wet than in the dry years (Table 5). The lowest N concentrations in senescent leaves (i.e., high resorption proficiency) were found in the wet-deciduous *Jacquinia* in 1999 and 2000, and in the dry-deciduous *Bursera* in 2001 (Table 4). Foliar P concentrations in senescent leaves were below 0.5 mg g^{-1} in six species (one wet-deciduous, three dry-deciduous non-legumes and two dry-deciduous legumes) in the dry years (Table 5).

N and P resorption efficiencies

There was considerable interspecific variation in N and P RE, with values ranging from 0 to 78% (N) and 0 to 83% (P) (Figs. 3 and 4). Despite such variation, mean N and P RE increased significantly (P < 0.05) with decreasing mean annual precipitation. Mean RE values in the wet 1999 for both N (16%) and P (22%) were lower than in the two dry years (2000 and 2001; 33 and 36% N; 38 and 46% P, respectively). There was a notable decrease in the number of species with 0% N and P RE from the wet to the driest year: 34% of the species had 0% N RE during 1999 and 2000, but only 5% in 2001. Similarly, 27%, 19%, and 12% of the species in 1999, 2000, and 2001, respectively, showed P RE of 0%. Furthermore, in the wet year (1999) 81% of the species showed N RE values below 30%, while in the dry years only 44% of the species on average had N RE below 30%. The same trend was apparent with P RE: 54%, 33%, 18% of the species in 1999, 2000, and 2001, respectively, showed values below 30%. Some species like *Guapira* consistently showed very low N and P RE's regardless of the year, while others like *Piptadenia* showed higher values (above 35%) in the three years of study (Figs. 3 and 4).

Ordination

The first three axes of the PCA accounted for 92% of the variation in the data set (Table 6). Axis 1 explained 44% of the total variation, with increasing values indicating high foliar N in senesced leaves and high N and P foliar concentrations in mature leaves (Fig. 5a, Table 6). Axis 2 explained 31% of the total variation, with increasing values indicating lower N and P resorption efficiencies (Fig. 5a, Table 6). Axis 3 explained 17% of the total variation, with increasing values indicating higher P concentrations in senescent leaves (Fig. 5b, Table 6). The ordination analysis showed that Axis 1 did not delimit any clear species groups, since these 21 species showed a great range of variation in N concentration of senesced leaves, as well as in N and P concentrations in mature leaves. However, Axis 2 delimits the species regarding the N RE: species with high N RE like legumes, the wet deciduous and some drought-deciduous non-legumes, and the low N RE like other drought-deciduous non-legumes, and *Piranhea* (Figure 5a). Axis 3 segregated the wet-deciduous species because of their high P concentrations in senescent leaves (Figure 5b). Interestingly, most legumes tended to group because of intermediate to high N concentrations in senescent leaves, high to intermediate N and P RE and intermediate to high P proficiency (low P concentrations in senesced leaves).

There were four significant ($P < 0.05$) positive correlations among traits (Table 7). Leaf N was positively correlated to leaf P and N in senesced leaves. Also, N RE and P RE were positively correlated.

DISCUSSION

This study with 21 dominant woody species provides new and more representative values of nutrient resorption in the Chamela tropical dry forest. We found higher mean values (32% for N and 39% for P) than the 22% (N) and 26% (P) reported by Rentería *et al*. (2005) for six tree species, in the same years and study site. Our values are still low compared to the average N and P resorption efficiencies (50%) reported by Aerts (1996) and to the efficiencies reported for tropical dry forest species in India (Lal *et al*. 2001) and Venezuela (Medina 1984) and for Australian sclerophyllous species (Wright and Westoby 2003). The ranges of variation of RE in this study (0-78% and 0-83% for N and P, respectively) were wider than the 4-66% for N and 25-89% for P in sclerophyllous species of Australia (Wright and Westoby 2003) and the 26-83% for N and 16-80% for P in tropical dry forest species of India (Lal *et al*. 2001). Together these results suggest that although the species may resorb

nutrients in substantial amounts to support new growth, this is a highly variable species-specific process.

Mean senescent-leaf N and P concentrations (i.e., a measure of resorption proficiency) in this set of 21 species (18.3 mg g^{-1} for N; 0.96 mg g^{-1} for P) were 19% and 40% lower, respectively, than values reported by Rentería *et al*. (2005) for six species in the tropical dry forest of Chamela. Nevertheless, they still suggest incomplete nutrient resorption when compared with those reported by Killingbeck (1996) for complete resorption (N< 7 mg g^{-1} and P< 0.4 mg g^{-1}).

Annual variation in resorption

The higher mean RE values for both N and P and the lower senescent leaf P concentrations during 2001, one of the two dry years, support previous findings in this tropical dry forest regarding nutrient RE and P resorption proficiency at Chamela (Rentería *et al*. 2005) which suggest an increase in resorption with decreasing water availability. Nevertheless, our results showed that individual species may not respond to the annual variation in precipitation similarly with all measures of resorption. For example, the wet-deciduous *Jacquinia* (sampled only during the wet 1999 and the dry 2000), responded to the annual variability in both P RE and proficiency, but not in N. The drought-deciduous *Guettarda* showed only a weak response in N RE to contrasting precipitation, and none in the other three measures of resorption. Such responses may reflect among-species variation in the timing of leaf-fall, since not all the species drop their leaves at the same time. This time-lag may be related to environmental constraints such as soil water deficit or changes in photoperiod. For example, species like *Plumeria* seem to be sensitive to soil water deficit, dropping their leaves soon after the last summer rains and before many other drought deciduous species (Vizcaíno 1978, L. Rentería pers. obs.).

Foliar N and P concentrations

The N:P foliar ratio in this study (mean=19) was similar to that reported for a set of six species (18) by Rentería *et al*. (2005). This would suggest P limitation to biomass production following Koerselman y Meuleman (1996) criteria. Both mean N:P foliar ratios were higher than the ratio (11) reported by Jaramillo y Sanford (1995) for a different site in the Chamela forest. This confirms previous suggestions that N:P ratios may indicate P limitation that occurs at local scales (Rentería *et al*. 2005). Our results suggest that P limitation may also occur at the species level. For example,

species like *Cordia, Erythrina, Gliricidia, Guapira, Helietta, Piptadenia* and *T. chrysantha* showed high N:P foliar ratios (≥17) irrespectively of the year, while others such as *Bauhinia, Bursera, Piranhea, Plumeria, Samyda* and *T. impetiginosa* clearly showed variation in the N:P foliar ratios in response to precipitation (i.e. lower values in the wet 1999 and higher ratios in the dry years of 2000 and 2001). At the community level, the overall increase in the mean N:P foliar ratio in the dry years supports previous findings that nutrient limitation in this forest is mediated by water availability (Rentería *et al.* 2005).

Species groups

      Examination of the PCA results indicated that the species of this tropical dry forest showed tendencies to be grouped based on resorption efficiency measures and N and P concentrations in mature leaves. We found a wide range of variation in resorption efficiency among species with contrasting leaf phenologies. The wet-deciduous species share common traits which grouped them in the ordination space: low P proficiency (high P concentrations in senescent leaves), high N proficiency (low N concentration in senescent leaves) and intermediate to high N and P RE. In general, the species examined here presented a wide range of strategies for nutrient conservation.

      Although the legumes did not conform a homogeneous group, it is interesting that they consistently shared the same general area of the ordination space. They all showed both intermediate to high N and P RE and P resorption proficiencies while having intermediate to low N resorption proficiencies. The higher N RE in the N-fixing (49%) than in the non N-fixing (26%) drought deciduous species in this study is opposed to previous reports (Killingbeck 1996 and references there in), which indicated that temperate species with N-fixing actinorhyzal symbionts had lower N RE than non N-fixing species. Our results also differed from findings with tropical deciduous tree species in India (Singh 2004), in which N RE of legumes (57%) was lower than in non-legume (66%) species. These data make difficult to establish a generalization concerning N RE in N-fixing and non N-fixing plants. Similarly, available data on N and P resorption proficiency (Killingbeck 1996; Singh 2004) do not allow to establish a general trend when N-fixing and non N-fixing species are compared.

Table 1. The 21 tree species of the tropical dry forest in Chamela, Jalisco, Mexico, listed in alphabetical order. Phenological groups (PG): 1) Drought-deciduous; 2) Wet-deciduous; 3) Semievergreen. Abb=Abbreviation of species name.

Species	Abb.	PG	Family/subfamily
1 *Adelia oaxacana* (Muell. Arg.) Hemsl.	Adel	1	Euphorbiaceae
2 *Bahuinia ungulata* L.	Bahu	1	Leguminosae/ Caesalpinoideae
3 *Bursera instabilis* Mc Vaugh y Rzed.	Burs	1	Burceraceae
4 *Piranhea mexicana* Standl. Radcl.–Sm. [=*Celaenodendron mexicanum* Standl.].	Pira	3	Euphorbiaceae
5 *Coccoloba liebmannii* Lindau	Cocc	2	Polygonaceae
6 *Colubrina heteroneura* (Grises.) Standl.	Colu	1	Rhamnaceae
7 *Cordia alliodora* (Ruiz y Pav.) Oken.	Cord	1	Boraginaceae
8 *Erythrina lanata* Rose var. *occidentalis* (Standl.) Krukoff y Barneby	Eryt		Leguminosae/ Papilionoideae
9 *Forchhammeria pallida* Liebm. [=*F. lanceolata* Standl.].	Forc	2	Capparaceae
10 *Gliricidia sepium* (Jacq.) Kunth ex Steudel.	Glir	1	Leguminosae/ Papilionoideae
11 *Guapira* cf. *macrocarpa* Miranda	Guap	1	Nyctaginaceae
12 *Guettarda elliptica* Sw. [=*G. macrosperma* Donn. Sm.].	Guet	1	Rubiaceae
13 *Helietta lottiae* Chiang	Heli	1	Rutaceae
14 *Ipomoea wolcottiana* Rose	Ipom	1	Convolvulaceae
15 *Jacquinia pungens* (A. Gray)	Bone	2	Theophrastaceae
16 *Lonchocarpus eriocarinalis* Micheli	Lonc	1	Leguminosae/ Papilionoideae
17 *Piptadenia constricta* (Micheli) Macbr. [=*Pityrocarpa oblicua* (Pers.) MacBride].	Pipt	1	Leguminosae/ Papilionoideae
18 *Plumeria rubra* L.	Plum	1	Apocynaceae
19 *Samyda mexicana* Rose	Samy	1	Flacourtiaceae
20 *Tabebuia chrysantha* (Jacq.) Nicholson	T.chr	1	Bignoniaceae
21 *Tabebuia impetiginosa* (Mart.) Standl. [=*T. palmeri* Rose]	T.imp	1	Bignoniaceae

Table 2. Leaf mass per area (LMA; g m^{-2}) of mature and senescent leaves of tree species of the tropical dry forest in Chamela, Jalisco, México. Values are means of three years with one standard error, except for the wet-deciduous species (*Jacquinia, Coccoloba* and *Forchhammeria*) wich were measured during two years.

Species	LMA	
	Mature	**Senescent**
Aadelia	63.1 ± 2.4	84.7 ± 4.6
Bahuinia	37.1 ± 1.6	47.6 ± 2.7
Bursera	50.7 ± 2.6	63.7 ± 2.5
Coccoloba	132.5 ± 21.4	140.9 ± 24.5
Colubrina	49.0 ± 1.8	82.8 ± 6.6
Cordia	67.9 ± 3.3	84.1 ± 4.0
Erythrina	35.5 ± 1.6	62.4 ± 17.6
Forchhammeria	163.9 ± 21.8	153.4 ± 6.1
Gliricidia	48.7 ± 1.8	58.9 ± 4.1
Guapira	66.3 ± 3.7	117.7 ± 6.9
Guettarda	64.4 ± 3.1	105.1 ± 14.9
Helietta	61. 2 ±.14	107.9 ± 23.7
Ipomoea	44.4 ± 1.1	57.4 ± 2.7
Jacquinia	66.3 ± 3.3	102.8 ± 4.5
Lonchocarpus	72.5 ± 3.1	86.6 ± 5.2
Piptadenia	68.1 ± 3.3	75.7 ± 2.7
Piranhea	83.7 ± 1.7	128.2 ± 12.5
Plumeria	54.9 ± 1.1	102.0 ± 6.3
Samyda	82.6 ± 5.7	126.1 ± 40.2
T. chrysantha	43.6 ± 2.2	59.1 ± 3.9
T. impetiginosa	58.1 ± 1.8	63.2 ± 2.8
Mean	**67.7 ± 6.8**	**91 ± 6.6**

Table 3. Foliar N:P mass ratios of tree species during three years in the tropical dry forest in Chamela, Jalisco, México. Values are means with one standard error. Years with different letters are significantly different (Tukey; P<0.05). Total annual precipitation was 1131 mm (1999), 545 mm (2000), and 440 mm (2001).

Species	1999	2000	2001
Adelia	10.7 ± 1.1b	14.6 ± 1.1b	20.7 ± 1.3a
Bauhinia	15.0 ± 2.7b	20.9 ± 1.3a	22.4 ± 0.6a
Bursera	8.3 ± 0.7c	25.9 ± 1.9a	15.3 ± 0.6b
Coccoloba	6.5 ± 0.4b	12.9 ± 0.5a	n.d.
Colubrina	11.0 ± 1.0b	17.2 ± 3.8ab	19.2 ± 1.0a
Cordia	16.7 ± 0.6a	17.1 ± 2.4a	20.4 ± 0.5a
Erythrina	24.1 ± 2.9a	20.7 ± 0.9a	21.3 ± 1.5a
Forchammeria	8.1 ± 0.3b	15.8 ± 1.3a	n.d.
Gliricidia	25.4 ± 2.5a	20.4 ± 0.5b	23.4 ± 0.4a
Guapira	22.4 ± 1.2a	23.6 ± 2.4a	26.3 ± 0.9a
Guettarda	13.7 ± 1.9a	17.7 ± 2.6a	18.8 ± 1.2a
Helietta	19.8 ± 2.0ab	17.4 ± 1.0b	24.1 ± 1.6a
Ipomoea	19.9 ± 1.2b	21.9 ± 0.6ab	25.5 ± 1.3a
Jacquinia	5.1 ± 0.4b	13.0 ± 2.5a	n.d.
Lonchocarpus	20.4 ± .8a	21.2 ± 0.8a	18.0 ± 0.5b
Piptadenia	25.1 ± 3.3a	19.4 ± 0.8b	30.2 ± 1.3a
Piranhea	7.6 ± 1.2b	19.0 ± 2.0a	14.2 ± 0.6a
Plumeria	11.0 ± 1.1b	23.8 ± 2.2a	19.6 ± 0.5a
Samyda	13.9 ± 0.3b	17.9 ± 3.8a	22.2 ± 1.7a
T. chrysantha	19.3 ± 2.0a	16.9 ± 1.4a	21.1 ± 1.1a
T. impetiginosa	8.6 ± 0.3b	18.1 ± 1.8a	19.9 ± 0.3a
Mean	**14.9 ± 1.4b**	**18.8 ± 0.7a**	**21.2 ± 0.8a**

n.d. = not determined

Table 4. Foliar N concentrations (mg g^{-1}) of senescent leaves of tree species during three years in the tropical dry forest in Chamela, Jalisco, México. Values are means with one standard error. Years with different letters are significantly different (Tukey; $P<0.05$). Total annual precipitation was 1131 mm (1999), 545 mm (2000), and 440 mm (2001).

	Foliar N		
Species	**1999**	**2000**	**2001**
Adelia	n.d.	15.6 ± 1.3a	10.2 ± 0.4b
Bauhinia	n.d.	16.0 ± 0.9b	20.0 ± 1.1a
Bursera	n.d.	11.3 ± 1.3a	7.9 ± 0.6b
Coccoloba	15.9 ± 1.5a	10.8 ± 1.4b	n.d.
Colubrina	15.5 ± 1.3a	16.6 ± 1.0a	20.0 ± 1.2a
Cordia	19.1 ± 1.8a	21.4 ± 1.4a	22.8 ± 1.0a
Erythrina	n.d	25.3 ± 3.5a	15.2 ± 0.6b
Forchhammeria	18.4 ± 0.8a	15.7 ± 0.4b	n.d.
Gliricidia	20.4 ± 1.4a	20.9 ± 0.7a	n.d.
Guapira	24.5 ± 1.4b	28.6 ± 0.6a	26.4 ± 0.6ab
Guettarda	16.4 ± 1.4a	21.6 ± 2.3a	16.9 ± 0.1a
Helietta	n.d.	16.6 ± 1.5a	18.1 ± 2.3a
Ipomoea	n.d.	28.6 ± 2.4a	14.7 ± 0.7b
Jacquinia	7.8 ± 0.3a	7.6 ± 0.6a	n.d.
Lonchocarpus	19.7 ± 1.5a	16.4 ± 0.7ab	13.8 ± 1.0b
Piptadenia	21.6 ± 1.0a	22.6 ± 1.8a	21.9 ± 1.3a
Piranhea	13.6 ± 0.9b	16.7 ± 0.9a	10.9 ± 0.2b
Plumeria	n.d.	20.0 ± 1.5a	14.3 ± 0.6b
Samyda	n.d.	16.8 ± 0.5a	14.7 ± 0.5a
T. chrysantha	n.d.	27.2 ± 1.8a	24.5 ± 1.4a
T. impetiginosa	n.d.	20.9 ± 0.7a	21.4 ± 0.8a
Mean	**18.5 ± 0.6ab**	**19.2 ± 0.6a**	**17.2 ± 0.5b**

n.d. = not determined

Table 5. Foliar P concentrations (mg g^{-1}) of senescent leaves of tree species during three years in the tropical dry forest in Chamela, Jalisco, México. Values are means with one standard error. Years with different letters are significantly different (Tukey; $P<0.05$). Total annual precipitation was 1131 mm (1999), 545 mm (2000), and 440 mm (2001).

	Foliar P		
Species	**1999**	**2000**	**2001**
Adelia	n.d.	0.8 ± 0.04a	0.5 ± 0.08b
Bauhinia	n.d.	0.8 ± 0.02a	0.9 ± 0.06a
Bursera	n.d.	0.8 ± 0.06a	0.3 ± 0.03b
Coccoloba	1.8 ± 0.03a	0.6 ± 0.07b	n.d.
Colubrina	1.8 ± 0.2a	0.8 ± 0.03b	0.8 ± 0.1b
Cordia	1.4 ± 0.2a	1.2 ± 0.1a	0.9 ± 0.06a
Erythrina	n.d.	1.2 ± 0.07a	0.4 ± 0.03b
Forchammeria	1.9 ± 0.03a	0.9 ± 0.04b	n.d.
Gliricidia	1.2±0.03a	0.6 ± 0.1b	n.d.
Guapira	2.3 ± 0.2a	1.2 ± 0.04b	0.9 ± 0.03b
Guettarda	1.3 ± 0.2a	0.8 ± 0.03a	0.7 ± 0.04a
Helietta	n.d.	0.7 ± 0.07a	0.6 ± 0.1a
Ipomoea	n.d.	1.3 ± 0.1 a	0.3 ± 0.04b
Jacquinia	1.9 ± 0.1a	0.4 ± 0.03b	n.d.
Lonchocarpus	1.7 ± 0.1a	0.9 ± 0.02b	0.4 ± 0.07c
Piptadenia	1.7 ± 0.1a	1.3 ± 0.2ba	0.8 ± 0.04b
Piranhea	1.1 ± 0.1a	1.1 ± 0.1a	1.0 ± 0.06a
Plumeria	n.d.	0.9 ± 0.06	0.4 ± 0.04
Samyda	n.d.	0.7 ± 0.01a	0.5 ± 0.01a
T. chrysantha	n.d.	1.1 ± 0.07a	1.0 ± 0.07a
T. impetiginosa	n.d.	1.1 ± 0.03a	1.1 ± 0.04a
Mean	**1.6 ± 0.05a**	**0.9 ± 0.02b**	**0.7 ± 0.02c**

n.d. = not determined

Table 6. Loadings of six continuous traits in the three first principal components of PCA for species of the tropical dry forest in Chamela, Jalisco, México. Variance (%) explained by each axis in parentheses. A coefficient with absolute value >0.33 is equivalent to a correlation with the axis at P < 0.05. N RE = nitrogen resorption efficiency; P RE = phosphorus resorption efficiency; Nsen = nitrogen concentration in senescent leaves; Psen = phosphorus concentration in senescent leaves.

	Principal Components		
Trait	**Axis 1**	**Axis 2**	**Axis 3**
Explained variation	(43.9)	(31.0)	(17.2)
Leaf N	**0.5199**	-0.2088	-0.35
Leaf P	**0.5688**	-0.0659	-0.007
N RE	-0.1004	**-0.6988**	-0.062
P RE	-0.1322	**-0.6805**	0.1466
Nsen	**0.5843**	-0.0182	0.0361
Psen	0.1929	-0.0178	**0.9224**

Table 7. Correlation coefficients (r) among traits used in PCA of the 21 species of the tropical dry forest in Chamela, Jalisco, México. Significant correlations (P<0.05) in bold. N RE= nitrogen resorption efficiency; P RE= phosphorus resorption efficiency; Nsen= nitrogen concentration in senescent leaves, Psen=phosphorus concentration in senescent leaves.

	Foliar N	Foliar P	N RE	P RE	Nsen	Psen
Foliar N	0.1000					
Foliar P	**0.7463**	1.000				
N RE	0.168	-0.1080	0.1000			
P RE	-0.0014	-0.0633	**0.8444**	0.1000		
Nsen	**0.7640**	**0.8091**	-0.1111	-0.1840	0.1000	
Psen	-0.0264	0.2540	-0.0693	0.0686	0.3192	0.1000
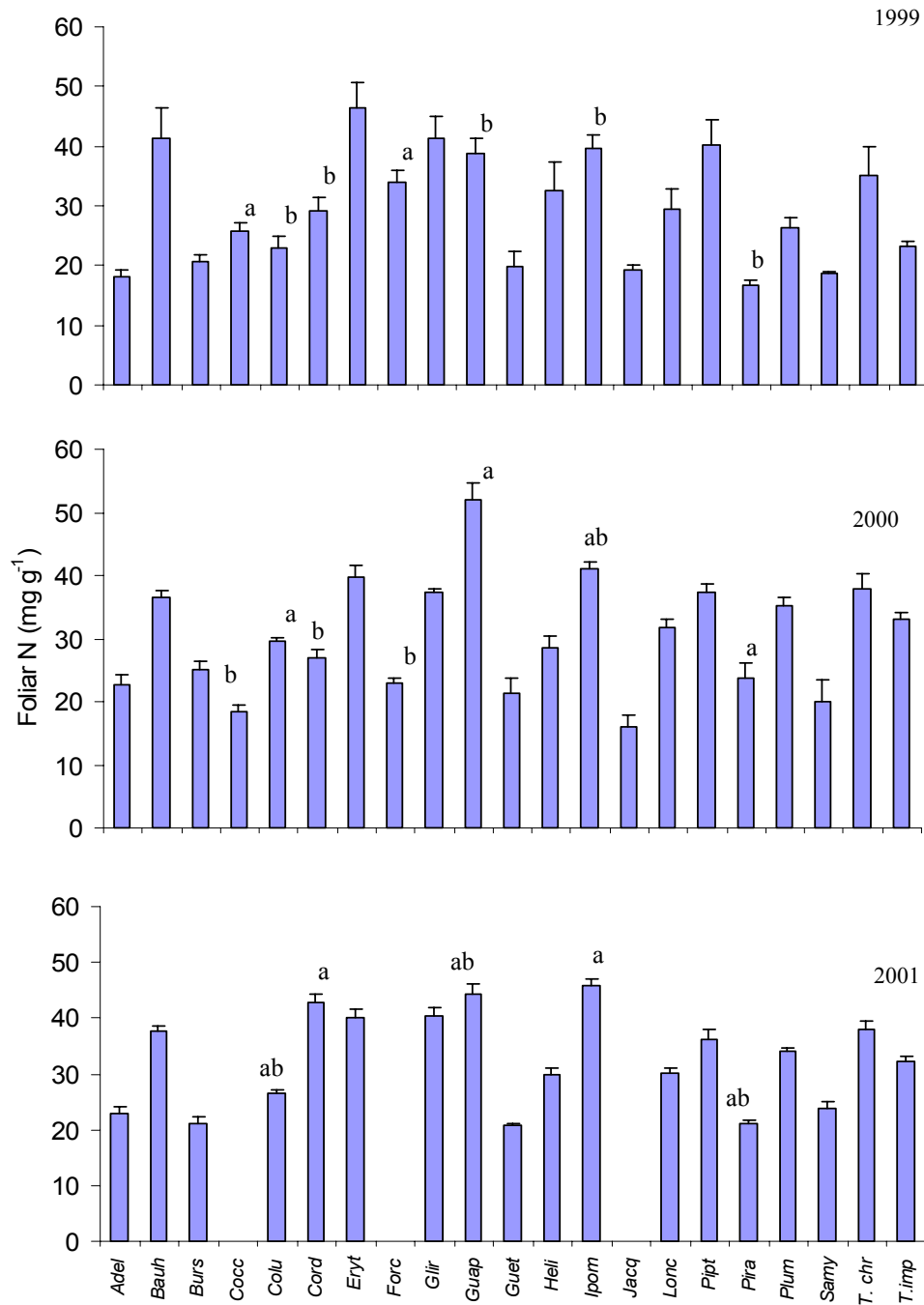
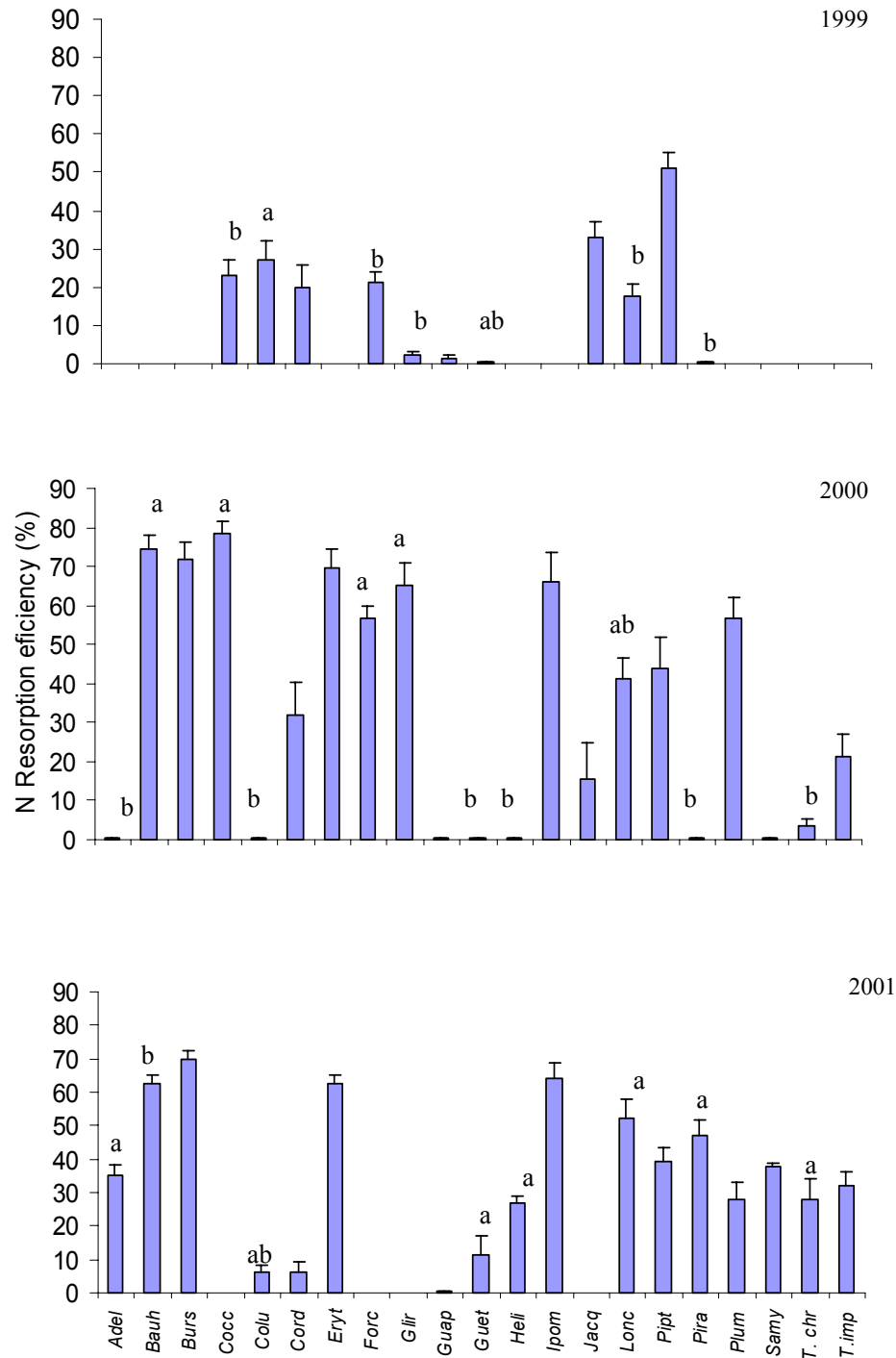Figure 1. N concentrations (mg g^{-1}) in mature leaves of tree species during three years in the tropical dry forest of Chamela, Jalisco, México. Total annual precipitation was 1131 mm (1999), 545 mm (2000), and 440 mm (2001). Values are means with one standard error. Different letters represent significant differences (P< 0.05) among years for each species. Abbreviation of the species names follows the same order as in Table 1.
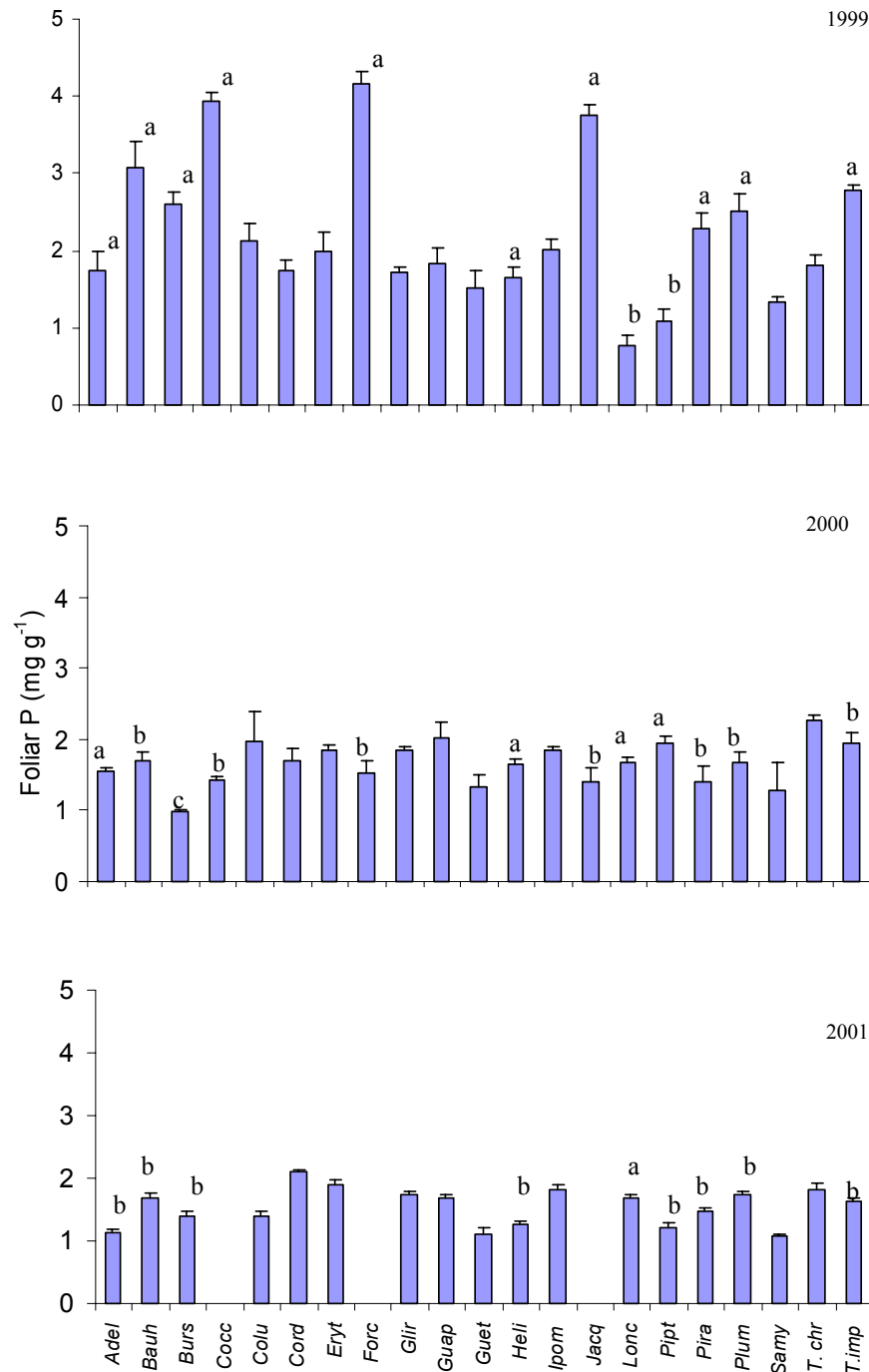
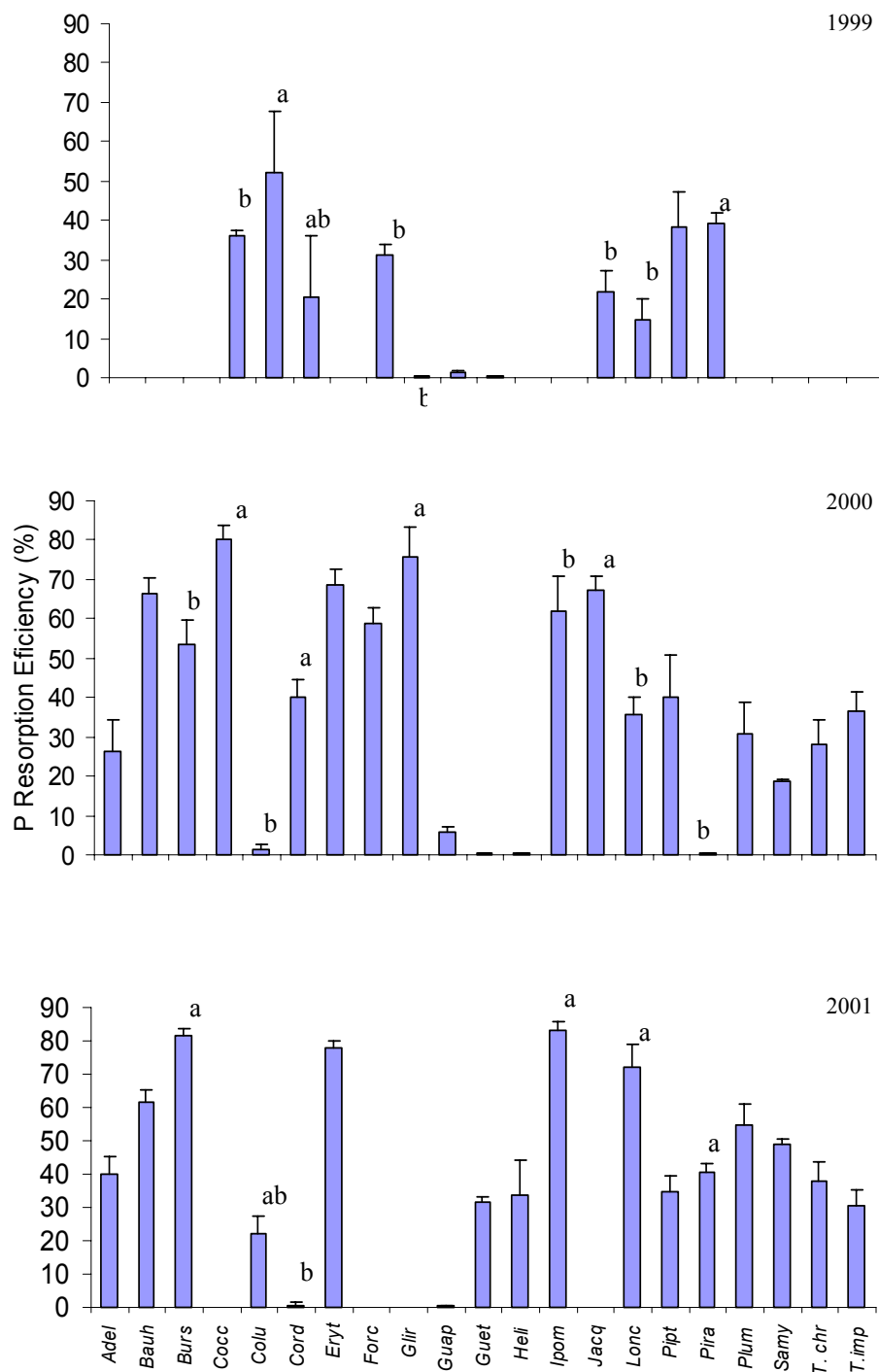Figure 2. P concentrations (mg g^{-1}) in mature leaves of tree species during three years in the tropical dry forest of Chamela, Jalisco, México. Total annual precipitation was 1131 mm (1999), 545 mm (2000), and 440 mm (2001). Values are means with one standard error. Different letters represent significant differences (P< 0.05) between years of each species. Species names follows the same order as in Table 1.

Figure 3. N resorption efficiency (%) of tree species during three years in the tropical dry forest of Chamela, Jalisco, México. Total annual precipitation was 1131 mm (1999), 545 mm (2000), and 440 mm (2001). Values are means with one standard error. Different letters represent significant differences (P< 0.05) between years of each species. Abbreviation of the species names follows the same order as in Table 1.

Figure 4. P resorption efficiency (%) of tree species during three years in the tropical dry forest of Chamela, Jalisco, México. Total annual precipitation was 1131 mm (1999), 545 mm (2000), and 440 mm (2001). Values are means with one standard error. Different letters represent significant differences (P< 0.05) between years of each species. Abbreviation of the species names follows the same order as in Table 1.
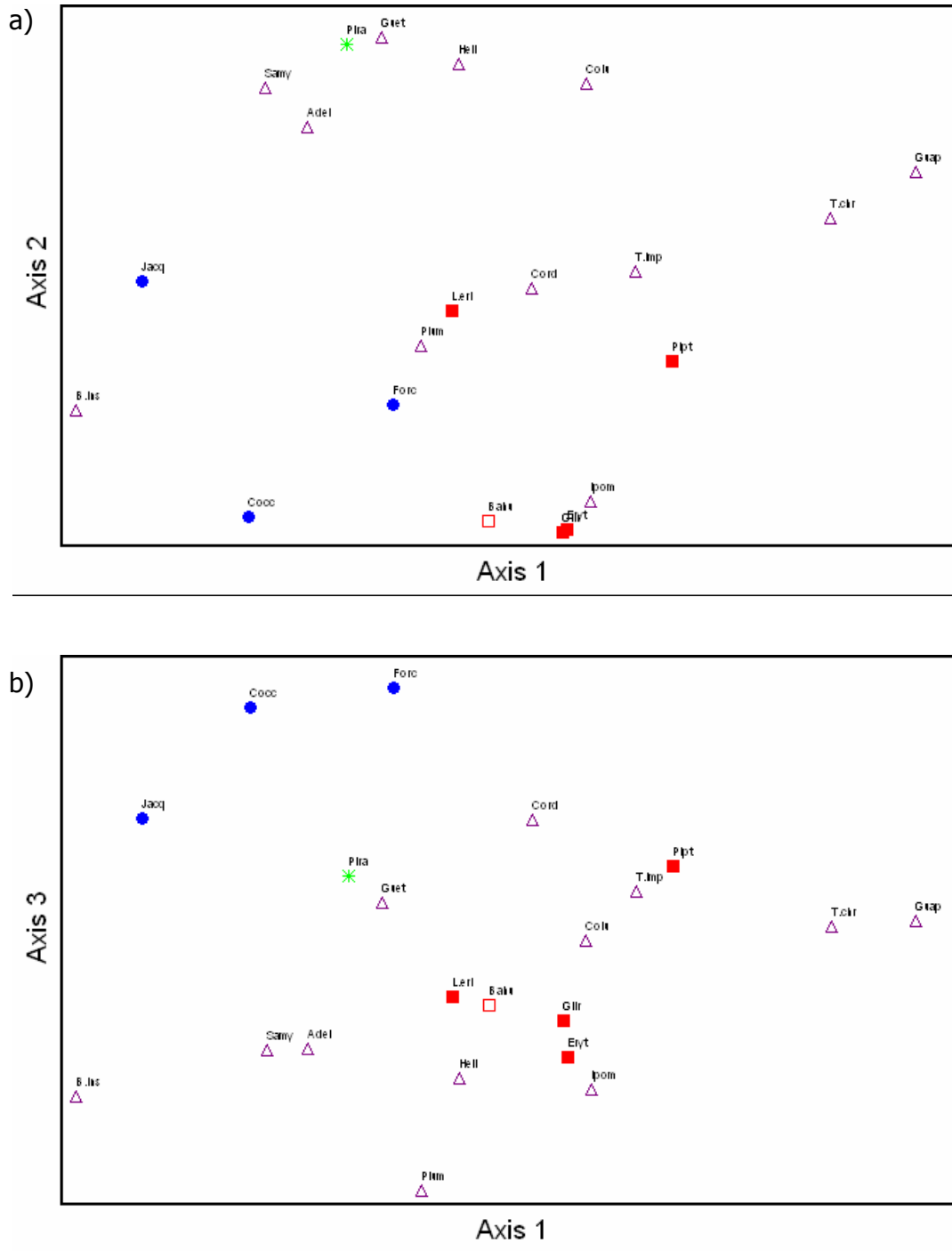
Figure 5. PCA Ordination results for five traits of 21 species of the tropical dry forest in Chamela, Jalisco, Mexico. Axes 1, 2, and 3 explained 43.9, 31, and 17.2% of the variation, respectively. Symbols indicate the four selected groups that could potentially show different biogeochemical properties. For the abbreviation of the species names see Table 1.

ORIGINAL ARTICLE

**Lyliana Y. Rentería · Víctor J. Jaramillo ·
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Nitrogen and phosphorus resorption in trees of a Mexican tropical dry forest

Abstract Resorption efficiency (RE) and proficiency, foliar nutrient concentrations, and relative soil nutrient availability were determined during 3 consecutive years in tree species growing under contrasting topographic positions (i.e., top vs. bottom and north vs. south aspect) in a tropical dry forest in Mexico. The sites differed in soil nutrient levels, soil water content, and potential radiation interception. Leaf mass per area ($g\ m^{-2}$) increased during the growing season in all species. Soil P availability and mean foliar P concentrations were generally higher at the bottom than at the top site during the 3 years of the study. Leaf N concentrations ranged from 45.4 to 31.4 mg g^{-1}. Leaf P varied from 2.3 to 1.8 mg g^{-1}. Mean N and P RE varied among species, occasionally between top and bottom sites, and were higher in the dry than in the wet years of study. Senesced-leaf nutrient concentrations (i.e., a measure of resorption proficiency) varied from 13.7 to 31.2 mg g^{-1} (N) and 0.4 to 3.3 mg g^{-1} (P) among the different species and were generally indicative of incomplete nutrient resorption. Phosphorus concentrations in senesced leaves were higher at the bottom than at the top site and decreased from the wettest to the the driest year. Soil N and P availability were significantly different in the north-

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and south-facing slopes, but neither nutrient concentrations of mature and senesced leaves nor RE differed between aspects. Our results suggest that water more than soil nutrient availability controls RE in the Chamela dry forest, while resorption proficiency may be interactively controlled by both nutrient and water availability.

Introduction

Nutrient resorption is the process by which nutrients are translocated from senescing leaves prior to abscission and stored into other plant tissues (Killingbeck 1986). This process makes a species less dependent on current nutrient uptake and is thus a major nutrient conservation mechanism, with important implications at both the population and the ecosystem levels. Foliar resorption can provide a substantial percentage of the nitrogen and phosphorus used annually by forests (Ryan and Bormann 1982). Nutrients that are not resorbed will be circulated through litterfall. Litter must be decomposed in the soil and its nutrients remineralized to become available again for plant uptake (Aerts and Chapin 2000).

It has often been suggested that species from low-nutrient habitats have higher nutrient resorption efficiencies (percentage of a nutrient withdrawn from mature leaves before abscission) than species from habitats with high nutrient availability (Aerts 1996). However, available evidence shows that nutrient resorption efficiency (RE) appears not to be very responsive to changes in nutrient supply and may not explain the distribution of species over habitats differing in soil fertility (Aerts and Chapin 2000). The lack of nutritional control on nutrient resorption raises the question of which other factors are involved (Aerts and Chapin 2000), and soil moisture availability is among several possible controls proposed (Boerner 1985; Del Arco et al. 1991; Escudero

et al. 1992; Pugnaire and Chapin 1993; Demars and Boerner 1997).

Resorption proficiency is a parameter describing the minimum level to which a nutrient is reduced during senescence, and has also been used to quantify nutrient resorption (Killingbeck 1996). Higher proficiencies correspond to lower final nutrient concentrations in senesced leaves. Resorption proficiency seems to be more responsive than RE to nutrient availability (Killingbeck 1996).

The importance of nutrient resorption as a demand-driven regulatory mechanism to match a plant's current growth rate and developmental stage is receiving increasing attention (Aerts and Chapin 2000). However, because of the emphasis on temperate deciduous forests, many of the recent generalizations are derived from temperate-biased data sets (e.g., see Aerts 1996; Killingbeck 1996). Until recently, only a few studies have been published on nutrient resorption in tropical forests. A negative (Vitousek 1998; Cordell et al. 2001) or lack of (Lal et al. 2001) correlation between RE and soil nutrient availability has been reported.

Although leaf nutrient concentration may reflect site fertility, the high interspecific variation found in growth rates causes tissue concentrations of wild plants to be less sensitive indicators of soil nutrient availability (Chapin 1980). Studies on the relationship between leaf nutrient concentration and nutrient availability in the tropics report conflicting results. In Hawaii, Harrington et al. (2001) found that foliar nutrients are controlled largely by nutrient supply. Austin and Vitousek (1998) also reported that a decline in soil P availability corresponded to a decrease in foliar P concentrations, but this was not so with N. In contrast, Lal et al. (2001) found no difference in mean foliar P between two sites with contrasting fertility in a dry tropical forest in India. The scarcity of information for tropical dry forest does not allow for an in depth analysis of the relationship between soil fertility and leaf nutrient status (Jaramillo and Sanford 1995).

In this paper, we report results of a field study in which we examine hypotheses relating soil nutrient availability to foliar nutrient concentrations and nutrient RE in a tropical dry forest ecosystem in western Mexico. We focused on the resorption of N and P, as these nutrients are the most important growth-limiting nutrients in many terrestrial ecosystems (Chapin 1980; Vitousek and Howarth 1991). The objectives of this study were: (1) to determine and compare foliar N and P concentrations and RE of tree species growing in contrasting topographic positions or slope aspects that differ in soil nutrient and water contents; (2) to determine if N and P resorption efficiencies and proficiencies were related to soil N and P availability, and (3) to determine whether foliar nutrient concentrations were related to nutrient RE. Our interest was to compare mature individuals of the same species growing in contrasting sites. We hypothesized that individuals of a given species growing in sites with lower soil nutrients or water (i.e., the top site of the watershed or the south-facing slope, respectively) would have lower foliar N and P concentrations but higher nutrient RE than those growing in more fertile or wetter sites (i.e., the bottom site of the watershed or the north-facing slope, respectively).

Materials and methods

Study area

The study was conducted at the Estación de Biología Chamela nature reserve (Universidad Nacional Autónoma de México) located on the Pacific coast of Jalisco, México (19°29′N, 105°01′W). The landscape is dominated by low hills with steep slopes (>20°). Mean annual precipitation is 746 mm (1983–2001; F. García-Oliva, unpublished data) mainly concentrated between July and November. The dominant vegetation type is a highly diverse tropical dry forest with trees 4–15 m tall, a well-developed understory of shrubs, and a strongly seasonal phenology (Lott et al. 1987). With few exceptions, the species have no leaves for several months during the dry season each year (Bullock and Solís-Magallanes 1990; Martínez-Yrízar and Sarukhán 1990). Lott (1985) reported 758 plant species from 107 families at the station, with the Leguminosae as the most important family with 15% of the species. Aboveground live biomass ranges from 70 to 85 Mg ha^{-1} (Martínez-Yrízar et al. 1992; Jaramillo et al. 2003) and belowground biomass from 17 to 31 Mg ha^{-1} (Castellanos et al. 1991; Jaramillo et al. 2003). Annual litterfall varies between 3.1 and 4.2 Mg ha^{-1} yr^{-1} (Martínez-Yrízar et al. 1996). The principal soil parent material is Cretaceous rhyolite (Campo et al. 2001). Soils are sandy clay-loams, poorly developed, classified in the USDA system as Typic Ustorthents and in the FAO system (1998) as Regosol (Cotler et al. 2002). Kaolinite is the dominant clay mineral (Campo et al. 2001) and the pH is 6.9 (García-Oliva et al. 1999).

Study site

The study was carried out in Watershed I, one of five contiguous small watersheds (12–28 ha) gauged for long-term ecosystem research (Sarukhán and Maass 1990). Three permanent plots were located along the watershed elevation gradient. The bottom of the watershed at 60 m a.s.l. has less potential solar radiation interception (SRI = 2,454 MJ m^{-2} year^{-2}; Galicia et al. 1999), greater soil water content (18.1 mm, Bouyoucos blocks; Galicia et al. 1999) and higher soil nutrient levels (extractable P = 28.2 ppm and total N = 2.3%, 0–20 cm depth; Martínez-Yrízar et al. 1996) than the upper part of the watershed at 160 m a.s.l. (SRI = 4,387 MJ m^{-2} year^{-2}; soil water content = 10.5 mm; extractable P = 8.8 ppm and total N = 1.3%). Plots with contrasting slope aspect in the middle position of the watershed have different SRI (north aspect slope at 100 m a.s.l., 3,651 MJ m^{-2} year^{-2}; south aspect slope at 120 m a.s.l., 4,478 MJ m^{-2} year^{-2}; Galicia et al. 1999) and soil water content (north-facing slope, 12.8 mm; south-facing slope, 10.8 mm; Galicia et al. 1999). The differences between the slopes are not as marked as between the bottom and top sites. To assess N and P foliar RE under contrasting conditions, we compared the top and bottom sites and the north- and south-facing slopes within the watershed.

Field methods

The study was conducted during the 1999, 2000, and 2001 growing seasons. Total annual precipitation was 1,131, 545, and 440 mm, respectively. The well above average precipitation in 1999 was due to two tropical summer storms that affected the region (data from the Sistema Meteorológico Nacional, Mexico). To compare soil nutrient availability, foliar nutrient concentrations, and RE between the top and bottom sites, four dominant species (A. Pérez-Jiménez, unpublished data) were chosen: two legume trees, *Lonchocarpus eriocarinalis* Micheli and *Piptadenia constricta* (Pers.) J. F. Macbr. and two non-legume trees, *Cordia alliodora* (Ruiz and Pav.) Oken (Boraginaceae) and *Guapira* cf. *macrocarpa* Miranda (Nyctaginaceae). To compare the north and the south-facing slopes, two dominant non-legume species were chosen: *Plumeria rubra* L. (Apocynaceae) and *Tabebuia impetiginosa* (Mart.) Standl [*T. palmeri* Rose] (Bignoniaceae). The species were chosen based on their availability at the contrasting sites since they have a heterogeneous distribution on the landscape. In April 1999, 3–8 available mature individuals of each species with comparable diameter at breast height (5–10 cm dbh) were selected and tagged. Fully expanded sun live leaves (5–15) were collected from the crown of each tree 1 month after the beginning of the rainy season (July–August). Attached senesced leaves (5–15, yellow and ready to drop) were collected at the onset of the dry season by gently shaking the branch to detach them (Killingbeck and Costigan 1988). Because leaf abscission does not occur simultaneously in all the species, the senesced leaves were collected in different months (November, December or January). Also, because of the high annual variation in the timing of leaf-fall, senesced leaves of *T. impetiginosa* were collected only during 2000 and 2001 and those of *Plumeria rubra* only in 2001.

Results from the 1999 and 2000 growing seasons indicated that leaf mass per area (LMA, g m^{-2}) was higher in senesced than in mature leaves. To determine if this was due to the sampling of senesced leaves belonging to different leaf cohorts, LMA estimates were obtained from leaves marked at the start of the 2001 growing season. Three individuals of four species (*L. eriocarinalis*, *Erythrina lanata* Rose subsp. *occidentalis* (Standl.) Krukoff and Barneby, *G. macrocarpa,* and *T. impetiginosa*) were chosen at the top and at the bottom sites. In July 2001, five sun-exposed terminal twigs or branches of each individual tree were marked. Ten fully expanded leaves within each of these branches were tagged. Five leaves of each individual (one leaf per branch) were collected monthly from August to December. After collection all leaves were placed between damp papers, stored in sealed plastic bags and measured on the day of sampling. *Cordia alliodora* and *Piptadenia constricta* were not included in this evaluation. All species will be referred to by their generic name hereafter.

Laboratory methods

looseness-1Single side surface area of all leaves without the petiole was measured with a Delta-T Image Analyzer, oven-dried at 70°C for 48 h, and weighed. All leaves from each individual tree were pooled after measurement. LMA was obtained by dividing the dry weight by the leaf area. Leaves were then ground in a Thomas Scientific mill to pass a 40-mesh screen. Total nitrogen and phosphorus were determined after acid digestion by a semi-Kjeldahl method. Samples were determined colorimetrically with an auto-analyzer (Bran-Luebbe Auto Analyzer III, Norderstedt, Germany; method No. 696-82W; Technicon Industrial System 1977).

Resorption calculation

Because LMA increased during the growing season in all species (see Results), RE was not calculated on a mass basis (Schlesinger et al. 1989). Species in which LMA increases as a result of the accumulation of carbon compounds with tissue age have lower nutrient concentrations in older leaves. This suggests an apparent resorption of foliar nutrients, when in fact there may be a slight or no change in content per unit leaf area. Thus, to estimate RE on a leaf area basis, element concentration was first converted to foliar content by multiplying LMA (g cm^{-2}) by concentration (mg g^{-1}) to yield content per unit area. Resorption (%) was calculated as the content of mature leaves minus that of senesced leaves, divided by content of mature leaves (Killingbeck and Costigan 1988). N and P concentrations in senesced leaves were used as a measure of resorption proficiency (Killingbeck 1996); lower final nutrient concentrations correspond to higher proficiencies, which are usually expressed as percentages.

Relative soil N and P availability

To establish the relationship among relative soil nutrient availability, foliar nutrient concentrations, and nutrient RE, we determined the relative soil N and P availability in all sites (topographic positions and slopes) using ion exchange resin bags during 2000 and 2001. The bags were made of nylon stocking and filled with 15 ml of anion resin and 15 ml of cation resin (IONAC C 251, H form). In 2000, three resin bags were buried at 3 cm depth beneath the canopy of individual trees of several species in May before the beginning of the rainy season and retrieved in December at the onset of the dry season. Fine root productivity and turnover are heavily concentrated in the first 5 cm of soil in this forest (Castellanos et al. 2001). The resin bags were placed 50–60 cm away from the trunk of each of five individuals of *Lonchocarpus* and *Guapira* at the top and bottom sites, and beneath five individuals of *Plumeria* and *Tabebuia* in the north- and south-facing slopes (i.e., a total of ten individuals of each species). Because variation among resin bags was high, four bags per tree in each of four individuals per species were used in 2001. Two

additional species (*Cordia* and *Piptadenia*) were included in the comparison between top and bottom sites that year. The retrieved resin bags were placed in plastic bags prior to analysis in the laboratory. Total inorganic available N (ammonium plus nitrate) and P (phosphate) were determined by 2 M KCl extraction and measured colorimetrically with an autoanalyzer (Bran-Luebbe Auto Analyzer III).

Statistical analyses

Data were analyzed using repeated measures analysis of variance (RMANOVA, von Ende 1993) with two between-subject factors (site and species) and one within-factor (year). Tukey's tests were used to compare years and species. A Student two-sample *t*-test was used to compare soil nutrient availability between sites. Computations were performed with SYSTAT 7.0 (SPSS, Chicago, IL). Huynh-Feldt and Greenhouse-Geiser corrections were estimated but they did not modify the significance of any *P* value. RE data were arcsine square-root transformed (Sokal and Rohlf 1995) prior to analysis to satisfy ANOVA assumptions. Nitrogen concentrations in senesced leaves did not require transformation but P data were log-transformed. All values are means with one standard error in their original scale of measurement.

Results

Seasonal variation of LMA in marked leaves

LMA of all species increased during the growing season in both bottom and top sites. The increment ranged from 25% to 47% (averaged over sites) and was primarily due to a decrease in leaf area during leaf senescence, rather than to changes in leaf weight, which remained almost constant. LMA of all species in both sites showed significant differences (*P*<0.005) between the first and the last dates. *Lonchocarpus* attained the greatest LMA prior to abscission (90.1±7.1 g m^{-2}) and *Erythrina* the lowest (34.8± 2.5 g m^{-2}).

Comparison between top and bottom sites

Relative soil N and P availability

Mean relative soil N availability at the top site was 39.2±3.1 and 48.7±3.8 μg N bag^{-1} at the bottom site. Mean relative soil P availability at the top site was 10.1±1.6 and 54.6± 4.2 μg P bag^{-1} at the bottom site. There were no clear differences in relative soil N availability between sites in any species, except for *Guapira*, which had a significantly higher relative soil N availability at the bottom than at the top site (Fig. 1a). In contrast, relative soil P availability in all species was significantly higher at the bottom than at the top site (Student's *t*-test, *P*<0.05; Fig. 1b).
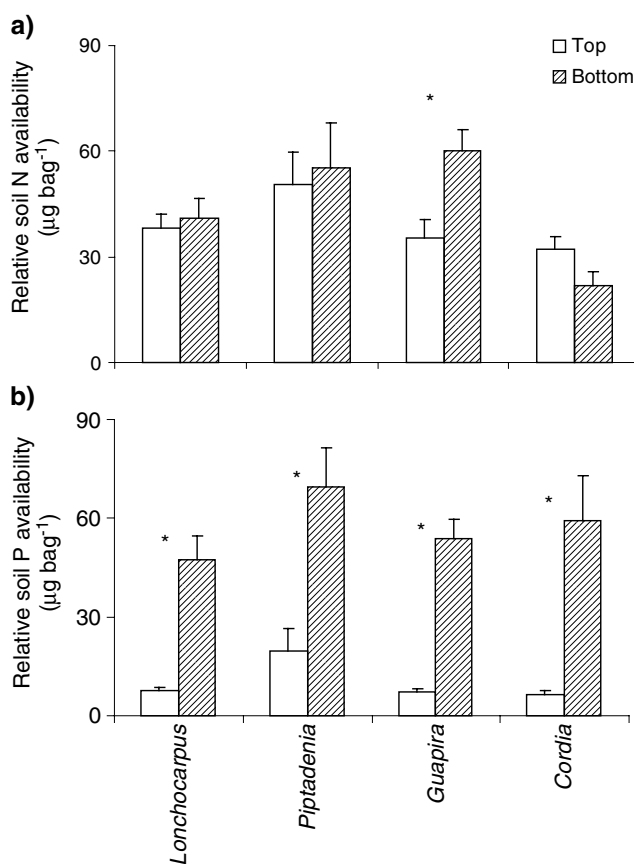
Fig. 1 Soil N (**a**) and P (**b**) availability (μ bag^{-1}) beneath the canopy of individuals of tree species at the top and bottom sites in the tropical dry forest of Chamela, Jalisco, Mexico. Values are means with one standard error. Significant differences between sites are indicated on the top of the *bars* (**P*<0.05). Individuals of *Guapira* and *Lonchocarpus* showed the same pattern during 2000 and 2001; therefore, values are the average from both years. Results for the other two species correspond to 2001, the driest year sampled. Total annual precipitation was 545 mm (2000) and 440 mm (2001)

Leaf mass per area

LMA of mature leaves (all years pooled) ranged from 51.8±1.0 to 77.9±3.2 g m^{-2} (Table 1). LMA in senesced leaves was higher than mature leaves in all the species with an increase of only 6% in *Piptadenia* and 58% in *Guapira*. The other species showed a mean 20% increment. LMA of both mature and senesced leaves of all species showed significant inter-annual variations (*P*<0.001; data not shown). There were no significant site effects (top vs. bottom; *P*>0.05) on LMA of mature and senesced leaves in either year.

Foliar N and P concentrations

Foliar N and P concentrations of mature leaves ranged from 12.4 to 66.0 mg g^{-1} and from 1.0 to 4.8 mg g^{-1}, respectively. Mean N and P concentrations (species and sites pooled) were not significantly different among sampling years (*P*=0.503). In general, there were no differences

Table 1 Leaf mass per area (*LMA*) of mature and senesced leaves of tree species in the tropical dry forest in Chamela, Jalisco, Mexico

Species	LMA (g m^{-2})	
	Mature	Senesced
Lonchocarpus eriocarinalis	77.9±3.0	97.7±3.2
Piptadenia constricta	75.0±3.2	80.2±6.5
Guapira macrocarpa	63.6±3.5	104.2±4.9
Cordia alliodora	63.9±2.4	84.9±4.0
Plumeria rubra	51.8±1.0	123.0±6.2
Tabebuia impetiginosa	57.7±2.0	62.5±3.2

Values are means of 3 sampling years (averaged over sites and slopes) with one standard error

in N concentrations within species when comparing topographic positions (Fig. 2a–c), except for *Cordia* in 2001, which showed higher N concentrations at the top than at the bottom site (*P*<0.05). Foliar P concentration (mean of all species and years) was higher at the bottom (2.5± 0.1 mg g^{-1}) than at the top site (1.8±0.1 mg g^{-1}; *P*=0.001). This site difference was significant (*P*<0.01) each year of the study. Within species, foliar P concentrations were also generally higher at the bottom than at the top site

(Fig. 2d–f) during the 3 sampling years. Except for one case (*Cordia* in 1999), the mean foliar N:P mass ratio was greater at the top than at the bottom site (*P*<0.001; Table 2).

Mean N concentrations in senesced leaves (averaged over species) did not generally differ between top and bottom sites (Table 3) and did not change significantly in wet and dry years (year comparison: *P*>0.10 for top site, but *P*=0.0148 for bottom site, where the 2000 mean was greater than the mean for 2001). Within-species comparisons showed few differences between sites and were not consistent during the 3 years of study. In contrast, mean P concentrations in senesced leaves (averaged over species) were lower at the top than at the bottom site during the 3 years of study (*P*<0.01). P concentrations decreased from the wet (1999) to the dry years at both sites (*P*<0.01; but 1999 and 2000 were not different at the bottom site), with the lowest mean concentrations occurring in 2001 at both sites (Table 3). Within-species comparisons indicated, except in a few cases, consistently lower P concentrations at the top than at the bottom site during the 3 years of study, and a general decrease in concentrations in all species from wet to dry years.

Fig. 2 Foliar N (**a–c**) and P (**d–f**) concentrations (mg g^{-1}) of mature leaves of tree species during 3 sampling years at the top and bottom sites in the tropical dry forest of Chamela, Jalisco, Mexico. Total annual precipitation was 1,131 mm (1999), 545 mm (2000), and 440 mm (2001). Values are means with one standard error. Significant differences between sites are indicated on the top of the *bars* (**P*<0.05)
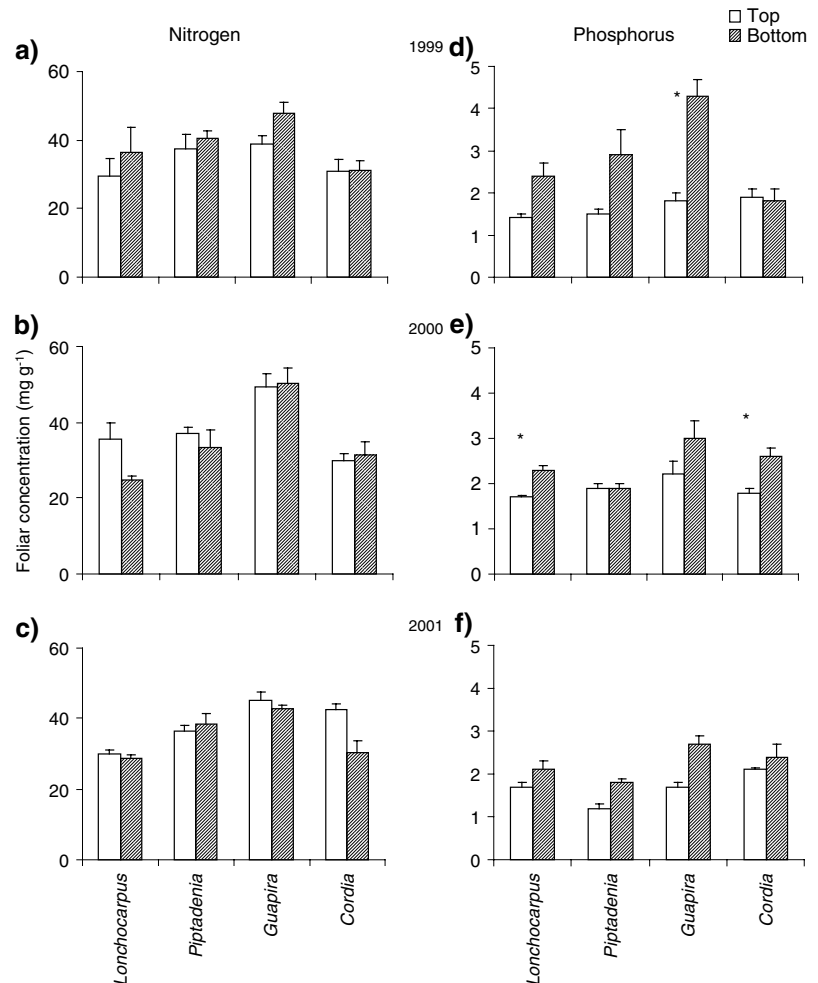
Table 2 Foliar N:P mass ratios of tree species at the top and bottom sites in the tropical dry forest, Chamela, Jalisco, Mexico

Year/species	Top	Bottom
1999 (1131 mm)		
Lonchocarpus	20.4±2.8	13.0±1.8
Piptadenia	25.1±3.3	17.3±3.5
Guapira	22.4±1.2	10.0±1.2
Cordia	16.6±3.1	17.1±4.8
Mean	**21.3±1.3**	**14.3±1.5**
2000 (545 mm)		
Lonchocarpus	21.2±2.3	11.3±0.6
Piptadenia	19.4±1.0	16.2±2.2
Guapira	23.6±2.4	15.3±1.9
Cordia	17.1±0.5	12.1±1.9
Mean	**20.7±1.1**	**14.0±1.0**
2001 (440 mm)		
Lonchocarpus	18.0±0.5	14.6±1.5
Piptadenia	30.2±1.3	21.3±1.9
Guapira	26.3±0.9	16.9±1.2
Cordia	20.1±0.6	13.7±2.4
Mean	**23.4±0.9**	**16.9±1.0**

The top site is drier and has lower soil nutrient levels than the bottom site (see Study site). Total annual precipitation is indicated in parentheses. Values are means with one standard error

N and P resorption efficiencies

Interspecific variation in RE was high. RE of N during the 3 years of study varied from 0% in *Guapira* to 52% in *Piptadenia*, while mean RE of P varied from 0%, also in *Guapira* to 60% in *Lonchocarpus*. Only in 2000 (except in *Guapira*) were RE values of N significantly higher at the top than at the bottom site (Fig. 3b). RE of P was also higher at the top site in *Lonchocarpus* and *Cordia* (Fig. 3e). In contrast, *Guapira* and *Cordia* (in 1999) and *Cordia* (in 2001) had higher RE of N at the bottom than at the top site ($P<0.05$, Fig. 3a and c). RE of N and P were not significantly correlated with foliar N or P concentrations. Interestingly, RE of N and P of both legume species (*Lonchocarpus* and *Piptadenia*) and *Cordia* at the bottom site increased during the dry 2001 when compared to the previous and also dry 2000. RE of both N and P in *Lonchocarpus* apparently increased from wet to dry years at the drier top site as well.

Comparison between north- and south-facing slopes

Relative soil N and P availability

Based on *Plumeria* and *Tabebuia* resin bags, there were no significant differences in relative soil N availability between the two slopes in 2000 (Fig. 4a). In contrast, the relative soil P availability in that year was greater in the south- (8.9±1.2 μg bag^{-1}) than in the north-facing slope (5.1±0.2 μg bag^{-1}; means for both species), although the difference was of only 1 μg bag^{-1} below *Tabebuia* (Fig. 4c). Opposite results were found in 2001, with no

Table 3 Foliar N and P concentrations of senesced leaves of tree species during the 3 sampling years at the top and bottom sites in the tropical dry forest, Chamela, Jalisco, México

	Top	Bottom	*P*-value
Nitrogen			
1999			
Lonchocarpus	19.8±1.5	25.5±1.8	**
Piptadenia	21.6±1.0	27.5±1.9	**
Guapira	24.5±1.4	24.1±1.5	NS
Cordia	19.1±1.8	13.7±1.4	*
Mean	**21.8±0.8**	**23.7±1.2**	NS
2000			
Lonchocarpus	16.4±0.7	25.6±2.4	***
Piptadenia	22.6±1.8	26.9±4.2	NS
Guapira	26.2±2.5	31.2±1.2	NS
Cordia	21.4±1.4	23.4±2.0	NS
Mean	**21.9±1.1**	**27.1±1.6**	**
2001			
Lonchocarpus	13.8±1.0	16.1±2.8	NS
Piptadenia	21.9±1.3	25.0±1.5	NS
Guapira	26.4±0.6	25.3±0.7	NS
Cordia	22.8±1.0	16.7±1.2	***
Mean	**20.8±1.0**	**21.4±1.1**	NS
Phosphorus			
1999			
Lonchocarpus	1.7±0.1	2.6± 0.1	***
Piptadenia	1.7±0.2	2.2± 0.1	NS
Guapira	2.3±0.4	3.3± 0.1	*
Cordia	1.4±0.3	2.6± 0.4	*
Mean	**1.9±0.2**	**2.7± 0.1**	***
2000			
Lonchocarpus	0.9±0.0	2.4±0.4	***
Piptadenia	1.3±0.2	1.7±0.1	NS
Guapira	1.2±0.0	2.3±0.1	***
Cordia	1.2±0.1	3.0±0.8	***
Mean	**1.2±0.1**	**2.2±0.2**	***
2001			
Lonchocarpus	0.4±0.1	0.9±0.3	*
Piptadenia	0.8±0.0	1.3±0.1	***
Guapira	0.9±0.0	2.3±0.3	***
Cordia	1.2±0.1	1.4±0.2	NS
Mean	**0.8±0.0**	**1.5±0.1**	***

The top site is drier and has lower soil nutrient levels than the bottom site (see Study site). Total annual precipitation was 1,131 mm (1999), 545 mm (2000), and 440 mm (2001). Values are means with one standard error. *$P<0.1$, **$P<0.05$, ***$P<0.01$, NS = not significant ($P>0.1$)

significant difference between slopes in soil P availability, but a higher relative soil N availability in the south- (43.1± 6.0 μg bag^{-1}) than in the north-facing slope (18.6 ± 4.9 μg bag^{-1}; Student's *t*-test, $P<0.05$, Fig. 4b and d).

Leaf mass per area

Mean LMA of mature leaves of *Plumeria* and *Tabebuia* was lower than in the other species (Table 1). LMA of senesced
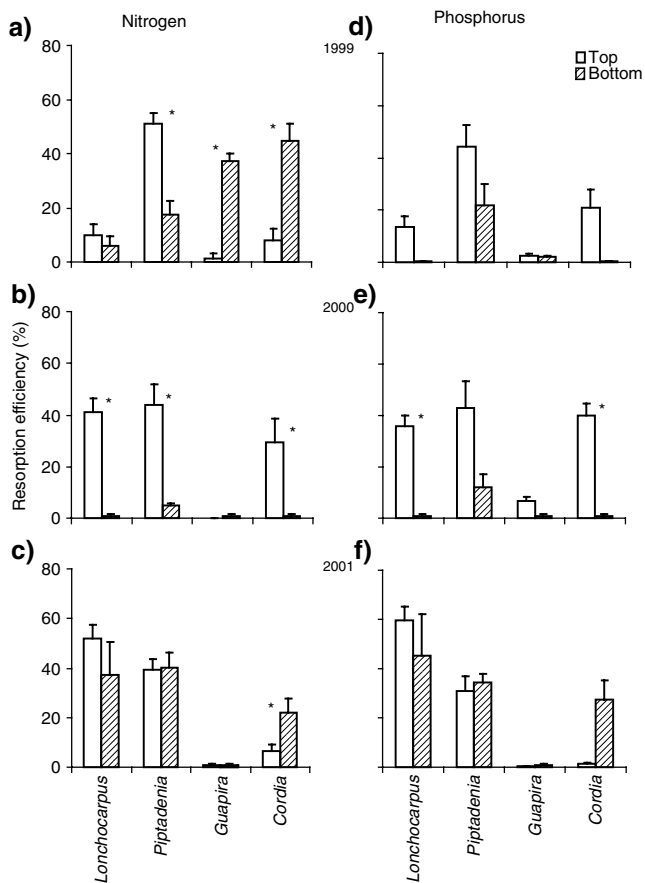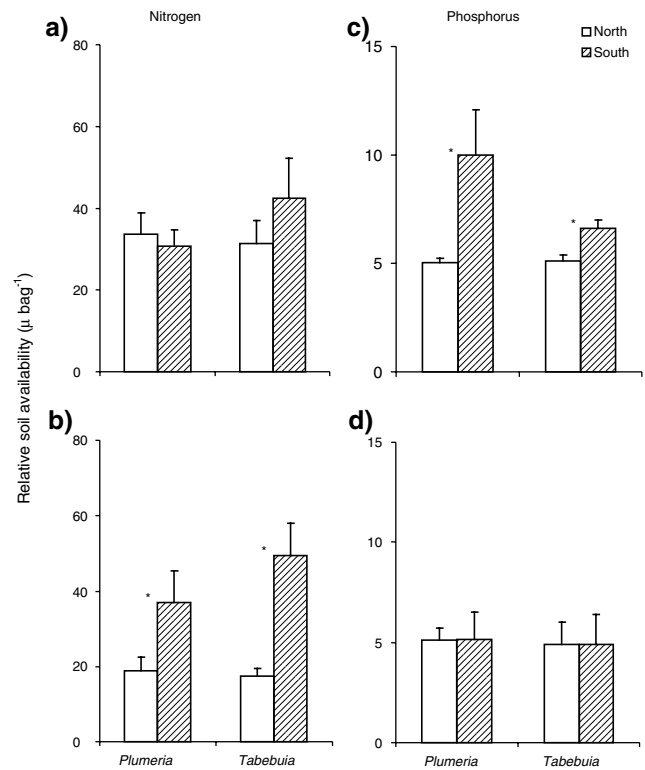
Fig. 3 N (**a–c**) and P (**d–f**) resorption efficiency (%) of tree species during 3 sampling years at the top and bottom sites in the tropical dry forest of Chamela, Jalisco, Mexico. Total annual precipitation was 1,131 mm (1999), 545 mm (2000), and 440 mm (2001). Values are means with one standard error. Significant differences between sites are indicated on the top of the *bars* (*$P<0.05$)

Fig. 4 Soil N (**a**, **b**) and P (**c**, **d**) availability (μ bag^{-1}) beneath the canopy of individuals of tree species during 2 sampling years in slopes with contrasting aspect in the tropical dry forest of Chamela, Jalisco, Mexico. Total annual precipitation was 545 mm (2000) and 440 mm (2001). Values are means with one standard error. Significant differences between sites are indicated on the top of the *bars* (*$P<0.05$)

leaves in these species was also higher than in mature leaves. LMA of mature leaves differed significantly among years ($P=0.001$; data not shown). The repeated measures analysis of variance did not show significant differences between slopes.

Foliar N and P concentrations

The differences in leaf N and P concentrations among the 3 years were significant ($P<0.001$), with the lowest N and the highest P concentrations in 1999 (Fig. 5a and b). There were no differences in mature leaf N concentrations between the two slopes in any of the species (Fig. 5a). Only *Plumeria* showed significantly higher leaf P concentrations in the north- than in the south-facing slope in 1999 and 2000 (Fig. 5b). In general, both species had similar leaf N and P concentrations. Foliar N:P mass ratios of *Plumeria* were higher on the south-facing slope in 1999 and 2000 ($P<0.05$), but *Tabebuia* did not show differences between slopes in any year (Table 4).

N and P concentrations of senesced leaves were 40–60% lower than in mature leaves. There were no signif-

icant differences ($P>0.05$) between slopes in N and P concentrations of senesced leaves of either species. *Plumeria* showed lower N and P concentrations in senesced leaves (13.9 ± 0.7 and 0.5 ± 0.0 mg g^{-1}, respectively) than *Tabebuia* (21.3 ± 0.6 and 1.09 ± 0.0 mg g^{-1}, respectively).

N and P resorption efficiencies

N and P resorption efficiencies in *Tabebuia* were similar among years (2000 and 2001; see field methods) and between slopes; mean values were $27.0\pm3.7\%$ and $31.7\pm3.8\%$, respectively. RE of N in *Plumeria* was higher in the south-($27.8\pm10.2\%$) than in the north-facing slope ($6.7\pm4.5\%$; $P=0.059$), and RE of P was also higher in the south-($56.1\pm6.\%7$) than in the north-facing slope ($20.1\pm7.4\%$; $P=0.005$).

Discussion

Nutrient resorption

The tree species in our study site showed low mean N and P resorption efficiencies: 22% of the N and 26% of the P
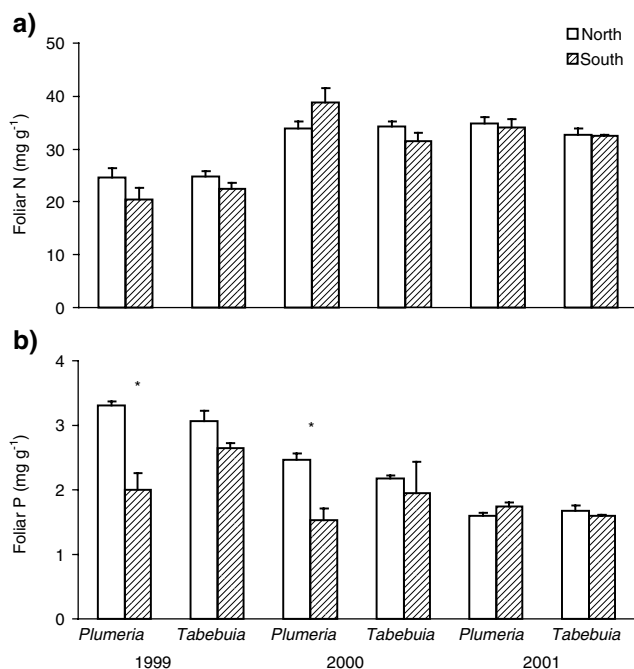
Fig. 5 Foliar N (**a**), and foliar P (**b**) concentrations (mg g^{-1}) of mature leaves of tree species during 3 sampling years in slopes with contrasting aspect in the tropical dry forest of Chamela, Jalisco, Mexico. Total annual precipitation was 1,131 mm (1999), 545 mm (2000), and 440 mm (2001). Values are means with one standard error. Significant differences between sites are indicated on the top of the*bars* (*$P<0.05$)

was resorbed from senescing leaves. These values are low compared to the average N and P resorption efficiencies (50%) found in a large literature survey (Aerts 1996), and are also lower than the 58% (N) and 50% (P) reported for a tropical dry forest in India (Lal et al. 2001) and the 65% (N) and 64% (P) documented for deciduous species in tropical dry forest in Venezuela (Medina 1984). More recently, Wright and Westoby (2003) reported a mean 34% proportional resorption of N (RE *sensu* Killingbeck 1996;

Table 4 Foliar N:P mass ratios of tree species in slopes with contrasting aspect in the tropical dry forest, Chamela, Jalisco, Mexico The south- is drier than the north-facing slope. Total annual precipitation is indicated in parentheses. Values are means with one standard error

Year/species	South	North
1999 (1131 mm)		
Plumeria	10.5±1.0	7.5±0.6
Tabebuia	8.5±0.2	8.1±0.3
Mean	**9.5±0.5**	**7.9±0.3**
2000 (545 mm)		
Plumeria	27.8±3.8	13.8±0.8
Tabebuia	19.5±4.7	15.7±0.4
Mean	**25.0±3.1**	**14.8±0.5**
2001 (440 mm)		
Plumeria	19.6±0.6	21.4±0.9
Tabebuia	20.3±0.3	19.5±0.4
Mean	**19.8±0.4**	**20.5±0.6**

range 4–66%) and a mean P resorption of 63% (range 25–89%) in 60 sclerophyllous species of Australia. The range of RE variation in our study of six dominant species was 0–52 and 0–60% for N and P, respectively.

Senesced-leaf N and P concentrations (i.e., a measure of resorption proficiency) in the Chamela species were high and indicative of incomplete nutrient resorption when compared to the values reported by (Killingbeck 1996; $N<0.7\%$ and $P<0.04\%$) for complete resorption. Exceptions to this were *Plumeria* and *Lonchocarpus* both with 0.4 mg g^{-1} (0.04%) in the south-facing slope and the top site, respectively, suggesting complete foliar P resorption in 2001. The overall mean N concentration (22.6 mg g^{-1} = 2.3%) in senesced leaves was higher and the P concentration (1.6 mg g^{-1} = 0.16%) similar to those reported for deciduous tropical dry forest species in India (Lal et al. 2001; 0.98 and 0.14, respectively). The high nutrient concentrations in senesced leaves of the species in our study were consistent with the high N and P concentrations in litterfall of the Chamela dry forest (Jaramillo and Sanford 1995; Díaz 1997; Campo 2001).

Resorption and soil nutrient availability

A repeated suggestion from early studies on nutrient resorption was that plants from nutrient-poor environments had a higher nutrient RE than those from nutrient-rich environments (Aerts and Chapin 2000). In our study, only during 2000, one of the years with rainfall below average (545 mm), RE of N was higher at the top than at the bottom site despite their similarity in soil N availability. Our results supported the hypothesis that P resorption efficiency was greater with lower soil P availability (top site) than with higher availability (bottom site), again only in 2000. This negative relationship between P resorption efficiency and soil P availability is consistent with results from a temperate forest in sites that differed in soil P availability (Boerner 1985; Kost and Boerner 1985). Nevertheless, our results mostly agree with those obtained from shrubs (Killingbeck and Costigan 1988; Minoletti and Boerner 1994), from species of a tropical dry forest (Lal et al. 2001), and from Mediterranean species (Knops and Koenig 1997), in which no relation was found between RE and nutrient availability. Wright and Westoby (2003) also reported that N and P resorption efficiencies of Australian sclerophyllous species did not differ under contrasting soil nutrient conditions.

If we used proficiency, a complementary measure of resorption based on senesced-leaf nutrient concentration (Killingbeck 1996), our results indicated that both N and P resorption proficiencies reflected relative soil nutrient availability. The overall between-site similarity in soil N availability was reflected in generally similar mean senesced-leaf N concentrations at the different topographic positions. On the other hand, P resorption proficiency was negatively correlated with relative soil P availability: individuals of a species growing at the bottom site with higher soil P had lower mean proficiencies (i.e., higher mean P concentrations) than those growing at the top site.

This result was consistent during the 3 years of study and is similar to findings reported by Wright and Westoby (2003) for sclerophyllous perennial species. They found that N and P concentrations in senesced leaves of plants occurring in nutrient poor soils were lower (i.e., had a higher resorption proficiency) than those of species growing on richer soils. In contrast, Lal et al. (2001) found no difference in senesced-leaf P concentrations of deciduous species between soils of different fertility in a tropical dry forest. Also, they found higher senesced-leaf N concentrations in the less fertile soil. On the other hand, Cordell et al. (2001) reported greater resorption proficiency of *Metrosideros polymorpha* in N-limited than in fertilized plots, but found no correlation with its ability to reduce P. Our results and those of Lal et al. (2001) support the argument concerning a lack of correlation in the species' ability to reduce both N and P simultaneously in leaves (Cordell et al. 2001).

Resorption and water availability

Estimates of RE in this study showed high annual variability. The highest mean REs for both N (26%) and P (25%) were recorded during 2001, one of the two dry years (440 mm). In the wet 1999 (1,131 mm), N and P resorption efficiencies were lower (19% and 11%, respectively). These results support Killingbeck (1996) concerning the need to assess RE for several years for a better description of the magnitude of foliar nutrient resorption. Results from a given year alone would have yielded different conclusions concerning the magnitude of RE in the Chamela dry forest. RE seems to vary in relation to a number of factors like soil water availability (Escudero et al. 1992), soil fertility (Stachurski and Zimka 1975), and plant nutrient status (Aerts 1996), among others. The annual differences found in our study suggest that N and P resorption efficiency at Chamela is a nutrient conservation mechanism that responds to water availability, the major functional control in this tropical dry forest. RE tends to be higher under drier conditions.

In contrast to RE, mean senesced-leaf N concentrations showed little inter-annual variability, whereas mean P concentrations decreased consistently from the wet 1999 to the dry 2001. This suggests that greater P conservation (i.e., higher proficiency) occurs with decreasing water availability in this forest. Changes in senesced-leaf N and P concentrations in response to changes in rainfall regimes have also been documented by Wright and Westoby (2003). In this case, however, perennial sclerophyllous species showed higher nutrient concentrations under drier conditions.

The increase in RE of both N and P at the bottom site, with higher P availability, during the dry 2001 (440 mm) in three of the four species when compared to the previous dry year (2000, 545 mm) may be related to the pattern of rainfall distribution during the growing season. Interestingly, precipitation at the end of the growing season in 2000 (September and October) was 268 mm but only 86 mm in 2001. This suggests that temporal variations in water availability during the rainy season may over-

ride differences in soil nutrients, especially P in our study, so that RE increased under drier conditions. Physiological responses of individual species undoubtedly mediate the effect of this water-nutrient interaction, as exemplified by *Guapira*. This species showed remarkably low RE and high N and P concentrations in senesced leaves (i.e., low resorption proficiency), regardless of changes in water or soil nutrient availability.

Seasonal differences in rainfall distribution also appeared to affect the species capacity to reduce P, but not N, in senesced leaves. The lowest P concentrations in senesced leaves of most species at the top and bottom sites were recorded in 2001. The lower precipitation at the end of the 2001 growing season apparently promoted P conservation regardless of relative differences in soil nutrient conditions. This suggests that water and nutrient availability interactively control nutrient resorption proficiency in this tropical dry forest.

Foliar N and P concentrations and soil nutrient availability

Leaf nutrient concentration, in some instances, reflects site fertility (Chapin 1980). In the present study, foliar P concentration was positively correlated with soil P availability. Species at the bottom site of the watershed with a higher relative soil P availability showed mean higher foliar P concentrations than individuals of the same species at the top site, where relative soil P availability was lower. This result is similar to the pattern observed in *M. polymorpha* in Hawaii (Austin and Vitousek 1998; Harrington et al. 2001) where foliar P concentrations reflected soil P availability. In contrast, Lal et al. (2001) reported no differences of deciduous species in foliar nutrient concentrations between two sites with different soil fertility in a tropical dry forest in India. Studies in temperate sites report conflicting results. Whereas Boerner (1984, 1985) and Del Arco et al. (1991) found that foliar P and soil P availability were positively correlated, Kost and Boerner (1985) and Minoletti and Boerner 1994 found no correlation. Despite the differences in foliar concentrations between our sites, there were no differences in relative soil N availability. This result contrasts with studies in temperate ecosystems where foliar N concentrations were high in sites with high N availability (Boerner 1985) and low in infertile sites (Kost and Boerner 1985; Minoletti and Boerner 1994). It is perhaps the nature of nutrient limitation at a particular site that determines the extent to which foliar N or P may or may not reflect changes in soil nutrient availability. Similar to the findings of Schlesinger et al. (1989), Aerts (1996), and Lal et al. (2001), mature leaf N and P concentrations in our species were not related to RE.

Koerselman and Meuleman (1996) proposed the use of the N:P mass ratio in plant tissues as an indicator of the type of nutrient limitation. They suggested that at N:P ratios >16, community biomass production was P-limited; at N:P ratios <14, plant growth was N-limited, and at N:P ratios between 14 and 16, co-limitation by N and P occurred.

Recently, the value to establish co-limitation by N and P was revised so that ratios lower than 14 may indicate such a condition (Güsewell et al. 2003). By these criteria, the mean N:P foliar ratio in our study (18) would suggest P limitation to biomass production at our study site. Available evidence suggests that soluble P pools in upper soil and litter plus mineralized P pools in soil at the onset of the rainy season may be large enough to compensate annual aboveground P return (Campo et al. 1998). Moreover, P fertilization of the tropical dry forest of Chamela did not increase litterfall production at the community level and species showed variable responses in trunk growth to fertilization (V.J. Jaramillo and J.M. Maass, unpublished data). Together, these results would suggest that this dry forest may not be limited by P availability. However, the N:P ratios at the top site during the 3 years of study (range 16.6–30.2) indicated that P limitation may occur at a local level. Furthermore, the consistently higher N:P ratio (averaged over species) at the top than at the bottom site reflected the site differences in foliar P concentrations and relative soil P availability. Such site differences in N:P ratios and their slight increase in the dry 2001 suggest nutrient limitation in this forest is mediated by water availability as well. This was also evident in the drier south-facing slope, where N:P ratios changed from N (9.5) to P (19.8–25) limitation from the wet to the dry years. Trees at the wetter sites (bottom site and north-aspect slope) showed N, P or co-limitation by N and P, with no discernible patterns, except that *Plumeria* and *Tabebuia* showed consistently higher N:P ratios in the drier than in the wet years.

Methodological considerations

Recently, Heerwaarden et al. (2003) proposed that current measures of nutrient RE lead to a substantial underestimation of the "real" RE due to changes in leaf area or leaf mass during senescence. They introduced a new parameter to correct for the effect of leaf shrinkage during senescence in area-based RE, the fractional change of measurement basis for leaf shrinkage ($FCMB_{area}$). Based on the marked leaves, the $FCMB_{area}$ estimates for our species vary from 0.24 to 0.34. We thus calculated the real RE (*sensu* Heerwaarden et al. 2003) for these species. The mean real RE of 45% for N and of 48% for P were higher than the uncorrected values. Importantly, a re-analysis of our resorption data indicated that the trends, differences, and similarities reported above (see Results) were still valid with the corrected values. However, ignoring the changes in leaf area during senescence may lead to a significant underestimation of the resorption process.

Conclusions

The general lack of correlation among N and P resorption efficiencies and soil nutrient availability, and between RE and foliar nutrient concentrations, together with the annual and between-site variations suggest that water controls RE more than soil nutrient availability in the Chamela dry forest. On the other hand, the relation between nutrient resorption proficiency (i.e., senesced-leaf nutrient concentrations) and soil nutrient availability, and the higher P proficiency observed with decreasing water availability suggest that resorption proficiency is interactively controlled by both nutrient and water availability.

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CONSIDERACIONES FINALES

El objetivo general de esta tesis fue explorar por primera vez para el bosque tropical seco de Chamela una definición de grupos funcionales de plantas que podrían tener efectos similares en procesos biogeoquímicos del ecosistema con base en atributos foliares y en un atributo ecofisiológico, la reabsorción de N y P. Como un objetivo particular se propuso estudiar los patrones de reabsorción de N y P y algunos atributos foliares, y su relación con la disponibilidad de nutrientes y agua.

Los resultados de la evaluación de los patrones de reabsorción mostraron un hallazgo que por una parte no debería ser sorprendente, dado que la dinámica de los bosques tropicales secos está dominada principalmente por la disponibilidad del agua. Sin embargo, se encontró que los patrones de reabsorción de N y P en Chamela estuvieron claramente relacionados con las diferencias en la precipitación total anual. La oportunidad que ocurrió al realizar la evaluación durante tres años consecutivos con marcadas diferencias en la precipitación total anual, permitió establecer un primer parámetro para la reabsorción de nutrientes en Chamela que indicó que la variabilidad anual de la precipitación, que puede estar influida por fenómenos meteorológicos, tiene un fuerte impacto sobre algunos procesos biogeoquímicos como la reabsorción de los nutrientes.

La medición de atributos foliares en individuos de 58 especies de árboles adultos creciendo en condiciones naturales de campo, no se había realizado con anterioridad en Chamela. Este trabajo realizado en el área de la cuencas experimentales, provee una extensa base datos sobre características foliares con implicaciones biogeoquímicas importantes para la evaluación del efecto de las especies en los procesos ecosistémicos. Esta primera aproximación en la determinación de grupos funcionales de plantas, indicó que existe una gran variación en los atributos foliares de las especies, la cual, se encuentra dentro del ámbito de variación de muchos otros ecosistemas iguales y diferentes a nivel global. Así mismo, la evaluación de características foliares clave cuyas correlaciones tienen implicaciones significativas a nivel global, permitió sugerir un modelo conceptual sobre las características que comparten las especies del bosque tropical seco de Chamela (Fig. 1). El modelo nos muestra como la similitud entre las características foliares evaluadas permitió

identificar grupos de especies que claramente impactarán de manera diferencial el ciclaje de los nutrientes. Dichas características de importancia biogeoquímica, tienen implicaciones sobre algunos procesos como la descomposición y la productividad primaria. Las concentraciones foliares de carbohidratos solubles, lignina y nitrógeno son indicadores de la calidad de la hojarasca, y pueden determinar las tasas de descomposición. El LMA indica el grosor de las hojas y está relacionado con la tasa fotosintética. La eficiencia de reabsorción de N y P es un atributo ecofisiológico relacionado con la conservación de los nutrientes que tiene implicaciones sobre la concentración final de nutrientes que tendrá la hojarasca.

El modelo propuesto sugiere, por ejemplo, que las leguminosas fijadoras de nitrógeno comparten atributos con cierto grado de variabilidad. Presentan baja concentración de carbohidratos solubles y altas concentraciones relativas de lignina y nitrógeno foliar. Así mismo, presentan hojas gruesas, presumiblemente con baja capacidad fotosintética, y alta eficiencia en la reabsorción de N y P foliar. El conjunto de estas características sugerirían que las leguminosas potencialmente fijadoras de N serían especies con hojarasca de baja calidad para la descomposición, relativamente poco productivas y con una buena capacidad de conservación de los nutrientes. A diferencia de estas especies, otras como las leguminosas no fijadoras y las deciduas de lluvias, también serían especies relativamente poco productivas y con buena eficiencia de reabsorción de N y P, pero con mayor calidad relativa de su hojarasca, en comparación con las leguminosas fijadoras. Por otra parte, las especies caducifolias no leguminosas, mostraron una gran variabilidad en sus atributos foliares. Algunas comparten características de las leguminosas fijadoras, pero otras se ubican con calidad intermedia de follaje para la descomposición, baja capacidad para conservar nutrientes pero con LMA que indicaría altas tasas fotosintéticas.

Este modelo, permite entender como la medición de atributos foliares en conjunto con una variable ecofisiológica como la reabsorción de N y P, en un importante número de especies representativas de un ecosistema, contribuyen a la definición de grupos de especies que comparten características que tiene implicaciones directas sobre la biogeoquímica del ecosistema. La aplicación del modelo en el bosque caducifolio de Chamela, provee una herramienta útil que proporciona información sobre el ciclaje de los nutrientes a nivel ecosistémico y permite generar hipótesis para nuevos proyectos de investigación. El conocimiento de atributos foliares y sus implicaciones biogeoquímicas en grupos de especies podrían también aplicarse en programas de restauración y manejo de ecosistemas. Por ejemplo, en el caso de un

esquema de restauración en donde se desea mantener las funciones ecosistémicas es necesario la introducción de especies leguminosas en la etapa inicial que provean el N necesario para promover el establecimientos y crecimiento de especies posteriormente (Walker, 1993) ya que la trayectoria de la restauración en el largo plazo está fuertemente influenciada por la composición inicial de especies. Así mismo, la tasa de descomposición al inicio de la es cerca de cero o nula debido a la falta de materia orgánica, por lo se podría pensar que la introducción de especies con alta calidad química en su hojarasca (Chapin, *et al*. 2002). Es así que especies leguminosas como *Piptadenia constricta, Lonchocarpus eriocarinalis, Glricidia sepium* y *Eritrina lanata* serían importantes en un programa de restauración. Además especies de alta calidad química en la hojarasca como *Jacaratia maxicana, Trichilia trifolia, Tohuinia paucidentata, Plumeria rubra, Bursera instabilis*, entre otras, podrían asegurar una importante acumulación de materia orgánica. Y por último especies con baja eficiencia de reabsorción (que aseguren la entrada de nutrientes al suelo vía hojarasca) como *Cordia alliodora, Guettarda elliptica, Guapira macrocarpa y Helietta lottiae*, pero sin olvidar que la variación anual en la reabsorción mostro variaciones importantes, así que cualquier programa de restauración deberá considerar que la disponibilidad de agua (en función de la precipitación total anual) influirá sobre la trayectoria del programa. Además a este respecto, Burgos y Maass (2004) presentaron recientemente un modelo conceptual sobre la dinámica de la vegetación post-disturbio en Chamela el cual también puede ser utilizado para hacer recomendaciones en términos de restauración y conservación del ecosistema.

Por otra parte, los atributos foliares clave que son de fácil medición, pueden proveer una útil base para el desarrollo de modelos regionales y ecosistémicos. Sin embargo, el estudio adicional de experimentos de descomposición y evaluación de la capacidad fotosintética a nivel específico, serán necesarios para validar algunos aspectos del modelo que en primera instancia parecen ambiguos y/o contradictorios.

La evidencia presentada en este trabajo representa un importante paso en el conocimiento de la biogeoquímica de los bosques tropicales caducifolios. Su aplicación en ecosistemas similares dependerá de si las correlaciones entre las variables foliares se mantienen, pero provee una base para el diseño de proyectos que planteen la evaluación de este tipo de características foliares.
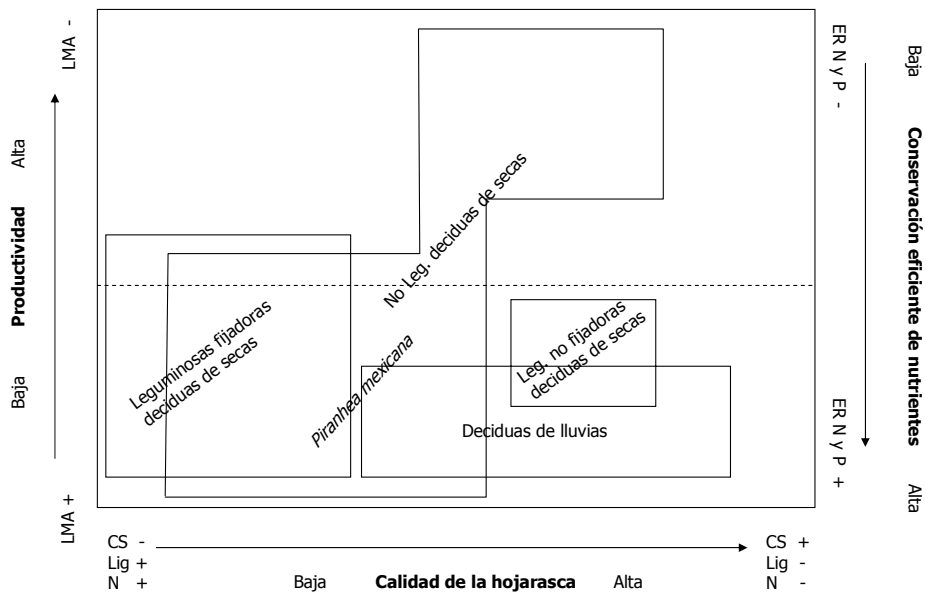
Fig. 1 Modelo conceptual que muestra la distribución de las especies del bosque tropical seco de Chamela en relación con las características foliares de interés biogeoquímico. Se indican la calidad de la hojarasca en función de las concentraciones foliares de carbohidratos solubles (CS), lignina (Lig) y nitrógeno (N). Se indica a la masa foliar específica (LMA) como un indicador de la productividad dada su relación inversa con la capacidad fotosintética de las plantas. La línea punteada indica la separación entre las especies de mayor y menor capacidad de conservación de nutrientes indicada por la eficiencia de reabsorción de N y P.

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