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**Diversidad y almacenes de carbono y nitrógeno en bosques tropicales caducifolios secundarios de la región de Chamela, Jalisco, con diferentes historias de uso**

# T E S I S

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me apoyaron y me amaron,

A la abue porque la quiero mucho,

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# INDICE

# RESUMEN

El bosque tropical caducifolio es considerado por muchos autores como uno de los ecosistemas con mayor presión antropogénica. Su conversión a cultivos o praderas ha ocasionado entre otras cosas, la pérdida de la diversidad, la pérdida de biomasa y con ella la liberación de carbono y nutrientes, lo cual, tiene efectos tanto a escalas locales como globales. La estructura y el funcionamiento de este ecosistema, en la región de Chamela (México) se han estudiado por casi 30 años. También se han evaluado los efectos inmediatos de su transformación por roza-tumba y quema a cultivos y praderas, pero se desconocen los efectos de transformaciones más severas (maquinaria) y/o la respuesta de la vegetación a largo plazo a éstos y otros tipos de uso. Para comenzar a abordar estos aspectos de la regeneración del bosque tropical caducifolio, se seleccionaron seis bosques secundarios que crecieron en sitios desmontados con maquinaria 30 años atrás y que fueron objeto de diferentes usos previos al abandono: a) desarrollo para vivienda (HD), b) praderas para ganadería (P), y c) sin uso posterior al disturbio (NU).

En la primera parte del estudio se comparó la diversidad y la estructura vegetal entre los tres tipos de uso, teniendo como premisa que las dos variables seguirían el patrón P < HD < NU. Para ello, se establecieron 10 parcelas de 40 x 2.5 m, que cubrieron 0.1 ha en cada uno de los sitios. En ellas se midieron e identificaron hasta especie todos los individuos de más de 1 cm de diámetro a la altura del pecho y mínimo 2 m de altura, y se clasificaron en cuatro categorías diamétricas: 1–3, 3,1–5, 5,1–10, y >10 cm. La densidad total de árboles varió de 2575 a 4745 individuos ha$^{-1}$ y el área basal total varió de 12.5 a 14.6 m$^2$ ha$^{-1}$. Se identificaron 87 especies vegetales, siendo LEGUMINOSAE la familia dominante en número de individuos y riqueza de especies. De éstas, la especie no nativa *Mimosa arenosa* (wild) Poir. var. Leiocarpa Barneby fue la más abundante, representando entre el 42 y 52% del área basal total en cada tipo de uso. Las principales diferencias entre los tipos de uso se dieron en los individuos de 1-3 cm de DAP, que correspondieron al 47% del total de los árboles registrados. Los sitios NU mostraron una mayor densidad, área basal y riqueza en esta categoría diamétrica que los sitios P y HD. En los sitios NU, además, no se registraron individuos de *M. arenosa* en la categoría 1-3 cm, pero sí de especies propias del bosque, lo que sugiere que esta especie está siendo reemplazada. Los resultados de este capítulo sugieren que las diferencias encontradas están fuertemente relacionadas con el uso actual del que son objeto estos bosques, y que las especies de bosque primario son reclutadas diferencialmente en un proceso que ocurre en escalas de décadas.

En la segunda parte del estudio se compararon la biomasa y los almacenes de carbono y nitrógeno, así como los potenciales de mineralización neta de nitrógeno entre los tres tipos de uso. Al igual que en la primera parte del estudio, la premisa fue que tanto la biomasa como los almacenes seguirían el patrón P < HD < NU. La biomasa de árboles se obtuvo a partir del área basal, utilizando las ecuaciones alométricas de Martínez-Yrízar et al. (1992). Además, se obtuvo la biomasa de plántulas y del mantillo en microparcelas (25 x 25 cm). La biomasa del

material leñoso muerto caído fue estimada usando la técnica del intercepto planar. La biomasa de raíces se cuantificó únicamente en los sitios NU para evaluar el potencial de recuperación del sistema radicular, en trincheras de 2 x 0.5 x 0.4 m. Se estimaron los almacenes de carbono y nitrógeno en cada uno de estos compartimientos y, en el suelo, colectando muestras compuestas sistemáticamente hasta una profundidad de 60 cm. El potencial de mineralización se estimó a una profundidad de 0 -10 cm, mediante incubaciones anaerobias por 15 días.

La biomasa total aérea varió de 40 a 50 Mg/ha y la de raíces de 10 a 13 Mg/ha. El almacén total de carbono en el ecosistema fue de 81.4 MgC/ha y el de nitrógeno fue de 6.6 Mg/ha. Ninguna de estas cuatro variables difirió significativamente entre las historias de uso. La biomasa y los almacenes de carbono y nitrógeno en árboles de 1-3 cm de DAP y la biomasa muerta total y sus almacenes de carbono y nitrógeno fueron mayores en NU que en P y HD. No se registraron diferencias en los almacenes de nitrógeno inorgánico ni en los potenciales de mineralización y nitrificación entre los tipos de uso. La biomasa total (aérea y raíces) y los almacenes escosistémicos de C y N de estos bosques secundarios representan el 48%, 59% y 85% de la biomasa total y de los almacenes ecosistémicos de C y N, respectivamente, de los bosques primarios de la región de Chamela. Este estudio representa la primera cuantificación del almacén ecosistémico (biomasa aérea y subterránea y perfil del suelo) de C y N en bosques tropicales caducifolios secundarios de la región de Chamela, y representan el potencial de recuperación del bosque caducifolio en la zona, luego de ser objeto de transformación con maquinaria y de historias de uso diferentes.

El conjunto de resultados de este estudio indica que las posibles diferencias en la sucesión secundaria debidas a los efectos a corto plazo de los diferentes tipos de uso han desaparecido después de casi 30 años de sucesión. Aunque se esperaba que el tipo de uso tuviera un impacto a largo plazo en las variables estudiadas no se encontraron grandes diferencias entre los tipos de uso, excepto para aquellos casos en los que los resultados reflejaron, aparentemente, el uso reciente de estos bosques. Pero al comparar los valores de los bosques secundarios con los del bosque primario se encontró que, 30 años han sido aparentemente suficientes para que el almacén de N del suelo y un porcentaje muy alto del almacén de C alcancen los valores cercanos a los del bosque primario. No así para las demás variables estudiadas. Los resultados también indican, en contraste con la aparente estabilidad de las comunidades dominadas por *Mimosa* según Ortiz (2001), que la regeneración con especies del bosque primario es un proceso activo en estos bosques.

# ABSTRACT

Tropical dry forest is considered one of the most endangered ecosystems by anthropogenic pressure. Its conversion to crops or pastures has caused diversity and biomass loss, and carbon and nutrients release with effects on both local and global scales. The structure and function of this ecosystem type in the Chamela Region (Mexico) have been under study for almost 30 years. The immediate effects slash-and-burn of the tropical dry forest have also been evaluated, but the effects of disturbance by heavy machinery and the long-term vegetation response to these and other land uses have not yet been evaluated. To address these aspects of tropical dry forest regeneration, we selected six secondary forests that grew on sites felled with machinery 30 years ago and were subjected to different pre-abandonment land uses: a) housing development (HD), b ) pasture for livestock grazing (P), and c) no use (NU).

In the first chapter we compared diversity and vegetation structure by establishing modified Gentry plots (40 x 2 m) covering 0.1 ha at each site. We measured and identified to species all individuals ≥ 1 cm diameter at breast height (DBH )and at least 2 m high. They were classified into four diameter classes: 1-3, 3,1-5, 5,1-10, and > 10 cm. Total tree density ranged from 2,575 to 4,745 individuals ha$^{-1}$ and total basal area ranged from 12.5 to 14.6 m$^2$ ha$^{-1}$. We identified 87 species total. The Leguminosae was the dominant plant family both in terms of number of individuals and species richness. Of these, the non-native species *Mimosa arenosa* (wild) Poir. var. Leiocarpa Barneby was the most important, representing 42 to 52% of the total basal area in each land-use type. The main differences between land-use types occurred in the1-3 cm DBH size-class, which accounted for 47% of the total number of trees. NU sites showed higher density, basal area, and richness than P and HD in this size-class. In addition, there were no individuals of *M. arenosa* 1-3 cm DBH in NU sites, but primary forest species were present, suggesting that this species is being replaced. Overall, the results suggest that species of primary forest are differentially recruited in a process that occurs on decadal scales, strongly associated to the current use experienced by these forests.

In the second chapter we compared biomass and carbon and nitrogen pools, as well as potential net nitrogen mineralization. Tree biomass was estimated from basal area data with the allometric equations of Martínez-Yrízar et al. (1992). In addition, seedling and litter biomass were obtained from 25 x 25 cm microplots. Downed woody debris was estimated with the planar-intercept method. Root biomass was quantified in the NU sites by digging trenches (2 X 0.5 m) to a 40 cm depth. We estimated carbon and nitrogen pools in each of these vegetation compartments, and in the soil, by collecting composite samples to a 60 cm depth.

Soil potential net nitrogen mineralization was estimated at a depth of 0-10 cm, by anaerobic incubations for 15 days.

Total aboveground biomass varied from 40 to 50 Mg/ha and root biomass from 10 to 13 Mg/ha. Total ecosystem pools were 81.4 MgC/ha and 6.6 Mg N ha$^{-1}$. None of these four totals differed significantly among the land-use types. Biomass and carbon and nitrogen pools in trees 1-3 cm DBH, as well as total dead biomass, and its carbon and nitrogen pools were higher in the NU land-use type than in P and HD. There were no differences in inorganic nitrogen pools or in potential net nitrogen mineralization and nitrification among land-use types. Total biomass (above and belowground) and ecosystem C and N pools of these secondary forests represented 48%, 59%, and 85%, respectively, of the total biomass and ecosystem C and N pools of primary forests in the Chamela region. This study is the first to quantify ecosystem C and N pools (above- and belowground biomass and soil) in secondary tropical dry forests in the Chamela region and represents the recovery potential for tropical dry forest in the area when it is subjected to transformation by heavy machinery and to different land uses.

Together, the results from this study indicated that any differences in secondary succession due to the short-term effects of the different land uses have disappeared after nearly 30 years of succession. Although, we expected a long-term effect on the variables measured, we found no significant differences among land-use types, except for cases in which the results apparently reflected the impact of recent use. When we compared results for secondary forests with those from the primary forest, we found that 30 years have been apparently sufficient for soil N, and to a high degree soil C, to achieve values similar to those in primary forest. This was not so for other variables. The results also showed that regeneration of primary forest species is an active process in these secondary forests, but to different degrees in the land-use types, in contrast to the apparent stability in communities dominated by *Mimosa* suggested by Ortiz (2001).

# Capítulo I
## Introducción general

# INTRODUCCIÓN GENERAL

El disturbio es una fuerza, agente o proceso biótico o abiótico que causa una perturbación (respuesta) en un componente ecológico o sistema, con relación a un sistema o estado de referencia, definido por características específicas (Rykiel, 1985). Chapin *et al.* (2002) lo definen como un evento relativamente discreto en el tiempo y en el espacio que altera la estructura de las poblaciones, las comunidades y los ecosistemas y causa cambios en la disponibilidad de los recursos o en el ambiente físico. El disturbio puede ser de origen natural como los huracanes, inundaciones o incendios, y de origen antrópico, derivado de las actividades humanas como la agricultura, la ganadería y la explotación de recursos forestales (Chazdon, 2003). Aunque los disturbios antropogénicos varían en los diferentes tipos de bosques y las zonas culturales del mundo, los efectos asociados a la transformación de los mismos siguen un patrón "general": causan, a tasas aceleradas, la alteración tanto de la estructura y la composición de la vegetación (Uhl *et al.*, 1982), como de los almacenes y la dinámica de los nutrimentos (Currie y Nadelhoffer, 2002), a escalas locales, regionales y globales. Una vez que la vegetación ha sido removida, muchos de estos nutrimentos se pierden del ecosistema por la deforestación, la combustión, la lixiviación y la erosión (Jaramillo *et al.*, 2003; Hughes *et al.*, 2000). De igual forma, el disturbio antropogénico ocasiona el aumento en las emisiones de $CO_2$ (Kauffman y Uhl, 1990) y de la emisión de otros gases de efecto invernadero, con efectos negativos para la biodiversidad y pérdidas en la productividad de los bosques (Murphy y Lugo, 1995). Igualmente, provoca la pérdida de fertilidad del suelo (Aweto, 1981; Toky y Ramakrischnan, 1981; Adedeji, 1984; Srivastava y Singh, 1989; Tiessen *et al.*, 1992) y la pérdida misma de suelo (Maass, 1995).

El proceso de sucesión secundaria de los ecosistemas depende del régimen de disturbio (severidad, intensidad, frecuencia, tipo y tamaño), de los mecanismos de regeneración y la disponibilidad de microhábitats para el establecimiento, y de nutrientes para el crecimiento (Uhl, 1987). Los mecanismos que determinan la sucesión secundaria son la dispersión de semillas de fuentes cercanas, el banco

de semillas, el banco de plántulas y el rebrote (Lieberman y Mingguang, 1992; Rico-Gray y García-Franco, 1992; Gerhardt, 1993; Miller y Kauffman, 1998a; Guariguata y Ostertag, 2001; Kennard *et al.*, 2002a), mientras que los procesos que la determinan, son la facilitación, las interacciones competitivas, la herbivoría y la variación estocástica del ambiente (Chapin *et al.*, 2002). Todos estos procesos que ocurren durante la sucesión originan comunidades vegetales con características estructurales y funcionales propias, que en el caso de los ecosistemas dominados por árboles se denominan bosques secundarios (Currie y Nadelhoffer, 2002). Los bosques secundarios son toda vegetación leñosa de carácter sucesional que se desarrolla sobre tierras cuya vegetación original fue destruida por actividades humanas (Smith *et al.*, 1997). Brown y Lugo (1990b) sugieren que los bosques secundarios se están convirtiendo en el tipo de cobertura vegetal más común en las regiones tropicales del planeta. También señalan que la sucesión secundaria es un proceso integral del desarrollo de los ecosistemas después de los disturbios naturales, pero que son los disturbios antrópicos los que han potenciado el aumento de este tipo de coberturas. Los bosques secundarios son importantes debido a que además del incremento de su área, tienen también el potencial de proveer muchos de los productos y servicios que normalmente se obtienen del bosque primario (Caamal y del Amo, 1987; Brown y Lugo, 1990a). Estudiar los bosques secundarios permite evaluar los efectos pasados y presentes de los disturbios producidos por las actividades humanas sobre la estructura y el funcionamiento de los ecosistemas (Brown y Lugo, 1990a; Currie y Nadelhoffer, 2002).

El tipo de cambio de uso del suelo más común en las zonas tropicales es la roza-tumba-quema. Éste tiene efectos directos sobre la estructura del bosque ya que generalmente se elimina el total de la vegetación presente por lo que hay una reducción drástica de la diversidad vegetal. Por ejemplo, Rzedowski (1978) y Burgos y Maass (2004) reportan que en la región de Chamela, el uso continuo de la roza tumba-quema para el mantenimiento de praderas, a largo plazo genera la pérdida de diversidad vegetal nativa y el establecimiento de matorrales espinosos cerrados. Además, se ha encontrado para el bosque estacional seco que este tipo de uso prolongado permite la colonización de espices exóticas

(Romero-Duque *et al.*, 2007; Molina y Lugo, 2006; Burgos y Maass, 2004; González-Iturbe *et al.*, 2002). Por otro lado, la roza-tumba-quema genera una reducción de la biomasa y los almacenes de nutrientes. Por ejemplo, en el bosque tropical húmedo la biomasa varía de 143 a 1174 Mg/ha, mientras que en praderas originadas a partir de estos bosques la biomasa varía de 53 a 119 Mg/ha (Hughes *et al.*, 2000 and referencias citadas). Para el caso del bosque tropical seco, la biomasa varía de 28 a 268 Mg/ha (Martínez-Yrízar, 1995), pero debido a la escasez de trabajos en esta área no se tiene un ámbito claro de la variación de la biomasa de las praderas originadas a partir de estos bosques. Estudios aislados como el de la región de Chamela, en la costa pacífica de Jalisco, México, sitúan la pérdida de biomasa en hasta un 82% (Jaramillo *et al.*, 2003). Otros estudios indican que los cambios en los almacenes ecosistémicos de nutrimentos debidos al cambio de uso de suelo se deben en su mayoría a estas pérdidas de biomasa, e indican que los almacenes del suelo son afectados en mucho menor grado (Hughes *et al.*, 2000; Kauffman *et al.*, 1993; Kauffman *et al.*, 1995; Trumbore *et al.*, 1995; Trumbore *et al.*, 1996). Al respecto, Murty *et al.* (2002) señalan que se pueden encontrar variaciones en el carbono del suelo de -50% hasta +160%, cuando se transforma el bosque a pradera, lo que sugiere que el tipo de uso del suelo determina la magnitud de la afectación de los almacenes de nutrimentos en el mismo. Este aspecto ha sido muy poco estudiado en los bosques tropicales secos de México.

De manera general, tanto los bosques tropicales húmedos (Gómez-Pompa *et al.*, 1976) como los bosques tropicales secos (Trejo y Dirzo, 2000) "cesan", en mayor o menor grado, su regeneración bajo sistemas de uso intensivo y extensivo. Así, en los sitios donde se remueve la vegetación y/o se realizan quemas suaves, las especies que dominan son las preexistentes (banco de semillas, banco de plántulas y rebrote), mientras que en los sitios donde se practica una remoción más severa (p.ej. con maquinaria), o se realizan quemas intensas, dominan las especies que llegan por dispersión (Kennard *et al.*, 2002a). A este respecto, Uhl *et al.* (1981) señalan que, en los bosques tropicales secos, las primeras especies leñosas que colonizan después de un disturbio, provienen, usualmente, de semillas que sobrevivieron a la quema o de semillas nuevas depositadas por el viento o

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por la dispersión de animales. Su establecimiento depende de la disponibilidad de agua, a diferencia de los bosques tropicales húmedos donde el establecimiento depende de la disponibilidad de luz (Durán *et al.*, 2002). Esta situación limita la sucesión temprana del bosque tropical seco, debido a las condiciones adeversas reinantes en este tipo de ecosistemas para el establecimiento de plántulas (Lieberman y Mingguang, 1992) y se exacerba cuando no hay fuentes de semillas cercanas.

Guariguata y Ostertag (2001) señalan que los trabajos publicados sobre la sucesión secundaria en el Neotrópico, la describen desde una perspectiva estructural, haciendo mayor énfasis en cuáles especies o grupos de especies dominan cada estado de la sucesión. Pero existe poca información desde la perspectiva funcional y mucho menos se han estudiado de manera conjunta las características funcionales y estructurales durante la sucesión. Los mismos autores señalan que los ecosistemas pueden recuperar más rápido las características funcionales que la composición florística existentes previas al disturbio. Además, durante la sucesión secundaria hay cambios en los patrones de asignación de biomasa de las plantas. En los estados sucesionales tempranos, la biomasa es principalmente asignada para la producción de hojas y raíces finas, mientras que en estados tardíos, la biomasa es asignada, en su mayoría, a la producción de material estructural y de soporte, como tallos leñosos y raíces gruesas (Guariguata y Ostertag, 2001).

En los bosques secundarios originados por actividades humanas, la cantidad de nutrimentos es generalmente mayor en el suelo que en la vegetación, por lo que el suelo provee un capital importante de nutrientes para la sucesión (Brown y Lugo, 1990a). Con la sucesión se acumula la biomasa aérea, aumenta consecuentemente la entrada de materia orgánica al suelo y con ella la de nutrimentos. Existen estudios que registran estos incrementos con el tiempo (Lamb, 1980; Williams-Linera, 1983; Werner, 1984; Silver *et al.*, 1996), pero otros que registran disminuciones (Uhl y Jordan, 1984). Por ejemplo, Harcombe (1980) en su revisión con respecto a la relación fertilidad del suelo – sucesión, indica que la vegetación es más o menos independiente de los nutrimentos del suelo en un

amplio intervalo de disponibilidad. El autor sugiere que la pérdida de nutrimentos como consecuencia del disturbio no afecta la sucesión.

La falta de patrones claros, especialmente en aspectos funcionales durante la sucesión de los bosques tropicales se debe, entre otras cosas, a diferencias en el efecto que la historia de uso tiene sobre la regeneración y a las características propias del ecosistema. Pero además, a la escasa investigación que existe sobre estos temas, epecialmente en el bosque tropical seco. Por esto es difícil señalar con qué éxito o a través de cuáles rutas ecológicas, el bosque tropical seco, puede regenerarse en áreas previamente clareadas.

Los bosques tropicales secos *sensu* Holdridge (1987) constituyen el ecosistema tropical más ampliamente distribuido y extenso del planeta. Cerca del 42% de toda la franja intratropical es bosque seco y el 49% de la vegetación de América Central y el Caribe es considerada bosque seco (Murphy y Lugo, 1995). Sin embargo, este ecosistema ha sufrido una gran presión antropogénica, hasta el punto de haber desaparecido de algunas regiones de Centro y Sur América (Janzen, 1983, 1988; Mares *et al.*, 1985). Globalmente, se estima que el 97% del área actual remanente de bosque tropical seco está en riesgo por una variedad de amenazas como resultado de las actividades humanas (Miles et al., 2006). El patrón de conversión del bosque tropical seco depende de las condiciones locales como la topografía, el tipo de suelo, la longitud de la estación seca, la existencia o no de conocimiento tradicional, las posibilidades económicas de los propietarios, el tipo de tenencia de la tierra y las políticas económicas y poblacionales de la zona (Maass, 1995). La magnitud, tanto temporal como espacial de la conversión, también varía. Thapa y Weber (1990), clasifican a los responsables de la deforestación en tres grupos generales: los cultivadores transitorios, los cuales son responsables del 45% de la pérdida de estos bosques, los ganaderos con poder económico que desmontan grandes áreas y los gobiernos de los países, que mediante políticas redistribuyen la tierra y determinan su uso.

Trejo y Dirzo (2000) reportan que de los bosques tropicales de México, los bosques tropicales secos cubren el 60%. Mencionan también que a comienzos de los años 90, sólo el 27% del área potencial de distribución del bosque tropical seco de México permanecía inalterada y que la tasa de deforestación era de 1.4%

anual. En la actualidad, se desconoce la tasa de transformación del bosque seco en el occidente de México, pero De Ita-Martínez (1983) reporta para la región de Chamela, localizada en la costa del estado de Jalisco, que el 3.8% del bosque tropical seco es convertido anualmente a agricultura, praderas y otros usos. Esto es particularmente alarmante dado que los bosques secos del occidente de México son los de mayor riqueza de especies y de endemismos, tanto de especies como de géneros, entre los bosques secos del Neotrópico (Gentry, 1995). La conservación de este ecosistema, así como la recuperación de algunas áreas, son necesarias para el mantenimiento de las funciones ecológicas y de su diversidad biológica. Sin embargo, para alcanzar estos objetivos es imperativo estudiar el patrón y la intensidad del disturbio, así como también la respuesta del bosque tropical seco al disturbio tanto a corto como a largo plazo, para generar alternativas viables de manejo y de restauración.

Aunque, como se mencionó anteriormente, los patrones y la magnitud de la transformación dependen de las condiciones locales, en la región de Chamela, la tendencia general es la remoción total de la vegetación mediante el sistema de roza-tumba-quema y la posterior introducción de pastos, en su mayoría de origen africano (Maass, 1995). Sin embargo, durante el período presidencial de Luis Echeverría, en México se estableció el Programa Nacional de Desmontes, en el cual, "*no se requería autorización para realizar los desmontes y se hacían los trabajos con maquinaria pesada y en caso de requerir utilizar la madera se levantaba un acta de existencias y se otorgaba documentación forestal de transporte, sólo para especies comerciales, el resto de la madera se apilaba y se quemaba*" (Limón, 2007). En la región de Chamela este programa fue aplicado mediante la tumba con maquinaria (bulldozer) y los terrenos tuvieron diferentes usos, entre ellos, el establecimiento de praderas y la construcción de conjuntos residenciales. En la región de Chamela no se ha realizado estudio alguno que evalúe los efectos a corto plazo de distrubios severos como el desmonte con maquinaria sobre la estructura y el funcionamiento del bosque tropical seco; y en ninguno de los dos casos (transformación tradicional o severa con maquinaria) se conoce con detalle lo que ocurre con la estructura y el funcionamiento del ecosistema una vez que la presión antropogénica se reduce o cesa y se produce

la sucesión secundaria. Tampoco se conoce en qué magnitud estas variables estructurales y funcionales de los bosques secundarios difieren de las de los bosques primarios.

Dada esta carencia de información, importante para entender el proceso de regeneración del bosque tropical seco, desde un punto de vista ecosistémico, se propone como objetivo general de este trabajo analizar aspectos estructurales y funcionales clave del bosque tropical seco secundario de la región de Chamela, Jalisco, México, en sitios cuyo bosque primario fue eliminado de la misma forma, pero que difieren en su historia de uso y abandono. Este objetivo permite abordar la sucesión secundaria en un marco temporal de décadas, enmarcado en la problemática general del cambio de uso del suelo del trópico seco en Latinoamérica. Para abordar este objetivo general, el proyecto incluye dos objetivos específicos:

1. Comparar la estructura y la diversidad de la vegetación de bosques secundarios con diferentes historias de uso.

2. Comparar los almacenes de carbono y nitrógeno y las tasas potenciales de mineralización de nitrógeno en el suelo de bosques secundarios con diferentes historias de uso.

Se espera que la información derivada de estos objetivos específicos provea elementos para determinar el impacto de la invasión de especies leñosas en el reestablecimiento de las propiedades estructurales y funcionales del ecosistema, para compararlas con las del bosque primario y de las praderas de la región.

Para cumplir con estos objetivos, se seleccionaron 6 sitios de estudio en la región de Chamela, en la costa Pacífica de Jalisco. De acuerdo con los residentes y/o propietarios, estos sitios estuvieron cubiertos de bosque tropical seco primario y comparten características similares. El bosque primario fue clareado con buldózer y quemado hace 30 años aproximadamente. Todos los bosques tienen tiempos similares de abandono (24 – 27 años), elevación (40 – 70 msnm), pendiente (cuatro sitios con 15%, uno con 25% y otro con 35%), y exposición (sur), pero tuvieron diferentes historias de uso:

1. Desarrollo residencial (HD): estos sitios fueron desmontados y quemados para desarrollar un proyecto residencial, durante el cual se construyeron

calles y banquetas que delimitan las cuadras donde se establecerían las residencias. El proyecto falló y los sitios fueron abandonados. La vegetación secundaria creció dentro de los terrenos originalmente designados para construir las viviendas. Desde entonces, estas áreas han sido objeto esporádicamente de corta selectiva y de pastoreo.

2. Praderas (P): estos sitios fueron desmontados y quemados para establecer áreas de pastoreo para el ganado. Allí se sembraron los pastos africanos *Panicum maximum* Jacq. (Zacate Guinea) y *Pennisetum ciliare* L. (Zacate Buffel). Este uso duró 6 años aproximadamente y desde entonces han sido objeto esporádicamente de corta selectiva y pastoreo.

3. No uso (NU): estos sitios fueron desmontados y quemados para tomar posesión de los terrenos y fueron abandonaos. En 1993 fueron incluidos dentro de las 13000 hectáreas de la Reserva de la Biosfera Chamela-Cuixmala. Dado que no fueron objeto de uso posterior al desmonte, son considerados como los de menor intensidad de uso.

La información generada hasta ahora del bosque tropical seco de la región de Chamela, hace referencia a la estructura y el funcionamiento del bosque primario y a los efectos inmediatos y mediatos de la transformación por roza-tumba y quema, y del establecimiento y uso de praderas. Estos estudios indican, por ejemplo, una disminución de 62 y 80% de la biomasa total aérea en diferentes tratamientos de intensidad de fuego (Kauffman *et al.* 2003). Jaramillo *et al.* (2003) encontraron una reducción de la biomasa aérea de individuos vivos de 60 a 15 Mg/ha y de la biomasa total aérea de 94 a 22 Mg/ha, debido a la transformación del bosque tropical seco primario a praderas. El almacén total aéreo de nitrógeno de las praderas correspondió al 17% del registrado en los bosques primarios (940 kg ha$^{-1}$; Jaramillo *et al.* 2003). Por otro lado, Castellanos *et al.* (2001) encontraron que la biomasa de raíces finas se redujo un 47% en los primeros 2 cm y 74% en los primeros 10 cm del perfil del suelo, debido a la roza-tumba-quema. La transformación del bosque tropical seco a pradera ocasiona también un aumento significativo en el contenido de nitrógeno inorgánico y del pH del suelo (García-Oliva y Maass, 1998) y una disminución de las tasas de mineralización

neta de nitrógeno (Ellingson et al., 2000). Sin embargo, se desconoce como y en que magnitud estas variables funcionales se recuperan durante la sucesión en estos bosques. Se sabe que la regeneracion de estos bosques luego de disturbios como la roza, tumba y quema, el uso como praderas y su abandono, ocurre con el establecimiento de la leguminosa no nativa *Mimosa arenosa* (Willd.) Poir. var. *leiocarpa* (DC.) Barneby (Ortiz, 2001), que forma bosques secundarios. Pero no existe información adicional sobre la estructura y diviersidad de los mismos, ni tampoco se ha evaluado el efecto a largo plazo de la historia de uso sobre ellos.

Dado que el rebrote es la principal respuesta de los bosques tropicales secos al disturbio, luego de éste y sin ningún tipo de manejo, no se deberían esperar cambios importantes en su composición florística durante la sucesión. Sin embargo, muchos estudios han demostrado que la frecuencia del rebrote disminuye con el incremento en la severidad del disturbio. Por ejemplo, Uhl *et al.* (1982), Kauffman (1991), Miller y Kauffman (1998b) encontraron que en los bosques tropicales secos el rebrote fue menos común después de fuegos intensos y repetitivos. Los fuegos intensos pueden disminuir el rebrote por la muerte del sistema radicular, lo que disminuye la reserva de carbohidratos para su crecimiento (Kauffman, 1991; Sampaio, 1995; Kennard *et al.*, 2002). Además, el disturbio que involucra la remoción de tallos y raíces (eliminando la regeneración vegetativa, típica del bosque tropical seco), puede, en el largo plazo, permitir sucesiones secundarias permanentes, disminuyendo la diversidad biótica en estos sitios (Hammond, 1995).

Con base en lo anterior, de manera general se espera que los sitios no sujetos a uso luego del desmonte con maquinaria, presenten un bosque más estructurado, más diverso, con mayor biomasa y almacenes de carbono y nitrógeno que aquellos sitios donde si se desarrollaron otros usos posteriores al desmonte.

La tesis consta de cuatro capítulos. El primero corresponde a esta Introducción general y los dos siguientes corresponden a cada uno de los objetivos específicos del trabajo de investigación. El segundo capítulo se titula "Structure and diversity of secondary tropical dry forests in Mexico, differing in their pior land-use history" y fue publicado en la revista Forest Ecology and

Management en el 2007. El tercer capítulo se titula: "Biomass, nutrient pools, and nitrogen mineralization in secondary tropical dry forests of Mexico, differing in their prior land-use history", que será sometido a publicación próximamente. El último es una sección donde se presentan algunas consideracines finales en el marco de la regeneración del bosque tropical seco.

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# Capítulo II

**Structure and diversity of secondary tropical dry forests in Mexico, differing in their prior land-use history**

*Diversidad y estructura de bosques tropicales secos secundarios de México que difieren en sus historia de uso.*

# Structure and diversity of secondary tropical dry forests in Mexico, differing in their prior land-use history

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Abstract

We compared the structure and diversity of secondary tropical dry forests, growing in sites cleared by bulldozer 30 years ago and subjected to different land uses prior to abandonment: (a) housing development (HD), (b) pasture (P), and (c) no use (NU). We sampled two forest sites representing each of the three former land-use types (i.e., a total of six sites) and measured the diameter at breast height (dbh) of all stems with dbh ≥1 cm and at least 2 m in height. All individuals were identified to species and classified into each of four dbh sizes-classes: 1 – 3, 3 – 5, 5 – 10, and ≥10 cm. No major differences in structure or diversity were evident among land-use types. Total tree densities varied from 2575 ± 55 to 4745 ± 985 individuals/ha and total basal areas ranged from 12.5 ± 2.6 to 14.6 ± 0.3 $m^2$/ha (mean and S.E.). Neither one differed significantly ($p < 0.05$) among land-use types. Overall, the most abundant tree size-class was the 1 – 3 cm dbh (47% of the total number of trees), whereas trees greater than 10 cm dbh were the least abundant (4%). We found significantly higher density and basal area ($p = 0.01$) in NU than in HD and P only in the smallest trees (1 – 3 cm dbh). We identified a total of 87 species in 28 families. The Leguminosae plant family had the greatest species richness and number of individuals in all land-use types. The HD land-use type showed lower total species richness than P and NU only with two of the four nonparametric estimators. Observed species richness decreased as dbh increased in all land-use types. At least 5 legumes were among the 10 most dominant species in all land-use types, of which the non-native *Mimosa arenosa* was the most dominant one. It represented between 42% and 52% of the total basal area in each land-use type. The secondary forests have reached, on average, 74% and 22% of the total density and basal area, respectively, of an average primary tropical dry forest of Mexico. The high number of individuals 1 – 3 cm dbh (48% of the total and 83% of the species) suggest that regeneration is occurring in all land-use types, although to different degrees. The absence of small individuals of *M. arenosa* and a high abundance of primary forest species at NU, suggest that *M. arenosa* is being replaced at these sites.

*Keywords*: Chamela; Disturbance; Heavy machinery; Mimosa arenosa; Regeneration

Introduction

Tropical dry forest (TDF) has been subjected to widespread alteration because human habitation and agricultural activities have developed in a large portion of its distribution (Maass, 1995; Murphy and Lugo, 1995). Such anthropogenic pressure has triggered a number of studies on ecosystem recovery after disturbance by agriculture (Donfack *et al.*, 1995; Maass, 1995; Miller and Kauffman, 1998a,b), grazing (Gerhardt, 1993; Aide *et al.*, 1995), fire (Sampaio *et al.*, 1993), and tree plantations (Mizrahi *et al.*, 1997). More recently, attention has been given to long-term (i.e. decadal) vegetation successional responses to natural or anthropogenic disturbances like slash-and-burn, grazing, and agriculture (e.g. Guariguata and

Ostertag, 2001; Kennard, 2002; Lawrence and Foster, 2002; Pereira *et al.*, 2003; Ruiz *et al.*, 2005). Some studies have shown that TDF more quickly recovers basal area and biomass than species composition after agriculture and/or grazing (Guariguata and Ostertag, 2001; Lawrence and Foster, 2002; Pereira *et al.*, 2003). Less attention has been given to vegetation responses to more severe anthropogenic disturbances like housing developments (e.g., Molina and Lugo, 2006), in which disturbance occurs with the use of heavy machinery to fell forests. The use of bulldozers generally causes diminution of soil porosity, water infiltration, soil moisture availability, aeration and rooting space, and can have substantial effects on soil fertility (Pinard *et al.*, 2000; Page-Dumroese *et al.*, 2006). It can also reduce soil physical quality, increase erosion, and can result in nutrient and organic matter loss (Zabowski *et al.*, 1994; Kozlowski, 1999; Pinard *et al.*, 2000). Site modifications produced by bulldozer use can substantially retard forest recovery (Guariguata and Dupuy, 1997).

Tropical dry forest is one of the most extensive and important tropical vegetation types in Mexico where it forms a nearly continuous strip on the Pacific coast, with major areas in western Jalisco and in the Balsas and Santiago river basins (Rzedowski, 1978; Challenger, 1998). It is also present in the Yucatan Peninsula in discontinuous forest patches. About 73% of the TDF area in Mexico shows, from light degradation up to total alteration of structure and function (Trejo and Dirzo, 2000), the latter associated to management. Such management commonly involves conversion to pasture and agricultural land (Challenger, 1998), by the use of machinery in the plains and through slash-and-burn in the hilly landscapes. Abandonment of unproductive lands promotes a landscape mosaic in which thorny plant communities and secondary forests, associated with the loss of native components, persist in the mid- and possibly the long-term (Rzedowski, 1978; Burgos and Maass, 2004). Thus, studies have recently focused on secondary forests in different regions of Mexico, such as the Yucatan Peninsula (Lawrence and Foster, 2002) and the state of Morelos (Saynes *et al.*, 2005).

Studies on TDF management through slash-and-burn in the Chamela region of Jalisco have reported abundant legume tree seedlings belonging to the Acacia and Mimosa genera 2 years after disturbance (Miller and Kauffman, 1998a,b). They suggested several conditions could explain this, including the low site aptitude for

native tree establishment and the absence of re-sprouting at high fire intensity. In addition, Ortiz (2001) reported *Mimosa arenosa* (wild) Poir. var. Leiocarpa Barneby, a non-native species, as the most dominant species in secondary forest sites in this region and suggested succession was arrested at these sites. To date, no attention has been given to long-term vegetation responses to severe anthropogenic disturbances after land abandonment in this region, despite that primary forest in Chamela is more species-rich than other dry forests in the Neotropics (Gentry, 1995). It remains an open question the degree to which species richness and forest structure recover after disturbance in this highly diverse tropical dry forest.

The Mexican government promoted the clearing of TDF by bulldozer during the 1970's along the Pacific coast of Jalisco. These areas were used for agriculture, cattle ranching, and for tourism and housing. Later abandonment of some of these sites allowed secondary vegetation to develop and provide an excellent opportunity to evaluate the regeneration of TDF. Thus, the overall objective of this study was to compare vegetation structure and diversity of secondary tropical dry forest sites, originally cleared by bulldozer, and subjected to different land-use practices prior to abandonment: (1) no use, (2) pasture, and (3) housing development. We expected higher diversity, density, and basal area in sites not subjected to land use after disturbance.

2. Study area description

The study was conducted in the Chamela region, on the Pacific coast of Jalisco, Mexico. The climate is highly seasonal with a pronounced dry season. Precipitation averages 746 mm (1983 – 2004), distributed mostly from June to October; on average annually, about 31% of the total annual precipitation falls in September (García-Oliva *et al.*, 1995, 2002). Mean temperature is approximately 25 °C, with a less than 5 °C difference between the coolest and warmest months. The landscape consists of low hills (50 – 160 m elevation) with steep convex slopes. Upland soils are relatively young, shallow (0.5 – 1 m depth) Typic Ustorthents. They are poorly structured, sandy loam in texture, derived from rhyolite, and have a pH of 6 – 6.5 (Solís, 1993). The flora of the Chamela region is comprised of at least 1149 vascular plant species, in 572 genera, and 125 families (Lott, 1993). The plant families with the

greatest species richness are Leguminosae, Euphorbiaceae, Rubiaceae, and Bignoniaceae, and more than 10% of the species are endemic to the states of Jalisco and Colima, Mexico.

3. Methods

After extensive road surveying of the area and interviewing local residents and site owners, we selected six secondary vegetation sites that, according to their accounts, had been originally covered by primary dry forest. These sites were subjected to different land uses but shared some features. The primary forest was cleared by bulldozer and burned approximately 30 years ago. All secondary forest sites had similar time since disturbance (24 – 27 years), elevation (40 – 70 masl), slope (15 – 35%), and aspect (south-facing slope), but had different land uses. These uses were: (a) housing development, (b) pasture, and (c) no use. Housing development (HD) sites were cut and burned for a construction project. The project failed and the sites were abandoned. Before abandonment, some streets were built with machinery and a secondary forest developed on the land originally designated to build houses. Since then, these sites have been subjected to sporadic selective cutting and cattle grazing. They were located in the Ejido San Mateo, 1 km away from the San Mateo village and approximately 10 km North of the Chamela Biological Station of the Instituto de Biología, UNAM (19º30′N, 105º03′W, Fig. 1). At the pasture sites (P), primary forest was cut and burned and the sites were seeded with the tropical forage grasses *Panicum maximum* Jacq. (Guinea grass) and *Pennisetum ciliare* L. (Buffel grass) for cattle production. These sites were grazed by cattle for 6 years and abandoned. They have been subjected to sporadic selective cutting and grazing since then. These sites were located near Quémaro village, approximately 20 km N of the Biological Station. The sites designated as no use (NU) were cut and burned to justify possession of the land and were abandoned. In 1993, these sites were included within the 13000 ha Biosphere Reserve of Chamela-Cuixmala (19º24′N, 104º58′W), 11 km S of the Station. Unlike the HD and P sites, the NU land-use type did not involve management after primary TDF was felled; therefore, we consider these sites as having a lower intensity of disturbance than the other land-use types. The secondary forests will be identified subsequently in the text by the abbreviation of their prior land use (HD, P, and NU).

We sampled two forest sites representing each of the three former land-use types (i.e., a total of six sites). We established ten 40 m x 2.5 m transects (0.1 ha), at least 7.5 m apart from each other, at each site. We measured the diameter at breast height (dbh) of all stems with dbh ≥ 1 cm and at least 2 m in height in each transect. All individuals were identified to species and classified into each of four dbh sizes-classes: 1 – 3 cm, 3 – 5 cm, 5 – 10 cm, and >10 cm. This dbh classification aided to evaluate successional trends at the sites. The data from all transects per site were used to calculate absolute and relative density (ind/ha) and basal area ($m^2$/ha), species richness, species similarity, and dominance. The importance value (IV) was calculated as: relative abundance + relative frequency + relative basal area for each species, where abundance was the number of individuals of the species at each site. Maximum IV was 300%.

We used nonparametric methods provided by Colwell's EstimateS program to approach true species richness. We used three estimators of species richness, as suggested for woody regenerating communities in secondary rain forests by Chazdon *et al.* (1998): incidence-based coverage (ICE) and Chao 2 estimators based on presence–absence of species and the abundance-based coverage estimator (ACE). For a complete description of these estimators see Chao and Lee (1992), Colwell and Coddington (1994), Chazdon *et al.* (1998), Gotelli and Colwell (2001). To compare species composition among the three land-use types we used Sørensen quantitative index and to compare species dominance we used rank/abundante plots (Magurran, 2004).

We used one-way ANOVA to examine differences in total density and total basal area among land-use types. This approach was also used to compare density and basal area among land-use types within each dbh size-class, and to examine differences in diversity with each estimator. In all cases, the experimental unit was the site, thus n = 2 for each land-use type in statistical analyses. When the ANOVA indicated a significant land-use effect ($p < 0.05$), means were compared with a Tukey post-hoc test. When data did not satisfy ANOVA assumptions after transformation (Sqr or log10), differences were assessed with a Kruskal–Wallis test. When a significant effect ($p < 0.05$) occurred, a mean rank multiple comparison of all groups was used. The slopes of rank/abundance plots were compared with a

Kolmogorov–Smirnov two-sample test. All statistical analyses were performed with Statistica 6.1.

## 4. Results

### 4.1. Density and basal area

Total tree densities including all size classes were 2575 ± 55, 2980 ± 30, 4745 ± 985 individuals/ha (mean and S.E.) in HD, P, and NU land-use types, respectively, and were not statistically different ( $p$ > 0.1). Inter-site variation in tree densities was low in HD and P land-use types (coefficients of variation (CV) of 2.1 and 1.0%, respectively), but was very high (CV = 20.8%) in NU. Overall, the most abundant tree size-class was the 1 – 3 cm dbh (47% of the total number of trees), whereas trees greater than 10 cm dbh were the least abundant (4%). Only 20 individuals (<1%) were greater than 15 cm dbh. The one-way ANOVA within each dbh class indicated a significantly higher density in NU than in HD and P only in the smallest trees (1 – 3 cm dbh; $F_{2,3}$ = 23.6, $p$ = 0.01; Fig. 2a).

Total tree basal areas were similar and amounted to 13.1 ± 2.2, 12.5 ± 2.6 and 14.6 ± 0.3 $m^2$/ha in HD, P, and NU secondary forests, respectively. In contrast to density, basal area of NU sites was similar (CV = 2.0%) between them, whereas between-site variation in the HD and P landuse types was higher (CV = 16.8% and 20.8%, respectively). Overall, trees in the 5 – 10 cm size-class comprised the greatest percentage of the basal area (Fig. 2b), representing from 30 to 61%. As was the case with density, there were significant differences in trees 1 – 3 cm dbh among land-use types ($F_{2,3}$ = 54; $p$ = 0.004). Again, the NU land-use type showed a significantly higher basal area than HD and P (Fig. 2b).

### 4.2. Diversity

We identified a total of 87 species in 28 families (1999 individuals, see Appendix). There were 18 families in the HD land-use type represented by 46 species and 501 individuals, 21 families in the P land-use type represented by 51 species and 574 individuals, and 23 families in the NU land-use type represented by 54 species and 924 individuals (Appendix). The Leguminosae had the greatest species richness and

number of individuals in all land-use types. This plant family represented 33% of the species in HD, 31% in P, and 30% in NU, and represented more than 50% of the total number of individuals in each of the three land-use types. Euphorbiaceae and Rubiaceae were present in secondary forests with considerably species richness (≤5 spp.) and with a lower percentage of individuals (<12%).

The nonparametric estimators indicated significant differences among land-use types in total species richness based on ICE ($KW_{(2,60)}$ = 20, $p$ < 0.001) and Chao2 ($F_{(2,60)}$ = 6.3, $p$ < 0.01) estimators, but not with ACE ($KW_{(2,60)}$ = 3.2 $p$ = 0.2) and Sobs ($KW_{(2,60)}$ = 3.5 $p$ = 0.18). The HD land use tended to show lower total species richness than P and NU. Observed species richness decreased as dbh increased in all land-use types (Fig. 3a). When comparisons among land-use types were performed by dbh size-classes, HD generally showed lower species richness in the smaller size-classes (<5 cm dbh; Fig. 3b–d). The highest species richness in the two larger size-classes (>5 cm dbh) occurred in the P land-use type (Fig. 3a–d). The Sørensen quantitative index showed that HD and P shared 56%, HD and NU shared 22%, and P and NU shared 32%, of the species.

Five species represented more than 50% of the total number of individuals in this study: *M. arenosa*, *Lonchocarpus lanceolatus* Benth., *L. minor* Sousa, *Apoplanesia paniculada* Presl., and *Cordia alliodora* (Ruiz and Pav.) Oken.. *M. arenosa* accounted for 26% and 44% of the total number of individuals in HD and P, respectively, but only 8% in NU. However, this species represented between 42% and 52% of the total basal area in each land-use type. This species showed a generally high relative abundance in HD and P in most dbh size-classes (Fig. 4a–d). In contrast, it was absent in the smallest size-class (1–3 cm dbh) in NU, but represented up to 79% of the relative abundance in the largest size-class (>10 cm) (Fig. 4a and d). Dominance also varied among dbh size-classes (Fig. 4). It was lower in the smallest trees and increased in the larger (≥5 cm dbh) size-classes. NU showed the lowest dominance in the smaller dbh size-class (1 – 3 cm) and P the highest in the >10 cm dbh size-class, but differences among land-use types were not significant. As indicated by the importance value, at least 5 legumes, common in primary forest, were among the 10 most dominant species in all land-use types (Table 1).

5. Discussion

We expected land use to have a long-term impact on the structure and diversity of secondary forests in the Chamela region. Apparently, however, potential initial differences in secondary succession due to the short-term effects of different land uses have mostly disappeared after nearly 30 years of secondary succession. No major differences among land-use types were evident, except in revealing cases which can be best interpreted as the result of current land use patterns of the secondary forests (see below). Our results also showed key similarities and differences with primary forest structure and diversity, which are discussed below.

5.1. Structure

Total density including all individuals ≥ 1 cm dbh in these secondary forests (2575 – 4745 ind/ha) lies within the range reported for the same diameter classes in primary TDF in Mexico (2030 – 7770 ind/ha), but basal area (12.5 – 14.6 $m^2$/ha) is well below (18.5 – 103.1 $m^2$/ha; Trejo, 1998). Thus, secondary forests in our study have reached, on average, about 74% of the density and 22% of the basal area of an average primary TDF in Mexico (Trejo, 1998). This percentage differs from findings in TDF of Yucatan, Mexico, where after 25 years of re-growth, basal area of secondary forest (individuals ≥ 1 cm dbh) represented 63% of that in primary TDF of the region (Lawrence and Foster, 2002). This could be related to the higher annual precipitation (1125 mm), less severe disturbance (slash-andburn), and different land use (maize cultivation) in the Yucatan than in the secondary forests of our study, which were subjected to disturbance by bulldozer (all sites) and are still subjected to some wood extraction (HD and P) or grazing (P). Density and basal area of individuals ≥ 3 cm dbh in secondary forests in this study represented 20% and 40%, respectively, of tose in primary TDF in Chamela (Jaramillo *et al.*, 2003). The percentages are much lower for large trees (≥10 cm dbh), with 5% and 14%, respectively, of values of primary TDF in this region (Durán *et al.*, 2002). Thus, structural differences between secondary and primary forests of the region are greater, if the larger trees are considered in the comparison.

The high number of individuals 1 – 3 cm dbh in our study is similar to results reported by Trejo (1998), who found that individuals < 3 cm dbh constituted up to 50%

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of the total number of individuals in primary TDF in México. The high densities of small individuals (1 – 3 cm dbh) in primary TDF could be reflecting some degree of disturbance, as reported by Trejo and Dirzo (2000). Individuals in the 1 – 3 cm dbh size-class have been frequently ignored in studies of structure and composition of secondary TDF (e.g. Nansen *et al.*, 2001; Ortiz, 2001; González-Iturbe *et al.*, 2002; Saha, 2003; Kalacska et al., 2004). In our study, they represented 48% of the total number of individuals and 83% of the species, but only 8% of the basal area. These results suggest that regeneration is occurring in all land-use types, although to different degrees. For example, the higher density and basal area in NU compared to the HD and P land-use types indicate greater regeneration in the former.

5.2. Diversity

Depauperate on-site regeneration mechanisms and substrate conditions promote opportunities for alien species invasions (e.g. Aide *et al.*, 1995, 2000; González-Iturbe *et al.*, 2002; Molina and Lugo, 2006). This was the case for the forests in this study, which showed a high dominance of the non-native legume *M. arenosa*, considered as ''typical'' of disturbed sites in this area (Lott, 1993) and in others (Francis and Liogier, 1991). Although controlling factors and patterns during plant establishment at the initial stages of secondary succession are not known at our study sites, Roth (1996) showed that *M. arenosa* invades only after disturbance has ceased and that it's not present in the soil seed bank of primary forests in the Chamela the region. Apparently, colonization by *M. arenosa* occurs within 5 years after the onset of secondary succession (Maza personal communication). It shows fase reproduction and dispersal, tolerance to low nutrient levels, and shade intolerance (Francis and Liogier, 1991), traits typical of invasive species (Gordon, 1998; Richardson *et al.*, 2000). Other results also indicate that *M. arenosa* may be fixing N in our secondary forest sites (Jaramillo et al., unpublished).

Lugo (2004) suggested that native species could tolerate or even benefit from alien species. For example, Aide *et al.* (2000) found that *Spathodea campanulata*, an invasive species of abandoned pasture-lands in Puerto Rico, favored the establishment of native species inducing changes in microclimate with its canopy. Also, Camargo-Ricalde (2002) found that the Mimosa genus in the Tehuacán-

Cuicatlán Valley of Mexico had a significant influence on soil chemical and biological properties, as well as micro-environmental factors which could allow establishment and growth of native species. This appeared to be happening in the secondary forests of our study, where primary forest species were sub-dominants in all sites. Moreover, although *M. arenosa* was the dominant species, the sites showed floristic patterns similar to those found in primary TDF in Mexico (Lott *et al.*, 1987; Rico-Gray *et al.*, 1988; Trejo and Dirzo, 2000) and elsewhere (Gentry, 1995), in that the Leguminosae was the better represented plant family in terms of species richness. Durán *et al.* (2002) reported that legumes represented 23% of the species in primary TDF of the Chamela region, followed by the Euphorbiaceae which represented 11%. Our study, in secondary forests of the same region, indicated that legumes represented 54% of the total number of tree species followed by the Euphorbiaceae with 11%.

Balvanera *et al.* (2002) reported high beta-diversity of primary TDF in Chamela and they attributed it to the impact of high environmental heterogeneity due to variations in aspect (north- and south-facing), in topography (crest, slope), and elevation, which affect incident radiation, evaporative demand, soil water holding capacity, and nutrient availability from the local to the watershed scale. The differences in floristic composition among the secondary forests of this study could be reflecting such high species turnover, since primary forest represents the species source for colonization and regeneration.

Some studies have supported the idea that land management in the Chamela region promotes persistent thorny communities, with the loss of native species in the mid- and possibly the long-term (Burgos and Maass, 2004) or an arrested succession (Ortiz, 2001). However, the high abundance of small individuals of primary forest species in all land-use types, indicated, that in spite of the prior land-use, primary forest regeneration was occurring. Nevertheless, primary forest regeneration seemed to be slower in sites still subjected to a certain degree of use, as HD and especially P, which showed a higher abundance of *M. arenosa* among the small individuals compared to the abundance of primary forest species. In contrast, the absence of small individuals of *M. arenosa* and a high abundance of primary forest species such as *L. lanceolatus* Benth., *L. minor* Sousa, *Caesalpinia eriostachys* Benth., *Guapira cf.*

*macrocarpa* Miranda, and *C. alliodora* (Ruiz and Pav.) Oken., among others, at NU, suggest that *M. arenosa* is being replaced at these sites. Apparently, primary forest species are differentially recruited in secondary forests in a process occurring at a decadal scale and related to current management practices. This has important implications when considering options for primary forest restoration, which could include the deliberate introduction of primary forest species, already known to establish and grow under the canopy of Mimosa-dominant secondary forests.

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TABLES

Table 1 Importance value (%) of the top 10 dominant species in secondary tropical dry forests in the Chamela region, Jalisco, Mexico, representing three land-use types

| Species | IV-HD | Species | IV-P | Species | IV-NU |
|---|---|---|---|---|---|
| *Mimosa arenosa* | 169 | *Mimosa arenosa* | 185 | *Mimosa arenosa* | 133 |
| *Apoplanesia paniculata* | 99 | *Apoplanesia paniculata* | 89 | *Lonchocarpus minor* | 123 |
| *Lonchocarpus minor* | 88 | *Amphypterigium adstringens* | 63 | *Lonchocarpus lanceolatus* | 121 |
| *Amphypterigium adstringens* | 69 | *Caesalpinia eriostachys* | 57 | *Croton pseudoniveus* | 99 |
| *Caesalpinia eriostachys* | 57 | *Ipomoea wolcottiana* | 36 | *Cordia alliodora* | 98 |
| *Casearia tremula* | 42 | *Cnidosculus spinosus* | 36 | *Caesalpinia eriostachys* | 88 |
| *Lonchocarpus eriocarinalis* | 41 | *Chloroleucon mangense* | 34 | *Piptadenia constricta* | 88 |
| *Caesalpinia platyloba* | 39 | *Coccoloba liebmanii* | 34 | *Casearia corymbosa* | 60 |
| *Jatropha sympetala* | 35 | *Heliocarpus pallidus* | 33 | *Guapira macrocarpa* | 59 |
| *Diphysa occidentalis* | 33 | *Caesalpinia coriaria* | 32 | *Casearia tremula* | 38 |

HD, housing development; P, pasture; NU, no use. Maximum IV = 300% = (relative abundance + relative frequency + relative basal area).

CAPTIONS TO FIGURES

Fig. 1. Site location in the study area. Modified from the map by Noguera et al. (2002).

Fig. 2. Density (individuals/ha) and basal area ($m^2$/ha) of trees in secondary tropical dry forests in the Chamela region, Jalisco, Mexico, representing three former land-use types. HD, housing development; P, pasture; NU, no use, dbh, diameter at breast height. Values are means ± standard error. Different letters indicate statistically significant differences ($p \leq 0.01$) in the 1–3 cm dbh sizeclass. There were no significant differences among land-use types in other dbh size-classes.

Fig. 3. Observed and estimated (Sobs, ACE, ICE and Chao2) species richness for each dbh size-class in secondary dry tropical forests in the Chamela region, Jalisco, Mexico, representing three former land-use types. HD, housing development; P, pasture; NU, no use. Different letters indicate a statistically significant difference ($p < 0.05$) among the land-use types.

Fig. 4. Rank/abundance plot for each dbh size-class in secondary dry tropical forests in the Chamela region, Jalisco, Mexico, representing three former land-use types: HD, housing development; P, pasture; NU, no use; M.a, *Mimosa arenosa*. Note, *M. arenosa* is not present in NU in the 1–3 cm dbh size-class.

FIGURES
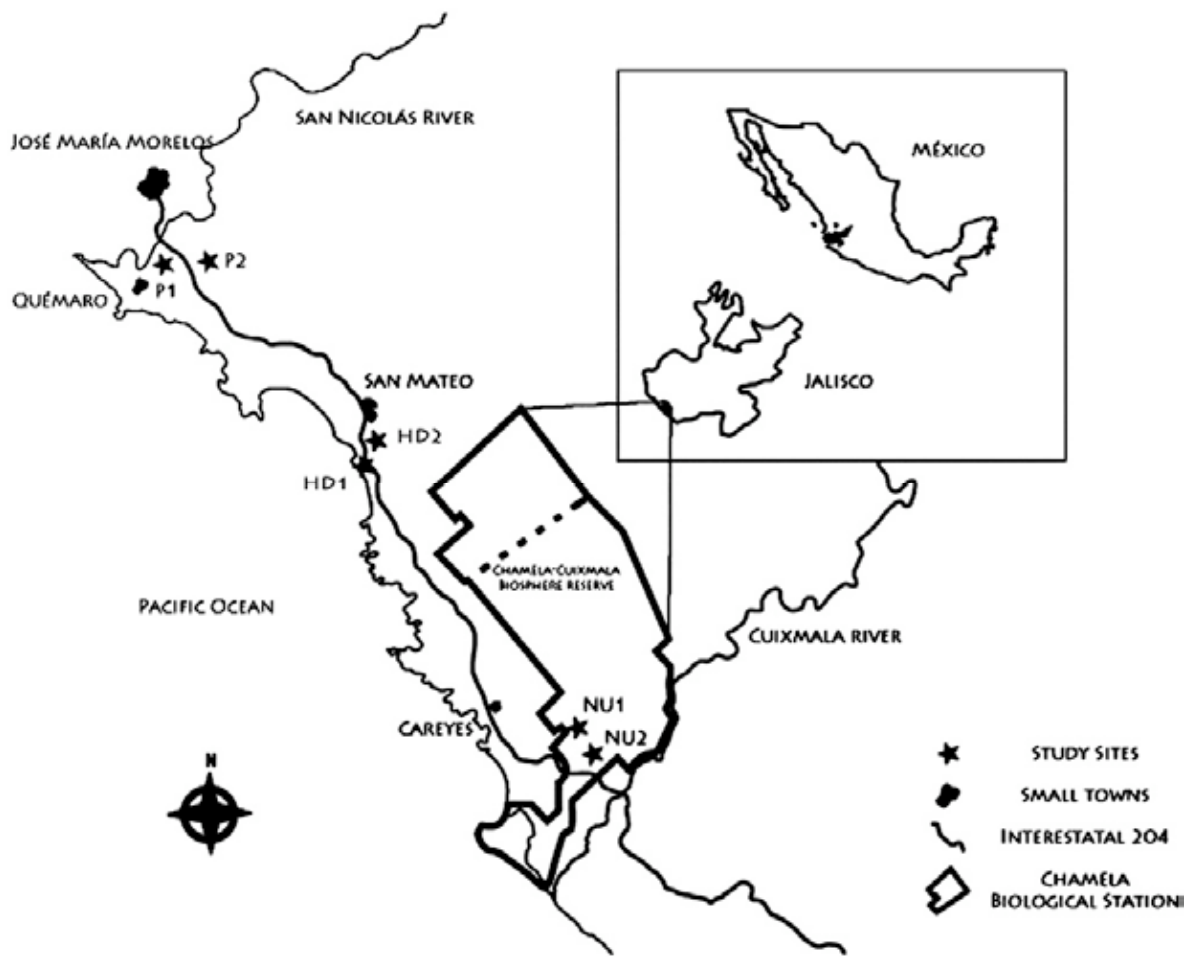


Figure1.
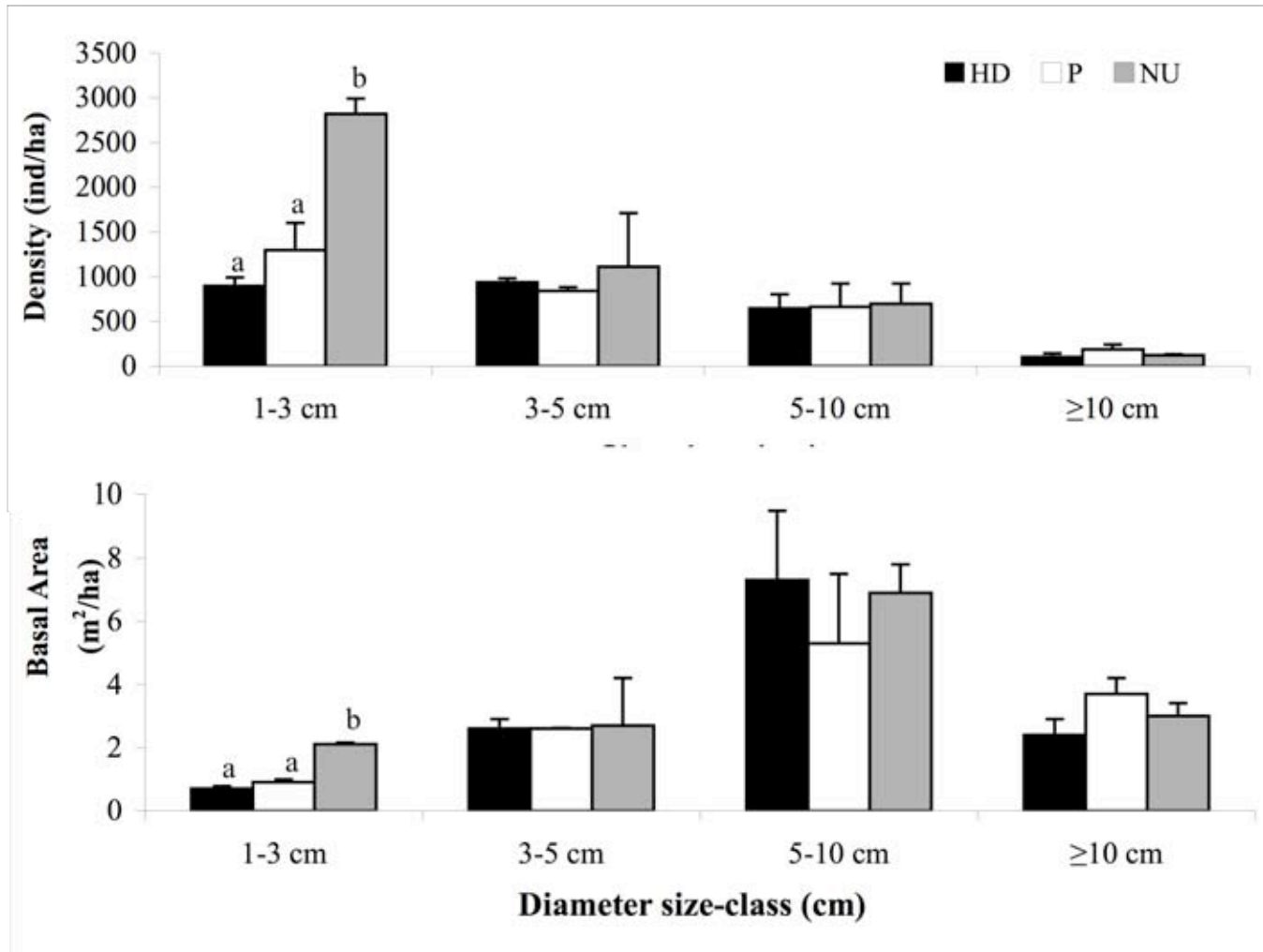
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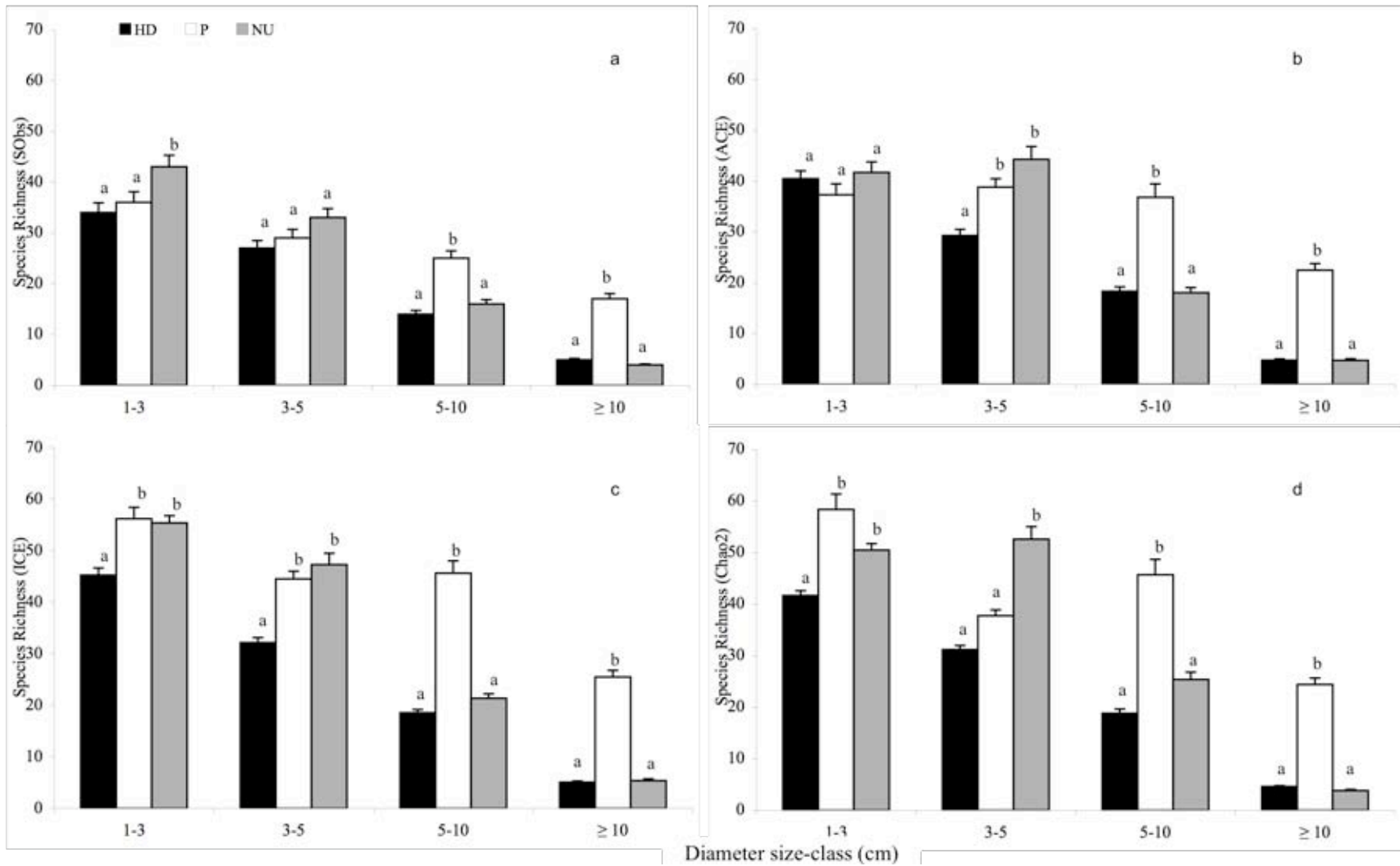
Figure 3.
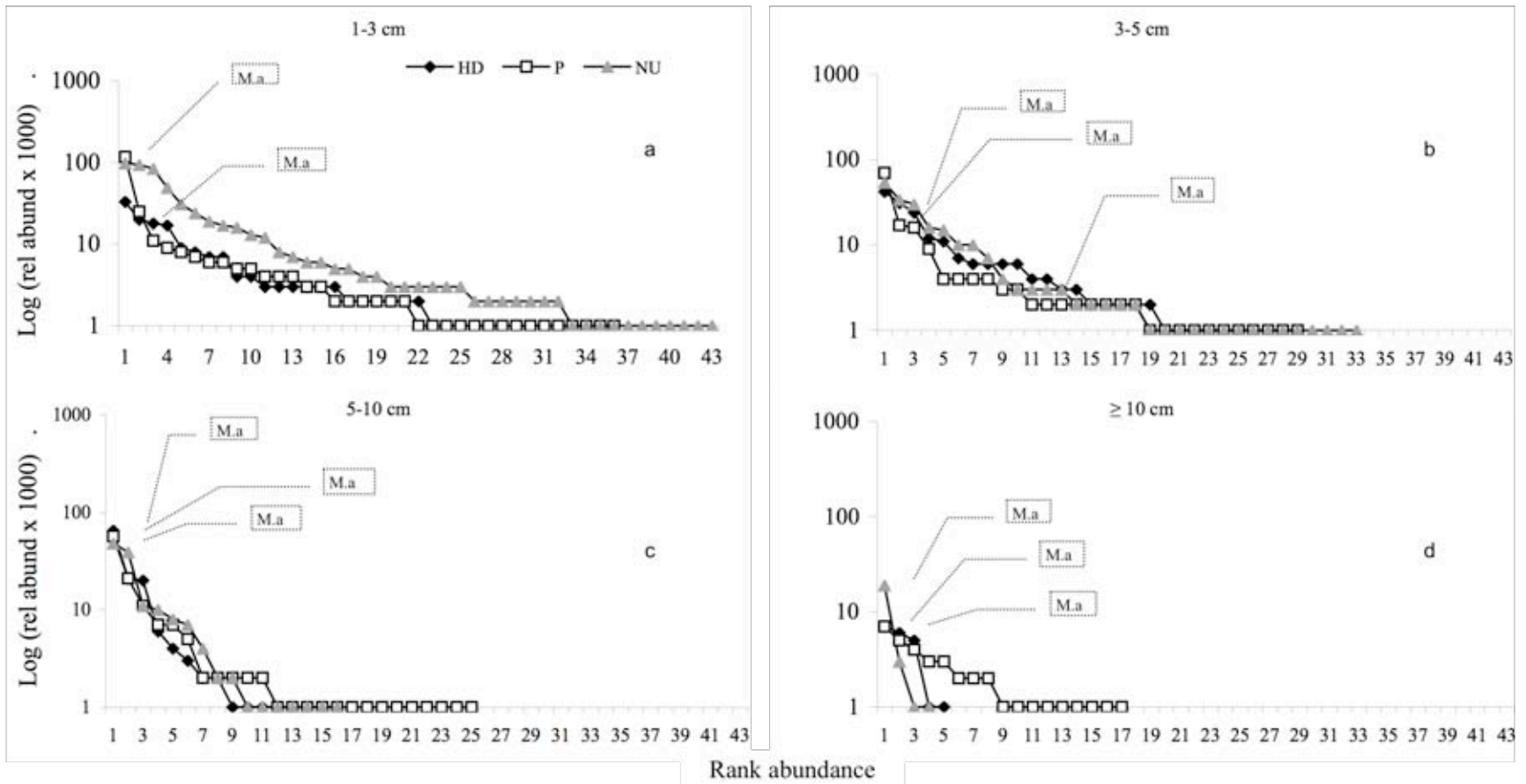
Figure 4.

Appendixes

Apendix A. Woody species in secondary dry tropical forests in the Chamela region, Jalisco, Mexico, representing three land-use types. HD, housing development; P, pasture; NU, no use. The legume *Mimosa arenosa* is the only non-native species.

| Family | Species | HD | P | NU |
|---|---|---|---|---|
| Achatocarpaceae | *Achatocarpus gracilis* H. Walt. | | X | X |
| Anacardiaceae | *Spondias purpurea* L. | X | X | X |
| Apocynaceae | *Rawolfia tetraphylla* L. | | | X |
| Bignoniaceae | *Tabebuia chrysantha* (Jacq.) Nicholson | | | X |
| | *Tabebuia impetiginosa* (Mart.) Standl. | X | | X |
| Bombacaceae | *Ceiba aesculifolia* (H.B.K.) Britt. & Baker. | X | | X |
| | *Ceiba grandiflora R*ose. | X | X | |
| Boraginaceae | *Bourreria* cf. *purpusii* T.S. Brandg. | X | | X |
| | *Cordia alliodora* (Ruiz & Pav.) Oken. | X | X | X |
| | *Cordia elaeagnoides* D.C. | | X | |
| | *Cordia gerascanthus* L. | X | X | |
| Burseraceae | *Bursera arborea* (Rose) Riley | X | X | |
| | *Bursera heteresthes* Bullock | | X | |
| | *Bursera instabilis* McVaugh & Rzed. | | X | |
| Capparaceae | *Capparis incana* H.B.K. | X | | |
| | *Capparis indica* (L.) Druce. | | | X |
| | *Capparis sp 1.* | X | | |
| | *Forchhammeria pallida* Liebm. | X | X | NU |
| Convolvulaceae | *Ipomoea wolcottiana* Rose | X | X | X |
| Ebenaceae | *Diospyros aequoris* Standl. | | | X |

| Family | Species | HD | P | NU |
|---|---|:--:|:--:|:--:|
| Euphorbiaceae | *Adelia oaxacana* (Muell. Arg.) Hemsl. | X | | |
| | *Bernardia spongiosa* McVaugh | | | X |
| | *Cnidosculus spinosus* Lundell | | X | |
| | *Croton alamosanus* Rose | X | X | X |
| | *Croton pseudoniveus* Lundell | X | | X |
| | *Croton roxanae* Croizat [C. fragilis H.B.K.] | | | X |
| | *Croton suberosus* H.B.K. | | | X |
| | *Jatropha malacophylla* Standl. | X | X | |
| | *Jatropha sympetala* Standl. & Blake | X | X | |
| | *Phyllanthus mocinianus* Baill. | | X | |
| Flacourtiaceae | *Casearia corymbosa* H.B.K. | | | X |
| | *Casearia obovata Schlechtendal* | | | X |
| | *Casearia sylvestris* Sw. | X | | X |
| | *Casearia tremula* (Griseb.) Wright | X | X | X |
| | *Samyda mexicana* Rose | X | | X |
| Hernandiaceae | *Gyrocarpus jatrophifolius* Domin | X | | |
| Julianaceae | *Amphipterygium adstringens* (Schlecht.) Schiede. | X | X | |
| Leguminosae | *Acacia farnesiana* (L.) Willd. | | X | |
| | *Aeschynomene amorphoides* (S. Wats.) Rose ex B.L. Rob. | | | X |
| | *Albizia tomentosa* (Micheli) Standl. | | | X |
| | *Apoplanesia paniculata* Presl. | X | X | X |
| | *Caesalpinia caladenia* Standl. | | X | |
| | *Caesalpinia coriaria* (Jacq.) Willd. | X | X | X |

| Family | Species | HD | P | NU |
|---|---|:---:|:---:|:---:|
| Euphorbiaceae | *Adelia oaxacana* (Muell. Arg.) Hemsl. | X | | |
| | *Bernardia spongiosa* McVaugh | | | X |
| | *Cnidosculus spinosus* Lundell | | X | |
| | *Croton alamosanus* Rose | X | X | X |
| | *Croton pseudoniveus* Lundell | X | | X |
| | *Croton roxanae* Croizat [C. fragilis H.B.K.] | | | X |
| | *Croton suberosus* H.B.K. | | | X |
| | *Jatropha malacophylla* Standl. | X | X | |
| | *Jatropha sympetala* Standl. & Blake | X | X | |
| | *Phyllanthus mocinianus* Baill. | | X | |
| Flacourtiaceae | *Casearia corymbosa* H.B.K. | | | X |
| | *Casearia obovata* Schlechtendal | | | X |
| | *Casearia sylvestris* Sw. | X | | X |
| | *Casearia tremula* (Griseb.) Wright | X | X | X |
| | *Samyda mexicana* Rose | X | | X |
| Hernandiaceae | *Gyrocarpus jatrophifolius* Domin | X | | |
| Julianaceae | *Amphipterygium adstringens* (Schlecht.) Schiede. | X | X | |
| Leguminosae | *Acacia farnesiana* (L.) Willd. | | X | |
| | *Aeschynomene amorphoides* (S. Wats.) Rose ex B.L. Rob. | | | X |
| | *Albizia tomentosa* (Micheli) Standl. | | | X |
| | *Apoplanesia paniculata* Presl. | X | X | X |
| | *Caesalpinia caladenia* Standl. | | X | |
| | *Caesalpinia coriaria* (Jacq.) Willd. | X | X | X |

| Family | Species | HD | P | NU |
|---|---|:-:|:-:|:-:|
| Leguminosae | *Caesalpinia eriostachys* Benth. | X | X | X |
| | *Caesalpinia platyloba* S. Wats. | X | X | X |
| | *Caesalpinia pulcherrima* (L.) Sw. | X | | X |
| | *Caesalpinia sclerocarpa* Standl. | X | X | X |
| | *Cassia atomaria L.* | | X | |
| | *Chloroleucon mangense (Jacq.) Britton & Rose* | X | X | X |
| | *Diphysa occidentalis* Rose | X | X | |
| | *Gliricidia sepium* (Jacq.) Steudel | | X | |
| | *Haematoxylum brasiletto* Karst. | X | X | |
| | *Lonchocarpus constrictus* Pitt. | X | | |
| | *Lonchocarpus eriocarinalis* Micheli. | X | X | X |
| | *Lonchocarpus lanceolatus* Benth. | | | X |
| | *Lonchocarpus magallanesii* Sousa | X | X | |
| | *Lonchocarpus minor* Sousa | X | | X |
| | *Lonchocarpus mutans* Sousa | | | X |
| | *Mimosa arenosa* (Willd.) Poir. var.*leiocarpa* (DC.) Barneby | X | X | X |
| | *Piptadenia constricta* (Pers.) J.F. Macbr. | X | | X |
| | *Pithecellobium dulce* (Roth.) Benth. | | X | |
| | *Zapoteca formosa* (Wlld.) H. Hern. subsp. *rosei* (Wiggins) H. Hern. [Calliandra formosa (Kunth) Benth.; C rosei Wiggins]. | | | X |
| Malpighiaceae | *Bunchosia palmeri* S. Wats.*sens. lat.* | | X | X |
| Menispermaceae | *Hyperbaena ilicifolia* Standl. | | | X |
| Nyctaginaceae | *Guapira* cf.*macrocarpa* Miranda | X | X | X |

| Family | Species | HD | P | NU |
|---|---|:---:|:---:|:---:|
| Ochnaceae | *Ouratea mexicana* (Humb. & Bonpl.) Engl. | | | X |
| Polygonaceae | *Coccoloba liebmannii* Lindau | | X | X |
| | *Ruprechtia costata Meisn.* | | X | |
| | *Ruprechtia fusca* Fern. [R. *standleyana* Cocucci] | X | X | |
| Rhamnaceae | *Karwinskia latifolia* Standl. | | X | |
| | *Ziziphus amole* (sessé & Moc.) M.C. Johnst. | | X | |
| Rubiaceae | *Allenanthus hondurensis* Standl. var. *parvifolia* L. Wms. | | | X |
| | *Exostema caribaeum* (Jacq.) Roem. & Schult. | X | X | X |
| | *Guettarda elliptica* Sw. | | | X |
| | *Hintonia latiflora* (Sessé & Moc. ex DC.) Bullock | | X | X |
| | *Randia sp 1.* | X | X | X |
| | *Randia sp 2.* | | X | |
| | *Randia sp 3.* | | X | |
| Rutaceae | *Esenbeckia berlandierii* Baill. subsp. *acapulcensis* (Rose) Kaastra | | | X |
| | *Esenbeckia nesiotica* Standl. | X | | |
| | *Helietta lottiae* Chiang | X | | |
| | *Zanthoxylum caribaeum* Lam. vel aff. | X | X | X |
| Sapindaceae | *Thouinia paucidentata* Radlk. | X | X | X |
| Sterculiaceae | *Guazuma ulmifolia* Lam. | | X | X |
| Theophrastaceae | *Jacquinia pungens* A.Gray | | X | X |
| Tiliaceae | *Heliocarpus pallidus* Rose. | | X | X |
| Verbenaceae | *Citharexylum hirtellum* Standl. | X | | |

# Capítulo III

**Biomass, nutrient pools, and nitrogen mineralization in secondary tropical dry forests of Mexico, differing in their prior land-use history ***

*Biomasa, almacenes de nutrientes y mineralización de nitrógeno de bosques tropicales secos secundarios que difieren en sus historias de uso*

Biomass, nutrient pools and nitrogen mineralization in secondary tropical dry forests of Mexico, differing in their prior land-use history

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Abstract

We compared carbon and nitrogen pools in aboveground and root biomass, and soil, and potential net nitrogen mineralization of secondary tropical dry forests growing in sites cleared by bulldozer 30 years ago and subjected to different land uses prior to abandonment: a) pasture (P), b) housing development (HD), and c) no use (NU). We sampled two forest sites representing each of the three former land-use types (i.e. a total of six sites). Total aboveground biomass (40 - 50 Mg/ha), total aboveground C pools (17 - 22 Mg/ha), and total aboveground N pools (115 - 192 kg/ha) did not differ significantly among land-use types. Biomass and C and N pools in the trees 1-3 cm dbh were significantly higher in the NU than in the other land-use types. Total dead biomass and C and N pools were also significantly higher in NU than in P. Mean root biomass was 12 Mg/ha, and mean root C and N pools were 5 MgC/ha and 138 kgN/ha. Soil C and N pools to a 60 cm depth were similar in all land-use types after soil bulk density correction. The total ecosystem carbon pool at NU was 81.4 ± 4.1 MgC/ha and the ecosystem N pool was 6566 ± 278 kgN/ha. No statistical differences were found in ammonium and nitrate pre-incubation pools, in potential net N mineralization (PNM) or in potential net N nitrification (PNN) among land-use types. The different original land uses did not generally show significant differences. Furthermore, 30 years of woody plant succession have not been enough for most ecosystem variables to attain primary forest values.

Key words: Carbon, Chamela, Disturbance, Nitrogen, Mineralization, Recovery.

Introducción

Recent estimates show that 53% of the world forests correspond to transformed natural forests, not including forest plantations (FAO, 2005). This phenomenon results from anthropogenic disturbances such as logging and conversion of forests to pasture and agricultural lands (Brown and Lugo, 1990b; Skole and Tucker, 1993). Given the growing prevalence of secondary forests in tropical regions and their potential relevance for the global carbon and nutrient cycles (Brown and Lugo, 1990b), the quantification of changes in biomass and nutrient pool sizes and fluxes is fundamental to the understanding of the effects of land-use/land-cover change on ecosystem function (Jaramillo *et al.*, 2003a). Research on the impact of both natural and anthropogenic disturbance on mature forests has focused on the immediate impacts (see Laurance and Bierregaard, 1997). Less attention has been given to forest responses to severe

anthropogenic disturbances, like heavy machinery use, particularly in the long-term.

Biomass accumulation in forest ecosystems after disturbance provides an index of carbon storage and the reestablishment of biological control over a variety of ecosystem processes (Swank *et al.*, 2001). Biomass and nutrient accumulation after disturbance is a function of different factors such as the disturbance regime (magnitude, frequency, severity and intensity), forest age, growing season length, soil humidity, and soil nutrient availability (see Uhl *et al.*, 1988; Fearnside and Guimares, 1996; Kimmins, 1996; Hughes *et al.*, 1999; Johnson *et al.*, 2001; Chapin *et al.*, 2002). There is considerable literature on biomass and carbon fluxes in secondary wet tropical forests previously subjected to different land uses (e.g. Hughes *et al.*, 1999, 2002; Johnson *et al.*, 2001; Jaramillo *et al.*, 2003b; Keller *et al.*, 2004; Mascaro *et al.*, 2005; Lawrence, 2005a), but biomass and nutrient pools and fluxes in secondary forests in the dry tropics remain poorly documented. Similarly, the effects of various land uses on tropical dry forest (TDF) regeneration have been under study only until recently (but see González-Iturbe *et al.*, 2002; Read and Lawrence, 2003a, 2003b; Lawrence, 2005b; Molina and Lugo, 2006). Some of these studies have shown that TDF recovers basal area, and above- and below-ground biomass more quickly than species composition after agriculture and/or cattle grazing (Guariguata and Ostertag, 2001; Lawrence and Foster, 2002; Pereira *et al.*, 2003, Molina and Lugo, 2006). Among the very few studies on secondary forest soil nutrients, Saynes *et al.* (2005) suggest that carbon and nitrogen soil pools and potential net N mineralization are similar to primary forests after 30 years of succession.

Tropical dry forests are among the most heavily utilized and perturbed by human activities and a far greater proportion of dry forests has been degraded or converted than moist and wet forests (Murphy and Lugo, 1986; Maass, 1995; Mooney *et al.*, 1995, Miles *et al.*, 2006). Tropical dry forest is one the most extensive and important tropical vegetation types in Mexico (Rzedowski, 1978; Murphy and Lugo, 1995; Challenger, 1998), where it represents 64% of the tropical vegetation (Masera *et al.*, 2001). It has been estimated that only 27% of the area originally covered by tropical dry forests in Mexico remained intact by the beginning of the

1990's (Trejo and Dirzo, 2000). Although the pattern and magnitude of forest transformation depend on local conditions, generally, vegetation is removed by slash-and-burn with the later introduction of African grasses (Maass, 1995). A previous study in the Chamela region on the coast of Jalisco documented biomass and nutrient pools in primary TDF and pastures (Jaramillo et al., 2003a). This study reported a reduction of 69 to 82% of the total aboveground biomass, 65% of the root biomass, 25% of total-ecosystem C pool, and up to 24% of the total-ecosystem N pool when TDF was converted to pasture. No information exists on the recovery of such pools due to woody plant invasion of abandoned sites in the region.

The Mexican government promoted the clearing of TDF by bulldozers during the 1970's along the Pacific coast of Jalisco. These areas were used for agriculture, cattle ranching, tourism or housing. Later abandonment of some of these sites allowed secondary vegetation to develop and thus providing an opportunity to evaluate the recovery of biomass and nutrient pools and fluxes of secondary TDF of known age and origin. The main objective of this study was to compare total aboveground- and below-ground phytomass, carbon and nitrogen pools, and potential net N mineralization in secondary tropical dry forest sites, originally cleared by bulldozer and subjected to different land-use practices prior to abandonment: 1) no use, 2) pasture, and 3) street construction for a housing development. We expected higher biomass and C and N pools in sites not subjected to land use after disturbance.

2. Study area description

The study was conducted in the Chamela region, on the Pacific coast of Jalisco, México. The climate is highly seasonal with a pronounced dry season. Precipitation averages 746 mm (1983-2004), distributed mostly from June to October; with 31% of the total annual precipitation recorded in September (García-Oliva *et al.*, 1995, García Oliva *et al.*, 2002). Mean temperature is 25ºC, with a less than 5ºC of difference between the coolest and warmest months. The region is characterized by a heterogeneous landscape of three relief forms: mountains, hills, and coastal zone. The low hills are between 50 and 160 masl and show steep convex slopes.

Soils are sandy-clay-loams, poorly developed (Cotler *et al.*, 2002), derived from rhyolite, and have a pH of 6-6.5 (Solís, 1993). The flora of the Chamela region includes 1149 vascular plant species, in 572 genera, and 125 families (Lott, 2002). The families with the greatest number of species are Leguminosae, Euphorbiaceae, Rubiaceae, and Bignoniaceae, and more than 10% of the species are endemic.

3. Methods

We selected six sites with secondary forest vegetation originally covered by primary dry forest, as established by interviewing old residents. These sites were subjected to different land uses but in all cases, the primary forest was cleared with bulldozer and burned approximately 30 years ago, and regeneration time was 24 to 27 years. The sites were also similar in elevation (40 to 70 masl), slope (15 in four of the six sites, 25% in one P site and 35% in one HD site), and aspect (south-facing slope). Three land uses were compared: a) housing development, b) pasture, and c) no use after clearing. Housing development (HD) sites were cut, burned and prepared for a construction project. Although some streets were built and paved, the project failed and the sites were abandoned. A secondary forest developed on the land originally designated to build houses, which has been subjected to sporadic selective cutting and cattle grazing. These sites were located in the Ejido San Mateo, approximately 10 km North of the Chamela Biological Station of the Instituto de Biología, Universidad Nacional Autonoma de Mexico  (19°30′N, 105°03′W, Figure 1). At the pasture sites (P), primary forest was cut, burned, and seeded with two tropical forage grasses: *Panicum maximum* Jacq. (Guinea grass) and *Pennisetum ciliare* L. (Buffel grass). These sites were grazed by cattle for six years and abandoned, and since then subjected to sporadic selective cutting and grazing. These sites were located near Quémaro village, approximately 20 km N of the Biological Station (Figure 1). The sites designated as no use (NU) were cut and burned to justify possession of the land and were abandoned. In 1993, these sites were included within the 13,000 ha Chamela-Cuixmala Biosphere Reserve (19°24′N, 104°58′W), 11 km S of the Station. Since the NU land-use type did not involve management after the primary TDF was felled, we consider these sites as

having a lower intensity of disturbance than the HD and P land-use types. The secondary forests will be identified subsequently in the text by the abbreviation of their former land use (HD, P, and NU).

## 3.1 Tree biomass

During the dry season of 2003 we sampled two forest sites representing each of the three land uses. In each site, ten 40 x 2.5 m transects (0.1 ha), at least 7.5 m apart from each other were established. The diameter at breast height (dbh) of all stems with dbh ≥ 1 cm and at least 2 m in height were recorded in each transect. All individuals were classified into each of four dbh sizes-classes: 1-3 cm, 3.1-5 cm, 5.1-10 cm and >10 cm. This dbh classification was used to evaluate regeneration trends at the sites. Aboveground tree biomass was estimated using an allometric equation developed at Chamela by Martínez-Yrízar *et al.* (1992; *Y = -a + (b x Log$_{10}$ basal area*). Live and standing-dead tree stems were noted.

## 3.2 Seedlings and litter

Plants less than 1 cm dbh and litter mass were sampled in ten 25 x 25 cm plots. Each plot was located randomly along each of the 40 m biomass transects. All plants with a dbh less than 1 cm rooted in the plot were clipped at ground level and placed in a paper bag. Forest floor litter within the plot was also collected and placed in a paper bag. Litter was classified as fine (leaves, flowers, fruits and seeds) and coarse (branches and small branches < 2.5 cm in diameter). All forest plants and litter were dried in an air circulating oven to constant weight at 60°C.

## 3.3 Aboveground necromass

Standing dead biomass comprised the amount of dead stems on live trees, and standing dead trees. Although standing dead stumps were present none of them fell within our 2.5 x 40 m transects. Standing dead biomass was estimated using the same allometric equation developed by Martínez-Yrízar *et al.* (1992). Downed woody debris was sampled non-destructively using the planar intercept technique (Kauffman *et al.*, 1995). Downed woody debris that intersected each sample plane was measured for diameter size and was partitioned into two

standardized size classes based on their diameter. Lengths of the sampling plane varied among particle size classes: 5 m for woody debris 2.54-7.6 cm diameter and 15 m for coarse woody debris ≥ 7.6 cm diameter. The diameter of coarse woody debris that intercepted the plane was measured to the nearest half centimeter. The quadratic mean diameter of fuel particles in two size classes was calculated through measurement of the diameter of 10 samples of woody debris. The woody debris mass was calculated using their specific gravity. This was obtained from the dry weight and volume determined by displacement of water after immersion (Barajas-Morales, 1987). Wood specific gravity was 0.66, 0.75, and 1.44 g cm$^3$ for sound wood 2.5-7.5 cm, and 0.64, 0.85, and 0.88 g cm$^3$ for sound wood > 7.5 cm in diameter, in HD, P, and NU, respectively.

## 3.4 Root biomass

In order to estimate maximum potential root regeneration we excavated roots only in sites with no past or recent management practices (NU sites). During the dry season of 2004 we established five of the ten transects for aboveground measurements in each site were randomly selected. One point was randomly located along each transect where a 2 x 0.50 m subplot was carefully excavated. To ensure unbiased sampling, the direction of the long axis of each subplot was also determined randomly. Roots were excavated to a 40 cm depth at 10 cm intervals because nearly 90% of the root biomass in primary TDF in Chamela is found in the top 40 cm of soil (Jaramillo et al., 2003a). Roots were separated in the field by sieving the soil through a wire mesh, placed in paper bags and transported to the laboratory. No attempt was made to separate live from dead roots. In the laboratory, roots from each depth were carefully washed out and manually separated into four diameter classes: 1.0-5.0 mm, 5.1-10.0 mm, 10.1-20.0 mm, and > 20 mm. Roots were oven-dried to constant weigh at 70°C. Fine roots (<1 mm in diameter) were sampled separately to the same depth with a soil core 5 cm in diameter because the trench sampling underestimated their biomass. Fine roots were separated on trays with two different mesh sizes (2- and 0.8 mm), collected with tweezers, and placed in a petri dish with water to eliminate soil particles. They were oven-dried to constant weight at 70°C.

3.5 Soil

During the dry season of 2004 we collected five compound soil samples (each one composed of four subsamples) in randomly located points at each of the six secondary forest sites. The samples were collected in 10 cm intervals down to the 20 cm depth, and in 20 cm intervals down to the 60 cm depth. All soil samples were sieved through a 2 mm mesh and dried at 80°C for 48 h.

*Carbon (C) and nitrogen (N) pools.* We extracted cores from each tree category, including dead stems on live trees, standing dead trees and standing stumps, to estimate C and N pools. All biomass samples were ground in a mill and soil samples were ground with a mortar, prior to nutrient analyses. To quantify C and N concentrations we used one to ten replicate samples of each tree category, biomass component (seedlings, litter, and downed woody debris), and of each root-size category at each soil depth. C concentrations in biomass and soil were determined in a Carbon Analyzer (CM 5012; UIC, Inc.) by combustion and coulometric detection. N concentrations were obtained with an acid digestion by a micro-Kjeldahl procedure and colorimetrically determined in a Bran Luebbe Auto Analyzer III, Nordestedt, Germany (Method No. 696-82WM, Technicon Industrial System 1997).

*Potential net N mineralization.* During the 2005 dry season, five compound soil samples (four subsamples each) in five randomly located points were collected at the six secondary forest sites. The samples were collected in 0-2.5 cm topsoil and the 2.5-10 cm depth, following Ellingson *et al.* (2000). From each of the five compound soil samples, one 10 g sub-sample was placed in 50 ml of 2N KCl and shaken thoroughly for 30 minutes. The supernatant was filtered through a Whatman 143 No.1 paper filter and stored under refrigeration (Robertson et al., 1999), until ammonium and nitrate were determined in a Bran Luebbe Auto Analyzer III (Nordestedt, Germany; method No. 696-82WM, Technicon Industrial Systems 1997). Another 100 g sub-sample was placed in 100 ml PVC (polyvinylchloride) tubes with a 0.17 mm mesh at the bottom, wetted to field capacity with deionized water, and incubated in a 1L jar for 15 days at 25°C. Potential net nitrogen mineralization was calculated as ammonium- plus nitrate-

nitrogen at the end of incubation minus the sum of the initial ammonium- and nitrate-nitrogen. Potential nitrification was calculated as the final nitrate-nitrogen concentration after incubation minus the initial value. To estimate microbial activity, evolved $CO_2$-C was collected in 10 ml traps of a 1M NaOH solution within the 1L jars. Jars were regularly aerated and the $CO_2$-C traps changed. Carbonates were precipitated by adding 5 ml of 1.5 M $BaCl_2$ and titrated with 0.5 M HCl. The $CO_2$-C values were corrected to soil dry weight.

## 3.6 Statistical analyses

We used one-way analysis of variance (ANOVA) to test for differences among land-use types in: a) total aboveground biomass (TAGB) and its components, b) C and N pools in TAGB and its components, c) total soil C and N pools, and d) potential net N mineralization. When the ANOVA indicated a significant factor effect ($p < 0.1$), means were compared with a Tukey *post-hoc* test. Data were transformed (Sqr and $Log_{10}$) to satisfy ANOVA assumptions. When these were not satisfied, differences in biomass and nutrient pools and potential net mineralization were assessed with a Kruskal-Wallis test. When a significant effect ($p < 0.1$) occurred, a mean rank multiple comparison of all groups was used.

## 4. Results

### 4.1. Aboveground biomass and C and N pools

Total aboveground biomass (TAGB) ranged from 40 to 50 Mg/ha and did not differ significantly among land-use types (Table 1). Live biomass represented 82-88% of the TAGB and varied between 36 and 41 Mg/ha. Live trees in the 5-10 cm dbh size-class comprised between 37 to 47% of the TAGB in all land-use types. In contrast, biomass in the 1-3 cm dbh size-class represented only between 5-11% of the TAGB and was significantly higher in NU than in the other land-use types ($F_{2,3}=35.9$, p =0.008; Table 1). Total aboveground necromass varied from 5 to 9 Mg/ha and represented 12-18% of the TAGB. It differed significantly between the NU and P land-use types ($F_{2,3}=6.6$, p =0.08; Table 1). Standing dead biomass varied from 2 to 5 Mg/ha and was significantly higher in NU than in HD and P ($F_{2,3}=7$, p <

0.07). Dead stems in live trees were 1.68, 0.75, and 1.96 Mg/ha in HD, P and NU, respectively. Downed woody debris represented 4-5% of the TAGB.

Carbon and nitrogen concentrations (mg g$^{-1}$) did not vary greatly among land-use types, except for seedlings (Table 2). Seedling C concentrations were lower ($F_{2,3}$ = 7, p = 0.07) and N concentrations higher in HD than in NU ($F_{2,3}$ = 9.2, p = 0.05; Table 2). Carbon concentrations were highest in standing dead biomass (480-488 mgC g$^{-1}$) and lowest in litter (372-380 mgC g$^{-1}$; Table 2). In contrast, N concentrations were highest in litter and seedlings (13-15 mgN g$^{-1}$; Table 2). Similar to biomass, total aboveground C pools (TAC) did not differ among land-use types and ranged from 17 to 22 MgC/ha (Table 1). The C pool in live biomass comprised 80-87% of the TAC. The C pool in dead biomass was significantly lower ($F_{2,3}$=7, p =0.07) in P than in NU (Table 1). Standing dead C pools represented 5-11% of the TAC (Table 1) and were significantly higher in NU than in HD and P ($F_{2,3}$=8, p =0.06). Total aboveground N pools (TAN) ranged from 115 to 192 kgN/ha and did not vary among land-use types (Table 1). N pools in live trees 1-3 cm DBH comprised less than 20% of total N pool, but differed significantly among the three land-use types ($F_{2,3}$ = 207.8, p = 0.0006). NU showed the highest (26 kgN/ha) and P the lowest (9 kgN/ha) N pool in this tree category. N pools in the total dead biomass were significantly higher ($F_{2,3}$=10.5, p =0.04) in NU than in P (Table 1).

4.2 Root biomass and C and N pools

In order to show root biomass and C and N pools variation, we will present disaggregated data of NU sites (NU1 and NU2). Total root biomass was 10.5 and 13.1 Mg/ha in NU1 and NU2, respectively. Between 41-49% of the total root biomass was in the top 20 cm of soil (Fig 2). However, root distribution varied with depth and by size-class between the two sites. The largest roots (> 20 mm) not only showed conspicuous differences in their distribution with depth between sites, but also in their biomass. For example, they represented 51% of the total root biomass in NU2 but only 28% in NU1 (Fig 2). Fine-root biomass (<1 mm) made up 3% of the total root biomass at both sites and 37-39% was in the top 10 cm of soil. The root:shoot ratios (total root biomass/(total live biomass + standing dead biomass) were 0.23 and 0.28 in NU1 and NU2 respectively.

Root C concentrations ranged from 40% to 44% across all size classes in both sites and were lower in the smaller than in the larger roots (Table 3). Root N concentrations varied between 0.7 and 1.8% and were lower in the largest roots (Table 3). Root N concentrations were somewhat lower in NU2 than in NU1. The root C pool was 4.5 and 5.6 MgC/ha in NU1 and NU2, respectively. The root N pool was 150.5 kgN/ha in NU1 and 125.6 kgN/ha in NU2.

## 4.3 Soil C and N pools

Soil bulk densities ranged from $0.9 \pm 0.1$ g/cm$^3$ at 10-20 cm in HD and NU to $1.9 \pm 0.4$ g/cm$^3$ at 20-40 cm in P (mean $\pm$ SE) and were generally higher at the P sites, originally subjected to grazing. Soil C concentrations varied from 0.6 to 1.7% and N concentrations from 0.8 to 2.0 mgN/g, in all soil depths and land-use types (Table 4). No significant differences were found among land-use types for soil C or N. Concentrations decreased with depth in both cases. For example, C and N concentrations at the 20-40 cm depth were 47 and 50% of those in the top 10 cm of soil. The soil C pool to the 60 cm depth was higher in the P land-use type (66 MgC/ha) than in HD and NU (50 and 55 MgC/ha respectively). However, the soil C pool in P after soil bulk density correction was 61 MgC/ha and thus similar to the other land-use types (Tabe 4). More than 55% of the soil C pool was in the top 20 cm of soil in all land-use types. The soil N pool to the 60 cm depth was higher in the P land-use type (7566 kgN/ha) than in HD and NU (5792 and 6208 kgN/ha respectively). The soil N pool after soil bulk density correction was 7114 kgN/ha. As was the case of soil C pools, soil N pools to the 60 cm depth were similar among land-use types after soil bulk density correction for P. Also, a high proportion (57–70%) of the soil N pool was in the top 20 cm of the soil. The total ecosystem C pool at NU was $81.4 \pm 4.1$ MgC/ha and the ecosystem N pool was $6566 \pm 278$ kgN/ha.

## 4.4 Potential net N mineralization

No significant differences were found in ammonium and nitrate pre-incubation pools, in potential net N mineralization (PNM) or in potential net N nitrification (PNN) among land-use types (Table 5). PNM was negative in all land-use types and varied from -1.6 µgN/g in HD to -2 µgN/g in P (0-10 cm; Table 5). PNN

was positive in all land-use types and ranged from 1.4 $\mu gNO_3$-N/g in NU to 1.8 $\mu gNO_3$-N/g in HD at 10 cm topsoil. There was notorious variation in PNN between P sites, with values in P1 4.3 times higher than in P2. Evolved $CO_2$-C varied from 44 to 49 $\mu gC$/g/day and did not differ ($p > 0.1$) among land-use types (Table 5).

5. Discussion

Tropical dry forests (TDF) are subjected to frequent disturbance, especially via slash-and-burn agriculture (Maass, 1995). Some of the short- and medium-term effects of this disturbance type on TDF have been studied, but long-term effects have not been frequently studied, especially in the west coast of México. Moreover, the long-term effects of more intense disturbance types like bulldozer clearing are basically unknown. Due to the lack of data about the long-term effect of different disturbance types on TDF biomass and nutrient pools and related aspects, management approaches are not yet clear. On a different scale, global carbon models do not include the effect of disturbances and the recovery of tropical forests (Vargas *et al.*, 2008), thus studies on secondary succession are needed to better establish both their contribution to C emissions and their potential as C sinks during regeneration.

This study is the first to estimate biomass and C and N pools in secondary TDF in the Chamela region and the first to estimate the long-term effects of bulldozer disturbance and differing land use histories in México. Other studies on the long term impacts of disturbance on mexican TDF have been conducted mostly in the Yucatan Peninsula, evaluating the effect of slash and burn agriculture (Lawrence and Foster, 2002; Eaton and Lawrence, 2006; Urquiza-Haas *et al.*, 2007) or the impact of fire (Vargas *et al.*, 2008).

Results of this study show that possible differences in secondary succession due to short-term effects of different land-use types have disappeared after nearly 30 years of succession. Although we expected land-use type to have a long-term impact in the phytomass and carbon and nitrogen pools, there were no large differences among land-use types, except for those variables in which values reflected, apparently, the recent use of these forests. However, we found interesting differences when we compared these results with others previously

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reported for grassland and primary forest in the Chamela region, and in TDF in other regions of the country and the world. It is within this context that we discuss the main results of this study.

5.1 Aboveground phytomass

A previous review of total aboveground biomass (TAGB) in primary TDF worldwide reported 28-268 Mg/ha (Martínez-Yrízar, 1995), whereas another previous review reported 78-320 Mg/ha (Murphy and Lugo, 1986). Jaramillo *et al.* (2003a) estimated 112 Mg/ha for primary TDF in the Chamela region, considering only those individuals ≥ 3 cm dbh. Although, TAGB of secondary forests in this study (40-55 Mg/ha) are within the range reported by Martínez-Yrízar (1995), they are in the lower biomass values for TDF. Similarly, live biomass of trees and seedlings (36-41 Mg/ha) is also lower than that reported of primary forest in the Chamela region (69 Mg/ha; Jaramillo *et al.*, 2003a), as well as dead aboveground biomass (DAGB, 5-9 Mg/ha) and woody debris (WDB - 1.8-1.9 Mg/ha) which are well below the estimates reported by Jaramillo *et al.* (2003a, 27-42 Mg/ha DAGB) and by Maass et al. (2002, 6-17 Mg/ha WDB) for primary TDF in the region.

There are few studies in secondary TDF to compare the results of this study. For example, Álvarez-Yepiz *et al.* (accepted) reported a higher TABG (61 Mg/ha) in secondary TDF of similar age (20-30 y) in Alamos (México), than in secondary forests of Chamela (40-55 Mg/ha). Secondary forests in Alamos were previously used for agriculture and sporadic grazing. Apparently, a lower intensity of site use through agriculture and sporadic grazing of secondary forests in Alamos, could partly explain the differences in biomass. Molina (1998) estimated 47 Mg/ha in live aboveground biomass of secondary TDF growing in an abandoned residential area in Puerto Rico, which is also greater than the 37 Mg/ha estimated for secondary forests from a similar land use (HD) in this study. Although both forests grow under similar climatic conditions (860 mm and 746 mm of rainfall for the Puerto Rican and Mexican sites, respectively), the lack of information on the type of disturbance and original land use of the former, does not allow us to make insightful comparisons.

Other studies have been conducted in secondary seasonally dry forests in the southern Yucatan Peninsula in Mexico. Read and Lawrence (2003a) reported twice the live biomass of individuals ≥ 1 cm dbh (60 – 98 Mg/ha) in seasonally dry semievergreen forests of similar age (25 y) than the live biomass estimated in this study (36-41 Mg/ha). Forests in their study were slashed and burned and cultivated with corn for a year. Eaton and Lawrence (2006) reported also higher woody debris (11.3 – 19.8 Mg/ha) in the Yucatan secondary forests than in secondary forests in this study (1.8-1.9 Mg/ha). Those forests in Yucatan have been from 1 to 16 years in succession and subjected to different cultivation cycles previous to abandonment. Thus, differences in vegetation structure and diversity and previous land-use explain the comparativley lower biomass in the Chamela secondary TDF. These results show the wide range of values for secondary seasonally dry forests, which are due to differences in structure and composition. For example, secondary forests in Chamela (TDF) did not show trees with dead stems ≥ 10 cm dbh which would eventually contribute to the woody debris pool and less than 5% of all trees sampled (1999 individuals) were standing dead trees (data not shown).

Oliver (1981) and Pastor and Post (1986) pointed that large rotten pieces of detritus may be present from a previous stand during aggradation and vigorous growth in an unmanaged stand, but only smaller size-classes are debris inputs at first from the aggrading stand. This seems to be the case in secondary forests of this study, where we found, on average, up to 4.5 fallen stems greater than 7.6 cm in diameter, but up to 33.5 fallen stems 2.5-7.6 cm in diameter (data not shown.

Bulldozer disturbance is perhaps the most severe type of disturbance due to the stripping of vegetation and the damage to the soil and root systems (Pinnard et al., 2000; Page-Dumroese et al., 2006). This may be worsened when certain land uses are practiced in those sites for long periods. Under such conditions, regeneration after abandonment of land use mainly occurs by seed rain, although most seeds of plants from the dry tropics have low dormancy and do not tolerate light and adverse soil conditions for prolonged periods (Durán et al., 2002). Thus alien species may colonize these sites, as documented in the Chamela region (Burgos and Maass, 2004; Romero-Duque et al., 2007), in Yucatan (González-Iturbe et al., 2002) and in Puerto Rico (Molina and Lugo, 2006). Molina and Lugo (2006)

showed alien species were extremely successful in terms of abundance, basal area, and importance value at her study site. Colonization by these species would evidently determine biomass and C and nutrient accumulation during forest regeneration. In this study we found differences in biomass and C and N pools when individuals in the early growth phase (1-3 cm dbh) were considered, and were higher in NU sites, where no individuals of *M. arenosa* were found in this dbh size class (Romero-Duque *et al.*, 2007). This suggests that *M. arenosa* slows down accumulation of aboveground biomass and aboveground C and N pools in these secondary forests. However, differences in plant densities in the 1-3 cm dbh size-class obscure the effects of changes in species composition.

## 5.2 Root biomass

There are no studies on total root biomass of secondary TDF to compare the results from Chamela. One study reported root biomass accumulation of the < 3 mm size fraction in a fire chronosequence of seasonally dry forest in the Yucatan peninsula (Vargas *et al.*, 2008). They estimated that these forests required close to 14 yr to reach 90% of the biomass in mature forests of the area. Biomass data for roots < 5 mm diameter in 30 yr old secondary TDF of Chamela indicate that such roots represent only 26% of the biomass in primary forest for the same size class. Such a great difference in small root accumulation is likely due to the nature of disturbance that induced secondary succession (fire in Yucatan compared to bulldozer removal in Chamela) and that reference forests in Yucatan and Chamela may not be comparable due to disturbance history as well (mature forest in Yucatan vs primary forest in Chamela).

Total root biomass in secondary forests of the Chamela region (10.5-13.1 Mg/ha) was in the lower end of that in primary TDF worldwide (8.5-58 Mg/ha; see Rentería-Rodríguez, 1997) and lower than in primary TDF of the Chamela region to a comparable soil depth (40 cm; 28 Mg/ha; Castellanos *et al.*, 1991) and 15 Mg/ha (Jaramillo et al., 2003a). Biomass of large roots (> 20 mm; 3-7 Mg/ha) represented 28 and 53% of the total root biomass at the NU sites and the biomass is similar to the biomass of large roots in primary forest of the Chamela region (4-6 Mg/ha; Jaramillo *et al.*, 2003a). These authors suggest that large roots decompose

between 7 to 13 yr after primary forest conversion to pasture. This suggests that biomass of large roots (> 20 mm diameter) in these secondary forests is biomass produced by woody species to comparable values of primary forests during 30 yr of growth. Interestingly, M. arenosa individuals account for only 18% of the total number of individuals at these NU sites (data not published) which suggests that a high proportion of large roots could belong to the primary forest species already dominant in this land-use type (Romero-Duque et al., 2007). Jaramillo and Sanford (1995) mentioned that the percentage of the total biomass in primary TDF allocated to roots is, on average, 27%. In the Chamela region, the percentage is 12% in primary TDF (Jaramillo et al., 2003a), which is 1.7 times lower than the 20% documented for secondary forests in this study. This is due to the greater aboveground biomass in primary than in secondary forests. However, the mean root:shoot ratio in secondary forest (0.25) is similar to the 0.20 reported by Jaramillo et al. (2003a) for primary TDF and are within the wide range of values (0.09-1.01) reported by Martinez-Yrizar (1995) for primary TDF worldwide. Guariguata and Ostertag (2001) indicated that biomass is primarily allocated to fine root and leaf production early in succession, whereas biomass is allocated, mostly to production of structural tissue, such as thick woody stems and roots in later stages. Apparently, secondary forests in Chamela are reaching a functionally similar stage to primary forests, despite the fact that after 30 yr of succession total biomass is still considerably lower than in primary forest.

5.3 C and N pools in phytomass

   C pools followed the same patterns than biomass; therefore we do not discuss any further the implications in this context. Despite the fact that total aboveground N pools (TAGBN) in NU sites were 1.4 and 1.6 times higher than in P and HD sites, respectively, no significant differences were found among the land-use types. However, similar to phytomass and the C pools, differences were found in the 1-3 cm dbh size-class. This could be due to the abundance of potentially N-fixing legumes in this size-class at NU (1375 ind ha$^{-1}$) compared to HD (610 ind ha$^{-1}$) and P (895 ind ha$^{-1}$) land-use types (Romero-Duque et al., 2007). Rentería-Rodríguez (2007) and Jaramillo (pers. comm.) indicate these legume species have

high leaf N concentrations and therefore could contribute to the higher aboveground N pools of NU sites.

Total aboveground N pools in secondary forests (115-192 kg ha-1) were well below the N pools in primary forests of the Chamela region (873 kg ha-1; Jaramillo *et al.*, (2003a). In contrast, root N pools were higher in secondary (125-150 kg ha-1) than in primary forest (106 kg ha-1). This is due to the higher root N concentrations in secondary forests (mean = 1.25%) than in primary forest (mean = 0.7%; calculated from Jaramillo *et al.*, 2003a), which result in a larger N pool, despite the fact that secondary forests showed a smaller root biomass. The higher root N concentration in secondary forest could be due to the dominance of potentially N-fixing legumes (Romero-Duque *et al.*, 2007) when compared to primary forest (Durán *et al.*, 2002). In addition, 56% of roots in secondary forests were less than 10 mm in diameter and had higher N concentrations (1.6%) than those of similar diameters in primary forest (0.7% N), which represented also a lower percentage (43%) of root biomass (Renteria-Rodriguez, 1997). Further studies are needed to evaluate the potential role of N-fixing legumes in these secondary TDF and in patterns of secondary succession in this region.

5.4 Soil C and N pools

Soil C pools in secondary forests were lower than in primary forest of the Chamela region (Jaramillo *et al.*, 2003a) estimated to the same depth (60 cm), but N pools were similar, even higher in P sites (see Table 4). These results may reflect the impact of bulldozer disturbance and the land use history. The use of heavy machinery has negative effects on soil nutrient pools due to removal of surface soil and soil compaction (Uhl *et al.*, 1982) and the exposure of soil organic matter to decomposition (Pinnard *et al.*, 2000), which promote short- and medium-term losses of soil C and nutrients. The main C and nutrient sources to the soil, such as surface litter and fine roots (Jaramillo and Sanford, 1995) are small in secondary forests of this study. Thus, an impoverished soil with low C inputs could explain their low soil C pools. In contrast, the similarity in soil N pools between secondary and primary forests could be due to the high root N concentrations and legume dominance in secondary forests (see above; Romero-Duque *et al.*, 2007).

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Interestingly, soil N pools in the first 10 cm of soil in secondary forests at Chamela (2232-2591 kgN/ha) were similar to soil N pools in early and mid-successional secondary forests (2010-2380 kgN/ha) in Morelos, Mexico (Saynes *et al.*, 2005), which are dominated by the N-fixing legume *Lysiloma microphyllum* Benth. (Cárdenas and Campo, 2007). Similarly, these forests showed higher soil C pools (45 MgC/ha) at the same depth than the secondary TDF of the Camela region (21 Mg/ha). Morelo's secondary forests have been growing for 20 to 30 years after land use abandonment. Higher soil C and N pools in Morelos may be due to lower intensity of both disturbance (slash and burn) and land-use history (corn agriculture).

5.5 Microbial activity and N mineralization

Microbial activity and N mineralization were measured in soil samples collected during the dry season, so results reflected soil conditions at this time of the year; nevertheless, they provide relevant information to compare the impact of land use history. A few studies have evaluated the short-term effects of slash and burn practices on N mineralization in TDF, but there are no comparable studies in secondary forests. For example, Ellingson et al. (2000) reported a decrease in the total N pool with a concomitant increase in $NH_4$-N during land-cover/land-use changes from TDF to pasture in the Chamela region. They pointed that total soil N losses depended on the fire severity, and suggested that high soil temperatures during the slash fires volatilized N at soil surface, pyromineralized organic N to $NH_4$-N and influenced soil biota at least to 5 cm in the soil profile. On the other hand, García-Mendez *et al.* (1991) reported twice the $NO_3$-N concentrations in pastures than in forest soils, but Ellingson *et al.* (2000) found that 2 years after pasture establsihment soil $NO_3$-N concentrations were significantly lower than those in forest soil. Both authors reported a significant decrease in rates of potential mineralization following conversion of TDF to pasture, and lower potential mineralization in pastures than in primary forests in the peak of the dry season.

Thirty years after bulldozer disturbance and different land uses, we found higher $NH_4$-N pools than $NO_3$-N$^-$ pools in the top 10 cm of soil. Moreover, we found soil inorganic N pools during the dry season (9-11 kg/ha) were in the lower range of

values reported for primary forest soils at the same season (11-28 kg/ha; Ellingson *et al.*, 2000). Similarly, both net potential N mineralization (-1.6 to -2 µgNH$_4$-N/g) and nitrification potential (1.4-1.8 µgNO$_3$-N/g) were lower than the values reported by Montaño-Arias *et al.* (2007) for primary forest soil (-0.3 µgNH$_4$-N/g and 7.2 µgNO$_3$-N/g). Idol *et al.* (2003) indicate that N availability, net N mineralization and nitrification tend to increase after harvest, and decline with increasing of forest age, although trends may vary by forest type. This pattern does not seem to hold in the Chamela region, where there is a temporary increase in soil inorganic N in recently established pastures (García-Méndez *et al.*, 1991), a decrease two years after pasture establishment (Ellingson *et al.*, 2000), and a stock in secondary forests after 30 yr of woody plant growth (this study) similar to that in primary TDF. Rodríguez *et al.* (2000) indicate that pools and potential N mineralization rates are responsive to the historic input of organic matter, both in quantity and quality.

The higher CO$_2$-C evolution in the top 2.5 cm of soil than in the lower 2.5-10 cm depth is consistent with results in primary forest soil (García-Oliva *et al.*, 1999). It is at that depth that microbial activity is greatest due to the transition between the surface litter layer and the mineral soil (Insam and Domsh, 1988). Morevoer, we found similar CO$_2$-C evolution in secondary forests of this study (44-49 µgCO$_2$-C/g/d) to that reported by Montaño-Arias *et al.* (2007) in incubations with primary forest soil from the Chamela region (40-51 µg/CO$_2$-C/g/d). This could suggest microbial community present at secondary forests is obtaining similar availability of organic compounds for organic matter decomposition. Finally, our results suggest that nitrification dominates N transformations in the Chamela forests, which in turn indicates that microorganisms are immobilizing NH$_4$-N and that C availability limits the mineralization process (Montaño-Arias *et al.*, 2007).


5.6 Ecosystem C and N pools

The estimates of these ecosystem pools at the NU sites, which include aboveground and belowground biomass and the soil profile, are the first for secondary forests in the Chamela region. The values represent the recovery potential of TDF in this area, since no activity was performed after disturbance at these sites. Total biomass (aboveground and roots) and the ecosystem C and N

pools of these secondary forests represent 48%, 59%, and 85% of the total biomass and ecosystem pools of primary TDF in the Chamela region reported by Jaramillo *et al.* (2003a; Table 6). These authors showed that primary forest conversion to pasture by slash and burn does not reduce soil C and N pools, but diminishes aboveground biomass. Aboveground C and N in secondary forests represent 40% and 23%, respectively, of that in primary forest. However, it is conceivable that disturbance with bulldozer results in significant soil C losses and thus soil C pools in secondary forests represent 72% of that in primary forest. In contrast, the fact that soil N pools are similar in secondary and primary forests suggests that secondary succession with woody species, many of them legumes, effectively restores N pools in the soil. Apparently then, the recovery of C and N pools with secondary succession proceeds in the following way: soil N > soil C > aboveground C > aboveground N.

It would seem that secondary succession with woody species plays a more relevant role in C than in N redistribution at the ecosystem level. Schlesinger (1997) showed that C pools are greater in soil than in the aboveground components. In this study, the soil C pool, excluding roots, represented 73% of the ecosystem C. If we compare this percentage to results in Jaramillo *et al.* (2003a) a pattern in the relative distribution of C in the ecosystem becomes apparent, in which secondary forests lie between the 54% in primary forest and 90% in pastures. In contrast, a much higher percentage of the ecosystem N pool occurs in the soil, either in primary forest (86%), secondary forest (97%) or pasture (98%).

Murphy and Lugo (1986) suggested that due to the simple structure of TDF and the coppicing capacity of species, they have the potential to return to a mature state faster than other vegetation types and therefore can be considered more resilient. However, resilience depends on the type of disturbance, especially when disturbance causes regeneration to depend more on propagule arrival than coppicing, as was the case in secondary forests of this study. If we consider the structure and diversity of these forests (Romero-Duque *et al.*, 2007) and results of the present study, we can argue that secondary forests in the Chamela region can more quickly recover biomass and C and N ecosystem pools than floristic diversity. This is consistent with what has been proposed for other tropical forests by

Guariguata and Ostertag (2001), Lawrence and Foster (2002), Pereira *et al.* (2003) and Molina and Lugo (2006).

Studies on TDF successional trends suggest that it may take between 45 yr for biomass and 95 yr for C for secondary forests to attain values similar to those in primary forest (Molina and Lugo, 2006). Vargas *et al.* (2008) estimated 50 yr for biomass and 70 yr for C in semievergreen TDF from the Yucatan peninsula, which is similar to the 40 to 60 years estimated for biomass by Read and Lawrence (2003a) in similar forests in the region. Alvarez-Yepiz et al. (accepted) estimated that secondary deciduous TDF required 50 to 100 years to attain similar biomass values to mature TDF in Northwest Mexico. Results from this study indicate that 30 yr old secondary forests in the Chamela region have attained 48% of primary forest biomass and C, including sites where there is no current use. Assuming a similar accumulation rate in the next decades, these secondary forests should require at least 60 yr to attain primary forest biomass. Although 30 years have apparently been sufficient for soil N pools to reach primary forest values and a very high percentage of primary forest soil C pools, data on the available N forms and microbial N transformations suggest that these soil processes have not reached primary forest values.

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TABLES

Table 1. Carbon (MgC/ha) and nitrogen (kgN/ha) pools in total aboveground biomass (Mg/ha) of secondary tropical dry forests in the Chamela region, Jalisco, Mexico representing three land-use types. P = pasture, HD = housing development, NU = no use. dbh = diameter at breast height. Values are means ± standard error. Means in the same row followed by different letters are statistically different. * = p<0.1, ** = p<0.05, *** = p<0.01, **** = p<0.005.

| Component | Biomasa | | | MgC/ha | | | kgN/ha | | |
|---|---|---|---|---|---|---|---|---|---|
| | HD | P | NU | HD | P | NU | HD | P | NU |
| Live biomasa | | | | | | | | | |
| Seedlings | 0.1 ± 0.0 | 0.1 ± 0.0 | 0.1 ± 0.0 | 0.03 ± 0.0 | 0.05 ± 0.0 | 0.05 ± 0.0 | 1.0 ± 0.4 | 1.6 ± 0.5 | 1.4 ± 0.0 |
| Woody | | | | | | | | | |
| 1-3 cm | 2.1 ± 0.3 | 2.6 ± 0.3 | 5.6 ± 0.2 b*** | 0.9 ± 0.1 | 1.1 ± 0.1 | 2.4 ± 0.0 b*** | 12.1 ± 0.8 | 9.2 ± 0.0 | 26.2 ± 0.8 c**** |
| 3.1-5 cm | 7.3 ± 0.9 | 7.2 ± 0.2 | 7.7 ± 4.4 | 3.1 ± 0.5 | 3.1 ± 0.1 | 3.3 ± 1.9 | 14.8 ± 0.7 | 15.1 ± 3.1 | 23.3 ± 17.1 |
| 5.1-10 cm | 20.3 ± 6.7 | 15.0 ± 6.2 | 19.2 ± 1.9 | 8.8 ± 2.7 | 6.4 ± 2.7 | 8.3 ± 1.1 | 24.2 ± 9.3 | 28.9 ± 14.2 | 35.1 ± 12.6 |
| >10 cm | 6.7 ± 1.5 | 10.7 ± 1.5 | 8.6 ± 1 | 2.8 ± 0.5 | 4.5 ± 0.6 | 3.7 ± 0.5 | 12.9 ± 8.3 | 17.9 ± 8.7 | 15.6 ± 0.5 |
| Total live | 36.5 ± 6.2 | 35.6 ± 7.2 | 41.3 ± 1.3 | 15.7 ± 2.5 | 15.2 ± 3.2 | 17.7 ± 0.3 | 65.2 ± 17.3 | 72.5 ± 19.5 | 101.0 ± 29.5 |
| Dead biomasa | | | | | | | | | |
| Standing dead | 2.0 ± 0.4 | 1.8 ± 0.2 | 4.9 ± 1 b* | 1 ± 0.2 | 0.9 ± 0.1 | 2.4 ± 0.5 b* | 15.6 ± 3.0 | 13.7 ± 2.6 | 37.9 ± 6.1 b** |
| Litter | | | | | | | | | |
| Fine | 0.7 ± 0.1 | 0.4 ± 0.2 | 0.7 ± 0.2 | 0.24± 0.0 | 0.14 ± 0.1 | 0.23 ± 0.1 | 13.1 ± 2.4 | 6.5 ± 2.3 | 11.6 ± 4.4 |
| Coarse | 1.3 ± 0.0 | 0.8 ± 0.2 | 1.3 ± 0.2 | 0.56 ± 0.0 | 0.35 ± 0.1 | 0.58 ± 0.1 | 17.3 ± 0.1 | 11.4 ± 2.8 | 25.0 ± 2.0 b** |
| Downed woody debris | | | | | | | | | |
| 2.5 - 7.6 cm sound | 0.4 ± 0.0 | 0.4 ± 0.2 | 0.4 ± 0.1 | 0.18 ± 0.0 | 0.2 ± 0.1 | 0.2 ± 0.1 | 2.8 ± 0.2 | 2.2 ± 0.7 | 2.5 ± 1.1 |
| > 7.6 cm sound | 1.4 ± 0.1 | 1.4 ± 0.5 | 1.5 ± 0.6 | 0.6 ± 0.0 | 0.6 ± 0.2 | 0.7 ± 0.2 | 8.8 ± 0.1 | 8.4 ± 0.4 | 13.5 ± 5.1 |
| Total necromass | 5.9 ± 0.6 | 4.9 ± 0.1 | 8.8 ± 1.2 b* | 2.6 ± 0.3 | 2.2 ± 0.0 | 4.0 ± 0.6 b* | 57.6 ± 5.7 | 42.3 ± 6.5 | 90.6 ± 9.9 b** |
| Total abovegroun biomass | 42.4 ± 6.8 | 40.5 ± 7.1 | 50.0 ± 0.0 | 18.3 ± 2.8 | 17.3 ± 3.2 | 21.7 ± 0.3 | 122.8 ± 23.0 | 114.8 ± 26.0 | 191.6 ± 19.6 |

Table 2. Carbon and nitrogen concentrations (mg/g) in aboveground biomass components of secondary tropical dry forests in the Chamela region. Jalisco. Mexico. representing three land-use types. P = pasture. HD = housing development. NU = no use. Values are means ± standard error. C concentration: *p = 0.07; N concentration: *p = 0.05

| Component | mgC/g | | | mgN/g | | |
|---|---|---|---|---|---|---|
| | P | HD | NU | P | HD | NU |
| Seedlings | 421.3 ± 2.5 | 410.6 ± 3.8 | 426.6 ± 2.8* | 14.6 ± 0.6 | 16.3 ± 0.5 | 13.1 ± 0.4* |
| Total woody | 428.2 ± 4 | 426.8 ± 8.8 | 427.9 ± 3.3 | 2.3 ± 0.2 | 2.7 ± 0.4 | 2.8 ± 0.5 |
| Standing dead | 480.5 ± 8.2 | 488 ± 6.3 | 487.3 ± 3.9 | 7.7 ± 0.4 | 7.7 ± 0.0 | 7.8 ± 0.3 |
| Litter | 372.3 ± 7.8 | 380.4 ± 5.5 | 377 ± 1.9 | 14.5 ± 0.7 | 15.5 ± 0.6 | 15.2 ± 0.6 |
| Downed debris | 450 ± 10.6 | 444.8 ± 14 | 449.6 ±10.8 | 6.3 ± 1.7 | 6.7 ± 0.4 | 7.9 ± 0.4 |

Table 3. Carbon and nitrogen concentrations (%) and C:N ratios in roots of secondary tropical dry forests in the Chamela region. Jalisco. Mexico. NU1 and NU2 are the two replicate sites of the NU (no use) land-use type.

| Root | %C | | %N | | C:N | |
|---|---|---|---|---|---|---|
| Diameter Category | NU1 | NU2 | NU1 | NU2 | NU1 | NU2 |
| ≤1 mm | 40.57 | 39.99 | 1.78 | 1.48 | 23 | 27 |
| 1.1-5 mm | 40.53 | 40.91 | 1.57 | 1.37 | 26 | 30 |
| 5.1-10 mm | 41.86 | 41.24 | 1.46 | 1.22 | 29 | 34 |
| 10.1-20 mm | 42.97 | 41.34 | 1.25 | 1.18 | 34 | 35 |
| >20 mm | 43.14 | 44.17 | 1.18 | 0.75 | 37 | 59 |

Table 4. Soil C and N concentrations (%) and pools (MgC/ha, kgN/ha) after soil bulk density, in secondary tropical dry forests of the Chamela region, Jalisco, Mexico, representing three land-use types. P = pasture. HD = housing development. NU = no use; Values are means ± standard error.

| Component | %C | mgN/g | Carbon pool (MgC/ha) | | | Nitrogen pool (KgN/ha) | | |
|---|---|---|---|---|---|---|---|---|
| | | | P | HD | NU | P | HD | NU |
| 0-10 cm | 1.7 ± 0.1 | 2.0 ± 0.1 | 20.2 ± 6.4 | 20.6 ± 8.9 | 23.2 ± 3.3 | 2450 ± 714 | 2232 ± 349 | 2591 ± 189 |
| 10-20 cm | 1.2 ± 0 | 1.3 ± 0 | 16.5 ± 6.9 | 10.1 ± 1.8 | 16.2 ± 0.9 | 2028 ± 619 | 1186 ± 9 | 1778 ± 281 |
| 20-40 cm | 0.8 ± 0.1 | 1.0 ± 0 | 13.9 ± 5.5 | 9.4 ± 2.0 | 9.6 ± 2.6 | 1140 ± 45 | 1257 ± 21 | 1109 ± 87 |
| 40-60 cm | 0.6 ± 0 | 0.8 ± 0.1 | 10.3 ± 3.1 | 9.3 ± 2.3 | 5.7 ± 1.1 | 1195 ± 43 | 1117 ± 279 | 731 ± 250 |
| Total soil 0-60 cm | 1.1 ± 0.2 | 1.3 ± 0.3 | 60.9 ± 31 | 49.5 ± 21.0 | 54.7 ± 5.0 | 7114 ± 1953 | 5792 ± 930 | 6208 ± 361 |

Table 5. Ammonium (kg$NH_4^+$/ha) and nitrate (kg$NO_3^-$/ha) pre-incubation pools, potential net mineralization (µg$NH_4^+$ + µg$NO_3^-$/g soil), potential net nitrification (µg $NO_3^-$/g soil) after 15-day incubations, and $CO_2$-C evolved (µg$CO_2$-C/g soil/day) of secondary tropical dry forests soils samples in the Chamela region, Jalisco, Mexico, representing three former land-use types:  HD = Housing development. P = pasture. NU = no use. Values are means ± standard error.

| Variable | P | | HD | | NU | |
|---|---|---|---|---|---|---|
| | 0-2.5 cm | 2.5-10 cm | 0-2.5 cm | 2.5-10 cm | 0-2.5 cm | 2.5-10 cm |
| $NH_4^+$ | 4.1 ± 0.7 | 3.5 ± 1.2 | 3.9 ± 0.1 | 2.8 ± 0.0 | 3.1 ± 0.7 | 2.4 ± 0.3 |
| $NO_3^-$ | 2.3 ± 0.3 | 1.3 ± 0.4 | 2.4 ± 0.8 | 1.9 ± 0.1 | 2.8 ± 0.1 | 1.2 ± 0.4 |
| P-Min | -1.1 ± 0.1 | - 0.9 ± 0.1 | - 0.7 ± 0.3 | - 0.9 ± 0.3 | - 1.1 ± 0.5 | - 0.7 ± 0.4 |
| P-Nit | 0.9 ± 0.5 | 0.7 ± 0.5 | 1.2 ± 0.3 | 0.6 ± 0.2 | 0.7 ± 0.1 | 0.7 ± 0.2 |
| $CO_2$-C | 26.1 ± 0.7 | 18.3 ± 1.7 | 30.7 ± 6.2 | 17.9 ± 3.4 | 25.2 ± 1.6 | 19.6 ± 2.4 |

Table 6. Biomass and nutrient pools of different land covers in the tropical dry forest region of Chamela, Jalisco, Mexico. P = pasture. HD = housing development. NU = no use. TAGB = total aboveground biomass (Mg/ha); TBGB = total belowground biomass (Mg/ha); C = carbon pool (MgC/ha); N = nitrogen pool (kgN/ha). Pasture and primary forest data are from Jaramillo *et al.* (2003a).

| Component | Pasture | Secondary forest | | | Primary forest |
|---|---|---|---|---|---|
| | | P | HD | NU | |
| TAGB | 22 | 40 | 42 | 50 | 112 |
| TBGB | 6 | - | - | 12 | 17 |
| Root:Shoot | 0.4 | - | - | 0.2 | 0.2 |
| Total Biomass | 28 | - | - | 62 | 129 |
| TAG-C pool | 10 | 18 | 19 | 23 | 58 |
| TBG-C pool | 2 | - | - | 5 | 7 |
| TAG-N pool | 126 | 135 | 142 | 218 | 940 |
| TBG-N pool | 44 | - | - | 138 | 106 |
| Soil C pool | 94 | 61 | 49 | 55 | 76 |
| Soil N pool | 5692 | 7114 | 5792 | 6208 | 6659 |

CAPTIONS TO FIGURES

Figure 1. Site location in the study area. Modified from the map by Noguera et al. (2002).

Figure 2. Root biomass (Mg/ha) by size-class distributed in top 40 cm of soil in two secondary tropical dry forests in the Chamela region. Jalisco. Mexico. representing the no use (NU) land-use type. Each value represents the mean of five replicate samples per site.
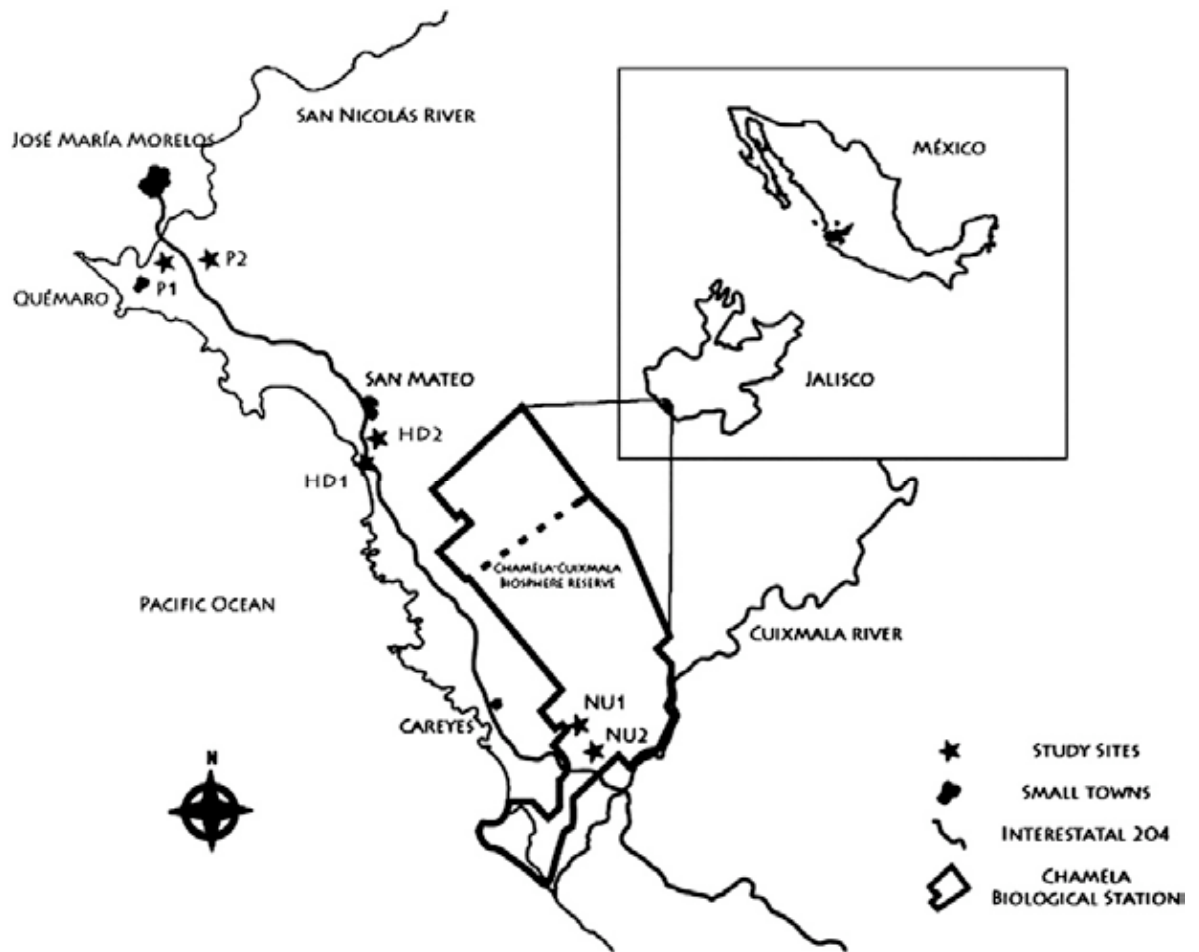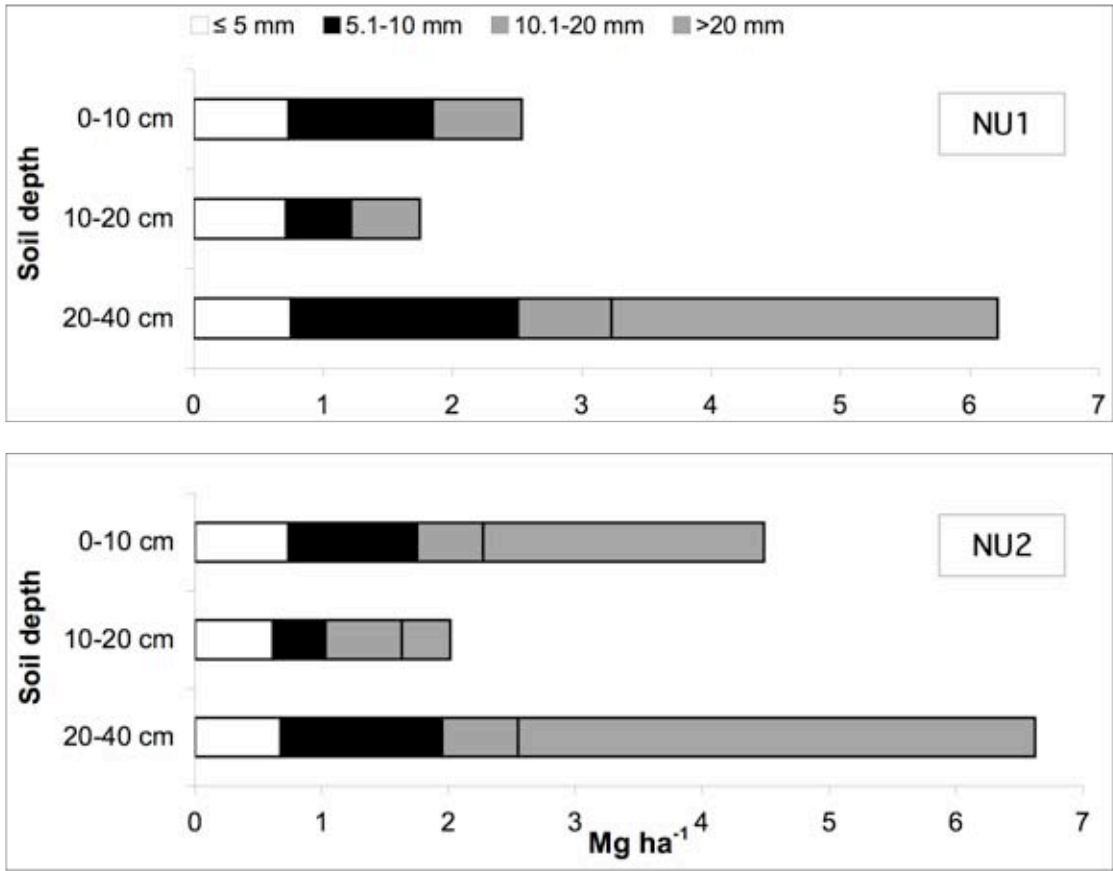
FIGURES



Figure 1.

FIGURES



Figure 1.

Figure 2.

# Capítulo IV

**Consideraciones finales**

# CONSIDERACIONES FINALES

El presente estudio tuvo dos objetivos generales: 1) comparar la estructura de la vegetación y la diversidad y 2) la biomasa y los almacenes de carbono y nitrógeno. así como el potencial neto de mineralización de nitrógeno del suelo. de bosques secundarios en la región de Chamela (Jalisco. México). derivados del desmonte con maquinaria (bulldozer) del bosque tropical seco . Estos bosques secundarios estuvieron sujetos a diferentes usos previos al abandono: 1) no uso (NU). 2) praderas (P) y 3) un desarrollo para vivienda (HD). Se consideró que la intensidad de uso de estos bosques. incluyendo el desmonte con bulldozer. seguía la secuencia: P > HD > NU. por lo que se esperaba encontrar mayor diversidad. densidad. área basal. biomasa y almacenes de carbono y nitrógeno en los sitios que no fueron usados luego del disturbio.

La falta de diferencias significativas entre los tipos de uso en variables como la densidad. el área basal. la biomasa y los almacenes de C y N. indica que las diferencias que pudieron existir inicialmente debidas a los efectos a corto plazo de los usos. han desaparecido luego de 30 años de regeneración de estos bosques. Las diferencias registradas en los árboles de 1-3 cm DAP que siguen el patrón (P ≈ HD) < NU para todas las variables. son interpretadas mejor. a la luz del uso actual del que son objeto estos bosques secundarios. Es decir. P y HD son aún objeto de tala selectiva y forrajeo. Así. el 52. 88 y 100% de los individuos de 1-3 cm de DAP de P. HD y NU. respectivamente. correspondió a individuos de especies del bosque primario y el porcentaje restante correspondió a individuos de *M. arenosa*. A diferencia de Ortíz (2001). quien sugiere que la sucesión en estos bosques está arrestada por la prevalencia de *M. arenosa*. los resultados del presente estudio indican que 30 años después del disturbio severo y de ser objeto de diferentes usos. la regeneración de estos bosques es un fenómeno activo. pero en diferentes grados. Esto coincide con lo reportado por Burgos y Maass (2004). quienes describen a los bosques secundarios de la zona. como comunidades persistentes en el tiempo. pero que eventualmente pueden regenerar un bosque primario.

Guariguata y Ostertag (2001) señalan que la sucesión secundaria en el Neotrópico se ha descrito. en general. desde una perspectiva estructural. haciendo un mayor énfasis en las especies o grupos de especies que dominan cada estado de la sucesión. Pero sostienen que existe poca información desde la perspectiva funcional y mucho menos estudios que conjunten las características funcionales y estructurales durante la sucesión. Los mismos autores señalan que los ecosistemas pueden recuperar más rápido las características funcionales que la composición florística existentes previas al disturbio. Sin embargo. los resultados del presente trabajo indican que ni la riqueza. ni los aspectos funcionales relacionados con las partes aéreas del bosque se han recuperado. luego de 30 años de regeneración. Esto sugiere que una estrategia de restauración del bosque tropical caducifolio. basada en los resultados de este estudio. debería incorporar aspectos tanto de la estructura como del funcionamiento. especialmente cuando éste ha sido objeto de un disturbio severo y de un uso intensivo. Dado que *M. arenosa* es una especie agresiva y de rápido crecimiento en sitios perturbados y que las especies del bosque primario se regeneran bajo su dosel. se podría considerar controlar la regeneración *M. arenosa* para favorecer la regeneración de especies del bosque primario. especialmente de leguminosas y otras especies. que además pueden influenciar la dinámica del N del ecosistema.

El presente estudio representa la primera cuantificación de los almacenes ecosistémicos de C y N en bosques tropicales caducifolios secundarios de México. Los resultados muestran el potencial de recuperación de la estructura y función del bosque tropical caducifolio en la zona. luego de un disturbio severo y de experimentar diferentes tipos de uso. Los resultados de este estudio. especialmente los de los sitios que no se usaron luego del disturbio muestran que. aunque el proceso de regeneración es lento. el potencial de recuperación es alto. Esto sugiere que para entender de manera integral la regeneración de este ecosistema y poder abordar su restauración. es preciso complementar esta clase de estudios con enfoques más dinámicos. como la sucesión. Ello permitirá entender. entre otras cosas. los factores que controlan la regeneración de *M. arenosa* y sus interacciones con otras especies. así como. la dinámica de los procesos funcionales durante la sucesión.

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Ortiz, T. 2001. Estructura arbórea en sitios perturbados y caracterizados por la presencia de Mimosa arenosa (Willd.) Poir. var leiocarpa (D.C.) Barneby, en el bosque tropical seco de la cosa de Jalisco, México. Tesis de Licenciatura. Facultad de Ciencias. UNAM. México.

# ANEXOS

# Forest Ecology and Management

# Structure and diversity of secondary tropical dry forests in Mexico, differing in their prior land-use history

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## Abstract

We compared the structure and diversity of secondary tropical dry forests, growing in sites cleared by bulldozer 30 years ago and subjected to different land uses prior to abandonment: (a) housing development (HD), (b) pasture (P), and (c) no use (NU). We sampled two forest sites representing each of the three former land-use types (i.e., a total of six sites) and measured the diameter at breast height (dbh) of all stems with dbh ≥1 cm and at least 2 m in height. All individuals were identified to species and classified into each of four dbh sizes-classes: 1–3, 3–5, 5–10, and >10 cm. No major differences in structure or diversity were evident among land-use types. Total tree densities varied from $2575 \pm 55$ to $4745 \pm 985$ individuals/ha and total basal areas ranged from $12.5 \pm 2.6$ to $14.6 \pm 0.3$ m²/ha (mean and S.E.). Neither one differed significantly ($p < 0.05$) among land-use types. Overall, the most abundant tree size-class was the 1–3 cm dbh (47% of the total number of trees), whereas trees greater than 10 cm dbh were the least abundant (4%). We found significantly higher density and basal area ($p = 0.01$) in NU than in HD and P only in the smallest trees (1–3 cm dbh). We identified a total of 87 species in 28 families. The Leguminosae plant family had the greatest species richness and number of individuals in all land-use types. The HD land-use type showed lower total species richness than P and NU only with two of the four nonparametric estimators. Observed species richness decreased as dbh increased in all land-use types. At least 5 legumes were among the 10 most dominant species in all land-use types, of which the non-native *Mimosa arenosa* was the most dominant one. It represented between 42% and 52% of the total basal area in each land-use type. The secondary forests have reached, on average, 74% and 22% of the total density and basal area, respectively, of an average primary tropical dry forest of Mexico. The high number of individuals 1–3 cm dbh (48% of the total and 83% of the species) suggest that regeneration is occurring in all land-use types, although to different degrees. The absence of small individuals of *M. arenosa* and a high abundance of primary forest species at NU, suggest that *M. arenosa* is being replaced at these sites.
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*Keywords:* Chamela; Disturbance; Heavy machinery; *Mimosa arenosa*; Regeneration

## 1. Introduction

Tropical dry forest (TDF) has been subjected to widespread alteration because human habitation and agricultural activities have developed in a large portion of its distribution (Maass, 1995; Murphy and Lugo, 1995). Such anthropogenic pressure has triggered a number of studies on ecosystem recovery after disturbance by agriculture (Donfack et al., 1995; Maass, 1995; Miller and Kauffman, 1998a,b), grazing (Gerhardt, 1993; Aide et al., 1995), fire (Sampaio et al., 1993), and tree plantations (Mizrahi et al., 1997). More recently, attention has been given

to long-term (i.e. decadal) vegetation successional responses to natural or anthropogenic disturbances like slash-and-burn, grazing, and agriculture (e.g. Guariguata and Ostertag, 2001; Kennard, 2002; Lawrence and Foster, 2002; Pereira et al., 2003; Ruiz et al., 2005). Some studies have shown that TDF more quickly recovers basal area and biomass than species composition after agriculture and/or grazing (Guariguata and Ostertag, 2001; Lawrence and Foster, 2002; Pereira et al., 2003). Less attention has been given to vegetation responses to more severe anthropogenic disturbances like housing developments (e.g., Molina and Lugo, 2006), in which disturbance occurs with the use of heavy machinery to fell forests. The use of bulldozers generally causes diminution of soil porosity, water infiltration, soil moisture availability, aeration and rooting space, and can have substantial effects on soil fertility

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(Pinard et al., 2000; Page-Dumroese et al., 2006). It can also reduce soil physical quality, increase erosion, and can result in nutrient and organic matter loss (Zabowski et al., 1994; Kozlowski, 1999; Pinard et al., 2000). Site modifications produced by bulldozer use can substantially retard forest recovery (Guariguata and Dupuy, 1997).

Tropical dry forest is one of the most extensive and important tropical vegetation types in Mexico where it forms a nearly continuous strip on the Pacific coast, with major areas in western Jalisco and in the Balsas and Santiago river basins (Rzedowski, 1978; Challenger, 1998). It is also present in the Yucatán Peninsula in discontinuous forest patches. About 73% of the TDF area in Mexico shows, from light degradation up to total alteration of structure and function (Trejo and Dirzo, 2000), the latter associated to management. Such management commonly involves conversion to pasture and agricultural land (Challenger, 1998), by the use of machinery in the plains and through slash-and-burn in the hilly landscapes. Abandonment of unproductive lands promotes a landscape mosaic in which thorny plant communities and secondary forests, associated with the loss of native components, persist in the mid- and possibly the long-term (Rzedowski, 1978; Burgos and Maass, 2004). Thus, studies have recently focused on secondary forests in different regions of Mexico, such as the Yucatan Peninsula (Lawrence and Foster, 2002) and the state of Morelos (Saynes et al., 2005).

Studies on TDF management through slash-and-burn in the Chamela region of Jalisco have reported abundant legume tree seedlings belonging to the *Acacia* and *Mimosa* genera 2 years after disturbance (Miller and Kauffman, 1998a,b). They suggested several conditions could explain this, including the low site aptitude for native tree establishment and the absence of re-sprouting at high fire intensity. In addition, Ortiz (2001) reported *Mimosa arenosa* (wild) Poir. var. *leiocarpa* Barneby, a non-native species, as the most dominant species in secondary forest sites in this region and suggested succession was arrested at these sites. To date, no attention has been given to long-term vegetation responses to severe anthropogenic disturbances after land abandonment in this region, despite that primary forest in Chamela is more species-rich than other dry forests in the Neotropics (Gentry, 1995). It remains an open question the degree to which species richness and forest structure recover after disturbance in this highly diverse tropical dry forest.

The Mexican government promoted the clearing of TDF by bulldozer during the 1970's along the Pacific coast of Jalisco. These areas were used for agriculture, cattle ranching, and for tourism and housing. Later abandonment of some of these sites allowed secondary vegetation to develop and provide an excellent opportunity to evaluate the regeneration of TDF. Thus, the overall objective of this study was to compare vegetation structure and diversity of secondary tropical dry forest sites, originally cleared by bulldozer, and subjected to different land-use practices prior to abandonment: (1) no use, (2) pasture, and (3) housing development. We expected higher diversity, density, and basal area in sites not subjected to land use after disturbance.

## 2. Study area description

The study was conducted in the Chamela region, on the Pacific coast of Jalisco, Mexico. The climate is highly seasonal with a pronounced dry season. Precipitation averages 746 mm (1983–2004), distributed mostly from June to October; on average annually, about 31% of the total annual precipitation falls in September (García-Oliva et al., 1995, 2002). Mean temperature is approximately 25 °C, with a less than 5 °C difference between the coolest and warmest months. The landscape consists of low hills (50–160 m elevation) with steep convex slopes. Upland soils are relatively young, shallow (0.5–1 m depth) Typic Ustorthents. They are poorly structured, sandy loam in texture, derived from rhyolite, and have a pH of 6–6.5 (Solís, 1993). The flora of the Chamela region is comprised of at least 1149 vascular plant species, in 572 genera, and 125 families (Lott, 1993). The plant families with the greatest species richness are Leguminosae, Euphorbiaceae, Rubiaceae, and Bignoniaceae, and more than 10% of the species are endemic to the states of Jalisco and Colima, Mexico.

## 3. Methods

After extensive road surveying of the area and interviewing local residents and site owners, we selected six secondary vegetation sites that, according to their accounts, had been originally covered by primary dry forest. These sites were subjected to different land uses but shared some features. The primary forest was cleared by bulldozer and burned approximately 30 years ago. All secondary forest sites had similar time since disturbance (24–27 years), elevation (40–70 masl), slope (15–35%), and aspect (south-facing slope), but had different land uses. These uses were: (a) housing development, (b) pasture, and (c) no use. Housing development (HD) sites were cut and burned for a construction project. The project failed and the sites were abandoned. Before abandonment, some streets were built with machinery and a secondary forest developed on the land originally designated to build houses. Since then, these sites have been subjected to sporadic selective cutting and cattle grazing. They were located in the Ejido San Mateo, 1 km away from the San Mateo village and approximately 10 km North of the Chamela Biological Station of the Instituto de Biología, UNAM (19°30′N, 105°03′W, Fig. 1). At the pasture sites (P), primary forest was cut and burned and the sites were seeded with the tropical forage grasses *Panicum maximum* Jacq. (Guinea grass) and *Pennisetum ciliare* L. (Buffel grass) for cattle production. These sites were grazed by cattle for 6 years and abandoned. They have been subjected to sporadic selective cutting and grazing since then. These sites were located near Quémaro village, approximately 20 km N of the Biological Station. The sites designated as no use (NU) were cut and burned to justify possession of the land and were abandoned. In 1993, these sites were included within the 13000 ha Biosphere Reserve of Chamela-Cuixmala (19°24′N, 104°58′W), 11 km S of the Station. Unlike the HD and P sites, the NU land-use type did not involve management after primary TDF was felled; therefore, we consider these sites as having a lower intensity of
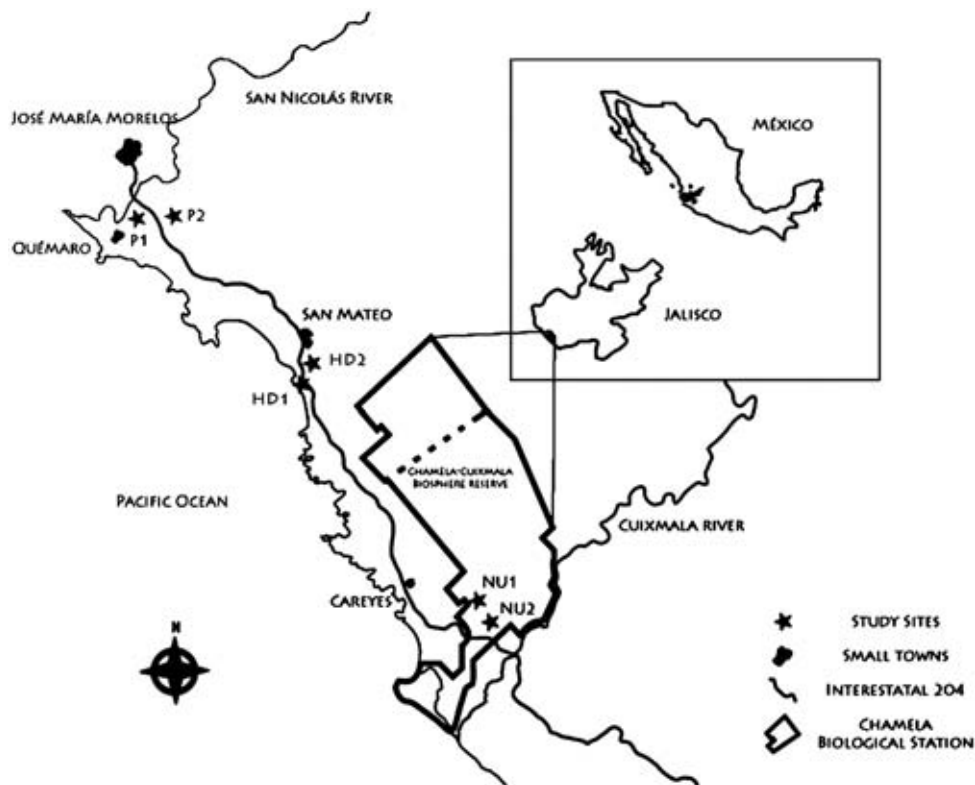
Fig. 1. Site location in the study area. Modified from the map by Noguera et al. (2002).

disturbance than the other land-use types. The secondary forests will be identified subsequently in the text by the abbreviation of their prior land use (HD, P, and NU).

We sampled two forest sites representing each of the three former land-use types (i.e., a total of six sites). We established ten 40 m × 2.5 m transects (0.1 ha), at least 7.5 m apart from each other, at each site. We measured the diameter at breast height (dbh) of all stems with dbh $\geq$ 1 cm and at least 2 m in height in each transect. All individuals were identified to species and classified into each of four dbh sizes-classes: 1–3 cm, 3–5 cm, 5–10 cm, and >10 cm. This dbh classification aided to evaluate successional trends at the sites. The data from all transects per site were used to calculate absolute and relative density (ind/ha) and basal area (m²/ha), species richness, species similarity, and dominance. The importance value (IV) was calculated as: relative abundance + relative frequency + relative basal area for each species, where abundance was the number of individuals of the species at each site. Maximum IV was 300%.

We used nonparametric methods provided by Colwell's EstimateS program to approach true species richness. We used three estimators of species richness, as suggested for woody regenerating communities in secondary rain forests by Chazdon et al. (1998): incidence-based coverage (ICE) and Chao 2 estimators based on presence–absence of species and the abundance-based coverage estimator (ACE). For a complete description of these estimators see Chao and Lee (1992), Colwell and Coddington (1994), Chazdon et al. (1998), Gotelli and Colwell (2001). To compare species composition among the three land-use types we used Sørensen quantitative index

and to compare species dominance we used rank/abundance plots (Magurran, 2004).

We used one-way ANOVA to examine differences in total density and total basal area among land-use types. This approach was also used to compare density and basal area among land-use types within each dbh size-class, and to examine differences in diversity with each estimator. In all cases, the experimental unit was the site, thus $n = 2$ for each land-use type in statistical analyses. When the ANOVA indicated a significant land-use effect ($p < 0.05$), means were compared with a Tukey *post-hoc* test. When data did not satisfy ANOVA assumptions after transformation (Sqr or $\log_{10}$), differences were assessed with a Kruskal–Wallis test. When a significant effect ($p < 0.05$) occurred, a mean rank multiple comparison of all groups was used. The slopes of rank/abundance plots were compared with a Kolmogorov–Smirnov two-sample test. All statistical analyses were performed with Statistica 6.1.

## 4. Results

### 4.1. Density and basal area

Total tree densities including all size classes were 2575 ± 55, 2980 ± 30, 4745 ± 985 individuals/ha (mean and S.E.) in HD, P, and NU land-use types, respectively, and were not statistically different ($p > 0.1$). Inter-site variation in tree densities was low in HD and P land-use types (coefficients of variation (CV) of 2.1 and 1.0%, respectively), but was very high (CV = 20.8%) in NU. Overall, the most abundant tree size-class
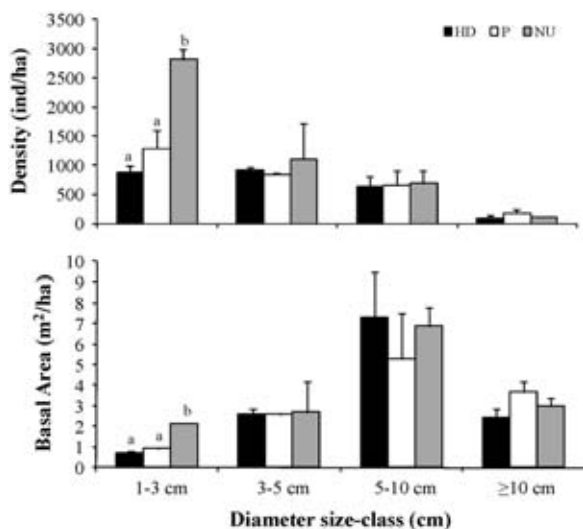
Fig. 2. Density (individuals/ha) and basal area (m²/ha) of trees in secondary tropical dry forests in the Chamela region, Jalisco, Mexico, representing three former land-use types. HD, housing development; P, pasture; NU, no use, dbh, diameter at breast height. Values are means ± standard error. Different letters indicate statistically significant differences ($p \leq 0.01$) in the 1–3 cm dbh size-class. There were no significant differences among land-use types in other dbh size-classes.

was the 1–3 cm dbh (47% of the total number of trees), whereas trees greater than 10 cm dbh were the least abundant (4%). Only 20 individuals (<1%) were greater than 15 cm dbh. The one-way ANOVA within each dbh class indicated a significantly higher density in NU than in HD and P only in the smallest trees (1–3 cm dbh; $F_{2,3} = 23.6$, $p = 0.01$; Fig. 2a).

Total tree basal areas were similar and amounted to 13.1 ± 2.2, 12.5 ± 2.6 and 14.6 ± 0.3 m²/ha in HD, P, and NU secondary forests, respectively. In contrast to density, basal area of NU sites was similar (CV = 2.0%) between them, whereas between-site variation in the HD and P land-use types was higher (CV = 16.8% and 20.8%, respectively). Overall, trees in the 5–10 cm size-class comprised the greatest percentage of the basal area (Fig. 2b), representing from 30 to 61%. As was the case with density, there were significant differences in trees 1–3 cm dbh among land-use types ($F_{2,3} = 54$; $p = 0.004$). Again, the NU land-use type showed a significantly higher basal area than HD and P (Fig. 2b).

### 4.2. Diversity

We identified a total of 87 species in 28 families (1999 individuals, see Appendix). There were 18 families in the HD land-use type represented by 46 species and 501 individuals, 21 families in the P land-use type represented by 51 species and 574 individuals, and 23 families in the NU land-use type represented by 54 species and 924 individuals (Appendix). The Leguminosae had the greatest species richness and number of individuals in all land-use types. This plant family represented 33% of the species in HD, 31% in P, and 30% in NU, and represented more than 50% of the total number of individuals in each of the three land-use types. Euphorbiaceae and Rubiaceae were present in secondary forests with considerably lower species richness ($\leq$5 spp.) and with a lower percentage of individuals (<12%).
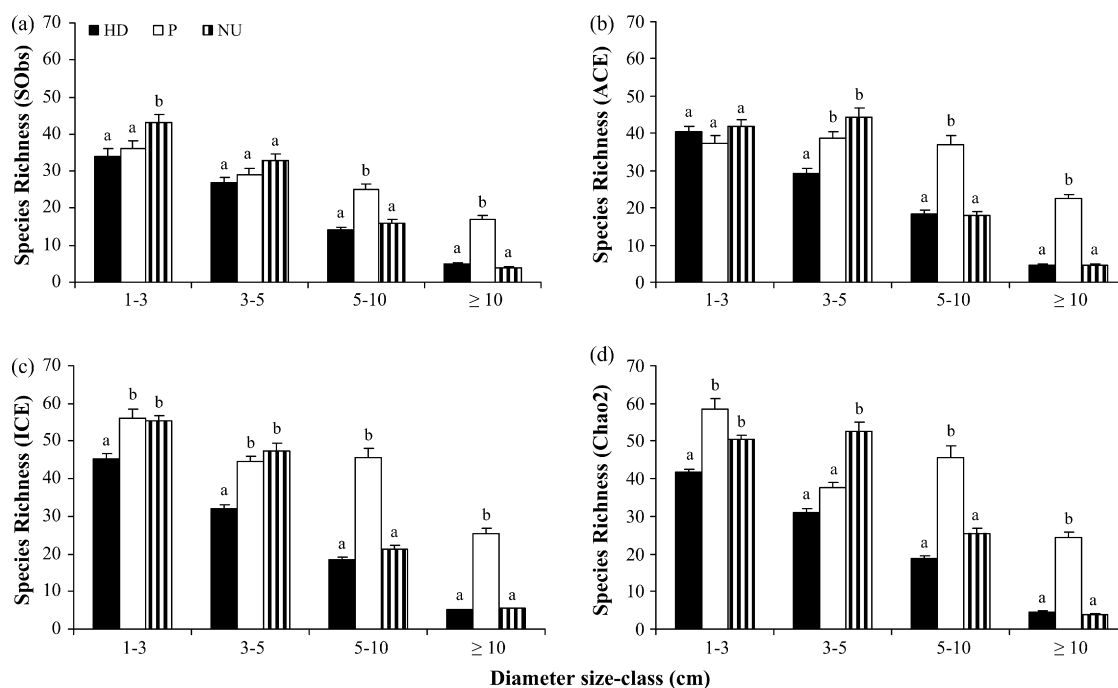


Fig. 3. Observed and estimated (Sobs, ACE, ICE and Chao2) species richness for each dbh size-class in secondary dry tropical forests in the Chamela region, Jalisco, Mexico, representing three former land-use types. HD, housing development; P, pasture; NU, no use. Different letters indicate a statistically significant difference ($p \leq 0.05$) among the land-use types.
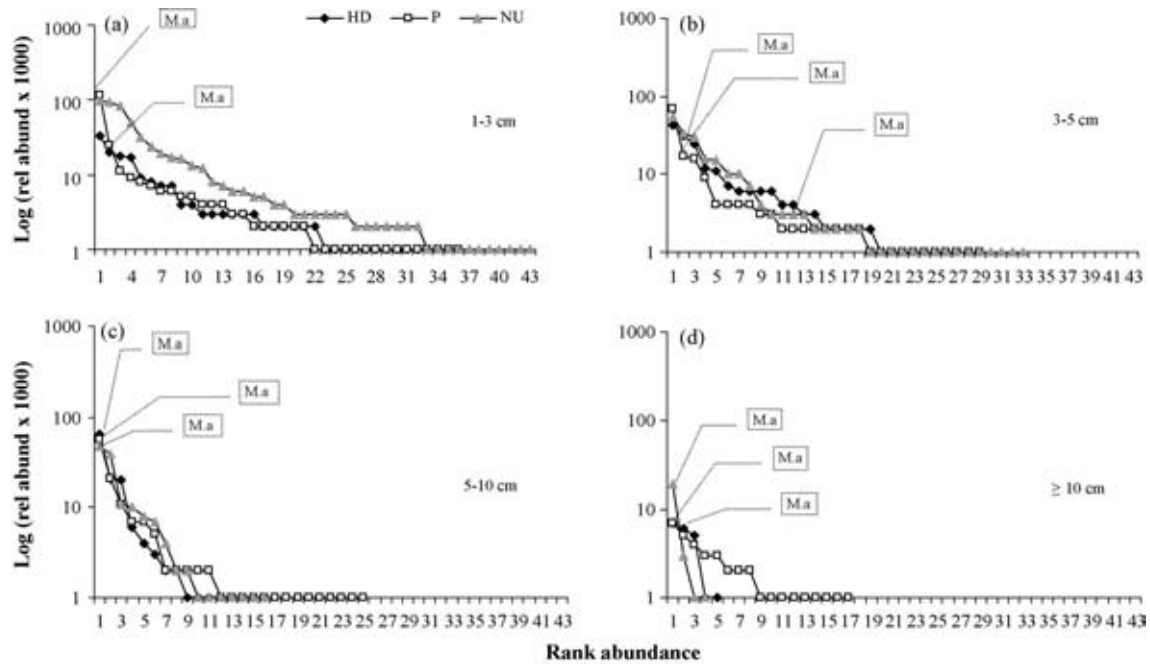
Fig. 4. Rank/abundance plot for each dbh size-class in secondary dry tropical forests in the Chamela region, Jalisco, Mexico, representing three former land-use types: HD, housing development; P, pasture; NU, no use; M.a, *Mimosa arenosa*. Note, *M. arenosa* is not present in NU in the 1–3 cm dbh size-class.

The nonparametric estimators indicated significant differences among land-use types in total species richness based on ICE ($KW_{(2,60)} = 20$, $p < 0.001$) and Chao2 ($F_{(2,60)} = 6.3$, $p < 0.01$) estimators, but not with ACE ($KW_{(2,60)} = 3.2$ $p = 0.2$) and Sobs ($KW_{(2,60)} = 3.5$ $p = 0.18$). The HD land use tended to show lower total species richness than P and NU. Observed species richness decreased as dbh increased in all land-use types (Fig. 3a). When comparisons among land-use types were performed by dbh size-classes, HD generally showed lower species richness in the smaller size-classes (<5 cm dbh; Fig. 3b–d). The highest species richness in the two larger size-classes (>5 cm dbh) occurred in the P land-use type (Fig. 3a–d). The Sørensen quantitative index showed that HD and P shared 56%, HD and NU shared 22%, and P and NU shared 32%, of the species.

Five species represented more than 50% of the total number of individuals in this study: *M. arenosa*, *Lonchocarpus lanceolatus* Benth., *L. minor* Sousa, *Apoplanesia paniculata*

Presl., and *Cordia alliodora* (Ruiz and Pav.) Oken. *M. arenosa* accounted for 26% and 44% of the total number of individuals in HD and P, respectively, but only 8% in NU. However, this species represented between 42% and 52% of the total basal area in each land-use type. This species showed a generally high relative abundance in HD and P in most dbh size-classes (Fig. 4a–d). In contrast, it was absent in the smallest size-class (1–3 cm dbh) in NU, but represented up to 79% of the relative abundance in the largest size-class (>10 cm) (Fig. 4a and d). Dominance also varied among dbh size-classes (Fig. 4). It was lower in the smallest trees and increased in the larger (≥5 cm dbh) size-classes. NU showed the lowest dominance in the smaller dbh size-class (1–3 cm) and P the highest in the >10 cm dbh size-class, but differences among land-use types were not significant. As indicated by the importance value, at least 5 legumes, common in primary forest, were among the 10 most dominant species in all land-use types (Table 1).

Table 1

Importance value (%) of the top 10 dominant species in secondary tropical dry forests in the Chamela region, Jalisco, Mexico, representing three land-use types

| Species | IV-HD | Species | IV-P | Species | IV-NU |
|---|---|---|---|---|---|
| *Mimosa arenosa* | 169 | *Mimosa arenosa* | 185 | *Mimosa arenosa* | 133 |
| *Apoplanesia paniculata* | 99 | *Apoplanesia paniculata* | 89 | *Lonchocarpus minor* | 123 |
| *Lonchocarpus minor* | 88 | *Amphypterigium adstringens* | 63 | *Lonchocarpus lanceolatus* | 121 |
| *Amphypterigium adstringens* | 69 | *Caesalpinia eriostachys* | 57 | *Croton pseudoniveus* | 99 |
| *Caesalpinia eriostachys* | 57 | *Ipomoea wolcottiana* | 36 | *Cordia alliodora* | 98 |
| *Casearia tremula* | 42 | *Cnidosculus spinosus* | 36 | *Caesalpinia eriostachys* | 88 |
| *Lonchocarpus eriocarinalis* | 41 | *Chloroleucon mangense* | 34 | *Piptadenia constricta* | 88 |
| *Caesalpinia platyloba* | 39 | *Coccoloba liebmanii* | 34 | *Casearia corymbosa* | 60 |
| *Jatropha sympetala* | 35 | *Heliocarpus pallidus* | 33 | *Guapira macrocarpa* | 59 |
| *Diphysa occidentalis* | 33 | *Caesalpinia coriaria* | 32 | *Casearia tremula* | 38 |

HD, housing development; P, pasture; NU, no use. Maximum IV = 300% = (relative abundance + relative frequency + relative basal area).

## 5. Discussion

We expected land use to have a long-term impact on the structure and diversity of secondary forests in the Chamela region. Apparently, however, potential initial differences in secondary succession due to the short-term effects of different land uses have mostly disappeared after nearly 30 years of secondary succession. No major differences among land-use types were evident, except in revealing cases which can be best interpreted as the result of current land use patterns of the secondary forests (see below). Our results also showed key similarities and differences with primary forest structure and diversity, which are discussed below.

### 5.1. Structure

Total density including all individuals $\geq 1$ cm dbh in these secondary forests (2575–4745 ind/ha) lies within the range reported for the same diameter classes in primary TDF in Mexico (2030–7770 ind/ha), but basal area (12.5–14.6 m$^2$/ha) is well below (18.5–103.1 m$^2$/ha; Trejo, 1998). Thus, secondary forests in our study have reached, on average, about 74% of the density and 22% of the basal area of an average primary TDF in Mexico (Trejo, 1998). This percentage differs from findings in TDF of Yucatán, Mexico, where after 25 years of re-growth, basal area of secondary forest (individuals $\geq 1$ cm dbh) represented 63% of that in primary TDF of the region (Lawrence and Foster, 2002). This could be related to the higher annual precipitation (1125 mm), less severe disturbance (slash-and-burn), and different land use (maize cultivation) in the Yucatán than in the secondary forests of our study, which were subjected to disturbance by bulldozer (all sites) and are still subjected to some wood extraction (HD and P) or grazing (P). Density and basal area of individuals $\geq 3$ cm dbh in secondary forests in this study represented 20% and 40%, respectively, of those in primary TDF in Chamela (Jaramillo et al., 2003). The percentages are much lower for large trees ($\geq 10$ cm dbh), with 5% and 14%, respectively, of values of primary TDF in this region (Durán et al., 2002). Thus, structural differences between secondary and primary forests of the region are greater, if the larger trees are considered in the comparison.

The high number of individuals 1–3 cm dbh in our study is similar to results reported by Trejo (1998), who found that individuals $< 3$ cm dbh constituted up to 50% of the total number of individuals in primary TDF in México. The high densities of small individuals (1–3 cm dbh) in primary TDF could be reflecting some degree of disturbance, as reported by Trejo and Dirzo (2000). Individuals in the 1–3 cm dbh size-class have been frequently ignored in studies of structure and composition of secondary TDF (e.g. Nansen et al., 2001; Ortiz, 2001; González-Iturbe et al., 2002; Saha, 2003; Kalacska et al., 2004). In our study, they represented 48% of the total number of individuals and 83% of the species, but only 8% of the basal area. These results suggest that regeneration is occurring in all land-use types, although to different degrees. For example, the higher density and basal area in NU compared to the HD and P land-use types indicate greater regeneration in the former.

### 5.2. Diversity

Depauperate on-site regeneration mechanisms and substrate conditions promote opportunities for alien species invasions (e.g. Aide et al., 1995, 2000; González-Iturbe et al., 2002; Molina and Lugo, 2006). This was the case for the forests in this study, which showed a high dominance of the non-native legume *M. arenosa*, considered as ''typical'' of disturbed sites in this area (Lott, 1993) and in others (Francis and Liogier, 1991). Although controlling factors and patterns during plant establishment at the initial stages of secondary succession are not known at our study sites, Roth (1996) showed that *M. arenosa* invades only after disturbance has ceased and that it's not present in the soil seed bank of primary forests in the Chamela the region. Apparently, colonization by *M. arenosa* occurs within 5 years after the onset of secondary succession (Maza personal communication). It shows fast reproduction and dispersal, tolerance to low nutrient levels, and shade intolerance (Francis and Liogier, 1991), traits typical of invasive species (Gordon, 1998; Richardson et al., 2000). Other results also indicate that *M. arenosa* may be fixing N in our secondary forest sites (Jaramillo et al., unpublished).

Lugo (2004) suggested that native species could tolerate or even benefit from alien species. For example, Aide et al. (2000) found that *Spathodea campanulata*, an invasive species of abandoned pasture-lands in Puerto Rico, favored the establishment of native species inducing changes in microclimate with its canopy. Also, Camargo-Ricalde (2002) found that the *Mimosa* genus in the Tehuacán-Cuicatlán Valley of Mexico had a significant influence on soil chemical and biological properties, as well as micro-environmental factors which could allow establishment and growth of native species. This appeared to be happening in the secondary forests of our study, where primary forest species were sub-dominants in all sites. Moreover, although *M. arenosa* was the dominant species, the sites showed floristic patterns similar to those found in primary TDF in Mexico (Lott et al., 1987; Rico-Gray et al., 1988; Trejo and Dirzo, 2000) and elsewhere (Gentry, 1995), in that the Leguminosae was the better represented plant family in terms of species richness. Durán et al. (2002) reported that legumes represented 23% of the species in primary TDF of the Chamela region, followed by the Euphorbiaceae which represented 11%. Our study, in secondary forests of the same region, indicated that legumes represented 54% of the total number of tree species followed by the Euphorbiaceae with 11%.

Balvanera et al. (2002) reported high beta-diversity of primary TDF in Chamela and they attributed it to the impact of high environmental heterogeneity due to variations in aspect (north- and south-facing), in topography (crest, slope), and elevation, which affect incident radiation, evaporative demand, soil water holding capacity, and nutrient availability from the local to the watershed scale. The differences in floristic composition among the secondary forests of this study could be reflecting such high species turnover, since primary forest represents the species source for colonization and regeneration.

Some studies have supported the idea that land management in the Chamela region promotes persistent thorny communities, with the loss of native species in the mid- and possibly the long-term (Burgos and Maass, 2004) or an arrested succession (Ortiz, 2001). However, the high abundance of small individuals of primary forest species in all land-use types, indicated, that in spite of the prior land-use, primary forest regeneration was occurring. Nevertheless, primary forest regeneration seemed to be slower in sites still subjected to a certain degree of use, as HD and especially P, which showed a higher abundance of *M. arenosa* among the small individuals compared to the abundance of primary forest species. In contrast, the absence of small individuals of *M. arenosa* and a high abundance of primary forest species such as *L. lanceolatus* Benth., *L. minor* Sousa, *Caesalpinia eriostachys* Benth., *Guapira cf. macrocarpa* Miranda, and *C. alliodora* (Ruiz and Pav.) Oken., among others, at NU, suggest that *M. arenosa* is being replaced at these sites. Apparently, primary forest species are differentially recruited in secondary forests in a process occurring at a decadal scale and related to current management practices. This has important implications when considering options for primary forest restoration, which could include the deliberate introduction of primary forest species, already known to establish and grow under the canopy of *Mimosa*-dominant secondary forests.

## Acknowledgements

## Appendix A. Appendix

Woody species in secondary dry tropical forests in the Chamela region, Jalisco, Mexico, representing three land-use types. HD, housing development; P, pasture; NU, no use. The legume *Mimosa arenosa* is the only non-native species.

| Family | Species | HD | NU | P |
|---|---|---|---|---|
| Achatocarpaceae | *Achatocarpus gracilis* H. Walt. | | X | X |
| Anacardiaceae | *Spondias purpurea* L. | X | X | X |
| Apocynaceae | *Rawolfia tetraphylla* L. | | X | |
| Bignoniaceae | *Tabebuia chrysantha* (Jacq.) Nicholson | | X | |
| | *Tabebuia impetiginosa* (Mart.) Standl. | X | X | |
| Bombacaceae | *Ceiba aesculifolia* (H.B.K.) Britt. & Baker. | X | X | |
| | *Ceiba grandiflora* Rose | X | | X |
| Boraginaceae | *Bourreria cf. purpusii* T.S. Brandg. | X | X | |
| | *Cordia alliodora* (Ruiz & Pav.) Oken. | X | X | X |
| | *Cordia elaeagnoides* D.C. | | | X |
| | *Cordia gerascanthus* L. | X | | X |
| Burseraceae | *Bursera arborea* (Rose) Riley | X | | X |
| | *Bursera heteresthes* Bullock | | | X |
| | *Bursera instabilis* McVaugh & Rzed. | | | X |
| Capparaceae | *Capparis incana* H.B.K. | X | | |
| | *Capparis indica* (L.) Druce. | | X | |
| | *Capparis* sp. 1 | X | | |
| | *Forchhammeria pallida* Liebm. | X | X | X |
| Convolvulaceae | *Ipomoea wolcottiana* Rose | X | X | X |
| Ebenaceae | *Diospyros aequoris* Standl. | | X | |
| Euphorbiaceae | *Adelia oaxacana* (Muell. Arg.) Hemsl. | X | | |
| | *Bernardia spongiosa* McVaugh | | X | |
| | *Cnidosculus spinosus* Lundell | | | X |
| | *Croton alamosanus* Rose | X | X | X |
| | *Croton pseudoniveus* Lundell | X | X | |
| | *Croton roxanae* Croizat [C. fragilis H.B.K.] | | X | |
| | *Croton suberosus* H.B.K. | | X | |
| | *Jatropha malacophylla* Standl. | X | | X |
| | *Jatropha sympetala* Standl. & Blake | X | | X |
| | *Phyllanthus mocinianus* Baill. | | | X |

**Appendix A** (*Continued*)

| Family | Species | HD | NU | P |
|---|---|---|---|---|
| Flacourtiaceae | *Casearia corymbosa* H.B.K. | | X | |
| | *Casearia obovata* Schlechtendal | | X | |
| | *Casearia sylvestris* Sw. | X | X | |
| | *Casearia tremula* (Griseb.) Wright | X | X | X |
| | *Samyda mexicana* Rose | X | X | |
| Hernandiaceae | *Gyrocarpus jatrophifolius* Domin | X | | |
| Julianaceae | *Amphipterygium adstringens* (Schlecht.) Schiede. | X | | X |
| Leguminosae | *Acacia farnesiana* (L.) Willd. | | | X |
| | *Aeschynomene amorphoides* (S. Wats.) Rose ex B.L. Rob. | | X | |
| | *Albizia tomentosa* (Micheli) Standl. | | X | |
| | *Apoplanesia paniculata* Presl. | X | X | X |
| | *Caesalpinia caladenia* Standl. | | | X |
| | *Caesalpinia coriaria* (Jacq.) Willd. | X | X | X |
| | *Caesalpinia eriostachys* Benth. | X | X | X |
| | *Caesalpinia platyloba* S. Wats. | X | X | X |
| | *Caesalpinia pulcherrima* (L.) Sw. | X | X | |
| | *Caesalpinia sclerocarpa* Standl. | X | X | X |
| | *Cassia atomaria* L. | | | X |
| | *Chloroleucon mangense* (Jacq.) Britton & Rose | X | X | X |
| | *Diphysa occidentalis* Rose | X | | X |
| | *Gliricidia sepium* (Jacq.) Steudel | | | X |
| | *Haematoxylum brasiletto* Karst. | X | | X |
| | *Lonchocarpus constrictus* Pitt. | X | | |
| | *Lonchocarpus eriocarinalis* Micheli. | X | X | X |
| | *Lonchocarpus lanceolatus* Benth. | | X | |
| | *Lonchocarpus magallanesii* Sousa | X | | X |
| | *Lonchocarpus minor* Sousa | X | X | |
| | *Lonchocarpus mutans* Sousa | | X | |
| | *Mimosa arenosa* (Willd.) Poir. var. *leiocarpa* (DC.) Barneby | X | X | X |
| | *Piptadenia constricta* (Pers.) J.F. Macbr. | X | X | |
| | *Pithecellobium dulce* (Roth.) Benth. | | | X |
| | *Zapoteca formosa* (Wlld.) H. Hern. subsp. *rosei* (Wiggins) H. Hern. [Calliandra formosa (Kunth) Benth.; C rosei Wiggins]. | | X | |
| Malpighiaceae | *Bunchosia palmeri* S. Wats. *sens. lat.* | | X | X |
| Menispermaceae | *Hyperbaena ilicifolia* Standl. | | X | |
| Nyctaginaceae | *Guapira* cf. *macrocarpa* Miranda | X | X | X |
| Ochnaceae | *Ouratea mexicana* (Humb. & Bonpl.) Engl. | | X | |
| Polygonaceae | *Coccoloba liebmannii* Lindau | | X | X |
| | *Ruprechtia costata* Meisn. | | | X |
| | *Ruprechtia fusca* Fern. [R. *standleyana* Cocucci] | X | | X |
| Rhamnaceae | *Karwinskia latifolia* Standl. | | | X |
| | *Ziziphus amole* (sessé & Moc.) M.C. Johnst. | | | X |
| Rubiaceae | *Allenanthus hondurensis* Standl. var. *parvifolia* L. Wms. | | X | |
| | *Exostema caribaeum* (Jacq.) Roem. & Schult. | X | X | X |
| | *Guettarda elliptica* Sw. | | X | |
| | *Hintonia latiflora* (Sessé & Moc. ex DC.) Bullock | | X | X |
| | *Randia* sp. 1 | X | X | X |
| | *Randia* sp. 2 | | | X |
| | *Randia* sp. 3 | | | X |
| Rutaceae | *Esenbeckia berlandierii* Baill. subsp. *acapulcensis* (Rose) Kaastra | | X | |
| | *Esenbeckia nesiotica* Standl. | X | | |
| | *Helietta lottiae* Chiang | X | | |
| | *Zanthoxylum caribaeum* Lam. vel aff. | X | X | X |
| Sapindaceae | *Thouinia paucidentata* Radlk. | X | X | X |
| Sterculiaceae | *Guazuma ulmifolia* Lam. | | X | X |
| Theophrastaceae | *Jacquinia pungens* A. Gray | | X | X |
| Tiliaceae | *Heliocarpus pallidus* Ro se. | | X | X |
| Verbenaceae | *Citharexylum hirtellum* Standl. | X | | |

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