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PATRONES, PROCESOS Y MECANISMOS DE LA COMUNIDAD REGENERATIVA DE UN BOSQUE TROPICAL CADUCIFOLIO EN UN GRADIENTE SUCESIONAL

TESIS

QUE PARA OBTENER EL GRADO ACADÉMICO DE

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PRESENTA

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Resumen

La sucesión secundaria es un proceso complejo, sobre todo en sistemas tropicales. Así, estudiar este proceso considerando pocos factores o sólo una visión teórica puede producir conclusiones demasiado limitadas y erróneas. El presente trabajo toma en cuenta aspectos de la visión holística y considera la presencia de mecanismos que, en conjunto y en interacción con algunos factores ambientales, pueden dar dirección al desarrollo sucesional de las comunidades regenerativas de los bosques tropicales estacionalmente secos que han sido perturbados.

Actualmente las altas tasas de deforestación, de cambio de uso del suelo y de abandono de tierras agropecuarias, en campos que fueron deforestados, originan sitios idóneos para el estudio de los procesos de sucesión secundaria y de regeneración natural de los bosques tropicales. Mientras que el conocimiento de la sucesión secundaria y la regeneración natural para los sistemas tropicales húmedos y templados es vasto, para las áreas tropicales estacionalmente secas es aún relativamente limitado. La presente investigación examinó los procesos de regeneración natural y de sucesión secundaria en pastizales abandonados y en vegetación madura del bosque tropical caducifolio, así como los factores y los mecanismos subyacentes a las trayectorias observadas. El sistema de estudio estuvo conformado por nueve parcelas (20 × 50 m) de diferente edad de abandono (años) situadas en tres categorías sucesionales: pastizales recién abandonados (0-1), tempranos (3-5) e intermedios (10-12), así como tres parcelas de bosque maduro.

Para caracterizar la estructura y la composición del banco de semillas y evaluar los mecanismos de sucesión presentes en esta fuente regenerativa (Capítulo II), en 2005 se obtuvieron 20 muestras del banco de semillas en cada una de las 12 parcelas. Los resultados mostraron un reemplazo de formas de crecimiento, con una dominancia fuerte de especies herbáceas al inicio de la sucesión, una integración del componente leñoso a los cinco años de abandono (sobre todo arbustos) y una contribución importante de árboles y de arbustos en los sitios de bosque maduro. Por otra parte, se observó la presencia de tres grupos sucesionales con base en su toleracia a ambientes hídricamente estresantes (*i.e.* alta radiación directa, baja disponibilidad de agua en el suelo, altas temperaturas del suelo): (i) especies muy tolerantes, (ii) especies de tolerancia intermedia, y (iii) especies poco tolerantes. Los tres grupos de especies mostraron un reemplazo a través del tiempo como

resultado de la facilitación. No se encontraron evidencias de inhibición o tolerancia como mecanismos sucesionales.

En el capítulo III se documentan las trayectorias sucesionales de la comunidad regenerativa y se contrastan con la dinámica de la misma; además, se evaluó el papel de factores biofísicos: apertura del dosel a nivel del sotobosque (%), matriz forestal circundante (%) y densidad de árboles y de arbustos (≥ 1 cm dap), como determinantes de la dinámica regenerativa de esta comunidad. Dentro de cada parcela se dispusieron, en 2004, 48 cuadros de 1 m^2 cada uno, dentro de los cuales todos los árboles y los arbustos de entre 10 y 100 cm de altura fueron monitoreados en la época de secas y lluvias en los años de estudio (2004-2007). En cada parcela se midieron los factores biofísicos, los cuales fueron utilizados como variables explicativas para los patrones de densidad de tallos, de densidad de especies y de cobertura foliar obtenidos de los valores puntuales de la cronosecuencia. El seguimiento de la cronosecuencia a través del tiempo, permitió evaluar la dinámica regenerativa de los sitios y confrontar los patrones de la dinámica regenerativa con los patrones predichos por la cronosecuencia. Los datos puntuales de la cronosecuencia mostraron que la densidad de tallos, la densidad de especies y la cobertura foliar incrementaron rápida y asintóticamente con el avance sucesional. Sin embargo, estos patrones no concordaron con las trayectorias observadas en la dinámica de las comunidades. Los datos dinámicos mostraron que la densidad de plantas y la cobertura foliar se redujeron con el avance sucesional, mientras que la densidad de especies fue independiente a la edad de abandono. De los factores biofísicos analizados, sólo la cobertura forestal de la matriz circundante mostró una relación positiva con la densidad de plantas.

Finalmente, en el capítulo IV se evaluó el papel de la precipitación de los años de estudio en la dinámica observada en la época de secas y la de lluvias. Se realizaron análisis de manera general para la comunidad, por forma de crecimiento (árbol y arbusto) y por origen (plántula y rebrote). Los resultados demostraron que las tasas de ganancia (*i.e.* tasas de reclutamiento, de ganancia de especies y de crecimiento en altura) están relacionadas con la época de lluvias y las de pérdida (*i.e.* tasas de mortalidad y pérdida de especies) con la de secas. Los años secos estuvieron asociados con reducciones fuertes en las tasas de regeneración de las comunidades, independientemente de la edad sucesional. Incluso con buena precipitación, en los años que estuvieron precedidos por años secos, se registró una reducción en biomasa y una desaceleración en las tasas de regeneración de las comunidades (*i.e.* mayores tasas de pérdida que de ganancia); los años precedidos por precipitaciones altas mostraron una aceleración en la tasa de regeneración. En términos de las formas de crecimiento y de origen de las plantas, sólo hubo diferencias entre rebrotes y plántulas. Los rebrotes presentaron tasas de mortalidad menores que las plántulas, de tal manera que el rebrote parece ser el principal mecanismo de mantenimiento de estas comunidades a lo largo de toda la sucesión.

Independientemente de la edad sucesional, la variación en la disponibilidad de agua parece jugar un papel fundamental en la dirección de desarrollo y en la tasa regenerativa de las comunidades en campos agropecuarios abandonados en los sistemas de bosque tropical caducifolio. Debido a la gran variación en la precipitación de estas regiones, aunado a los efectos del cambio climático (*e.g.* eventos intensos de El Niño), es posible que la regeneración natural de estos sistemas sea intermitente, pasando por periodos de ganancia, de pérdida y de estabilidad en términos de biomasa y de diversidad. El tener un proceso regenerativo y sucesional intermitente hace que los sistemas de bosque tropical caducifolio presenten una recuperación lenta de la estructura y la composición de especies de los bosques maduros.

Bajo escenarios cada vez menos óptimos en términos de variación climática y deforestación, el seguimiento temporal de la regeneración natural y la sucesión secundaria es clave para conocer más ampliamente el impacto de estos factores en campos agropecuarios abandonados de sistemas tropicales caducifolios.

Abstract

The secondary succession is a complex proccess mainly in tropical systems. Thus, if this process is studied considering few factors or since only one theoric vision the resulting conclusions can be too limited and wrong. This study takes-account aspects of the holistic vision and considers mechanisms that on the whole and interaction with some environmental factors can address the successional development of the regenerative communities from the seasonally dry tropical forest that have been perturbed.

Nowadays, the high deforestation rates, the land use change, and the abandoned fields, of sites that were deforested, generate suitable sites for the study of secondary succession and natural regeneration processes of tropical forests. While the knodlewge of the secondary succession and the natural regeneration for the humid tropical and temperate forests is vast, for the seasonally dry tropical areas this is yet limited. This research evaluated the natural regeneration and secondary succession processes on abandonment fields and old-growth forests from tropical dry forest, as well as the underlying factors and mechanisms to the observed trajectories. The study system was conforme by nine plots (20 × 50 m) with different fallow age (years) organizad in three successional categories: pastures recently abandoned (0-1), early (3-5), and intermediates (10-12), thus three old-growth forest plots.

For to characterized the structure and composition seed bank and to evaluate the successional mechanisms present in this regenerative source (Chapter II), in 2005 I obtained 20 samples of the seed bank in each in each one of the 12 plots. The results showed a growth forms turnover, with a strong domain of herbaceous species on the beginning succession, an incorporation of the woody component at the five fallow age (mainly shrubs), and an important contribution of trees and shrubs on old-growth forest sites. On the other hand, three successional groups, considering their watering stress tolerance (*i.e.*, high direct radiation, low water soil availability, high temperature soil), were observed: (i) high tolerant species, (ii) intermediate tolerant species, and (iii) low tolerant species. The three species groups showed a replacement along through the time as result of the facilitation mechanism. No evidences were observed of the successional mechanisms of inhibition or tolerance.

In the chapter III the successional trajectories of the regenerative community are documented and contrasted with their own dynamic. Furthermore, here was evaluated the role of some biophysic factors: understory light availability (%), surrounded forest matrix (%), and trees and shrubs density (≥ 1 cm dbh), as determinants of the regenerative dynamic of this community. In each plot were established, in 2004, 48 squares (1-m^2) where all trees and shrubs between 10 and 100 cm were recorded during dry and rainy season along study years (2004-2007). In each plot the biophysical characteristics were measured and used as explanatory variables for the plant and species density, and plant cover patterns from the chronosequence static data. The study of the chronosequence along time let to evaluate the regenerative dynamic of the sites and to contraste the regenerative dynamic with the predicted patterns from the chronosequence. The static data from the chronosequence showed a rapid and asymptotic increase in density plants, density species and plant cover with the fallow age. However, these patterns did not match with communities dynamic trajectories. The dynamic data showed that the plant density and plant cover decreased with the successional advance, while the species density was independent of the fallow age. Of the biophysic analyzed factors, only the surrounding forestal matrix showed a positive relation with the plant density.

Finally, in chapter IV the effects of inter-seasonal and inter-year rainfall variation on the dynamics of regenerative communities were evaluated. The whole community and separating shrubs from trees (*i.e.* growth-forms), and seedlings from sprouts (*i.e.* by origin), were analyzed. The results showed that the gain rates (*i.e.* rates of recruitment, species gain and height growth) are higher in the rainy season and the loss rates (*i.e.* rates of mortality and loss species) with the dry season. The dry years were associated with high reductions in the community regeneration rates, independently of the successional age. Even years with good precipitation, in the preceded years by dry years, a biomass reduction and a decrement in the community regeneration rates (*i.e.* higher loss than gain rates) were registered. The preceded years by good precipitation showed acceleration in the regeneration rate. In relation with the growth-forms and the plant origin, only differences between sprouts and seedlings were observed. The sprouts had lower mortality rates than the seedlings, thus the sprouts possiblely be the major mechanism of the maintenance of these communities along all succession.

Independently of the successional age, the water availability variation play a fundamental role on the address of the development and on the community regenerative rate on abandoned fields on tropical dry forest. Due to the high variation in the precipitation of these regions plus the climatic change effects (*e.g.* intense events of the ENSO) it is possible that the natural regeneration of these systems is intermittent with gain, loss, and stable periods of biomass and diversity. Have a successional and regenerative intermittent processes imply that the tropical dry forest has a slow recuperation of the structural and composition attributes from the old-growth forests.

Under less and less optimum of global climate change and deforestation, the long-term studies on natural regeneration and secondary succession are keys to understand understand the impact of these factors on abandoned fields of seasonally tropical systems.

CAPÍTULO I

INTRODUCCIÓN GENERAL

De acuerdo con la FAO (2009), uno de los factores más importantes que ha provocado la reducción de los bosques tropicales a nivel nacional y mundial es la deforestación asociada al establecimiento de campos agropecuarios. Estas actividades abarcan desde la tradicional roza, tumba y quema hasta la agricultura y la ganadería intensiva que emplean especies exóticas, agroquímicos y maquinaria pesada. A pesar del amplio desarrollo agropecuario, la pérdida de la productividad de los campos y/o los cambios socio-económicos (tales como la urbanización y la migración transnacional) en el ámbito rural, han promovido el abandono de campos agropecuarios (Ramankutty y Foley 1999, Grau *et al*. 2003, FAO 2009). Este proceso de abandono ha generado un importante aumento de bosques secundarios (Wright y Muller-Landau 2006, Hobbs y Cramer 2007), a tal grado que en la segunda mitad del siglo pasado Gómez-Pompa y Vázquez-Yanes (1974) ya hablaban de la “Era de vegetación secundaria”.

Un bosque secundario puede definirse como la vegetación que se desarrolla después de que la original ha sido perturbada significativamente o eliminada por eventos naturales u originados por el humano (Chokkalingam y De Jong 2001). En algunas regiones del mundo los bosques secundarios representan ya el principal tipo de cobertura vegetal (Brown y Lugo, 1990, FAO 2006) y en México abarcan cerca de 40% de la cobertura forestal de las regiones tropicales (Challenger y Soberón 2008). A nivel mundial, casi 60% de los bosques tropicales del mundo pueden considerarse como secundarios (FAO 2005).

Como resultado de las perturbaciones ecológicas producidas por las actividades agropecuarias, en los campos abandonados las condiciones físico-químicas del suelo, los niveles de disponibilidad de recursos y la naturaleza e intensidad de las interacciones bióticas que afectan al proceso de regeneración natural y de sucesión ecológica de las comunidades vegetales difieren de aquellas encontradas en los bosques maduros (Pickett y White 1985). Dependiendo del nivel de degradación producido, la comunidad podrá regenerarse naturalmente, *i.e.* a través de sus propios mecanismos, o bien necesitar la asistencia de actividades de restauración (Nepstad *et al*. 1991, Chazdon 2008).

Aunado al efecto de las actividades agropecuarias, en las últimas décadas han ocurrido cambios atmosféricos de alcance mundial, causados por un aumento en la emisión de gases de efecto invernadero de origen antrópico, que están produciendo modificaciones notables en los regímenes climáticos regionales y locales (Nakagawa *et al*. 2000, Sen 2009). Estos cambios climáticos también afectan la dinámica, la estructura y la composición de las comunidades vegetales en ambientes conservados y perturbados (Bazzaz 1998, Ravindranath y Sukumar 1998, Engelbrecht *et al*. 2006, Dale *et al*. 2001).

Se ha mostrado que algunas actividades de bajo impacto (*e.g.* extracción de productos no maderables y siembra tradicional; Chazdon 2008), en sinergia con el cambio climático, pueden tener impactos negativos en comunidades de plantas adultas (*e.g.* Martínez-Ramos *et al*. 2009, Brienen *et al*. 2010). En un escenario de actividades de mayor impacto, como la ganadería (Chazdon 2008), y considerando comunidades regenerativas (*i.e.* banco de semillas, plántulas y rebrotes), es posible que los efectos negativos sobre dichas comunidades sean mayores.

Ante el actual panorama de cambio de uso del suelo y de cambio climático global, algunas de las preguntas ecológicas que urge enfrentar, para lograr un mejor entendimiento y manejo de los bosques secundarios, son: ¿cuáles son los patrones sucesionales de las comunidades regenerativas de plantas en sistemas perturbados por actividades agropecuarias?, ¿cuáles son los mecanismos ecológicos que determinan la capacidad de regeneración de las comunidades regenerativas de plantas en esos sistemas?, ¿cuáles son los factores ambientales que determinan la dinámica regenerativa de las comunidades sucesionales vegetales?, ¿cómo impactan las fuertes variaciones climáticas contemporánes a dicha dinámica regenerativa? y ¿qué efectos producen las perturbaciones por el cambios de uso del suelo y la variación climática sobre la estructura y la composición en la dinámica sucesional de las comunidades vegetales?

Una forma de abordar estas preguntas es a través de un enfoque de estudio de largo plazo que permita entender, por un lado, el desarrollo natural de la vegetación en ambientes perturbados por actividades agropecuarias y, por el otro, evaluar los efectos relacionados con la variabilidad temporal de factores climáticos. En particular, realizar este tipo de estudios en bosques tropicales estacionalmente secos, como el bosque tropical caducifolio (*sensu* Rzedowski 1978), puede contribuir de manera importante al conocimiento de la regeneración natural y la sucesión secundaria. Estos bosques son los más amenazados por la deforestación y el cambio de uso del suelo en las regiones tropicales (Janzen 1988b, Miles *et al.* 2006) además de que son ecosistemas con una marcada estacionalidad climática en los que los cambios interanuales e interestacionales del clima son muy evidentes (Holdridge 1947, Murphy y Lugo 1986, Lebrija-Trejos 2009).

De manera general, el objetivo de la presente investigación fue caracterizar y entender los factores, los patrones y los mecanismos ecológicos involucrados en la regeneración natural y la sucesión secundaria del bosque tropical caducifolio en campos ganaderos abandonados en la región de Chamela, Jalisco, México. Este trabajo contribuye al conocimiento de la sucesión secundaria y la regeneración natural de ecosistemas terrestres con marcada estacionalidad climática. También se pretende que el conocimiento científico generado por esta investigación sea útil para un mejor entendimiento y manejo de los bosques tropicales caducifolios.

A continuación, se presenta una síntesis de elementos conceptuales y téoricos que dan sustento a la investigación abordada en esta tesis. Posteriormente se presentan los capítulos de la tesis junto con sus objetivos particulares y la descripción del área y del sistema de estudio.

REGENERACIÓN NATURAL Y SUCESIÓN SECUNDARIA

El proceso de regeneración natural de una comunidad vegetal puede definirse como la renovación de los elementos constituyentes de la misma (Martínez-Ramos 1994), o como la ganancia y/o la recuperación de la biomasa vegetal en un área determinada (Ewel 1980), ya sea que esté involucrada una sola especie (*e.g.* bosques mono-específicos) o especies diferentes. Este proceso puede darse con o sin la generación de nuevos individuos genéticamente diferentes, ya que estrictamente la regeneración a través de rebrotes no implica diferentes genets (por ejemplo, existen bosques completos de *Populus tremuloides* que sólo consisten ramets; Harper 1977). El proceso de regeneración natural depende, de manera general, de la disponibilidad de propágulos, de las condiciones físico-químicas, de la disponibilidad de recursos, de las interacciones bióticas y de los atributos biológicos de las especies que están presentes en un sitio en un momento determinado (Figura 1).

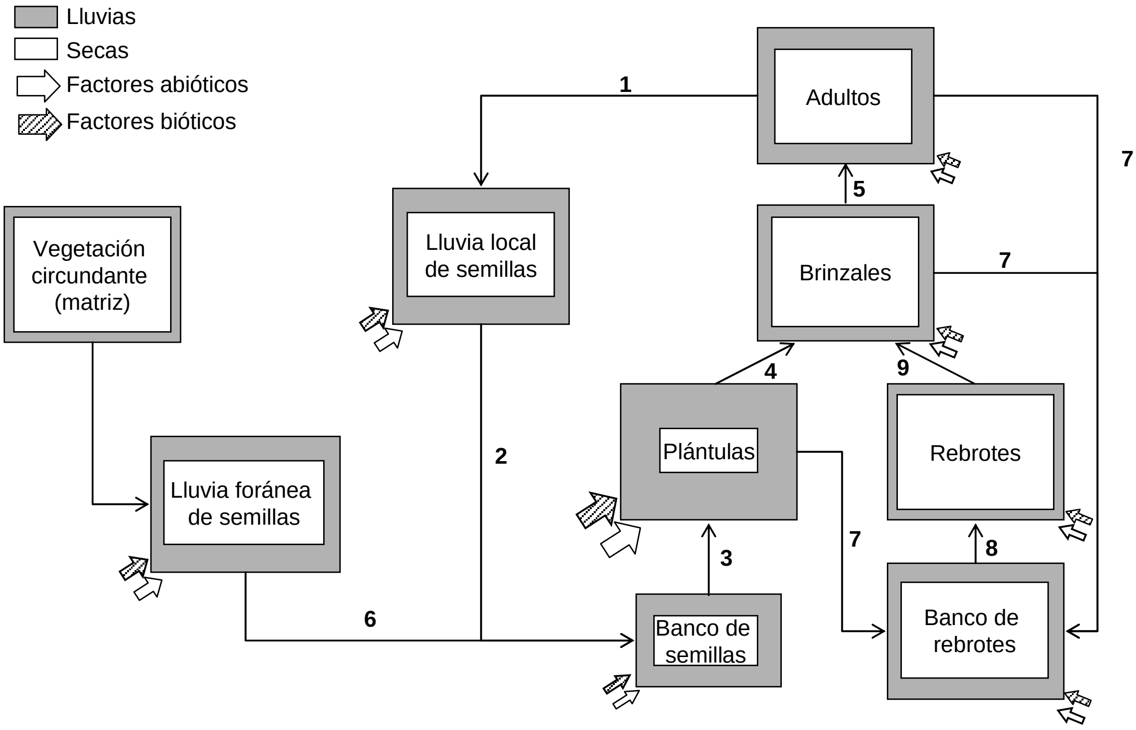

Figura 1. Esquema conceptual del proceso de regeneración natural de una comunidad vegetal de arbustos y de árboles. Las flechas delgadas y los números indican las rutas por las que pueden transitar los individuos durante sus diferentes estadios de vida hacia la fase adulta (reproductiva). La regeneración puede proceder a través de una ruta reproductiva sexual local, con semillas producidas por plantas adultas presentes en el sitio (ruta 1, 2, 3, 4, 5). También puede proceder a través de semillas producidas por plantas foráneas, encontradas en la vegetación aledaña (matriz), que llegan al sitio por medio de agentes de dispersión biótica o abiótica (ruta 6, 3, 4, 5). Otras rutas posibles pueden incluir la producción de propágulos vegetativos (rebrotes o ramets) que se desarrollan a partir de meristemos presentes en raíces o tallos de las plantas jóvenes (brinzales), de plantas adultas, de plántulas que después de ser dañadas rebrotan, o bien de remanentes de tejido vegetal (por ejemplo, bulbos, rizomas o restos de raíces y tocones; ruta 7, 8, 9, 5). El proceso de regeneración es complejo ya que las plantas nuevas en la comunidad pueden originarse de rutas que involucran tanto vías sexuales como vegetativas. Las transiciones son afectadas por factores bióticos (flechas con líneas diagonales; depredadores, patógenos, parásitos, herbívoros, competidores y mutualistas como hongos micorrizógenos, bacterias fijadoras de nitrógeno, polinizadores y dispersores de semillas -estos dos últimos en las fases reproductivas-) y abióticos (flechas blancas; temperatura, radiación solar, características físicas del suelo, disponibilidad de agua, luz y nutrientes en el suelo). El efecto de estos factores (indicado por el tamaño de las flechas) sobre la disponibilidad de las fuentes regenerativas (representada por el tamaño del rectángulo), en sus diferentes estadios de desarrollo, es diferente en la época de lluvias (rectángulos grises) y en la época de secas (rectángulo blanco). Por ejemplo, la disponibilidad de plántulas y rebrotes (en términos de densidad) durante la lluvia es mayor que en la época de secas; sin embargo, mientras

que los rebrotes parecen no reducirse demasiado en la época de secas, la disponibilidad de plántulas se ve fuertemente mermada por la alta radiación y la baja disponibilidad de agua en el suelo que provocan tasas de evapotranspiración altas y aumentan el estrés hídrico. Independientemente de la estación (aunque sí debe de haber cambios), el efecto de los factores bióticos y abióticos sobre las plántulas es mayor que sobre los rebortes que dependen de sus reservas de carbohidratos y agua almacenadas en los tallos o raices que les dieron origen (obsérvese el tamaño de las flechas blancas y con líneas diagonales). Es posible que en la época de secas, los factores abióticos (como las condiciones y los recursos) sean más restrictivos para el proceso regenerativo de la comunidad (*e.g.* mayor radiación, menor disponibilidad de agua, mayor presión evapotranspirativa). Sin embargo, por los grandes almacenes de carbohidratos y agua que los rebrotes poseen y/o la dependencia de recursos de su planta paternal (*i.e.* la planta de donde se originó el rebrote y con la que aún puede tener conexión), la época de secas mermará más fuertemente a las semillas y a las plántulas. En la época de lluvias, la disponibilidad de algunos factores abióticos aumenta, como la de agua en el suelo, pero la de otros, como la de luz disminuye, pudiendo limitar el desarrollo de las plantas. En la época de lluvias, las poblaciones de herbívoros pueden aumentar e impactar fuertemente a la regeneración natural, sobre todo a las semillas y las plántulas, las cuales poseen un contenido energético grande. A diferencia de los rebrotes, las plántulas poseen tejidos más suaves y apetecibles a los herbívoros. El impacto puede ser inverso en secas, en donde los rebrotes pueden mostrar una mayor supervivencia que las plántulas.

En un escenario en el que no haya limitación de propágulos, si las condiciones físico-químicas son adversas y los recursos limitados, es esperable que la regeneración sea limitada. Por otra parte, aun cuando las condiciones y la disponibilidad de recursos sean favorables para el desarrollo de la vegetación, si la disponibilidad de propágulos es reducida, puede esperarse que la regeneración también esté restringida. Aun en un escenario donde haya una buena disponibilidad de propágulos con condiciones favorables y sin recursos limitados, si las interacciones bióticas dominantes resultan ser negativas (*e.g.* interferencia/competencia, herbivoría, enfermedades, depredación) para la supervivencia, el crecimiento y la reproducción de los propágulos, es posible que la regeneración de la comunidad se vea también mermada. Por lo tanto, es esperable que la regeneración natural de una comunidad vegetal se desarrolle sin limitaciones (*i.e.* regeneración potencial) cuando haya una buena disponibilidad de propágulos, condiciones óptimas, disponibilidad de recursos e interacciones bióticas favorables para el desarrollo y la reproducción de los propágulos.

Las comunidades vegetales están sujetas a la acción recurrente de diversos agentes abióticos (tales como fuegos, tormentas y sequías severas, deslaves, terremotos, erupciones volcánicas, apertura de claros) o bióticos (desarrollo de epidemias y plagas), que alteran de manera súbita las condiciones físicas y químicas, los niveles de disponibilidad de recursos o la naturaleza y la intensidad de las interacciones bióticas. A estos agentes de alteración se les conoce con el término de disturbios ("disturbances" en inglés, *sensu* Rykiel 1985). La presencia de un disturbio no es necesaria para el desarrollo regenerativo de una comunidad, pero sí para el proceso de sucesión ecológica (Pickett y McDonnell 1989). El proceso de sucesión ecológica puede definirse, de manera general, como el reemplazamiento de especies a través del tiempo que se inicia con un disturbio y que puede culminar en el mismo estado o en diferentes estados alternativos al existente antes del disturbio (Drury y Nisbet 1973, Begon *et al.* 1996). Cuando después del disturbio queda un substrato estéril, sin vida, nos referimos a un proceso de sucesión primaria, como el que se desarrolla sobre lavas volcánicas (*e.g.* Del Moral 1999). Si después del disturbio permanece germoplasma vivo (*e.g.* semillas, meristemos en raíces y tallos, vegetación en pie) o suelo fértil, a partir del cual se pueda desarrollar vegetación, nos referimos a un proceso de sucesión secundaria (Drury y Nisbet 1973, Begon *et al.* 1996).

Si bien el proceso de regeneración natural no involucra necesariamente un proceso de sucesión ecológica, este último sí involucra al proceso de regeneración natural. Por ello, el proceso de sucesión, como lo discuten Pickett y McDonnell (1989), además de la presencia de un sitio alterado, producido por un disturbio, incluye los componentes de la regeneración natural: disponibilidad de propágulos de una o varias especies, condiciones ambientales, disponibilidad de recursos, interacciones bióticas y abióticas, además de los atributos de historia de vida que determinan el desarrollo diferencial de las especies a través del tiempo (Figura 2).

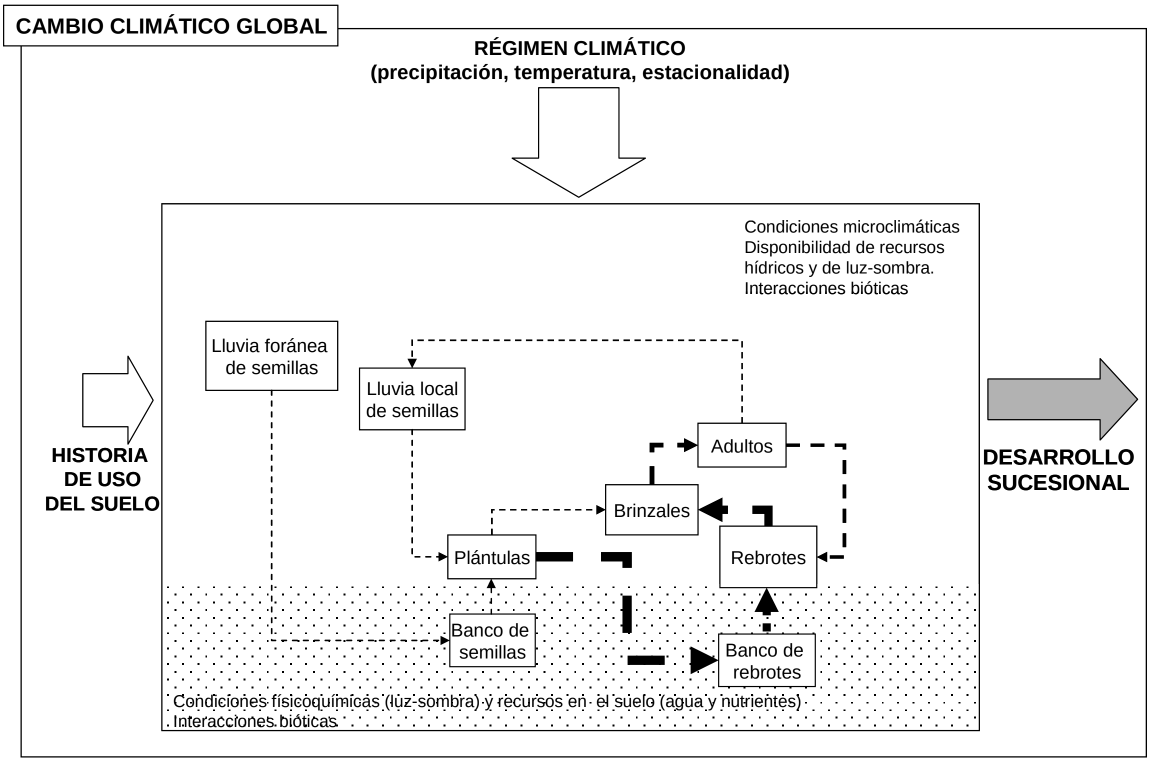

Figura 2. Esquema conceptual de los componentes que determinan el proceso de sucesión secundaria en un campo agropecuario abandonado. Los rectángulos indican diferentes estados de desarrollo de las fuentes regenerativas, el tamaño del rectángulo indica la disponibilidad, en términos de densidad, de cada estado de desarrollo; el área punteada representa el suelo. Las flechas discontinuas indican probabilidades de transición (en proporción con su grosor) entre estadios de vida de las plantas que son afectadas por todo el complejo de factores. Por ejemplo, la probabilidad de que una plántula llegue a ser un brinzal es menor que la probabilidad de que se convierta en rebrote (*e.g.* por herbivoría o estrés hídrico es posible que la plántula pierda toda su biomasa por arriba del suelo y que sus almacenes subterráneos le permitan reintegrarse a la comunidad como rebrote). Al momento de abandono, pueden estar presentes una o más especies de plantas, cada una con probabilidades de transición que están determinadas por propiedades intrínsecas de cada especie y del ambiente imperante. El proceso de sucesión secundaria puede iniciarse con la germinación de las semillas latentes en el suelo (banco de semillas), de las semillas recién dispersadas por las plantas presentes en el campo abandonado (lluvia local de semillas) y/o por las plantas que se encuentran fuera del campo (lluvia foránea de semillas). La sucesión también puede iniciarse con el desarrollo de meristemos vegetativos originados del banco de rebrotes o de plantas remanentes (*e.g.* de plántulas dañadas y deplantas adultas), así como con el desarrollo de la vegetación remanente al momento del abandono del campo (plántulas, rebrotes, brinzales y/o plantas adultas). La flecha blanca horizontal indica que la historia de uso del suelo es un factor determinante en la disponibilidad de propágulos, de recursos (*e.g.* disponibilidad de agua, luz-sombra, nutrientes), de condiciones microclimáticas (radiación, sombra, temperatura y humedad) y de las interacciones bióticas (herbivoría, depredación, mutualismo con bacterias, dispersión, polinización) presentes en el campo abandonado y que operan sobre las plantas por debajo del suelo, en el suelo y sotobosque. La flecha blanca vertical indica que la variación temporal en el régimen climático (precipitación, temperatura y estacionalidad) juega también un papel importante sobre el desarrollo de la vegetación al momento y después del abandono del campo, así como en los recursos, las condiciones y las interacciones bióticas dentro de la comunidad abandonada. La

variación climática también puede afectar los resultados de la historia de uso del suelo, Por ejemplo, en sequías fuertes la acumulación de combustible (*e.g.* hojarasca) aumenta, incrementando la frecuencia y la intensidad de incendios. Las probabilidades de transición entre las diferentes fuentes regenerativas son determinantes de la abundancia de las especies; estas probabilidades son cambiantes a través del tiempo y el espacio. Así, las probabilidades de transición pueden definir las posibilidades de colonización y de extinción local de especies a través del proceso sucesional (indicado por la flecha horizontal gruesa en tonos de gris). Más allá del régimen climático característico de cada región, hay factores globales como el cambio climático global que tendrán consecuencias sobre la variación climática de un lugar, así como en los efectos del manejo de uso del suelo.

SUCESIÓN SECUNDARIA, TEORÍAS

Históricamente se han planteado varias teorías sobre el proceso de sucesión secundaria. Entre las primeras están la propuesta hecha por Clements (1916) y la propuesta de Gleason (1926). De manera general, Clements (1916) visualizó a la sucesión ecológica como un proceso bien definido, en donde las comunidades son comparables a un organismo, con etapas de desarrollo específicas (*i.e.* etapas serales) y un fin determinado, el clímax. Este enfoque determinista, fue posiblemente la causa principal de controversia en torno a la visión “Clementsiana”, la cual fue lidereada por Ramensky (McIntosh 1983) y Gleason (1926). Sin embargo, pese a esta postura determinista, la teoría de Clements involucró aspectos mecanicistas (*i.e.* existencia de mecanismos que dirigen los procesos, causalidad; Connell y Slatyer 1977) y holísticos (*i.e.* el sistema observado es consecuencia de todos los componentes de dicho sistema como disturbios, características biofísicas del ambiente y características de las especies), que posteriormente fueron retomadas por otras teorías; inclusive Gleason (1926) hizo hincapié en la existencia de muchos factores y mecanismos que posibilitan la existencia de diversas rutas de desarrollo y sin un fin determinado.

Dentro de la visión mecanicista se contempla la existencia de factores importantes del proceso sucesional, tales como el tipo de disturbio (White y Pickett 1985), el ambiente físico (Drury y Nisbet 1973, Diamond 1975, Hobbs y Norton 2004), la disponibilidad de especies (Egler 1954, Pickett y McDonnell 1989), las habilidades de las especies para su establecimiento y su crecimiento en un ambiente determinado (Diamond 1975, Connell y

Slatyer 1977, Huston y Smith 1987, Pickett y McDonnell 1989), la capacidad de las especies para modificar el ambiente (*i.e.* Connell y Slatyer 1977) y la interacción entre especies (*e.g.* Connell y Slatyer 1977, Tilman 1985, Huston y Smith 1987). Así, la visión temprana de Clements (1916) encierra parte de los factores y los mecanismos influyentes en el proceso sucesional que han sido discutidos históricamente. Como se mencionó anteriormente, posiblemente el punto más controversial de la teoría de Clements fue la propuesta de que, para cada comunidad vegetal dentro de un ámbito climático determinado, existe una ruta de desarrollo sucesional predecible hacia un estado único llamado “clímax” (el cual a pesar de ser el estado más “estable” en el desarrollo de las comunidades, nunca está en completo equilibrio, ni libre de perturbaciones; Clements 1916). A pesar del determinismo “Clementsiano”, la implicación de numerosos factores y la complejidad del proceso que enmarcó Clements (1916), y que fue más evidente en la propuesta de Gleason (1926), ha sido clave en la generación de otras teorías (*e.g.* Pickett y McDonnell 1989).

Pickett y McDonnell (1989), con la llamada “teoría jerárquica de la sucesión”, establecieron la existencia de tres componentes fundamentales para el desarrollo sucesional: i) la disponibilidad de sitios abiertos, ii) la disponibilidad de especies, y iii) el desarrollo diferencial de las especies. Estos componentes están determinados a su vez por otros factores y mecanismos ecológicos y biológicos en una escala jerárquica cada vez más fina; de ahí el nombre de esta teoría. Sin embargo, la dinámica de una comunidad no depende del desarrollo aislado de estos factores y mecanismos (visión holística); las rutas que puede seguir una comunidad son tan variadas como los factores y los mecanismos que intervienen en su desarrollo (Gleason 1926). Por ejemplo, el desarrollo de una comunidad dependerá no solamente del tipo de disturbio inicial, sino también de la vegetación remanente en el sitio y de las características biofísicas del ambiente (*e.g.* suelo, topografía, matriz circundante), entre otros factores confinados a la disponibilidad de sitios. Ahora bien, si consideramos los factores involucrados en la disponibilidad de especies y en el desarrollo diferencial de las mismas, las rutas que puede tomar el desarrollo sucesional de una comunidad se vuelven más complejas y diversas.

La visión mecanicista y holística pueden observarse en la teoría de estados alternativos (Chesson y Huntly 1997, White y Jentsch 2004, Heil 2004). Esta teoría supone que: i) el desarrollo sucesional de una comunidad seguirá diferentes trayectorias, dependiendo de factores tales como las condiciones iniciales del sitio, la historia de uso del suelo, la disponibilidad de propágulos y la presencia de eventos azarosos que interactúan en el sistema, y ii) la existencia de estados alternativos de equilibrio. Los estados alternativos de equilibrio pueden entenderse como los espacios o los tiempos en los que el sistema permanece sin cambios abruptos o notorios, y se presentan a lo largo del desarrollo sucesional de una comunidad.

Las perturbaciones producidas por eventos climatológicos, tales como los huracanes y los eventos de sequía (acentuados actualmente por el cambio climático global; Timmermann *et al*. 1999, Nakagawa *et al*. 2000), sin duda modifican los factores, los mecanismos y los procesos involucrados en el desarrollo de la comunidad, alterando así, el patrón o la trayectoria de desarrollo (Chesson y Huntly 1997). Por ejemplo, como resultado de los eventos de El Niño (fase caliente del ENSO), en algunas regiones tropicales, la estación de sequía se prolonga y la época de lluvias se reduce en términos de tiempo y de cantidad (Timmermann *et al.* 1999, Nakagawa *et al*. 2000, Larkin y Harrison 2002), produciendo una alza en la tasa de mortalidad (sobre todo en plantas de tamaño pequeño) y una reducción en las tasas de ganancia como la de germinación y la de crecimiento de las plantas (Martínez-Ramos *et al*. 2009, Brienen *et al*. 2010). Por otro lado, estas sequías pueden impactar negativamente a las poblaciones de polinizadores y dispersores (Corlett y Lafrankie 1998), mermando indirectamente la disponibilidad de propágulos. Por el contrario, La Niña (la fase fría del ENSO) provocará una estación de lluvias prolongada y de mayor magnitud (Larkin y Harrison 2002), reduciendo fuertemente, y por un tiempo más prolongado, la luz a nivel del sotobosque. Estas nuevas condiciones de sombra y de humedad, pueden reducir las probabilidades de germinación y aumentar las tasas de mortalidad o de daño por herbivoros, hongos y otros patógenos (Hammond 1995, Peña-Claros y De Boo 2002).

Además de la incidencia directa en la dinámica regenerativa, las variaciones climáticas globales como las resultantes de los años de El Niño, también repercuten en la magnitud, la frecuencia y la duración de los disturbios que influyen en el desarrollo sucesional de una comunidad. Por ejemplo, las sequías fuertes pueden provocar que la magnitud (*i.e.* el grado de impacto) y la extensión (*i.e.* dimensión del área afectada) de los incendios en las actividades de roza-tumba y quema sean mayores, como resultado de una mayor acumulación de combustible (*e.g.* hojarasca y leña) y de un ambiente más seco (Dale *et al.* 2001). Esto incrementa el impacto en la disponibilidad de propágulos, que se reduce o merma por la mortalidad o el daño por incendios de magnitud y extensión mayor. Sin duda, los fenómenos climáticos globales como El Niño tienen repercusiones importantes y pueden jugar un papel preponderante en el desarrollo de los bosques maduros y de la vegetación secundaria. El impacto de las variaciones climáticas, en los procesos de regeneración natural y de la sucesión ecológica puede ser mayor en sistemas fuertemente estacionales como el bosque tropical caducifolio. La dinámica de estos sistemas depende principalmente de la disponibilidad de agua, es decir de la frecuencia, la magnitud y la duración de los eventos de lluvia, que se ven fuertemente modificados por fenómenos como El Niño (Timmerman *et al.* 1999, Nakagawa *et al.* 2000).

El presente trabajo de investigación considera aspectos de la visión mecanicista; es decir, la existencia de mecanismos claves (*i.e.* facilitación, tolerancia e inhibición), que en conjunto (visión holística) con factores causales definirán la dinámica sucesional de la comunidad regenerativa. Los factores incluidos son eventos estocásticos, como eventos fuertes de sequía o de lluvia, que en interacción con las condiciones del sitio, en donde se desenvuelve el fenómeno sucesional, y demás factores involucrados (*e.g.* historia de uso del suelo, disponibilidad de especies, desarrollo diferencial de las especies; Fig. 2) determinarán en cierto grado el desarrollo regenerativo y sucesional de la comunidad. Además, como establece la “teoría de reglas de ensamblaje”, se considera que este complejo de factores podrá actuar a manera de filtro ambiental, moldeando la composición, la estructura y las trayectorias de las comunidades vegetales a través del tiempo sucesional (Diamond 1975, Hobbs y Norton 2004).

REGENERACIÓN NATURAL Y SUCESIÓN SECUNDARIA EN LOS TRÓPICOS

Algunas de las teorías sobre la regeneración natural y la sucesión ecológica han sido desarrolladas y evaluadas con el estudio de sistemas de vegetación tropical, principalmente en el trópico húmedo (Gómez-Pompa y Vázquez-Yanes 1985, Denslow 1987, Martínez-Ramos y García-Orth 2007). El conocimiento generado sobre este tema abarca aspectos estructurales y de composición de la vegetación secundaria (Guariguata y Ostertag 2001, Peña-Claros 2003), dinámicos (Capers *et al*. 2005, Chazdon *et al*. 2007, Lebrija-Trejos *et al*. 2010a), funcionales (Poorter *et al*. 2010, Lebrija-Trejos *et al*. 2010b), de interacciones bióticas y abióticas (Augspurger 1984, Wright 2002, Ceccon *et al*. 2003, Comita *et al*. 2009), de efectos de la historia de uso del suelo (Romero-Duque *et al*. 2007, Álvarez-Yepiz *et al*. 2008, Chazdon *et al*. 2009), de restauración ecológica (Holl 1999, 2007) y a nivel paisaje (Uriarte *et al*. 2009). Aunque el conocimiento es amplio para los trópicos, la mayoría está restringido a los bosques tropicales húmedos, dejando de lado a los sistemas caracterizados por una estacionalidad fuerte y marcada (Sánchez-Azofeifa *et al.* 2005, ver revisiones Ceccon *et al*. 2006, Vieira y Scariot 2006, McDonald *et al*. 2010).

Se sabe que en los bosques tropicales húmedos, donde el agua de lluvia es abundante, uno de los factores principales que rige las dinámicas de la regeneración natural y de la sucesión ecológica es la disponibilidad de luz solar, la cual representa un recurso limitante para las comunidades vegetales de estos ecosistemas (Richards 1996). Las teorías sobre sucesión ecológica en los bosques tropicales húmedos se han desarrollado en gran medida considerando la variación temporal y espacial de la disponibilidad de la luz fotosintéticamente activa (Denslow 1987). Por ejemplo, se ha sugerido que las especies pioneras, muy demandantes de luz, son reemplazadas por especies con niveles crecientes de tolerancia a la sombra, a medida que transcurre el tiempo sucesional (Gómez-Pompa y Vázquez-Yanes 1985, Swaine y Whitmore 1988). Así, las especies del bosque tropical húmedo se han clasificado con base en sus respuestas, morfofuncionales, fisiológicas y demográficas a las variaciones del recurso lumínico (Bazzaz 1979, Bazzaz y Pickett 1980).

A diferencia de los bosques tropicales húmedos, la dinámica de los bosques tropicales caducifolios está principal y fuertemente vinculada al régimen de variación temporal de lluvias (Ewel 1977, Lieberman y Lieberman 1984, Murphy y Lugo 1986, Martínez-Yrízar y Sarukhán1990, Lieberman y Li 1992, Sovan y Singh 1994, Anaya *et al*. 2007, Lebrija-Trejos *et al*. 2010a), más que al régimen temporal de la disponibilidad de luz (pero ver Huante y Rincón 1998, Ceccon *et al*. 2003). Los bosques tropicales caducifolios se caracterizan por una estación de sequía fuerte y marcada (*e.g.* en la región de Chamela los meses de la época de secas presentan menos de 37 mm de lluvia mensual), que abarca desde tres hasta ocho meses (Galicia *et al*. 1999; datos obtenidos de http://www.ibiologia.unam.mx/ebchamela/www/clima.html), valores bajos de precipitación anual (desde 400 hasta 1800 mm) y una temperatura promedio de 25°C (Holdridge 1947). De acuerdo con Holdridge (1947), estos bosques tienen una evapotranspiración potencial anual de hasta cuatro veces mayor que la precipitación anual, dando como resultado un cociente de evapotranspiración potencial/precipitación mayor a uno (ETP/PP>1). Es decir, estos bosques pierden más agua anualmente a través de la transpiración y la evaporación que la que reciben por la lluvia, convirtiéndolos en sistemas estresados hídricamente, sobre todo en la estación de secas. Estas particularidades ambientales generan comunidades con características de estructura, composición y funcionamiento muy diferentes a las del bosque tropical húmedo (Tabla 1; Ewel 1977, Murphy y Lugo 1986).

Debido a los contrastes antes mencionados entre los bosques tropicales húmedos y los bosques tropicales caducifolios (Tabla 1), es razonable pensar que los factores y los mecanismos involucrados en la regeneración natural y la sucesión secundaria de estos dos ecosistemas sean distintos, y que los patrones y los mecanismos de recuperación a las perturbaciones producidas por el cambio de uso del suelo que sufren estos ecosistemas también sean diferentes.

Tabla 1. Características contrastantes entre los bosques tropicales caducifolios y bosques tropicales húmedos.

Características	**[a]Bosque tropical caducifolio**	**[b]Bosque tropical húmedo**	**Referencias**
Altura promedio del dosel (m)	12	30	[a]Trejo y Dirzo 2002, [b]Richards 1996
Número de especies de árboles por ha	35-90	50-200	[ab]Murphy y Lugo 1986
Número de estratos arbóreos	Dos	Tres como mínimo	[a]Trejo y Dirzo 2002, [b]Richards 1996
Caída de árboles	Poco frecuente	Frecuente	[a]Durán 2004, [b]Denslow 1987
Densidad de flujo de fotones (%) en el nivel del sotobosque	9-10	1-2	[a]Lebrija-Trejos *et al.* 2010b, [b]Chazdon y Fetcher 1984
Estacionalidad	Muy marcada	No marcada	[a]Bullock y Solís-Magallanes 1990,
Cociente de evapotranspiración potencial/precipitación (ETP/PP)	> 1	< 1	[ab]Holdridge 1947

EL CASO DE LOS BOSQUES TROPICALES CADUCIFOLIOS

FUENTES DE PROPÁGULOS

En los bosques tropicales caducifolios (*sensu* Rzedowski 1978), o también llamados, selvas bajas caducifolias (Miranda y Hernández-X 1963), tropical dry forests (Holdridge 1947) y seasonally dry tropical forests (Mooney *et al*. 1995), los factores dirigentes de la regeneración natural parecen ser la disponibilidad de agua en el suelo (recurso limitante) y la radiación solar (Lieberman y Li 1992, McLaren y McDonald 2003, Ceccon *et al*. 2006, Vieira *et al*. 2006, Lebrija-Trejos *et al*. 2010a); factores que en conjunto generan ambientes hídricamente estresantes (*i.e.* altas tasas de evapotranspiración; Camargo y Kapos 1995). Bajo estas características ambientales se ha propuesto que el mecanismo de regeneración más importante, de árboles y arbustos, en los bosques tropicales caducifolios, es la formación de rebrotes y no la formación de plántulas (*i.e.* desarrollo a partir de semillas; Ceccon *et al*. 2006, Vieira *et al.* 2006, Vieira y Scariot 2006, pero ver Ceccon *et al*. 2003). Es posible que la formación de rebrotes sea aun más importante en sitios perturbados, en donde los niveles altos de radiación y de temperatura y la baja disponibilidad de agua en el suelo limitan fuertemente la regeneración vía semillas (Camargo y Kapos 1995, Lebrija-Trejos *et al*. 2011).

Mientras que la germinación requiere de ciertas condiciones de luz, de temperatura, de nutrientes y de humedad del suelo (generadas en la estación de lluvias; Rincón y Huante 1994, Huante y Rincón 1998, Khurana y Singh 2001, Ceccon *et al*. 2003, Ceccon *et al*. 2006, Vieira y Scariot 2006), y el establecimiento y la supervivencia de las plántulas depende (además de los factores mencionados anteriormente) de la generación de sus propios recursos (*i.e.* a través de la fotosíntesis; Grime 1979), la formación de los rebrotes parece no tener dichas exigencias ambientales. La formación de los rebrotes depende principalmente de sus recursos almacenados (en raíces y/o tallos) y/o de los recursos provistos por la planta parental (*i.e*. a través de las conexiones existentes de tejido; Grime 1979, Chapin III *et al.* 1990, Hoffmann 1998, Knox y Clarke 2005).

Así, la dependencia grande de las plántulas hacia los factores ambientales, hacen pensar razonablemente que la probabilidad de establecimiento y de crecimiento de las plántulas en los ambientes que presentan niveles altos de radiación y disponibilidad baja de agua, sea menor que la de los rebrotes (Lieberman y Li 1992, Khurana y Singh 2001, Cabin *et al*. 2002, Marod *et al*. 2002, McLaren y McDonald 2003; pero ver Ceccon *et al*. 2003). Además, por los requerimientos ambientales la germinación y el establecimiento de las plántulas están confinados a la época corta de lluvias (Bullock 1995, Ceccon *et al*. 2006, Vieira y Scariot 2006).

Los rebrotes, al poseer un vigor mayor (*i.e.* tejidos más fuertes) y raíces más profundas que las plántulas, tienen probabilidades más grandes de supervivencia ante eventos de fuertes sequías e incendios (Sennerby-Forsse *et al*. 1992, Hoffmann 1998, Vesk and Westoby 2004, Lévesque *et al*. 2011). Por otro lado, en términos de interacciones bióticas se ha observado que los tejidos suaves de las plántulas, en relación a los de los rebrotes, las hacen más suceptibles a los herbívoros (Coley y Barone 1996).

Hasta el momento, los estudios proponen que la formación de rebrotes es el mecanismo principal de la regeneración natural en los bosques tropicales caducifolios. Sin embargo, hay algunos trabajos que han mostrado datos controversiales (Ceccon *et al*. 2002, 2003, 2004), que muestran que la regeneración natural inicial está dominada por las plántulas y no por los rebrotes. Si bien la regeneración puede estar dominada inicialmente por las plántulas, las condiciones ambientales adversas (*i.e*. hídricamente estresantes) y la limitación de recursos (*i.e.* agua) provocan tasas altas de mortalidad en las plántulas (McLaren y McDonald 2003, Ceccon *et al*. 2004) y promueven una regeneración posterior (*i.e.* persistencia) a través de los rebrotes (Hoffmann 1998, McLaren y McDonald 2003, Vieira *et al*. 2006).

En ambientes perturbados, el papel de mantenimiento de los rebrotes aumenta (Hoffmann 1998, Miller y Kauffmann 1998, McLaren y McDonald 2003, Vesk y Westoby 2004, Vieira *et al*. 2006). Se ha observado que las reservas de la planta, que se utilizan para la formación de los rebrotes, se movilizan después de cierto grado de daño (*e.g.* incendios, cortes; Kozlowski y Pallardi 1997, Hodgkinson 1998). Sin embargo, algunos estudios han observado que en disturbios intensos y frecuentes, es posible que la capacidad de producir rebrotes disminuya (Hodgkinson 1998).

Debido a las características de la lluvia y del banco de semillas en el bosque tropical caducifolio, se piensa que esta última fuente puede limitadamente contribuir a la formación de un banco de plántulas de árboles y de arbustos. Un porcentaje alto de las especies de árboles y de arbustos del bosque tropical seco, dispersan sus semillas a través del viento (entre 33 y 63%) o a través de sus propios mecanismos de dispersión, y sólo una fracción pequeña se dispersa a través de animales (Frankie *et al*. 1974, Justiniano y Fredericksen 2000, pero ver Ray y Brown 1994). De esta manera, las semillas parecen no tener barreras para arribar a los sitios disponibles (Teegalapalli *et al*. 2010). Aunque la dispersión de semillas se registra principalmente a finales de la época de secas (sobre todo de las especies dispersadas por el viento; Garwood 1983, Bullock y Solís-Magallanes 1990, Pérez y Santiago 2001, Sundarapandian *et al*. 2005, Flores-Rodríguez 2008, Martínez-Garza *et al*. 2011), algunos trabajos han reportado que también durante la época de lluvias existen eventos importantes de dispersión (sobre todo de las especies dispersadas por los animales;

Ray y Brown 1994, Martins y Engel 2007). Una vez que las semillas caen al suelo y forman parte del banco de semillas, el tiempo que permanecen viables es menos de un año (*i.e.* banco transitorio; Thompson y Grime 1979) ya que la mayoría de estas semillas germinan rapidamente (Rico-Gray y García-Franco 1992, Skoglund 1992, Miller 1999). Además de la permanencia corta de las semillas en el banco, se ha reportado que las densidades de semillas de árboles y de arbustos son bajas y que por el contrario, la mayor parte de las especies registradas en el banco de semillas son herbáceas (Campbell *et al*. 1990, Skoglund 1992, Ray y Brown 1994, Miller 1999, Martins y Engel 2007, Flores-Rodríguez 2008, Lemus-Herrera 2008). Con base en esto, es razonable pensar que el banco de plántulas, de árboles y de arbustos, proviene principalmente de la lluvia de semillas.

En sistemas pertubados, donde el banco de semillas ha sido fuertemente impactado (*e.g*. a través del uso de fuego, químicos, maquinaria pesada, pisoteo de ganado), la probabilidad de que a partir de éste se produzca un banco de plántulas es aún menor que en sitios conservados; la mayoría de estos bancos están compuestos, casi en su totalidad, por especies herbáceas (Miller 1999, Flores-Rodríguez 2008, Lemus-Herrera 2008). Por otro lado, en sitios perturbados, los árboles y los arbustos reproductivos son dañados parcial o totalmente. Bajo estas circunstancias, es probable que la lluvia local de semillas (*i.e*. originada por los componentes del mismo sitio) se reduzca fuertemente al igual que la lluvia foránea de semillas (*i.e*. semillas provenientes de fuentes externas al sitio perturbado; Khurana y Singh 2001, Martínez-Garza *et al*. 2011). Por ejemplo, si la extensión (*i.e*. el área) del disturbio es muy grande, es posible que la capacidad de dispersión por viento no logre traspasar esta barrera. Por otro lado, se sabe que en sitios abiertos la presencia de animales dispersores es baja, debido a los riesgos que les representan estos campos en términos de depredación y estrés (Janzen 1988b, Holl 1999).

CONDICIONES Y RECURSOS

Como hemos mencionado anteriormente, la disponibilidad baja de agua en el suelo en conjunto con los niveles altos de temperatura y de radiación solar parecen ser los factores dirigentes del proceso regenerativo en el bosque tropical caducifolio. Durante la época de lluvias, se ha observado que la disponibilidad de agua en el suelo aumenta y la radiación y la temperatura en el sotobosque disminuyen (Barradas 1991, Lebrija-Trejos *et al*. 2011), creando ambientes con menor demanda de evapotranspiración (*i.e*. menor estrés hídrico). Así, bajo estas nuevas condiciones ambientales se ha observado que la germinación, el establecimiento y el crecimiento de las plántulas y la producción y el crecimiento de los rebrotes están confinados principalmente a la época de lluvias (Khurana y Singh 2001, Ceccon *et al*. 2002, Vieira *et al.* 2006).

Sin embargo, pese a las condiciones óptimas y a la disponibilidad buena de recursos en la época de lluvias, existen otros factores ambientales que pueden impactar de manera negativa el proceso regenerativo. Por ejemplo, hay estudios que indican que durante la época de lluvias, la densidad de organismos que pueden dañar a las plantas pequeñas y a las semillas (*e.g*. herbivoros, patógenos), así como el nivel de daño (*e.g*. herbivoría, infestación) incrementan (Janzen 1981, Janzen 1988a, Filip *et al*. 1995, Hammond 1995, Coley y Barone 1996, Marini-Filho 2000, Cuevas-Reyes *et al*. 2006).

Por otro lado, algunos estudios proponen que en ambientes de estrés, como el generado en la época de secas en los bosques tropicales caducifolios, es posible que la facilitación sea un mecanismo clave en la regeneración natural de las comunidades (Dormann y Brooker 2002, Lebrija-Trejos *et al*. 2008). Debajo o cerca del dosel de una planta, las condiciones de radiación y temperatura son menores que en el campo abierto; este microambiente puede favorecer la supervivencia de plantas pequeñas, sobre todo en la época de secas o en campos perturbados (Vetaas 1992, Belsky *et al*. 1993, Veenendaal *et al*. 1996).

De manera general se ha observado que en sitios perturbados las condiciones de estrés hídrico se acentuan, los sitios perturbados presentan niveles mayores de radiación, de temperatura y baja disponibilidad de agua (Camargo y Kapos 1995, Lebrija-Trejos *et al*. 2008). Así, las condiciones ambientales en los sitios perturbados promueven tasas menores de germinación, de supervivencia y de crecimiento que en los bosques maduros (Vetaas 1992, McLaren y MCDonald 2003).

Por otro lado, algunos estudios han mostrado que el nivel de daño por animales es mayor en sitios perturbados que en sitios conservados (Coley y Barone 1996). Si bien la facilitación puede promover tasas mayores de supervivencia, sobre todo en sitios perturbados recientemente (donde las características ambientales son adversas y restrictivas para el establecimiento y supervivencia de las plantas), es lógico pensar que después de cierto tiempo (*i.e.* cuando las características ambientales son menos adversas y restrictivas), la facilitación resulte en algún tipo de interferencia (Connell y Slatyer 1977, McCook 1994, Butterfield 2009, Verdú *et al*. 2009), trayendo como resultado extinciones locales de especies. Es importante recordar que el tipo y la intensidad de las interacciones en un espacio determinado, son cambiantes en el tiempo y dependen de las características ambientales (Bradley 2009).

Los estudios de sucesión secundaria y de regeneración natural en los bosques tropicales caducifolios se han centrado principalmente en la vegetación leñosa juvenil y madura (*i.e.* árboles y arbustos ≥ 1.5 cm diámetro a la altura del pecho, dap), y pocos estudios se han enfocado en la comunidad regenerativa (*i.e.* banco de semillas, lluvia de semillas, banco de plántulas y banco de rebrotes), la cual se ve fuertemente reducida por filtros ambientales como la limitación de recursos, las condiciones adversas y las interacciones bióticas negativas como la depredación, el parasitismo y la competencia (Harper 1977). Se sabe que el proceso de germinación y el estado de plántula son las fases más críticas del establecimiento de las plantas (Harper 1977). Incluso la capacidad de rebrote presenta umbrales ambientales que limitan su establecimiento (Bond y Midgley 2001, Vieira *et al*. 2006).

CRONOSECUENCIAS Y ESTUDIOS DINÁMICOS DE LARGO PLAZO

Si bien el estudio de la sucesión secundaria inició hace casi un siglo (Clements 1916), en los últimos años se ha cuestionado la validez de los patrones sucesionales generales obtenidos a través de cronosecuencias. La mayoría de las investigaciones sobre sucesión ecológica se han basado en el empleo de esta técnica (Chazdon *et al*. 2007, Johnson y

Miyanishi 2008). Los procesos de sucesión pueden tomar décadas o cientos de años y el uso de cronosecuencias permite la evaluación de estos períodos largos de desarrollo, reemplazando el tiempo por el espacio. Pese a la ventaja que representa el uso de cronosecuencias, existe un supuesto importante que cumplir, el cual establece que todos los sitios que conforman la cronosecuencia deben diferir solamente en la edad, es decir, que todos los sitios deben compartir la misma historia de desarrollo y tener las mismas circunstancias bióticas y abióticas (Johnson y Miyanishi 2008), lo cual en la práctica es muy dificil de cumplir.

Sin duda, la violación a los supuestos implícitos en el uso de cronosecuencias limita su correcta aplicación; sin embargo, la mayoría de los estudios han pasado por alto dicha restricción (Chazdon *et al*. 2007, Johnson y Miyanishi 2008). Generalmente, los estudios basados en las cronosecuencias consideran y controlan sólo aspectos topográficos como el tipo de sustrato, la pendiente o la exposición, dejando de lado otros aspectos (*e.g.* la estructura y composición de las especies remanentes, las condiciones climáticas en el momento del disturbio y del abandono y la matriz de la vegetación circundante), que sin duda son importantes en el desarrollo diferencial de las comunidades de las cronosecuencias.

Recientemente se ha discutido que el alcance que tienen las cronosecuencias en la predicción del desarrollo sucesional en un sitio perturbado determinado es limitado (Foster y Tilman 2000, Chazdon *et al*. 2007, Johnson y Miyanishi 2008). De manera general, en los bosques tropicales secundarios (húmedos y secos), las cronosecuencias predicen un aumento en la riqueza de especies, la densidad de plantas y la biomasa a través del tiempo (Chazdon *et al*. 2007). Sin embargo, algunos estudios han comprobado que las predicciones de las cronosecuencias no concuerdan con el desarrollo real de las comunidades, habiendo inconsistencias entre lo esperado y lo observado (Kennard 2002, van Breugel *et al*. 2006, Brienen *et al.* 2009; pero ver Lebrija-Trejos *et al*. 2008 y 2010a). Por ejemplo, el alcance predictivo de las cronosecuencias parece estar confinado a algunos atributos estructurales, tales como el área basal, en donde la trayectoria positiva y la velocidad de acumulación observada a través del tiempo en la dinámica, ha respaldado lo predicho por las cronosecuencias. Sin embargo, por otro lado los datos dinámicos de la densidad de tallos, la altura de la vegetación y la diversidad de especies no respaldan, las trayectorias positivas esperadas por la cronosecuencia. En estos casos, los datos dinámicos muestran un desarrollo independiente a la edad de abandono; las trayectorias parecen estar más vinculadas con las características particulares del sitio (*i.e*. idiosincrático), como la historia de uso del suelo, la estructura y composición de la comunidad al momento de abandono, las variaciones climáticas durante el disturbio y en el momento del abandono (van Breugel *et al.* 2006, Chazdon *et al*. 2007, Johnson y Miyanishi 2008; pero ver Lebrija-Trejos *et al*. 2008 y 2010a).

Si bien las cronosecuencias pueden llevar a plantear hipótesis sobre la forma de las trayectorias sucesionales y las tasas de cambio de los atributos estructurales de la comunidad (Johnson y Miyanishi 2008, van Breugel *et al*. 2006), este enfoque está limitado para explorar los mecanismos ecológicos que subyacen a dichas trayectorias y tasas. La dinámica sucesional de la vegetación está gobernada por variables que no necesariamente son medibles a través la edad sucesional (*e.g*. la historia de uso del suelo, las especies remanentes, la matriz circundante y las condiciones ambientales al momento de abandono). Por otro lado, se ha propuesto que la composición de especies de una comunidad no sólo depende de la edad sucesional. Algunos factores extrínsecos, como la variación climática, también son importantes en la determinación de las especies presentes. Por ejemplo, las sequías fuertes pueden inducir en tasas de mortalidad altas para algunas especies, mientras que otras, pueden mostrar mayor resistencia (Foster y Tilman 2000, Chazdon *et al*. 2005, Engelbrecht *et al*. 2007, Lebrija-Trejos *et al.* 2008, Pineda-García *et al*. 2011).

El proceso sucesional puede tomar décadas (Finegan 1996), limitando seriamente la posibilidad de hacer un seguimiento real de una comunidad a través del tiempo. Por lo tanto, el seguimiento de una cronosecuencia a través del tiempo puede, en cierta medida, reducir los vacíos y las limitantes del uso único de cronosecuencias (Johnson y Miyanishi 2008). Con un enfoque que combine el método de cronosecuencias con el de monitoreo a través del tiempo, se puede tener información sobre estados sucesionales de edades avanzadas (> 80 años), imposibles de seguir horizontalmente desde sus inicios (*i.e*. recién abandonados). Además, el seguimiento del desarrollo individual de cada sitio incluido en la cronosecuencia permitirá conocer la dinámica de las comunidades vegetales en diferentes estados sucesionales y explorar los mecanismos involucrados en tal dinámica (*e.g*. Lebrija-Trejos *et al*. 2010a).

En este panorama, el presente trabajo estudiará las trayectorias de las comunidades regenerativas en diferentes estados sucesionales, a través del tiempo. Lo anterior con la finalidad de conocer, no sólo los patrones, sino también los mecanismos y los factores influyentes en dichas trayectorias.

OBJETIVOS

El presente trabajo de tesis está dirigido a identificar los patrones, los procesos y los mecanismos de la regeneración natural y la sucesión secundaria en comunidades regenerativas (semillas, plántulas, rebrotes y brinzales) de arbustos y de árboles, presentes en etapas iniciales (< 16 años) de la sucesión secundaria del bosque tropical caducifolio, desarrolladas en pastizales ganaderos abandonados de la región de Chamela, Jalisco, México.

Para cubrir este objetivo, se desarrollaron tres estudios. El primero, presentado en el Capítulo II, analiza los cambios en la abundancia, la diversidad y la composición de especies del banco de semillas a través de una cronosecuencia. La cronosecuencia abarcó pastizales ganaderos con 0 a 12 años de abandono y sitios de bosque maduro. El análisis incluyó la exploración de los mecanismos de facilitación, de tolerancia y de inhibición propuestos por Connell y Slatyer (1977), considerando las formas de crecimiento (herbáceas, arbustivas, arbóreas y trepadoras) de las especies presentes en el banco de semillas.

En el segundo estudio (Capítulo III), se analizaron las tendencias sucesionales de las comunidades regenerativas (plántulas, brinzales y rebrotes) de arbustos y de árboles, predichas por uso exclusivo de cronosecuencias, y se compararon con la dinámica de la comunidad observada durante un intervalo de tres años. Además de la edad de abandono, se exploraron factores biofísicos tales como la disponibilidad de luz en el sotobosque durante la época de lluvia, la densidad de tallos de arbustos y de árboles adultos (dap ≥ 1 cm) en los sitios de estudio y la cobertura de bosque alrededor de los sitios (matriz), como posibles variables explicativas de los patrones sucesionales obtenidos con la cronosecuencia y con la dinámica de las comunidades.

En el tercer estudio (Capítulo IV), se evaluó el papel de factores climatológicos globales, como la Oscilación del Sur El Niño (ENSO por sus siglas en inglés), que afectan de manera fundamental a los regímenes climáticos regionales y locales, en términos de los patrones interanuales e interestacionales de temperatura y de precipitación. En este contexto, se estudió el efecto de la variación temporal de lluvias durante el periodo de estudio (2004-2007) y de años previos, sobre la dinámica (tasas de ganancia y de pérdida de plantas y de especies en las estaciones de sequía y de lluvia) de las comunidades regenerativas a través de la sucesión. Además de analizar a estas comunidades en conjunto, se evaluó la dinámica de las plántulas, los rebrotes, los árboles y los arbustos de manera independiente. Esto tuvo la finalidad de evaluar si se presentaban respuestas diferenciales entre estos grupos.

Finalmente, en el Capítulo V se presentan la discusión y las conclusiones generales de este trabajo de investigación, haciendo una síntesis sobre los resultados más importantes y el alcance que éstos tienen en el contexto teórico de la sucesión secundaria y la regeneración natural de los bosques tropicales caducifolios en campos agropecuarios abandonados.

MÉTODOS

SITIO DE ESTUDIO

La presente investigación se realizó en el municipio de La Huerta, Jalisco, en donde se encuentran áreas rurales y la Reserva de la Biosfera Chamela-Cuixmala (19° 30’ N, 105° 03’ W; Figura 3). El clima de esta región, de acuerdo con la clasificación de Köppen modificado por García (1988), es Cálido Subhúmedo, Aw_0i. Con base en la información obtenida de los datos climáticos de 1978 a 2007 de la Estación de Biología Chamela, Instituto de Biología-UNAM, el promedio de temperatura mensual (± 1 e.e) es de 25.1°C ± 1.96°C y la precipitación media anual de 777.4 mm ± 47.7 mm. Cerca del 90% de lluvia cae en el período comprendido entre junio y octubre, y una fuerte sequía (<37 mm mensual) se presenta desde noviembre hasta mayo, con un promedio mensual de 12.1 ± 5.1 mm (http://www.ibiologia.unam.mx/ebchamela/www/clima.html; Figura 1, capítulo IV).

La zona de estudio se caracteriza por presentar una fuerte variación en el inicio y el término de la estación de lluvias, así como en la frecuencia y la magnitud de los eventos de lluvia, tanto entre años y dentro de un mismo año (Galicia *et al.* 1999). La presencia de períodos de sequía durante la época de lluvias (sequía intraestival, canículas o "drought spells" en inglés) es un factor recurrente que impacta el desarrollo de las comunidades vegetales, al igual que los eventos de lluvia en la época de secas (De Ita-Martínez y Barradas 1986, Páramo-Pérez 2009). Se ha observado que estos dos fenómenos, lluvias en secas y sequía intraestival, están relacionados con la cantidad de precipitación de ese año; los años con altas precipitaciones presentan mayor frecuencia de eventos de lluvia en la época de sequías mientras que los años con precipitaciones escasas aumentan la posibilidad de presentar eventos de sequía durante la época de lluvias (Galicia *et al.* 1999); aparentemente esta variación también está relacionado con los años de La Niña (*i.e.* años extremadamente lluviosos) y los años de El Niño (*i.e.* años extremadamente secos).

La vegetación predominante en el sitio de estudio es el bosque tropical caducifolio (Rzedowski 1978). El bosque de la región Chamela-Cuixmala ha sido catalogado como uno de los bosques tropicales caducifolios con mayor diversidad florística en América (Lott y Atkinson 2006). El promedio de la altura del dosel varía entre 5 y 10 m, las familias más importantes por su número de especies son Fabaceae, Euphorbiaceae y Asteraceae; los componentes leñosos más importantes, por su abundancia y número de especies, lo comprenden los árboles (229 especies) y los arbustos (227 especies), que en conjunto concentran 43% de las especies totales reportadas para la región de Chamela-Cuixmala (1149 especies de plantas vasculares; Lott y Atkinson 2006). El 57% de especies restantes, está conformado por lianas y bejucos (197 especies), epífitas (40 especies) y herbáceas predominantemente perennes (366; Lott y Atkinson 2006). La característica más sobresaliente de este tipo de vegetación es, sin duda, que la mayoría de las especies son caducifolias durante la temporada de secas, quedando desprovistas de follaje de cinco a ocho meses (Bullock y Solís-Magallanes 1990).

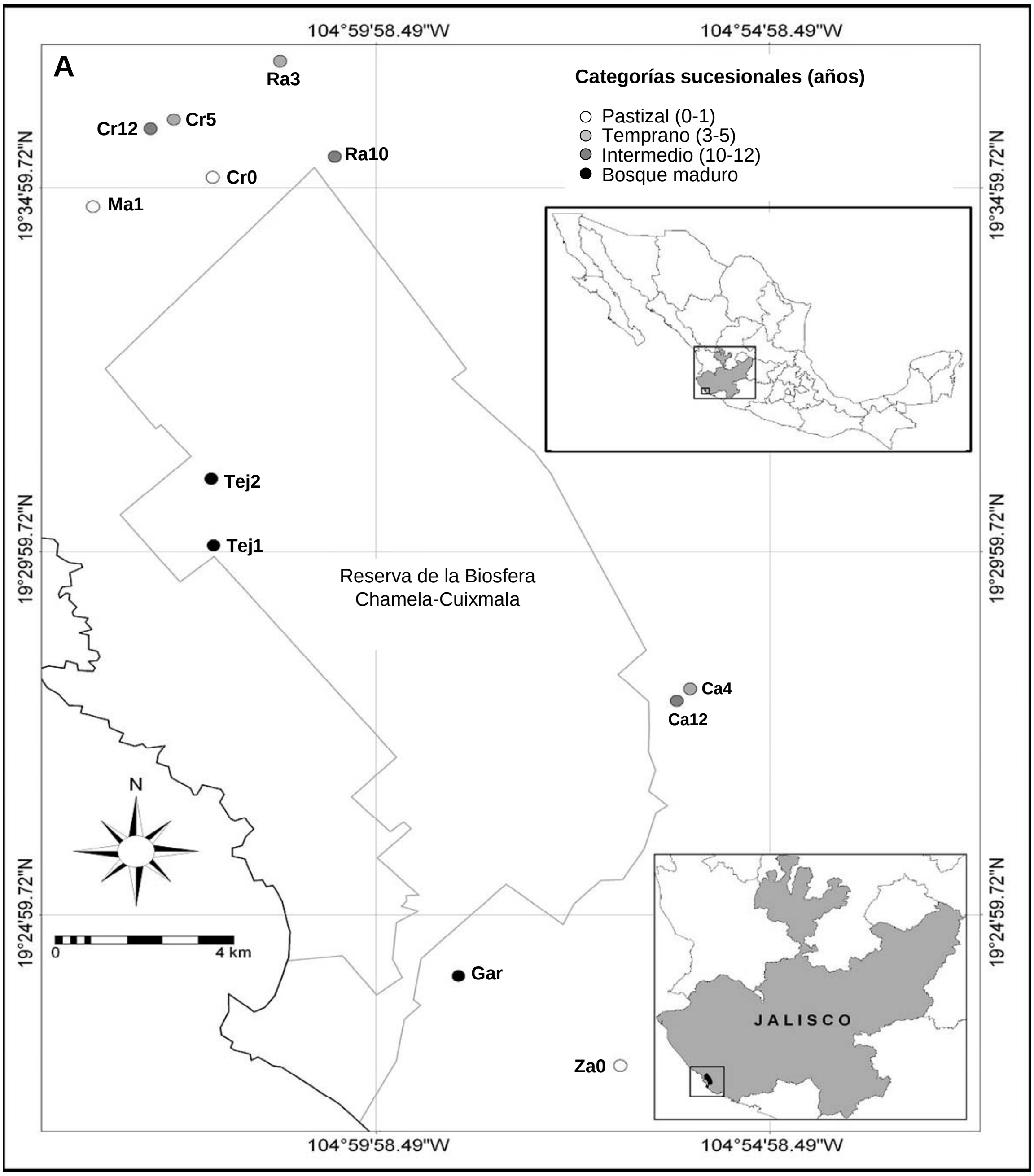

Figura 3. Localización geográfica de los doce sitios de estudio en la región de Chamela-Cuixmala, municipio de La Huerta, Jalisco. Cada punto representa un sitio de estudio, los colores diferentes indican cada una de las categorías sucesionales (ver recuadro de la parte superior izquierda) y las siglas identifican a los sitios (ver detalles en la Tabla 2). El área delimitada por el polígono (línea gris) corresponde a la Reserva de la Biosfera Chamela-Cuixmala.

La región es predominantemente montañosa y su relieve se encuentra dominado por lomeríos y algunas planicies aluviales que se presentan sobre todo cerca de la desembocadura de arroyos y de ríos. Las elevaciones montañosas representan 85% de la región y las planicies el 15% restante (De Ita-Martínez y Barradas 1986). La ganadería es la principal actividad que ha contribuido con el cambio del uso del suelo; esta actividad representa 60% del área transformada por las actividades humanas (Burgos y Maass 2004). Topográficamente, la actividad ganadera se concentra en laderas de pendientes intermedias, mientras que los valles son utilizados principalmente para actividades agrícolas (De Ita-Martínez y Barradas 1986). Las actividades agropecuarias realizadas en el área de estudio pueden considerarse de impacto bajo (Trilleras-Motha 2008), debido al suministro escaso de agroquímicos (*e.g*. herbicidas, fertilizantes) y a la falta de uso de maquinaria pesada para el arado de la tierra (*e.g*. tractores). De manera general, el manejo se resume en las actividades de roza-tumba y quema.

SISTEMA DE ESTUDIO

El sistema de estudio empleado en este trabajo, incluye sitios de bosque tropical caducifolio sin perturbación humana y sitios originalmente cubiertos por bosque tropical caducifolio, los cuales fueron desmontados y convertidos en pastizales para la crianza de ganado bovino, usados por algún tiempo y luego abandonados. Los campos abandonados se agruparon en las siguientes tres categorías de edad abandono: i) tres sitios con menos de un año, ii) tres de 3 a 5 años, y iii) tres de 8 a 12 años. También se estableció la categoría de bosques maduro (Old-Growth Forest en inglés) con tres sitios dentro de áreas conservadas. La Tabla 2 describe algunas características biofísicas de los sitios de estudio.

En cada sitio se instaló una parcela permanente de 20 x 50 m, dentro de la cual se establecieron 48 cuadros permanentes de 1 m^2 cada uno, distribuidos homogéneamente en toda el área de la parcela (1000 m^2) con la finalidad de cubrir la mayor heterogeneidad ambiental posible. Dentro de cada cuadro, los árboles y los arbustos entre 10 y 100 cm de altura (medida desde el suelo hasta la punta más alta de la copa) fueron marcados y monitoreados a lo largo de los tres años (de octubre de 2004 a octubre de 2007) que duró la presente investigación.

Se procuró establecer a los sitios de estudio en terrenos con una orientación sur y con un grado de inclinación semejante, lo anterior con el fin de asegurar un mismo nivel de radiación solar, escorrentía y otros factores asociados al relieve (Galicia *et al*. 1999, Auslander *et al*. 2003; Tabla 2). Para cada sitio se obtuvo la cobertura forestal de la matriz circundante (a través de imágenes satelitales), la densidad de tallos de árboles y de arbustos (dap ≥ 1 cm) y la apertura del dosel a una altura de 1.3 m sobre el suelo (ver detalles en el Capítulo III).

Finalmente, se obtuvo el porcentaje de agua contenido en el suelo a través de la densidad aparente de siete muestras cilíndricas de suelo (78.5 cm^3 cada muestra; 5 cm de diámetro y 10 cm de profundidad) tomadas a finales de agosto de 2006. Las muestras se obtuvieron, en cada una de las doce parcelas y fueron almacenadas en recipientes herméticos para su transportación al laboratorio. En un mismo día y a una misma hora (para controlar el efecto de la variación ambiental y temporal en las diferentes categorías sucesionales), se muestreó una parcela de cada categoría sucesional, es decir cuatro parcelas por día. Para cada una de las parcelas se obtuvo el promedio de agua contenida (%) en el suelo (Tabla 2). Cada una de las siete muestras se pesó antes (peso inicial, P_i) y después de secarse en un horno a 70°C por 48 horas (peso final, P_f), obteniéndose así el porcentaje de agua contenida en cada muestra (% Agua en el suelo = $(1-(P_f/P_i))*100$).

Para conocer la independencia de las variables biofísicas de los sitios se realizaron regresiones lineales. Los datos fueron transformados previamente para cumplir con los supuestos del análisis de regresión lineal.

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Tabla 2. Características biofísicas de los 12 sitios de estudio que incluyen pastizales ganaderos abandonados y sitios de bosque maduro, en el municipio de La Huerta, Jalisco, México. Los nombres codificados corresponden a las dos primeras letras del nombre del sitio y la edad en años de abandono: Zapata (Za0), Mateo (Ma1), Santa Cruz (Cr0), Caimán (Ca4), Ranchitos (Ra3), Santa Cruz (Cr5), Caimán (Ca12), Ranchitos (Ra10); para los sitios de bosque maduro (BM) el número sólo identifica al sitio: Gargollo (Ga), Tejón 1 (Tej1), Tejón 2800 (Tej2).

Sitio	Za0	Ma1	Cr0	Ca4	Ra3	Cr5	Ca12	Cr12	Ra10	Gar	Tej1	Tej2
Categoría sucesional	0-1			3-5			10-12			BM		
Edad de abandono (años)	0	1	0	4	3	5	12	12	10	BM	BM	BM
Exposición de ladera	S	SW	S	E	SE	SW	S	SW	SW	S	S	S
Pendiente del terreno (°)	20	26	25	30	15	18	20	25	28	22	23	28
Matriz forestal circundante (%)	39	44	28	54	47	61	64	80	63	100	100	100
Densidad de tallos (dap ≥ 1cm) [a]	0	255	306	505	186	996	834	732	774	644	641	652
Apertura del dosel (%) [b]	90.6 ± 10.5	60.2 ± 14.6	71.3 ± 16.2	58.3 ± 16.6	75.6 ± 14.6	44.6 ± 15.1	29.2 ± 12.5	23.7 ± 12.5	22.7 ± 13.8	8.7 ± 6.0	20.2 ± 8.7	17.6 ± 6.3
Contenido de agua en el suelo (%) [c]	7.3 ± 0.66	2.9 ± 0.61	Dato no disponible	6.5 ± 1.5	9.8 ± 1.6	7.5 ± 1.5	7.4 ± 1.1	10.0 ± 1.1	11.0 ± 0.5	14.0 ± 4.1	10.6 ± 1.7	10.5 ± 1.0

[a] La densidad de tallos/ha, es la densidad de árboles y de arbustos (≥1cm dap) registrada en el 2005 (datos no publicados de P Balvanera y colaboradores); [b] la apertura del dosel tomada al final de la época de lluvias, corresponde al promedio para cuatro años de registro (2004-2007) ± 1 error estándar (ver detalles en el Capítulo III); [c] el contenido de agua en el suelo es el promedio por sitio ± 1 error estándar. Con excepción de la densidad de tallos y la apertura del dosel ($y= -0.114x + 1.372$; $R^2= 52.1$, $p= 0.0001$) y la apertura del dosel y el contenido de agua en el suelo ($y= -0.112x + 1.375$; $R^2= 35.7$, $p= 0.05$), el resto de variables mostraron independencia.

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CAPÍTULO II

SUCCESSIONAL TRENDS IN SOIL SEED BANKS OF ABANDONED PASTURES OF A NEOTROPICAL DRY REGION

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Successional trends in soil seed banks of abandoned pastures of a Neotropical dry region

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Abstract: A chronosequence was used to study seed-bank communities during the first 12 y of tropical-dry-forest regeneration in abandoned pastures in Chamela, Mexico. Prediction that seeds of woody species replace those of herbaceous species during succession was tested and mechanisms of species replacement (facilitation, tolerance, inhibition) were assessed. Four successional categories (three sites each) were considered: pasture (0–1 y since abandonment), early (3–5 y), intermediate (10–12 y), and old-growth forest. At the end of the dry season, 20 cylindrical soil samples (10 cm diameter, 15 cm depth) were randomly obtained within a 20 × 50-m plot in each site. Seeds $\geq$1 mm were counted and identified. Overall, 2941 seeds and 102 morphospecies (52 taxonomically identified) were recorded. Seed bank density reduced, species diversity remained fairly constant and seeds of herbaceous species were replaced by those of woody species over the chronosequence. A clear species-by-species replacement pattern was detected, as expected under a mechanism of succession by facilitation. Twelve years after abandonment, a diverse seed bank of woody species did exist, indicating a fast recovery of the tropical-dry-forest regenerative potential; nonetheless, the structure and composition of the seed bank was still different from that in the old-growth forest.

Key Words: Chamela–Cuixmala, chronosequence, Mexico, natural regeneration, regenerative communities, secondary succession, tropical dry forest

INTRODUCTION

Tropical dry forests (TDF) are greatly threatened by their conversion to agricultural land, making the future of this biome largely dependent on conservation of remaining old-growth forests and regeneration and restoration of secondary forests (Dirzo *et al.* 2010, Sánchez-Azofeifa *et al.* 2009). This posits a challenge because understanding the ecological factors, processes and mechanisms that allow TDF regeneration is far from being complete (Quesada *et al.* 2009). For example, currently no more than five published studies on TDF seed-bank communities in old-fields exist (González-Rivas *et al.* 2009, Lemenih & Teketay 2006, Miller 1999, Rico-Gray & García-Franco 1992, Vieira & Scariot 2006).

Colonizing herbaceous plants are highly dependent on light to produce abundant seeds, which usually are able to stay dormant in the soil for long periods (Fenner 1985). Seed bank density of such herbaceous plants is expected to decline as TDF succession advances and light resources reduce in the understorey. In contrast, seeds of most woody species lack prolonged dormancy and suffer high predation rates (Briones-Salas *et al.* 2006, Garwood 1989, Janzen 1981, Khurana & Singh 2001), which makes their abundance in the soil largely dependent on local seed rain (Álvarez-Buylla & Martínez-Ramos 1990, Dalling & Denslow 1998). Thus, the abundance and diversity of seeds of woody species in the soil is expected to increase as more reproductive woody plants become established during succession.

The temporal changes undergone by seed-bank communities may allow the exploration of mechanisms underlying species replacement during succession (*sensu* Connell & Slatyer 1977). Such analysis is possible if the abundance and composition of mature plant communities are mirrored in the characteristics of the seed banks. There is some evidence indicating that this is true for woody species (Ceccon *et al.* 2006, Dalling & Denslow 1998). Three possible patterns can be expected to occur in

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seed-bank samples taken along a chronosequence, depending on the mechanisms underlying plant succession. If there is a change in the species composition of the seed bank over the chronosequence, following a species-by-species replacement pattern, a facilitation mechanism would be inferred. In contrast, if seeds of several woody species are found in recently abandoned fields but they disappear sequentially with successional time, a tolerance mechanism would be indicated. Finally, if species richness and composition of the seed bank increase during succession after the disappearance of a dominant early-colonizer species, an inhibition mechanism would be inferred.

In this paper we analyse structural and compositional changes of seed-bank communities over a chronosequence of abandoned cattle pastures (with fallow ages of 0–12 y) and old-growth TDF sites in western Mexico. We hypothesize that: (1) density, diversity, and species composition of seed-bank communities change with fallow age and plant growth form during the first 12 y of succession, (2) seeds of herbaceous species are replaced by seeds of woody species over succession, (3) abundance of seed-banks of woody species mirror the abundance of the species in the established community and (4) successional mechanisms (i.e. facilitation, tolerance or inhibition) can be inferred from patterns of species replacement in the seed bank over the chronosequence.

METHODS

Study site

This study was carried out in the municipality of La Huerta and in the Biosphere Reserve of Chamela–Cuixmala (19°30′N, 105°03′W; Figure 1a), in Jalisco, Mexico. The annual average temperature is 22 °C and the mean annual precipitation is 788 mm. Most rain (*c.* 93%) falls between June and October and from November to May a long dry season occurs. The dominant vegetation is TDF which is characterized by low-stature trees (maximum 12 m) and shrubs, developed mostly on slopes and ridges of low hills (Segura *et al.* 2004). The conversion of the TDF to cattle pastures is the main agriculture practice in the study region, representing about 60% of the total area affected by human activities (Burgos & Maass 2004). Slash-and-burn is a highly recurrent practice; after some years of use, the pastures are abandoned and plant communities, initially dominated by herbaceous species and shrubs, develop in the open sites (Burgos & Maass 2004).

Study system

We used a chronosequence as a study system. Increasing evidence indicates that the substitution of time by space implicit in chronosequences does not necessarily predict the temporal trajectories that would follow the succession in a given site over time (Chazdon *et al.* 2007, Johnson & Miyanishi 2008). Accordingly, with the aim of reducing predictive uncertainty associated with chronosequences, we considered four successional categories with three replicates each: ‘pasture’ (pastures of 0–1 y since abandonment), ‘early’ (pastures 3–5 y since abandonment), ‘intermediate’ (pastures 10–12 y since abandonment), and old-growth forest without any sign of human disturbance. The percentage of land in open conditions (active pasture and other agricultural land uses, and roads) in the matrix surrounded the studied sites diminished, on average, from 63% in pasture to 31% in intermediate successional categories (Figure 1b).

At each study site, 20 cylindrical soil samples (10 cm diameter, 15 cm depth) were randomly obtained within a plot of 20 × 50 m. This sampling effort (equivalent to 200 samples ha^{-1}) exceeded the recommendation of Butler & Chazdon (1998) in order to properly represent the seed bank in a given tropical forest area. Soil sampling was conducted in May 2005, towards the end of the dry season. Other studies have found that density and diversity of seed banks in TDFs peak during the dry season (Grombone-Guaratini & Rodrigues 2002, Martins & Engel 2007). Many woody species tend to produce seeds in the dry season (Bullock & Solís-Magallanes 1990, Foster 1986), while germination, seed predation, and/or damage by fungi are higher in the rainy season compared with the dry season.

Each soil sample was sifted using metallic sieves of different aperture size to remove soil and debris. Sifted material was inspected visually and with stereoscopic microscopes to separate all seeds of at least 1 mm diameter. Seeds were separated by unequivocal morphospecies that were identified to the lowest taxonomic level whenever possible. Samples of seed morphospecies were germinated in a greenhouse to obtain seedlings/plants that could be identified. Herbarium reference collections, specialized literature and specialists were consulted for taxonomic identification. All morphospecies were assigned to following plant growth forms: tree, shrub, woody climber, herbaceous climber, terrestrial herb and grass. Dispersal mode (animals, wind and gravity) was also assigned to each identified morphospecies. Because of the lack of tests on seed viability, density and diversity values of the studied seed banks could be overestimated (Simpson *et al.* 1989).

Data analysis

At the community level and for each growth form, values of seed density (seeds per area unit), species density (species per area unit) and species diversity (number

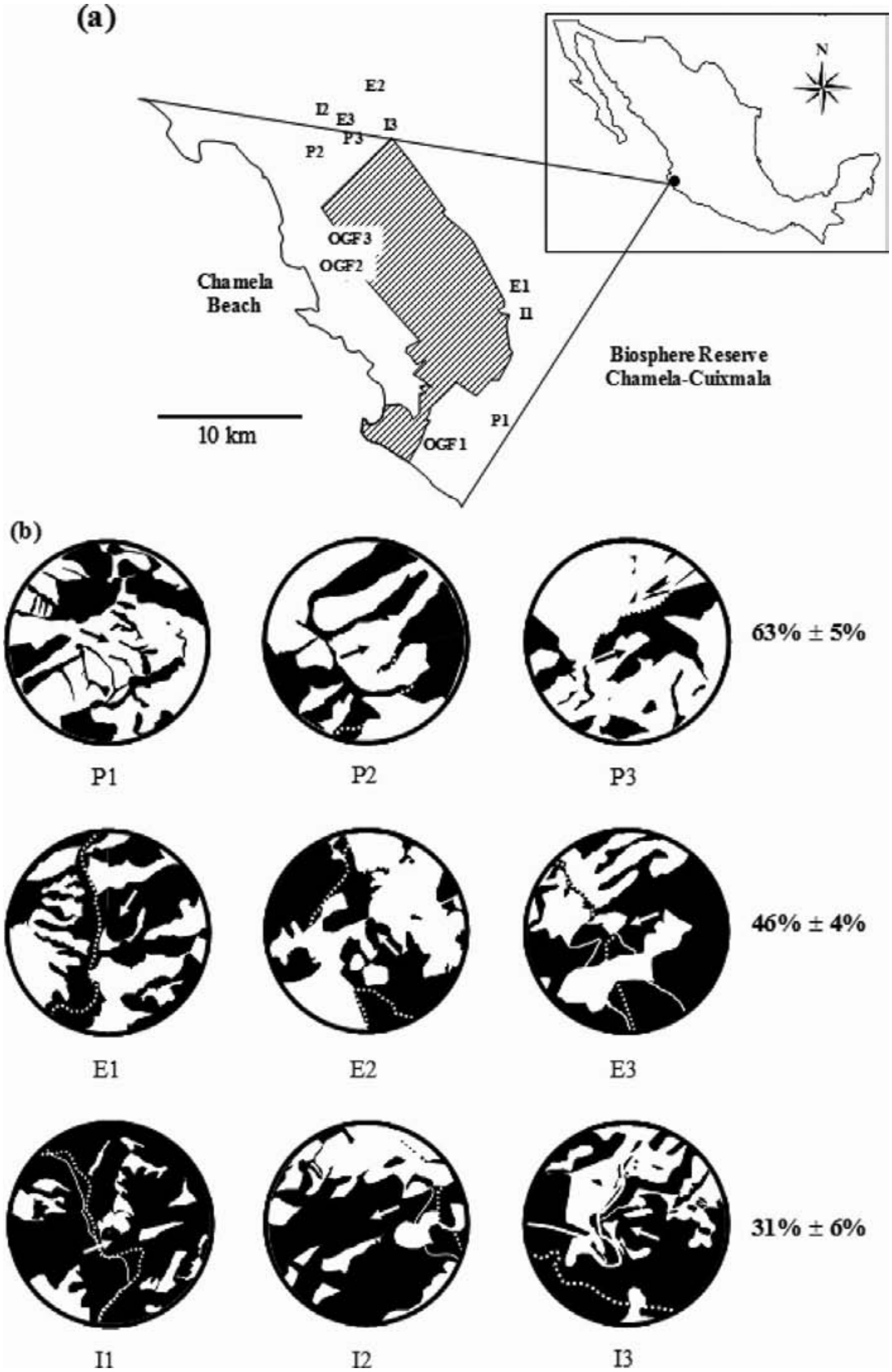

Figure 1. Geographic location of studied sites and matrix configuration surrounding each abandoned studied pastures at La Huerta Municipality (Jalisco), western Mexico. Map of location of 12 studied sites, three for each following successional categories; P: 'pasture' (0–1 y since abandonment), E: 'early' (3–5 y since abandonment), I: 'intermediate' (10–12 y since abandonment) and OGF: old-growth forest (a). Shaded area corresponds to the MAB Biosphere Reserve Chamela–Cuixmala. Matrix configuration around (in a circular area with a radius of 0.5 km) each studied site belonging to pasture, early and intermediate successional categories (b); in black are indicated areas covered with vegetation (secondary or old-growth forest) and in white open areas (active pastures, other agricultural fields, and roads), drawn from geo-referenced Google Earth® satellite images. Old-growth-forest sites were 100% covered by forest vegetation. Within the circular area, the position of the 20 × 50-m study plot is indicated by the tip of the black or white arrow. To the right, the mean and 1 SE of the percentage represented by open areas in each successional category is indicated.

and relative abundance of species, only for the whole community) were obtained. To do this, the program EstimateS 8.2 was used to generate a single trait value per plot, obtained from randomized accumulation curves of seeds and species, based on a matrix of species × samples for each plot; each cell of the matrix contained the number of seeds per species. Using the same program, two non-parametric estimators of the real number of species were also obtained for each plot. These estimators calculate the expected total number of species in a given site to determine, in a probabilistic way, the number of species missed by the sampling (Chao *et al.* 2005). ACE (based on species abundance) and ICE (based on species incidence) estimators were obtained, as they have been proved to be effective for plant communities (Magurran 2004). We used Fishers's α, which is insensitive to sample size (Magurran 2004), to quantify species diversity. Because of the small sample size for several morphospecies in most sites, it was not possible to calculate species diversity at the growth-form level.

One-way analyses of variance (ANOVA) were used to assess differences in seed density, species density and species diversity among the four successional categories. To fulfil the parametric criteria of ANOVA, the count response variables (seed density and species density) were log(x+1)-transformed. Bonferroni multiple comparison tests were used a posteriori to detect significant ($P \leq 0.05$) differences. Additionally, by lumping together sites of the same successional category, we constructed rank-abundance curves per successional category by plotting the seed density (seeds per m^2) of each species (logarithmic scale) as a function of species abundance rank (Magurran 2004). Log-log (potential) regression models, which approximate the Zipf–Mandelbrot model (Izák 2006), were fitted to each rank-abundance curve to calculate the ordinate (an estimator of species dominance) and the slope of the curve. An analysis of covariance (ANCOVA) was applied to test differences in community evenness (slope of the rank-abundance curve) among successional categories.

To assess the hypothesis of replacement of seeds from plants with different growth forms during succession, graphs of the percentage of total seeds represented by different growth forms as a function of successional category were constructed. To assess possible mechanisms of species replacement during succession (*sensu* Connell & Slatyer 1977), we did the following analyses. First, a Bray–Curtis similarity matrix (Austin 2005) was constructed considering values of seed density per species at each of the 12 studied sites. Second, a non-metric multi-dimensional scaling analysis (NMDS, Primer v.5) was used to ordinate the sites based on the Bray–Curtis similarity matrix. Multivariate analysis of variance (MANOVA) and a posteriori Bonferroni tests were performed to assess significant differences among successional categories over the ordination dimensions generated by the NMDS analysis. Finally, for each one of the 17 most-abundant species (with at least 15 seeds in all studied sites), we constructed graphs of the relative abundance of seeds as a function of successional category. The relative abundance of species was calculated by dividing the number of seeds of species *i* recorded in the three sites of a given successional category by the total number seeds of that species recorded in all studied sites. In the same way, to explore whether seed bank mirrored the abundance of mature plants, we calculated relative abundance of stems (diameter at breast height, dbh $\geq$ 1 cm) per successional category for the most abundant woody species recorded in the seed banks, based on data obtained in the same plots of our chronosequence (P. Balvanera, unpubl. data).

RESULTS

Overall, 2941 seeds in a total sampled area of 1.88 m^2 were recorded, corresponding to a mean density of 1560 seeds m^{-2} across all studied sites. In total, 102 unequivocal morphospecies were recorded (Appendix 1) from which 52% were identified to species, 23% to genus and 25% to family. Only 8.3% of total seeds were not taxonomically identified. From the identified taxa, 12 were trees (23.1%), five shrubs (9.6%), two woody climbers (3.8%), 14 herbaceous climbers (27%), 10 terrestrial herbs (19.2%) and six grasses (11.5%); three taxa (5.8%), identified at the family level, could not be associated to any growth form. Hereafter, we will refer to morphospecies as species.

Successional patterns and replacement among plant growth forms

Seed-bank density. Overall, seed density decreased from the younger to older successional categories ($F_{3,8} = 4.1$, $P = 0.05$; Figure 2a). However, this trend differed depending on plant growth form (Table 1). While seed density of herbaceous plants decreased ($F_{3,8} = 4.84$, $P = 0.03$), that of woody plants did tend to increase, although this trend was not significant ($F_{3,8} = 2.9$, $P = 0.09$). These patterns were mostly due to reductions in seed density of terrestrial herbs ($F_{3,8} = 7.24$, $P = 0.01$) and grasses ($F_{3,8} = 5.57$, $P = 0.02$), and an increase in the seed density of trees ($F_{3,8} = 10.4$, $P = 0.004$). Clearly, in proportional terms, seeds of herbaceous plants (mostly terrestrial herbs and grasses) were replaced by those of woody plants (mostly trees; Figure 3a, b).

Species density. Overall, species density did not vary among successional categories (Figure 2b). On average

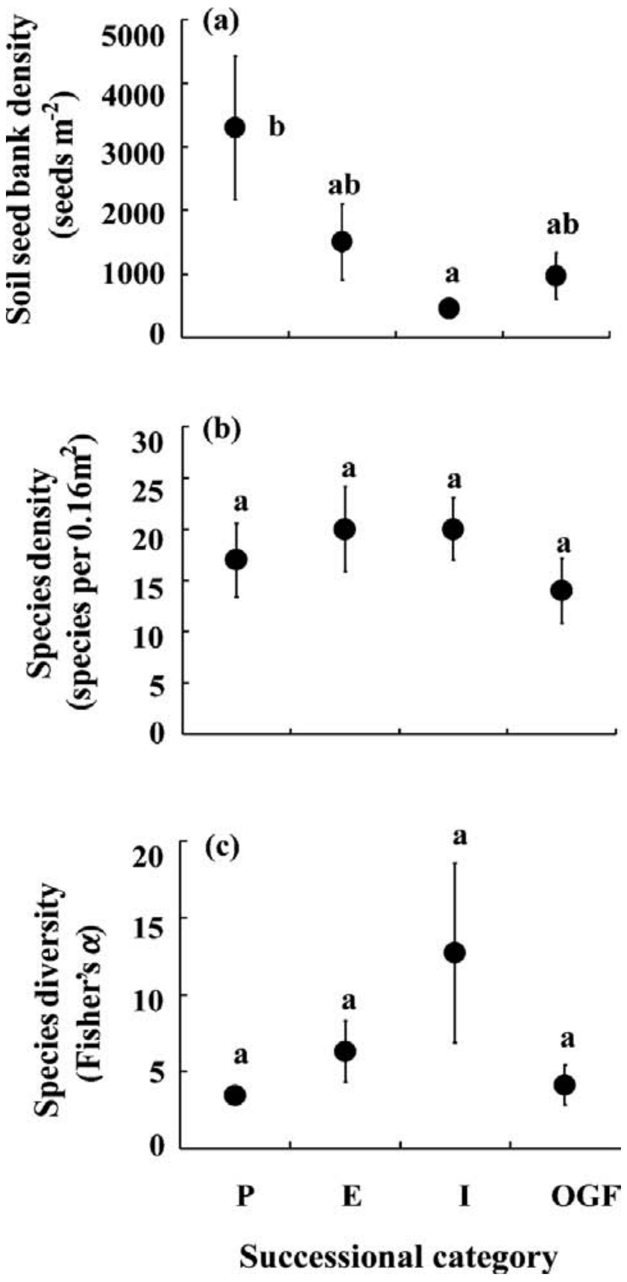

Figure 2. Seed-bank structural changes across four tropical dry-forest successional categories (as indicated in Figure 1) at La Huerta (Jalisco), eastern Mexico. Seed density (a), Species density (b), Fisher's α species diversity (c). Vertical lines indicate ±1 SE. Successional categories that do not share same letters are statistically different ($P \leq 0.05$).

(±SE), 18 ± 2 species per 0.16 m^2 per site were recorded. The expected species density calculated using non-parametric estimators did not vary among successional categories either. These estimators indicated the existence of twice as many species per site (ACE = 43 ± 14, ICE = 41 ± 7), when compared with our sampling effort. Species density, however, changed over the chronosequence depending on growth-form categories (Table 1). Species density of herbaceous plants declined ($F_{3,8} = 7.2$, $P = 0.01$), but increased for tree species ($F_{3,8} = 4.6$, $P = 0.04$). Species density of shrubs and woody climbers remained similar over the chronosequence. The relative frequency of herbaceous species was clearly replaced by that of woody species (mainly trees) over the chronosequence (Figure 3c, d).

Species diversity. For the whole seed-bank community ($F_{3,8} = 0.67$, $P = 0.59$; Figure 2c), as well as for herbaceous and woody plants separately, Fisher's α diversity index exhibited a maximum in the intermediate successional category, but this peak was not significant (Table 1). The slope of the rank-abundance curve, however, differed significantly among successional categories (ANCOVA successional category × species rank-abundance interaction: $F_{3,153} = 61.8$, $P < 0.001$), showing a diversity maximum in the intermediate category (Figure 4). In the pasture category, the slope of the rank-abundance curve was very pronounced ($b = -2.12$) with the three most abundant species representing 83% of all seeds. In the early category, the slope was less pronounced ($b = -1.68$), and percentage of three most abundant species reduced to 67%. The intermediate category showed the highest evenness (flattest slope, $b = -1.12$) and lowest percentage of three most abundant species (48%). In the old-growth forest, the slope ($b = -1.57$) was steeper when compared with the intermediate category, and three species represented 76% of total seeds. While in the pasture and early successional categories the dominant species were herbaceous, in the intermediate and old-growth forest woody species were dominant (Figure 4). The second most abundant species in the old-growth forest was a herbaceous Amaranthaceae species which was not found in earlier successional categories.

Species replacement over the chronosequence

NMDS minimized stress (0.05) with three dimensions in the ordination of the sites. Successional categories differed only along dimension-1, following a sequence of younger to older categories ($F_{3,8} = 22.1$, $P = 0.0003$; Figure 5). Pasture differed significantly ($P < 0.01$) from the intermediate and old-growth forest categories; the early category was not different from pasture but differed from intermediate and old-growth forest categories. The intermediate category was different from the old-growth forest. Groups of species showed maximum relative densities at different successional categories. Eight species (seven herbaceous and one shrub) had their greatest relative abundance in the pasture and early categories (Figure 6a-h), four herbaceous species in the early

Table 1. Seed-bank changes in density, species density and species diversity over a chronosequence of abandoned pastures and old-growth-forest (OGF) sites at Chamela, Mexico. Pasture: 0–1 y since abandonment, Early: 3–5 y since abandonment, Intermediate: 10–12 y since abandonment, OGF: old-growth forest. Values are mean ± 1 SE for different growth forms. Only seeds of species classified by growth forms are included. For each case, successional categories not sharing the same superscript letter differ significantly ($P \leq 0.05$).

	Pasture	Early	Intermediate	OGF
Density (seeds per 0.16 m^2)				
Trees	1 ± 0^{a}	2 ± 2^{a}	28 ± 16^{ab}	96 ± 42^{b}
Shrubs	14 ± 12^{a}	3 ± 3^{a}	6 ± 6^{a}	9 ± 2^{a}
Woody climbers	1 ± 1^{a}	0 ± 0^{a}	0 ± 0^{a}	0 ± 0^{a}
Herbaceous climbers	126 ± 112^{a}	23 ± 8^{a}	3 ± 2^{a}	5 ± 4^{a}
Terrestrial herbs	364 ± 154^{b}	179 ± 109^{ab}	17 ± 8^{ab}	18 ± 18^{a}
Grasses	110 ± 54^{b}	99 ± 74^{b}	16 ± 8^{ab}	0 ± 0^{a}
All woody plants	15 ± 14^{a}	6 ± 24^{a}	34 ± 22^{ab}	106 ± 43^{b}
All herbaceous plants	489 ± 168^{b}	201 ± 109^{ab}	19 ± 7^{a}	23 ± 17^{a}
Species density (species per 0.16 m^2)				
Trees	1 ± 1^{a}	1 ± 1^{a}	4 ± 1^{ab}	4 ± 1^{b}
Shrubs	1 ± 0^{a}	1 ± 1^{a}	0 ± 0^{a}	2 ± 0^{a}
Woody climbers	0 ± 0^{a}	0 ± 0^{a}	0 ± 0^{a}	0 ± 0^{a}
Herbaceous climbers	4 ± 2^{a}	4 ± 1^{a}	2 ± 1^{a}	1 ± 0^{a}
Terrestrial herbs	2 ± 1^{a}	2 ± 1^{a}	1 ± 0^{a}	0 ± 0^{a}
Grasses	3 ± 1^{b}	3 ± 1^{b}	3 ± 1^{b}	0 ± 0^{a}
All woody species	2 ± 1^{a}	3 ± 1^{a}	5 ± 1^{ab}	6 ± 2^{b}
All herbaceous species	9 ± 2^{b}	10 ± 1^{b}	6 ± 2^{b}	2 ± 1^{a}
Species diversity (Fisher's α)				
All woody species	1 ± 1^{a}	2 ± 1^{a}	3 ± 1^{a}	1 ± 1^{a}
All herbaceous species	2 ± 0^{a}	2 ± 0^{a}	4 ± 3^{a}	1 ± 1^{a}

category (Figure 6i-l), two tree species in the intermediate category (Figure 6m, n), and three (two woody and one herbaceous) species in the old-growth forest categories (Figure 6o-q).

Seed bank mirrored the abundance of established individuals in four of five woody species analysed (Figure 6m, n, o, q). The exception was the shrub *Mimosa arenosa*, which seeds were only found in the pasture category while its stem abundance was highest in the early successional category (Figure 6a).

DISCUSSION

The fact that a third of the total recorded species in our chronosequence were represented by a single seed (singletons), concurs with the finding that rare species are typical of seed banks in tropical forests (Garwood 1989) and suggests that our sampling effort missed even more rare species. According to ACE and ICE estimators, our sampling effort potentially overlooked approximately half of the possible extant species. The aggregated pattern of spatial distribution of the seeds, common in TDFs (Condit *et al.* 2000, Hubbell 1979), could also contribute to increasing the probability of missing species with our random sampling design (Butler & Chazdon 1998). Despite these sampling limitations, we were able to detect clear successional patterns. These patterns support the hypothesis that herbaceous plants are replaced by woody plants during succession and suggest that a facilitation mechanism drives species replacement in the studied TDF successional system, as discussed below.

Successional patterns and replacement among plant growth forms

Seed bank density. Reduction in the seed bank density along the chronosequence parallels successional trends described in TDFs (González-Rivas *et al.* 2009, Rico-Gray & García-Franco 1992) and temperate deciduous forests (Hyatt & Casper 2000, Roberts & Vankat 1991). For example, in north Yucatan, Mexico, the density of the seed bank in a cornfield 1 y after abandonment was five times greater than in cornfields with fallow ages of more than 30 y (Rico-Gray & García-Franco 1992). In Nicaragua, the seed bank density in a 4-y-old secondary TDF was doubled when compared to a 14-y-old secondary forest (González-Rivas *et al.* 2009).

As predicted, we observed a progressive replacement of seeds of herbaceous plants by those of woody plants over the chronosequence. This pattern is concurrent with the general successional patterns observed in the secondary succession of forest communities (Bazzaz

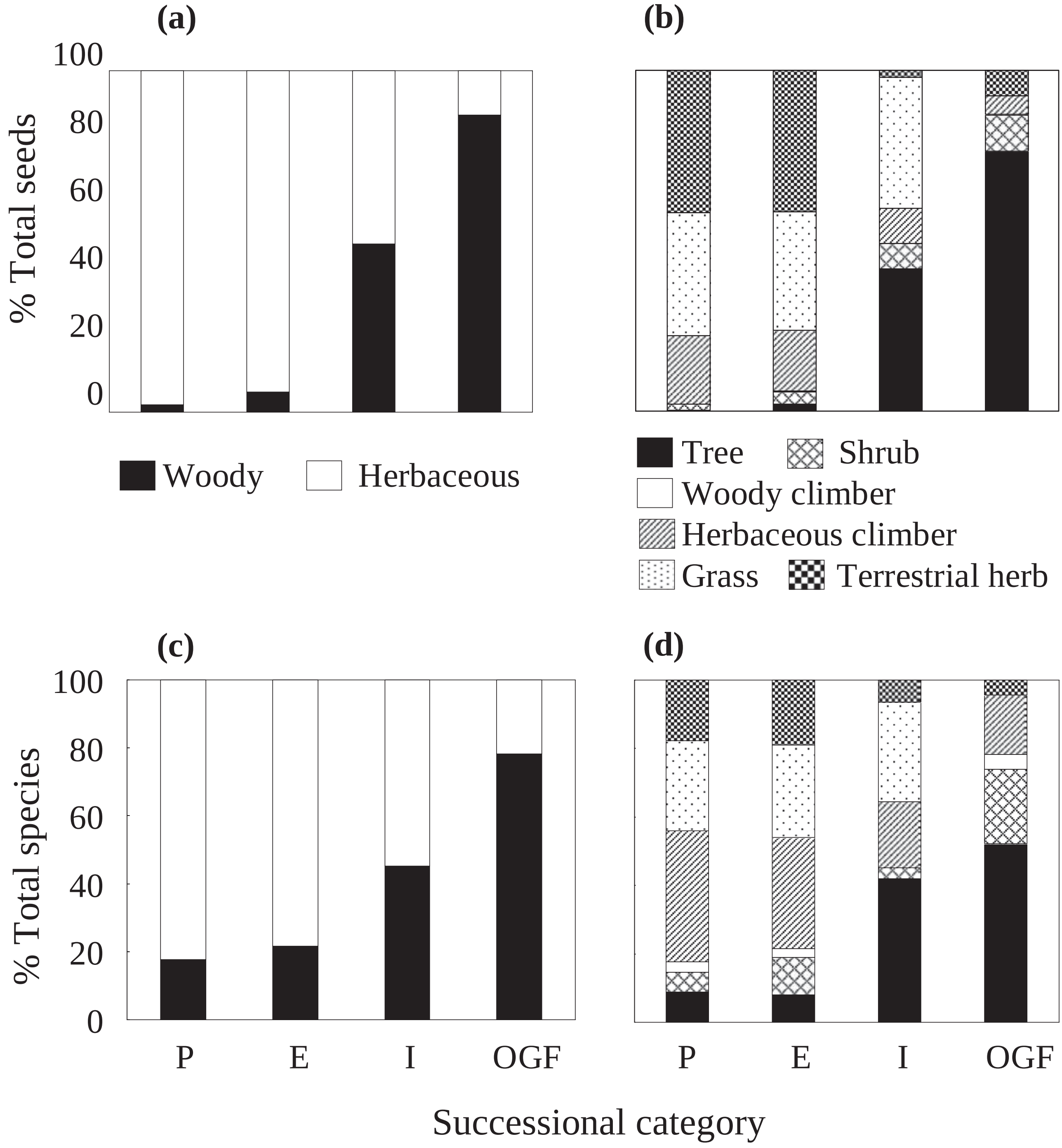

Figure 3. The relative contribution of different plant growth forms to the total number of seeds and species recorded in the seed-bank at four TDF successional categories (as indicated in Figure 1) at La Huerta (Jalisco), eastern Mexico. Proportion of total seeds represented by woody (trees, shrubs and woody climbers) and herbaceous (terrestrial herbs, herbaceous climbers and grasses) plants (a); proportion of total seeds represented by different growth-forms (b); proportion of total species density represented by woody and herbaceous plants (c); proportion of total number of species represented by different growth-forms (d).

1996, Bekker *et al.* 2001, Lemenih & Teketay 2006, Lyaruu *et al.* 2000, Roberts & Vankat 1991). The reduction of reproductive populations of heliophilic forbs may explain the rapid decrease of seeds of herbaceous plants over the chronosequence. As succession advances the forest canopy closes, reducing light resources in the understorey. This effect is particularly marked in the rainy season, when TDF leaf area index maximizes (Barradas 1991). In this season, forest canopy openness at 1.30 m above ground at our intermediate successional sites was

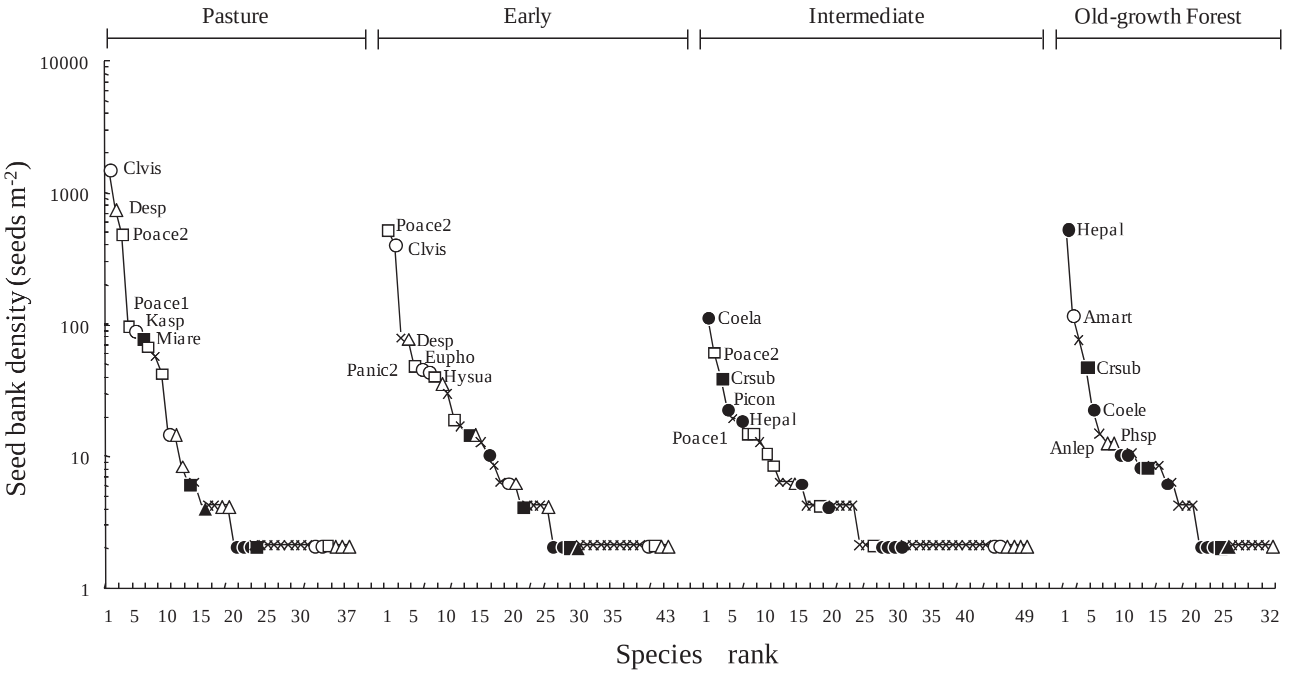

Figure 4. Rank-abundance curves for seed-bank communities of four TDF successional categories at Chamela, Mexico. Successional categories as indicate in Figure 1. White circles correspond to herbaceous terrestrial, white squares to grass, white triangles to herbaceous climber, black circles to tree, black squares to shrub and black triangles to woody climber species. Species acronyms for the six most abundant species at each successional category as follows: Amart = Amaranthaceae, Anlep = *Antigonon cf. leptopus*, Coele = *Cordia elaeagnoides*, Clvis = *Cleome viscosa*, Crsub = *Croton suberosus*, Desp = *Desmodium* sp., Eupho = Euphorbiaceae, Hepal = *Heliocarpus pallidus*, Hysua = *Hyptis suaveolens*, Kasp = *Kallstroemia* sp., Micua = *Mimosa quadrivalvis*, Miare = *Mimosa arenosa*, Pani1 = *Panicum* sp. 1, Pani2 = *Panicum* sp. 2, Phsp = *Phaseolus* sp. 1, Picon = *Piptadenia constricta*, Poace1 = Poaceae sp. 1, Poace2 = Poaceae sp. 2. Note y-axis is scaled logarithmically.

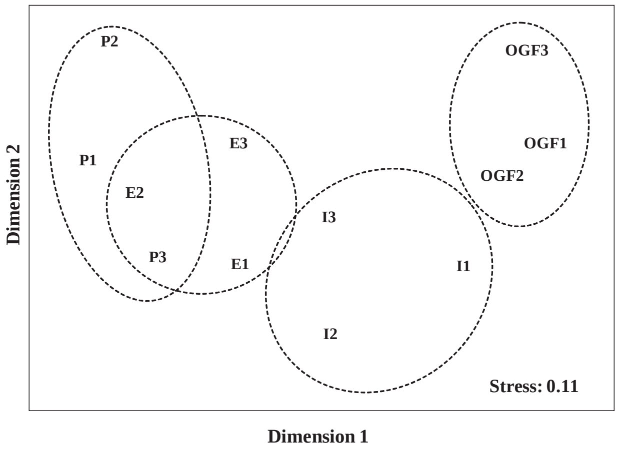

Figure 5. NMDS ordination of abandoned pasture and old-growth TDF sites from Chamela, Mexico. Sites are designated by successional category as indicated in Figure 1. Dashed ellipses include sites of same successional category. See text for further details.

similar to that in the old-growth-forest sites (15% vs 12%, S. Maza-Villalobos, pers. obs.).

Despite there being a clear increasing trend in the representation of seeds of woody plants over the chronosequence, seeds of grasses were still abundant in the 10–12-y-old secondary forest sites. Long-lasting seed dormancy (Baskin & Baskin 1985), together with seed dispersal from nearby active pastures (Dupuy & Chazdon 1998), may explain such prevalence. Because such sites were mostly surrounded by secondary or old-growth forest vegetation, we believe that seed dormancy was the main determinant. Thus, our results indicate that a legacy of the agricultural activity, expressed in the high proportion of seeds of exotic species of grass (e.g. *Panicum* sp., *Rhynchelytrum repens*), persist for several years after field abandonment.

The increase of seeds from woody species over the chronosequence could result from an increase in the abundance of reproductive individuals (i.e. increasing local seed rain) and of seeds dispersed from nearby sources. The fact that abundance of seeds from common woody species paralleled that of stems of the same species over the chronosequence supports the former possibility. After some years of succession, the developing forest canopy can provide food, shelter, perching and nesting sites for seed-dispersing mammals and birds (Holl 1999, Janzen 1988). At the same studied chronosequence, abundance of frugivorous bats (Avila-Cabadilla *et al.* 2009) and birds (J. Schondube, pers. comm.) increased substantially in the pastures of more than 5 y since abandonment, which

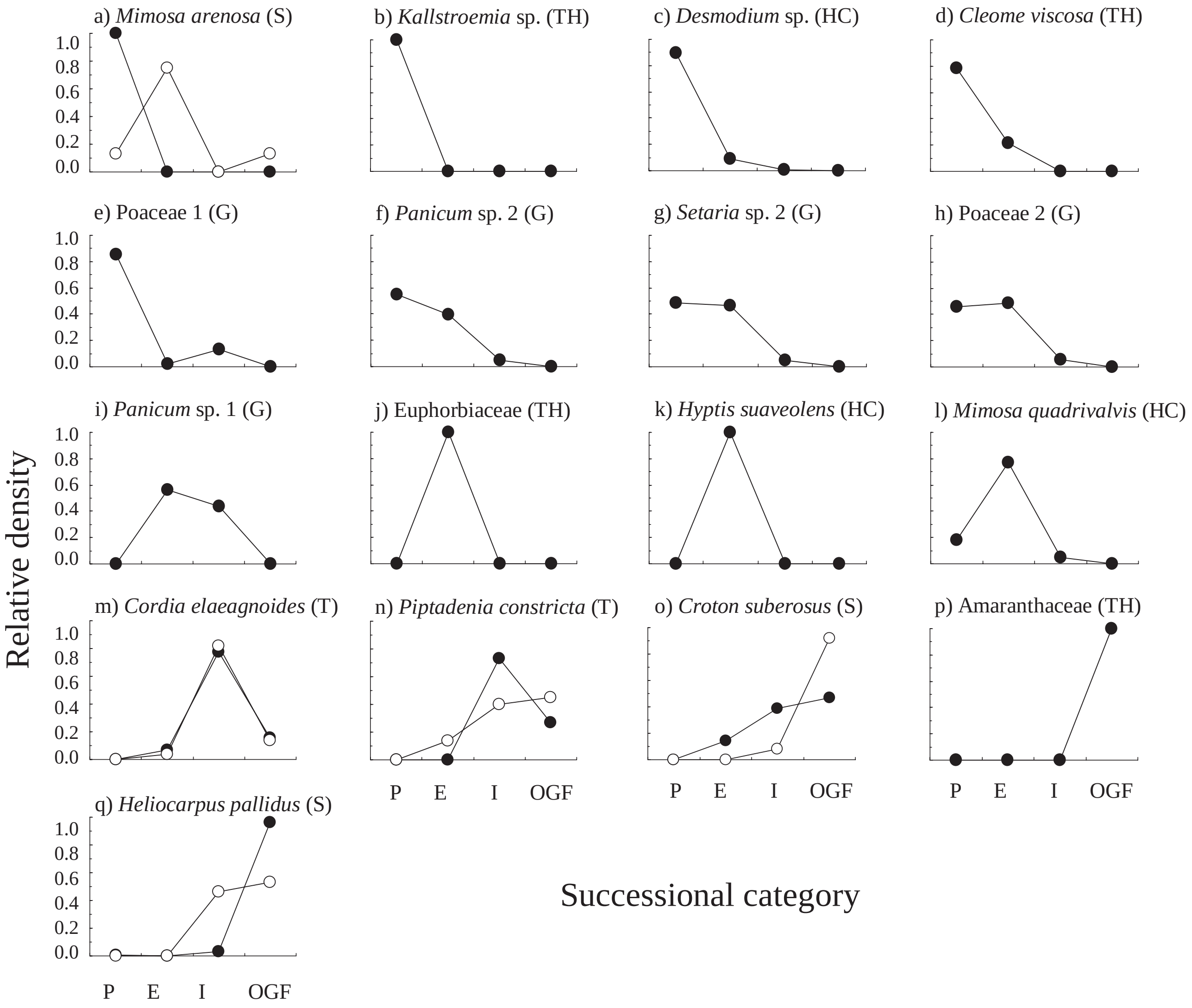

Figure 6. Chronosequence changes in the relative density of the 17 most abundant species in the seed-bank of abandoned pastures and old-growth TDF sites at the Municipality of La Huerta, western Mexico. Successional categories as indicated in Figure 1. After the species name, in parentheses the species growth-form is indicated: T = tree, S = shrub, TH = terrestrial herb, HC = herbaceous climber and G = grass. In (a), (m), (n), (o) and (q) lines connected by open circles indicates changes among successional categories of the relative abundance of stems with dbh ≥1 cm.

concurs with the evident increase in the abundance and species diversity in the seed bank of trees in the 10–12 y old secondary forests. Also, several TDF woody species are widely dispersed by wind (Bullock 1995, Gentry 1995, Greene *et al.* 2008). The fact that at early successional sites there were seeds but not stems of the wind-dispersed species *C. suberosus* (Figure 6o) support that exogenous seed dispersal is important for some species.

The dominance of seeds of woody plants in the old-growth forest was largely related to small seeds produced by a few species that fruit copiously during the dry season (e.g. *H. pallidus* and *C. elaeagnoides*) and to seeds of species that may remain dormant in the soil due to an impermeable seed coat (e.g. the legumes *Acacia farnesiana*, *Caesalpinia* sp., *Senna atomaria*). Large seeds were not found in the seed bank. This might be because large-seeded species produce fruits and disperse during the rainy season (Bullock & Solís-Magallanes 1990, Garwood 1989) when seed predation and germination occur (Janzen 1981, Khurana & Singh 2001).

Species density. The uniform pattern shown by species density over the chronosequence is similar to that found in a successional chronosequence of burned sites (up to 26 y after abandonment) of Mediterranean vegetation in Australia (Wills & Read 2007). In our case, this pattern resulted from a combination of the reduction of herbaceous and grass species and the increase of woody species over the chronosequence, as occurred in seed banks of secondary TDF in Nicaragua (González-Rivas *et al.* 2009). Such replacement of species with different growth forms is consistent with the tendencies of secondary succession observed in different terrestrial plant systems (Lyaruu *et al.* 2000, Roberts & Vankat 1991).

Species diversity. The hump-like successional pattern in species diversity in the seed bank was parallel to the one observed in several tropical and temperate forest successional systems, where species diversity increases to an upper value to later decrease with successional time (Bazzaz 1975, Bekker *et al.* 2001). The peak of species diversity observed in the intermediate successional category resulted from a mixture of seeds from herbaceous species, which were dominant in pasture and early successional sites and seeds of woody species, which were abundant in the seed bank of old-growth forest. Furthermore, the highest number of rare species (with one or two seeds) was recorded at the intermediate successional category.

Species replacement and successional mechanisms

In our study system, we did not find any herbaceous or woody species present over all successional categories. This result suggests that species are not able to establish along the whole environmental gradient sampled by our chronosequence. The clear parallel between the abundance of seeds and stems of woody species over the chronosequence strongly supports this idea and concurs with the observation that seed banks of woody species are mostly determined by local seed rain (Ceccon *et al.* 2006, Dalling & Denslow 1998). This parallelism enables us to explore mechanisms of species replacement during succession (*sensu* Connell & Slatyer 1977).

Our results do not lend support to the existence of a tolerance mechanism of replacement of species. We did not find in the recently abandoned pastures seeds of an initial pool of species from which some species disappear and other remain over the chronosequence. In fact, our NMDS analysis indicates that species found in the younger successional categories were totally different from those found in later successional ones. Our results do not support the existence of a successional inhibition mechanism because there was not a single dominant species in the seed bank of earlier successional categories and because species density did not change over the chronosequence. Instead, our results show the existence of groups of species that have their maximum regenerative potential (via soil seeds) at different successional stages. Such segregation of species over succession therefore suggests the existence of a mechanism of facilitation in which stages of colonization, development, facilitation and replacement dictate the change in the structure and species composition in the successional community. In our chronosequence, the pioneer, colonizing, group would include short-lived forbs like *Cleome viscosa*, *Kallstroemia* sp., *Desmodium* sp. and grass species, as well as the shrub *M. arenosa.* In the seed bank of intermediate sites, most of these species were replaced by woody species like *C. elaeagnoides*, *C. suberosus*, *Piptadenia constricta* and *H. pallidus*. These species were also abundant in the old-growth forest.

In young TDF secondary vegetation in Mexico it is common to observe abundant populations of *Mimosa* species. It has been proposed that once established these shrub species inhibit secondary succession in old fields (Burgos & Maass 2004). However, in our chronosequence the seeds of *M. arenosa* were found only in the recently abandoned pastures, nonetheless abundance of stems of this species showed a maximum in the early successional category. This suggests that potential for regeneration of this species beyond early successional stages is quite poor. Recent studies indicate that *Mimosa* species could play a facilitating, instead of an inhibitory, role in succession (Lebrija-Trejos *et al.* 2008). These shrubs are associated with nitrogen-fixing bacteria and their foliage can create favourable shady conditions which facilitate establishment and development of seedlings of tree species (Khurana & Singh 2001). Abundant and diverse communities of seedlings and saplings of woody species have been observed under the canopies of *Mimosa* in TDFs dominated by these shrubs (Romero-Duque *et al.* 2007). Furthermore, in the studied chronosequence, established populations of *M. arenosa* dominate in the 3–5-y-old secondary forest but its abundance diminishes remarkably in the intermediate successional category and was practically absent in the old-growth forest. Thus, *M. arenosa* in our system could be a facilitator more than an inhibitor species, supporting the idea that a facilitation mechanism operates during the studied old-field TDF succession.

CONCLUSION

Our chronosequence study indicates that the structure and composition of seed banks strongly change over the first 12 y of TDF succession in abandoned pastures. A critical breakpoint did occur at 10–12 y after pasture abandonment, when seeds of early forb and grass species were replaced in abundance and diversity by those of woody species. At this stage, diverse seeds of tree species were found, but the structure and composition of the seed bank was still distinguishable from that in the old-growth forest. A clear replacement of groups of seed species was observed over the chronosequence, suggesting that facilitation is a possible successional mechanism in our studied system. Future experimental and long-term studies are needed to test the chronosequence trends here documented, and assess the importance of such trends for the TDF regeneration in old fields.

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Appendix 1. Species recorded at seed-bank communities in a chronosequence of abandoned pastures and old-growth tropical dry forest sites at Chamela, Mexico. Where applicable, growth-form (GF; T: tree, S: shrub, WC: woody climber, TH: terrestrial herb, HC: herbaceous climber, U: unknown) and dispersal syndrome (DS; A = animal, both epizoochory and endozoochory, W = wind, G = gravity and U = unknown) are indicated. Unidentified species (morphospecies) are indicated by the prefix MSP. Successional categories: P = 'pasture' (0–1 y since abandonment), E = 'early' (3–5 y since abandonment), I = 'intermediate' (10–12 y since abandonment), OGF = old-growth forest. For each successional category there were three sites. Figures indicate the number of seeds recorded per species per 1.88 m^2 at each site, per species in all sites (last column) and for all species at each site (last row).

FAMILY	GF	DS	P1	P2	P3	E1	E2	E3	I1	I2	I3	OGF1	OGF2	OGF3	TOTAL
Amaranthaceae															
MSP1	TH	U	0	0	0	0	0	0	0	0	0	0	0	56	56
MSP2	U	U	0	0	0	0	0	0	0	0	0	0	2	2	4
Asteraceae															
Mikania micrantha H.B.K.	WC	W	0	0	0	1	0	0	0	0	0	0	0	1	2
MSP3	TH	U	0	1	0	0	0	0	0	0	0	0	0	0	1
MSP4	TH	U	7	0	0	0	0	0	0	0	0	0	0	0	7
Boraginaceae															
Cordia alliodora (Ruiz & Pav.) Oken.	T	W	0	0	0	0	0	0	1	0	0	0	0	0	1
Cordia elaeagnoides DC.	T	W	0	0	0	5	0	0	51	0	4	0	11	0	71
Burseraceae															
Bursera sp.	T	A	0	0	0	0	0	0	0	0	0	0	3	0	3
Capparaceae															
Cleome viscosa L.	TH	A	68	606	38	5	150	38	0	0	1	0	0	0	906
Convolvulaceae															
Ipomoea clavata (G. Don) v. Ooststr.	HC	G	0	0	0	0	0	0	1	0	0	0	0	0	1
Ipomoea hederifolia L.	HC	G	0	0	0	0	1	0	0	0	0	0	0	0	1
Ipomoea nil (L.) Roth.	HC	G	1	0	0	0	0	0	0	1	0	0	1	0	3
Ipomoea wolcottiana Rose	T	W	0	0	0	0	0	0	1	0	0	0	1	0	2
Merremia aegyptia (L.) Urb.	HC	G	1	6	0	0	0	2	0	0	0	0	0	0	9
MSP5	HC	U	0	0	0	4	0	0	0	0	0	0	0	0	4
Cucurbitaceae															
MSP6	HC	U	2	0	0	0	0	0	0	0	0	0	0	0	2
Euphorbiaceae															
Croton suberosus H.B.K.	S	G	0	0	0	0	1	6	19	0	0	12	4	7	49
Euphorbia heterophylla L.	TH	G	0	0	0	1	0	0	0	0	0	0	0	0	1
MSP7	TH	G	0	0	0	22	0	0	0	0	0	0	0	0	22
Fabaceae															
Acacia farnesiana (L.) Willd.	S	A	3	0	0	0	0	1	0	0	0	0	0	4	8
Apoplanesia paniculata Presl	T	W	0	0	0	0	0	0	0	1	0	2	3	0	6
Caesalpinia sp.	T	G	0	0	0	0	0	0	2	0	0	0	0	1	3
Desmodium sp.	HC	G	341	15	1	3	8	26	1	3	0	0	0	0	398
Lonchocarpus constrictus Pitt.	T	G	1	0	0	0	0	1	0	0	0	0	0	0	2
Mimosa arenosa (Willd.) Poir.	S	G	0	38	0	0	0	0	0	0	0	0	0	0	38
Mimosa quadrivalvis L.	HC	G	3	0	1	0	14	3	0	1	0	0	0	0	22
MSP8	HC	U	0	0	0	0	0	3	0	0	0	0	0	0	3
MSP9	U	U	0	1	0	1	0	0	0	0	0	0	0	0	2
Phaseolus sp. 1	HC	G	0	1	0	5	0	2	0	0	0	0	0	0	8
Phaseolus sp. 2	HC	G	0	0	0	0	0	0	0	0	0	1	5	0	6
Phaseolus sp. 3	HC	W	1	1	0	0	0	0	0	0	0	0	0	0	2
Piptadenia constricta (Micheli & Rose) J.M. Macbr.	T	W	0	0	0	0	0	0	0	0	11	0	0	4	15
Senna atomaria (L.) I. & B.	T	A	0	1	0	0	0	0	0	1	0	0	0	1	3
Flacourtiaceae															
Casearia corymbosa Kunth	T	A	0	0	0	1	0	0	1	1	1	0	0	0	4
Julianiaceae															
Amphipterygium adstringens (Schlecht.) Shiede.	T	W	0	0	0	0	0	0	0	0	0	0	5	0	5
Labiatae															
Hyptis suaveolens (L.) Poit.	TH	G	0	0	0	21	0	0	0	0	0	0	0	0	21
Malvaceae															
MSP10	S	U	0	0	0	0	0	0	0	0	0	0	1	0	1
Passifloraceae															
Passiflora foetida L.	HC	A	0	0	0	0	0	0	0	1	0	0	0	0	1
Poaceae															
Panicum sp. 1	G	A	0	0	0	8	1	0	6	1	0	0	0	0	16
Panicum sp. 2	G	A	20	0	12	3	20	0	0	1	2	0	0	0	58
Poaceae sp. 1	G	U	175	13	43	31	211	2	0	1	28	0	0	0	504
Poaceae sp. 2	G	U	0	0	46	0	1	0	0	7	0	0	0	0	54

Appendix 1. Continued.

FAMILY	GF	DS	P1	P2	P3	E1	E2	E3	I1	I2	I3	OGF1	OGF2	OGF3	TOTAL
Rhynchelytrum repens (Willd.) C.E. Hubb.	G	W	0	1	0	0	0	0	0	0	0	0	0	0	1
Setaria sp.	G	A	6	0	14	7	12	0	0	1	1	0	0	0	41
Polygonaceae															
Antigonon cf. leptopus Hook. & Arn.	HC	G	1	0	0	0	0	0	0	0	0	0	6	0	7
Coccoloba sp.	S	A	0	0	0	0	0	2	0	0	0	0	0	0	2
Rhamnaceae															
Gouania sp.	WC	W	0	2	0	0	0	0	0	0	0	0	0	0	2
Rubiaceae															
Hintonia latiflora (Sessé & Moc. ex DC.) Bullock	HC	W	0	0	0	0	0	1	0	0	0	0	0	0	1
Solanaceae															
Solanum deflexum Greenm.	TH	A	0	0	0	0	0	3	0	1	0	0	0	0	4
Tiliaceae															
Heliocarpus pallidus Rose	T	W	0	1	0	0	0	0	1	0	8	42	42	174	268
Zygophyllaceae															
Kallstroemia sp.	TH	G	0	43	0	0	0	0	0	0	0	0	0	0	43
Unknown															
MSP11	U	U	18	1	8	3	1	10	3	4	0	0	2	1	51
MSP12	U	U	0	0	0	0	0	0	6	0	0	12	24	0	42
MSP13	U	U	1	0	0	37	0	0	0	0	0	0	0	0	38
MSP14	U	U	0	0	0	2	0	0	6	3	0	0	1	0	12
MSP15	U	U	1	0	0	1	0	7	0	0	0	1	0	0	10
MSP16	U	U	0	0	0	5	1	0	0	1	0	0	2	0	9
MSP17	U	U	0	0	0	0	0	0	0	0	0	0	0	7	7
MSP18	U	U	0	0	0	1	0	0	0	0	0	1	0	4	6
MSP19	U	U	0	0	0	2	0	1	1	1	0	0	0	0	5
MSP20	U	U	0	1	1	1	0	1	0	0	0	0	0	0	4
MSP21	U	U	0	0	0	0	0	0	0	0	0	0	4	0	4
MSP22	U	U	0	0	0	0	0	1	2	0	0	0	0	0	3
MSP23	U	U	2	0	0	0	0	0	0	1	0	0	0	0	3
MSP24	U	U	0	0	0	0	0	2	0	1	0	0	0	0	3
MSP25	U	U	0	0	0	0	0	0	0	3	0	0	0	0	3
MSP26	U	U	0	0	0	0	0	0	0	3	0	0	0	0	3
MSP27	U	U	3	0	0	0	0	0	0	0	0	0	0	0	3
MSP28	U	U	0	0	0	0	0	0	2	0	0	0	0	0	2
MSP29	U	U	0	0	0	0	0	0	0	0	0	0	2	0	2
MSP30	U	U	0	0	0	0	0	0	0	0	0	0	2	0	2
MSP31	U	U	0	0	0	0	0	1	0	0	1	0	0	0	2
MSP32	U	U	0	0	0	0	0	0	0	0	2	0	0	0	2
MSP33	U	U	0	0	1	0	0	0	0	0	1	0	0	0	2
MSP34	U	U	0	0	0	0	0	0	0	0	2	0	0	0	2
MSP35	U	U	0	0	0	1	0	0	0	0	0	0	0	0	1
MSP36	U	U	0	0	0	1	0	0	0	0	0	0	0	0	1
MSP37	U	U	0	0	0	1	0	0	0	0	0	0	0	0	1
MSP38	U	U	0	0	0	0	0	0	1	0	0	0	0	0	1
MSP39	U	U	0	0	0	0	0	0	1	0	0	0	0	0	1
MSP40	U	U	0	0	0	0	0	0	1	0	0	0	0	0	1
MSP41	U	U	0	0	0	0	0	0	1	0	0	0	0	0	1
MSP42	U	U	0	0	0	0	0	0	1	0	0	0	0	0	1
MSP43	U	U	0	0	0	0	0	0	0	1	0	0	0	0	1
MSP44	U	U	0	0	0	0	0	0	0	1	0	0	0	0	1
MSP45	U	U	0	0	0	0	0	0	0	1	0	0	0	0	1
MSP46	U	U	0	0	0	0	0	0	0	1	0	0	0	0	1
MSP47	U	U	0	0	0	0	0	0	0	0	0	1	0	0	1
MSP48	U	U	0	0	0	0	0	0	0	0	0	1	0	0	1
MSP49	U	U	0	0	0	0	0	0	0	0	0	0	1	0	1
MSP50	U	U	0	1	0	0	0	0	0	0	0	0	0	0	1
MSP51	U	U	0	0	0	0	0	0	0	0	1	0	0	0	1
MSP52	U	U	0	0	0	0	0	1	0	0	0	0	0	0	1
MSP53	U	U	1	0	0	0	0	0	0	0	0	0	0	0	1
MSP54	U	U	1	0	0	0	0	0	0	0	0	0	0	0	1
MSP55	U	U	1	0	0	0	0	0	0	0	0	0	0	0	1
MSP56	U	U	0	0	0	0	0	1	0	0	0	0	0	0	1
MSP57	U	U	0	0	0	0	0	1	0	0	0	0	0	0	1

Appendix 1. Continued.

FAMILY	GF	DS	P1	P2	P3	E1	E2	E3	I1	I2	I3	OGF1	OGF2	OGF3	TOTAL
MSP58	U	U	0	0	0	0	0	0	0	0	1	0	0	0	1
MSP59	U	U	0	0	0	0	0	0	0	0	0	0	0	1	1
MSP60	U	U	0	1	0	0	0	0	0	0	0	0	0	0	1
MSP61	U	U	0	1	0	0	0	0	0	0	0	0	0	0	1
Total			658	735	165	173	421	116	109	42	64	73	122	263	2941

CAPÍTULO III

EARLY REGENERATION OF TROPICAL DRY FOREST FROM ABANDONED PASTURES: CONTRASTING CHRONOSEQUENCE AND DYNAMIC APPROACHES

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Early Regeneration of Tropical Dry Forest from Abandoned Pastures: Contrasting Chronosequence and Dynamic Approaches

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ABSTRACT

Old field secondary succession of tropical dry forests (TDFs) is poorly understood, particularly regarding the dynamics of seedlings, saplings, and sprouts (regenerative communities). We used chronosequence and dynamic approaches to: (1) document successional trajectories of regenerative communities during the first dozen years of regeneration in abandoned pastures at Chamela, Mexico; (2) test the usefulness of chronosequences to predict the dynamics of regenerative communities along time; and (3) assess the influence of surrounding forest matrix, stand density, and understory light availability (in the rainy season) as driving factors of such dynamics. More than 1000 plants and 95 species of shrubs and trees 10–100 cm tall were monitored between 2004 and 2007 in nine abandoned pastures (0–12 yr since abandonment) and two old-growth forest (OGF) sites; gain and loss rates of plants, species, and plant cover were obtained. Chronosequence predicted a rapid and asymptotic increase of plant density, species density, and plant cover toward the OGF values. Such prediction did not match with dynamic data that showed negative or neutral net community rates of change, independently of fallow age. Recruitment and species gain rates increased with the amount surrounding forest matrix. No other effect of the explored factors was detected. Strong rainfall shortenings could be responsible for the high loss and low gain rates of plants and species recorded in most sites. We highlight the critical role of supra-annual rainfall variability on the dynamics of TDF regenerative communities and the poor predictive value of chronosequences in forest systems subjected to strong environmental temporal variation.

Abstract in Spanish is available at http://www.blackwell-synergy.com/loi/btp.

Key words: Chamela; community dynamics; Mexico; natural regeneration; saplings; seedlings; sprouts.

Tropical dry forest (TDF) is one of the biomes most threatened by deforestation and conversion to agriculture (Sánchez-Azofeifa *et al.* 2005, Miles *et al.* 2006). Frequently, agricultural fields are abandoned allowing dry forest regeneration and secondary succession, which may result in the recovery of some biodiversity and ecosystem functionality (Janzen 1988). The understanding of how, at what rate, and to what extent TDF regeneration occurs in abandoned agriculture fields remains poor (Vieira & Scariot 2006, Chazdon *et al.* 2007, Lebrija-Trejos *et al.* 2008), and this lack of knowledge might limit the ability to conserve, restore, and sustainable manage secondary TDF.

Chronosequence studies predict that structural attributes of tropical forests, such as stand density, species diversity, and biomass, increase rapidly after field abandonment, attaining within a few decades their original values; the same studies, however, also suggest that species composition takes a longer time to recover (Rico-Gray & García-Franco 1992; Kennard 2002; Chazdon *et al.* 2007; Lebrija-Trejos *et al.* 2008, 2010a). Such successional patterns emerged from studies conducted in communities of shrubs and trees ≥ 1 cm diameter at breast height (dbh). Scant information is available for seedlings, saplings and sprouts of shrubs and trees (regenerative communities) despite these early plant stages are critical to forest regeneration and succession (Capers *et al.* 2005, Comita *et al.* 2009).

Recent long-term dynamic studies of secondary forests on permanent plots have challenged the predictions emerged from chronosequences (Chazdon *et al.* 2007, Johnson & Miyanishi 2008). These studies show a weak or no correlation between actual forest regeneration rates and those predicted by chronosequences. For example, Chazdon *et al.* 2007 found that only basal area accumulation followed in some extent the chronosequence trend while species density, species richness, species composition, and stem density followed different trajectories. This disparity emerges from the fact that factors affecting regeneration (*e.g.*, land use history, surrounding matrix, availability of seed dispersers, microclimate, topography, and soil heterogeneity) are not equivalent among old fields of same age, as assumed by chronosequences, but change substantially from site to site (Chazdon *et al.* 2007, Comita *et al.* 2009). Because chronosequences may fail to predict community dynamics at a given site (Chazdon *et al.* 2007, Johnson & Miyanishi 2008), direct measurements of community rates of change are needed to understand the factors and mechanisms driving forest regeneration and succession (Johnson & Miyanishi 2008). Therefore, the analysis of regeneration in old fields would be better addressed by including both chronosequence and dynamic approaches (Foster & Tilman 2000, Letcher & Chazdon 2009, Lebrija-Trejos *et al.* 2010a).

The regeneration processes depend on gains and losses of individuals and species. Gains depend on the availability of propagules, local conditions, and resources affecting establishment, survival, and growth of plants; losses are due to mortality and biomass reduction caused by adverse conditions, limited resources, and damage by natural enemies (Hammond 1995, Lebrija-Trejos *et al.* 2010b). In turn, the availability of propagules depends on seed sources in the surrounding matrix (Aide *et al.* 1995, Martínez-Garza *et al.* 2009), seeds produced *in situ* by isolated vegetation,

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and propagules remaining in the abandoned field (Miller & Kauffman 1998a, Miller 1999, Romero-Duque *et al.* 2007). During early succession (< 15 yr), local seed rain is expected to be positively related to stand density because more shrubs and trees would result in more seeds, sprouting, and perching sites for seed dispersers (Holl 2007). Because soil water potential has been shown to be positively correlated with stand density, due to increased shade in young secondary TDFs (Lebrija-Trejos *et al.* 2010b), survival and growth of regenerative plants may increase with stand density during early succession. This can be expected particularly in tropical dry areas where solar radiation, and evaporation, is very high even during the rainy season; at Chamela, for example, clear sky conditions can last as much as seven hours during this season (García-Oliva *et al.* 2002). Higher gain rates of individuals, species or biomass are therefore expected to occur as stand density increases during early succession.

In contrast to the positive effects of stand density, other factors may have opposing effects on secondary forest dynamics. During the rainy season, when the forest foliage is produced (Maass *et al.* 1995), light availability (PAR) in the understory is reduced to 20 percent (Parker *et al.* 2005). In secondary TDFs of around 10 yr old, forest canopy openness can be as low as 15 percent (Lebrija-Trejos *et al.* 2010b) and in old-growth TDF under 5 percent (Barradas 1991). Such light reduction may lower survival and/or growth of seedlings, depending on the species (*e.g.*, Rincón & Huante 1993, Huante & Rincón 1998). Furthermore, in the rainy season, dense cover of understory vegetation provide habitat for rodents and microhabitats (*i.e.*, humid, hot, and dark) for micro-organisms that might increase predation on seeds and plants (Hammond 1995, Peña-Claros & De Boo 2002). As secondary forest develops, reductions in the understory light environment and higher predation pressures might therefore slow regenerative dynamics.

This paper is focuses on seedlings, saplings and sprouts that are critical stages in regeneration processes and poorly studied in successional TDF. The dynamics of these regenerative stages is faster than that of the established shrubs and trees, and thus processes can be analyzed within relatively short time periods. We analyze successional trajectories of TDF regenerative communities, using chronosequence and dynamic approaches. Specifically, we address following questions: what are the successional trajectories of plant density, species density, and plant cover predicted by a chronosequence along the first 12 yr of regeneration in abandoned pastures? What are the actual rates of change of these community structural traits through time? Do community structural changes predicted by the chronosequence match those observed at individual old fields through time? Do surrounding forest matrix, stand density, and understory light availability (in the rainy season) influence the community rates of changes of regenerative communities?

METHODS

STUDY SITE.—The study was conducted at the Chamela region (La Huerta municipality and the Chamela-Cuixmala Biosphere Reserve; 19°30′ N, 105°03′ W; Fig. S1A) in Jalisco, Mexico. The mean annual temperature is 25°C (1978–2007), and mean annual precipitation is 788 mm with a wide interannual variation (from 384 to 1393 mm); most of the annual rainfall (*ca* 93%) occurs from June to October, with a dry season from November to May. Total annual rainfall variation for the previous 29 yr (climatic data from Chamela Biological Field Station) is shown in Fig. S1B. The main vegetation type is a TDF whose canopy height varies between 5 and 10 m, most plants (> 95%) annually dropping their leaves in dry season. Small areas of tropical semi-deciduous forests are along riparian zones supporting taller and denser vegetation (Lott *et al.* 1987). TDF covers about 30 percent of La Huerta municipality while rural towns and communal lands cover the rest (Sánchez-Azofeifa *et al.* 2009); cattle pasture fields (60% of total area in 1990), crops, and managed forests dominate the landscape (Burgos & Maass 2004).

STUDY SYSTEM AND EXPERIMENTAL DESIGN.—The study sites were located within an area of about 100 km^2. Nine abandoned pastures, with fallow ages ranging from < 1 to 12 yr, and two old-growth forest (OGF) sites were selected (Fig. S1A). Fallow age was obtained through semi-structured interviews to landowners and by biophysical traits (Trilleras 2008; Table 1). The minimal distance between study sites was 1.5 km, and between 0.5 and 4.5 km between abandoned pastures and OGF (Fig. S1A). Terrain slope and aspect were homogenized as much as possible to control topographical effects. At each abandoned pasture, a site of 120 × 90 m

TABLE 1. *Biophysical characteristics of nine abandoned pastures and two old-growth forests (OGF) sites at Chamela, Mexico. The acronym name for each pasture site is composed by two letters followed by the number of years since abandonment in 2004 (fallow age).*

Site	Za0	Ma1	Cr0	Ca4	Ra3	Cr5	Ca12	Cr12	Ra10	Gar	Tej
Fallow age in 2004 (yr)	0	1	0	4	3	5	12	12	10	OGF	OGF
Terrain aspect	S	SW	S	E	SE	SW	S	SW	SW	S	S
Terrain slope (°)	20	26	25	30	15	18	20	25	28	22	23
Surrounding forest matrix (proportion)	0.39	0.44	0.28	0.54	0.47	0.61	0.64	0.80	0.63	1.00	1.00
Stand density[a]	0	680	1140	1440	640	8620	8040	8660	8780	7300	8580
Vegetation canopy openness (%)[b]	99.8 ± 0.0	52.0 ± 5.3	50.5 ± 5.6	57.4 ± 5.1	91.1 ± 2.0	22.6 ± 3.6	32.0 ± 2.6	8.5 ± 0.6	5.9 ± 0.7	5.3 ± 5.0	18.7 ± 19.0

[a] Stems/0.18 ha of trees and shrubs with dbh ≥ 1 cm (Chazdon *et al.* 2011).

[b] Mean ± SE of 24 measurements per site; sites Za0, Ma1, and Cr0 were lumped in a single point as EP in Fig. 4.

was delimited with four parallel metallic barbed wires (spaced every 30 cm; 1.20 m total height) to exclude cattle but no wild animals (the bigger herbivore in the area is the white tailed deer that can jump such exclusion). A permanent plot of 50×20 m ($1000\ \text{m}^2$) was established in each site and 24 square 1-m^2 subplots (delimited corners with 0.5 m tall PVC poles) were randomly established in the plot.

Biophysical characteristics.—Information on the surrounding forest matrix, stand density, and understory light availability were obtained to evaluate their effects on community changes. The remaining forest cover in the matrix surrounding each plot was calculated using Google Earth geospatial images. As described in detail by Maza-Villalobos *et al.* (2011), a Google Earth geospatial image, corresponding to the rainy season of the 2004 and 2005 yrs, was used to estimate forest cover (including old growth and secondary forests) within a circular area of 500 m radius around each study site.

In November 2004, at each study site, stand density (trees and shrubs dbh ≥ 1 cm) was inventoried in an area of $1800\ \text{m}^2$ (30×60 m) that enclosed our studied permanent plots. In October 2004 canopy openness (CO%) was measured at 1.3 m aboveground. At the center of each subplot, at each cardinal orientation CO% reading was taken with a spherical concave crown densiometer obtaining a mean value per each subplot. Studies have shown that photosynthetic flux density is tightly related with relative canopy openness (Anten & Ackerly 2001).

Collecting data.—To document structural attributes, all seedlings, sprouts, and small saplings of shrubs and trees (10–100 cm height) were recorded and tagged within the 1-m^2 subplots at the end of the rainy season in October 2004. For each plant, height (from the ground to the tip of the plant's canopy), maximum ($D_{\max}$) and minimum ($D_{\min}$) crown diameters, and taxonomic identity were obtained. Taxonomic nomenclature followed Lott (2002); specimens of reference were obtained outside of the plots and vouchers are available from the authors. To quantify temporal changes, another census was conducted in October 2007. New plants reaching a height of 10 cm or more (recruits) were recorded, and surviving initial plants were remeasured.

Data and statistical analyses.—To test chronosequence predictions and the effects of biophysical characteristics on regenerative dynamics, we calculated annual rates of change for community structural attributes. Plant and species density were expressed as the number of recorded plants or species per $24\ \text{m}^2$, the low plant density in several plots hindered to estimate species richness by rarefaction. Crown cover per plant (CC_i) was obtained from $D_{\max}$ and $D_{\min}$ measurements of each recorded plant i, assuming an ellipsoid crown shape as $CC_i = \pi \times (D_{\min}/2) \times (D_{\max}/2)$. Total community plant cover per plot (CC) was obtained summing up all CC_i records in the 24 1-m^2 subplots.

To characterize successional trajectories, excluding the OGF sites, different regression models (linear, potential, logarithmic, polynomial) were fitted to the chronosequence data; plant density, species density, or plant cover as response variable and fallow age as the independent variable. Count variables were $\ln(x+1)$ transformed before analysis to meet homoscedasticity and parametric criteria. The model explaining the higher amount of variance (R^2, $P \leq 0.05$) was selected.

For assessing the chronosequence predictions, for each plot and for a 3-yr period (from October 2004 to October 2007), we calculated ratios of community change in plant density, species density, and plant cover. This time period was selected because we believe that it is enough to detect significant structural community changes in the chronosequence trajectories that can be unequivocally tested against the observed dynamic data. The best-fitted regression models adjusted to the chronosequence data were used to predict the initial (PT_{2004}) and final x trait value (PT_{2007}) at each one of the nine studied abandoned pastures. These values were used to compute a predicted community ratio of change (PR) as $PR_x = \ln[(PT_{2007}+1)/(PT_{2004}+1)]$, where x represents a structural trait. Using the dynamic data, for each structural trait, we calculated an observed community ratio of change as $OR_T = \ln[(OT_{2007}+1)/(OT_{2004}+1)]$; where OT_{2007} represents the recorded value of a given structural trait x at the final of the study period (2007). To assess the predictive power of the chronosequence, for each structural trait, OR_x was correlated with PR_x using Pearson correlation coefficient analysis considering one-tailed significant level of $P \leq 0.05$ under the hypothesis that chronosequence predicts the directionality of the successional change.

To quantify the regenerative community dynamics, for each plot we calculated annual rates of recruitment, mortality, and growth. Recruitment rate (RR_D) was calculated as $RR_D = [[(n+r)/n]^{1/t}] - 1$, where n is the number of plants present at the initial census, r is the number of new recruited plants (10–100-cm height) surviving until the final census and t is the number of years elapses between census ($t = 3$). Mortality rate (MR_D) was calculated as $MR_D = 1 - [[1 - (m/n)]^{1/t}]$ where m is the number of initial plants that died during the 3 yr period. Outgrowth rate (OR_D) was calculated as $OR_D = 1 - [[1 - (o/n)]^{1/t}]$, where o is the number of initial plants passing 100 cm height during the 3 yr period. The annual net rate of change in community density (NRC_D) was calculated as: $NRC_D = RR_D - MR_D - OR_D$, where D indicating plant density.

Using the same rationality and S for species density, we calculated annual rates of species gain (GR_S, incorporation of new species), species loss (LR_S, disappearing from previously recorded species due to mortality), and species transition (TR_S, species disappearing from previously recorded species due to plant outgrowth, *i.e.*, species represented by plants reaching more than 100 cm height) using the same equations described above. In this case, n was the initial number of species, r the number of new-recorded species, m the number of disappearing species, and o the number of transitioning species. The net rate of change in species density (NRC_S) was calculated as: $NRC_S = GR_S - LR_S - TR_S$. Finally, using C for foliage cover, we calculated annual rates of plant cover gain (GT_C; resulted from recruitment of new plants and the increase of cover of initial surviving plants), plant cover loss (LR_C; resulted from the mortality and cover reductions of initial surviving plants), and plant cover transition (TR_C; cover of individuals outgrowing

100 cm height). The net community rate of change in cover (NRC_C) was calculated as $NRC_C = GR_C - LR_C - TR_C$.

To asses the influence of biophysical factors on community dynamic, the following relationships were assessed by simple regression analysis: (i) plant recruitment and species gain rates increase with surrounding forest matrix and stand density, (ii) mortality and species loss rates reduce and outgrowth rate increases with stand density, (iii) mortality rate decreases and outgrowth rate increases as understory light availability increases. In these analyses, OGF sites were included and the three recently abandoned pasture sites (0–1 yr old in 2004) were lumped in a single data point to increase sample sizes in the calculations of the community rates of change. Because the estimation of the community rates of change was based on sample sizes that were different in every site, the number of initial individuals was used as weights in the regression models.

RESULTS

A total of 1068 shrub and trees 10–100 cm tall, representing 95 morphospecies (66 identified to species, 13 to genus or family levels), were recorded. Overall, the studied TDF regenerative communities showed very low densities among years and plots (mean ± SE = 0.77 ± 0.13 plants/m^2) varying from 0.13 to 1.83 plants/m^2. Mean species density was also very low, 0.3 ± 0.04 species/m^2 for the 2 yr and all plots, varying from 0.04 to 0.92 species/m^2. Community cover varied from 0.01 to 0.14 m^2/m^2 with a mean of 0.04 ± 0.07 m^2/m^2 among years and plots, *i.e.*, on average, only 4 percent of the ground was covered by shrubs and trees 10–100 cm tall.

The percentage of surrounding forest cover of each site varied nearly three fold, from 28 percent in the younger abandoned pastures to 80 percent in the older ones (Table 1). Stand density ranging from zero, in a recently abandoned pasture (Za0), to 8780 stems/ha in a 10 yr old site (Ra10; Table 1). The percentage of canopy openness varied almost 17 times between the smallest (Ra10 = 5.9 ± 0.7%) to the highest (Za0 = 99.8 ± 0.7%) values; sites with similar fallow age strongly differed in canopy openness (Table 1).

SUCCESSIONAL TRAJECTORIES AND COMMUNITY RATES OF CHANGE.—TDF regenerative communities exhibited asymptotic (potential model) chronosequence trajectories in plant density, species density, and plant cover. In all cases, a fast growing phase during the first 3 yr of abandonment was followed by reduced rates of increase (Fig. 1).

Overall, observed community rates varied among sites independently of fallow age (Fig. 2). The only exception was the species gain rate (Fig. 2E) with a negative trajectory (logarithmic model) declining rapidly with fallow age. Net rate of change for all studied structural traits was quite low, in most cases negative or zero; such rates did result from high mortality/loss rates, moderate recruitment/gain rates, and almost null outgrowth/transition rates in most sites (Fig. 2).

MATCH BETWEEN CHRONOSEQUENCE AND DYNAMIC REGENERATION TRENDS AND EFFECTS OF FACTORS.—The community rates of change predicted by the chronosequence for the structural traits did not match the observed rates. While the chronosequence predicted positive rates for all traits, the observed net community rates of change were mostly negative or zero (Fig. 2). Correlations between

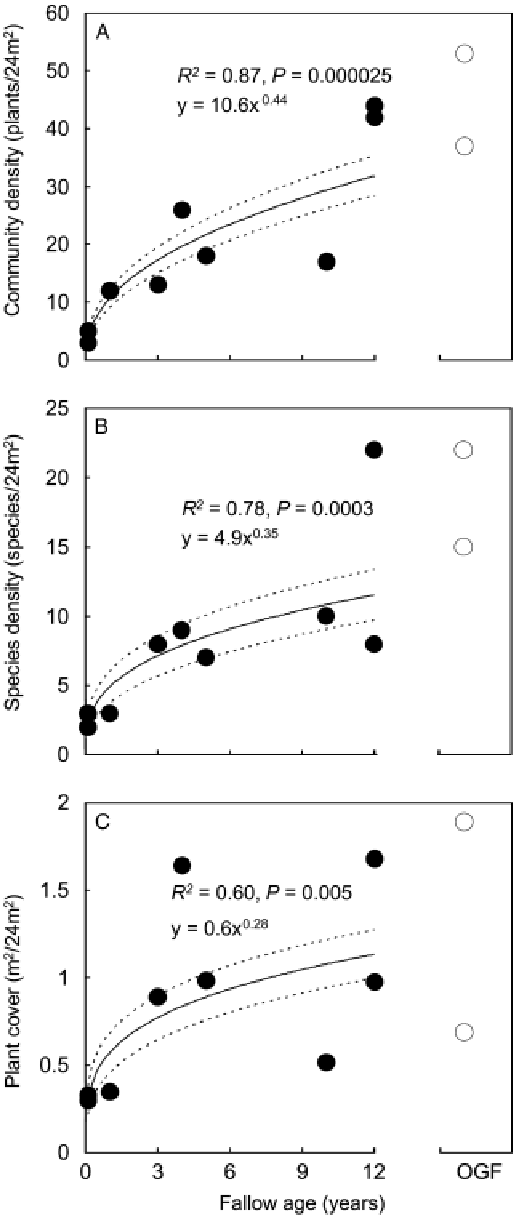

FIGURE 1. Chronosequence trajectories for structural traits of tropical dry forest regenerative communities (trees and shrubs 10–100 cm tall) in abandoned pastures (black circles) at Chamela, Jalisco, Mexico. (A) Plant density, (B) species density, and (C) plant cover. Values correspond to the year 2004. Dotted lines are the 95% confidence bands of the adjusted potential regression models. Old-growth forest sites (OGF, white dots) are excluded of the regression models. At each graph, the proportion of variance explained by the adjusted model (R^2), the corresponding significance P value, and model parameter values are provided.

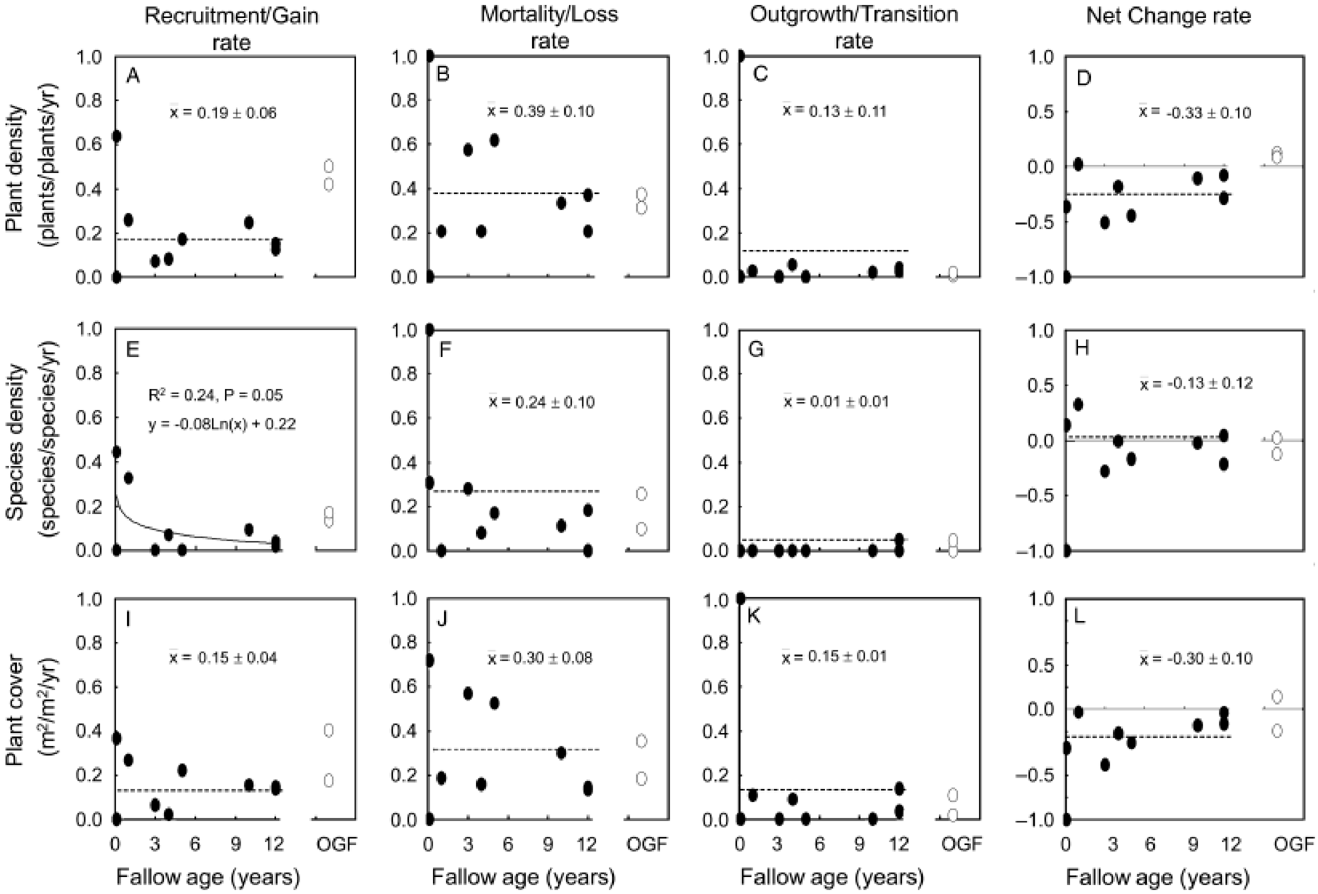

FIGURE 2. Relationships between community rates of change of regenerative communities and fallow age at Chamela, Mexico. Mean community annual rates of change correspond to the period October 2004 to October 2007. Net community annual rates of change result from the balance among recruitment/gain, mortality/loss, and outgrowth/transition rates for each structural variable. In cases where no significant relationships between a community rate and fallow age was found, an horizontal line indicates the mean community rate of change value across all abandoned pastures (also shown in numbers ± 1 SE). For species gain rate (*E*), the significant adjusted logarithmic curve is showed indicating R^2, significance *P* value and parameter model values. White dots indicate old-growth forest (OGF) sites (not included in the community rate-fallow age relationships).

predicted and observed community rates were not significant for any of the studied structural traits (Fig. 3).

No relationship was found between any of the community rates and stand density or light availability. The only significant relationships were between recruitment (Fig. 4A) or species gain rate (Fig. 4B) and surrounding forest matrix; these relationships were positive and linear and significant only when pastures of 0–1 yr of abandonment (Table 1) were removed from the analyses. In these pastures, 70 percent of the recruits were sprouts while in the other sites it was 40 percent on average.

DISCUSSION

Plant densities of regenerative communities in our chronosequence were similar to those recorded in other successional TDF. For example, density of shrubs and trees ≤ 1 m height in a 100 yr old secondary TDF in Pinkwae, Ghana (745 mm/yr; Swaine *et al.* 1990) was in the same order of magnitude (2.8 plants/m^2) than the mean plant density of our OGF sites (1.8 plants/m^2). Similarly, density of woody plants ≤ 1 m height in secondary TDFs of 10–20 yr old in Mozambique (930 mm/yr; Campbell *et al.* 1990) was similar (0.52–1.34 plants/m^2) to the plant density of our 10–12 yr old secondary forests (1.1 plants/m^2). In contrast, plant density values recorded in our regenerative communities were four to 14 times lower than those reported for comparable abandoned cattle pastures in tropical rain forest areas (Benítez-Malvido *et al.* 2001). Such noticeable difference may be result of the lower forest productivity and harsher environmental conditions prevailing in tropical dry areas. TDFs have smaller trees than tropical rain forests (*e.g.*, Ewel 1977, Lebrija-Trejos *et al.* 2008), which may result in lower propagules availability for regeneration. Also, in TDF areas, dryness and high irradiation may impose strong environmental restrictions for production, establishment, survival and growth of propagules, especially in pasture environments (Vieira *et al.* 2008, Suresh *et al.* 2010).

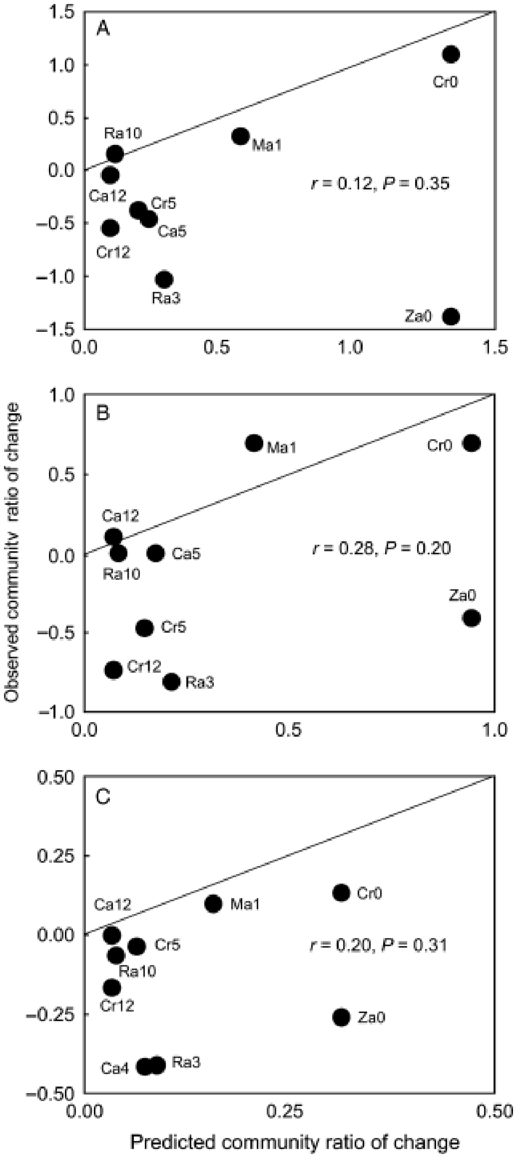

FIGURE 3. Relationships between observed and predicted (from the chronosequence) community ratios of change of structural traits of tropical dry forest regenerative communities in abandoned pastures at Chamela, Mexico. (A) Plant density, (B) species density, (C) plant cover. The continuous diagonal line represents a 100 percent correspondence between observed and predicted rates. Each dot represents one abandoned pasture site and tags the acronym name and fallow age of the site. Pearson correlation coefficient (*r*) and associated significance (*P*) value are indicated in each case.

In years with a short rainy season, water availability may not be enough for accumulating the required resources to survive (Engelbrecht *et al.* 2006, Slot & Poorter 2007, Suresh *et al.* 2010), to produce seeds (Bullock & Solís-Magallanes 1990) and or to resprout (Latt *et al.* 2000) during the long dry season. In this context, it is noticeable that the driest and hottest years of the last 29 yr in Chamela occurred during the studied period (Fig. S1B). Correspondingly, mortality did surpass recruitment, causing decrement in plant density in most of our sites (see below). Events of higher mortality than recruitment rates in regenerative communities are frequent in TDFs (Swaine *et al.* 1990, Lieberman & Li 1992).

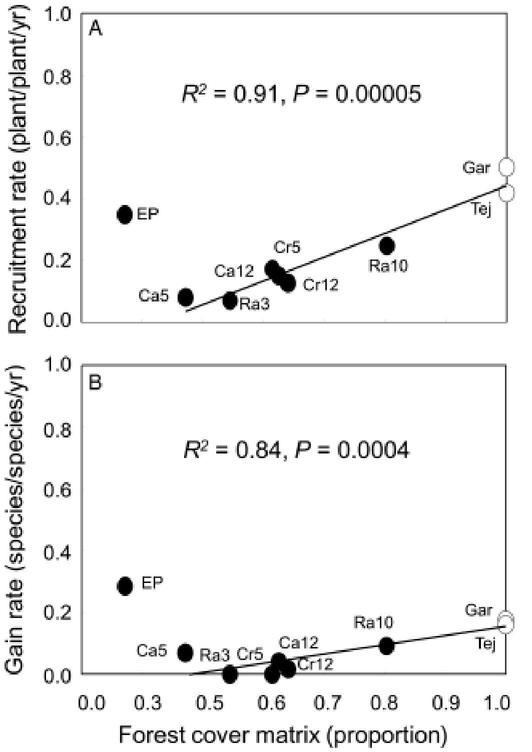

FIGURE 4. Relationships between community rates of change of regenerative plants and the proportion of surrounding forest matrix (in a circular area of 500 m radius) for abandoned pastures (3–12 yr since abandonment, black dots) and old-growth forest sites (white dots) at Chamela, Mexico. (A) Recruitment rate and (B) gain rate. Excluding the outlier EP point (mean of pastures with 0–1 yr of abandonment), R^2 and *P* values for the adjusted linear regression are indicated. EP point was excluded because sprouts (> 70% all plants) dominated this successional category.

CHRONOSEQUENCE TRENDS.—Our chronosequence trajectories showed that TDF regeneration start with low plant/species density and plant cover values progressing rapidly and asymptotically toward of OGF values. In humid tropical areas, density of small woody plants increase rapidly during the first 20 yr and then decline as succession advances; such trend results of the dynamics of entrance and disappearance of abundant pioneer species determined by changes in understory light availability (Swaine & Hall 1983, Chazdon *et al.* 2007). In tropical dry regions, soil water availability more than light resources may drive succession (see below). High evapotranspirative demand (Camargo & Kapos 1995) and the facilitation role of colonizer species can be fundamental in the dynamics of regenerative communities during early TDF succession (Lebrija-Trejos 2009).

It is likely that dispersed seeds arriving from nearby seed sources found in the matrix could contribute to the rapid recovery of regenerative communities indicated by our chronosequence. In fact, more than a third of the matrix area surrounding our old fields was covered by forest vegetation. Several woody species of TDF produce anemochorous seeds (Bullock 1995) that can travel dozen or hundred meters (Greene *et al.* 2008). Also, zoochorous seeds could have arrived from the matrix; ongoing studies in our chronosequence have detected active assemblages of frugivore bats and birds in our abandoned pastures > 3 yr fallow age (Ávila-Cabadilla *et al.* 2009). Also, cattle raising activities practiced at Chamela are of low intensity, with no use of machinery, low agrochemicals inputs, low livestock densities, and retaining shrubs and trees within the pastures (Burgos & Maass 2004, Trilleras 2008). Such practices seem to have had relatively low impact on soil properties (Trilleras 2008) and could favor local seed rain. These aspects could influence in the rapid recovery suggested by the chronosequence. The rapid recovery of TDF plant communities in old fields seems to operate in other TDF regions (*e.g.*, Campbell *et al.* 1990).

Chronosequence studies in Mexican TDF areas (Lebrija-Trejos *et al.* 2008, Chazdon *et al.* 2011) with shrubs and trees dbh ≥ 1 cm documented similar successional trends to ours, but predicted faster successional convergence to the OGF structure. It is well established that survival and growth increases as plants reach larger size (*e.g.*, Sarukhán *et al.* 1984). Therefore, the difference in such successional convergence rate could be due to differences in vital rates between the regenerative (small) and the mature (large) plants. High mortality, low recruitment, and low growth rates of regenerative plants could impose slow successional rates of change that could accelerate as plants reach larger sizes and, consequently, higher survival and growth.

DO CHRONOSEQUENCES MATCH DYNAMIC RATES?—Overall, the results emerging from our dynamic study did not match the successional structural trends predicted by the chronosequence. Thus, our study concurs with others (Chazdon *et al.* 2007) in pointing out that chronosequences have limitations to confidently predict successional dynamics (Johnson & Miyanishi 2008).

The pasture sites Cr0 and Ma 1 did show higher gain rates than loss rates of plants and species, paralleling with chronosequence predictions (Fig. 3). Such results are consistent with the hypothesized input of colonizing species, with high recruitment and growth rates, at the beginning of succession (*e.g.*, Grime 1979) as has been observed during the first years of succession in tropical rain forest areas (*e.g.*, van Breugel *et al.* 2006). In contrast to these two pasture sites, our other recently abandoned pasture (Za0) showed a negative community rate of change. This pasture was cleaned and burned by the owner before abandonment, leaving no isolated shrubs or trees (Table 1). In this site, outgrowth rate was higher than recruitment rate and all plants were sprouts. After slash and burn, sprouts can persist and grow thanks to their carbohydrate stocks, and their physical vigor (Hoffmann 1998, Miller & Kauffman 1998b, Vesk & Westoby 2004). Low recruitment could be due to the elimination of the seed bank and vegetative meristems by the clearance and fire. Because Za0 had similar surrounding matrix than the other recently abandoned pastures, the absence of seedling recruits in this site suggest that the land use history may be more critical than landscape factors for the regenerative dynamics at the beginning of the secondary succession.

EFFECTS OF FACTORS ON TDF REGENERATIVE DYNAMICS.—How strongly were the observed dynamics of the studied regenerative communities related to surrounding forest matrix, stand density, and light availability?

We found evidence that plant recruitment and species gain rates increased with the amount of surrounding forest matrix which support the hypothesis that remnant forests function as an important seed source for early forest regeneration in old fields (Chazdon 2003). Evidence that most recruits were sprouts in the recently abandoned pastures explains the higher recruitment and species gain rates than that expected under the observed recruitment–matrix relationship. It is well know that in TDF areas an important regenerative mechanism is resprouting (Rico-Gray & García-Franco 1992, Miller & Kauffman 1998b, Miller 1999, Vieira & Scariot 2006). At Chamela, a study showed that 50 percent of the plants and more than 60 percent of the species recruited 16 mo after pasture abandonment were sprouts (Miller & Kauffman 1998a, b). It is likely that after a first important wave of regeneration from sprouts and dormant soil seeds, new recruits emerge from dispersed seeds arriving from the surrounding forest matrix increasing abundance and species number. This idea is supported because the abandoned pastures had only three species, in coincidence with the known fact that regeneration sprouting has low species diversity (Bond & Midgley 2001), and that seedlings represented over 60 percent of total recruits in most of our studied sites > 3 yr fallow age.

Because most community rates of change were not related either to fallow age, surrounding forest matrix, stand density, or light availability we believe that the strong temporal variability in water rainfall availability, occurring before and over our studied period, did override the expected effects of these factors. From 2000 to 2005 very low annual rainfalls and high temperatures occurred at Chamela (Fig. S1B). Particularly, in 2005, a severe El Niño Southern Oscillation event took place. During that year, annual rainfall (383 mm) was less than half of the long-term mean annual rainfall (788 mm), being the driest of the previous 29 yr. Moreover, the mean annual temperatures during the studied period (2004–2007; average = 26.5°C) were the highest in last previous 26 yr (1978–2003; average = 24.8°C). During such dry and warm episodes, negative soil water potentials (resulting from a combination of high evaporation demands, high radiation loads, vapor pressure deficits, and high exposure to wind desiccation) can be exacerbated, particularly in recently abandoned pastures (Camargo & Kapos 1995), reducing the survival, recruitment and growth of regenerative plants.

Drought has been identified as an important agent of mortality and a strong limiting factor for growth of seedlings, small saplings of tropical tree species (*e.g.*, Marod *et al.* 2002, McLaren & McDonald 2003, Engelbrecht *et al.* 2006). In TDF environments, drought can also lower seed/sprout production (*e.g.*, Slot & Poorter 2007, Poorter & Markesteijn 2008) and increase mortality of mature trees (Suresh *et al.* 2010), which may result in lower recruitment rates at the community level. It has been documented that TDF tree species store resources obtained during previous rainy seasons to produce flowers in the dry season (Bullock & Solís-Magallanes 1990). Thus, shrubs and trees may fail to produce seeds (and hence seedlings) due to water shortages during present or previous growing seasons. It is interesting to note that community rates of change were negative or zero even when the last 2 yr (2006, 2007) of our study had annual rainfall above the long-term average (Fig. S1B), suggesting that the recovery of regenerative communities from long lasting and severe droughts involves periods of more than 2 yr. In synthesis, the evidence that mortality and species loss rates were high, and growth, recruitment and species gain rates were quite low, across most studied sites (Fig. 2), suggests that drought was a preponderant factor affecting the dynamics of the regenerative communities in abandoned pastures and OGF sites.

Strong supra-annual variation in rainfall has been indicated as an important factor affecting tree community organization and dynamics in old-growth TDF (Kelly & Bowler 2002). Our study suggests that such variation may be also important for the dynamics of regenerative successional communities in abandoned pastures.

CONCLUSIONS

Successional chronosequence trajectories predict a rapid recovery of structural trait values of regenerative TDF communities at abandoned pastures at Chamela. Community rates of change predicted by the chronosequence, however, were not matched by the observed rates. Excluding recently abandoned pastures, recruitment and species gain rates increased with the amount of surrounding forest matrix. The null influence of fallow age, stand density or light availability on the community rates of change, indicate the preponderance of others driving factors of the regenerative process. We suggest that rain water availability is a major driving factor of the TDF regeneration in abandoned pastures, but research encompassing longer time periods than ours are needed to assess such hypothesis. As a corollary, we emphasize that chronosequence approach has low predictive value, especially in strong seasonal forest systems and in plant communities undergoing rapid dynamics. Hence, dynamics studies are critical to understand the processes and mechanisms underlying TDF secondary succession.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

FIGURE S1. Geographic localization of the study sites and climatic patterns at Chamela, Mexico.

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CAPÍTULO IV

EFFECTS OF ENSO AND TEMPORAL RAINFALL VARIATION IN THE DYNAMICS OF REGENERATIVE COMMUNITIES OVER THE OLD-FIELD SUCCESSION IN A TROPICAL DRY FOREST

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Effects of ENSO and temporal rainfall variation in the dynamics of regenerative communities over the old-field succession in a tropical dry forest

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Summary

1. The effects of the temporal variation of rainfall on the successional dynamics of terrestrial seasonal ecosystems are poorly understood. Here, we studied the effects of inter-seasonal and inter-year rainfall variation on the dynamics of regenerative communities over the old-field succession of a tropical dry forest at Chamela, Mexico. Particularly, we focused on the effects caused by a severe El Niño Southern Oscillation (ENSO) event occurred in 2005.

2. We established permanent plots in sites representing a chronosequence of Pasture (abandoned cattle pastures, 0-1 years fallow age), Early (3-5 years), Intermediate (10-12 years), and Old-Growth Forest successional categories (n = 3 sites per category). At each site, seedlings and sprouts of shrubs and trees 10 to 100-cm height were identified, measured, and monitored over four years. Monthly rates of recruitment, growth, and mortality, as well as the rates of gain and loss of species were calculated per season (dry *vs*. rainy), year, and successional category, considering the whole community and separating seedlings from sprouts, and shrubs from trees.

3. Community rates changed in a complex way in response to rainfall variation, with almost no effect of successional category. Mortality and species loss rates peaked in the dry season of the ENSO year and were still high in the following year; however, after two rainy years mortality peaked in the rainy season. Growth, recruitment and species gain rates were higher in the rainy season but they were significantly reduced after the ENSO event. Overall, seedlings exhibited a higher mortality rate than did sprouts while shrubs and trees exhibited similar rates in all analysed traits.

4. Synthesis. The severe drought produced by the ENSO event strongly impacted both the dynamics and trajectory of succession, creating transient fluctuations in the abundance and species richness of the studied communities. Although such fluctuations were smoothed out by

subsequent rainy years, there was a net decline in plant density and species density in most successional stages. Therefore, we conclude that strong drought events have critical consequences for regeneration dynamics, because they can delay the successional recovery of tropical dry forests in abandoned fields.

Key-words: Plant-climate interactions, Plant community structure and diversity, Forest regeneration, Secondary succession, ENSO, Chamela, Mexico, Seedlings, Sprouts

Introduction

Most theoretical and empirical studies on forest succession have focused on the role of light availability on the dynamics of tree communities in evergreen forest ecosystems (e.g. Horn 1974; Denslow 1980; Finegan 1984). In contrast, few studies have approached the role of water availability on succession (e.g. Chazdon, Redondo & Vilchez 2005), even in strongly seasonal ecosystems (Verdú *et al*. 2009). In the seasonal tropical dry forest (TDF), which is a major biome in the world (Brown and Lugo 1982), water availability plays a critical ecological role (Murphy & Lugo 1986; Lebrija-Trejos *et al*. 2010), affecting functional, demographic, community, and ecosystem attributes of woody plants (Bullock, Mooney & Medina 1995; Dirzo *et al*. 2011).

Availability of water for TDF plants depends critically on the frequency, magnitude, and duration of rainfall events; these events vary widely among seasons, within seasons, and among years (García-Oliva, Ezcurra & Galicia 1991; Sen 2009). Furthermore, current scenarios of global climate change predict that severe drought events, such as those caused by the El Niño Southern Oscillation (ENSO), will increase both in intensity and frequency in tropical regions (Timmermann *et al*. 1999; Nakagawa *et al*. 2000). Under such scenarios it is critical to understand to what extent temporal rainfall variability affects natural regeneration and succession of seasonal dry ecosystems in abandoned agricultural fields, which have become dominant components of contemporaneous tropical a non-tropical landscapes (Dale *et al*. 2001; Chazdon *et al*. 2007).

Temporal variation in rainfall, especially when strong drought episodes occur, has been shown to have important effects on demographic rates of woody TDF plants at their early life-cycle stages (Veenendaal *et al*. 1996; Kuhurana & Singh 2001; Marod *et al*. 2002; McLaren &

McDonald 2003), as is also the case for plants in other tropical forest systems (e.g. Chazdon, Redondo & Vilchez 2005; Feeley et al. 2011). While recruitment and growth have been mostly linked with the rainy season, mortality has been observed to occur mostly during the dry season (Lee 1989; Lieberman & Li 1992; Khurana & Singh 2001; Slot & Poorter 2007; Schumacher *et al*. 2008). We can also expect that rates of gain and loss of species parallel these seasonal changes in rates of performance and mortality, as variation in species number tends to be correlated with changes in abundance (Gotelli & Colwell 2001). However, more studies are needed to verify the strength of such linkages, especially in successional environments in the dry tropics.

During secondary succession, seedlings and sprouts of shrub and tree species may respond in different ways to changes in the levels of water availability. Overall, survival and growth rates tend to be lower for seedlings than for sprouts (Grime 1979; Miller & Kauffman 1998; Kennard *et al*. 2002), and sprouting has been proposed to be a major regenerative mechanism in TDF where strong water shortages may limit survival and growth of seedlings (Bond & Midgley 2001; Vieira & Scariot 2006; Busby, Vitousek & Dirzo 2010). Likewise, in ecosystems outside the TDF, shrubs have been shown to have higher recruitment, growth, and or survival rates than trees under the harsh conditions of early successional environments (Grime 1979; Bellingham & Sparrow 2000). Therefore, we hypothesize that the survival and growth of sprouts and shrubs would be higher than that of seedlings and trees at early successional stages and that such differences would reduce as succession advances.

Although it has been proposed that temporal variation in rainfall may affect the long-term dynamics of tree communities in TDFs (Kelly & Bowler 2002; Slot & Poorter 2007), little is known about the temporal signature of such effects (Suresh, Dattaraja & Sukumar 2010). Effects of the amount of rainfall within a given season on plant survival could be expected to be immediate because, for example, a severe and prolonged drought may cause embolism problems and lead to the rapid death of plants (Páramo 2009). In contrast, current plant growth and recruitment would vary not only with water availability in a given season but also with the amount of rainfall of previous seasons because such past rainfall events affects the storage of photosynthates needed for future biomass gain and seed production (Yu *et al*. 2008; Hill & Edwards 2010; Bullock & Solís-Magallanes 1990; Viera & Scariot 2006). Overall, however, there is a lack of knowledge about the potential lag effects caused by rainfall regimes on the regeneration and successional dynamics of TDF.

In this paper we studied the effects of temporal rainfall variation on the dynamics of regenerating communities of shrubs and trees (plants 10-100 cm height) over the old-field succession of a TDF in western Mexico. In a previous paper (Maza-Villalobos, Balvanera & Martínez-Ramos 2011) we analysed successional patterns of these communities, which strongly suggested that rainfall temporal variability plays a critical role on such dynamics. Here, we explicitly evaluate the importance of inter-annual and inter-seasonal rainfall events on rates of plant recruitment, growth, and mortality as well as on species gain and loss rates over the period of October 2004 to October 2007. We placed a special consideration on assessing the effects caused by the strong ENSO event that occurred in 2005, which produced the driest of the previous 30 years in the study area. Specifically, we tested the following hypotheses: i) plant mortality and species loss rates are linked to dry seasons and drought years while recruitment, growth, and species gain rates are linked to rainy seasons and rainy years, ii) trees and seedlings are more prone than shrubs and sprouts to mortality during drought events, iii) growth, recruitment, and species gain rates depend more on historical rainfall events than survival rates, and iv) effects caused by rainfall temporal variability on regenerative community dynamics are higher at early than late successional stages.

Materials and Methods

STUDY SITE

The study was conducted at the Chamela-Cuixmala Biosphere Reserve (19°30´ N, 105°03´ W), and surrounding rural areas in the La Huerta municipality, Jalisco, Mexico. Mean annual temperature is 22.1 °C and mean annual precipitation is 731 mm with wide inter-annual (384 to 1393 mm) and season variation (Fig. 1). Almost 93% of the annual rainfall occurs from June to October, with a long dry season from November to the end of May. The main vegetation type is TDF; in the study area 1149 plant species (45% tree and shrub species) have been recorded (Lott 2002; Lott & Atkinson 2006). Canopy height varies between 5 and 10-m (Durán *et al.* 2002) and most trees and shrubs have small diameters at breast height (dbh < 10-cm). During the dry season around 95% of all the plants drop their leaves. The TDF covers about 30% of La Huerta municipality while rural agricultural lands cover the rest (Sánchez-Azofeifa *et al.* 2009). By 1990, different agriculture activities reduced 60% of the area historically covered by TDF. Presently, the landscape is dominated by pasture fields, crops, and managed forests (Burgos & Maass 2004).

STUDY SYSTEM AND EXPERIMENTAL DESIGN

Twelve abandoned cattle pasture sites, with fallow ages ranging from 0 to 12 years, and three conserved old-growth forest sites (OGF) were selected. These sites were classified in four successional categories, each with three sites: Pasture (P; 0-1 years), Early (E; 3-5 years), Intermediate (I; 10-12 years), and Old-Growth Forest. At each site, an area of 120 × 90-m (1.08 ha) was delimited with metal barbed wire posed (three parallel lines separated 50-cm each) to exclude cattle but not wild animals; in OGF only stakes were used to limit the study area. A permanent plot of 50 × 20-m was established at each site and 48 subplots (delimited in the corners with 0.5-m tall PVC poles) of 1-m^2 each were randomly established in each plot. Maza-Villalobos, Balvanera & Martínez-Ramos (2011) provide details of the geographical location, biophysical and land use history characteristics of the study sites.

In October 2004, at the end of the rainy season, for each subplot, we tagged and measured all trees and shrubs with heights between 10 and 100-cm (from the ground level to the apical growth bud). Each recorded plant was measured in height and classified as a sprout, if it presented a physical connection with another plant, or a seedling, if cotyledons were present or if there was no evidence of it re-sprouting from other plants. Taxonomic identification followed the nomenclature provided by Lott (2002); specimens of reference were obtained outside of the plots and vouchers are available from the authors. Additional censuses were conducted over the following three years. In total, we did eight censuses, four at the end of the rainy seasons (October 2004, November 2005, November 2006, and October 2007), three at the initiation of the rainy season (September 2005, June 2006, and August 2007; in 2005 the rainy season began late; Fig. 1) and one in the middle of the rainy season (September 2006). During these censuses new seedlings and sprouts reaching a height of 10-cm or more (hereafter referred to as recruits) were recorded, measured and identified while surviving plants were re-measured for height.

Rainfall data used in this study comes from the meteorological system owned by the Chamela Biological Field Station, Institute of Biology, National Autonomous University of

Mexico (www.ibiologia.unam.mx/ebchamela/www/clima.html). All study sites are within a radius of 17-km from the Station.

DATA AND STATISTICAL ANALYSIS

We calculated plant recruitment, growth, and mortality rates, as well as species gain and loss rates per successional category, separating dry seasons from the rainy ones, and for each studied year. These calculations were conducted considering the whole community, separating plant growth forms (shrubs *vs*. trees) and separating plant regeneration strategies (seedlings *vs*. sprouts). In sum, we monitored community dynamics over three one-year periods (which did not coincide with calendar years but for simplicity we will refer here after as years), encompassing three periods within dry seasons (October 2004 to September 2005, November 2005 to June 2006, and November 2006 to August 2007) and three within rainy seasons (September 2005 to November 2005, June 2006 to November 2006, and August 2007 to October 2007). It should be noted that duration of these periods (hereafter referred as seasons) was variable. Therefore, to have a standardized time scale of analysis, we calculated monthly rates per season. Recruitment rate (*RR*) was calculated as $RR = [[(n + r)/n)]^{30/t}]- 1$, where n is the number of plants present at the beginning of the season, r is the number of new recruits recorded within a season and that survive until the end of that season, and t is the number of days elapsed between censuses conducted at the beginning and end of a given season. Mortality rate (*MR*) was calculated as $MR = 1-[[1-(m/n)]^{30/t}]$ where m is the number of initial plants that died from the beginning to the end of a given season. Growth rate (*GR*) was calculated as $GR = (h_f - h_i)/(h_i)]*(30/t)$ where h_i and h_f are the plant height at the beginning and end of the season, respectively. Gain and loss rates of species were obtained using the same formulas for recruitment and mortality as mentioned before, but in theses cases *n* was the number of species, *r* the number of new species, and *m* the number of species lost within a season. While the recruitment and mortality rate depend from the number of plant inicial, the probabilities of these rates will be exponential but since the growth rate does not depend of the n, this rate is lineal (Harper 1977).

Repeated measure analyses of variance were used to evaluate the effects of calendar year (three levels: October 2004-November 2005, November 2005-November 2006, November 2006-October 2007), season (two levels: rainy and dry), and successional category (four levels: Pasture, Early, Intermediate, and Old-Growth Forest) for each of the studied regenerative community rates. This analysis was also conducted for the whole community. In addition, the analysis was performed introducing the factor regenerative strategy (two levels: seedlings and sprouts) or growth form factor (two levels: trees and shrubs), separately. When necessary, response variables with non-normal errors were transformed [log (x+1)] to fulfil the parametric criteria required by parametric analyses. All analyses were performed using Data Desk 6.1.

Results

TEMPORAL VARIATION IN RAINFALL

During the studied period, the first year registered far below the long-term mean annual rainfall recorded in our study locality (Fig. 1). In that year (2005) occurred a severe ENSO event causing a very long dry season, resulting in the driest year of the previous three decades (Fig. 1). In the two previous years (2003 and 2004) annual rainfall was close to the long-term mean, and in the two years following to the ENSO year (2006 and 2007) annual rainfall was substantially above this long-term mean.

COMMUNITY RATES OF CHANGE AFFECTING PLANT DENSITY

RECRUITMENT RATE

On average, considering the whole community, recruitment rate varied significantly among seasons ($F_{1,38} = 25.3$, $P < 0.0001$) and years ($F_{2,38} = 3.3$, $P = 0.05$). Recruitment was ten times higher in the rainy season (mean ± S.E = 0.20 ± 0.07 plant plant^{-1} m^{-1}) compared to the dry season (0.02 ± 0.003) and, on average, was substantially higher in the ENSO year (0.21 ± 0.09) than in the following two years (0.03 ± 0.01 and 0.09 ± 0.06, 2006 and 2007 respectively; Fig. 2a). Although recruitment rate, on average, was higher in the Pasture (0.25 ± 0.14) than in the other successional categories (Early: 0.06 ± 0.02, Intermediate: 0.06 ± 0.02, and OGF: 0.08 ± 0.03) in two of the three studied years, the high inter-site variation did not result in significant differences among the successional categories. In addition, over all years, seasons, and successional categories, recruitment rate was nor significantly different between trees (0.09 ± 0.022) and shrubs (0.11 ± 0.04), nor between seedlings (0.12 ± 0.05) and sprouts (0.10 ± 0.05).

The magnitude of the differences in recruitment rate between seasons varied among the years (significant year × season interaction: $F_{2,38} = 11.4$, $P = 0.0001$). During the rainy season of the ENSO year, recruitment rate was much higher in the rainy than in the dry season over all successional categories. In contrast, in the rainy season of the following two years recruitment was strongly reduced, approaching the values recorded in the dry season for most successional categories (Fig. 2a).

Overall, recruitment rate of trees varied among years ($F_{2,38} = 14.4$, $P \leq 0.0001$) and seasons ($F_{1,38} = 12.3$, $P = 0.002$), following the temporal changes observed across the successional categories in the whole community. However, while in the ENSO year this rate was clearly higher in the rainy season and showed peaks in the Pasture and Old-Growth Forest categories, it was quite similar and very low over all successional categories and seasons in the second and third years (Fig. 2b). Recruitment rate of shrubs did not vary among years but it was twenty times higher in the rainy season (0.20 ± 0.08) compared to the dry season (0.01 ± 0.003; $F_{1,38}$ = 20.5, P = 0.0002). In the first and last studied years, this rate significantly decreased in the Pasture compared to the other successional categories for the rainy season ($F_{3,38}$ = 4.0, P = 0.02; Fig. 2c).

Recruitment rate of seedlings did not vary among years nor among successional categories and, on average, it was ten times higher in the rainy season (0.22 ± 0.10) compared to the dry season (0.02 ± 0.00; $F_{1,44}$ = 14.4, P = 0.001; Fig. 2d). Recruitment rate of sprouts varied significantly among years ($F_{2,44}$ = 5.1, P = 0.01) and seasons ($F_{1,44}$ = 6.7, P = 0.02) but not among successional categories. On average, recruitment rate of sprouts was six times higher in the rainy season (0.18 ± 0.11) compared to the dry season (0.02 ± 0.00); however, during the following two years to the ENSO event, this rate was similarly low between seasons in all successional categories (significant year × season interaction: $F_{2,44}$ = 4.2, P= 0.02; Fig. 2e).

MORTALITY

On average, considering the whole community, there were significant effects of season ($F_{1,32}$ = 6.1, P = 0.02) and year ($F_{2,32}$ = 24.6, P < 0.0001) but not of successional category on mortality rate. On average, mortality rate in the dry season was almost twice as high (0.028 ± 0.004 plant plant^{-1} m^{-1}) compared to the rainy season (0.015 ± 0.005) and it showed a maximum in the ENSO year (0.05 ± 0.01; Fig. 2f). During this year, mortality in the rainy season tended to be higher in the Pasture than in the other successional stages. In the following two years, however, mortality was not related to successional category. Interestingly, after two rainy years (2006, 2007; Fig. 1) mortality was higher in the rainy than in the dry season (Fig. 2f).

Over years, seasons, and successional categories, trees (0.024 ± 0.005) the shrubs (0.019 ± 0.004) displayed similar mortality rates. The tree mortality rate did not vary among successional categories but it was different among years ($F_{2,44} = 10.73$, $P = 0.0002$), with the highest mortality found in the ENSO year (Fig. 3g). In the first two studied years (2005, 2006), tree mortality was higher in the dry than in the rainy season, in most successional categories; however, in the last studied year (2007) this pattern reversed (year × season interaction: $F_{2,44} = 10.8$, $P = 0.0001$; Fig. 2g). The shrub mortality rate varied among years ($F_{2,44} = 17.15$, $P < 0.0001$) and seasons ($F_{1,44} = 8.63$, $P = 0.01$), showing maximum mortality in the ENSO year (Fig. 2h). On average, shrub mortality was higher in the dry season (0.03 ± 0.01) compared to the rainy season (0.01 ± 0.001). In the last studied year (2007) shrub mortality was almost zero and no differences among successional categories were detected.

Overall, the mortality rate of seedlings (0.030 ± 0.005) was twice as high ($F_{1,22} = 102.1$, $P < 0.0001$) as that of sprouts (0.015 ± 0.004). Seedling mortality varied among years ($F_{2,44} = 14.42$, $P < 0.0001$), and seasons ($F_{1,44} = 4.89$, $P = 0.03$) but not among successional categories. Overall, the highest mortality occurred in the ENSO year, and mortality rate was twice as high in the dry season (0.04 ± 0.01) compared to the rainy season (0.02 ± 0.01). Over most successional categories, the highest mortality occurred in the dry season of the ENSO year (0.08 ± 0.02). In the following year, mortality was also higher in the dry than in the rainy season but in the third year (2007) seedling mortality was much higher in the rainy than in the dry season (year × season interaction: $F_{2,44} = 12.19$, $P < 0.0001$) with the dry season mortality rate being close to zero (Fig. 2i).

Sprouts exhibited mortality rates that differed among years ($F_{2,44} = 12.37$, $P < 0.0001$) and seasons ($F_{1,44} = 5.06$, $P = 0.03$) but not among successional categories. The highest mortality rate occurred in the ENSO year (0.04 ± 0.01) and, on average, mortality was higher in the dry season (0.02 ± 0.01) compared to the rainy season (0.01 ± 0.01); however, in the third year (2007) shrubs exhibited almost zero mortality in most successional categories, independently of season (Fig. 2j).

GROWTH

On average, considering the whole community there were significant effects of year ($F_{2,38} = 188.1$, $P < 0.001$) and season ($F_{1,38} = 3203.8$, $P < 0.0001$) but not of successional category on growth rate. Overall, growth was higher in the rainy season (0.90 ± 0.04 cm cm^{-1} m^{-1}) compared to the dry season (0.25 ± 0.01). Plant growth in the rainy season showed important variation among years, with the year after the ENSO event (2006) exhibiting the lowest growth rate value (Fig. 2k). In contrast, growth during the dry season was quite stable over the three years. Overall, differences between trees and shrubs and between seedlings and sprouts were not significant. Variation in the growth rates of trees, shrubs, seedlings and sprouts over the years, seasons, and successional categories generally paralleled those observed for the whole community (Fig. 2k-o).

COMMUNITY RATES AFFECTING SPECIES DENSITY

SPECIES GAIN RATE

On average, and for the whole community, the species gain rate varied among years ($F_{2,38} = 16.28$, $P < 0.0001$) and seasons ($F_{1,38} = 40.57$, $P < 0.0001$) but not among successional categories. Overall, the species gain rate was four times higher in the rainy season (0.12 ± 0.02

species species^{-1} m^{-1}) compared to the dry season (0.03 ± 0.003) and it showed minimum values one year after the ENSO event (2006; 0.04 ± 0.01). There were no significant interactions between growth form and season, year, or successional category (Fig. 3a-c). Thus, the changes in the species gain rate among seasons, years, and successional categories for trees and shrubs were generally the same as those observed in the whole community, except that the gain rate of tree species in the rainy season was still low two years after the ENSO event, and was less of a strong pattern for shrubs (Fig. 3b,c).

SPECIES LOSS RATE

At the whole community level, species loss rate varied between seasons ($F_{1,38} = 4.39$, $P = 0.05$) and among years ($F_{2,38} = 3.72$, $P = 0.03$) but not among successional categories. On average, this rate was higher in the rainy season (0.10 ± 0.01) compared to the dry season (0.05 ± 0.01; Fig. 3d). However, species loss rate was quite similar between seasons during the ENSO year and after the following year (2006) but it was much higher in the rainy season (0.11 ± 0.02) compared to the dry season (0.03 ± 0.01) in 2007 (year × season interaction: $F_{2,38} = 4.63$, $P = 0.01$).

Regarding growth form and species loss rates (Fig. 3e,f), the only significant effect that we detected was that of a season x year interaction ($F_{2,44} = 5.41$, $P = 0.008$) for trees. Although, on average, species loss rate was higher in the rainy (0.11 ± 0.03) than in the dry season (0.03 ± 0.01), this difference appeared to be mostly due to the seasonal changes that occurred in the rainy year of 2007 (Fig. 3e).

SUCCESSIONAL TRAJECTORIES IN PLANT AND SPECIES DENSITY

Figure 4 shows the temporal trajectories of plant density (Fig. 4a-e) and species density (Fig. 4f-h) over the four studied years for each successional category. The occurrence of ENSO in 2005 produced important fluctuations in both density and diversity, at the whole community level and separating trees from shrubs and seedlings from sprouts. Such fluctuations were smoothed over by the occurrence of two rainy years (2006 and 2007) subsequent to the ENSO year. In most successional categories, growth forms, and regenerative strategies, plant density and species density maintained similar values or decreased over time (Fig. 4). However, there were some exceptions. Tree density increased over time in all successional categories but most strongly in the Intermediate and Old-Growth Forest categories; as a result, differences among these successional categories and the younger ones became more pronounced over time (Fig. 4b). Stem density (but not species density) of shrubs increased over time in the Pasture but not in the other successional categories (Fig. 4h), which resulted in a convergence of stem density of shrubs over time in the Pasture, Early and Intermediate categories (Fig. 4c). Finally, sprout density increased with time in the Pasture, Early and Intermediate categories but decreased in the Old-Growth Forest; as a result, after three years, the density of sprouts exhibited similar values in all successional categories (Fig. 4e).

Discussion

Our study shows that successional dynamics of regenerative communities of the TDF at Chamela was governed by strong inter-annual and inter-seasonal rainfall variation, which included an ENSO event. Overall, the effects of rainfall variation were independent of successional category, which indicate the predominance of global factors (ENSO, climatic regimes) over those of local origin and related to successional age on such dynamics.

TEMPORAL CHANGES IN REGENERATIVE COMMUNITY RATES

RECRUITMENT

As expected, recruitment rate peaked in the rainy season. In TDFs, most wind-dispersed species produce seeds during the dry season that germinate in the following rainy season, while most animal dispersed species produce seeds during the rainy season that germinate either shortly afterwards or in some cases remain dormant until favourable growth conditions occur (Frankie, Baker & Opler 1974; Bullock & Solís-Magallanes 1990; Khurana & Singh 2001; Grombone-Guaratini & Rodrigues 2002; Martins & Engel 2007). These reproductive behaviours result in the largest recruitment of seedlings occurring during the rainy season, as our study documents. The recruitment rate of sprouts also peaked in the rainy season, which suggests the high importance of water availability thresholds for triggering the development of vegetative meristems present in roots, stumps or stems of parental plants.

In contrast, our results do not support the expectation that the recruitment rate ought to peak in rainier years. This rate was at its minimum in the rainy years of 2006 and 2007 (Fig. 1). Furthermore, the highest recruitment rate that we found occurred during a dry year (2005). These unexpected results can be explained based on the hypothesis that the storage of water reserves and photosynthetic products, which are critical for future vegetative (*i.e.* sprout production) and sexual reproduction (*i.e.* seed yield), is determined by past rainfall events (Reich & Borchert 1984; Bullock & Solís-Magallanes 1990; Kozlowski & Pallardy 1997; Latt, Nair & Kang 2000; Poorter *et al.* 2010). Thus, the important reduction in recruitment during the two years that followed the drought caused by ENSO could result from a strong shortage of stored reserves, and, consequently, from a reduction in the sprouting and reproductive activity of shrubs and trees. The fact that recruitment was depleted during two consecutive years after a severe drought suggests that sexual and vegetative reproduction depend on reserves accumulated over long-time periods. Consistent with this hypothesis, we believe that the peak of recruitment during the ENSO year (2005) resulted from the sprouting, flowering and seeding activity stimulated by reserves stored during the previous three years which received twice as much or more the amount of rainfall recorded in 2005 (Fig. 1). Aspects such as the failure of seed production due to a reduction of pollination agents (in animal pollinated plants) could also play an important role in the reduction of recruitment after the ENSO year.

The only significant effects of successional category on the dynamics of regenerating communities were related to recruitment rate of shrubs. Such effects were linked to the high recruitment (84% of total recruits) of the shrub *Mimosa arenosa* (Willd.) Poir., in one of our Pasture sites, where several adult individuals of this species were also present (S. Maza-Villalobos, pers. obs.). This species, and others of the same genus, is often found as a pioneer plant in abandoned pastures and cornfields (Romero-Duque, Jaramillo & Pérez-Jiménez 2007; Lebrija-Trejos *et al*. 2008). The abundance of this species in the early stages of succession can be attributed to its high capacity to germinate (92-100%) and withstand high temperatures and low soil water availability in disturbed sites (Camargo-Ricalde, Dhillion & García-García 2004).

MORTALITY

Small plants, such as seedlings and sprouts, are very sensitive to changes in the levels of soil water availability (Harper 1977; Comita *et al*. 2009). In TDFs, incoming solar radiation and temperature increase in the dry season, producing high evapotranspirative demands for plants (Camargo & Kapos 1995; Lebrija-Trejos *et al*. 2010, 2011), which could lead to the death of the plant, particularly when drought conditions remain for long-time periods. The fact that mortality rate of seedlings and sprouts peaked during the ENSO year (when the dry season persisted for eight months, Fig. 1) documents such vulnerability to drought, even for TDF shrubs and trees adapted to live in such water-limited environments (Murphy & Lugo 1986). Also, as expected, seedlings were more prone than sprouts to drought conditions as they had an overall mortality rate higher than that of sprouts, as has been also found in other studies (*e.g*. Miller & Kauffman 1998). Small amounts of maternal resources contained in the cotyledons, small sizes, limited root systems and soft tissues of seedlings make them susceptible to biotic and abiotic damages (Milton 1979; Coley 1980; Coley & Barone 1996; Castro-Díez *et al*. 1998), and vulnerable to drought (Hoffmann 1998; Bond & Midgley 2001). In contrast, larger sizes, larger root systems, and higher parental resources of sprouts (Sennerby-Forsse, Ferm & Kauppi 1992) make them more tolerant to physical or biotic damages, and to withstand better strong water shortages (Hoffmann 1998; McLaren & McDonald 2003; Vieira *et al*. 2006).

However, our results only partially support the prediction that the mortality rate of regenerating plants should peak in the dry season and during drier years. A striking and unexpected result was that the drought-related mortality reversed after two rainy years that followed to the ENSO event. The fact that in the rainy year of 2007 mortality rates were higher in the rainy than in the dry season can be attributable to two possible causes. First, it is known that in rainy years TDF plants can store non-structural carbohydrates used for survival during drought spells and dry seasons (Khurana & Singh 2001; McLaren & McDonald 2003; Poorter *et al.* 2010). Thus, we believe that the high precipitation that occurred in 2006 (Fig. 1) enabled to plants to store reserves that were important to survive during the dry season of the following year. Second, it is possible that in rainy years factors other than drought become important agents of mortality for regenerative plants. Biotic damages caused by herbivores and pathogens have been shown to be important sources of mortality for seedlings and small plants in TDF during the rainy season (Janzen 1981; Filip *et al*. 1995; Coley & Barone 1996; Khurana & Singh 2001; Cuevas-Reyes, Quesada & Oyama 2006). Thus, after two consecutive rainy years the strength of these mortality agents could intensify. We do not believe that light limitation *per se* was a major source of mortality in rainy years because although light availability in the understory was strongly reduced over the first twelve years of succession (Magaña 2005, Maza-Villalobos, Balvanera & Martínez-Ramos 2011) mortality was independent of successional category in all studied years. Whether biotic damages or soil nutrient limitation were the major mortality agents in the rainy season of rainy years should be further investigated.

GROWTH

Our results support the prediction that growth rate is higher in the rainy season than in the dry season but not the expectation that growth rate peaks in rainier years. Plant growth was substantially reduced during the year having the maximum rainfall. A plausible explanation for this unexpected result is that growth rate in a given rainy season depends on the photosynthetic products gathered during previous years (Kumar & Toky 1994; Poorter *et al*. 2010). Thus, it is possible that the growth reduction observed in the rainy season of 2006 resulted from a massive shortage of stored reserves caused by the severe drought produced by the ENSO event in the previous year. Conversely, the high growth rates observed in 2004 and 2007 could result from the occurrence of previous rainy years (Fig. 1), which enabled the plants to store reserves. These patterns were independent of growth form (shrubs or trees) and plant regeneration strategy (seedlings or sprouts), which suggests the existence of a general plant functional response to temporal changes in rainfall. Also, because the growth rates we measured were independent of successional category, we believe that light availability in the understorey during the rainy season, or other factors associated with successional age (e.g. herbaceous cover, biomass of woody plants), were not as important as water availability for plant growth.

SPECIES GAIN AND LOSS RATES

The prediction that species gain rate ought to peak in the rainy season and during rainier years was only partially supported by our results. This rate, both for shrubs and trees, behaved in a complex way; it was much higher in the rainy season than in the dry season, peaked in the driest year, and was low during the two rainy years that followed the ENSO event. The fact that these fluctuations resemble a mixture of those observed for the community-wide recruitment and growth rates (Figs 2a and 3a), strongly suggests that the gain of species during a given rainy season is also greatly affected by the rainfall of past years. We believe that the reduction in the species gain rate after the ENSO year indicates that several shrub and tree species fail to produce seeds or sprouts as a consequence of having exhausted their reserves after a severe drought year. It is interesting to note that the species gain rate for seedlings, recorded in the rainy season two years after the ENSO year, was lower than that for sprouts. This difference suggests that for several species the consequences of a severe drought for reproductive processes affecting seedling production (e.g. flowering, pollination, fruiting, seed germination) are more drastic compared to processes affecting sprouting. In addition, it is possible that high rates of seed and seedling predation reduced species gain rate during the rainy season of rainier years, although we did not directly measure this in our study.

Regarding the species loss rate, our results do not support the expectation that this rate ought to peak in the dry season and during drier years. Overall, this rate was higher during the rainy season, and peaked in a rainy year, which suggests that factors other than drought were involved in the loss of species from our regenerative communities. As discussed previously for the mortality rate patterns, such factors can be of a biotic nature, including seed predation, herbivory, pathogenic diseases, and plant-plant interactions, which often intensify during the rainy season. However, the species loss rate was also high in the dry season, especially in the ENSO year (Fig. 3), which may indicate the importance of drought for species loss.

EFFECTS OF THE TEMPORAL VARIATION IN RAINFALL ON SUCCESSIONAL TRAJECTORIES

While the temporal variation in rainfall had strong effects on the dynamics of the studied regenerating communities, successional category did not show important effects over such dynamics. This indicates that site factors related to fallow age played a minor role with respect to the effects caused by global (ENSO) and regional climatic factors. The net effect of the temporal variation in rainfall on the dynamics of the studied regenerative communities resulted in a negative or stable temporal trajectories in plant and species density over the four-year study period. Such finding highlights that severe drought episodes, like those caused by ENSO, may delay the recovery process of the TDF in abandoned agriculture fields.

An increasing number of studies have pointed out the importance of ENSO events in tropical forests ecology. It has been documented ENSO effects on growth trajectories of pioneer trees in secondary TDF (Brienen *et al*. 2010) and on tree demography (e.g. Condit, Hubbell & Foster 1995; Martínez-Ramos, Anten & Ackerly 2009), reproductive behaviour of trees (e.g.

Curran *et al*. 1999; Wright & Calderón 2006), forest dynamics (e.g. Feeley *et al*. 2011), biomass dynamics and carbon balance (e.g. Philips *et al*. 1998; Rolim *et al*. 2005), and successional dynamics (e.g. Chazdon, Redondo & Vilchez 2005) in other tropical forest biomes.

Conclusion

Successional dynamics of TDF regenerating communities was strongly affected by temporal variability in rainfall. In general, recruitment, growth, and species gain peaked in the rainy season, while mortality peaked in the dry season and, unexpectedly, species loss rate peaked in the rainy season. These overall patterns, however, were driven by the occurrence of a severe drought during the ENSO event of 2005. Our study shows that global factors like ENSO can play a paramount role, controlling the tempo of TDF regeneration in abandoned fields. Under scenarios of global climate change, which predict an increase in the frequency and severity of drought causing phenomena, such as ENSO, long-term studies are urgently needed to understand the impact of global climate change on the successional process of secondary forests in tropical areas. This is particularly relevant as the conservation of biodiversity and ecosystem functions and services will depend on the resilience of tropical forests to withstand the disturbances caused by agriculture and global climate change.

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Fig. 1. Long-term inter-annual and seasonal variation of rainfall in the study area of La Huerta, Western Mexico. Inset is shown annual rainfall records from1978 to 2007; grey bars correspond to rainfall values during the four years of present study. The arrows point the ENSO years: 1982 (585.2 mm), 1986 (545.6 mm), 1991 (611 mm), 1997 (679 mm), 2001 (392 mm), and 2005 (384 mm). In the larger graph is shown monthly rainfall variation from 2003 to 2007. Note the strong drought episode caused by El Niño Southern Oscillation event occurred in 2005, which produced the drier year in the last three decades before 2007.

Fig. 2. Seasonal variation of recruitment, mortality, and growth rates of regenerating communities over the secondary succession of a tropical dry forest in abandoned pastures in Western Mexico. Each graph shows mean monthly (± 1 S.E, n = 3) community rates in the dry (open bars) and rainy season (black bars) over three year-periods, at four successional categories: P = Pasture (pastures with 0-1 of abandonment in 2004), E = Early (pastures with 3-5 years of abandonment), I = Intermediate (pastures with 10-12 years of abandonment), and OGF = Old-Growth Forest. Graphs in the left column correspond to recruitment rates, graphs in the middle column correspond to mortality rates, and graphs in the right column to growth rates for the whole community (a, f, k), trees (b, g, l), shrubs (c, h, m), seedlings (d, i, n), and sprouts (e, j, o), respectively. Note the different scale of the y-axis in the different graphs.

Fig. 3. Seasonal variation of species gain and loss rates of regenerating communities (seedlings and sprouts) of shrubs and trees over the secondary succession of the tropical dry forest in abandoned cattle pastures in Western Mexico. Each graph shows mean monthly (± 1 S.E, n = 3) community rates in the dry (open bars) and rainy season (black bars) over three studied year-

periods, at four successional categories (as described in Fig. 3). Graphs in the left column correspond to species gain rates; graphs in the right column correspond to species loss rates for the whole community (a, d), for trees (b, e), and for shrubs (c, f). Note different scale of the y-axis in different graphs.

Fig. 4. Temporal changes in plant density (left column) and species density (right column) of regenerative communities (plants 10-100 cm) at four TDF successional categories in Western Mexico. Temporal changes are shown for the whole community (a, f), trees (b, g), shrubs (c, h), seedlings (d), and sprouts (e). Different colour-grey dots represent a successional category: white, Pasture (pastures with 0-1 of abandonment in 2004); light grey, Early (pastures with 3-5 years of abandonment); dark grey, Intermediate (pastures with 10-12 years of abandonment); black, Old-Growth Forest. Each dot represents mean values (± 1 S.E, n = 3).

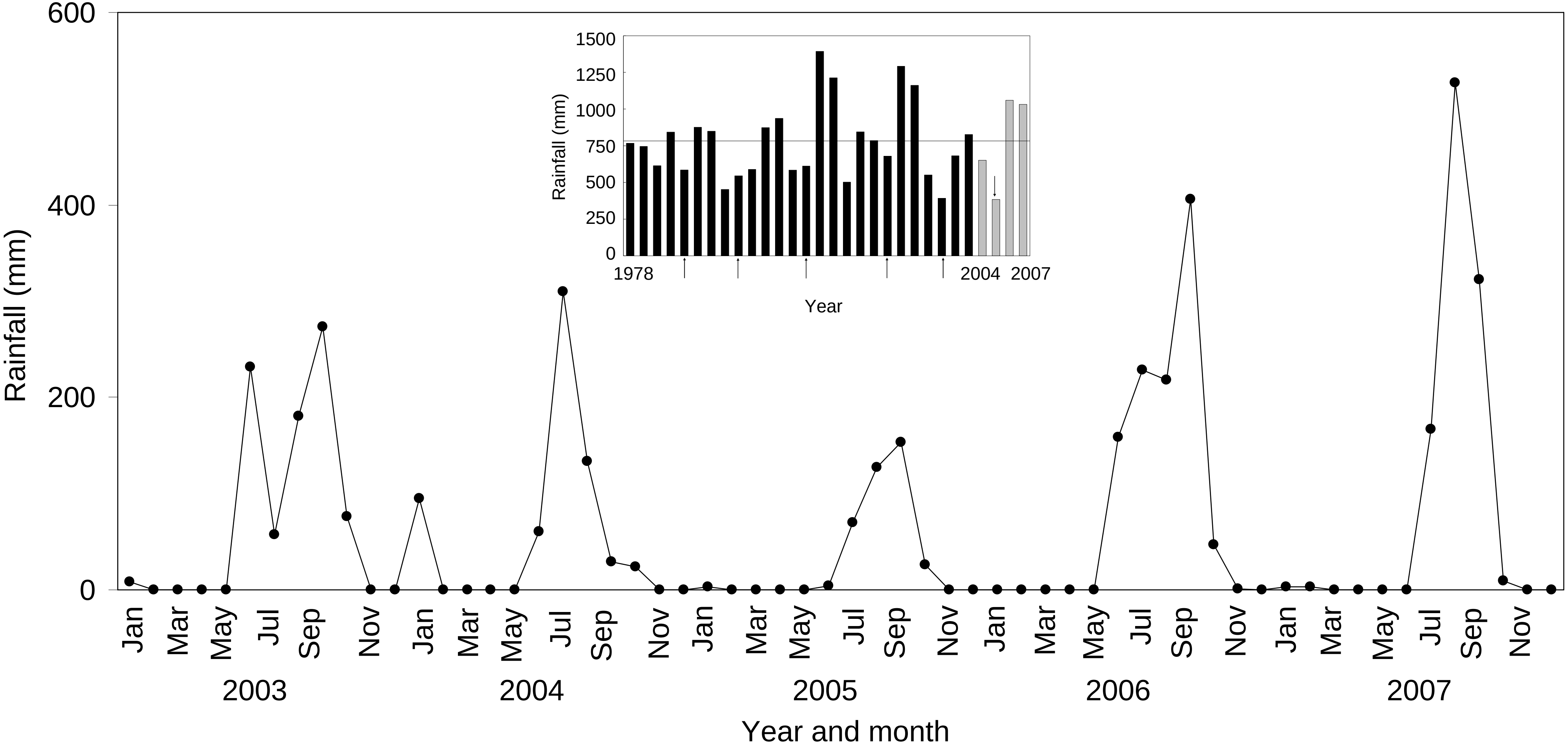
Rainfall (mm)
600
400
200
0
Jan
Mar
May
Jul
Sep
Nov
2003
2004
2005
2006
2007
Year and month
Rainfall (mm)
1500
1250
1000
750
500
250
0
1978
2004
2007
Year

Fig. 1

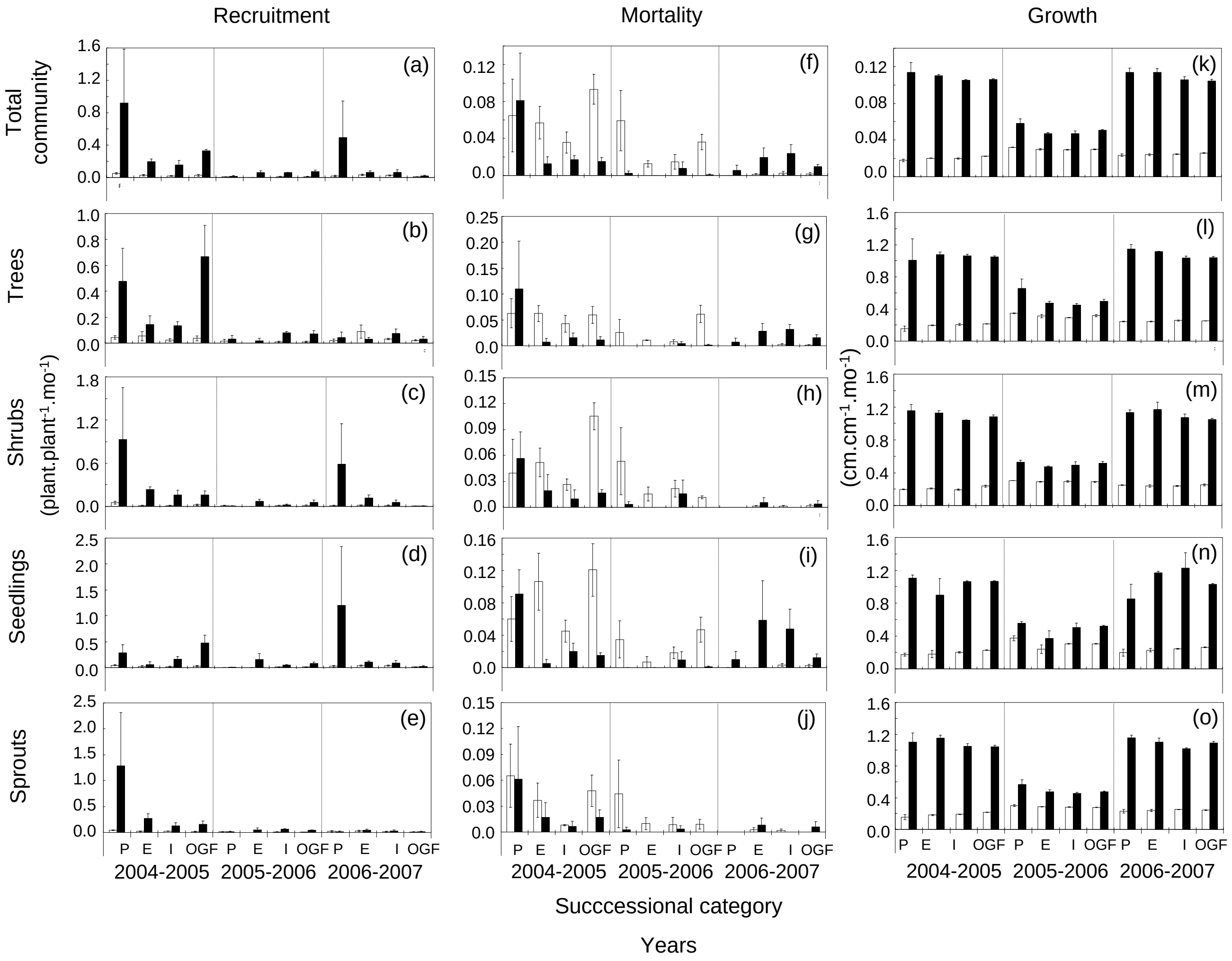
Recruitment
Mortality
Growth
Total community
Trees
Shrubs
Seedlings
Sprouts
(plant.plant-1.mo-1)
(cm.cm-1.mo-1)
(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
(i)
(j)
(k)
(l)
(m)
(n)
(o)
P
E
I
OGF
2004-2005
2005-2006
2006-2007
Succcessional category
Years

Fig. 2

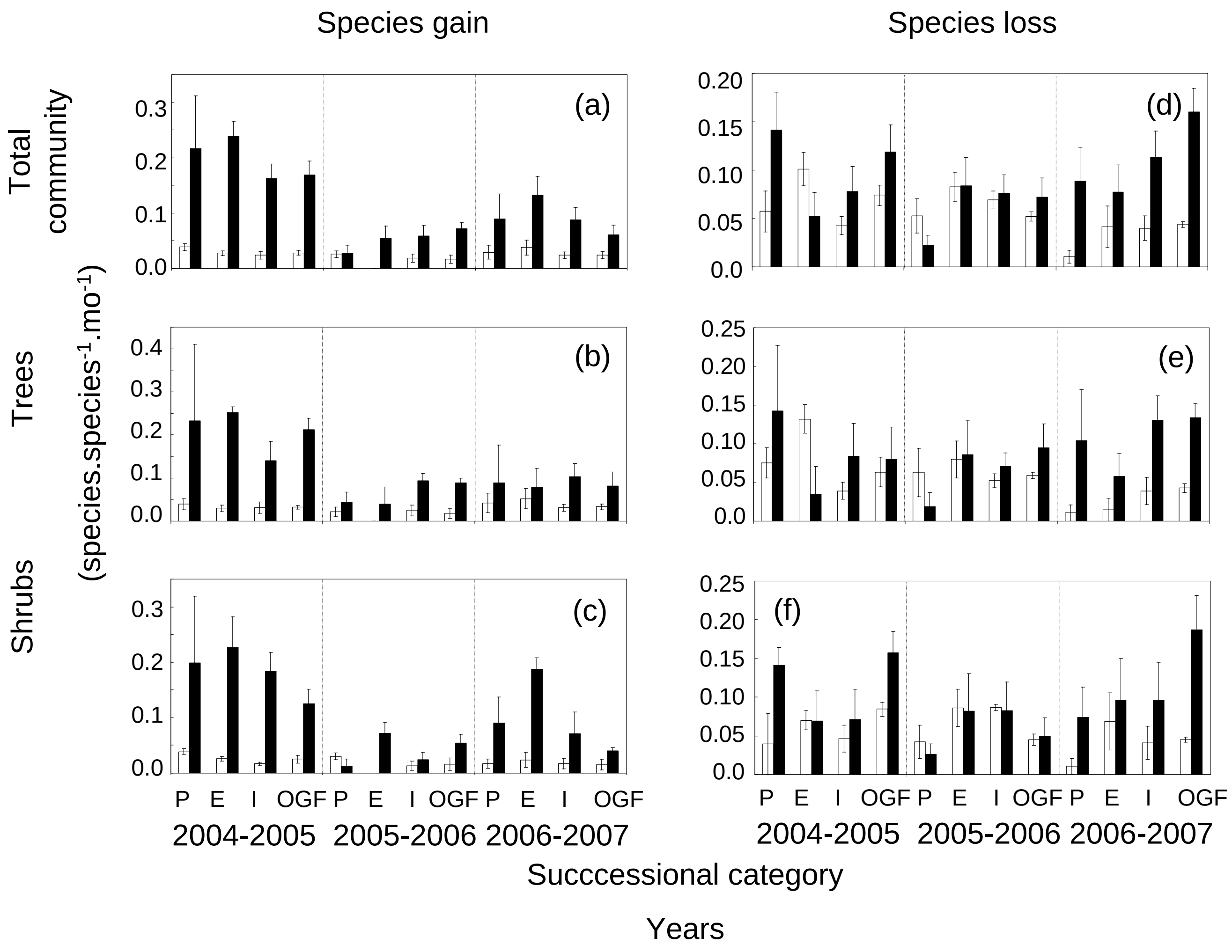
Species gain
Species loss
Total community
Trees
Shrubs
(species.species-1.mo-1)
(a)
(b)
(c)
(d)
(e)
(f)
0.0
0.1
0.2
0.3
0.4
0.05
0.10
0.15
0.20
0.25
P
E
I
OGF
2004-2005
2005-2006
2006-2007
Succcessional category
Years

Fig. 3

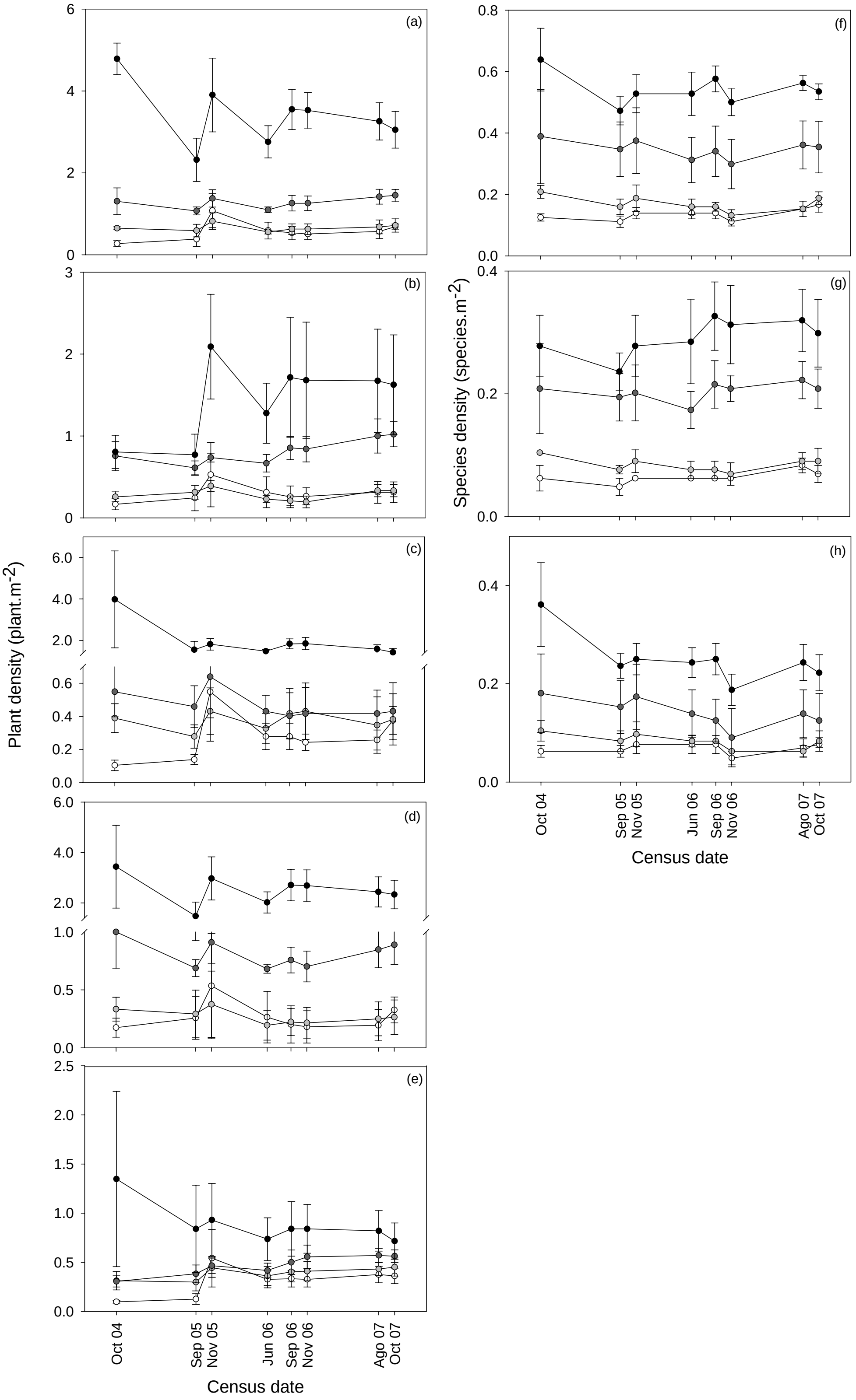
(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
Plant density (plant.m^{-2})
Species density (species.m^{-2})
Census date
Census date
Oct 04
Sep 05
Nov 05
Jun 06
Sep 06
Nov 06
Ago 07
Oct 07
0
2
4
6
1
3
0.0
0.2
0.4
0.6
2.0
4.0
6.0
0.5
1.0
1.5
2.0
2.5
0.8

Fig. 4

CAPÍTULO V

DISCUSIÓN GENERAL Y CONCLUSIONES

En este último capítulo se retoman los resultados más sobresalientes de la presente investigación doctoral. Los resultados se discuten en el contexto del nuevo conocimiento generado con los tres estudios realizados, en torno a los patrones, los procesos y los mecanismos involucrados en la regeneración natural y la sucesión secundaria del bosque tropical caducifolio. También se resaltan diferencias entre los procesos sucesionales que ocurren en estos bosques con respecto a aquellos del bosque tropical húmedo.

En los pastizales ganaderos abandonados las características ambientales difieren por mucho de aquellas que prevalecen en el bosque original (Capítulo 2, Lebrija-Trejos *et al.* 2010b). La historia de uso del suelo, la vegetación circundante, los remanentes de vegetación, los atributos físico-químicos del suelo y la topografía del terreno, entre otras variables, determinan las características ambientales existentes en los campos recién abandonados y, por ende, el curso de los procesos de la regeneración natural y de la sucesión secundaria (Capítulo 1, Figura 2). Además, es posible que el desarrollo de la vegetación secundaria esté afectado por la interacción entre las variables ambientales intrínsecas a los campos abandonados y las variables climatológicas (Ravindranath y Sukumar 1998, Dale *et al*. 2001). Esto podría ser particularmente crítico a medida que cambian los regímenes climáticos regionales y locales, como resultado del cambio climático global (Nakagawa *et al*. 2000, Sen 2009). Tal interacción es esperable particularmente en ecosistemas fuertemente estacionales, en los que el agua de la lluvia resulta un recurso clave para el desarrollo de las comunidades vegetales y los procesos del ecosistema (Jaramillo *et al*. 2011).

PATRONES SUCESIONALES

Atributos estructurales.- El presente estudio partió de la predicción de que las condiciones ambientales (*e.g*. radiación solar, temperatura), la disponibilidad de recursos (*e.g.* cantidad de agua en el suelo) y las fuentes de propágulos *(e.g.* relacionadas con la densidad de arbustos y de árboles adultos) cambian con la edad sucesional, favoreciendo un aumento en la abundancia, en la cantidad de especies y en la biomasa de las comunidades regenerativas con el incremento de la edad. Considerando los patrones de la cronosecuencia obtenidos del estudio del banco de semillas (Capítulo II) y del estudio de las comunidades de plantas (Capítulo III), esta predicción se cumplió. Efectivamente, los atributos estructurales analizados (densidad de semillas, densidad de plantas, densidad de especies y cobertura) aumentaron de manera asintótica hacia los valores del bosque maduro con la edad sucesional (Fig. 2, Capítulo II, Fig. 1, Capítulo III). Estas trayectorias sucesionales concuerdan con muchos de los patrones de sucesión secundaria de una gran variedad de ecosistemas terrestres; la mayoría obtenidos con el uso de cronosecuencias (Johnson y Miyanishi 2008, Chazdon *et al*. 2007, Lebrija-Trejos *et al.* 2010a).

Sin embargo, las trayectorias obtenidas de la cronosecuencia para las comunidades regenerativas (Capítulo II), difirieron de aquellas generadas, en otros estudios, para comunidades de arbustos y de árboles grandes (tallos con dap ≥ 1 cm). Para estas últimas comunidades, se ha encontrado que después de 12-20 años de sucesión del bosque tropical caducifolio, en campos agropecuarios abandonados, los valores de densidad de tallos, densidad de especies y de área basal son muy parecidos (mayor al 90%) a aquellos del bosque maduro (Lebrija-Trejos *et al.* 2010a, Chazdon *et al*. 2011). En contraste, en las comunidades de plántulas y de rebrotes estudiados, los valores de la densidad de plantas y de especies alcanzaron menos del 60% de los valores del bosque maduro. Tal discrepancia puede reflejar el hecho de que en las comunidades de plántulas y de rebrotes operan tasas mayores de mortalidad y de crecimiento que en las comunidades de plantas adultas, convirtiéndolas en comunidades más dinámicas en términos estructurales (*i.e.* densidad de tallos, densidad de especies y biomasa).

Por un lado las comunidades regenerativas de plántulas y de pequeños rebrotes son más susceptibles a las condiciones ambientales adversas (*e.g.* altos niveles de radiación solar), la limitación de recursos (*e.g.* disponibilidad de agua en el suelo) y las interacciones bióticas negativas (*e.g.* herbivoría) relacionadas con fuertes sequías, que en conjunto representan fuertes filtros ambientales para el establecimiento y la permanencia de las plantas (Harper 1977). Por otro lado, si bien las plántulas y los rebrotes pueden presentar mayores tasas de crecimiento que las plantas adultas, también se ha observado que las plántulas y los rebrotes pueden prescindir de buena parte de sus tallos como respuesta a la sequía o por efecto de herbívoros en dicha estación (Observaciones personales). Así, es razonable pensar que una vez que las plantas pequeñas aumentan en tamaño la probabilidad de supervivencia aumenta, volviéndose más estables estructuralmente; de esta manera se incrementa la acumulación de plantas, de especies y de biomasa en la comunidad sucesional (Capítulo III).

Considerando los resultados de la cronosecuencia obtenidos en la presente tesis y aquellos publicados por otros autores (Murphy y Lugo 1986, Rico-Gray y García-Franco 1992, Lebrija-Trejos *et al*. 2008), se puede proponer que el bosque tropical caducifolio posee una recuperación sucesional rápida en los campos agropecuarios abandonados. Estos resultados apoyan la teoría que propone que los bosques tropicales caducifolios experimentan tasas de regeneración y de sucesión más rápidas que las de los bosques tropicales húmedos, lo cual se atribuye a la menor complejidad estructural y menor riqueza de especies de los bosques tropicales caducifolios (Ewel 1977, Ewel 1980, Murphy y Lugo 1986). Sin embargo, la mayoría de estos resultados, incluyendo este trabajo, provienen de áreas en donde las actividades agropecuarias realizadas se basan en técnicas tradicionales de uso del suelo de bajo impacto (*e.g*. barbecho, sin uso de agroquímicos y/o maquinaria pesada) y en las que existen aún grandes superficies cubiertas con remanentes de bosque maduro o con bosque secundario en edad intermedia y avanzada de desarrollo (Capítulo II y III). Debería evaluarse cómo se modifican las trayectorias sucesionales en áreas donde las actividades agropecuarias son más intensivas y donde la cobertura forestal nativa remanente es muy reducida.

Las trayectorias sucesionales predichas por la cronosecuencia empleada en esta tesis no fueron sustentadas por la dinámica observada en las comunidades regenerativas a través de los cuatro años de estudio. En lugar de observarse un aumento asintótico de los atributos estructurales con la edad sucesional, se observó una disminución de la densidad de especies y de la cobertura foliar con el tiempo, y un cambio casi nulo en términos de la densidad de plantas (Figura 3, Capítulo III). La falta de concordancia entre lo predicho por la cronosecuencia y lo observado en la dinámica de la vegetación, también se ha documentado parcialmente, en algunos atributos, para comunidades sucesionales de árboles y arbustos grandes de otros bosques tropicales caducifolios (Lebrija-Trejos *et al.* 2008; sin embargo ver Lebrija-Trejos *et al*. 2010b) y húmedos (van Breugel *et al*. 2006, Chazdon *et al*. 2007).

Considerando que la edad de abandono, no necesariamente, es la variable más importante para predecir el comportamiento temporal de las comunidades sucesionales (Johnson y Miyanishi 2008), en el Capítulo III se evaluaron otras variables del ambiente que se proponen como determinantes del proceso sucesional. De los factores analizados, la densidad de tallos ≥ 1cm dap, la apertura del dosel y la cobertura forestal de la matriz circundante, el último factor fue el único que mostró un efecto positivo en la tasa de reclutamiento de plantas (R^2= 0.91) y de ganancia de especies en la comunidad de plantas (R^2= 0.84).

Composición de especies.- Las comunidades de semillas encontradas en los pastizales ganaderos, con 0-12 años de abandono, fueron muy diferentes en la composición de especies a las encontradas en el bosque maduro (Capítulo II). Mientras que el banco de semillas de los pastizales recién abandonados (< 1 año) estuvo dominado por especies de plantas herbáceas, el banco de semillas de los sitios de bosque maduro estuvo dominado por especies de árboles y de arbustos, tal y como se ha reportado en otros bosques tropicales caducifolios (Rico-Gray y García-Franco 1992, Miller 1999b). En los sitios con 10-12 años de abandono la composición de especies del banco de semillas, aunque estuvo dominada por especies de arbustos y de árboles, fue aún muy diferente de la encontrada en el bosque maduro. Estos resultados concuerdan con otros estudios sucesionales, de zonas tropicales húmedas o estacionalmente secas, que indican que la recuperación de atributos estructurales es más rápida que la recuperación de la composición de especies (Chazdon *et al*. 2007, Lebrija-Trejos *et al*. 2008).

Los resultados del estudio del banco de semillas (Capítulo II) no sustentaron la teoría de la composición florística inicial (Egler 1954). Esta teoría establece que después de la colonización inicial de un grupo florístico amplio, las especies alcanzan picos de abundancia y persisten o desaparecen durante el proceso de sucesión, en función de sus atributos de su historia de vida (por ejemplo, longevidad) o de su tolerancia a la variación de recursos y de condiciones. Los resultados obtenidos muestran que al inicio de la sucesión, el banco de semillas se compone de un número contado de especies y ninguna de estas especies fue encontrada a través de toda la cronosecuencia. Por el contrario las especies mostraron una distribución segregada en la cronosecuencia, formando grupos de especies que se reemplazaron a través de la secuencia sucesional, tal y como lo predice la teoría de Connell y Slatyer (1977) cuando opera un mecanismo de sucesión por facilitación (ver más adelante; Capítulo II). Este patrón de grupos de especies que se reemplazan a través del proceso sucesional, ha sido observado en las comunidades de árboles y de arbustos adultos en el bosque tropical caducifolio de Nizanda, Oaxaca (Lebrija-Trejos *et al.* 2010a), así como en la comunidad regenerativa de árboles, arbustos y bejucos (10-100 cm de altura) de nuestra zona de estudio (Magaña-Rodríguez 2005).

Formas de crecimiento.- En el banco de semillas se observó un recambio de diferentes formas de crecimiento (plantas herbáceas, arbustivas, arbóreas y trepadoras) a través de la cronosecuencia (Capítulo II). Las especies caracterizadas por ciclos cortos de vida, tasas altas de crecimiento y de reproducción, con estrategias de historia de vida tipo *r* (*e.g.* herbáceas terrestres, trepadoras herbáceas) dominaron el banco de semillas en los pastizales recién abandonados (representando más del 97% del total de semillas y más del 80% de las especies). Dentro de estas especies se encuentran: *Cleome viscosa* L., *Desmodium procumbens* (Mill.) Hitchhc, var. *longipes* (Schindl.) Schubert., *Kallstroemia maxima* (L.) Hook. & Arn., *Panicum* sp. 2., *Hyptis suaveolens* (L.) Poit., y *Mimosa quadrivalvis* L. Este grupo fue reemplazado paulatinamente, durante los primeros 12 años de sucesión, por otro grupo de especies de ciclos de vida largos, tasas bajas de crecimiento y de reproducción y con estrategias de historia de vida tipo *k* (en su mayoría árboles y arbustos; *e.g*. *Cordia elaeagnoides* DC., *Croton suberosus* H.B.K. y *Piptadenia constricta* (Pers.) J.F. Macbr.). En el bosque maduro, las plantas herbáceas representaron menos del 20% de la densidad total de las semillas y de las especies (Figuras 3 y 4, cap. II). Estos resultados concuerdan con las generalidades propuestas en varias teorias sobre sucesión (Gómez-Pompa y Vázquez-Yanes 1981, Huston y Smith 1987), que indican la existencia de un proceso de reemplazamiento de especies a lo largo del tiempo en el desarrollo de una comunidad.

La disminución en la abundancia de semillas y en el número de especies de las plantas herbáceas en el banco de semillas a través de la sucesión, puede ser indicativa de una reducción de las poblaciones de plantas herbáceas heliófilas y al decaimiento de la actividad reproductiva de las plantas herbáceas a medida que avanza la sucesión. Tal reducción pudo ser causada por el fuerte descenso de recursos lumínicos en el sotobosque, a medida que avanzó el proceso sucesional y se desarrolló el dosel del bosque secundario. Al aumentar la complejidad del bosque (por ejemplo, en su índice de área foliar), aumenta la intercepción de luz en las partes altas del dosel durante la época de lluvias y con ello disminuye la luz a nivel del suelo (Capítulo III; Barradas 1991, Parker *et al*. 2005, Lebrija-Trejos *et al*. 2011). Además, las condiciones ambientales resultantes del establecimiento temprano de las especies pioneras herbáceas pudieron favorecer el desarrollo de las especies de árboles y de arbustos, quienes fueron aumentando su representación y reemplazando a las herbáceas en el banco de semillas. También el establecimiento de *Mimosa arenosa* (Willd.) Poir., especie pionera, pudo desempeñar esta función de facilitación (Capítulo II,); sin embargo, estas ideas deberían abordarse en otros estudios para su comprobación (ver discusión más adelante).

FACTORES Y MECANISMOS INFLUYENTES EN LA DINÁMICA REGENERATIVA

El estudio de la sucesión a nivel del banco de semillas (Capítulo II) permitió explorar los mecanismos de tolerancia, inhibición y facilitación, propuestos por Connell y Slatyer (1977), que explican el reemplazo de especies a través de la sucesión. Aun cuando la presencia de semillas de especies herbáceas fue importante en los bosques maduros, no se registró especie alguna (herbácea, arbustiva o arbórea) que estuviese presente en el banco de semillas a través de toda la cronosecuencia. Este patrón no apoya a la tolerancia como mecanismo sucesional para las comunidades regenerativas estudiadas. Según la teoría, el mecanismo de tolerancia opera cuando un grupo de especies colonizan simultáneamente un sitio abierto y, con el paso del tiempo, las especies persistentes son aquellas que tienen mayor longevidad o que son tolerantes a condiciones cada vez más limitadas en recursos (Connell y Slatyer 1977). Tampoco se encontró la dominancia total de una sola especie en un determinado estado sucesional, lo que hubiese apoyado la presencia del mecanismo de inhibición (Connell y Slatyer 1977). Por lo tanto, se postuló (Capítulo II) que el mecanismo sucesional que determinó el reemplazamiento de especies en las comunidades regenerativas estudiadas fue el de facilitación. La facilitación opera cuando la colonización de especies pioneras modifica las condiciones ambientales y la disponibilidad de recursos, facilitando el establecimiento de otras especies. Esta sustitución de especies se repite con el tiempo, lo que resulta en una serie de reemplazos de grupos de especies con diferentes requerimientos ambientales a través del proceso sucesional. Sin embargo, es necesario realizar estudios a mayor plazo que permitan evaluar si la facilitación da lugar a procesos de inhibición.

Además de los factores ambientales y los mecanismos intrínsecos al sitio en sucesión, el aumento del número de especies y de diversidad de formas de crecimiento con el avance sucesional (Capítulos II y III), pudo responder a factores que se encontraron en la matriz circundante al campo en sucesión. Entre estos factores se pueden señalar la disponibilidad de agentes bióticos de dispersión de semillas y la extensión de bosques remanentes (en los que se encuentra un acervo potencial de semillas que pueden ingresar por dispersión al campo en sucesión). Además, en el mismo sistema de estudio empleado en esta tesis, se ha documentado que la actividad de los murciélagos y las aves dispersoras de semillas aumenta con la edad sucesional, sobre todo después de los primeros cinco años de abandono (Ávila-Cabadilla *et al*. 2009, J. Shondube, comentarios personales). En concordancia, también se encontró que la tasa de reclutamiento de plántulas aumentó con la cantidad de la matriz forestal circundante a los pastizales abandonados (Figura 4, Capítulo III).

Algunas investigaciones han señalado que las especies arbustivas y arbóreas del género *Mimosa* detienen el desarrollo sucesional del bosque tropical caducifolio en campos agropecuarios abandonados del occidente de México (Ortíz-Ávila 2001, Burgos y Maass 2004). Sin embargo, existen algunas evidencias que contradicen este punto de vista. Primero, en los sitios estudiados en Chamela, en el banco de semillas de los sitios con más de cinco años de abandono no se encontraron semillas, plántulas o rebrotes de *M. arenosa* (Capítulo II; Magaña-Rodríguez 2005). Segundo, se ha documentado que la longevidad de las especies del género *Mimosa* en los bosques secundarios es corta (< 30 años, Brienen *et al*. 2009). Tercero, se ha observado que bajo la cobertura de las plantas del género *Mimosa* en los bosques secundarios se desarrolla una comunidad regenerativa diversa de otras especies leñosas (Romero-Duque *et al*. 2007, Lebrija-Trejos *et al*. 2008). Cuarto, existe una regeneración pobre o nula de especies del género *Mimosa* en bosques secundarios con más de 30 años de abandono (Lebrija-Trejos *et al*. 2008).

Por el contrario, es posible que las especies de este género funcionen como especies facilitadoras en el proceso sucesional del bosque tropical caducifolio. Esto debido a que diferentes especies del género *Mimosa* tienen alta tolerancia a los sitios abiertos (*i.e.*con temperaturas elevadas del suelo y tasas altas de evaporación), en los que alcanzan tasas altas de germinación y de crecimiento (Camargo-Ricalde *et al*. 2004). La presencia de estas especies pueden propiciar el establecimiento de especies con menor tolerancia a condiciones hídricas estresantes (*i.e*. especies de etapas sucesionales más avanzadas; Lebrija-Trejos *et al*. 2008). El presente trabajo de investigación no evaluó la comunidad regenerativa establecida bajo del dosel de *Mimosa arenosa*. Sin embargo, Lebrija-Trejos *et al.* (2008) han reportado a *Amphypteringium adstringens* Schiede ex Schlech., *Apoplanesia paniculata* Presl., *Euphorbia schlechtendalii* Boiss., *Lysiloma divaricatum* (Jacq.) J. F. Macbr. y *Senna atomaria* (L.) Irwin & Barneby., como parte de las especies establecidas bajo el dosel de *Mimosa tenuiflora* (Willd.) Poir. X., y *M. acantholoba* var., *eurycarpa* (Willd.) Poir. var. *eurycarpa* (B.L. Rob.) Barneby, en un bosque tropical caducifolio en la región del Itsmo de Tehuantepec, Oaxaca.

En el sistema sucesional de bosque tropical caducifolio fue posible identificar tres grupos de especies, caracterizados por su nivel de tolerancia a condiciones hídricas estresantes. Estos grupos pueden ser análogos a los que se presentan en los bosques tropicales húmedos (Denslow 1987). Los grupos identificados son: i) especies muy tolerantes; presentes sobre todo al inicio de la sucesión (*e.g. M. arenosa*, *Mimosa acantholoba* (Willd.) Poir., *Piptadenia flava* (Spreng. Ex DC.) Benth.), ii) especies de tolerancia intermedia, distribuidas a casi todo lo largo de la sucesión (*e.g. Coccoloba liebmanii* Lindau, *Jacquinia pungens* A. Gray., *Zapoteca formosa* (Willd.) H. Hern.), y ii) especies no tolerantes, presentes solamente en estados sucesionales más avanzados (*e.g. Spondias purpurea* L., *Apoplanesia paniculata* Presl., *Jacaratia mexicana* A. DC.).

Las especies muy tolerantes, aquí reportadas, se registraron como semillas (*M. arenosa),* plántulas (*P. flava* y *M. arenosa*) y rebrotes (*M. arenosa* y *M. acantholoba*). Estas especies poseen frutos dehiscentes, por lo que es probable que las plántulas se hayan originado a partir de semillas producidas *in situ*. En los mismos sitios donde las semillas, las plántulas y los rebrotes fueron registrados, se observaron plantas adultas, lo cual puede confirmar el origen de las plántulas y la formación de rebrotes. Propágulos de alguna de estas especies también han sido reportadas en otros sitios sucesionales jóvenes de bosques tropical caducifolio (Miller y Kauffman 1998, Romero-Duque *et al*. 2007, Brienen *et al*. 2009).

De estos tres grupos, con diferente tolerancia al estrés hídrico, solamente los dos grupos extremos han sido identificados en las comunidades de arbustos y de árboles adultos en otros bosques tropicales caducifolios (Lyaruu *et al*. 2000, Lemenih y Teketay 2006, Lebrija-Trejos 2009). Lo anterior confirma que la comunidad regenerativa (semillas, plántulas y rebrotes) tiene que pasar fuertes filtros ambientales, como los altos niveles de radiación y de evaporación en la mayor parte del año (*i.e*. estación de sequía y días secos dentro de la estación de lluvias), la baja disponibilidad de agua en el suelo y los efectos de la herbivoría y la depredación, para establecerse en la comunidad adulta de estos sistemas.

Solo la cobertura forestal presente en la matriz circundante, entre todas las variables independientes analizadas, influyó sobre la dinámica de las comunidades regenerativas estudiadas. La tasa de reclutamiento de plantas y la tasa de ganancia de especies aumentó al incrementarse esta cobertura (Fig. 4, cap. III); más allá de esta relación, la dinámica de las comunidades regenerativas mostró un comportamiento particular a las características y a la historia propia del sitio (Fig.3, cap. IV). Muy probablemente, tal comportamiento estuvo asociado a factores que no fueron analizados explícitamente en la presente investigación doctoral, tales como las características del paisaje, las condiciones ambientales locales al momento de abandono y la historia del uso del suelo. Estas variables, como ya se ha discutido con anterioridad, no están implícitas en la edad de abandono.

Se ha propuesto, en el contexto de la teoría sucesional de los bosques tropicales caducifolios, que la reproducción asexual es el mecanismo reproductivo más importante, debido a la resistencia ante condiciones adversas y su dependencia de recursos (Vesk y Westoby 2004). De las 132 especies de árboles y de arbustos (entre 10 y 100 cm de altura) registradas en este estudio, 46% se originó exclusivamente a partir de semilla, es decir tres veces más que las especies que se reprodujeron exclusivamente a través de rebrote (15.2%) y 38.6% se reprodujo tanto por semilla como por rebrote. Si bien la contribución de rebrotes no superó a la contribución de plántulas, en términos de densidad de plantas (Figura 3, Capítulo IV), y las tasas de reclutamiento y de crecimiento fueron similares a las de las plántulas, la tasa de mortalidad de los rebrotes fue menor que la de las plántulas, como se ha reportado en otros estudios (McLaren y McDonald 2003; Figura 4, Capítulo IV). Estos resultados confirman la idea de que la producción de rebrotes juega un papel clave en la regeneración natural como un mecanismo de mantenimiento de los bosques tropicales caducifolios (Vieira *et al.* 2006, Lévesque *et al.* 2011). Por otro lado, la baja cantidad de especies regeneradas exclusivamente a través de rebrotes y la falta de evidencia de composición florística inicial (Egler 1954), permiten sostener que en este sistema el proceso de sucesión no es de autosucesión. Si bien, las especies presentes al inicio de la sucesión fueron registradas como plántulas y como rebrotes provenientes de las fuentes locales (*i.e.* dentro del sitio), las especies posteriores, de sitios maduros, es muy probable que hayan llegado de fuentes externas al sitio (no todas las especies se encontraron como adultos dentro del sitio de estudio). Además, la mayoría de las plantas a lo largo de la sucesión, pero sobre todo en sitios sucesionalmente avanzados, se regeneraron a través de semillas y no por rebrotes.

EFECTO DE FACTORES CLIMATOLÓGICOS SOBRE LA DINÁMICA SUCESIONAL

La variación temporal de la lluvia (Capítulo IV) se identificó como el factor explicativo preponderante del comportamiento dinámico de las comunidades regenerativas estudiadas. Durante el periodo de cuatro años de estudio, en el año de 2005 (383.8 mm anual), se presentó el evento de EL Niño más severo en las últimas décadas y el año más seco de los 30 años previos en la región. Antes y después de este evento se presentaron años lluviosos, especialmente en 2006 (1059.4 mm anual) y 2007 (1032.1 mm anual), años en los que la precipitación anual superó por mucho el valor promedio anual (1978-2008; 788 mm) de largo plazo. Las variaciones interanuales e interestacionales de la lluvia tuvieron un impacto fundamental en las tasas de mortalidad, de crecimiento y de reclutamiento de plantas y en las tasas de ganancia y de pérdida de especies a lo largo de la cronosecuencia, independientemente de la edad sucesional. El evento de El Niño tuvo en consecuencia general un retardo en la dinámica de recuperación y sucesión de las comunidades regenerativas. Los resultados obtenidos muestran que factores climáticos globales (como El Niño), que actúan independientes de la edad sucesional, juegan un papel crítico en la dirección de la sucesión secundaria del bosque tropical caducifolio (Capítulo IV).

La regeneración y la sucesión de una comunidad dependen de las condiciones físico-químicas, de la disponibilidad de recursos, de la naturaleza e intensidad de las interacciones bióticas, de la disponibilidad de propágulos y del desempeño de las especies en los sitios perturbados (Figuras 1 y 2). Varios de estos componentes fueron afectados por la variación temporal de la lluvia. Así, en el Capítulo IV se discutió que la disponibilidad de propágulos está vinculada con eventos de lluvia de años pasados. Se propuso que la producción de propágulos (semillas y rebrotes) depende del almacenamiento de productos de la fotosíntesis, en la forma de energía, y de agua que se acumulan por uno o más periodos de crecimiento. De esta manera, un año con lluvia abundante y regularmente distribuida durante el periodo de lluvias, muy posiblemente permitirá en el futuro una producción abundante de semillas y de rebrotes, mientras que un año con lluvias escasas conducirá en el futuro a una producción baja o nula de propágulos (pero ver Soriano *et al.* 2011). Esto explica porqué, en general, los años que fueron precedidos por años lluviosos tuvieron mayor tasa de reclutamiento de plántulas y de rebrotes mientras que en los dos años que siguieron al fuerte evento de sequía, provocado por El Niño, tal tasa fue cercana a cero, independientemente de la edad sucesional. (Figura 4A)

De una forma parecida a la anterior, la tasa de crecimiento en altura, que fue máxima en la estación de lluvias, tuvo una reducción importante un año después del evento de El Niño y tuvo valores máximos en los veranos que fueron precedidos por años lluviosos, independientemente de la edad sucesional ((Figura 4C; Capítulo IV). Este patrón sugiere que el crecimiento también puede depender del nivel y tipo de productos fotosintéticos y de agua almacenados en años previos, en nuestro caso del 2003 (826.21 mm anual). Por último, la tasa de mortalidad de plántulas y de rebrotes, que alcanzó generalmente máximos en las épocas de sequía (Figura 4B), varió directamente con la cantidad de lluvia caída en cada año. En el año de El Niño la mortalidad fue máxima y en los años lluviosos de 2006 y 2007 la mortalidad fue mínima. De hecho, en el año de 2007, la mortalidad máxima no ocurrió en la época de sequía sino en la de lluvia. Como se

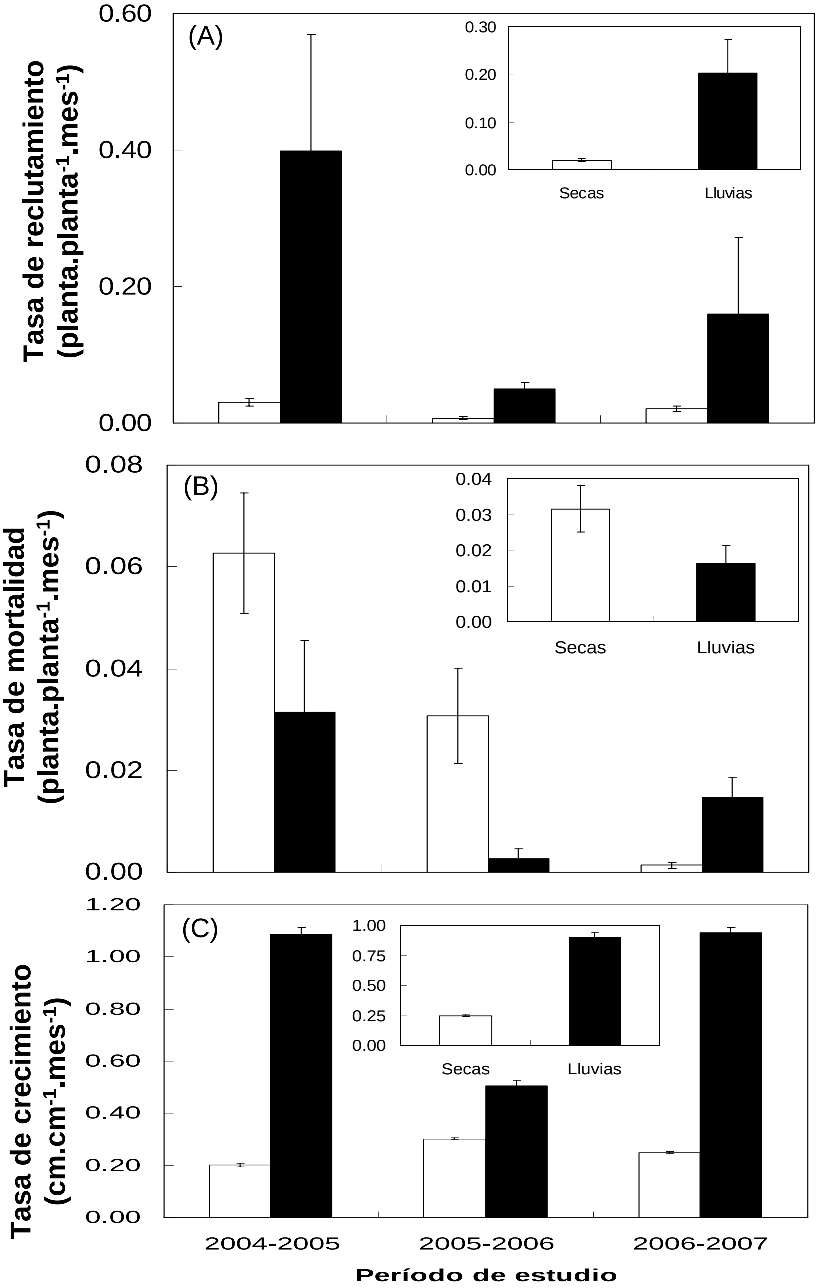

Figura 4. Tasas vitales de desarrollo de la comunidad regenerativa total (plántulas y rebrotes) de árboles y arbustos en los diferentes años de estudio durante la época de secas (barras blancas) y la época de lluvias (barras negras). Las gráficas internas, representan el comportamiento general de la tasa vital durante la época de secas y de lluvias. En todos los casos se consideraron los doce sitios de estudio; las barras indican el promedio ± 1 error estándar.

discutió en el Capítulo IV, este resultado sugiere, por un lado, que cuando ocurre un año con disponibilidad de lluvia alta, las plantas pueden almacenar agua y recursos que les ayudan a sobrevivir durante la siguiente estación de sequía. Por el otro lado, sugiere que en un año lluvioso, durante la estación de lluvias, operan otros factores de mortalidad, muy probablemente relacionados con enemigos naturales en la forma de herbívoros, patógenos, parásitos y /o interferencia planta-planta (Capítulo IV). Otra posible causa de la mortalidad alta en años lluviosos, puede estar relacionada con el tipo de suelo en donde se desarrolla la comunidad; por ejemplo, suelos con poca filtración pueden provocar anegación (E. Ceccon, comentarios personales). Sin embargo, este no fue nuestro caso, los suelos en donde se desarrollaron las comunidades estudiadas presentaron buenos niveles de filtración (Trilleras-Motha 2008). Estos aspectos aún se encuentran abiertos a futuras investigaciones.

Un aporte original de esta tesis es la demostración de que la variación interanual e interestacional de la lluvia juega un papel crucial en la dinámica de las comunidades regenerativas, durante la sucesión secundaria del bosque tropical caducifolio en los pastizales ganaderos abandonados. La incidencia del fenómeno de El Niño produjo oscilaciones transitorias en las trayectorias temporales de la densidad de plantas y la densidad de especies de las comunidades regenerativas, que fueron amortiguadas por los años lluviosos que siguieron a este evento (Figura 4, Capítulo IV). La sequía severa ocasionada por El Niño, tuvo como resultado global el que estas variables estructurales quedaran sin cambio o que disminuyesen al final de un periodo de cuatro años. Bajo el contexto del cambio climático global, es posible que los procesos de regeneración y de sucesión de bosques secundarios, en regiones tropicales estacionalmente secas, se vean modificados de manera importante por el aumento en la frecuencia y la intensidad de sequías y lluvias extremas. Dada esta situación, es necesario realizar más estudios que aborden de manera puntual los efectos del cambio climático en comunidades secundarias y maduras de los bosques tropicales caducifolios.

CONCLUSIONES

Los resultados de esta tesis muestran que la dinámica de la sucesión secundaria de comunidades regenerativas del bosque tropical caducifolio, desarrollada en pastizales ganaderos abandonados, no puede ser predicha a través del uso único de cronosecuencias. La gran variación temporal en la disponibilidad de agua de lluvia, junto con las características ambientales intrínsecas de los campos abandonados, determinaron que las comunidades regenerativas siguiesen trayectorias temporales diferentes a aquellas predichas por la cronosecuencia.

La dinámica sucesional de las comunidades regenerativas, en sistemas agropecuarios abandonados y de bosque maduro del bosque tropical caducifolio está fuertemente determinada por la variabilidad temporal de la precipitación. Bajos niveles de precipitación afectan negativamente el proceso regenerativo de estas comunidades; además, el efecto de la precipitación parece tener vigencia no sólo en ese momento, sino también un año después.

Bajo sistemas caracterizados por fuertes sequías y alta variabilidad en la precipitación, es la facilitación el mecanismo que permite el desarrollo sucesional de las comunidades regenerativas. A través de este mecanismo, se producen las condiciones necesarias para el establecimiento y éxito de especies poco tolerantes al estrés hídrico. Sin embargo, son necesarios estudios de mayor tiempo que permitan evaluar si además de la facilitación existe algún tipo de inhibición en fases de desarrollo más avanzadas (*i.e.* juveniles y adultos).

En un escenario de incremento de bosques secundarios, de origen agropecuario, y de cambios globales climáticos, son necesarios estudios de largo plazo que nos permitan entender el impacto que estos factores tienen sobre el proceso regenerativo y sucesional de estos sistemas en bosques tropicales caducifolios.

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