



UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO
POSGRADO EN CIENCIAS BIOLÓGICAS
FACULTAD DE CIENCIAS

**ANATOMÍA DEL XILEMA DE ESPECIES SUCESIONALES EN UN BOSQUE TROPICAL
CADUCIFOLIO: UN ENFOQUE ECOLÓGICO**

TESIS

QUE PARA OPTAR POR EL GRADO DE:

DOCTORA EN CIENCIAS

PRESENTA:

ISABEL EUNICE ROMERO PÉREZ

TUTOR PRINCIPAL DE TESIS: Dr. Jorge Arturo Meave del Castillo
FACULTAD DE CIENCIAS, UNAM

COMITÉ TUTOR: Dra. Teresa Margarita Terrazas Salgado
INSTITUTO DE BIOLOGIA, UNAM

Dr. Horacio Armando Paz Hernández
INSTITUTO DE INVESTIGACIONES EN ECOSISTEMAS Y SUSTENTABILIDAD, UNAM

CD. MX., ENERO, 2021.



Universidad Nacional
Autónoma de México



UNAM – Dirección General de Bibliotecas
Tesis Digitales
Restricciones de uso

DERECHOS RESERVADOS ©
PROHIBIDA SU REPRODUCCIÓN TOTAL O PARCIAL

Todo el material contenido en esta tesis esta protegido por la Ley Federal del Derecho de Autor (LFDA) de los Estados Unidos Mexicanos (México).

El uso de imágenes, fragmentos de videos, y demás material que sea objeto de protección de los derechos de autor, será exclusivamente para fines educativos e informativos y deberá citar la fuente donde la obtuvo mencionando el autor o autores. Cualquier uso distinto como el lucro, reproducción, edición o modificación, será perseguido y sancionado por el respectivo titular de los Derechos de Autor.



UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO
POSGRADO EN CIENCIAS BIOLÓGICAS
FACULTAD DE CIENCIAS

**ANATOMÍA DEL XILEMA DE ESPECIES SUCESIONALES EN UN BOSQUE TROPICAL
CADUCIFOLIO: UN ENFOQUE ECOLÓGICO**

TESIS

QUE PARA OPTAR POR EL GRADO DE:

DOCTORA EN CIENCIAS

PRESENTA:

ISABEL EUNICE ROMERO PÉREZ

TUTOR PRINCIPAL DE TESIS: Dr. Jorge Arturo Meave del Castillo
FACULTAD DE CIENCIAS, UNAM

COMITÉ TUTOR: Dra. Teresa Margarita Terrazas Salgado
INSTITUTO DE BIOLOGIA, UNAM

Dr. Horacio Armando Paz Hernández
INSTITUTO DE INVESTIGACIONES EN ECOSISTEMAS Y SUSTENTABILIDAD, UNAM

MÉXICO, CD. MX., 2021.

COORDINACIÓN DEL POSGRADO EN CIENCIAS BIOLÓGICAS
FACULTAD DE CIENCIAS
DIVISIÓN ACADÉMICA DE INVESTIGACIÓN Y POSGRADO
OFICIO FCIE/DAIP/476/2020
ASUNTO: Oficio de Jurado

M. en C. Ivonne Ramírez Wence
Directora General de Administración Escolar, UNAM
P r e s e n t e

Me permito informar a usted que en la reunión ordinaria del Subcomité de Biología Evolutiva, Ecología, Manejo Integral de Ecosistemas y Sistemática del Posgrado en Ciencias Biológicas, celebrada el día **23 de marzo de 2020** se aprobó el siguiente jurado para el examen de grado de **DOCTORA EN CIENCIAS** de la estudiante **ROMERO PÉREZ ISABEL EUNICE** con número de cuenta **302630707** con la tesis titulada: **“Anatomía del xilema de especies sucesionales en un bosque tropical caducifolio: un enfoque ecológico”**, realizada bajo la dirección del **DR. JORGE ARTURO MEAVE DEL CASTILLO**:

Presidente:	DRA. ANGELINA MARTÍNEZ YRÍZAR
Vocal:	DR. PEDRO GUILLERMO ÁNGELES ÁLVAREZ
Secretario:	DRA. TERESA MARGARITA TERRAZAS SALGADO
Suplente:	DR. MARCELO RODRIGO PACE
Suplente:	DRA. SILVIA AGUILAR RODRÍGUEZ

Sin otro particular, me es grato enviarle un cordial saludo.

A T E N T A M E N T E
“POR MI RAZA HABLARÁ EL ESPÍRITU”
Cd. Universitaria, Cd. Mx., a 03 de diciembre de 2020

COORDINADOR DEL PROGRAMA



DR. ADOLFO GERARDO NAVARRO SIGÜENZA



COORDINACIÓN DEL POSGRADO EN CIENCIAS BIOLÓGICAS

Unidad de Posgrado, Edificio D, 1º Piso. Circuito de Posgrados, Ciudad Universitaria
Alcaldía Coyoacán. C. P. 04510 CDMX Tel. (+5255)5623 7002 <http://pbiol.posgrado.unam.mx/>

AGRADECIMIENTOS INSTITUCIONALES

Agradezco al Posgrado en Ciencias Biológicas, UNAM.

Agradezco los siguientes apoyos económicos recibidos:

Del Consejo Nacional de Ciencia y Tecnología (CONACyT) la beca No. 270104 para realizar mis estudios de doctorado.

Del Programa de Apoyo a la Investigación e Innovación Tecnológica (PAPIIT – UNAM), a través de los proyectos IN218416 y IN217620 otorgados a Jorge A. Meave del Castillo, el financiamiento para llevar a cabo el trabajo de campo y de laboratorio, así como la beca para la obtención de grado.

Del Programa de apoyo a los estudios de Posgrado (PAEP) dos becas para presentar los resultados de mi investigación en dos congresos internacionales.

Del programa “Scholarships of the Ministry of Education, Youth and Sports in support of Foreign Nationals' Study at Public Institutions of Higher Education in Czech Republic” la beca para una estancia de investigación en la Universidad de Mendel.

Agradezco a mi Tutor Principal Dr. Jorge Meave y a los miembros del Comité Tutor: Dra. Teresa Terrazas y Dr. Horacio Paz.

AGRADECIMIENTOS A TÍTULO PERSONAL

Agradezco al Dr. Jorge Meave por ser parte fundamental en mi formación académica desde hace poco más de una década, por estar siempre al pendiente de absolutamente todos los asuntos logísticos durante mi formación académica y por brindarme apoyo académico y personal.

Agradezco a los miembros del jurado, Dra. Angelina Martínez-Yrizar, Dr. Guillermo Ángeles, Dra. Silvia Aguilar, Dr. Marcelo Pace y Dra. Teresa Terrazas, quienes aceptaron gustosamente revisar esta tesis y la enriquecieron enormemente.

Agradezco al Biol. y Técnico Académico Marco Antonio Romero Romero, a la Dra. Mariana Hernández Apolinar, al Dr. Pedro Eloy Mendoza y a la Dra. Alicia Rojas por el soporte técnico brindado para la elaboración de esta tesis.

Agradezco a Armando Rodríguez y a Rocío González por su amabilidad, paciencia y apoyo con mis trámites.

Agradezco al Dr. Edgar Javier González Liceaga quien contribuyó a hacer posible esta tesis a través de los análisis estadísticos de los Capítulos 2, 3 y 6.

Agradezco al Dr. Frans Bongers y al Dr. Eduardo Pérez García por su contribución al Capítulo 2 de esta tesis y por su apoyo académico y personal.

Agradezco al Dr. Carlos Martorell, a la Dra. Clara Tinoco, al Dr. Fernando Pineda, al Dr. Francisco Mora y a la Dra. Teresa Terrazas por aceptar formar parte del comité evaluador de mi candidatura.

I am grateful to Dr. Vladimír Gryc, Dr. Kyriaki Giagli, Dr. Hanuš Vavrčík, Dr. Jan Tippner, Dr. Tomáš Kolář and Dr. Peter Radermacher, from the Department of Wood Science and Wood Technology, for their support during my research stay at Mendel University.

I thank Dr. Pieter Baas for the ideas that inspired the Chapter 6 variability analyses of this thesis.

AGRADECIMIENTOS A TÍTULO PERSONAL

Gracias a la Vida, por brindarme la oportunidad de coincidir con personas maravillosas. Esta tesis es el resultado de la interacción académica y personal con ustedes.

Teresa Terrazas: Gracias por haberme presentado el interesante y hermoso mundo de la anatomía de la madera, el cual ahora me apasiona enormemente. Gracias por brindarme su tiempo, apoyo y enseñanzas. Gracias por haberme aceptado en su grupo de trabajo y brindarme conocimientos, espacios y herramientas para desarrollar esta tesis. Gracias por enviarme constantemente a las musas de la inspiración. Gracias por compartir conmigo viajes, aventuras y el asombro de observar y descubrir cosas en el campo y en el laboratorio. Gracias por estar siempre al pendiente, por revisar cada texto, por motivarme y guiarme con sabiduría y paciencia. Gracias por la convivencia y por ser parte de historias sobre un árbol misterioso y una chamarra inteligente. Algún día Ale y Maty leerán esto y comprenderán que también les agradezco a ellos: porque la cartita de Ale me ha acompañado y motivado durante horas de trabajo en la computadora, y las ocurrencias de Maty me han dado alegría e inspiración.

Edgar: Gracias por tu paciencia y por presentarme el mundo de R y de los GLMMs de la forma más amena, paciente, agradable y digerible posible. Disfruté mucho cada reunión de trabajo contigo. Gracias a ti he aprendido la belleza de las Matemáticas aplicadas a la Biología. Gracias por tu amistad.

Consuelo Bonfil, Saddhajoti e Irene Pisanty: Gracias por su apoyo y por adoptarme en su laboratorio y en sus hogares. Airene gracias por presentarme el maravilloso mundo de la Ecología.

Mariana Hernández, Bruno Barrales, Jaime Zúñiga e Irene Sánchez: Gracias por brindarme su apoyo y comprensión, así como conocimientos, espacios y herramientas para la elaboración de esta tesis.

Alice: Gracias por tu constante apoyo en el laboratorio. Gracias por enseñarme con infinita paciencia, dedicación y cuidado, desde técnicas anatómicas, hasta la ubicación de objetos e instrumental del laboratorio que utilicé para elaborar esta tesis. Gracias por intentar ser un microscopio viviente para orientar los cortes anatómicos de *Jacaratia*. Gracias los momentos divertidísimos, por ser testigo y apoyo durante los despistes absolutos. Gracias por escucharme, por tus sabias palabras y por tu amistad.

Marcelo: Gracias por tu inmenso apoyo académico y personal. Gracias por escucharme, animarme, aconsejarme, considerarme, motivarme e impulsarme. Gracias por enseñarme la técnica para por fin lograr ver los cortes de *Jacaratia*. Gracias por tu amistad.

Irma Trejo: Gracias por brindarme un espacio para elaborar esta tesis. Gracias por tu apoyo constante, por tantos momentos divertidos, gracias por tu amistad.

Vero, Edgar y Nancy: Gracias por la convivencia y su amistad, por darme ánimos y apoyarme constantemente. Gracias por llevarme al lado oscuro y fabuloso de la estadística y del uso de R. Vero: gracias por tu compañía durante el doctorado. Nancy gracias por tantos momentos divertidos, por tu apoyo constante, tus palabras, y gracias por confiar repetida y ciegamente en mí.

Lalo: Gracias por tu apoyo constante, por tolerar e inclusive alimentar la creatividad de cierto porcentaje de la población y por compartir el hermoso e inspirador mundo de las orquídeas.

Marco Romero: Gracias por tu infinita paciencia y por el constante apoyo tanto académico como personal, llueve, truene o relampaguee.

AGRADECIMIENTOS A TÍTULO PERSONAL

Hanuš: Děkuji mnohokrát, for your all your support and kindness, I enjoyed a lot your stories and the lessons of how to not be a datel during cambium sampling. Thank you Vladimír, Kyra, Anna, Ginevra, Jiří, Radím, Jan and Eva (algún día espero terminar de escuchar la historia), for your kindness and support.

Georg von Arx, Alan Crivellaro, Marco Carrer and Angela Prendin: Thank you for such a nice and interesting quantitative wood anatomy course. Georg also thank you for my first snowball. Giacomo: Thank you for your support.

Pacho: gracias por ayudarme a recolectar *Acacia* y por revisar con detalle mi proyecto de investigación.

Julieta Rosell y Mark Olson: Gracias por su apoyo personal y académico. Mark además quisiera expresar mi enorme agradecimiento por regalarme un libro muy especial y crucial para mi formación académica.

Marco Virgilio y Rey David: Gracias por su amistad y los agradables y divertidos viajes de campo. Rey David gracias por ayudarme a ubicar y recolectar plantas, gracias por encontrar el hobbo entre una maraña de Mimosas espinosas, por compartir historias y lugares muy especiales y por los momentos divertidos en campo que compartimos con Moi y con ¡Úrsula Úrsula Úrsula!

Daniel, Alejandro, Marysol, Arantza, Maribel y Rubí (Plant Anatomy Rules!): Gracias por su apoyo y por su amistad. Dany gracias por tantos momentos divertidos, por la convivencia a la hora de la comida, por compartir conmigo tu asombro por la Biología y la Anatomía vegetal. Ale Alegrías gracias por proveerme de alimentos durante la elaboración de esta tesis y por tu apoyo técnico y personal constante. Marysol gracias por cada momento divertido y por enseñarme la importancia de vestir elegantemente para el campo. Arantza gracias por tu apoyo y compañía durante horas de mediciones en el analizador.

Irenka: Gracias por tu disposición a ayudarme con el trámite de la candidatura. Gracias por tu amistad y tu apoyo. Gracias por tantas y tantas pláticas y por tu paciencia. Gracias por compartir historias.

Silvia Salas: Gracias por tu amistad, por tu apoyo constante en mi vida personal y académica. Gracias por compartir café, vivencias y tu hermosísimo rancho.

Nihaib y Erick: Gracias por compartir su espacio y su zona de estudio, y gracias por su amistad.

Marce, Betito, Le Moi y Kouat: Gracias por su amistad, compañía y apoyo.

Gerardo Heavy: Gracias por hacer ameno y divertido el trabajo en el lab y en el campo. Gracias por compartir quesadillas, estrellas, nieve derretida y tus fabulosas historias.

Montu, Mary, ¡Albeeert!, Biaanni, Meli, Nidis, Darinka, Ceci, Angie y Lilí: Gracias por su amistad, su cariño y su apoyo constante. Gracias por tantísimos momentos geniales y divertidos.

Chucho: Gracias por tu amistad, por guiarme y apoyarme justo en los momentos de mi vida que más lo he necesitado. Gracias OoOo gran Marco y Flor.

Mónica: Gracias por tu amistad, el café, la chamba, el control de calidad, las pláticas y el apoyo constante.

Míra y Ondra: Děkujeme. Quizá mañana celebremos este logro académico obtenido.

Ale, Adri, Sandra: Gracias por su amistad y su apoyo. Gracias Rashid por ayudarme a organizar conceptos durante mi candidatura y gracias a Lñaki por prestarnos su pizarrón.

AGRADECIMIENTOS A TÍTULO PERSONAL

Mamá: Como expreso en la dedicatoria de esta tesis, las palabras no me son suficientes para agradecerte todo. Infinitas gracias por ser mi mamá Bióloga y por ser parte del equipo Lulú-Eu.

Papá: Gracias por estar y por tu amor incondicional. Gracias por tus enseñanzas y consejos que han mejorado mi vida inmensamente. Gracias por escucharme y alegrarme bajo cualquier circunstancia.

Madrina Carmen y Padrino Poncho: Gracias por ser mis Padrinos en todo el sentido de la palabra, desde siempre en mi vida. Las palabras no me alcanzan para agradecerles todo.

Tía Isa: Gracias por tu cariño, apoyo, compañía y comprensión. Gracias por tantos momentos divertidos y por acompañarme con tu presencia y con hermosas y especiales artesanías elaboradas por ti.

Gaby: Gracias por tu amistad constante, gracias por apoyarme, acompañarme y ayudarme a seguir adelante. Gracias a ti y a tu familia que me han abierto las puertas de sus corazones y de su hogar.

Bety, Rocío, Marianita: Gracias por su amistad, por su apoyo constante, gracias por los momentos divertidos, por compartir vivencias. Gracias por siempre estar ahí.

Tanis: Gracias por tu apoyo incondicional y por los momentos pampalinescos. Estimada Lic. en Biopolitología Edurne: Gracias por ser un gran nodo y por recibirme incondicionalmente en tu hogar. Gracias a ambas por escucharme, por tantas risas, por su cariño, por su amistad, por las conversaciones de voz y de percusión. Gracias por alegrar e iluminar mi vida.

Alí, Georgina y Rodrigo, mis hermanitos académicos: Gracias por su amistad. Amiguísima: 🥰 Gracias por ser la Lamparita que alumbra nuestros caminos, por las risas y los pasteles biológico-matemáticos. Mi muy estimado Rodko: infinitas gracias por todo, por tu apoyo personal y académico, conocerte dio un giro muy especial a mi vida. Geo: Gracias por tu apoyo, por compartir caminos y avanzar como equipo.

Gracias Clau y Dino por recibirme en su hogar, por apoyarme, y gracias Clau por tus deliciosas comidas. Gracias Bau y Bety por su amistad. Gracias Lito (Bau), Bryan, Aldo y Adrián. Gracias a ustedes Nizanda tiene un lugar especial en mi vida y en mi corazón.

A mi mamá,

Te dedico esta tesis con mucho cariño,

como una forma de agradecerte lo que las palabras no alcanzan a expresar.

Gracias por tu infinito amor.

A mi abuelito,

También te dedico esta tesis por haberme motivado, cuando era niña, a estudiar y concluir una carrera profesional a cambio de poner sobre aquella mesa larga tus preciados libros y regalarme los que yo eligiera. Apá Benjamín tu intención y tu cariño se quedaron en mi mente y en mi corazón. Sé que me acompañas a cada paso de mi camino y que de cierta forma viste concluidos mis logros.

ÍNDICE

Resumen.....	1
Abstract.....	3
Capítulo 1. Introducción general	5
Capítulo 2. Differential performance of 50 canopy tree species along tropical dry forest succession.....	18
Capítulo 3. Wood anatomy of dominant species with contrasting ecological performance in tropical dry forest succession.....	47
Capítulo 4. Wood density, deposits and mineral inclusions of successional tropical dry forest species.....	60
Capítulo 5. Wood anatomy of 13 species from a tropical dry forest secondary vegetation.....	73
Capítulo 6. Wood anatomical spectrum of early and late-successional tropical dry forest communities.....	118
Capítulo 7. Discusión general y conclusiones.....	138
Referencias	149
Anexos.....	157
Anexos Capítulo 2.....	158
Anexos Capítulo 5.....	178
Anexos Capítulo 6.....	183

RESUMEN

Las especies presentes en la vegetación secundaria (especies sucesionales) derivada del bosque tropical caducifolio (BTC) enfrentan escasez de agua durante una estación seca prolongada y distintos filtros ambientales asociados al gradiente sucesional, y presentan diferentes respuestas fenológicas. El xilema secundario del tallo de las plantas contiene diversas posibilidades de atributos funcionales relacionados con la hidráulica, el soporte mecánico y el almacenamiento de recursos. El estudio partió de la premisa de que el análisis de las características del xilema secundario del tallo de las especies sucesionales puede contribuir a dilucidar la relación entre el ambiente, las funciones del tallo y su desempeño ecológico. El estudio se realizó en la región de Nizanda, Oaxaca, México, donde existen importantes áreas de vegetación secundaria con distintas edades de abandono. La primera fase del estudio consistió en analizar el desempeño ecológico de 50 especies leñosas presentes en la vegetación secundaria mediante la construcción de modelos lineales generalizados mixtos (GLMMs), con la edad sucesional como variable explicativa (intervalo de 2 a 70 años de abandono). Estos modelos integran dos variables de desempeño ecológico: la presencia y el área basal, siendo esta última un indicador de la acumulación de biomasa en el tallo. A continuación, para los análisis del xilema secundario, se eligieron 13 especies (tres exclusivas de la vegetación secundaria y 10 que crecen tanto la vegetación secundaria como en el bosque maduro). A través de la producción y observación de cortes del xilema secundario, se describieron las características anatómicas del tallo de especies que coexisten en las comunidades sucesionales tempranas (< 5 años de abandono) y tardías (> 50 años de abandono); se construyeron GLMMs para estimar y comparar las medias de los rasgos anatómicos entre especies, así como su variación intraespecífica. Asimismo, se evaluó la densidad de madera y se describieron los contenidos celulares y las inclusiones minerales. Las especies sucesionales mostraron una amplia diversidad de patrones de acumulación de área basal con respecto a la edad sucesional, de valores de densidad de la madera y de características anatómicas del xilema secundario, que en conjunto sugieren multifuncionalidad. Como las especies estudiadas crecen en un ambiente estacionalmente seco, se esperaba que presentaran características relacionadas con la respuesta a los cambios estacionales en la precipitación. Inesperadamente, los límites de las marcas de crecimiento son comúnmente inconspicuos. Sin embargo, todas las especies estudiadas presentaron células de parénquima que rodean los elementos conductores de agua, las cuales usualmente se asocian con la resistencia a la sequía. En congruencia con lo encontrado en otras especies tropicales, la mayoría de las especies estudiadas presentaron porosidad difusa y las marcas de crecimiento estuvieron dadas por diversas características anatómicas. La especie temprana dominante *Mimosa eurycarpa* y la especie dominante tardía *Lysiloma divaricatum* fueron las únicas que presentaron porosidad anular. Los bajos índices de vulnerabilidad en la madera tardía de ambas especies sugieren una resistencia alta al estrés hídrico. Las especies sucesionales presentaron

densidades de madera desde 0.10 g/cm^3 (*Jacaratia mexicana*) hasta 0.92 g/cm^3 (*Lysiloma divaricatum*) y mostraron una baja variabilidad intraespecífica a pesar de las diferencias conspicuas en las condiciones ambientales entre las comunidades tempranas y tardías. Las especies con alto contenido de agua en la madera se restringieron a las comunidades tardías. La densidad de madera de las dos especies de Cactaceae no difirió significativamente de la densidad de madera de especies de árboles paquicaules como *Bursera simaruba* y *Cnidoscolus megacanthus*. Los compuestos fenólicos y los cristales fueron comunes en la mayoría de las especies; algunas presentaron gomas. Las especies estudiadas (excepto *Jacaratia mexicana*), presentaron almidón abundante almacenado en el parénquima, lo cual podría representar una fuente de carbono para la producción de biomasa. Se encontró que el parénquima axial y el radial pueden ser desde escasos hasta abundantes. El componente principal del xilema secundario puede estar conformado por fibras vivas septadas, no septadas, gelatinosas (siendo estas últimas apreciablemente abundantes en algunas especies), una mezcla de las anteriores, o incluso puede no presentar fibras (*Jacaratia mexicana*). El parénquima radial, junto con las fibras septadas, podría tener un papel importante en el almacenamiento de agua del tallo en estas especies. Aparentemente sólo las dos especies de Cactaceae y la especie de Caricaceae carecen de una propiedad de redundancia hidráulica, ya que en ellas predominan los vasos solitarios; en el resto de las especies los grupos de más de 10 vasos son comunes. Los intervalos registrados para la media de los diámetros de vasos, el número de vasos por mm^2 , el grosor de fibras y el número de vasos por grupo fueron amplios, y los coeficientes de variación y la desviación estándar de estas variables fueron grandes. Las fibras vivas de paredes delgadas podrían representar una disyuntiva entre costos altos en el mantenimiento de biomasa y el almacenamiento de agua. Las especies estudiadas mostraron características anatómicas en el tallo que sugieren diferentes mecanismos de resistencia a la sequía, en congruencia con lo descrito para otras especies sucesionales de BTC, así como diferentes costos de producción de biomasa, la cual aparentemente resulta de diferentes combinaciones anatómicas. Las especies con baja densidad de madera, fibras vivas (las dos cactáceas, *Jacaratia mexicana*, *Bursera simaruba* y la especie de fenología invertida *Bonellia macrocarpa*) podrían constituir un grupo funcional, siendo el almacenamiento de agua en el tallo uno de los mecanismos de evasión de la sequía; por el contrario, las especies con un contenido bajo de agua en la madera y fibras de paredes gruesas con lúmenes reducidos (principalmente leguminosas) podrían ser tolerantes a la sequía (i.e., ser capaces de seguir funcionando con poca agua ambiental). Las características anatómicas altamente variables de los vasos, así como las distintas combinaciones de arreglos y tipos celulares en el xilema secundario del tallo podrían ser clave para entender el desempeño ecológico diferencial de las especies a lo largo del gradiente sucesional.

Palabras clave: Densidad de la madera; estrés hídrico; GLMMs; rebrotes; sucesión temprana y tardía.

ABSTRACT

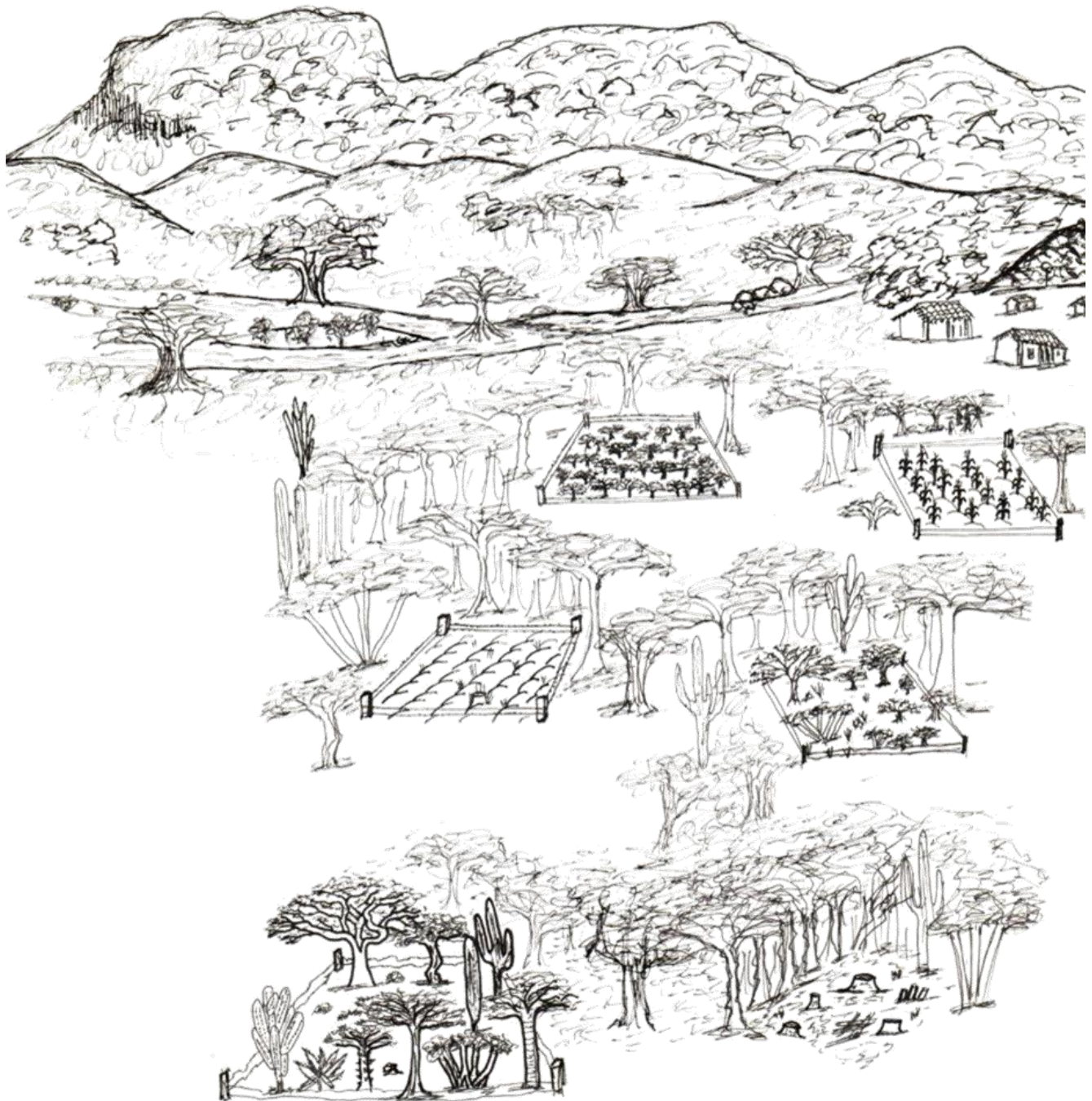
Species occurring in secondary tropical dry forest (successional species; TDF) face water shortage during a well-marked dry season along with gradual changes in environmental filters over the successional gradient, and have different phenological responses. Wood tissue encompasses diverse possibilities of functional traits in terms of stem hydraulics, mechanical support and resource storage. The study departed from the premise that the analysis of the characteristics of the secondary xylem in the stems of successional species may contribute to elucidate the relationship between environment, stem functions and ecological performance. The study was conducted in Nizanda, Oaxaca state, Mexico, where there are numerous patches of secondary vegetation of different ages across the region, derived from agriculture and grazing. In the initial phase of the study, the ecological performance of 50 woody species growing in secondary vegetation was analyzed, by constructing generalized linear mixed models (GLMMs), with successional age as the explanatory variable (range from 2 to 70 years of abandonment); these models integrate two variables of ecological performance: presence and basal area, the latter of which indicates stem biomass accumulation. Next, for secondary xylem analyses, 13 species were chosen (three of which are exclusive of secondary vegetation and 10 that are present both in secondary vegetation and mature forest). Through the production and observation of secondary xylem sections, stem anatomical characteristics of species that coexist in early successional communities (< 5 years of abandonment) and late ones (> 50 years of abandonment) was described. GLMMs were constructed to estimate and compare the mean values of the anatomical features between species, as well as their intraspecific variation. Likewise, wood density was analyzed, and cellular contents as well as mineral inclusions were described. Successional species had highly diverse patterns of basal area accumulation along the successional gradient, along with variable wood density values and anatomical characteristics of secondary xylem, all of which suggests multifunctionality. Since the studied species grow in a seasonally dry environment, I expected that they would exhibit characteristics associated with responses to seasonal changes in precipitation. Unexpectedly, growth marks boundaries were often microscopically inconspicuous; however, all the studied species had parenchyma cells surrounding the vessels, a feature usually related to drought resistance. In consistency with other tropical species, most of my studied species had diffuse porosity and growth marks were given by various anatomical features. The only ring porous species were *Mimosa eurycarpa* (an early dominant species) and *Lysiloma divaricatum* (a late dominant species). Low vulnerability indexes in the latewood of both species suggest high water stress resistance. Wood density of successional species ranged from 0.10 g/cm³ (*Jacaratia mexicana*) to 0.92 g/cm³ (*Lysiloma divaricatum*). Overall, species growing in both early and late communities showed low intraspecific variability, despite in their life cycle, due to anthropogenic activities, and conspicuous differences in environmental conditions. Species with high wood

water content were exclusive of late communities. Wood density did not differ between the two columnar cacti (*Pachycereus pecten-aboriginum* and *Pilosocereus collinsii*) and tree species with high wood water content such as *Bursera simaruba* and *Cnidoscolus megacanthus*. Phenolic compounds and crystals were common in most species; some had gums. All of the studied species (except for *Jacaratia mexicana*) had abundant starch stored in parenchyma cells, which could be a carbon source for biomass production. In the studied species, axial and radial parenchyma was scarce to abundant. The main component of secondary xylem could include living septate fibers, non-septate fibers, gelatinous fibers (which in some species were appreciably abundant), a mixture of these, or it not had fibers at all (*Jacaratia mexicana*). Radial parenchyma, together with septate fibers, could play an important role in stem water storage in these species. Apparently, only the two Cactaceae species and the Caricaceae species lack a hydraulic redundancy property, as solitary vessels predominated in their secondary xylem; in the rest of the species groups of more than 10 vessels were common. The ranges for mean vessel diameters, number of vessels per mm², fiber thickness and number of vessels per group were wide; in general, mean coefficient of variation and mean standard deviation of these variables were large. Thin-walled living fibers could represent a trade-off between high costs in biomass maintenance and water storage. The studied species showed stem anatomical characteristics that suggest different mechanisms of resistance to drought, in consistency with other TDF successional species; these features also suggest different costs of biomass production, apparently consisting of different anatomical combinations. Species with low wood density and the presence of living fibers (the two Cactaceae, *Jacaratia mexicana*, *Bursera simaruba* and the inverted phenology species *Bonellia macrocarpa*) could represent a functional group, with stem water storage being one of the mechanisms of drought evasion; in contrast, species with low wood water content and thick-walled fibers with narrow lumina (mainly legume species) could be drought tolerant (i.e., able to continue functioning despite drought). Highly variable anatomical characteristics of the vessels, together with different combinations of cell arrangements and types in the stem secondary xylem could be key to understand the differential ecological performance of the species observed along the successional gradient.

Keywords: Wood density; water stress; GLMMs; resprouts; early and late succession.

CAPÍTULO 1

Introducción general



CAPÍTULO 1. INTRODUCCIÓN GENERAL

Generalidades de la sucesión secundaria del bosque tropical caducifolio

El bosque tropical caducifolio (BTC), *sensu* Rzedowski (1978), es un tipo de vegetación que se desarrolla en regiones que presentan una marcada estacionalidad en la precipitación, con un periodo de lluvias de alrededor de seis meses (Brown y Lugo 1990). Esta característica confiere una fisonomía particular en la comunidad: la mayoría de las especies sólo tienen hojas durante la época de lluvias y el dosel alcanza alturas de 15 m cuando mucho (Gerhardt *et al.* 1992; Holbrook, 1995; Mooney *et al.* 1995).

En las regiones donde se desarrolla el BTC se llevan a cabo actividades agrícolas y ganaderas que remueven casi en su totalidad la biomasa aérea de la vegetación, por lo que las condiciones ambientales del sitio se modifican drásticamente (Trejo y Dirzo 2000; Lebrija-Trejos *et al.* 2011). El primer paso para establecer una milpa o un pastizal para el ganado es el desmonte del sitio por roza-tumba y quema. Cuando el sitio es abandonado después de un cierto tiempo de uso, inicia la regeneración de la vegetación a través del proceso ecológico de sucesión secundaria (Pickett 1976). A lo largo de esta tesis se define como especie sucesional a cada especie presente en la vegetación secundaria (*i.e.*, la comunidad vegetal que se desarrolla en sitios donde el BTC fue desmontado con fines agrícolas o ganaderos, que posteriormente fueron abandonados); se considera especie sucesional independientemente de si ésta crece normalmente en el bosque maduro, o de si es exclusiva de la vegetación secundaria.

El bosque previo al disturbio antropogénico tiene una estructura comunitaria particular que crea condiciones ambientales en su interior muy distintas en comparación con las que predominan en un sitio deforestado y abandonado. Al remover la cobertura vegetal original, la cantidad de luz y la temperatura del aire se incrementan, lo cual también provoca una disminución en la humedad ambiental y mayores tasas de evapotranspiración; esto, aunado a la marcada época de sequía, reduce la cantidad de agua disponible en el suelo (Lebrija-Trejos *et al.* 2011; Méndez-Alonzo *et al.* 2013; Pineda-García *et al.* 2013).

Filtros ambientales y desempeño ecológico de las especies sucesionales

La teoría ecológica ha propuesto que las condiciones ambientales actúan como filtros que limitan la presencia de ciertas especies en un hábitat particular (Keddy 1992a; 1992b; Cornwell *et al.* 2006). El desempeño ecológico de una especie se puede determinar analizando la capacidad de sobrevivir, crecer (aumento de la biomasa) o reproducirse de un conjunto de individuos presentes en un hábitat particular (Violle *et al.* 2007). Hay características que pueden afectar ciertas funciones, por ejemplo, la capacidad de adquirir recursos o la habilidad de tolerar condiciones ambientales desfavorables y de competencia entre individuos que coexisten en el hábitat (Keddy 1992b). Las características morfo-fisiológicas que tienen impacto sobre algún componente del desempeño ecológico se denominan atributos funcionales (Violle *et al.* 2007). Los filtros ambientales y las interacciones biológicas (p.ej., la competencia) pueden actuar simultáneamente, así como tener distintos efectos, tanto en el desempeño ecológico como en los atributos funcionales de las especies (Cornwell *et al.* 2006).

Las especies de plantas que componen a la comunidad vegetal que se está regenerando pueden pertenecer a uno de dos grupos: las que sobrevivieron después del disturbio en forma de tocón o en el banco de semillas, y las especies que llegan en forma de propágulo de los alrededores (Vieira y Scariot 2006). Las plantas presentes antes del disturbio enfrentan cambios drásticos en su ciclo de vida, es decir, tienen que sobrevivir después de que su biomasa aérea fue removida y volver a crecer en las nuevas condiciones ambientales. Las especies de plantas que no estaban en el sitio tienen que ser capaces de dispersarse y posteriormente establecerse, sobrevivir y crecer en las nuevas condiciones ambientales.

Las especies presentes en etapas sucesionales tempranas enfrentan condiciones ambientales poco favorables para llevar a cabo sus funciones vitales, las cuales representan filtros ambientales generados por el disturbio antropogénico (Lebrija-Trejos *et al.* 2010b). Conforme pasa el tiempo y la vegetación se desarrolla, algunos de los individuos que conforman a la comunidad en regeneración incrementan su tamaño, incluyendo a algunos

de los nuevos individuos que llegan y logran establecerse (Álvarez-Yépiz *et al.* 2008). Este incremento en biomasa influye en la estructura de la comunidad, ya que la densidad de individuos, la cobertura del dosel y el área basal aumentan; a su vez, estos cambios modifican el ambiente en el que se desarrolla la vegetación secundaria (Lebrija-Trejos *et al.* 2010b; Pineda-García *et al.* 2013). Así, los filtros ambientales cambian, ya que en las etapas tardías la competencia por recursos como el espacio y la luz se incrementan con respecto a las etapas iniciales; además, la temperatura disminuye, lo cual incrementa el agua disponible para las plantas y disminuye sus tasas de pérdida por evapotranspiración (Guariguata y Ostertag 2001; Garnier *et al.* 2004; Lebrija-Trejos *et al.* 2010a). La comunidad vegetal de las etapas sucesionales tardías en algunos casos puede ser similar al bosque maduro, tanto en su estructura y diversidad como en las condiciones ambientales que genera (Lebrija-Trejos *et al.* 2011).

Interacción de las plantas con los cambios en el ambiente durante el proceso sucesional

La sucesión secundaria en el BTC representa un gradiente ambiental caracterizado por distintos factores limitantes para el desarrollo de las plantas, aunado al estrés hídrico debido a la marcada estacionalidad en la precipitación. Una vez que las especies logran llegar a un sitio, no todas pueden sobrevivir, crecer y reproducirse a medida que los filtros ambientales siguen cambiando (Connell y Slatyer 1977). Se observa el cambio en la dominancia de unas especies por otras y la estructura de la vegetación cambia, en parte, dependiendo del éxito de cada una (Finegan 1996; Chazdon *et al.* 2010). Este éxito está dado por rasgos que les confieren a las plantas distintas capacidades de resistencia a las condiciones bióticas y abióticas propias de cada edad sucesional, así como de captura y uso de los recursos disponibles (Ackerly *et al.* 2004; Lavorel *et al.* 2007; Violle *et al.* 2007; Poorter *et al.* 2008). Las especies de plantas que tienen atributos asociados con la capacidad de tolerar la falta de agua, almacenarla, o de evadir el estrés hídrico, pueden sobrevivir y crecer en las etapas tempranas. En el mecanismo de evasión la planta posee atributos físicos o metabólicos que funcionan como barrera a la desecación, y la planta no sufre falla

hidráulica general, mientras que en el mecanismo de tolerancia a la sequía, el sistema hidráulico puede seguir funcionando en condiciones desfavorables sin sufrir daños, o posee mecanismos de reparación de daños (Levitt 1980; McDowel *et al.* 2008). Por otro lado, las especies presentes en etapas tardías, además de enfrentar la disponibilidad reducida de agua durante la época de sequía (Lebrija-Trejos *et al.* 2011), también enfrentan la disminución en recursos como el espacio (Lebrija-Trejos *et al.* 2010). Por ello, las especies en las etapas tardías con atributos que les confieren tanto resistencia al estrés hídrico como habilidades competitivas (p.ej., eficiencia alta de captura de recursos y capacidad de acumular biomasa rápidamente) pueden tener mejor desempeño ecológico con respecto a las especies que cohabitan el sitio (Finegan 1984; Ackerly *et al.* 2004; Lebrija-Trejos *et al.* 2010b; Lohbeck *et al.* 2014; Pineda-García 2015).

El tejido vascular secundario del tallo de las plantas

Las plantas interactúan con el ambiente que las rodea a través de sus raíces, tallos y hojas (Durante *et al.* 2011), y las características de estos órganos determinan sus funciones (Carlquist 2001). Las funciones principales del tallo son el transporte y el almacenamiento de agua y nutrientes, así como el soporte mecánico. El xilema secundario en el tallo es un tejido complejo compuesto de conjuntos de células especializadas: los elementos de vaso, las células del parénquima radial y axial, y las fibras, tanto libriformes como no libriformes (Carlquist 2001; Segala-Alves *et al.* 2002). El agua es transportada de forma pasiva a través de los vasos por evapotranspiración. El transporte activo de agua y de nutrientes, así como su almacenamiento, se lleva a cabo en las células de los parénquimas axial y radial (Zimmermann 1983; Carlquist 2015); en algunos casos también las fibras septadas llevan a cabo dicha función. El soporte mecánico está dado principalmente por las fibras (Carlquist 1977), aunque los vasos también cumplen esta función.

Las características y la distribución de las células que componen el xilema secundario del tallo afectan las funciones de transporte hídrico, soporte mecánico y almacenamiento de recursos. En cuanto al transporte hídrico, el diámetro del lumen del vaso está asociado

con una propiedad hidráulica importante: los vasos más anchos son capaces de transportar mayor cantidad de agua que los vasos estrechos (Zimmerman, 1983). Sin embargo, cuando el agua escasea en el ambiente la capacidad de transporte hídrico del xilema disminuye debido a la interrupción de la columna de agua bajo presiones negativas (cavitación), lo cual puede provocar que los vasos se llenen de aire (embolismo), impidiendo el transporte de agua (Zimmermann 1983; Tyree y Zimmermann 2002). Esta situación puede tener repercusiones en la supervivencia y el crecimiento de la planta, aunque la intensidad del daño varía en función de los otros componentes anatómicos del tejido (López *et al.* 2005; Lens *et al.* 2013; Trifilò *et al.* 2014). El número de vasos y su distribución espacial también influyen en la seguridad durante la conducción hídrica. La redundancia es una propiedad de la arquitectura hidráulica del árbol, la cual consiste en que si un vaso está bloqueado, el agua puede pasar a uno adyacente a través de sus paredes contiguas (Cruiziat *et al.* 2002). Por lo tanto, la presencia de un gran número de vasos en el tejido, aunado a que muchos de éstos se encuentren agrupados, impiden que el transporte de agua se vea gravemente afectado cuando la disponibilidad de agua es baja (Ewers *et al.* 2007).

En cuanto a las funciones de las fibras, la lignina se acumula en sus paredes secundarias, y mientras más grande sea su diámetro y más gruesas sean sus paredes, más lignina contienen, lo que le confiere al xilema secundario más dureza y resistencia al daño mecánico, a la vez que aportan mayor soporte mecánico al individuo (Larjavaara *et al.* 2010). Por último, la función de almacenamiento comúnmente está asociada con el parénquima axial y radial (Carlquist 2015; Morris *et al.* 2016).

Ciertas combinaciones de características aportan ventajas al desempeño de la planta, pero generalmente conllevan un costo asociado. Las restricciones se dan al nivel de la estabilidad y la seguridad mecánicas, así como de la habilidad de crecer y competir por recursos, entre otros (Gartner 1995). Las disyuntivas principales se pueden dar entre caracteres que aportan seguridad hidráulica y eficiencia en la conducción (Pineda-García *et al.* 2015), así como entre la seguridad hidráulica y los costos de producción y de mantenimiento de la biomasa. Una disyuntiva asociada al diámetro de los vasos es que vasos anchos teóricamente aumentan la eficiencia del transporte hídrico; sin embargo,

cuando la disponibilidad de agua en el suelo es baja, el riesgo de embolismo en los vasos anchos es mayor que en los vasos estrechos (Cochard 2006). Entre la seguridad en el transporte de agua y la producción de biomasa hay otra disyuntiva, ya que mientras más lignina se acumule en las paredes secundarias de las fibras, mayor será el soporte mecánico del tejido que pueda evitar el colapso irreversible o el daño de las células (De Micco y Aronne 2012); sin embargo el refuerzo mecánico de los tejidos requiere una mayor inversión en los costos de producción de la biomasa.

Planteamiento del problema

Las especies presentes en la vegetación secundaria derivada del BTC experimentan una sequía estacional muy marcada que genera condiciones ambientales limitantes para su desarrollo. Además, la deforestación con fines agrícolas, que es común en estos sitios, trae como consecuencia que las plantas que forman parte de la vegetación original experimenten cambios drásticos en su ciclo de vida y en el ambiente que las rodea (Madeira *et al.* 2009; Lebrija-Trejos *et al.* 2010b; Lebrija-Trejos *et al.* 2011). Al cesar el disturbio, la vegetación comienza a regenerarse, lo que genera cambios en las condiciones bióticas y abióticas, y se da un reemplazo de especies de plantas que enfrentan distintas condiciones (Connell y Slatyer 1977); en particular, destaca el estrés hídrico en las etapas sucesionales tempranas y la competencia por recursos en las etapas sucesionales tardías. En dichas condiciones, algunas especies son capaces de alcanzar valores altos de biomasa y de área basal en los extremos del gradiente sucesional (Álvarez-Yépez *et al.* 2008; Lebrija-Trejos *et al.* 2010a). Los patrones de acumulación de biomasa usualmente se basan en las especies dominantes (Finegan 1996; Alvarez-Añorve *et al.* 2012; Schönbeck *et al.* 2015), lo cual oculta el comportamiento del resto de las especies de la comunidad vegetal. Sin embargo, los cambios sucesionales en las comunidades vegetales son resultado de las respuestas individuales de las especies que las componen (Connell y Slatyer 1977; Chazdon *et al.* 2010). Por ello, para entender profundamente el proceso ecológico de la sucesión secundaria es

importante subsanar la falta de conocimiento sobre el cambio en variables estructurales (p.ej., el área basal) de las especies involucradas (Madeira *et al.* 2009).

Las plantas que componen a la vegetación en recuperación interactúan con el ambiente que las rodea a través de sus órganos, los cuales poseen distintos atributos morfo-fisio-fenológicos. Algunas de estas características están asociadas al crecimiento, a la reproducción y a la supervivencia de las plantas, por lo que pueden afectar la capacidad de superar los filtros ambientales asociados al gradiente sucesional (Pickett 1976; Violle *et al.* 2007; Selaya *et al.* 2008; Lebrija-Trejos *et al.* 2010b). El xilema secundario del tallo contiene diversas posibilidades de atributos funcionales, ya que sus características afectan la eficiencia y seguridad con la que se conduce el agua (Pratt *et al.* 2007; Lens *et al.* 2011), el almacenamiento de recursos y el soporte mecánico (Carlquist 1977; Carlquist 2009; Apgaua *et al.* 2015, 2016; Baas *et al.* 2016). Debido al vínculo entre las características estructurales del xilema y las funciones que desempeña una planta, las características del xilema afectan su capacidad de sobrevivir, la cantidad de biomasa acumulada en el tallo y la velocidad a la que éste crece (Craven *et al.* 2013; Hoeber *et al.* 2014).

La densidad de la madera es una propiedad física relacionada con el soporte mecánico tanto a nivel de la planta, como al del sistema de transporte hídrico del xilema secundario (Hacke *et al.* 2001), que se ha utilizado ampliamente para predecir el desempeño ecológico de las especies (Chave *et al.* 2009; Poorter *et al.* 2008). Los valores altos de densidad de la madera suelen asociarse con el crecimiento lento (Osunkoya *et al.* 2007; Poorter *et al.* 2008) y con una mayor supervivencia, y con mayor soporte y protección de daños mecánicos (Hacke *et al.* 2001).

Preguntas de investigación e hipótesis

Las especies presentes en la vegetación secundaria derivada de un BTC enfrentan estrés hídrico estacional, así como cambios en su desempeño ecológico, en las condiciones ambientales y en los recursos disponibles, los cuales están asociados al proceso sucesional. El desarrollo de esta investigación doctoral estuvo guiado por la siguiente pregunta:

¿contribuye el análisis de las características del xilema secundario del tallo de las especies sucesionales a dilucidar la relación entre las funciones del tallo y su desempeño ecológico? Las características del xilema secundario determinan la eficiencia y vulnerabilidad en el transporte hídrico, el almacenamiento de agua y almidón, y la asignación diferencial de recursos (p.ej., agua y carbono) para la producción de la biomasa que compone a los tallos de las especies sucesionales. Por ello, hipotetizamos que las características del xilema secundario tienen implicaciones en la capacidad de resistencia a la sequía, supervivencia y acumulación de biomasa de las especies sucesionales.

Para abordar la pregunta general, planteamos dos preguntas relacionadas con el desempeño ecológico y con el xilema secundario de las especies involucradas en el proceso sucesional: La primera pregunta es: ¿cómo varía la acumulación de biomasa que compone los tallos de las especies leñosas del dosel con respecto a la edad sucesional? Para responderla, el área basal (suma de las áreas transversales de los tallos de cada especie, medidas al 1.30 m de altura) se utilizó como una medida indirecta de la biomasa, mientras que la edad sucesional se utilizó como *proxy* de las condiciones y los recursos a lo largo del gradiente (Lebrija-Trejos *et al.* 2011)., La segunda pregunta es ¿cuáles son las características físicas y anatómicas del xilema secundario del tallo de las especies presentes en comunidades sucesionales tempranas y tardías? Además, planteamos las siguientes preguntas sobre la posible relación entre las características del xilema secundario del tallo, sus funciones y el desempeño ecológico: (iii) ¿las especies que coexisten en las comunidades sucesionales tempranas presentan formas similares de resistir las condiciones ambientales que caracterizan a estos sitios?; (iv) ¿las especies presentes en comunidades sucesionales tardías presentan características anatómicas del xilema secundario asociadas con la estacionalidad en la precipitación?; y por último, (vi) ¿cómo es la asignación de recursos en el tallo de las especies que coexisten tanto en las comunidades tempranas como en las tardías?

Objetivo general

El objetivo principal de esta investigación doctoral fue analizar las características del xilema del tallo de especies sucesionales en un BTC, las cuales se enfrentan a cambios ambientales asociados al gradiente sucesional y a una fuerte estacionalidad en la precipitación, a fin de contribuir a dilucidar algunos posibles mecanismos de resistencia al estrés hídrico, así como la forma de asignación de recursos para la producción y el mantenimiento de la biomasa que conforma el tallo de estas especies.

Objetivos particulares

1. Analizar el desempeño ecológico a lo largo del gradiente sucesional, medido a través de la presencia y el área basal, de un número considerable de especies leñosas presentes en el dosel de la vegetación secundaria.
2. Determinar las características físicas y anatómicas del xilema del tallo de las especies que forman parte de la vegetación secundaria.
3. Evaluar las características anatómicas del xilema del tallo de las especies sucesionales principales que coexisten en los extremos del gradiente sucesional (comunidades sucesionales tempranas y tardías).

Estructura y contenido la tesis doctoral

La presente tesis doctoral está conformada por siete capítulos, en los que se abordan los objetivos planteados para esta investigación. En este primer capítulo se establece el marco teórico, así como las preguntas, objetivos e hipótesis de la investigación. El objetivo del Capítulo 2 fue atender la falta de conocimiento sobre el desempeño ecológico individual, medido a través del área basal, de un número considerable de especies involucradas en el proceso de sucesión secundaria, en una comunidad vegetal muy diversa, la cual presenta una fuerte estacionalidad en la disponibilidad de agua que limita el desarrollo de las plantas.

El xilema del tallo es un tejido de gran complejidad, por lo que en los Capítulos 3, 4, 5 y 6 se analizó a distintos niveles. Además, dado que la sucesión secundaria en el bosque tropical caducifolio involucra un número de especies elevado, y considerando la complejidad de los procedimientos para estudiar los caracteres anatómicos, fue necesario limitar el número de especies de estudio. Por lo tanto, el Capítulo 2, que aborda la respuesta a los cambios en el área basal de cada especie asociados a la edad sucesional, fue la base para elegir a las especies de estudio de los capítulos posteriores.

El objetivo del Capítulo 3 se enfocó en caracterizar anatómicamente el xilema del tallo de las especies sucesionales dominantes, así como en generar hipótesis sobre los posibles mecanismos de resistencia a la sequía en las especies presentes en la vegetación secundaria. Este capítulo incluye el desarrollo de la estrategia metodológica para obtener los resultados de las variables anatómicas cuantitativas, por lo que funge como protocolo de investigación del Capítulo 6.

La densidad de la madera es una variable usualmente relacionada con la inversión en la producción de biomasa de una planta, a la vez que se trata de una variable compleja debido a que emerge de los componentes anatómicos del tejido del tallo. La concepción inicial de esta variable surgió dentro de la disciplina forestal, por lo que es relativamente nueva para los ecólogos y por lo tanto aún hay incongruencias en la forma de medirla, así como en su uso como atributo funcional. Por estas razones, en el Capítulo 4 se aborda parte de esta problemática, además de caracterizar y analizar a nivel comunitario e

intraespecífico los valores de densidad de la madera de las especies sucesionales dominantes (*i.e.*, las que acumulan mayor área basal con respecto al resto de las especies). Cabe mencionar que en este capítulo se utiliza la observación de cortes anatómicos como una herramienta para identificar algunos contenidos celulares en el xilema secundario de las especies estudiadas, los cuales podrían estar estrechamente relacionados con su desempeño sucesional, y teóricamente con los valores de densidad de madera que presentan.

A continuación, en el Capítulo 5 se describen las características anatómicas cualitativas del xilema del tallo de trece especies presentes en etapas sucesionales tardías, y se discuten algunas características anatómicas que comúnmente se han asociado con los mecanismos de resistencia a la sequía. Posteriormente, en el Capítulo 6 se analizan las características anatómicas cuantitativas del xilema que poseen las especies que están presentes en las comunidades sucesionales tempranas, así como en las comunidades tardías. Sin embargo, la forma en la que se analizan cuantitativamente los componentes anatómicos en la actualidad, tanto a nivel celular como a nivel poblacional, no es estadísticamente la más adecuada. Por lo tanto, en el Capítulo 6 se utilizó un método estadístico novedoso que permite resolver la problemática actual sobre las métricas anatómicas.

Finalmente, en el capítulo 7 se discute de forma integral (*i.e.*, considerando en conjunto los resultados de los capítulos 2 a 6), cómo el análisis de las características del xilema secundario de especies sucesionales en un bosque tropical caducifolio puede contribuir a dilucidar algunos de los posibles mecanismos relacionados con la eficiencia en el transporte hídrico, la resistencia a daños por cavitación, el almacenamiento de agua y almidón, el soporte mecánico, y con el mantenimiento y la producción de biomasa.

Área de estudio

Los estudios se llevaron a cabo en los alrededores del poblado conocido localmente como Nizanda, el cual pertenece al Municipio de Asunción Ixtaltepec, Distrito de Juchitán, Oaxaca. La región de Nizanda se centra en las coordenadas $16^{\circ}39'30''$ N y $95^{\circ}00'40''$ O, correspondientes a la vertiente pacífica del Istmo de Tehuantepec, en el sur de México (Pérez-García *et al.* 2010; Fig. 1). La altitud de la zona varía desde *ca.* de 100 m s.n.m. a más de 750 m s.n.m en la cima del Cerro Naranjo (SPP 1981).

La temperatura media anual es de 27.7°C y la precipitación media anual es de 898 mm. Las lluvias caen con una marcada estacionalidad, distinguiéndose una época seca de noviembre a abril y una lluviosa de finales de mayo a mediados de octubre, en la cual se concentra más de 90 % de la precipitación (Pérez-García *et al.* 2001; Fig. 1). Los vientos dominantes provenientes del norte azotan con gran velocidad la región durante todo el año.

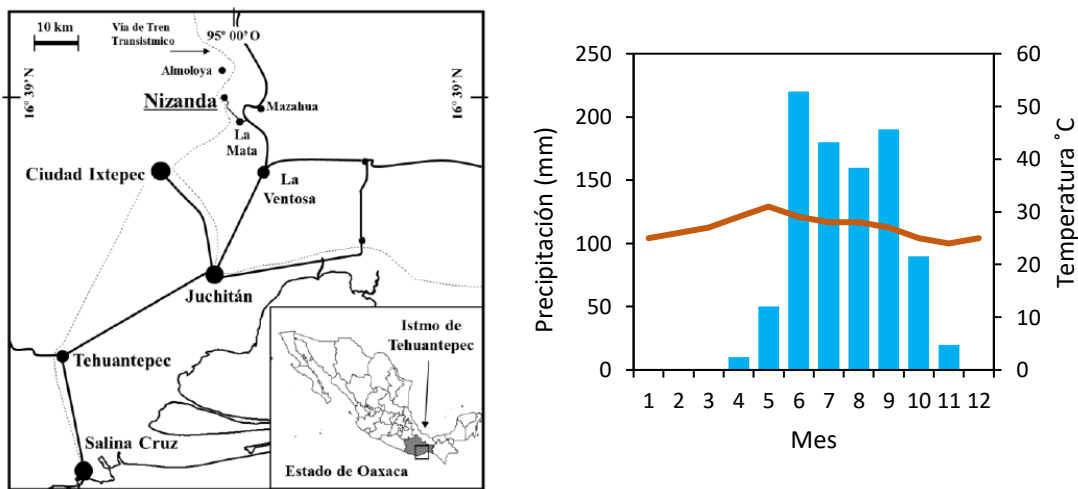
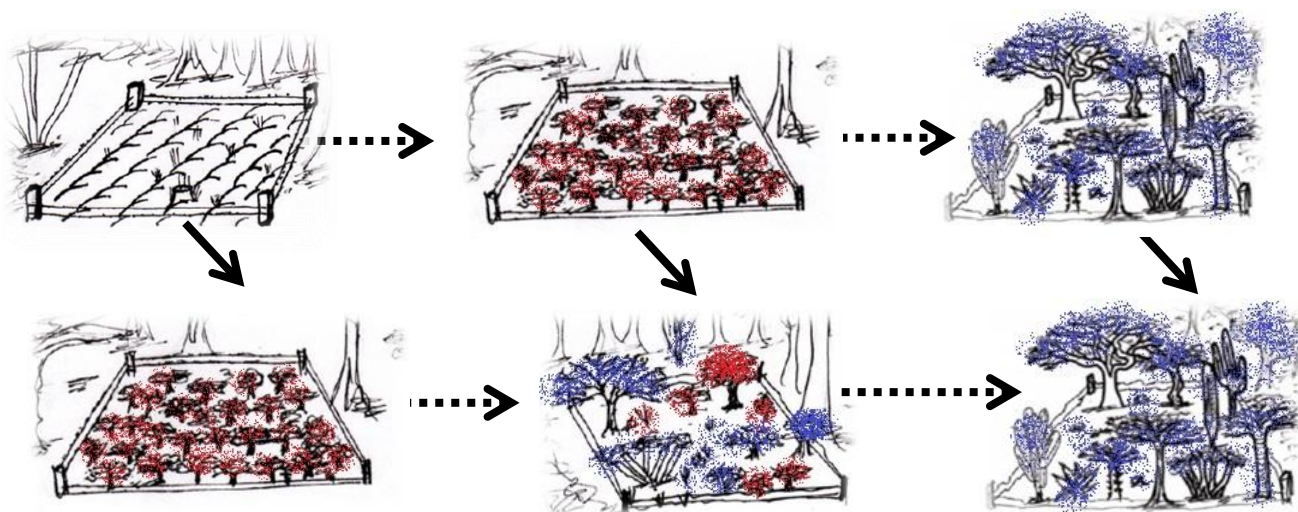


Figura 1. Localización del área de estudio en el Istmo de Tehuantepec, Oaxaca, México, y diagrama ombrotérmico correspondiente a la estación meteorológica de Ciudad Ixtepec, que es la más cercana a Nizanda.

CAPÍTULO 2

Differential performance of 50 canopy tree species along tropical dry forest succession



Differential performance of 50 canopy tree species along tropical dry forest succession

Abstract

Community assembly mechanisms through succession remain elusive due to its complexity, including changing environmental conditions that drive species' entry and persistence in the canopy of the recovering vegetation, especially in water-limited, highly diverse ecosystems. We asked: how is the ecological performance of canopy species during secondary succession in a tropical dry forest (TDF)? And, at which point of the successional gradient each species is more successful, i.e. attains high basal area values (BA)? This study was conducted in a tropical dry forest region of southern Mexico with secondary vegetation of different age development. We integrated two ecological variables for assessing 50 canopy adult tree species performances: the presence of the species in the system as well as their BA, which is an indicator of biomass accumulation. Occurrence and BA data were gathered in 11 annual vegetation surveys conducted in 15 permanent plots representing a successional range from 0 to 70 years after abandonment. We described each species' BA, given that it is present in a plot, by constructing composite models with successional age as explanatory variable. We tested the effect of age on each species' BA by comparing the models with null models that lacked successional age as predictor. Successional age explained variation in BA in 21 species, with some of them attaining maximum BA values at early successional stages (including two dominant early successional *Mimosa* species), and others at advanced successional stages (including the dominant late successional *Lysiloma divaricatum*). Several species showed unexpected responses including fluctuating, bell-shaped and asymptotic patterns. The BA of nine species did not respond to successional age. The two early successional *Mimosa* species had complementary behaviours. Exploring individual species BA variation along the successional gradient by using a novel statistical analysis revealed a large variety of patterns, suggesting divergence among species in their resource acquisition and tolerance to physical environmental conditions.

Keywords: GAMMs; GLMs; permanent plots; species basal area; species presence; successional patterns; temporal autocorrelation

Introduction

Vegetation recovery through secondary succession is a widely studied ecological phenomenon (Clements, 1916; Gleason, 1927; McIntosh, 1981; Finegan, 1996; Meiners *et al.* 2015). Despite a plethora of studies addressing this topic, successional patterns have not been fully understood and the mechanisms involved remain elusive. This is particularly true for some ecological systems, such as tropical dry forests (TDF), which have received less attention (Gillespie *et al.* 2000; Murphy & Lugo, 1995; Quesada *et al.* 2009; Derroire *et al.* 2016).

The assembly of the species along secondary succession may be related to the differential ecological performance of each species, but information on individual species patterns is virtually non-existent for many ecosystems given the complexity of secondary succession, especially in highly diverse systems, and the continuously changing conditions that drive the entry and persistence of species in successional communities (Gleason, 1939; Guariguata & Ostertag, 2001; Arroyo-Rodríguez *et al.* 2017). Many studies in the tropics have inferred successional patterns from chronosequence analyses (i.e., based on plots differing in time since abandonment assuming to represent a single successional pathway; Pickett, 1989; Foster & Tilman, 2000; Kennard *et al.* 2002; Letcher & Chazdon, 2009; Poorter *et al.* 2016; Rozendaal *et al.* 2019), while fewer have used monitoring-through-time approaches, mostly focusing on early succession (e.g., the first 20 years; Chazdon *et al.* 2007; van Breugel, *et al.* 2007; Maza-Villalobos *et al.* 2011; Mesquita *et al.* 2015, Norden *et al.* 2015, Rozendaal *et al.* 2017). Unfortunately, the time frameworks attainable by these two approaches, both in terms of resolution and extent, have been insufficient to fully comprehend community successional dynamics through the analysis of the successional patterns of the species composing the community.

Relative dominance of a species is inherently related to its capacity to accumulate basal area (BA), thus, analysing changes in the BA of the most abundant species in a given community has led to a valuable knowledge regarding general successional patterns of species assemblages for certain forest ecosystems; some species (referred to as pioneers) dominate early stages of forest recovery, and these are subsequently replaced by shade-tolerant species (Whitmore, 1989; Finegan, 1996; van Breugel *et al.* 2007; Álvarez-Añorve *et al.* 2012; Schönbeck *et al.* 2015). However, the light-demanding pioneer versus shade-tolerant guild contrast may be an oversimplification, as many species are

widely spread out over the entire successional gradient (Powers *et al.* 2009). Each species could be better adapted to a different successional moment, so that at each successional stage only a few species would become conspicuous structural components, attaining either large densities or biomass stocks (Finegan, 1996; Lebrija-Trejos *et al.* 2010b).

TDF hosts a high plant species richness, and displays rapid changes in the regeneration environment (Madeira *et al.* 2009; Lebrija-Trejos *et al.* 2010b; Lebrija-Trejos *et al.* 2011; Ferreira-Nunes *et al.* 2014), as well as in canopy structure and species diversity (e.g., Ruiz *et al.* 2005; Derroire *et al.* 2016). The relatively long dry season creates harsh conditions with high temperatures and water shortage, both of which limit vegetation recovery in recently abandoned fields (Lebrija-Trejos *et al.* 2011; Pineda-García *et al.* 2013). Despite limitations to plant growth, at early successional stages pioneer species establish and rapidly attain high BA values relative to other species (Álvarez-Yépiz *et al.* 2008; Lebrija-Trejos *et al.* 2010a). Later in succession, BA values and regeneration environment are more similar to those found in mature forest conditions (Romero-Duque *et al.* 2007; Lebrija-Trejos *et al.* 2011), where the occurring plant species face new environmental filters such as stronger density-dependent competition for resources (Westoby, 1984; Tilman, 1985; Peterson & Squiers, 1995). Between these two extremes, the pioneer contribution to community BA is gradually superseded by the contribution of mature forest species (Romero-Duque *et al.* 2007; Lebrija-Trejos *et al.* 2010a; Ferreira-Nunes *et al.* 2014). As succession proceeds, individual plant growth results in an increment of the area occupied by each of their stems, and community-level BA increases in a more or less predictable fashion (Ruiz *et al.* 2005; Lebrija-Trejos *et al.* 2010a; Dupuy *et al.* 2012; but see Mora *et al.* 2015). Yet, it is uncertain what the individual contribution is of the different species to such increase along a successional gradient. General patterns focusing on dominant species may conceal the behaviours of the large assemblage of other species with lower structural importance in the community. Successional changes in plant communities represent the integrated outcome of the individual species responses (Connell & Slatyer, 1977; Chazdon *et al.* 2010), and therefore we need to analyse quantitatively the BA patterns of species that participate in the process. Such deficiency is particularly far-reaching in tropical forest systems given the large number of species that they host (Madeira *et al.* 2009).

In this study, we analyse the ecological performance, through changes in BA, of a relatively large group of canopy species that occur at various stages of the succession, using a novel modelling approach. For the successional TDF of Nizanda, southern Mexico, a unique representation of the entire successional gradient is available, which has resulted from combining the chronosequence approach with the continuous monitoring of permanent plots (Lebrija-Trejos *et al.* 2010a). This study design enabled us to address two main questions: (i) how is the ecological performance of canopy species during secondary succession in a TDF? and (ii) at which point of the successional gradient each species is more successful, *i.e.* attains high BA values? To answer these questions, for each species we modelled its BA as a function of successional age (*i.e.*, time since abandonment), while recognising that BA is necessarily conditioned on the probability of a species being present in a successional plot. Successional age has proven to be a good predictor of environment in the forest interior, with factors such as soil-water and space availability, drastically differing between young and late successional stands (Read & Lawrence, 2003; Lebrija-Trejos *et al.* 2011; Pineda *et al.* 2013). We hypothesised that these changing environmental filters operating along a successional gradient are important drivers of plant species' ecological performance; we predicted that successional age (as a *proxy* of these filters) would explain BA variation in individual species. We also hypothesised that TDF species differ in their ability to overcome successional shifts in environmental filters, thus we expected species to have higher BA values at different successional ages.

Materials and methods

Study site

The study was conducted in Nizanda, Oaxaca, Mexico (16° 39' 30" N, 95° 00' 40" W). Elevations are around 250 m a.s.l. The regional climate is characterised by a mean annual temperature of 27.7 °C and an average total annual precipitation of 902.3 mm, with 90% falling between late May and mid-October. Although the area is covered by a mosaic of different vegetation types (Pérez-García *et al.* 2010), largely associated with a complex geological substrate (Pérez-Gutiérrez *et al.* 2009), TDF is the dominant forest type in the region, which develops mostly on relatively shallow Leptosols derived from siliciclastic phyllite (C. Miguel Talonia, pers. comm.). Subsistence agriculture has been practiced

for decades in Nizanda and its surroundings, which has resulted in the presence of numerous secondary vegetation stands of different ages across the landscape (Gallardo-Cruz *et al.* 2012).

Field survey

The data used in this analysis were gathered in 11 annual vegetation surveys (2003-2013) conducted in the same 15 permanent plots as Lebrija-Trejos *et al.* (2008) (20 × 20 m), whose initial ages (i.e., time since abandonment) ranged between 0 and 60 years. The spatial arrangement of the plots across the landscape is shown in Gallardo-Cruz *et al.* (2012); mean distance between plots is 1.31 km (SD = 0.7). The surveys took place yearly at the end of the rainy season (October-November), following the protocol of Lebrija-Trejos *et al.* (2008). Callipers were used to measure the diameter of stems with DBH \geq 1 cm and less than \sim 2 cm DBH, and diametric tapes for stems with \sim 2 cm or higher DBH. Over this study period and in all plots, we recorded a total of 95 canopy plant species (DBH \geq 1 cm), including trees, shrubs and succulents. From this set, we selected the 50 canopy tree species (see Table S1 in Supporting Information 1; Chapter 2 Annexes), which contributed for at least 80 % of the total BA in each plot in 2008. Taxon nomenclature was based on www.theplantlist.org, last accessed on July 28, 2017.

Data analysis

An appropriate analysis of the performance variables needed to consider data structure. Given the sampling design, a time series was produced for each species in each plot where it was recorded at the canopy level (DBH \geq 1 cm; see Lebrija-Trejos *et al.* 2008). The unequal successional age of the plots at the start of the study period has two consequences: first, such time series started at different moments of the succession; and secondly, they overlapped in different plots. Therefore, the first step in the analysis consisted in modelling the occurrence probability for any given species along the entire range of successional ages observed over the study period (0-70 years). To this end, we constructed presence/absence models (PA) through generalized linear mixed models (GLMMs); we used a logistic link function and a binomial error distribution, with age as a fixed effect and plot as a random effect, to account for among-plot variation (this model is referred to as PA1; see details in Supporting information 1, Fig. S1, in Annexes of Chapter 2). For each species, we first discarded those plots where

it was never recorded because of the impossibility to ascertain whether the plot conditions were adequate or not to host it. For those species for which PA data were invariable across successional ages in the remaining plots, the fitted model was a constant with a value of 1. Further, in those cases where a given species was recorded in a single plot only (i.e., a single time series was available for this species), no random factor was included, i.e. a GLM was fitted. From here onwards, we constructed GLMMs for most remaining species. For some species GLMMs did not converge due to insufficient variation in the data (insufficient number of zero data); for these species we fitted a Firth's bias reduced logistic regression (logistf; Heinze *et al.*, 2013). Figure S1a provides a flow diagram illustrating the steps and decisions involved in the construction of GLMM and GLM models.

Next, we constructed a null model (henceforth PA0) by excluding successional age as a variable from the PA1 model (Fig. S1b, in Annexes of Chapter 2). We used Akaike's Information Criterion corrected for small sample sizes (AICc) to compare these two PA models for each species. Due to sample size limitations for some species, we made the conservative decision that competing models had similar empirical support whenever ΔAICc was < 10 given the observed complexity in the data (Anderson & Burnham, 2002; see Fig. S1c in Supporting information 1, in Annexes of Chapter 2).

For 15 species AICc values associated to PA models could be calculated (Fig. 1). For 35 species AICc could not be calculated because a Firth logistic regression was used, thus precluding comparisons between PA0 and PA1 (Fig. 1; *PA1 in Table S2, in Supporting information 1, in Annexes of Chapter 2).

The BA of each species was calculated for every plot \times year combination. BA of individual species was scaled to 1 ha (i.e., m^2/ha ; see Lebrija-Trejos *et al.*, 2008 for further details). Generalised additive mixed models (GAMMs) were used to describe changes in a species' BA across successional ages. This phase of the modelling was conditioned to the presence of the species in any given plot (i.e., we modelled BA given presence). We used an exponential link function and a gamma error distribution (as the response variable is positive and continuous), defining age as a fixed effect and plot as a random effect (BA1 model). For BA we were mostly able to account for the temporal autocorrelation in the time series obtained for each plot; we achieved this by including a correlation structure of order 1 (i.e., only the BA from the previous year influences the BA of the current year) at the plot level. The strength of autocorrelation was estimated through the statistic Φ (range: -1 to 1,

with no autocorrelation at $\Phi = 0$, negative correlation at $\Phi = -1$ and positive at $\Phi = 1$). For those species recorded in a single plot only, no plot random factor was included in the BA1 model (Fig. S2a). We also constructed a null model (i.e., no age effect, henceforth BA0), and compared it with BA1 using the same procedure as with PA data using AICc (Fig. S2b, c). All decision rules followed in constructing BA1 and BA0 models are illustrated in full detail in Figure S2 (Supporting information 1, in Annexes of Chapter 2).

To model BA changes along successional age for each species we constructed a composite model that resulted from the product of the selected PA and BA models. We obtained a BA model conditioned on the species' occurrence in the plots. Wald's 95 % confidence intervals were calculated for this model to reflect the uncertainty in the BA estimates. Finally, we assembled the resulting models into a single graph to visualise the joint behaviours of the analysed species in order to gain an integrated depiction of the whole community successional development. This visualisation was first done based on the predicted absolute BA values and then by plotting the proportional BA values to represent the relative contributions of the various species to the community-level BA accumulation pattern.

To assess the goodness of fit of each composite model to the observed time series, we calculated an R^2 coefficient conditional on the plot (R^2_c) as the squared correlation between the observed BA data (BA_{obs}) and the estimated BA (BA_{est}) from the composite model, as follows:

$$R^2_c = (\text{cor}(BA_{obs}(\text{age}), \exp(\log(BA_{est}(\text{age}))+\text{RE}(\text{plot}))))^2$$

where cor is correlation and RE(plot) is the random effect associated to each plot. R^2_c measures the goodness of fit between observed and estimated BA values at the plot level, and it was calculated because no R^2 has been developed for Gamma-distributed mixed effect models (Nakagawa and Schielzeth, 2012).

Model fitting was performed in R (R Core Team, 2015) using packages lme4 (GLMMs; Bates *et al.*, 2015), logistf (Firth's bias reduced logistic regression; Heinze *et al.*, 2013) and gamm4 (GAMMs; Wood & Scheipl, 2014). Results were plotted with ggplot2 (Wickham, 2009).

Results

Modelling species' presence/absence

Seven of the 15 species for which Akaike's Information Criterion (AICc) values could be calculated (Fig. 1) PA1 was selected over PA0 (Fig. 1, Table S2 in Supporting Information 1, in Annexes of Chapter 2), while for the other eight species discrimination between their PA0 and PA1 models was not detected (either $PA0 \leq PA1$ or $PA1 \leq PA0$ in Fig. 1 and Table S2).

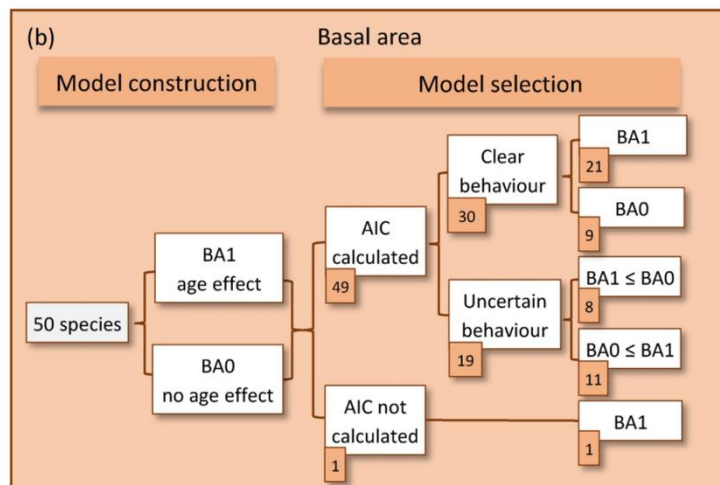
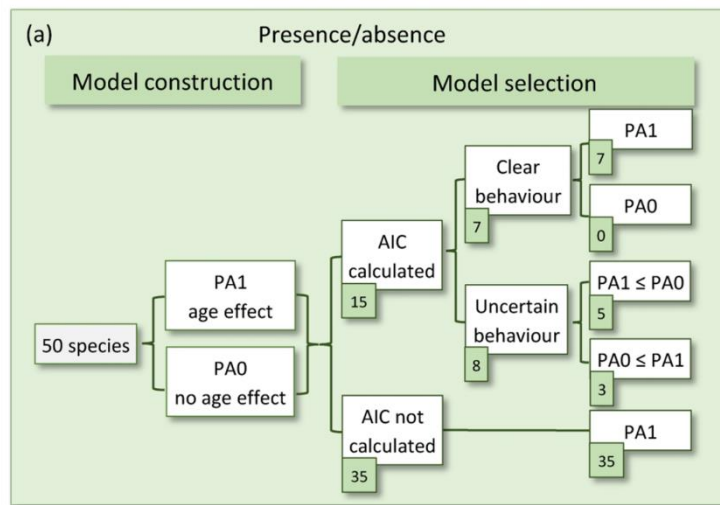


Figure 1. Distribution of models of the ecological performance of 50 species along succession in a tropical dry forest of southern Mexico. Composite models involved the construction of (a) presence/absence (PA), and (b) basal area (BA) models. For each model type, two models were considered: one that included an age (time since abandonment) effect (PA1 and BA1), and one that did not include it (PA0 and BA0). Model selection was performed using AICc; when $\Delta AICc < 10$, we considered the behaviour of the data uncertain, as models were similarly supported. Yet, we distinguish here the model with smaller AICc by placing it on the left side of the \leq symbol; PA1 or BA1 were included in the composite model when AICc could not be estimated.

Modelling species' basal area given presence in each plot

AICc could be calculated for all 50 species models but one (Fig. 1; Table S2; *Schoepfia schreberi* was the exception), 30 species had a clear behaviour ($\Delta\text{AICc} > 10$), and for 19 (out of 49) the model selection procedure resulted in uncertainty. For 21 out of 30 species age affected BA (i.e., BA1 model had better support than BA0; Fig. 1b; Table S2); this situation is exemplified by *Mimosa eurycarpa*, *M. tenuiflora* and *Lysiloma divaricatum* in Fig. 2a, b, c. For five species, including *Mimosa tenuiflora* and *Bursera simaruba* (Fig. 2b, e), a high temporal autocorrelation was estimated at the plot level ($|\Phi| \geq 0.5$; Table S2); that is, their BA at any given year was strongly influenced by the corresponding value in the previous one. The other nine species showed no age effect on their BA (the model only including BA0 had the best support; Fig. 1b; Table S2); this situation is exemplified by *Lonchocarpus lanceolatus* (Fig. 2f).

The 19 species showing uncertain behaviours consisted of two subgroups depending on which BA model had the smallest AICc (Fig. 1b; Table S2). In eight species, exemplified by *Phyllostylon rhamnoides* (Fig. 3a), age seemed to have an effect on BA variation, but the null model could not be discarded (BA1 = BA0 in Fig. 1 and Table S2). For the remaining 11 species, illustrated by *Acacia cochliacantha* (Fig. 3b) and *Bonellia macrocarpa* (Fig. 3c), the opposite was true, as the null model had the smallest AICc, but the BA1 model could not be discarded (BA0 = BA1 in Fig. 1b and Table S2).

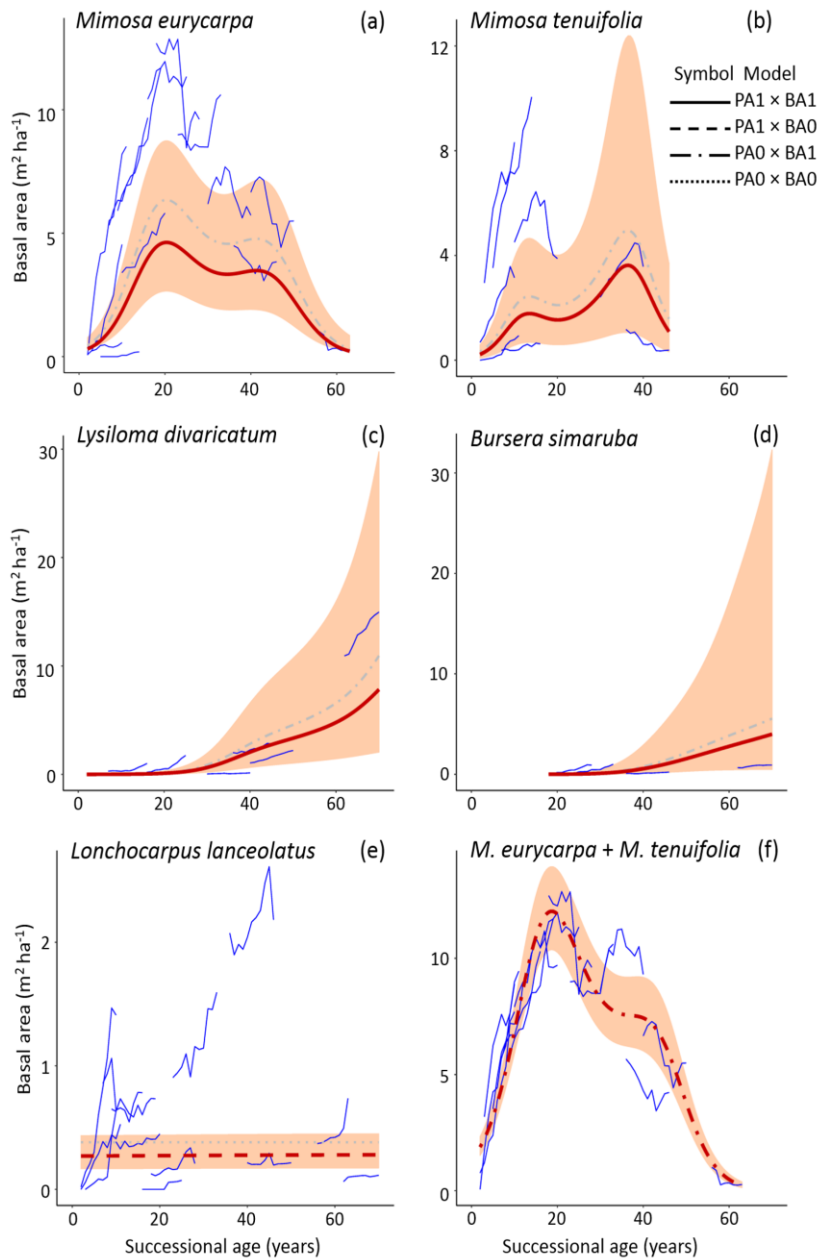


Figure 2. Modelled patterns of basal area change for six TDF successional species. The last panel (f) represents the composite model constructed with the combined data for two early successional *Mimosa* species. The best supported models are indicated by thick red lines, while grey lines denote models with similar support (i.e., $\Delta\text{AICc} < 10$); line type denotes different composite model types. Blue thin lines show the observed trajectories in individual plots. Orange bands around the best composite models are Wald's 95% confidence intervals.

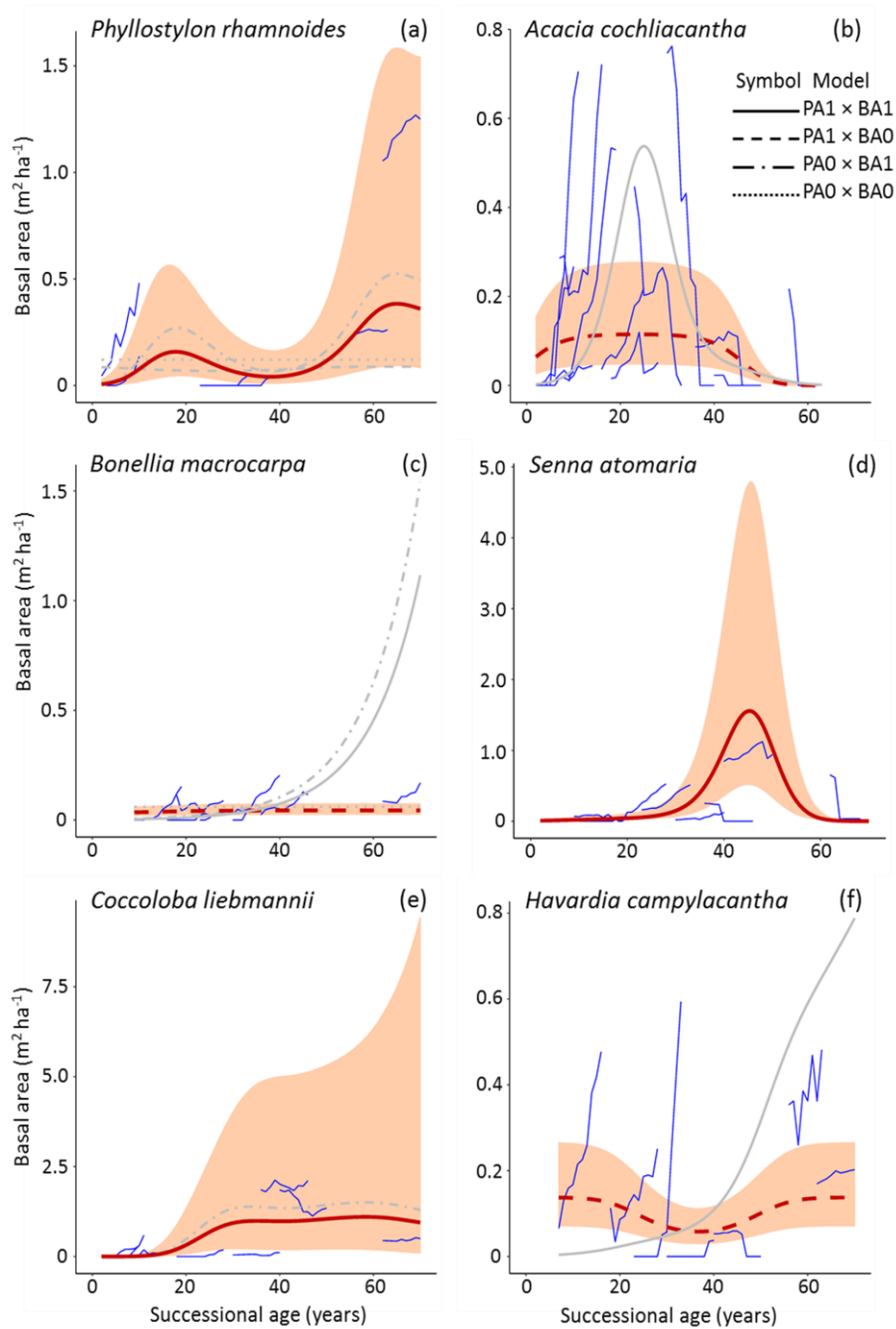


Figure 3. Representative modelled patterns of basal area change for individual species during secondary succession. The best supported models are indicated by thick red lines, while grey lines denote models with similar support (i.e., $\Delta AICc < 10$); line type denotes different composite model types. Blue thin lines show the observed trajectories in individual plots. Orange bands around the best composite models are Wald's 95 % confidence intervals.

Composite model for each species ($PA \times BA$)

Composite models were constructed for all 50 species (Figure 1d in Supporting Information 2). For 29 species fallow age affected BA through succession (BA_1 , and $BA_1 \leq BA_0$), whereas for the remaining 20 species age did not have such an effect (BA_0 , and $BA_0 \leq BA_1$; Fig. 1b).

Among the 21 out of the 30 species with a clear effect of age on BA (only BA_1 ; Fig. 1b), a variety of composite-model patterns over successional age was found (Table S2; Supporting Information 2). For example, *Mimosa eurycarpa* and *M. tenuiflora* showed a bimodal pattern (Fig. 2a, b), whereas ten typical mature forest species, exemplified by *Lysiloma divaricatum* (Fig. 2c), had initial low BA values that increased exponentially over time. A small group of species (*Senna atomaria*, Fig. 3d; *Senna holwayana*, *Exostemma caribaeum*, and *Aeschynomene compacta* in Supporting Information 2) showed a bell-shaped pattern, with BA peaking at intermediate or advanced successional stages. *Coccoloba liebmannii* was the only species with an initial increase in BA that stabilised at a maximum value (Fig. 3e).

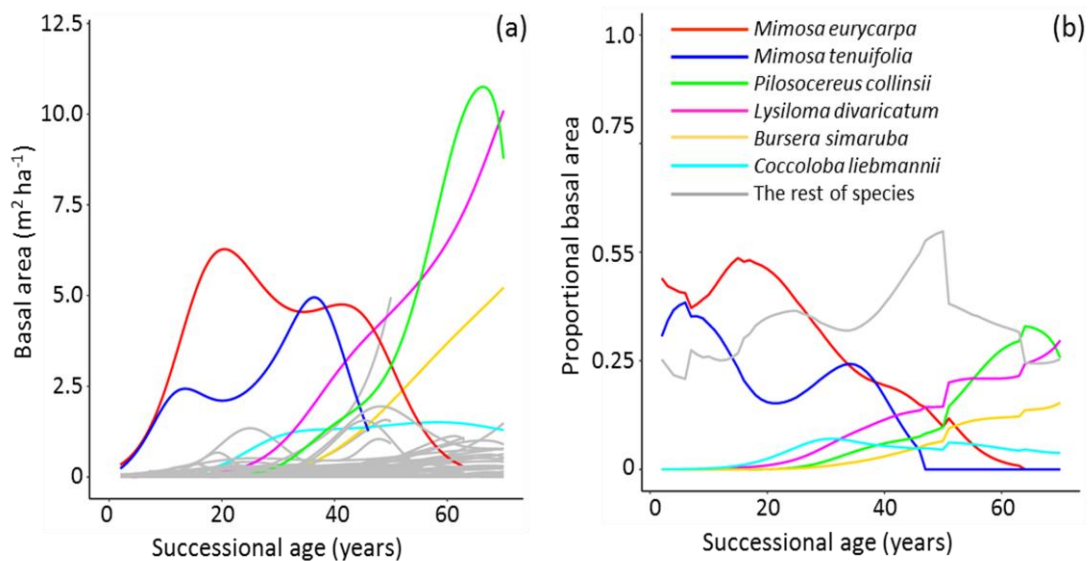


Figure 4. Integrated depiction of the modelled basal area changes along succession. (a) Absolute basal area values predicted by the composite models constructed for 50 successional species. (b) Relative contributions of successional species to community-level changes of basal area along succession. The coloured lines show the composite models for the six pioneer and mature forest dominant species, while the grey lines represent the rest of the species, either separately by species (a) or integrated into a single bin (b).

Three species attained high BA values along the broad successional gradient examined. *Mimosa eurycarpa* was the most successful species at early stages (up to 12.87 m²/ha at six years of abandonment), followed by *M. tenuiflora* (10.05 m²/ha at 14 years). *Lysiloma divaricatum* was the most successful species at advanced stages (with a maximum observed value of 14.96 m²/ha at 70 years).

BA variation among plots was important in some species. For example, *M. eurycarpa* showed two different responses in different plots, so that averaging those responses (i.e., the composite model) produced a response that did not fully align to any of them (Fig. 2a). *Acacia cochliacantha* is another example (Fig. 3b), as we observed some plots with large BA values at intermediate fallow ages, and some with low values at these same ages. Such variation explains our inability to select between a platykurtic pattern (PA1 × BA0 model; dashed line in Fig. 3b), and a leptokurtic one (PA1 × BA1 model; continuous line in Fig. 3b). Additionally, model selection was also difficult for those species with a low within plot autocorrelation, given by near-zero Φ values (for example, *Bonellia macrocarpa* and *Havardia campylacantha*, Fig. 3c, f).

Integrated community-level basal area accumulation pattern

The joint visualisation of all composite models shows the behaviour of each species in relation to the modelled changes in BA of the co-occurring species (Fig. 4a), showing the replacement of the BA of dominant pioneer species by dominant late successional ones. More interesting, however, is the pattern that results when the proportional BA values are plotted against successional time (Fig. 4b); in this case, it becomes clear that the sharp increase in BA of mature forest species towards late successional stages is attenuated by the contributions of an increasingly larger array of species to community-level BA.

The case of Mimosa species

Three extra analyses were performed for two species, *Mimosa eurycarpa* (MIEU) and *M. tenuiflora* (MITE), that showed complementary behaviours in their basal areas, as at the onset of succession a high BA in one corresponded to a low value in the other. First, when we analysed *M. eurycarpa* excluding plots where *M. tenuiflora* was the main species (MIEU_{wt}; 8 plots), we found that

successional age explained BA variation in a bell-shaped pattern (BA1 was the best-supported model), peaking at intermediate ages (Supporting Information 2). Notably, BA predictability from one year to the next increased under this scenario ($\phi = 0.89$ in MIEU_{wt} vs. 0.23 in MIEU). Likewise, when we excluded plots where *M. eurycarpa* had very high values (MITE_{wt}), the effect of age on *M. tenuiflora* BA became evident (i.e., BA1 was the best-supported model for MITE_{wt}; Table S2).

Finally, presence was independent of age when combining the data of the two *Mimosa* species (MIEU + MITE = MIMI; Fig. 2d), and age explained BA changes along succession and had a nearly bell-shaped pattern.

Discussion

Studies on tropical dry forest succession have identified key environmental filters that drive their recovery; overall, the regeneration environment shifts along succession from high light availability, high soil and air temperatures and particularly high water stress, to milder conditions regarding all these factors in older stands (Lebrija-Trejos *et al.* 2010b, 2011; Lohbeck *et al.* 2013). In this study we hypothesised that the changing environmental filters operating over the successional dry forest gradient, measured indirectly through successional age, would be important drivers of canopy species ecological performance, and expected that for most of the 50 study species successional age would explain their BA variations. On the whole, a large proportion of species displayed the foreseen behaviour. Unexpectedly, for nine species we observed a lack of response to successional age in their BA, which suggests a non-response behaviour to the changing environmental filters associated with the vegetation recovery process. Moreover, our study allowed us to visualise the community-level pattern of biomass accumulation over succession resulting from the absolute and relative contributions to this structural attribute of the 50 canopy tree species analysed.

Differential species performance along succession

We expected the successional age when performance is optimal, defined by peaks in BA patterns, to differ between species. Indeed, most of the 21 species showing clear responses in their BA to successional age attain their optimal performance at either extreme of the successional gradient. For

these species, the most common pattern was a non-linear increase in BA with successional age (the two pioneer *Mimosa* species showed a non-linear decrease), although the rate of BA accumulation differs notably between them. However, the remaining species showed a broader range of successional behaviours, including fluctuating, bell-shaped and asymptotic patterns.

For the same study system, Lebrija-Trejos *et al.* (2010a) distinguished two ecological guilds and concluded that BA of the pioneer guild (comprising five species) was replaced by the late successional guild (88 species) at about 40 years after stand abandonment. Our study revealed that the patterns of these two guilds are essentially determined by the individual dynamics of two dominant species: *Mimosa eurycarpa* is largely responsible for successional change in BA of the pioneer group, while the pattern observed for the mature forest guild is also mainly accounted for by *Lysiloma divaricatum*. General patterns previously reported for other tropical dry forests (e.g., Maza-Villalobos *et al.* 2011) may also represent the locally dominant species, with responses of less prominent species going unnoticed.

Most species display their maximum BA values near the extremes of the recovery process, but there is also a clear group species that may be classified as transitional, as their BA values peak halfway along the successional axis. Interestingly, this group is exclusively composed of legume species (*Acacia cochliacantha*, *Aeschynomene compacta*, *Senna holwayana* and *S. atomaria*), which is in agreement with previous findings of tropical dry forest succession studies (Madeira *et al.* 2009; Williams-Linera *et al.* 2010).

Despite the large number of species participating in the recovery process of this community, only three species are clear dominants over succession. Starting at very early stages (ca. 2-3 years after abandonment), *Mimosa eurycarpa* or *M. tenuiflora* become dominant and retain this role during the subsequent four decades of succession; after losing dominance, they can persist in successional stands as old as 60 years or more, with very low frequencies. In turn, only one species, *Lysiloma divaricatum* stands out as the sole dominant species in more advanced successional stages. Although all these three species are wind-dispersed, it is more likely that shared features granting competitive advantage, such as higher growth rates, and probably their ability to withstand fire disturbance (Rico-Gray & García-Franco, 1992), explain this dominance (Dalling & Hubbell, 2002).

The case of the Mimosa species

The two *Mimosa* species that are the structural dominants in early successional stands may have a similar ecological niche and appear to exclude each other: in no case do they share dominance at the same site and moment, as the BA of either one always largely exceeded the other. Our current understanding of the successional process in this tropical dry forest is still insufficient to explain this mutually exclusive behaviour. One possibility is that the dominance of either species represents an alternative successional pathway, probably associated with stochastic processes and niche dynamics (Norden *et al.* 2015; Arroyo-Rodríguez *et al.* 2017). Yet, *Mimosa eurycarpa* clearly is the most common successional species in the region (Lebrija-Trejos *et al.* 2008), and future studies will have to elucidate the underlying causes of such differences in the distribution and abundance of these congeneric taxa, including the potential role of biotic interactions (particularly competition), history of disturbance, light regime and soil features (Huante *et al.* 1995; Kennard *et al.* 2002; Ceccon *et al.* 2006; Álvarez-Yépiz *et al.* 2008). In this scenario of divergent BA patterns, competition between these two ecologically similar species may be the key, in line with predictions of the limiting similarity hypothesis (Whittaker, 1965; Li *et al.* 2015) and Huston and Smith's (1987) total suppression pattern, according to which species possessing a combination of features that confer them with a competitive advantage over others will have higher biomass throughout succession.

At present, even the sources from which these two species dispersed initially into successional stands in the region are uncertain, as both of them are extremely rare in old growth forest in the area, even in canopy gaps (Dechnik-Vázquez *et al.* 2016). In other Mexican tropical dry forests, other congeneric species play similar roles in the recovery process (*M. arenosa* in western Mexico, *M. bahamensis* in the Yucatán Peninsula and *M. antioquiensis* along the central coast of Oaxaca; Romero-Duque *et al.* 2007; Rico-Gray & García-Franco, 1992; Salas-Morales *et al.* 2007; Roig-Juñent *et al.* 2012). Given the strong and long-lasting dominance exerted by these *Mimosa* species, further research is needed on their potential negative effects in the recovery process in the study area, for example by delaying the transit towards old growth forest.

Mature forest species present in successional fallows

Environmental variables in advanced successional stages such as photosynthetically active radiation, air and soil temperature, air relative humidity, and soil water potential are very similar to those prevailing in mature forest (Lebrija-Trejos *et al.* 2010a, 2011; Pineda *et al.* 2013). Thus, we also expected that the BA of the two main contributors to community structure in the regional mature forest on phyllite, namely *Lysiloma divaricatum* and *Jacaratia mexicana* (Muñoz, 2015), would increase exponentially with successional age and attain large values of this variable in old stands. However, only *L. divaricatum* fully matched these predictions. In our local mature forest stands, a few individuals of *J. mexicana* contribute to community structure with high BA values. Therefore, the reasons why we failed to observe the expected pattern for this species may be manifold: this species may establish in more advanced successional stages than *L. divaricatum*, or the successional range comprised in our study may be too short for this species to reach BA values similar to those of mature forest.

In disagreement with our hypothesis, the performance of some mature-forest species was found to be independent of successional age. For nine species (18 % of the total) this was clearly the case, but 20 more species BA may potentially be independent of successional age. This result implies that these species are capable of accumulating biomass equally well under contrasting environmental conditions. This behaviour, exemplified by the sub-canopy plant *Bonellia macrocarpa* and the canopy tree *Phyllostylon rhamnoides*, is suggestive of a strongly limited propagule transport to successional stands (Zapata & Arroyo, 1978; Holl 1999; Guariguata & Ostertag, 2001; Wijdeven & Kuzee, 2001), which could explain the seemingly episodic appearance of these species along the successional gradient. Yet, other factors superseding the age-related processes cannot be ruled out (Arroyo-Rodríguez *et al.* 2017), for example micro-environmental variations (Quigley & Platt 2003; Ceccon *et al.* 2004), herbivory patterns (Filip *et al.* 1995; Dalling & Hubbell, 2002), life history attributes (Huston & Smith, 1987), and management history (Read & Lawrence 2003; Ceccon *et al.* 2006; Álvarez-Yépiz *et al.* 2008; Jakovac *et al.* 2016; Mora *et al.* 2015). In spite of some efforts to identify those attributes that lead species to display succession-independent behaviours (e.g., Huante *et al.* 1995; Kammesheidt, 2000; Lohbeck *et al.* 2014; Sanaphre-Villanueva *et al.* 2017), further research is needed to fully understand the interplay of the multiple factors potentially involved.

Considerations on the modelling approach

Our modelling approach allowed us to cope with analytical problems associated with the combined use of the chronosequence and longitudinal monitoring methods, which is increasingly popular in successional studies across many ecosystems (e.g., Foster & Tilman 2000; Lutz 2015; Rozendaal *et al.* 2017). Our composite model accounts for two ecological processes underlying individual species performance: their capacity to establish at a particular location and their subsequent growth and development (Chazdon *et al.* 2007; Cingolani *et al.* 2007). Thus, in order to examine basal area-related patterns, we decided to consider species occurrences in the stands, which resulted in the construction of BA models conditioned on the presence of a species in a particular stand. The best-supported models thus constructed must be interpreted as a mean successional behaviour for the species.

Our modelling approach also combined the data from the different sites included in the chronosequence that have been monitored over time, so that the experimental design is fully acknowledged. This was achieved through the inclusion of random effects, which accounted for the different environmental conditions particular to each site. Also, GAMMs allowed us to analyse successional changes in BA in a flexible manner, and to identify data-based patterns, instead of trying to adjust theoretical, pre-established models to the data (e.g., Huisman *et al.* 1993). Additionally, we considered the fact that observed BA can be affected by its values in previous years, irrespective of successional age (i.e., temporal autocorrelation). Thus, by controlling for temporal autocorrelation we were able to identify those species whose growth in BA was insensitive to the particular environmental conditions in any given year.

Ecosystems as diverse as tropical dry forests often harbour many rare species (Murphy & Lugo, 1995), and therefore we attempted to include as many species as possible in our analysis. Yet, the low abundances of many rare species imposed limitations on the statistical procedure, so that we were unable to conclusively assess the effect of successional age on their performance. The sensitivity of the modelling approach to low numbers of individuals constitutes an important shortcoming, and the only way we envision to deal with it is to minimize the number of under-represented species by increasing sample size as much as possible, while acknowledging the significant increases in the associated time and monetary costs. Nonetheless, the performance

models for rare species reported here provide a first insight into the key successional times for the entrance, growth and permanence of these species in the community.

Conclusions

Exploring individual species BA variation along the successional gradient by using a novel statistical analysis revealed a large variety of patterns, suggesting divergence among species in their resource acquisition and tolerance to physical environmental conditions. To date, much of the research pursuing an understanding of the successional process in human-modified ecosystems has focused on the analysis of the dynamics of community state variables. In some cases, efforts have been made to dissect such patterns into broad successional guilds. Despite the pivotal contributions of these studies, in highly diverse systems these general patterns may mask unforeseen ways in which multiple species occurring in the community perform along the course of succession. Only by understanding the full spectrum of these trajectories will we be able to take full advantage of the potential of successional forests to serve as functional reservoirs of the vanishing biodiversity of tropical regions.

Acknowledgments

We are grateful to the people of Nizanda for their continuous support and permission to work in their lands. Gerardo Cervantes and Flor Vega kindly assisted in field work, and Rodrigo Muñoz with data processing. We are grateful to Marco A. Romero-Romero for artwork. This study was funded by Consejo Nacional de Ciencia y Tecnología (CONACYT, grants SEMARNAT-2002-C01-0267 and CB-2009-01-128136) and Programa de Apoyo a Proyectos de Investigación e Innovación Tecnológica (PAPIIT-UNAM, grants IN216007-3 and IN218416).

References

- Alvarez-Añorve, M.Y., Quesada, M., Sánchez-Azofeifa, G.A., Avila-Cabadilla, L.D. & Gamon, J.A. (2012) Functional regeneration and spectral reflectance of trees during succession in a highly diverse tropical dry forest ecosystem. *American Journal of Botany*, **99**, 816-826.
- Álvarez-Yépiz, J.C., Martínez-Yrizar, A., Búrquez, A. & Lindquist, C. (2008) Variation in vegetation structure and soil properties related to land use history of old-growth and secondary tropical dry forests in northwestern Mexico. *Forest Ecology and Management*, **256**, 355-366.
- Anderson, D.R. & Burnham, K.P. (2002) Avoiding pitfalls when using information-theoretic methods. *The Journal of Wildlife Management*, **66**, 912-918.
- Arroyo-Rodríguez, V., Melo, F.P.L., Martínez-Ramos, M., Bongers, F., Chazdon, R.L., Meave, J.A., Norden, N., Santos, B.A., Leal, I.R. & Tabarelli, M. (2017) Multiple successional pathways in human-modified tropical landscapes: new insights from forest succession, forest fragmentation and landscape ecology research. *Biological Reviews*, **92**, 326-340.
- Bates D., Maechler, M., Bolker, B. & Walker, S. (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, **67**, 1-48.
- Burnham, K.P. & Anderson, D.R. 2004. Multimodel inference understanding AIC and BIC in model selection. *Sociological Methods and Research*, **33**, 261-304.
- Ceccon, E., Sánchez, S. & Campo, J. (2004) Tree seedling dynamics in two abandoned tropical dry forests of differing successional status in Yucatán, Mexico: a field experiment with N and P fertilization. *Plant Ecology*, **170**, 277-285.
- Ceccon, E., Huante, P. & Rincón, E. (2006) Abiotic factors influencing tropical dry forests regeneration. *Brazilian Archives of Biology and Technology*, **49**, 305-312.
- Chazdon, R.L., Letcher, S.G., van Breugel, M., Martínez-Ramos, M. & Bongers, F. (2007) Rates of change in tree communities of secondary Neotropical forests following major disturbances. *Philosophical Transaction of the Royal Society B*, **362**, 273-289.
- Chazdon, R.L., Finegan, B., Capers, R.S., Salgado-Negret, B., Casanoves, F., Boukili, V. & Norden, N. (2010) Composition and dynamics of functional groups of trees during tropical forest succession in Northeastern Costa Rica. *Biotropica*, **42**, 31-40.

- Cingolani, A. M., Cabido, M., Gurvich, D. E., Renison, D. & Díaz, S. (2007). Filtering processes in the assembly of plant communities: Are species presence and abundance driven by the same traits? *Journal of Vegetation Science*, **18**: 911-920.
- Clements, F. E. (1916) Plant succession: an analysis of the development of vegetation. Publication No. 242. Carnegie Institute, Washington, DC.
- Connell, J. H. & Slatyer, R. O. (1977). Mechanisms of succession in natural communities and their role in community stability and organization. **111**: 1119-1144.
- Dalling, J.W. & Hubbell, S.P. (2002) Seed size, growth rate and gap microsite conditions as determinants of recruitment success for pioneer species. *Journal of Ecology*, **90**, 557-568.
- Dechnik-Vázquez, Y.A., Meave, J.A., Pérez-García, E.A., Gallardo-Cruz, J.A. & Romero-Romero, M.A. (2016) The effect of treefall gaps on the understorey structure and composition of the tropical dry forest of Nizanda, Oaxaca, Mexico: implications for forest regeneration. *Journal of Tropical Ecology*, **32**, 89-106.
- Derroire, G., Balvanera, P., Castellanos-Castro, C., Decocq, G., Kennard, D.K., Lebrija-Trejos, E., Leiva, J.A., Odén, P.-C., Powers, J.S., Rico-Grey, V., Tigabu, M. & Healey, J.R. (2016) Resilience of tropical dry forests – a meta-analysis of changes in species diversity and composition during secondary succession. *Oikos*, **125**, 1386-1397.
- Dupuy, J.M., Hernández-Stefanoni, J.L., Hernández-Juárez, R.A., Tetetla-Rangel, E., López-Martínez, J.O., Leyequién-Abarca, E., Tun-Dzul, F. & May-Pat, F. (2012) Patterns and correlates of tropical dry forest structure and composition in a highly replicated chronosequence in Yucatan, Mexico. *Biotropica*, **44**, 151-162.
- Ferreira-Nunes, Y.R., da Luz, G.R., Rebleth, S., de Souza, D.L.d.S., das Dores Magalhães-Veloso, M., do Espírito-Santo, M.M. & dos Santos, R.M. (2014) Floristic, structural, and functional group variations in tree assemblages in a Brazilian tropical dry forest: effects of successional stage and soil properties. *Tropical Dry Forests in the Americas: Ecology, Conservation, and Management*, pp. 325-349. Taylor & Francis Group, Boca Raton.
- Filip, V., Dirzo, R., Maass, J.M. & Sarukhán, J. (1995) Within- and among-year variation in the levels of herbivory on the foliage of trees from a Mexican Tropical Deciduous Forest. *Biotropica*, **27**, 78-86.

- Finegan, B. (1996) Pattern and process in neotropical secondary rain forests: the first 100 years of succession. *Trends in Ecology & Evolution*, **11**, 119-124.
- Foster, B.L. & Tilman, D. (2000) Dynamic and static views of succession: testing the descriptive power of the chronosequence approach. *Plant Ecology*, **146**, 1-10.
- Gallardo-Cruz, J.A., Meave, J.A., González, E.J., Lebrija-Trejos, E.E., Romero-Romero, M.A., Pérez-García, E.A., Gallardo-Cruz, R., Hernández-Stefanoni, J.L. & Martorell, C. (2012) Predicting tropical dry forest successional attributes from space: is the key hidden in image texture? *PLoS One*, **7**, e30506.
- Gallardo-Cruz, J.A., Meave, J.A. & Pérez-García, E.A. (2005) Estructura, composición y diversidad de la selva baja caducifolia del Cerro Verde, Nizanda (Oaxaca), México. *Boletín de la Sociedad Botánica de México*, **76**, 19-35.
- Gillespie, T.W., Grijalva, A. & Farris, C.N. (2000) Diversity, composition, and structure of tropical dry forests in Central America. *Plant Ecology*, **147**, 37-47.
- Gleason, H.A. (1927) Further views on the succession-concept. *Ecology*, **8**, 299-326.
- Gleason, H.A. (1939) The individualistic concept of the plant association. *American Midland Naturalist*, 92-110.
- Guariguata, M.R. & Ostertag, R. (2001) Neotropical secondary forest succession: changes in structural and functional characteristics. *Forest Ecology and Management*, **148**, 185-206.
- Heinze, G., Ploner, M., Dunkler, D. & Southworth, H. (2013) logistf: Firth's bias reduced logistic regression. R package version 1.21.
- Huante, P., Rincón, E. & Acosta, I. (1995) Nutrient availability and growth rate of 34 woody species from a tropical deciduous forest in Mexico. *Functional Ecology*, **9**, 849-858.
- Huisman, J., Olff, H. & Fresco, L.F.M. (1993) A hierarchical set of models for species response analysis. *Journal of Vegetation Science*, **4**, 37-46.
- Huston, M. & Smith, T. (1987) Plant succession: life history and competition. *The American Naturalist*, **130**, 168-198.
- Jakovac, C.C., Bongers, F., Kuyper, T.W., Mesquita, R.C.G. & Peña-Claros, M. (2016) Land use as a filter for species composition in Amazonian secondary forests. *Journal of Vegetation Science*, **27**, 1104-1116.

- Kammesheidt, L. (2000) Some autecological characteristics of early to late successional tree species in Venezuela. *Acta Oecologica*, **21**, 37-48.
- Kennard, D.K., Gould, K., Putz, F.E., Fredericksen, T.S. & Morales, F. (2002) Effect of disturbance intensity on regeneration mechanisms in a tropical dry forest. *Forest Ecology and Management*, **162**, 197-208.
- Lebrija-Trejos, E., Bongers, F., Pérez-García, E.A. & Meave, J.A. (2008) Successional change and resilience of a very dry tropical deciduous forest following shifting agriculture. *Biotropica*, **40**, 422-431.
- Lebrija-Trejos, E., Meave, J.A., Poorter, L., Pérez-García, E.A. & Bongers, F. (2010a) Pathways, mechanisms and variability of tropical dry forest succession. *Perspectives in Plant Ecology, Evolution and Systematics* **12**, 267-275.
- Lebrija-Trejos, E., Pérez-García, E. A., Meave, J. A., Bongers, F. & Poorter, L. (2010b). Functional traits and environmental filtering drive community assembly species-rich tropical system. *Ecology*, **91**: 386-398.
- Lebrija-Trejos, E., Pérez-García, E.A., Meave, J.A., Poorter, L. & Bongers, F. (2011) Environmental changes during secondary succession in a tropical dry forest in southern Mexico. *Journal of Tropical Ecology*, **27**, 477-489.
- Letcher, S.G. & Chazdon, R.L. (2009) Rapid recovery of biomass, species richness, and species composition in a forest chronosequence in northeastern Costa Rica. *Biotropica*, **41**, 608-617.
- Li, S.P., Cadotte, M.W., Meiners, S.J., Hua, Z.S., Jiang, L. & Shu, W.S. (2015) Species colonisation, not competitive exclusion, drives community overdispersion over long-term succession. *Ecology Letters*, **18**, 964-973.
- Lohbeck, M., Poorter, L., Lebrija-Trejos, E., Martínez-Ramos, M., Meave, J.A., Paz, H., Pérez-García, E.A., Romero-Pérez, I.E., Tauro, A. & Bongers, F. (2013) Successional changes in functional composition contrast for dry and wet tropical forest. *Ecology*, **94**, 1211-1216.
- Lohbeck, M., Poorter, L., Martínez-Ramos, M., Rodríguez-Velázquez, J., van Breugel, M. & Bongers, F. (2014) Changing drivers of species dominance during tropical forest succession. *Functional Ecology*, **28**, 1052-1058.
- Lutz, J.A. (2015) The evolution of long-term data for forestry: large temperate research plots in an

- era of global change. *Northwest Science*, **89**, 255-269.
- Madeira, B.G., Espírito-Santo, M.M., Neto, S.D.Â.N., Nunes, Y.R.F., A. Sánchez-Azofeifa, G., W. Fernandes, G. & Quesada, M. (2009) Changes in tree and liana communities along a successional gradient in a tropical dry forest in south-eastern Brazil. *Plant Ecology*, **201**, 291-304.
- Martínez-Yrizar, A., Sarukhán, J., Pérez-Jiménez, A., Rincón, E., Maass, J.M., Solís-Magallanes, A. & Cervantes, L. (1992) Above-ground phytomass of a tropical deciduous forest on the coast of Jalisco, México. *Journal of Tropical Ecology*, **8**, 87-96.
- Maza-Villalobos, S., Balvanera, P. & Martínez-Ramos, M. (2011) Early regeneration of tropical dry forest from abandoned pastures: contrasting chronosequence and dynamic approaches. *Biotropica*, **43**, 666-675.
- McIntosh, R.P. (1981) Succession and Ecological Theory. *Forest Succession: Concepts and Application* (eds D. C. West, H. H. Shugart & D. B. Botkin), pp. 10-23. Springer, New York, NY.
- Meiners, S.J., Cadotte, M.W., Fridley, J.D., Pickett, S.T.A. & Walker, L.R. (2015) Is successional research nearing its climax? New approaches for understanding dynamic communities. *Functional Ecology*, **29**, 154-164.
- Mesquita, R.d.C.G., Massoca, P.E.d.S., Jakovac, C.C., Bentos, T.V. & Williamson, G.B. (2015) Amazon rain forest succession: stochasticity or land-use legacy? *BioScience*, **65**, 849-861.
- Mora, F., Martínez-Ramos, M., Ibarra-Manríquez, G., Pérez-Jiménez, A., Trilleras, J. & Balvanera, P. (2015) Testing chronosequences through dynamic approaches: time and site effects on tropical dry forest succession. *Biotropica*, **47**, 38-48.
- Murphy, P. G. & Lugo, A. E. (1995) Dry forests of Central America and the Caribbean. In S. H. Bullock, H. A. Mooney & E. Medina (Eds), *Seasonally dry tropical forests* (pp. 9-33). Cambridge, UK: Cambridge University Press.
- Muñoz, R. (2015) *Dinámica de la estructura y la diversidad de un bosque tropical caducifolio del Istmo de Tehuantepec, Oaxaca, México*. B.Sc. Thesis, Mexico City: Universidad Nacional Autónoma de México.
- Nakagawa, S. & Schielzeth, H. (2012) A general and simple method for obtaining R² from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, **4**, 133-142.
- Norden, N., Angarita, H.A., Bongers, F., Martínez-Ramos, M., Granzow-de la Cerda, I., van Breugel,

- M., Lebrija-Trejos, E., Meave, J.A., Vandermeer, J., Williamson, G.B., Finegan, B., Mesquita, R. & Chazdon, R.L. (2015) Successional dynamics in Neotropical forests are as uncertain as they are predictable. *Proceedings of the National Academy of Sciences of the USA*, **112**, 8013-8018.
- Pérez-García, E.A., Meave, J.A., Villaseñor, J.L., Gallardo-Cruz, J.A., & Lebrija-Trejos, E. (2010). Vegetation heterogeneity and life-strategy diversity in the flora of the heterogeneous landscape of Nizanda, Oaxaca, Mexico. *Folia Geobotanica*, **45**, 143-161.
- Pérez-Gutiérrez, R., Solari, L.A., Gómez-Tuena, A., & Valencia, V.A. (2009). El terreno Cuicateco: ¿cuenca oceánica con influencia de subducción del Cretácico Superior en el sur de México? Nuevos datos estructurales, geoquímicos y geocronológicos. *Revista Mexicana de Ciencias Geológicas*, **26**, 222-242.
- Peterson, C.J. & Squiers, E.R. (1995) Competition and Succession in an Aspen-White-Pine Forest. *Journal of Ecology*, **83**, 449-457.
- Pickett, S.T.A. (1989) Space-for-time substitution as an alternative to long-term studies. *Long-term studies in ecology*, pp. 110-135. New York, N.Y.: Springer.
- Pineda-García, F., Paz, H. & Meinzer, F.C. (2013) Drought resistance in early and late secondary successional species from a tropical dry forest: the interplay between xylem resistance to embolism, sapwood water storage and leaf shedding. *Plant, Cell & Environment*, **36**, 405-418.
- Poorter, L., Bongers, F., Aide, T.M., Almeyda Zambrano, A.M., Balvanera, P., Becknell, J.M., ... Rozendaal, D.M.A. (2016) Biomass resilience of Neotropical secondary forests. *Nature*, **530**, 211-214. doi:10.1038/nature16512
- Powers, J.S., Becknell, J.M., Irving, J. & Pérez-Aviles, D. (2009) Diversity and structure of regenerating tropical dry forests in Costa Rica: geographic patterns and environmental drivers. *Forest Ecology and Management*, **258**, 959-970.
- Quesada, M., Sanchez-Azofeifa, G.A., Alvarez-Añorve, M., Stoner, K.E., Avila-Cabadilla, L., Calvo-Alvarado, Castillo, A., Espírito-Santo, M.M., Fagundes, M., Fernandes, G.W., Gamon, J., Lopezaraiza-Mikel, M., Lawrence, D., Morellato, L.P.C., Powers, J.S., Neves, F.S., Rosas-Guerrero, V., Sayago, R. & Sanchez-Montoya, G. (2009) Succession and management of tropical dry forests in the Americas: Review and new perspectives. *Forest Ecology and Management*, **258**, 1014-1024.
- Quigley, M.F. & Platt, W.J. (2003) Composition and structure of seasonally deciduous forests in the

- Americas. *Ecological Monographs*, **73**, 87-106.
- R Core Team (2019) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Read, L. & Lawrence, D. (2003) Recovery of biomass following shifting cultivation in dry tropical forests of the Yucatan. *Ecological Applications*, **13**, 85-97.
- Rico-Gray, V. & García-Franco, J.G. (1992) Vegetation and soil seed bank of successional stages in tropical lowland deciduous forest. *Journal of Vegetation Science*, **3**, 617-624.
- Roig-Juñent, F.A., Villanueva-Díaz, J., Jiménez-Osornio, J.J., Hayden, W.J., Barajas-Morales, J. & Luckman, B.H. (2012) *Anatomía de maderas en comunidades rurales de Yucatán* INIFAP, Durango, México.
- Romero-Duque, L. P., Jaramillo, V. J. and Pérez-Jiménez, A. (2007). Structure and diversity of secondary tropical dry forests in Mexico, differing in their prior land-use history. *Forest Ecology and Management*, **253**: 38-47.
- Rozendaal, D.M.A., Chazdon, R.L., Arreola-Villa, F., Balvanera, P., Bentos, T.V., Dupuy, J.M., ... Bongers, F. (2017) Demographic drivers of aboveground biomass dynamics during secondary succession in neotropical dry and wet forests. *Ecosystems*, **20**, 340-353.
- Rozendaal, D.M.A., Bongers F., Aide, T.M., Alvarez-Dávila, E., Ascarrunz, N., Balvanera, P...Poorter, L. (2019). Biodiversity recovery of Neotropical secondary forests. *Science Advances*, **5**: eaau3114.
- Ruiz, J., Fandiño, M.C. & Chazdon, R.L. (2005) Vegetation structure, composition, and species richness across a 56-year chronosequence of dry tropical forest on Providencia Island, Colombia. *Biotropica*, **37**, 520-530.
- Salas-Morales, S. H., Schibli, L., Nava-Zafra, A., & Saynes-Vásquez, A. (2007) Flora of the coast of Oaxaca, Mexico (2): floristic annotated list of Huatulco National Park. *Botanical Sciences*, **81**: 101-130.
- Sanaphre-Villanueva, L., Dupuy, J.M., Andrade, J.L., Reyes-García, C., Jackson, P.C. & Paz, H. (2017) Patterns of plant functional variation and specialization along secondary succession and topography in a tropical dry forest. *Environmental Research Letters*, **12**, 055004.
- Schönbeck, L., Lohbeck, M., Bongers, F., Martínez-Ramos, M. & Sterck, F.J. (2015) How do light and water acquisition strategies affect species selection during secondary succession in moist tropical

- forests? *Forests*, **6**, 2047-2065.
- Tilman, D. (1985) The resource-ratio hypothesis of plant succession. *The American Naturalist*, **125**, 827-852.
- van Breugel, M., Bongers, F. & Martínez-Ramos, M. (2007) Species dynamics during early secondary forest succession: recruitment, mortality and species turnover. *Biotropica*, **39**, 610-619.
- Westoby, M. (1984) The self-thinning rule. *Advances in Ecological Research*, **14**, 167-225.
- Whittaker, R.H. (1965) Dominance and diversity in land plant communities. *Numerical relations of species express the importance of competition in community function and evolution*, **147**, 250-260.
- Whitmore, T.C. (1989) Canopy gaps and the two major groups of forest trees. *Ecology*, **70**, 536-538.
- Wickham, H. (2009) ggplot2: elegant graphics for data analysis. Springer, New York.
- Williams-Linera, G., Alvarez-Aquino, C., Hernández-Ascención, E. & Toledo, M. (2010) Early successional sites and the recovery of vegetation structure and tree species of the tropical dry forest in Veracruz, Mexico. *New Forests*, **42**, 131-148.
- Wood, S. & Scheipl, F. (2014) gamm4: Generalized additive mixed models using mgcv and lme4. R package version 0.2-3.
- Zapata, T.R. & Arroyo M.T.K. (1978) Plant reproductive ecology of a secondary deciduous tropical forest in Venezuela. *Biotropica*, **10**, 221-230.

For Supporting Information see annexes of Chapter 2 at the end of this thesis

Supporting Information 1

Table S1. List of species included in the study, along with their family affiliation and acronyms.

Table S2. Models for presence/absence (PA) and basal area (BA) responses to successional age for 50 species of a tropical dry forest.

Table S3. Range of age presence (years of abandonment) in the successional gradient of the 50 species included in the study, the number of plot-age combinations in which they are present (plot-age frequency), and their corresponding ranks.

Figure S1. Diagrams depicting model construction and selection for presence/absence (PA) data. (a) Construction of the PA0 model. (b) Construction of the PA1 model. (c) Model comparison and selection.

Figure S2. Diagrams depicting the model construction and selection for basal area (BA) data. (a) Construction of the BA0 model. (b) Construction of the BA1 model. (c) Model comparison and selection.

Supporting Information 2

Patterns of basal area changes of 50 species during secondary succession in a tropical dry forest in southern Mexico.

CAPÍTULO 3

Wood anatomy of dominant species with contrasting ecological performance in tropical dry forest succession

Romero, E., González, E.J., Meave, J.A. y Terrazas, T. (2020). Wood anatomy of dominant species with contrasting ecological performance in tropical dry forest succession, *Plant Biosystems - An International Journal Dealing with all Aspects of Plant Biology*, **154**: 524-534. <https://doi.org/10.1080/11263504.2019.1651775>





Wood anatomy of dominant species with contrasting ecological performance in tropical dry forest succession

Eunice Romero^{a,c} , Edgar J. González^a , Jorge A. Meave^a  and Teresa Terrazas^b 

^aDepartamento de Ecología y Recursos Naturales, Facultad de Ciencias, Universidad Nacional Autónoma de México, Ciudad Universitaria, Mexico City, Mexico; ^bInstituto de Biología, Universidad Nacional Autónoma de México, Ciudad Universitaria, Mexico City, Mexico; ^cPosgrado en Ciencias Biológicas, Unidad de Posgrado, Circuito de Posgrados, Ciudad Universitaria, Mexico City, Mexico

ABSTRACT

Environmental restrictions faced by successional species (those occurring in recovering vegetation) change gradually between early and late succession. In tropical dry forest (TDF), legume species dominate early succession, that is, accumulate more biomass than coexisting species, but later are gradually replaced by late successional species. Stem anatomical traits are involved in water conduction efficiency and safety, and thus biomass accumulation. We hypothesized that anatomical characteristics of dominant species may explain their status in their respective successional community. We analyzed the wood anatomy of TDF dominant successional species: *Mimosa eurycarpa* and *M. tenuiflora* (early successional), *Lysiloma divaricatum* (late successional), and *Euphorbia schlechtendalii* (successionally ambiguous). Anatomical variables and indices were estimated and compared between species through linear modeling. Unexpectedly, *Mimosa* species differed in porosity type, which is one characteristic linked to water stress tolerance. *M. eurycarpa* and *L. divaricatum* are ring-porous (an uncommon feature in tropical species), whereas *M. tenuiflora* and *E. schlechtendalii* displayed diffuse porosity. *M. eurycarpa* had the lowest vulnerability index (VI) and the highest relative hydraulic conductivity. Within-individual differences in relative water conduction in ring-porous species, driven by high vessel density in earlywood and low VI in latewood, likely represent a highly advantageous strategy in water-stressed successional environments.

ARTICLE HISTORY

Received 15 December 2018
Accepted 15 July 2019

KEYWORDS

Earlywood; fiber dimensions; latewood; relative hydraulic conductivity; Runkel ratio; vessel density; vessel diameter; vulnerability index



Introduction

When a site that underwent severe anthropogenic modifications is abandoned, the plant community can recover through secondary succession (Drury and Nisbet 1973; Pickett 1976). As this process unfolds vegetation cover and biomass increase, and species turnover takes place. In advanced successional stages, some communities attain attributes similar to those existing in the pre-disturbance condition (Whittaker 1953; Finegan 1996). Tropical dry forest (TDF) occurs in tropical regions with a well-marked dry season lasting up to seven months, which may result in high water stress for plants (Brown and Lugo 1990). Deforestation for agriculture or livestock ranching enhances such regional climatic constraints, as sites devoid of vegetation cover are subjected to high temperatures and solar irradiance (Lebrija-Trejos et al. 2011; Pineda-García et al. 2013). Thus, species occurring in recovering communities face continuous changes in resource availability and environmental conditions, such as water, space and light, which in turn are driven by the development of plant community structure (Lebrija-Trejos et al. 2010b).

Temporal changes in species composition largely reflect contrasting performances among species, because not all of

them are able to survive, grow and reproduce under these changing conditions in a successional community (Connell and Slatyer 1977; Pineda-García et al. 2016). Particularly, early secondary TDF vegetation across large areas in the Neotropics consists of a thorny low forest dominated by different species of *Acacia* and *Mimosa*, which are prevalent in the forest for at least 20 years, but often persist in it for several more decades (Burgos and Maass 2004; Lebrija-Trejos et al. 2010a). With time, these legume species are gradually replaced by late successional or typical mature forest species (Lebrija-Trejos et al. 2010a).

Also, species replacements are largely associated with the different functional traits they have, among which anatomical features can be important. Plants interact with their environment and uptake resources through their roots, stems and leaves (Durante et al. 2011), and these organs' traits determine their functions (Carlquist 2001). Given the underlying link between structure and function, the wood anatomical features of the stem affect the amount of biomass accumulated by a plant (Craven et al. 2013), its growth speed (Hoeber et al. 2014), as well as water conduction efficiency and safety (Pratt et al. 2007; Lens et al. 2013). Three

CONTACT Teresa Terrazas  tterrazas@ib.unam.mx  Instituto de Biología, Universidad Nacional Autónoma de México, Ciudad Universitaria, Mexico City, Mexico

 Supplementary data for this article is available online at <https://doi.org/10.1080/11263504.2019.1651775>.

© 2019 Società Botanica Italiana

basic cell types make up the wood in angiosperm stems, namely fibers, vessel elements and parenchyma cells, with each of these bearing different functions and production costs. Lignin accumulation in the secondary walls of fibers is directly related to cell diameter and cell wall thickness; such accumulation results in wood that is hard and more resistant to mechanical damage, although these two latter properties require larger biomass investments (Larjavaara and Muller-Landau 2010). Vessel lumen diameter is associated with wood hydraulic properties, as wider vessels conduct more water (Zimmermann 1983). However, a mechanical trade-off is also implied, as the risk of embolism heightens with an increase in vessel lumen diameter if soil water is limited (Cochard 2006). Vessel density and distribution also influence water conductance safety (Ewers et al. 2007; Zanne et al. 2010; von Arx et al. 2013). Redundancy in the hydraulic architecture of a tree is given by a large density of vessels along with an increased level of vessel grouping. A potential consequence of redundancy is that if one vessel is blocked, water could continue its movement to adjacent vessels through their contiguous walls (Tyree et al. 1994; Cruziat et al. 2002). When water is scarce, some vessels may become inoperative due to air embolism, and in these cases redundancy may be useful to maintain water transport through alternative routes (Ewers et al. 2007). Parenchyma spatial arrangement has been associated with maintenance of water transport through refilling of embolized conduits and with embolism prevention by conferring high hydraulic capacitance (Morris et al. 2016). Also it has been found that angiosperm species with large vessels tend to have axial parenchyma packed around them, suggesting an important role in long-distance xylem water transport (Morris et al. 2018). Water availability at the time of conduit development is closely linked to final cell size, and thus, it affects conduit diameter size (Gartner et al. 1990). In some species classified as ring-porous, large differences in vessel diameter and fiber wall thickness between the early and late phases of the wood growing period allows the distinction between earlywood (produced early in the season) from latewood (produced later in it). In contrast, in species with diffuse porosity latewood may be sometimes recognized exclusively by few layers of more lignified fibers or by marginal parenchyma (Tarelkin et al. 2016). In ring-porous species, earlywood vessels with large diameters display different efficiency and vulnerability hydraulic properties that differ from latewood vessels with small diameters, and this has been interpreted as one of the major adaptations among temperate trees (IAWA 1989; Woodcock 1994; Domec and Gartner 2002).

Species occurring in recovering vegetation (which can be collectively referred to as successional species) face environmental restrictions that gradually change in nature and intensity between early and late successional stages. We hypothesized that, among these successional species, the dominant ones, which make the largest contribution in biomass to a successional community, display important anatomical characteristics that may explain their status in the community. Specifically, we expected dominant species at early stages to have wood anatomical features associated

with low hydraulic vulnerability, which ultimately enhances their ability to withstand water stress. Similarly, we expected dominant species at late successional stages to display anatomical features associated with an efficient resource uptake that enhances growth rates, biomass accumulation, and mechanical support. To test this hypothesis, for every dominant species in the early and late communities of a tropical dry forest, we: (1) quantified various anatomical traits, including vessel and fiber dimensions, and vessel distribution; (2) estimated their relative hydraulic conductivity and the vulnerability index; and (3) compared these variables between species.

Material and methods

Study area

The study was conducted in Nizanda, Oaxaca, southern Mexico (16° 39' 30" N, 95° 00' 40" W). Although mature TDF still covers large areas in the region, agriculture has been practiced there for a very long time, which explains the numerous secondary vegetation patches of different ages across the region (Gallardo-Cruz et al. 2012). Mean annual temperature is 27.6 °C and average total annual rainfall is 902.6 ± 355.4 mm (±SD), with 90% of it falling during the rainy season; in addition to the strong seasonality, annual precipitation is highly unpredictable, as indicated by the coefficient of variation (39.7%; CICESE 2015).

Secondary succession in the study area and species selection

The abandonment of agricultural fields triggers a secondary succession process that has been studied extensively in the region (Lebrija-Trejos et al. 2008; Brienen et al. 2009; Lebrija-Trejos et al. 2010a, 2010b, 2011). Regarding TDF successional environmental gradient characterization, forest structure changes significantly with time shaping the local environment (basal area from 0 to 25 m²/ha and total crown cover from 0 to 7.2 m; Lebrija-Trejos et al. 2008, 2010b). During wet season, soil water availability and relative humidity are greater in late-successional sites than early ones (soil water potential changed significantly from -45 to -18 kPa and relative humidity from 67 to 74%), while vapor pressure deficit decreased around 0.5 kPa from early to old sites; light as well as air and soil temperatures decrease with plant community development (75–15% of open-sky radiation, 31.7 to 29.3 °C and +2.5 °C to -0.5 °C relative to ambient, respectively), which makes early-successional sites sunny, hot, and dry (Lebrija-Trejos et al. 2010b, 2011).

For this study, we selected the dominant species based on previous knowledge about their ecological performance (i.e., presence and abundance along the successional gradient; Pérez-García et al. 2001; Gallardo-Cruz et al. 2005; Lebrija-Trejos et al. 2010a; Pérez-García et al. 2010; Romero-Pérez 2014; Romero et al. submitted). Only three species stand out as being dominant in the secondary vegetation of Nizanda (i.e., they attain high basal area and high density of

individuals in comparison with other species also present in the recovering vegetation: *Mimosa eurycarpa* Robinson, *Mimosa tenuiflora* (Willd.) Poir in early successional plots, and *Lysiloma divaricatum* (Jacq.) J.F. Macbr. (Fabaceae) in late successional plots.

In Nizanda, recovering tropical dry forest is a diverse community, with the presence of at least 57 woody species (Lebrija-Trejos et al. 2010a). The majority of these successional species (50) have been also recorded in mature tropical dry forest stands of the region and are considered typical of it (Pérez-García et al. 2010). For this study, we selected two of the seven successional species absent in the mature forest, namely *M. eurycarpa* and *M. tenuiflora*. We also selected two species from the large group occurring in secondary forests, having different abundance patterns along the successional gradient (Romero-Pérez 2014), and also occurring in mature forest stands, namely *L. divaricatum* (present from early to late successional plots, it attains higher basal area values in late successional plots and also in mature forest plots), and *Euphorbia schlechtendalii* Boiss. (Euphorbiaceae, present from middle to late successional plots and also present in mature forest of the study region).

Regarding dominance patterns of the selected species, the two *Mimosa* are notorious for their dominance at early stages of succession, although *M. eurycarpa* is more frequent than *M. tenuiflora*. Both *Mimosa* species are still dominant during the subsequent four decades of succession, after which they gradually lose dominance. These *Mimosa* species can persist as big trees (up to ca. 9 m tall and 18 cm DBH [diameter at 1.30 m]) in successional stands as old as 60 years or more, but with very low frequencies. In contrast, *Lysiloma divaricatum* (up to 11 m tall and 27.3 cm DBH in successional stands) is a nonthorny Fabaceae that occurs in stands as young as two years old, where it has a low frequency, although it gradually becomes the only dominant species in late successional stages.

The reason to include *Euphorbia schlechtendalii* in the study was somewhat different. Unlike the aforementioned legumes, this species does not attain dominance at any stage of the successional gradient. However, there is an interesting ecological ambiguity related to it: in the TDF of Nizanda this is a relatively common mature forest species (Gallardo-Cruz et al. 2005), as well as a successional species, as its presence has been recorded in secondary stands as young as 25 years of age (Romero-Pérez 2014). Yet, *E. schlechtendalii* has been reported as an early dominant species in secondary TDF stands in other regions of Mexico differing in latitude and precipitation (Trejo-Vázquez 1998). We expected that the comparative analysis of its wood anatomy would be useful as a first insight into explaining its successional ambiguity.

Sample collection

Three adult healthy-looking individuals with straight stems of each species were selected in the field (see Appendix 1 in [Supplementary material](#)). A wood sample was collected with a saw from the main stem of each individual, and

immediately fixed in a glycerin–ethanol–water solution (1:1:1), in which they remained for three months until sectioning. Transverse, tangential and radial sections (20 μm thick) were cut with a sliding microtome (Leica 2000 R, Wetzlar, Germany). The sections were dehydrated with ethanol (50%, 70%, and 96%), stained with safranin-fast green, and mounted with synthetic resin.

Anatomical description and measurements

Wood anatomical traits were described following IAWA recommendations (IAWA 1989) with an optical Olympus microscope. All vessel and fiber variables were measured with Image Pro v. 6.1. We measured the tangential vessel diameter of 45 vessels per individual of diffuse-porous species, and 90 vessels per individual in ring-porous species (45 earlywood and 45 latewood vessels), as we distinguished differences within the same growth ring. For each individual, in 10 optical microscopic fields at 4X zoom (area in one optical field = 3 mm²), we counted the number of vessels, the number of vessel groups, and the number of vessels per group. In the case of fibers, tangential diameter and lumen diameter we measured 50 cells per individual.

Statistical analyses

Generalized linear mixed-effects models (GLMM) were constructed to describe and compare mean anatomical traits among species (Appendix 2 in [Supplementary material](#)). For every response variable (vessel tangential diameter, number of vessels/3 mm², number of vessels per group, fiber diameter, and fiber lumen) we constructed two basic models: a model assuming differences in the estimated means between species, and a model that did not assume this (null model). Further models were constructed to examine the influence of explanatory variables: porosity type, earlywood vs latewood, family, and dominance in early succession (see Appendix 2 in [Supplementary material](#)). Model selection for each response anatomical variable was performed using the sample-corrected Akaike Information Criterion (AICc; Burnham and Anderson 2003). Model fitting was performed in R (R Core Team 2015), using the lme4 package (Bates et al. 2015).

We explored two appropriate probability error distributions for each anatomical response variable (Appendix 2 in [Supplementary material](#)): for positive continuous variables (i.e., vessel diameter, fiber diameter, and fiber lumen), we used the log-normal and gamma distribution; for the number of vessels per 3 mm², models assumed either a Poisson or a negative binomial distribution; and for the number of vessels per group, the error distribution was either a one-inflated Poisson or a one-inflated negative binomial. One-inflated distributions were used because of the large number of solitary vessels (which were taken as groups containing one vessel element only).

All derived variables (i.e., not measured directly in the wood sample) were not modeled but calculated from the means estimated from the above-mentioned models. We calculated mean number of vessels per mm² as:

mean number of vessels per $3 \text{ mm}^2/3$,

mean fiber wall thickness was calculated as:

$$(\text{mean fiber diameter} - \text{mean fiber lumen})/2,$$

and the mean Runkel ratio as:

$$2 \times (\text{mean fiber wall thickness}/\text{mean fiber lumen}).$$

Finally, for each species, we calculated the relative hydraulic conductivity (RHC; Fahn et al. 1986) as:

$$r^4 \times \text{number of vessels}/\text{mm}^2,$$

where r is vessel radius, and the vulnerability index (VI; Carlquist 1977) as:

$$\text{vessel tangential diameter}/\text{number of vessels per mm}^2$$

Results

General wood features

Growth rings were typically delimited by radially flattened latewood fibers, which were associated with marginal parenchyma in the three legumes (Figures 1, 2). *L. divaricatum* and *M. eurycarpa* had ring-porous wood, whereas *E. schlechtendalii* and *M. tenuiflora* presented diffuse-porous wood. In all four species, most vessels were solitary or in small groups, although clusters up to seven vessels were observed in *M. tenuiflora* and up to eight in *E. schlechtendalii*. Vessel elements had simple perforation plates and alternate intervacular pits. Distribution of axial parenchyma was apotracheal and paratracheal; in particular, it was apotracheal reticulate in *E. schlechtendalii* (Figure 2(D)), vasicentric to confluent in *L. divaricatum* and in *M. eurycarpa* (Figure 2(A,C)), and aliform to confluent bands in *M. tenuiflora* (Figures 1(B)). Regarding cell contents, starch grains were common (Figure 2(B)), and the legumes showed abundant crystalliferous strands. In all four species, fibers had very small simple pits and abundant gelatinous fibers in bands, mostly in the latewood. Rays were heterogeneous uni-, bi- to 4-seriate, with laticifers in *E. schlechtendalii* and homogeneous bi- to 3-seriate in *M. eurycarpa* and *L. divaricatum* but uni to bi-seriate in *M. tenuiflora* (Figure 1(E-H)).

Among species comparison of anatomical features

Quantitative features describing the wood of the four successional tree species are shown in Appendix 3 (vessel dimensions and vessel distribution estimated means), Appendix 4 (fiber estimated dimensions), and Appendix 5 (RHC and VI), in Supplementary material. Some differences between species were observed regarding vessel diameter. Ring-porous wood species (*L. divaricatum* and *M. eurycarpa*) had smaller vessel diameters than diffuse-porous species (*E. schlechtendalii* and *M. tenuiflora*) (Appendix 2 shows that "earlywood vs latewood" model had the lowest AICc, indicating differences in vessel diameter; Figure 3(A, C, D) and Appendix 3 shows which estimated means differ between them: see confidence intervals around each mean; any overlapping of upper or lower limits indicate no significant differences). When the

wood of ring-porous species was divided into earlywood and latewood, vessel dimensions of species with diffuse porosity (whole-wood) turned out to be equal to those of the earlywood vessels produced by ring-porous species (Figure 3(B)). The vessel diameter model that included porosity type (which establishes that mean vessel diameter differs between diffuse- and ring-porous species) was the best supported (Appendix 2 in Supplementary material), showing that mean vessel diameter in latewood was smaller than mean vessel diameter in earlywood, and also smaller than in whole wood (Figure 3(B)). Among the four species, *M. eurycarpa* had considerably greater number of vessels per mm^2 (Figure 4(A)), whereas vessel abundance did not differ between the other species.

Although *E. schlechtendalii* had on average more vessels per group than the other species (Figure 4(B); Appendix 3 in Supplementary material), data produced insufficient evidence to conclude that the number of vessels per group differs between species (i.e., null model and species model were equally supported; Appendix 2). On average, all species had 1.56 vessels per group (Appendix 3 in Supplementary material). However, the confidence interval around the estimated mean for *E. schlechtendalii* (as many as 2.88 vessels per group) was broader than for the other species (Figure 4(B)). Mean fiber diameters differed between diffuse- and ring-porous species, as the porosity-type model had the lowest AICc among all models considered (Appendix 2 in Supplementary material). Mean fiber diameter did not differ statistically between *E. schlechtendalii* and *M. tenuiflora*, and neither did it differ between *L. divaricatum* and *M. eurycarpa* (Figure 4(C)). Fiber lumina was larger for *E. schlechtendalii* (family model was the best supported model, Appendix 2; Appendix 4), and Runkel ratio was lower than that for the legume species (Figures 4(D), 5; Appendix 5 in Supplementary Materials). Fiber wall thickness differed among all species, with *M. tenuiflora* having the thickest fiber walls, and *E. schlechtendalii* the thinnest ones (Figures 4(E), 5).

Figure 6 shows the comparisons of RHC and VI among species. RHC did not differ between the earlywood of *M. eurycarpa* and the whole-wood of *M. tenuiflora*, although it was more variable in the former. The whole-wood of *M. tenuiflora* and *E. schlechtendalii*, and the earlywood of *L. divaricatum* shared equally high VI and equally low RHC values; in contrast, the latewood of both *L. divaricatum* and *M. eurycarpa* had equally low values for RHC.

Discussion

In this study, we hypothesized that xylem anatomical traits of dominant early and late successional species could explain, at least partially, their dominance in their respective communities during secondary succession. We found that the two main dominant successional species, namely *Mimosa eurycarpa* (in early succession) and *Lysiloma divaricatum* (in more advanced stages; see Methods), are ring-porous, an anatomical feature that may confer on them the expected hydraulic properties; apparently, *M. eurycarpa* shows low

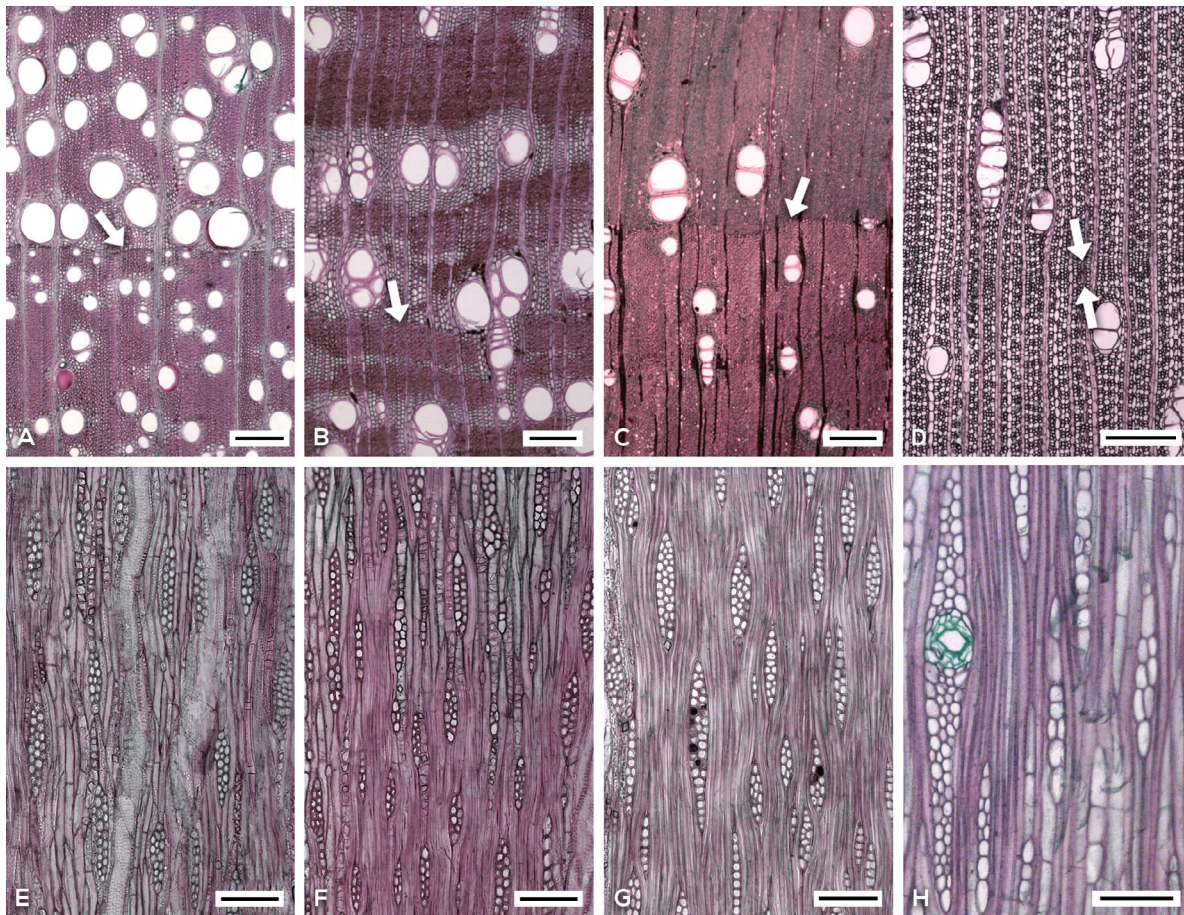


Figure 1. Anatomical comparison of four important successional tree species in a tropical dry forest. (A–D) Transverse sections; growth mark boundary is highlighted with an arrow. (E–H) Tangential sections showing rays. (A, E) *Mimosa eurycarpa*. (B, F) *Mimosa tenuiflora*. (C, G) *Lysiloma divaricatum*. (D, H) *Euphorbia schlechtendalii*. Bar is 200 μm in A–C, 100 μm in E–H; 300 μm in D.

hydraulic vulnerability in the dry season, whereas *L. divaricatum* displays an efficient water uptake in the rainy season. Surprisingly, we did not observe the expected similarities between the two early successional dominant species, with the most striking difference being related to porosity type.

L. divaricatum, the only dominant late successional species, also occurs in early successional sites; we thus foresaw the presence of certain characteristics in its wood that could somehow allow this species to withstand the limiting water conditions prevailing in those sites. In consistency with this expectation, we found evidence suggesting that its latewood is hydraulically safe, while the RHC of its earlywood is virtually the same as that recorded for the whole-wood of *M. eurycarpa*. Although no differences were found for vessel diameter in the latewood of these two species, the lower vessel density in *L. divaricatum* likely imposes a limit to its performance in early succession, as it cannot attain high water conduction. Moreover, its earlywood has high VI values, which implies that *L. divaricatum* may not be able to recover readily after the severe water stress experienced under these conditions. In both ring-porous species, there are probably variable degrees of hydraulic efficiency and security in their wood, as indicated by the differences between earlywood and latewood; such within-stem functional differentiation has been observed for several temperate forest species (Woodcock 1994; Domec and Gartner

2002), as well as in some tropical taxa from very dry regions (Fichtler and Worbes 2012). The ring-porous species studied by us seem to have an efficient water uptake in the rainy season, while the features of the vascular tissue produced in the dry season may be rather associated with hydraulic safety (Domec and Gartner 2002). Notoriously, earlywood vessels observed in the different species resemble each other more closely than the vessels of earlywood and latewood produced by the same species (Figure 3(B)). The high variability between early- and latewood emerges as a potentially important feature associated with their dominance.

Vessel density and degree of vessel grouping (number of vessels per group) are variables associated to the maintenance of the hydraulic function under drought stress, with vessel redundancy being the underlying mechanism (Ewers et al. 2007). Our results showed that vessel grouping did not differ significantly among the four species, so probably this feature does not play a functional role as important as previously thought (Halis et al. 2014; Ayup et al. 2015) or it can be related to the occurrence of paratracheal parenchyma. Yet, further studies are needed to confirm these possibilities.

Regarding RHC, the two early dominant species (*M. eurycarpa* and *M. tenuiflora*) appear to have a greater capacity to conduct water than the dominant species in more advanced stages (*L. divaricatum*), with *M. eurycarpa* being the species that attains the highest mean value and variability in its

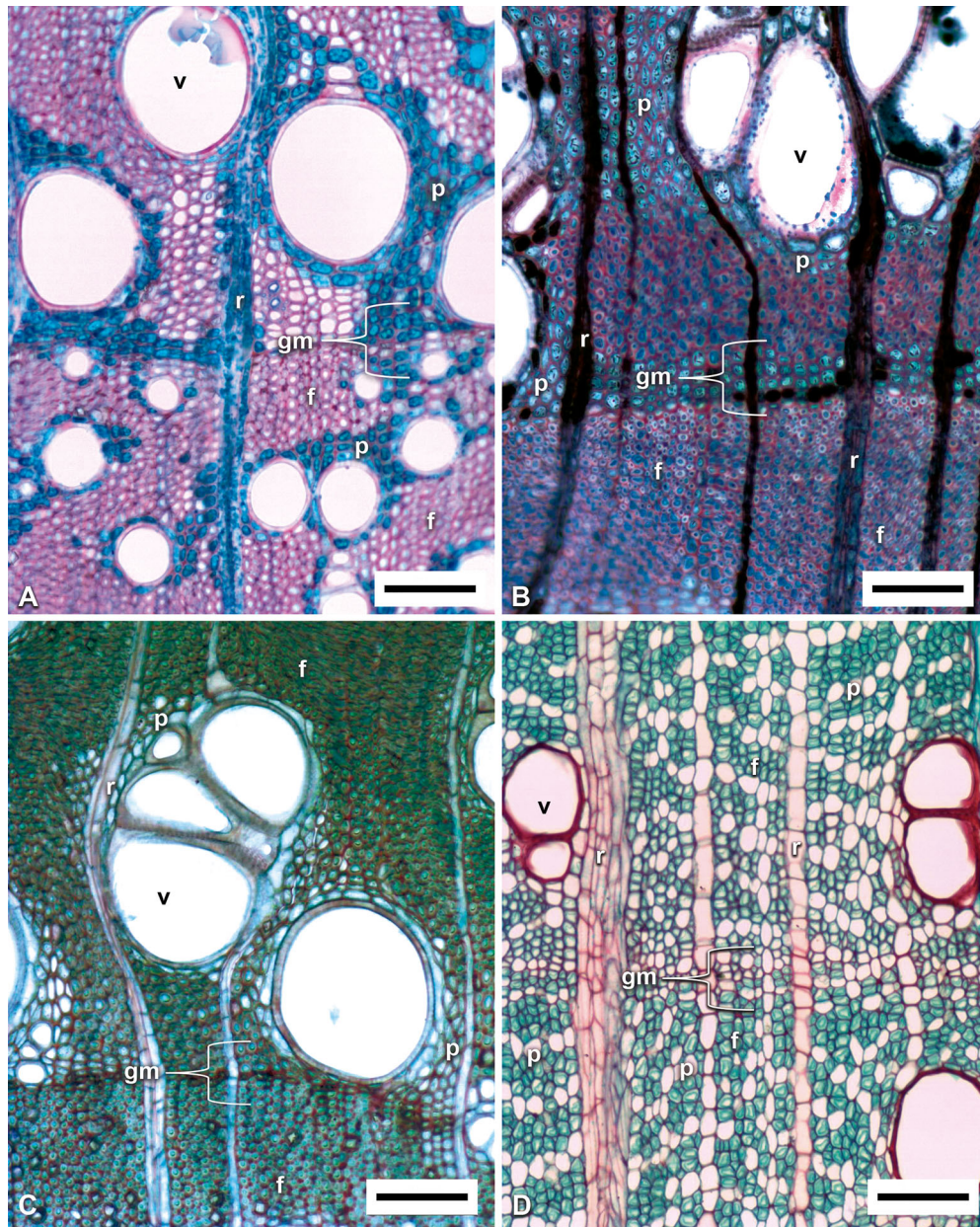


Figure 2. Detail of anatomical cell types view in transverse sections. (A) *Mimosa eurycarpa*. (B) *Mimosa tenuiflora*. (C) *Lysiloma divaricatum*. (D) *Euphorbia schlechtendalii*. Bar is 100 μm . f = fiber, gm = growth mark, p = axial parenchyma, r = ray, v = vessel.

earlywood. In *M. tenuiflora*, whole-wood RHC was undistinguishable from earlywood RHC in *M. eurycarpa*, although this lack of difference was mostly due to the large variation in vessel diameter and distribution in *M. eurycarpa*. It is likely that this variation allows for rapid adjustments in *M. eurycarpa* to changes in water availability throughout the year (Fichtler and Worbes 2012).

E. schlechtendalii and, unexpectedly, *M. tenuiflora* showed high VI. This result was expected for *E. schlechtendalii* given its absence in the early-successional water-stressed environment, but not for *M. tenuiflora*, given its dominance in some early stands. The banded paratraqueal parenchyma in *M. tenuiflora* may be associated with its ability to cope with hydraulic vulnerability, as parenchyma cells surrounding the vessels can store water, thus protecting them from hydraulic failure (Taneda and Sperry 2008; Zheng and Martínez-

Cabrera 2013; Trifilò et al. 2014; Carlquist 2015). *M. tenuiflora* has nearly as much mean percentage of parenchyma per 2 mm^2 ($24.6\% = 5\%$ radial plus 19.6% axial) as *E. schlechtendalii* ($31.5\% = 19.8\%$ radial + 11.7% axial) and more than *M. eurycarpa* ($14.5\% = 3.8\%$ radial + 10.7% axial) and *L. divaricatum* ($21.5\% = 8.2\%$ radial + 13.3% axial). Moreover, *M. tenuiflora* also seems to have the highest amount of axial parenchyma of the four species (19.6% ; unpublished data) which may increase the probability of connection with vessels, thus influencing water transport maintenance. This parenchyma feature may be associated with the persistence of the leaves in *M. tenuiflora*, as this species retains its foliage for a longer time than *M. eurycarpa* (Maldonado-Romo 2014). Moreover, we also observed in *M. tenuiflora* a RHC similar to the most dominant successful species (*M. eurycarpa*, Figure 6(A)); together with the above-described parenchyma

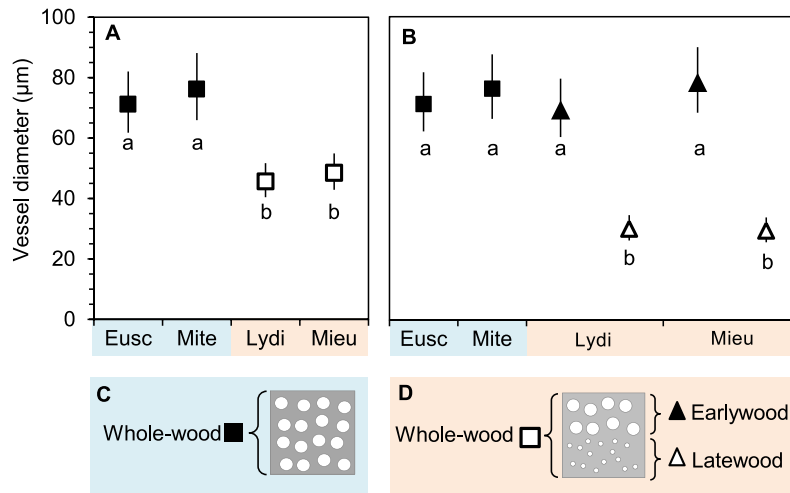


Figure 3. Anatomical comparison of vessel diameter estimated means of four successional tree species in a tropical dry forest. Different letters indicate significant differences. Eusc, *Euphorbia schlechtendalii*; Mite, *Mimosa tenuiflora*; Lydi, *Lysiloma divaricatum*; Mieu, *Mimosa eurycarpa*. (A) Species model; estimated means between species are different. (B) wood zone model; estimated means between wood zones are different. (C) diffuse-porous wood scheme; open circles represent vessels. (D) ring-porous wood scheme; tissue produced during rainy season (closed triangle, earlywood) can be clearly distinguished from tissue produced later during growth season (open triangle, latewood). Confidence intervals are shown. Model comparison was made with AICc.

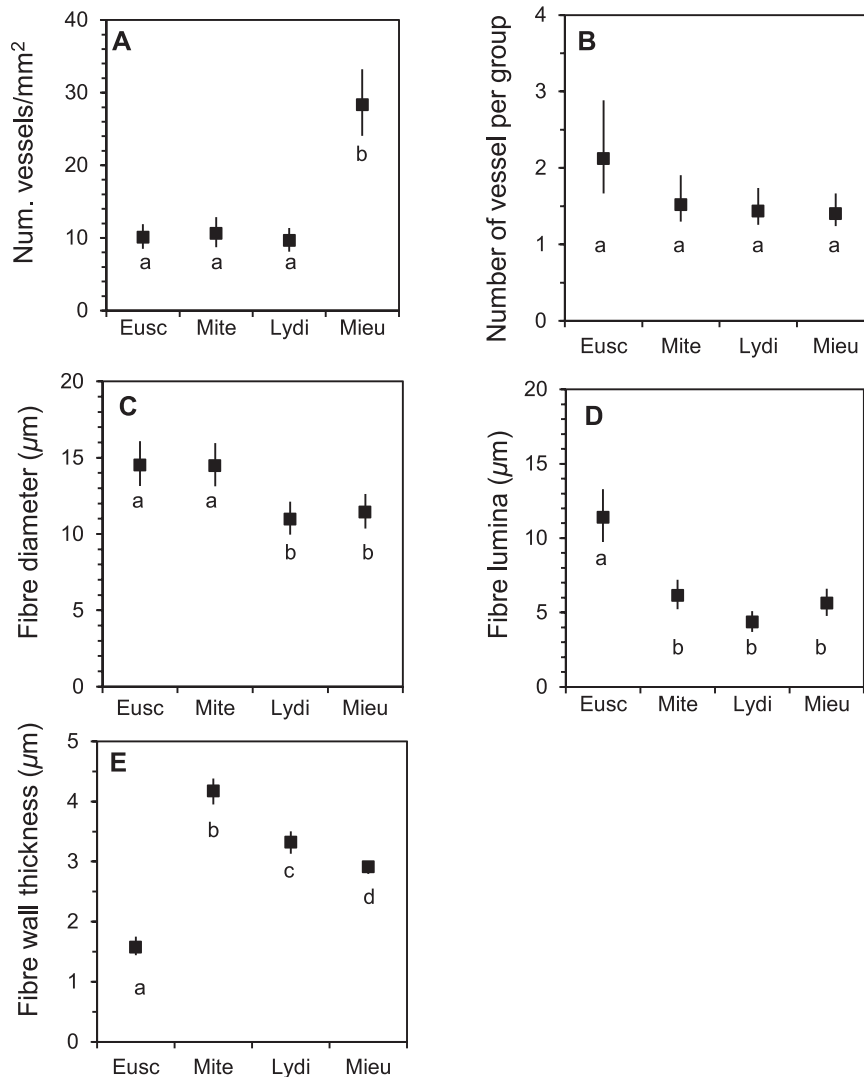


Figure 4. Comparison of anatomical features among four important successional tree species in a tropical dry forest. Different letters indicate significant differences. Eusc, *Euphorbia schlechtendalii*; Mite, *Mimosa tenuiflora*; Lyd, *Lysiloma divaricatum*; and Mieu, *Mimosa eurycarpa*. (A) Number of vessels per mm²; (B) number of vessel per group; (C) fiber diameter; (D) fiber lumina diameter; (E) fiber wall thickness.

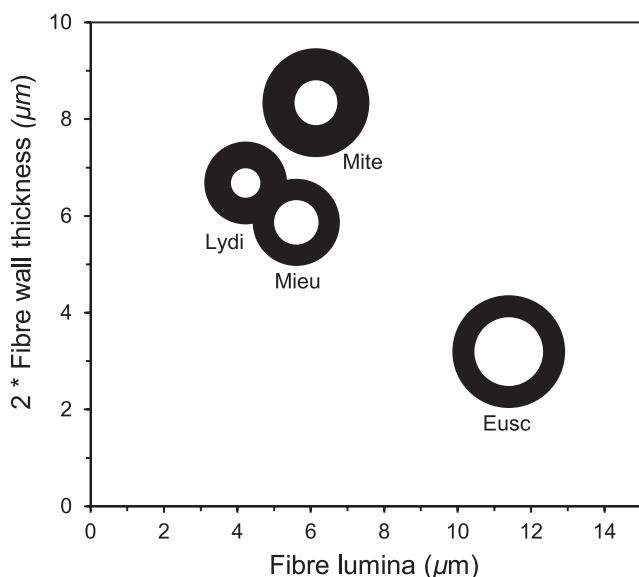


Figure 5. Runkel ratio of four important successional tree species. Open black dots represent estimated mean fiber dimensions (wall thickness, lumen width, and cell width). Eusc, *Euphorbia schlechtdalii*; Mite, *Mimosa tenuiflora*; Lydi, *Lysiloma divaricatum*; Mieu; *Mimosa eurycarpa*.

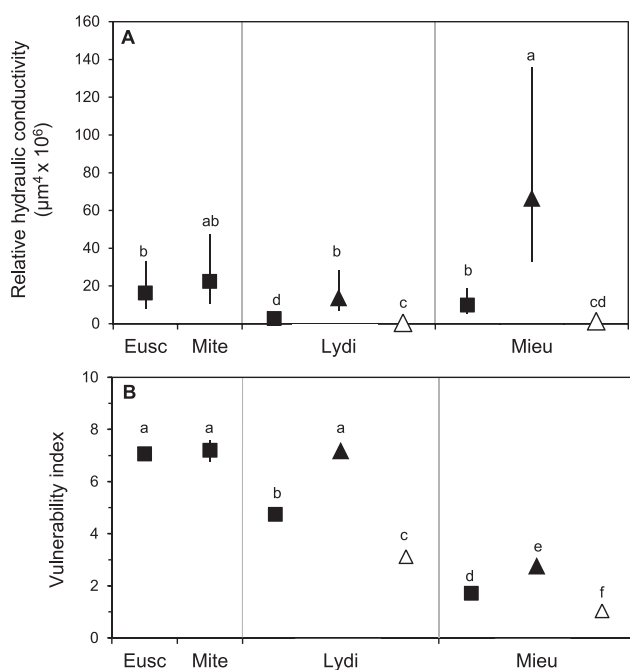


Figure 6. Relative hydraulic conductivity (A) and vulnerability index (B) for four important successional tree species in a tropical dry forest. Eusc, *Euphorbia schlechtdalii*; Mite, *Mimosa tenuiflora*; Lydi, *Lysiloma divaricatum*; Mieu, *Mimosa eurycarpa*. Whole-wood variables of *L. divaricatum* and *Mimosa eurycarpa* were divided in latewood, and earlywood. Closed squares, whole-wood; closed triangles, earlywood; open triangles, latewood.

feature, such high RHC seems to be advantageous for fast biomass production. The combination of these two traits may explain why *M. tenuiflora* can grow successfully in harsh early successional environments. Fiber lumen area, fiber wall fraction, and fiber wall to lumen ratio can explain wood density, which is an important physical property that has been linked with mechanical strength and with a growth-mortality tradeoff (Poorter et al. 2008; Osazuwa-Peters et al. 2017). Thus, regarding biomass production costs Runkel ratio

may indicate how is the trade-off between abundance and lumen vs wall thickness when having similar density.

We anticipated that *E. schlechtdalii* would differ from the three legumes studied both in fiber and vessel dimensions, as well as parenchyma distribution, partly because of its different familial affiliation (Euphorbiaceae). Indeed, their values of fiber diameter, lumina and wall thickness were different from those recorded in the legumes. Nonetheless, its vessel features and associated emergent properties (i.e. RHC and VI) were remarkably similar to those of *M. tenuiflora*. The anatomical features observed in *E. schlechtdalii* (vessel diameter size and distribution, and parenchyma distribution) do not confer hydraulic safety, which is one reasonable explanation for its absence in early successional stages. Future studies on the hydraulic architecture of *E. schlechtdalii* individuals growing in different communities may support this possibility. It is likely that tree height plasticity may explain the ecological success of this species in early stages of other TDFs; the species has been reported to grow as a shrub (I. Trejo-Vázquez pers. comm.), while in our study site, it is a tree as tall as 8 m. Thus, it seems that in Nizanda the height of this species promotes a high hydraulic conductivity, rather than minimizing the risk of xylem hydraulic damage associated with drought, as reported for other tropical species (Rowland et al. 2015; Zach et al. 2010).

Competitive advantages of the most successful early dominant species

Notwithstanding the strong water-related environmental filters operating in early succession, *M. eurycarpa* is remarkable, as it reaches considerably higher basal area values (a common structural variable interpreted as a proxy of biomass production) than any other successional species in early stands, including its congeneric *M. tenuiflora* (Lebrija-Trejos et al. 2011; Romero et al. unpublished). For this reason, we predicted that *M. tenuiflora* would depart from the others in certain anatomical features that would guarantee its success in early succession. In consistency with this idea, *M. eurycarpa* showed the lowest vulnerability index of all species examined, especially for its latewood, so probably this species conducts water even at the end of the growing season.

Our results for *M. eurycarpa* whole-wood suggest that this species does not face the expected trade-off between high efficiency in water conduction at the cost of low water security (Sperry et al. 2008; Gleason et al. 2016); hydraulic safety in this species is likely possible not only due to small vessel diameter, but also to a large investment in large numbers of vessels. The anatomical characteristics of *M. eurycarpa* probably ensure highly efficient water conduction when water is available, while they may reduce its hydraulic vulnerability when this resource is scarce; similar patterns have been reported for other species growing in environments with unpredictable water availability (De Micco et al. 2008). Initially, we anticipated a low RHC for this species. This was true only when the analysis was conducted at the whole-wood level. Conversely, when the analysis was dissected by earlywood and latewood, *M. eurycarpa* turned out to have

the highest RHC in its earlywood among the four species. Such a high RHC is an outcome from its considerably high frequency and diameter of vessels.

One important expectation in our study was that the wood of the two early dominant species, namely *M. eurycarpa* and *M. tenuiflora*, would largely resemble to each other due to their congeneric status (although they are not so closely related phylogenetically; Simon et al. 2011). Surprisingly, our results revealed large differences in their anatomical features, the most important of which are porosity type and vessel density, specially ring porosity, which is a rare trait in Mimosoideae (Evans et al. 2006).

Although the two early congeneric dominant species (*M. eurycarpa* and *M. tenuiflora*) have similar ecological behaviors (Lebrija-Trejos et al. 2008; Romero et al. submitted; see Methods), *M. tenuiflora* does not make a structural contribution to successional forests as high as that of *M. eurycarpa*. The diffuse porosity of *M. tenuiflora* probably enables this species to attain a high hydraulic efficiency in the rainy season, and thus to accumulate biomass rapidly; however, such vessel features may also entail high costs in hydraulic safety during the dry season. Considering vessel diameter, we may conclude, in agreement with Montaña-Arias et al. (2013), that *M. tenuiflora* is vulnerable to hydraulic stress. This may well be an explanatory factor of the comparatively lesser dominance of *M. tenuiflora* in the regional TDF secondary succession.

Considerations on the statistical analysis

Anatomical variation among and within species is high, and there is a large variety of procedures to quantify it (Scholz et al. 2013). At present, there is a strong need for standardized statistical analysis of anatomical features (Ewers and Fisher 1989; Mencuccini et al. 2010; von Arx et al. 2013; Wegner et al. 2013). In fact, some wood anatomical studies have overlooked statistical issues (Montaña-Arias et al. 2013). For example, since multiple measurements are usually performed in a single individual, no independence can be assumed among them, and thus pseudoreplication becomes a problem when making inferences (Hurlbert 1984; Lazic 2010). A solution is to average over all measurements done on the same individual (Hurlbert 1984; Kroodsmá et al. 2001); however, this procedure largely reduces sample size, which can strongly affect statistical power (Schank and Koehnle 2009). A better option is the use of mixed models, which account for both the within- and between-individual variation, providing more accurate estimates than those obtained assuming independence (Lazic 2010). This is the statistical approach we used in this study. Furthermore, an additional consideration is the error distribution we assume on the response variable. Given that such distribution is not known *a priori*, the exploration of alternative distributions is advisable (Dick 2004). We suggest that our analytical approach be routinely applied in the study of many anatomical variables often measured repeatedly on a single individual.

Concluding remarks

Our results suggest that the two early dominant species display different strategies to cope with drought stress in early successional stages. By examining earlywood and latewood separately, which has commonly been done for temperate species (Woodcock 1994; Domec and Gartner 2002) but infrequently for tropical trees, we were able to observe differences in RHC and VI within a single individual. Such variation, along with a high vessel density, could be the key to the ecological success of the pioneer *M. eurycarpa*, as this combination of anatomical characteristics seems to be advantageous. Among the four studied species, *M. eurycarpa* is apparently characterized by the lowest VI during the dry season and the highest RHC during the rainy season. New studies are needed to further support this conclusion. Within-individual differences in relative water conduction in successional ring-porous species, driven by high vessel density and diameter in earlywood and low VI in latewood, seems to represent a highly advantageous strategy in water-stressed successional environments.

Acknowledgements

This study is part of the requirements for ER to obtain the Doctor of Science degree from the Posgrado en Ciencias Biológicas (PCB), Universidad Nacional Autónoma de México (UNAM). We are grateful to the people of Nizanda for their continued hospitality and support. We thank Francisco Mora and Bartolino Reyes for their assistance in field work, Alicia Rojas for her technical support in laboratory, Bianca Santini for reviewing the manuscript and for her critical ideas, and Julio César Monero Rojas for helping with artwork.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

Funding for this research was provided by the Consejo Nacional de Ciencia y Tecnología (CONACYT), grant no. 270104; and Programa de Apoyo a Proyectos de Investigación e Innovación Tecnológica-Universidad Nacional Autónoma de México (PAPIIT-UNAM); grant no. IN218416.

ORCID

Eunice Romero  <http://orcid.org/0000-0002-8282-3005>
 Edgar J. González  <http://orcid.org/0000-0001-9113-1070>
 Jorge A. Meave  <http://orcid.org/0000-0002-6241-8803>
 Teresa Terrazas  <http://orcid.org/0000-0001-7749-5126>

References

- Ayup M, Chen Y-N, Nyongesah MJ, Zhang Y-M, Rajput VD, Zhu C-G. 2015. Xylem anatomy and hydraulic traits of two co-occurring riparian desert plants. *Iawa J.* 36(1):69–83.
- Bates D, Mächler M, Bolker B, Walker S. 2015. Fitting linear mixed-effects models using lme4. *J Stat Softw.* 67:1–48.
- Brienen RJW, Lebrija-Trejos E, Van Breugel M, Pérez-García EA, Bongers F, Meave JA, Martínez-Ramos M. 2009. The potential of tree rings for

- the study of forest succession in southern Mexico. *Biotropica*. 41(2): 186–195.
- Brown S, Lugo AE. 1990. Tropical secondary forests. *J Trop Ecol*. 6(1): 1–32.
- Burgos A, Maass JM. 2004. Vegetation change associated with land-use in tropical dry forest areas of Western Mexico. *Agric Ecosyst Environ*. 104(3):475–481.
- Burnham KP, Anderson DR. 2003. Model selection and multimodel inference: a practical information-theoretic approach. New York (NY): Springer Science & Business Media.
- Carlquist S. 1977. Ecological factors in wood evolution: a floristic approach. *Amer J Bot*. 64(7):887–896.
- Carlquist S. 2001. Comparative wood anatomy: systematic, ecological, and evolutionary aspects of dicotyledon wood. New York (NY): Springer-Verlag.
- Carlquist S. 2015. Living cells in wood. 1. Absence, scarcity and histology of axial parenchyma as keys to function. *Bot J Linn Soc*. 177(3): 291–321.
- Centro de Investigación Científica y de Educación Superior de Ensenada (CICESE). 2015. Base de datos climatológica nacional (Sistema CLICOM). <http://clicom-mex.cicese.mx> Accessed May 2018 4.
- Cochard H. 2006. Cavitation in trees. *C R Phys*. 7(9–10):1018–1026.
- Connell JH, Slatyer RO. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *Amer Nat*. 111(982):1119–1144.
- Craven D, Hall JS, Ashton MS, Berlyn GP. 2013. Water-use efficiency and whole-plant performance of nine tropical tree species at two sites with contrasting water availability in Panama. *Trees-Struct Funct*. 27(3):639–653.
- Cruziat P, Cochard H, Améglio T. 2002. Hydraulic architecture of trees: main concepts and results. *Ann For Sci*. 59(7):723–752.
- De Micco V, Aronne G, Baas P. 2008. Wood anatomy and hydraulic architecture of stems and twigs of some Mediterranean trees and shrubs along a mesic-xeric gradient. *Trees-Struct Funct*. 22(5):643–655.
- Dick EJ. 2004. Beyond 'lognormal versus gamma': discrimination among error distributions for generalized linear models. *Fish Res*. 70(2–3): 351–366.
- Domec JC, Gartner BL. 2002. How do water transport and water storage differ in coniferous earlywood and latewood? *J Exp Bot*. 53(379): 2369–2379.
- Drury WH, Nisbet CT. 1973. Succession. *J. Arnold Arbor*. 54(3):331–368.
- Durante M, Maseda PH, Fernández RJ. 2011. Xylem efficiency vs. safety: acclimation to drought of seedling root anatomy for six patagonian shrub species. *J Arid Environ*. 75(5):397–402.
- Evans JA, Gasson PE, Lewis GP. 2006. Wood anatomy of the Mimosoideae (Leguminosae). *Iawa J*. 5:1–117.
- Ewers FW, Fisher JB. 1989. Techniques for measuring vessel lengths and diameters in stems of woody plants. *Amer J Bot*. 76(5):645–656.
- Ewers FW, Ewers JM, Jacobsen AL, López-Portillo J. 2007. Vessel redundancy: modeling safety in numbers. *Iawa J*. 28(4):373–388.
- Fahn A, Werker E, Baas P. 1986. Wood anatomy and identification of trees and shrubs from Israel and adjacent regions. Jerusalem: Israel Academy of Sciences and Humanities.
- Fichtler E, Worbes M. 2012. Wood anatomical variables in tropical trees and their relation to site conditions and individual tree morphology. *Iawa J*. 33(2):119–140.
- Finegan B. 1996. Pattern and process in Neotropical secondary rain forests: the first 100 years of succession. *Trends Ecol Evol (Amst)*. 11(3): 119–124.
- Gallardo-Cruz JA, Meave JA, Pérez García EA. 2005. Estructura, composición y diversidad de la selva baja caducifolia del Cerro Verde, Nizanda (Oaxaca), México. *Bot Sci*. 76:19–35.
- Gallardo-Cruz JA, Meave JA, González EJ, Lebrija-Trejos EE, Romero-Romero MA, Pérez-García EA, Gallardo-Cruz R, Hernández-Stefanoni JL, Martorell C. 2012. Predicting tropical dry forest successional attributes from space: is the key hidden in image texture? *PLoS One*. 7(2): e30506.
- Gartner BL, Bullock SH, Mooney HA, Brown VB, Whitbeck JL. 1990. Water transport properties of vine and tree stems in a tropical deciduous forest. *Amer J Bot*. 77(6):742–749.
- Gleason SM, Westoby M, Jansen S, Choat B, Brodribb TJ, Cochard H, Delzon S, Hacke UG, Jacobsen AL, Johnson DM, et al. 2016. On research priorities to advance understanding of the safety–efficiency tradeoff in xylem. *New Phytol*. 211(4):1156–1158,.
- Halis Y, Benhaddya ML, Bachi OE, Lahcini A, Belhamra M. 2014. Vessel deviations as a determinant of intervessel connectivity and hydraulic integrity in the stem wood of six Fabaceae trees. *Trees-Struct Funct*. 28(4):1225–1234.
- Hoerber S, Leuschner C, Köhler L, Arias-Aguilar D, Schuldt B. 2014. The importance of hydraulic conductivity and wood density to growth performance in eight tree species from a tropical semi-dry climate. *For Ecol Manage*. 330:126–136.
- Hurlbert SH. 1984. Pseudoreplication and the design of ecological field experiments. *Ecol Monogr*. 54(2):187–211.
- IAWA Committee. 1989. IAWA list of microscopic features for hardwood identification with an appendix on non-anatomical information. *IAWA Bull Ns*. 10:219–332.
- Kroodsma DE, Byers BE, Goodale E, Johnson S, Liu WC. 2001. Pseudoreplication in playback experiments, revisited a decade later. *Animal Behav*. 61(5):1029–1033.
- Larjavaara M, Muller-Landau HC. 2010. Rethinking the value of high wood density. *Funct Ecol*. 24(4):701–705.
- Lazic SE. 2010. The problem of pseudoreplication in neuroscientific studies: is it affecting your analysis? *BMC Neurosci*. 11(1):5
- Lebrija-Trejos E, Bongers F, Pérez-García EA, Meave JA. 2008. Successional change and resilience of a very dry tropical deciduous forest following shifting agriculture. *Biotropica*. 40(4):422–431.
- Lebrija-Trejos E, Meave JA, Poorter L, Pérez-García EA, Bongers F. 2010a. Pathways, mechanisms and variability of tropical dry forest succession. *Perspect Plant Ecol Evol Syst*. 12(4):267–275.
- Lebrija-Trejos E, Pérez-García EA, Meave JA, Bongers F, Poorter L. 2010b. Functional traits and environmental filtering drive community assembly species-rich tropical system. *Ecology*. 91(2):386–398.
- Lebrija-Trejos E, Pérez-García EA, Meave JA, Poorter L, Bongers F. 2011. Environmental changes during secondary succession in a tropical dry forest in Mexico. *J Trop Ecol*. 27(5):477–489.
- Lens F, Tixier A, Cochard H, Sperry JS, Jansen S, Herbette S. 2013. Embolism resistance as a key mechanism to understand adaptive plant strategies. *Curr Opin Plant Biol*. 16(3):287–292.
- Maldonado-Romo A. 2014. Fenología foliar y reproductiva de la comunidad arbórea del bosque tropical caducifolio en Nizanda, Oaxaca, México. Faculty of Sciences, Bachelor's degree thesis. Mexico City: Universidad Nacional Autónoma de México, p107.
- Mencuccini M, Martínez-Vilalta J, Piñol J, Loepfe L, Burnat M, Alvarez X, Camacho J, Gil D. 2010. A quantitative and statistically robust method for the determination of xylem conduit spatial distribution. *Am J Bot*. 97(8):1247–1259.
- Montaño-Arias SA, Camargo-Ricalde SL, Pérez-Olvera CP. 2013. Ecoanatomía de los elementos de vaso de la madera de cinco especies del género *Mimosa* (Leguminosae-Mimosoideae). *Bot Sci*. 91(1): 1–10.
- Morris H, Plavcová L, Cvecko P, Fichtler E, Gillingham MAF, Martínez-Cabrera HI, McGlenn DJ, Wheeler E, Zheng J, Ziemirńska K, Jansen S. 2016. A global analysis of parenchyma tissue fractions in secondary xylem of seed plants. *New Phytol*. 209(4):1553–1565.
- Morris H, Gillingham MAF, Plavcová L, Gleason SM, Olson ME, Coomes DA, Fichtler E, Klepsch MM, Martínez-Cabrera HI, McGlenn DJ, et al. 2018. Vessel diameter is related to amount and spatial arrangement of axial parenchyma in woody angiosperms. *Plant Cell Environ*. 41(1): 245–260.
- Osazuwa-Peters OL, Wright SJ, Zanne AE. 2017. Linking wood traits to vital rates in tropical rainforest trees: Insights from comparing sapling and adult wood. *Am J Bot*. 104(10):1464–1473.
- Pérez-García EA, Meave J, Gallardo C. 2001. Vegetación y flora de la región de Nizanda, istmo de Tehuantepec, Oaxaca, México. *Acta Bot Mex*. 56: 19–88.
- Pérez-García EA, Meave JA, Villaseñor JL, Gallardo-Cruz JA, Lebrija-Trejos E. 2010. Vegetation heterogeneity and life-strategy diversity in the flora of the heterogeneous landscape of Nizanda, Oaxaca, México. *Folia Geobot*. 45(2):143–161.

- Pickett S. 1976. Succession: an evolutionary interpretation. *Amer Nat.* 110(971):107–119.
- Pineda-García F, Paz H, Meinzer FC. 2013. Drought resistance in early and late secondary successional species from a tropical dry forest: the interplay between xylem resistance to embolism, sapwood water storage and leaf shedding. *Plant Cell Environ.* 36(2):405–418.
- Pineda-García F, Paz H, Meinzer FC, Angeles G. 2016. Exploiting water versus tolerating drought: water-use strategies of trees in a secondary successional tropical dry forest. *Tree Physiol.* 36(2):208–217.
- Poorter L, Wright SJ, Paz H, Ackerly DD, Condit R, Ibarra-Manríquez G, Harms KE, Licona JC, Martínez-Ramos M, Mazer SJ, et al. 2008. Are functional traits good predictors of demographic rates? Evidence from five Neotropical forests. *Ecology.* 89(7):1908–1920.
- Pratt RB, Jacobsen AL, Ewers FW, Davis SD. 2007. Relationships among xylem transport, biomechanics and storage in stems and roots of nine Rhamnaceae species of the California chaparral. *New Phytol.* 174(4):787–798.
- R Core Team. 2015. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. Available: www.R-project.org. Accessed Feb 2017 2
- Romero IE, González EJ, Mejía-Domínguez NR, Pérez-García EA, Bongers F, Meave JA. submitted. Differential performance of 50 canopy tree species through tropical dry forest succession.
- Romero-Pérez IE. 2014. Atributos funcionales y desempeño de especies arbóreas durante la sucesión secundaria de un bosque tropical caducifolio. Faculty of Sciences, Master degree thesis. Mexico City: Universidad Nacional Autónoma de México, p. 88
- Rowland L, da Costa ACL, Galbraith DR, Oliveira RS, Binks OJ, Oliveira AAR, Pullen AM, Doughty CE, Metcalfe DB, Vasconcelos SS, et al. 2015. Death from drought in tropical forests is triggered by hydraulics not carbon starvation. *Nature.* 528(7580):119–122.
- Schank JC, Koehnle TJ. 2009. Pseudoreplication is a pseudoproblem. *J Comp Psychol.* 123(4):421–433.
- Scholz A, Klepsch M, Karimi Z, Jansen S. 2013. How to quantify conduits in wood? *Front Plant Sci.* 4:1–11.
- Simon MF, Grether R, Queiroz LPD, Särkinen TE, Dutra VF, Hughes CE. 2011. The evolutionary history of *Mimosa* (Leguminosae): toward a phylogeny of the sensitive plants. *Am J Bot.* 98(7):1201–1221.
- Sperry JS, Meinzer FC, McCulloh KA. 2008. Safety and efficiency conflicts in hydraulic architecture: scaling from tissues to trees. *Plant Cell Environ.* 31(5):632–645.
- Taneda H, Sperry JS. 2008. A case-study of water transport in co-occurring ring- versus diffuse-porous trees: contrasts in water-status, conducting capacity, cavitation and vessel refilling. *Tree Physiol.* 28(11):1641–1651.
- Tarelkin Y, Delvaux C, De Ridder M, El Berkani T, De Cannière C, Beeckman H. 2016. Growth- ring distinctness and boundary anatomy variability in tropical trees. *Iawa J.* 37(2):275–277.
- Trejo-Vázquez RI. 1998. Distribución y diversidad de selvas bajas de México: relaciones con el clima y el suelo. Faculty of Sciences, PhD thesis. Mexico City: Universidad Nacional Autónoma de México, p 210.
- Trifilò P, Barbera PM, Raimondo F, Nardini A, Gullo M. 2014. Coping with drought-induced xylem cavitation: coordination of embolism repair and ionic effects in three Mediterranean evergreens. *Tree Physiol.* 34(2):109–122.
- Tyree MT, Davis SD, Cochard H. 1994. Biophysical perspectives of xylem evolution: is there a tradeoff of hydraulic efficiency for vulnerability to dysfunction?. *Iawa J.* 15(4):335–360.
- von Arx G, Kueffer C, Fonti P. 2013. Quantifying plasticity in vessel grouping-added value from the image analysis tool ROXAS. *Iawa J.* 34(4):433–445.
- Wegner L, von Arx G, Sass-Klaassen U, Eilmann B. 2013. ROXAS—an efficient and accurate tool to detect vessels in diffuse-porous species. *Iawa J.* 34(4):425–432.
- Whittaker RH. 1953. A consideration of climax theory: the climax as a population and pattern. *Ecol Monograph.* 23(1):41–78.
- Woodcock DW. 1994. Occurrence of woods with a gradation in vessel diameter across a ring. *Iawa J.* 15(4):377.
- Zach A, Schuldt B, Brix S, Horna V, Culmsee H, Leuschner C. 2010. Vessel diameter and xylem hydraulic conductivity increase with tree height in tropical rainforest trees in Sulawesi, Indonesia. *Flora.* 205(8):506–512.
- Zanne AE, Westoby M, Falster DS, Ackerly DD, Loarie SR, Arnold SEJ, Coomes DA. 2010. Angiosperm wood structure: global patterns in vessel anatomy and their relation to wood density and potential conductivity. *Amer J Bot.* 97(2):207–215.
- Zheng J, Martínez-Cabrera HI. 2013. Wood anatomical correlates with theoretical conductivity and wood density across China: evolutionary evidence of the functional differentiation of axial and radial parenchyma. *Ann Bot.* 112(5):927–935.
- Zimmermann MH. 1983. Xylem structure and the ascent of sap. Springer series in wood science. New York: Springer-Verlag.

CAPÍTULO 4

Wood density, deposits and mineral inclusions of successional tropical dry forest species

Romero, E., Dávalos-Sotelo, R., Meave, J.A. y Terrazas, T. (2020). Wood density, deposits and mineral inclusions of successional tropical dry forest species. *European Journal of Forest Research*, 139: 369–381.

<https://doi.org/10.1007/s10342-019-01236-9>





Wood density, deposits and mineral inclusions of successional tropical dry forest species

Eunice Romero^{1,4} · Raymundo Dávalos-Sotelo² · Jorge A. Meave¹ · Teresa Terrazas³

Received: 19 June 2019 / Revised: 26 September 2019 / Accepted: 3 October 2019 / Published online: 17 October 2019
© Springer-Verlag GmbH Germany, part of Springer Nature 2019

Abstract

Wood water content, wood dry mass fraction, wood deposits and mineral inclusions separately affect wood mechanical properties, as well as plant survival and growth rates. Tree species occurring in recovering vegetation from deforestation face water stress, which is a particularly strong environmental filter in tropical dry forest regions. In this study, we analyze wood density and its associated variables of tree species present in early and late successional communities. We assessed and compared their wood density, wood water content, wood dry mass fraction, as well as wood cellular deposits, secretory elements and mineral inclusions which were described through anatomical sections. Wood density ranged from 0.10 g/cm³ (*Jacaratia mexicana* in late successional community) to 0.92 g/cm³ (*Lysiloma divaricatum* in early successional community). Successional species showed low intraspecific variability, despite large differences in the environmental conditions in the communities where they grow. Species with high wood water content were restricted to late successional communities, and pioneers showed higher wood density than non-pioneer species, which supports the linkage between high wood density and harsh environmental filtering through hydraulic safety. Wood density did not differ between columnar cacti (*Pachycereus pecten-aboriginum* and *Pilosocereus collinsii*) and tree species such as *Bursera simaruba*. Starch, tannins and crystals were abundant in most successional species and some species had gums; these deposits could potentially influence wood density and hydraulic, defense and storage plant functions. Our results suggest that modifications in the life cycle of successional tropical dry forest tree species due to anthropogenic activities may not be an important source of wood density variation.

Keywords Early successional species · Functional attributes · Late successional species · Wood anatomy · Wood dry mass fraction · Wood water content

Communicated by Martina Meincken.

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s10342-019-01236-9>) contains supplementary material, which is available to authorized users.

✉ Teresa Terrazas
tterrzas@ib.unam.mx

¹ Departamento de Ecología y Recursos Naturales, Facultad de Ciencias, Universidad Nacional Autónoma de México, Ciudad Universitaria, 04510 Coyoacán, Ciudad de México, Mexico

² Instituto de Ecología, A.C., 091070 Xalapa, Veracruz, Mexico

³ Instituto de Biología, Universidad Nacional Autónoma de México, Ciudad Universitaria, 04510 Coyoacán, Ciudad de México, Mexico

⁴ Posgrado en Ciencias Biológicas, Unidad de Posgrado, Circuito de Posgrados, Ciudad Universitaria, C.P. 04510 Mexico City, Mexico

Introduction

Wood density is defined as the amount of mass present in a given volume of a plant's secondary vascular tissue (Williamson and Wiemann 2010b). Initially, this variable was examined by foresters and wood technologists (Echenique-Manrique and Robles Fernández 1993; Russell 2005), who considered it the most important physical property of timber and developed standardized protocols to quantify it. The main goals of wood density quantification are defining wood potential uses, predicting its quality, strength and flexibility (Nogueira et al. 2005; Oluwadare and Ashimiyu 2007), and assessing its commercial value through estimation of the amount of dry mass (Cannell 1989). These calculations have been oriented mainly for commercial species from temperate climates in North America, and with intermediate wood density values; such species are the most widely used because species with low and high wood density values are difficult

to process with machines (ASTM 2014; Williamson 1975; Green and Evans 2001; Silva-Guzmán et al. 2010).

Currently, wood density is a plant functional trait widely included in ecological analyses, as it is thought to be correlated with multiple functions affecting the ecological performance of plants (Zanne et al. 2010; Beeckman 2016; Violle et al. 2007; Chave et al. 2009). Among other things, wood density has been interpreted as a surrogate of growth and survival rates, and as an indicator of a plant's competitive ability for light and space (King et al. 2006; Poorter et al. 2008; Francis et al. 2017). Wood density is also an important variable in studies on environmental services and biological conservation (Slik et al. 2008; Meave et al. 2012).

By definition, wood density quantification requires the total extraction of water from wood tissue (ASTM 2010). As simple as this procedure may sound, it actually faces several difficulties that must be dealt with properly. The particular method used to measure wood dry weight varies depending on the amount of water and the occurrence of cellular volatile extractives such as tannins (Echenique-Manrique and Robles Fernández 1993; ASTM 2010). Wood contains both free water and bounded water, and these fractions represent different levels of difficulty for their extraction (i.e., require different amounts of energy to be extracted). Forestry protocols provide precise methods for obtaining dry mass at constant weight, based on the 'endpoint' concept (i.e., the moment at which a given specimen no longer contains any water). Yet, identifying the endpoint may not be straightforward, as the wood tissue may continue to lose weight even after the water has been completely extracted. Such extra weight reduction, which may be confounded with loss of water, is related to the volatilization of some compounds known as extractives (ASTM 2010) which can be indirectly observed through deposits located within the cell walls or in cell lumina. Different species may contain variable amounts of deposits (gums, latex, resins, starch and tannins; Hillis 1987; Schmidt et al. 2016) which can affect dry weight and the volume of the piece to be measured (Nearn 1955; Hernández 2007). In commercial species, deposits may vary from almost imperceptible quantities to nearly 20% of wood dry weight (Wangaard and Granados 1967). The potential of volatile substances to cause water content overestimation has led to specific procedures in forestry protocols for their extraction (Panshin and de Zeeuw 1980).

In the context of the ecological-functional approach of wood density, the large majority of studies include non-commercial gymnosperms and angiosperms from different ecosystems (Chave et al. 2006; Ackerly 2004). These studies use diverse non-standardized protocols [see reviews by Baker et al. (2004), and by Williamson and Wiemann (2010b)], or protocols in which wood density measurement is treated briefly, not taking into account the presence of deposits and mineral inclusions in measuring dry weight

(e.g., Pérez-Harguindeguy et al. 2013). Despite these methodological caveats regarding the measurement of wood density, this trait has been increasingly included in functional analysis (Larjavaara and Muller-Landau 2010; Williamson and Wiemann 2010b).

Each variable involved in wood density calculations relates in some way to ecological performance. Wood water content, wood dry mass and the type and abundance of deposits and mineral inclusions are variables associated with certain plant functions. Plant growth is defined as the net increase in dry mass (Hunt 1982), so this latter variable is associated to tissue production and resource allocation (Percy et al. 1991), and it has been incorporated in allometric equations for estimating local or regional carbon stocks (Henry et al. 2010). Likewise, the amount of material contained in cell walls is associated to wood mechanical strength (Panshin and de Zeeuw 1980). As for cellular deposits and inclusions, they may affect plant survival and growth rates, given their known association to nutrient and resource storage, and to water transport. For example, starch is a source of energy that may be transported to different points of demand like flower buds (Carlquist 2001). Tannins and latex are associated to defense against herbivores and resistance to pathogens (William 1983; Konno 2011), and crystals to mechanical resistance (He et al. 2014). Moreover, the occurrence of gums occluding vessel lumina in some species interferes with water movement (de Micco et al. 2016). A greater amount of dry mass relative to water content decreases pathogen attacks (Holbrook 1995) and confers greater mechanical resistance to physical damage (Panshin and de Zeeuw 1980). Some plant species from arid environments are able to store water in their stems, thus wood water content can help infer how much water is potentially available in the dry season (Holbrook 1995). Also, wood density has been used for gaining insight into successional mechanisms, as it has been associated to the ways in which plants cope with changing environmental filters (Chave et al. 2009; Pineda-García et al. 2013, 2015; Letcher et al. 2015).

Tropical dry forests (TDF), once the most extensive forest ecosystem in the tropics (Murphy and Lugo 1986), have undergone severe deforestation in the last decades, resulting in the presence of large areas covered with secondary vegetation (Trejo and Dirzo 2000). TDF develop in regions with a well-marked dry season, which results in water stress for plants, particularly in early successional stages (Lebrija-Trejos et al. 2011; Pineda-García et al. 2013). For TDF species, it has been hypothesized that wood density is indicative of their capacity to cope with the harsh early successional environment, either through tolerance or evasion mechanisms (Markesteyn et al. 2011; Méndez-Alonzo et al. 2012), and high wood density has been related to a water acquisition strategy under low-water conditions (Chave et al. 2009).

For a better understanding of the possible influence of wood density on plant function, to perform an accurate carbon assessment, and for selecting appropriate uses for wood, a precise knowledge of wood physical properties in particular ecosystems is required. Thus, the goals of this study were (1) to characterize wood density of tree species present in TDF secondary vegetation, (2) to infer how much water their wood can hold through assessing wood dry mass fraction, and (3) to describe, through anatomical sections, wood deposits and mineral inclusions, which are variables associated to wood density. Specifically, we analyzed these variables between and within early and late successional communities, and within species occurring in both early and late communities.

Plant species in recovering (successional) TDF are subjected to changing environmental filters over time, with water availability being the most important one (Lebrija-Trejos et al. 2011; Pineda-García et al. 2013). Also, as part of the preparation of the agricultural fields, many of these plants have their aboveground biomass totally removed, severely modifying their life cycle. Thus, we hypothesized that environmental and life cycle changes are a source of variation in the physical properties of the wood of TDF successional species. We expected differences in wood density between individuals of the same species growing in early and late successional stands. Also, we expected successional stage to affect wood density values, given that water availability in early stages is lower than later in succession (Lebrija-Trejos et al. 2011; Pineda-García et al. 2013), and that wood water content determines wood density (Dinwoodie 2000), since dense tissues have also been linked to hydraulic safety (Holbrook 1995; Hacke et al. 2000; Pineda-García et al. 2015) and harsh environmental filtering (Francis et al. 2017). Particularly, for early successional communities we expected higher wood density values and lower wood water contents than in late communities. Late successional communities are more complex both structurally (Kennard 2002; Peña-Claros 2003; Lebrija-Trejos et al. 2008) and in terms of species composition (Derroire et al. 2016) than early communities, so we expected higher variation in wood density among species in late successional communities.

Materials and methods

Study area and successional communities

This study was conducted in the region surrounding Nizanda, Oaxaca state (16° 39' 30" N and 95° 00' 40" W), Mexico. The regional climate is warm subhumid, with summer rains. Mean annual temperature is 27.6 °C and mean annual rainfall is 902.6 mm (CICESE 2015). Rains fall with a marked seasonality, which results in a strong

distinction between a dry season from November to April, and a rainy season from the end of May to mid-October. Most of Nizanda region is covered by TDF (Pérez-García et al. 2010).

In the study region, agricultural practices have had significant impacts, which have resulted in the presence of numerous old fields and secondary forest with different ages (years after abandonment; Lebrija-Trejos et al. 2008). The main crop is rain-fed corn cultivated through slash-and-burn system, which leaves numerous remnants of the vegetation occurring prior to the anthropogenic disturbance. In early successional communities (0 to < 2 years since abandonment), multi-stemmed individuals of different tree species resprouting from a base (stump) damaged by fire and logging are common, as reported for other TDF regions (Saha and Howe 2003; Bhaskar et al. 2014). Late stands (> 60 years since abandonment) resemble TDF mature forest community in structure (basal area, canopy height and density of individuals) and species richness. Individual trees in late successional stands may be both plants that resprouted early in succession or plants that established from seed at any moment of the succession. Ground-level (regeneration) environmental conditions contrast greatly between early and late stands, particularly in the rainy season (Lebrija-Trejos et al. 2011).

Species selection and sampling of individuals

Species selection was based on previous studies on mature and successional vegetation in the area (Pérez-García et al. 2010; Lebrija-Trejos et al. 2010). At least 57 woody species have been recorded in the TDF successional vegetation; 50 of them also occur in mature forest stands (Pérez-García et al. 2010), whereas the seven remaining ones are considered pioneers, due to their absence in mature TDF. For this study, we selected three pioneer species and ten non-pioneer species (13 species in total; Table 1), because of their high frequency in all TDF successional communities (in plots with ages ranging between 2 and > 50 years).

Wood samples were collected both in early and late successional stands, with the following design. In three young sites (< 5 years of age), six individuals of eight of the 13 species were sampled, as the remaining five were absent there (see 'early community' in Table 1). Selection of individuals was based on size (ca. 30 cm height and 1 cm in diameter; see Table S1 in Supplementary Material). Individuals of seven species had more than two stems resprouting from a stump (Fig. 1c), whereas individuals of *L. divaricatum* did not show evidence of resprouting from a stump even though they may have two stems; Fig. 1c). In turn, for late succession, wood samples were collected in seven older stands (> 50 years of age), for all 13 selected species (Table 1).

Table 1 List of 13 woody species occurring in a secondary tropical dry forest (TDF) of Nizanda, Oaxaca, Mexico

Species	Early	Late	Family
Non-pioneer species			
<i>Bonellia macrocarpa</i> (Cav.) B. Ståhl & Källersjö	1	1	Primulaceae
<i>Bursera simaruba</i> (L.) Sarg.	0	1	Burseraceae
<i>Coccoloba liebmanii</i> Lindau	1	1	Polygonaceae
<i>Cnidoscolus megacanthus</i> Breckon ex Fern.Casas	0	1	Euphorbiaceae
<i>Jacaratia mexicana</i> A.DC	0	1	Caricaceae
<i>Lonchocarpus lanceolatus</i> Benth.	1	1	Leguminosae
<i>Lysiloma divaricatum</i> (Jacq.) J.F. Macbr.	1*	1	Leguminosae
<i>Pilosocereus collinsii</i> (Britton & Rose) Byles & G.D. Rowley	0	1	Cactaceae
<i>Pachycereus pecten-aboriginum</i> (Engelm. ex S.Watson) Britton & Rose	0	1	Cactaceae
<i>Phyllostylon rhamnoides</i> (J.Poiss.) Taub.	1	1	Ulmaceae
Pioneer species			
<i>Acacia cochliacantha</i> Willd.	1	1*	Leguminosae
<i>Mimosa eurycarpa</i> Herzog	1	1*	Leguminosae
<i>Mimosa tenuiflora</i> (Willd.) Poir.	1	1*	Leguminosae

Pioneer species, absent in mature TDF and particularly abundant in early successional stands; non-pioneer species, present in mature TDF but also occurring in successional plots, in some cases even in very young ones. Early successional stands with < 2 years of development after abandonment; Late, successional stands with > 50 years after abandonment. 0, absence; 1, presence; 1*, presence but with low frequency. Species names standardized according to the plant list (www.theplantlist.org, last accessed March 2019)

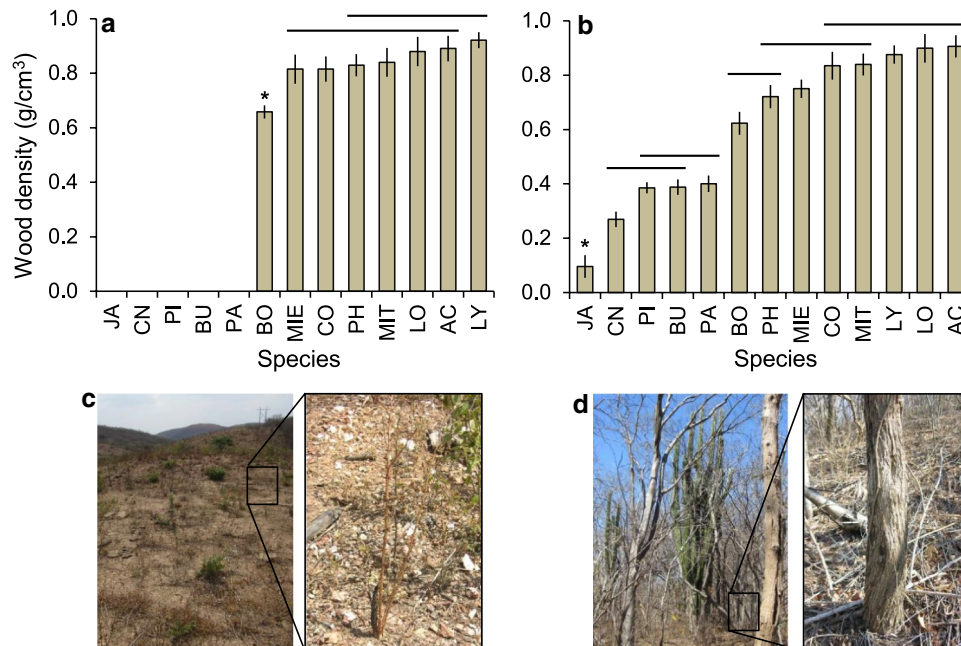


Fig. 1 Wood density of the stem of 13 woody species occurring in a secondary tropical dry forest with two different ages of successional development. **a** Early successional community: sites with 2 years of abandonment; species without a bar are absent in early successional communities, **b** late successional community: sites with > 60 years of abandonment. The letters indicate groups of species with similar wood density values (early ANOVA, $P < 0.001$ and $F 19.125$; late $F 263.99$, $P < 0.001$). Lines are standard deviations. Horizontal bars denote species in a group without significant differences (post hoc

Scheffé test, $P < 0.001$), and asterisks show species with significant differences from the rest of the species, **c** photographs showing an early successional community, and an individual of *M. eurycarpa*, **d** photographs showing a late successional community, and an individual of *M. eurycarpa*. AC, *A. cochliacantha*; BO, *B. macrocarpa*; BU, *B. simaruba*; CO, *C. liebmanii*; CN, *C. megacanthus*; JA, *J. mexicana*; LO, *Lonchocarpus lanceolatus*; LY, *L. divaricatum*; MIE, *M. eurycarpa*; MIT, *M. tenuiflora*; PA, *P. pecten-aboriginum*; PH, *P. rhamnoides*; PI, *P. collinsii*

Wood sample collection

For each individual sampled in the young stands, a cylinder 1 cm long was cut with a saw near the base of its tallest stem. For individuals in the late stands, a section of the main stem 5–6 cm wide was cut with a saw 30 cm above the ground. Each sample so collected was divided into two fractions; the first one, aimed at wood density measurement, was kept in a resealable plastic bag and placed in a cooler to minimize evaporation of the wood free water; in turn, the second piece was fixed in a formaldehyde, alcohol and acetic acid solution (Ruzin 1999) for anatomical analysis.

Measurement and calculation of wood physical properties

After removing the bark from each wood sample, fresh volume, fresh weight and dry weight were measured with an analytical balance. Fresh volume was calculated through the water displacement method (ASTM 2010), whereby a plastic cup with distilled water was placed on the balance. A dissection needle was inserted into each wood sample before carefully immersing it in the water, ensuring that the sample did not touch the plastic cup walls. The weight of the water displaced by the sample was recorded immediately. Samples were air-dried and then oven-dry weight was determined after keeping them at 105 °C for 72 h, following Williamson and Wiemann (2010b), and ASTM (2010). Oven-dry weight was measured with an analytical balance. For each sample, wood density (WD) values were calculated, as well as wood water content (WWC), defined as the weight of moisture contained in a piece of wood expressed as a percentage of its oven-dry weight (Panshin and de Zeeuw 1980), and wood dry mass fraction (DMF) with the following equations:

$$\text{WD} = \text{dry weight/fresh volume} \quad (1)$$

$$\text{WWC} = ((\text{fresh weight} - \text{oven-dry weight}) / \text{oven-dry weight}) \times 100 \quad (2)$$

$$\text{DMF} = \text{oven-dry weight/fresh weight} \quad (3)$$

For wood cellular inclusions and deposits qualitatively description in each species, 20–25 µm wood sections (transverse, tangential and radial) were made with a sliding microtome (Leica 2000R, Wetzlar, Germany). Wood sections were examined with an optical microscope (Olympus BX51) and photographs were taken using a digital camera (Evolution LC Color) adapted to the optical microscope. The occurrence of inclusions and deposits in the axial and radial parenchyma cells, fibers and vessel lumina were recorded. Abundance of deposits and inclusions was assessed qualitatively with the following ordinal scale: 0, no evidence of

cellular deposits or inclusions; 1, very scarce; 2, scarce; 3, abundant; 4, very abundant.

Statistical analysis

Software StatSoft Inc. (2007) was used for all statistical analysis. Student's *t* tests with unequal variances for independent samples were performed for comparisons of mean WD, WWC and DMF, between early and late successional plots, as well as comparisons of mean WD between pioneer species and non-pioneer species in young and older stands.

Pearson correlations were performed for WD, WWC and DMF. Comparisons of species mean WD within early ($S=8$) and late ($S=13$) plots were performed through ANOVA; post hoc Scheffé tests were used to assess pairwise differences in species means. For the eight species that were present both in young and older stands, comparison of mean WD between successional stages for each species was conducted with Student's *t* tests. For all statistical tests, significance was set at $\alpha=0.05$.

Results

Comparison of physical wood properties between young and older successional stands

Overall, mean WD for the entire TDF successional community (i.e., considering all 13 species present both in early and late successional plots) was 0.70 g/cm³ (± 0.23 standard deviation), with a coefficient of variation = 33%, with a minimum mean value of 0.10 g/cm³ (± 0.04 SD; *J. mexicana*), and a maximum of 0.92 g/cm³ (± 0.03 SD; *L. divaricatum* in early plots; Fig. 1, Table S2 in Supplementary Material). When dissecting WD data by successional category, this variable was significantly higher in early than in late succession (0.78 ± 0.14 g/cm³ vs. 0.61 ± 0.27 g/cm³; $P < 0.001$; Table S2). The same pattern was true for mean wood dry mass fraction (0.68 ± 0.06 in early plots vs. 0.53 ± 0.21 in late plots; $P < 0.0001$). By contrast, mean WWC was significantly higher ($P < 0.001$) in late ($148.91 \pm 179.31\%$) than in early (48.44 ± 16.21) plots. In early stands, mean WD was significantly higher ($P < 0.05$) in pioneer species (0.82 ± 0.10 g/cm³) than in non-pioneer species (0.75 ± 0.16 g/cm³), and the same pattern was found in late plots (pioneers, 0.83 ± 0.07 g/cm³; non-pioneers, 0.55 ± 0.27 g/cm³ ($P < 0.001$)).

All correlations between the three analyzed variables were significant. Particularly, DMF was positively correlated with WD ($r=0.96$; $P < 0.001$), WWC was negatively correlated both with WD ($r=-0.81$; $P < 0.001$) and DMF ($r=-0.84$; $P < 0.001$).

Species wood density in early and late successional plots

Bonellia macrocarpa WD differed significantly from the rest of the species present in early plots (Fig. 1a). Additionally, in late plots, various groups of significantly different species were distinguished, representing a gradient of increasing WD values (Fig. 1b). In these latter plots, *J. mexicana* WD differed from all other species. Other three species also had relatively low WD values; WD mean in the cacti *P. pecten-aboriginum* ($0.40 \pm 0.03 \text{ g/cm}^3$) and *P. collinsii* ($0.39 \pm 0.02 \text{ g/cm}^3$) were indistinguishable from WD in the tree *B. simaruba* ($0.39 \pm 0.03 \text{ g/cm}^3$). The remaining eight species were also variable, with WD values ranging from $0.62 \pm 0.04 \text{ g/cm}^3$ in *B. macrocarpa* to a maximum value of $0.91 \pm 0.04 \text{ g/cm}^3$ in *A. cochliacantha* (Fig. 1b; Table S2 in Supplementary Material).

Comparison within each species wood density between early and late successional communities

Among the eight species that were present both in early and late successional plots, significant differences ($P < 0.05$ in all cases) in mean WD were found only for three of them, one pioneer and two non-pioneers, with values for young plots always being larger than values for older plots: *M. eurycarpa*, $0.81 \pm 0.05 \text{ g/cm}^3$ in early plots versus $0.75 \pm 0.03 \text{ g/cm}^3$ in late plots; *P. rhamnoides*, $0.83 \pm 0.04 \text{ g/cm}^3$ versus $0.72 \pm 0.04 \text{ g/cm}^3$; *L. divaricatum*, $0.92 \pm 0.03 \text{ g/cm}^3$ vs. $0.88 \pm 0.03 \text{ g/cm}^3$ (Fig. 2).

Wood water content and wood dry mass fraction

WWC was highly variable in late plots compared to early successional plots (Fig. 3a, b), and species with $\text{WWC} > 150\%$ were found only in late plots. In early successional communities, *B. macrocarpa* was the species with the highest WWC (Fig. 3a) and the lowest DMF (Fig. 3c), while in late plots, it was *J. mexicana* (Fig. 3b, d). For the eight species that occurred both in early and late successional plots, WWC was significantly higher in late ($148.91 \pm 179.31\%$) than in early successional ones ($48.44 \pm 16.21\%$; $P < 0.001$), and conversely, dry mass fraction was higher in early (0.68 ± 0.06) than in late plots (0.53 ± 0.21 ; $P < 0.001$).

Cellular deposits and mineral inclusions

Table 2 shows the type and presence in each species of observed cellular deposits and inclusions (see location and abundance details in Fig. 4, and in Table S3 provided in Supplementary Material). Occurrence and abundance of these materials varied greatly (from being absent to very

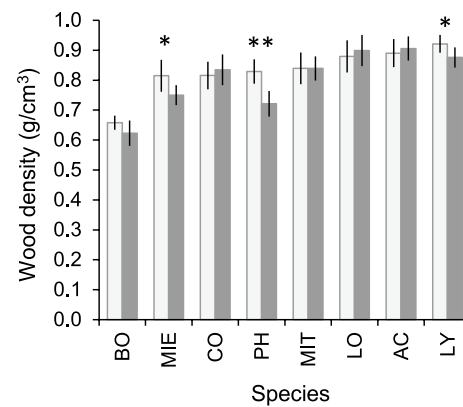


Fig. 2 Wood density of the stem of eight woody species occurring in a secondary tropical dry forest with contrasting successional development: light gray bars indicate early successional communities (sites < 2 years of abandonment), and dark bars indicate late successional communities (sites > 50 years of abandonment). *t* tests were performed to compare wood density mean value between a same species present in early and late successional community; asterisks denote significant differences * $P < 0.05$; ** $P < 0.01$. AC, *A. cochliacantha*; BO, *B. macrocarpa*; BU, *B. simaruba*; CO, *C. liebmanii*; CN, *C. megacanthus*; JA, *J. mexicana*; LO, *L. lanceolatus*; LY, *L. divaricatum*; MIE, *M. eurycarpa*; MIT, *M. tenuiflora*; PA, *P. pecten-aboriginum*; PH, *P. rhamnoides*; PI, *P. collinsii*

abundant) depending on species and, in some cases also on successional stage. All but one species had starch (*J. mexicana* being the exception), commonly located in axial and radial parenchyma (Tables 2 and S3), whereas two species, namely *C. liebmanii* and *B. simaruba*, had starch in septate fibers. Cellular deposits observed in some species were tannins and starch (Table 2 and Fig. 4). Crystals were observed in the wood tissue of all legume species (pioneers and non-pioneers; Tables 1, 2, and Fig. 4), as well as in three species of other families (*C. liebmanii*, *J. mexicana* and *P. rhamnoides*; Fig. 4).

Discussion

In this study, we analyzed WD along with other associated physical properties that can potentially affect the ecological performance of TDF successional species. Unexpectedly, most of these successional species showed low intraspecific variability, despite large differences in the environmental conditions they experience in the various successional communities where they grow, suggesting that, at the species level, environmental and life cycle changes are not an important source of variation in wood physical properties. High WD has been linked with hydraulic and harsh environmental filtering, and accordingly we found that species with high WWC were restricted to late successional communities, and that pioneers showed higher WD than non-pioneers.

Fig. 3 Wood water content and dry mass fraction of wood stem samples of 13 successional tree species, which occur in two successional TDF communities: **a** and **c** early successional communities (2 years of abandonment), **b** and **d** late successional communities (> 60 years of abandonment). AC, *A. cochliacantha*; BO, *B. macrocarpa*; BU, *B. simaruba*; CO, *C. liebmanii*; CN, *C. megacanthus*; JA, *J. mexicana*; LO, *L. lanceolatus*; LY, *L. divaricatum*; MIE, *M. eurycarpa*; MIT, *M. tenuiflora*; PA, *P. pecten-aboriginum*; PH, *P. rhamnoides*; PI, *P. collinsii*

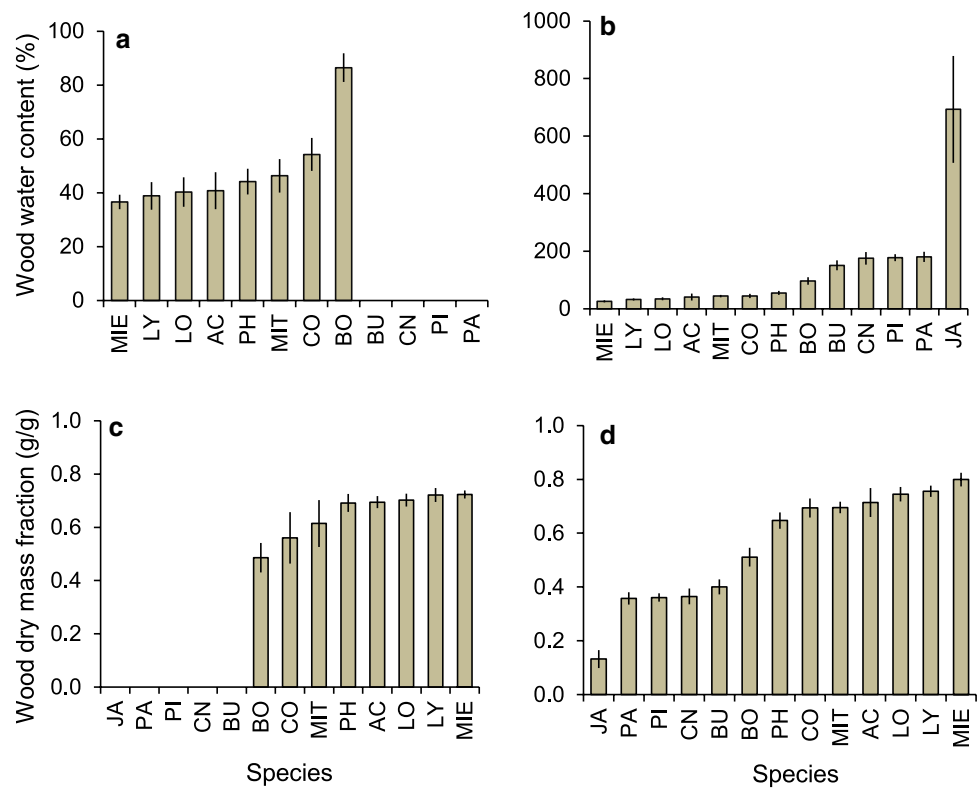


Table 2 Cellular deposits and mineral inclusions observed presence (asterisks) in anatomical sections in 13 woody successional tree species of a tropical dry forest

Species	Starch	Crystals	Gums	Tannins	Resin	Silica bodies
<i>Acacia cochliacantha</i>	*	*	*			
<i>Bursera simaruba</i>	*	*		*	*	
<i>Cnidocolobus megacanthus</i>	*					
<i>Coccoloba liebmanii</i>	*	*	*	*		
<i>Jacaratia mexicana</i>		*				
<i>Bonellia macrocarpa</i>	*					*
<i>Lonchocarpus lanceolatus</i>	*	*	*			
<i>Lysiloma divaricatum</i>	*	*	*	*		
<i>Mimosa eurycarpa</i>	*	*	*			
<i>Mimosa tenuiflora</i>	*	*	*	*		
<i>Pachycereus pecten-aboriginum</i>	*					
<i>Phyllostylon rhamnoides</i>	*	*		*		
<i>Pilosocereus collinsii</i>	*					

Coupled to the structural and floristic complexity of the late TDF tree successional communities (Lebrija-Trejos et al. 2008), our results show that they also have a high diversity in WD and other associated physical properties. Regarding cellular deposits and mineral inclusions, we found that starch and tannins were abundant in most successional species, while some have gums and crystals. Thus, the variability in the occurrence and abundance of these inclusions and deposits could potentially affect the resulting values of WD through dry mass content values, and it may also influence the ecological performance of successional species.

Physical wood properties and the ecology of species present in TDF recovering vegetation

Mean WD values of successional species included in this study are highly variable and have a differential distribution along the successional gradient. These WD values are within the range of compiled values reported for Mexican TDF species: 0.16 g/cm³ (*J. mexicana*) to 1.4 g/cm³ (corresponding to *Guaiacum sanctum* L.), one of the highest values recorded worldwide), mean = 0.64 ± 0.17 SD, and a coefficient of variation = 27% (Barajas-Morales

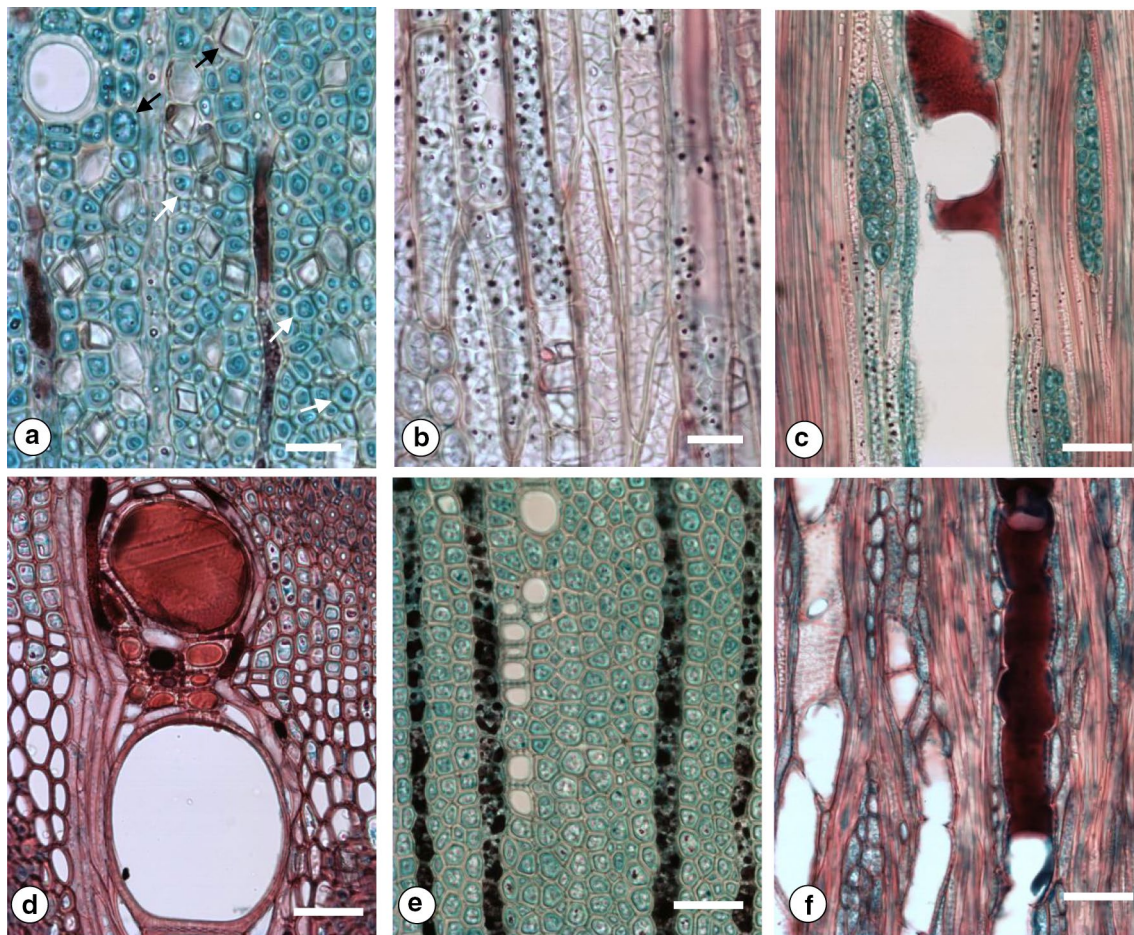


Fig. 4 Cellular deposits and mineral inclusions observed in woody successional tree species of a tropical dry forest. **a** Cleared transverse section of *L. divaricatum* in an early successional community (<2 years of abandonment), showing crystals, and starch in axial parenchyma (black arrows), starch in fibers (white arrows), and tannins in radial parenchyma, **b** and **c** cleared tangential sections of the pioneer species *Mimoso eurycarpa* in an early successional community; in **(b)** tannins starch and crystals can be observed in axial parenchyma, and starch in radial parenchyma; in **(c)** gums inside vessel,

starch in radial parenchyma, and starch and tannins in axial parenchyma are shown, **d** transverse section of pioneer species *M. tenuiflora* in a late successional community (>50 years of abandonment), gums in vessel lumens, and starch and tannins in axial parenchyma can be observed, **e** transverse section of *C. liebmanii* in early successional community, with tannins in radial parenchyma, and starch in septate fibers, **f** tangential section of *L. lanceolatus* in early community, showing gums in vessel lumen, and starch in axial and radial parenchyma. Scale bars in **(a, b)** = 20 μm , and in **(c-f)** = 50 μm

1987; Ordóñez et al. 2015), although none of the species included in this study surpass 1.0 g/cm^3 . The highest WD values are found in early successional communities, and are given by a high WWC and low DMF. Conversely, the lowest WD values can be found in late communities. WD, WWC and DMF differed between early and late communities, which is consistent with a previous study in a dry region (Bastin et al. 2015), suggesting that the environmental differences in early and late successional communities, probably related to water availability, could be affecting those wood properties at community level.

Both early and late successional species in TDF face dry-season soil drought, and have different drought resistance mechanisms, such as sapwood water reserves (drought avoidance) and leaf shedding (drought tolerance; Pineda-García

et al. 2013; Wolfe and Kursar 2015). Nevertheless, species face a stronger water availability filtering early in succession, so we expected that species with the ability to function with low-water (tolerant species) would be dominant in early successional communities. Thus, as expected, species with the lowest WD and DMF are present only in the late successional communities, while species present in the early stands showed the highest WD values, with *L. divaricatum* having the highest WD of all the species distributed along the successional gradient. We also observed less variability in the values of WD and WWC in the early communities than in the more advanced ones. These results provide evidence that supports the hypothesis that states that selection favors high WD in dry habitats (Chave et al. 2009; Bhaskar et al. 2014).

Species considered as TDF pioneers (i.e., with high density of individuals in sites with < 5 years of age, namely *M. eurycarpa*, *Mimosa tenuiflora* and *A. cochliacantha*) have higher WD than non-pioneer species. These results are in disagreement with those for other species classified as pioneers from other vegetation types, like tropical rainforest (Larjavaara and Muller-Landau 2010; van Gelder et al. 2006). A likely explanation to this controversy may be that TDF pioneer species differ from tropical rainforest pioneers regarding the environmental filters they face (those being water and light; Letcher et al. 2015). Probably most TDF pioneer species are water conservative species with a drought tolerance mechanism (Pineda-García et al. 2015), but detailed studies are needed to examine this hypothesis further.

Regarding late community and mature TDF species, *J. mexicana* is a very interesting species, as we found that its wood reaches a considerably high WWC, which results in the lowest WD of all successional species, lower than a co-occurring Euphorbiaceae tree species (*Cnidococcus megacanthus*), and even lower than its own bark (E. Romero, unpublished results). Bark tissue is known to play a mechanical role (Niklas 1999; Rosell and Olson 2014) that mostly applies to branches, although for *J. mexicana* it appears to contribute practically to the mechanical support at whole individual level. For this species, it also seems to be a trade-off between mechanical support and water storage, as reported for other species (Pineda-García et al. 2015).

Particularities in WD and WWC can give insights into the mechanisms underlying an atypical ecological performance. For example, *B. macrocarpa* differs from the rest of the successional species as it is the only species with inverted phenology (A. Maldonado, unpublished results). One hypothesis that could explain how this species can retain its leaves during dry season is that it has deep roots that can take deep water, and that this water is subsequently stored in the stem; this drought-avoidance mechanism has been observed in other TDF species (Pineda-García et al. 2013). Accordingly, *B. macrocarpa* is the only species differing from the rest of the species in the early successional communities, as it has the lowest WD and the highest WWC.

We expected that environmental and life cycle changes would have an effect on wood physical properties of successional species, but our results did not support this hypothesis consistently. We had anticipated that there would be clearly marked intraspecific differences in WD between individuals present in early successional communities from those growing in more advanced stages of the succession, but significant differences were found only in three species. Such homogeneity across successional stages suggests that most species present in both early and late communities do not display high intraspecific plasticity in WD, although the environmental conditions and the individuals' physiognomy

in both communities are drastically different (Lebrija-Trejos et al. 2011). In agreement with this possibility, Williamson and Wiemann (2010a) reported, for tropical wet forest pioneers, that specific gravity variation may not be controlled environmentally, but genetically, and that it is closely related to the individuals' age. Ewel (1980) reports small differences between wood density of pioneer and mature forest species in dry environments. Furthermore, Kenzo et al. (2017) found that, at the community level, WD does not differ even between wet and dry forest types, and that tree life form does not affect WD in dry forests. Yet, our results were unexpected, as other studies have found differences in WD even within single individuals, for example branches and stems, pith and near the bark, base and apex, as well as between juvenile and mature wood (Wiemann and Williamson 1989; Henry et al. 2010; Gryc et al. 2011; McCulloh et al. 2011; Fortunel et al. 2013). One likely explanation is from an ontogenetic viewpoint, resprouting individuals in early communities are adults, as the stump from where their stems come from were adults before their aboveground biomass was removed. Interestingly, *L. divaricatum* was one of the few species with significant intraspecific differences. Based on our field observations, *L. divaricatum* is the only species whose individuals probably came always from seed and not from the stump of a previous adult, supporting the above-stated hypothesis; further studies that assess ontogenetic differences are needed to confirm it.

Highlighting wood density of Cactaceae species

Our results showed that WD of the two Cactaceae species included in this study did not differ from the WD of other tree species, such as *B. simaruba* and *C. megacanthus*. WD similarity may indicate that these cacti species are potentially capable of storing a similar amount of carbon as other tree species. For this reason, it is important to include Cactaceae species for TDF biomass estimations, since they are important components of TDF structure (Martínez-Yrizar et al. 1992). In an ecological context, these species with low WD may constitute a functional group with water storage as the main avoidance mechanism of drought resistance, as reported for other TDF tree species (Paz et al. 2015).

Wood cellular deposits and inclusions in successional TDF species

Successional species have different types and abundances of cellular deposits and inclusions which could potentially influence their WD through dry mass values, as well as influence its ecological performance. Wood anatomy can be a useful tool to understand WD of each species. In addition, it can be used to indirectly infer whether what is being lost during the drying process is water only or also certain

volatile compounds, and if dry mass is partly made up of crystals. The group of species found in both early and late successional communities present medium to high WD values, and it consists mainly of species of the legume family. Overall, Fabaceae are characterized by high WD (Chave et al. 2006) and by having crystals in their wood (Evans et al. 2006), thus it is possible that the crystals contribute to a higher WD. Deposits that potentially can be extracted from wood observed in the successional species included tannins, gums and starch, while the observed mineral inclusions that are likely related to dry mass were crystals and silica bodies. Because tannins and starch are volatile compounds and they were abundant in several species, it is likely that, for those species, this type of substance may evaporate during the drying process along with free and bound water.

Starch is common and abundant among TDF successional species and it probably plays an important role in their carbohydrate reserves, as reported for other species (Plavcová and Jansen 2015). *Jacaratia mexicana* was the only species in which starch was not observed. Some species had tannins, and these contents may be associated to herbivory defense (William 1983). Further research is needed to assess the importance of cellular deposits and mineral inclusions in the ecological performance of successional species, especially during the dry season.

Methodological considerations

The use of high-precision procedures for assessing WD may help solving controversies regarding WD as a functional attribute. A starting point could be the adjustment of WD measurements taking into account the diversity of the tissue of the species of interest, which can include different types and abundances of WWC and cellular deposits and inclusions. In addition, we recommend measuring WD and adjusting WD measurements for each species in collaboration with wood technologists and forestry engineers, following more precise protocols (e.g., ASTM 2010, 2014, 2016), and in appropriate facilities (e.g., a place where humidity remains constant during dry weight measurement). We also recognize the need for future quantitative studies evaluating the type, amount and distribution of deposits in wood in order to evaluate wood properties.

As WWC, wood deposits and mineral inclusions can affect WD values (Wangaard and Granados 1967; Reva et al. 2015). Here, we provide some methodological considerations derived from our results. Since the amount of WWC of successional species is extremely variable (particularly in late successional communities), we suggest that drying treatments should be adopted for each species, taking into account WWC and DMF (which in some species may include crystals and deposits). The possible consequence of over drying wood is that other substances may evaporate in

the wood besides the free and bounded water (ATSM 2010). To obtain more precise dry weight values, and subsequently WD, in species with high WWC (for example Burseraceae, Cactaceae and Euphorbiaceae species), it is recommended to increase drying time. An undesirable effect of stopping the drying of wood samples at 72 h could be that such time is insufficient to extract all the water, with a potential overestimation of WD values. In addition, although there is no clear correlation between WD and the presence of crystals in the wood (Hietz et al. 2015), the influence of the latter cannot be discarded. For biomass estimates, the possible consequences of ignoring a high abundance of crystals in the wood (for example in Fabaceae species) could be that a large percentage of biomass would be composed by crystals rather than by cellulose and lignin.

Conclusions

WD, WWC and DMF of TDF successional species, as well as the occurrence and abundance of cellular deposits and mineral inclusions in their wood are highly variable. Unexpectedly, our results suggest that the severe modifications in the life cycle of successional TDF woody species due to anthropogenic activities do not represent an important source of WD variation. In turn, this suggests that the wood produced by trunk reiterations from felled trees (sprouts from stumps) in early successional communities may be ontogenetically the same as the wood produced by individuals in late successional stands.

WD values have different sources of variation at different levels; therefore, WD is an emergent property that results from complex interactions among different variables such as those analyzed in this study. Thus, before using WD as a functional attribute that predicts the ecological performance of certain species in a particular system, it is convenient to consider the variables that influence WD values, which may actually be functional attributes themselves; this includes the assessment of cellular deposits and mineral inclusions through anatomy sections.

Acknowledgements This study is part of the requirements for ER to obtain the Doctor of Science degree from the Posgrado en Ciencias Biológicas (PCB), Universidad Nacional Autónoma de México (UNAM). Funding for this research was provided by Consejo Nacional de Ciencia y Tecnología (CONACyT), Grant No. 270104 (ER) and Programa de Apoyo a Proyectos de Investigación e Innovación Tecnológica-Universidad Nacional Autónoma de México (PAPIIT-UNAM); Grant No. IN218416 (JAM). We are grateful to the people of Nizanda for their continued hospitality and support, to UNAM Population Ecology research group who gave the permission and support to use the required equipment and facilities, particularly to Mariana Hernández Apolinar and Pedro Eloy Mendoza Hernández who provided technical support in laboratory. We are grateful to Rey David López Mendoza for field assistance, Alicia Rojas-Leal for laboratory assistance and Julio César Montero Rojas for artwork.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

References

- Ackerly D (2004) Functional strategies of chaparral shrubs in relation to seasonal water deficit and disturbance. *Ecol Monogr* 74:25–44
- American Society for Testing and Materials (ASTM) (2010) Standard test method for specific gravity of wood and wood-based materials. ASTM D2395–07. Annual book of ASTM standards. ASTM, West Conshohocken
- American Society for Testing and Materials (ASTM) (2014) Standard methods of testing small clear specimens of timber. ASTM D143. Annual book of ASTM standards. ASTM, West Conshohocken
- American Society for Testing and Materials (ASTM) (2016) Standard test methods for direct moisture content measurement of wood and wood-base materials. ASTM D4442–15. vol 04.10 in Wood. Annual book of ASTM standards. ASTM, West Conshohocken
- Baker TR, Baker TR, Phillips OL, Malhi Y et al (2004) Variation in wood density determines spatial patterns in Amazonian forest biomass. *Glob Change Biol* 10:545–562
- Barajas-Morales J (1987) Wood specific gravity in species from two tropical forests in Mexico. *IAWA J* 8:143–148
- Bastin J-F, Fayolle A, Tarelkin Y et al (2015) Wood specific gravity variations and biomass of central African tree species: the simple choice of the outer wood. *PLoS One* 10:e0142146
- Beeckman H (2016) Wood anatomy and trait-based ecology. *IAWA J* 37:127–151
- Bhaskar R, Dawson TE, Balvanera P (2014) Community assembly and functional diversity along succession post-management. *Funct Ecol* 28:1256–1265
- Cannell MGR (1989) Physiological basis of wood production: a review. *Scand J For Res* 4:459–490
- Carlquist S (2001) Comparative wood anatomy: systematic, ecological, and evolutionary aspects of dicotyledon wood. Springer, New York
- Chave J, Muller-Landau HC, Baker TR, Easdale TA, Steege H, Webb CO (2006) Regional and phylogenetic variation of wood density across 2456 neotropical tree species. *Ecol Appl* 16:2356–2367
- Chave J, Coomes D, Jansen S, Lewis SL, Swenson NG, Zanne AE (2009) Towards a worldwide wood economics spectrum. *Ecol Lett* 12:351–366
- CICESE Centro de Investigación Científica y de Educación Superior de Ensenada (2015) Base de datos climatológica nacional (Sistema CLICOM). <http://clicom-mex.cicese.mx>. Accessed 4 May 2018
- de Micco V, Balzano A, Wheeler E, Baas P (2016) Tyloses and gums: a review of structure, function and occurrence of vessel occlusions. *IAWA J* 37:186–205
- Derroire G, Tigabu M, Odén PC et al (2016) Resilience of tropical dry forests—a meta-analysis of changes in species diversity and composition during secondary succession. *Oikos* 125:1386–1397
- Dinwoodie JM (2000) Timber: its nature and behaviour. E & FN Spon, London
- Echenique-Manrique R Robles, Fernández VF (1993) Ciencia y tecnología de la madera (Science and technology of wood). Universidad Veracruzana, Xalapa
- Evans JA, Gasson PE, Lewis GP (2006) Wood anatomy of the Mimosoideae (Leguminosae). *IAWA J Suppl* 5:1–117
- Ewel J (1980) Tropical succession: manifold routes to maturity. *Biotropica* 12:2–7
- Fortunel C, Ruelle J, Beauchêne J, Fine PVA, Baraloto C (2013) Wood specific gravity and anatomy of branches and roots in 113 Amazonian rainforest tree species across environmental gradients. *New Phytol* 202:79–94
- Francis EJ, Muller-Landau HC, Wright SJ et al (2017) Quantifying the role of wood density in explaining interspecific variation in growth of tropical trees. *Glob Ecol Biogeogr* 26:1078–1087
- Green DW, Evans JW (2001) Evolution of standardized procedures for adjusting lumber properties for change in moisture content. Gen Tech Rep FPL-GTR-127 US Department of Agriculture, Forest Service, Forest Products Laboratory, Madison
- Gryc V, Vavrčik H, Horn K (2011) Density of juvenile and mature wood of selected coniferous species. *J For Sci* 57:123–130
- Hacke UG, Sperry JS, Pittermann J (2000) Drought experience and cavitation resistance in six shrubs from the Great Basin, Utah. *Basic Appl Ecol* 1:31–41
- He H, Veneklaas EJ, Kuo J, Lambers H (2014) Physiological and ecological significance of biomineralization in plants. *Trends Plant Sci* 19:166–174
- Henry M, Besnard A, Asante WA et al (2010) Wood density, phytomass variations within and among trees, and allometric equations in a tropical rainforest of Africa. *For Ecol Manag* 260:1375–1388
- Hernández RE (2007) Moisture sorption properties of hardwoods as affected by their extraneous substances, wood density, and interlocked grain. *Wood Fiber Sci* 39:132–145
- Hietz P, Horsky M, Prohaska T, Lang I, Grabner M (2015) High-resolution densitometry and elemental analysis of tropical wood. *Trees* 29:487–497
- Hillis WE (1987) Heartwood and tree exudates. Springer, New York
- Holbrook NM (1995) Stem water and storage. In: Gartner BL (ed) Plant stems. Physiology and functional morphology. Academic Press, Cambridge, pp 151–169
- Hunt R (1982) Plant growth curves. The functional approach to plant growth analysis. Edward Arnold Ltd, London
- Kennard DK (2002) Secondary forest succession in a tropical dry forest: patterns of development across a 50-year chronosequence in lowland Bolivia. *J Trop Ecol* 18:53–66
- Kenzo T, Sano M, Yoneda R, Chann S (2017) Comparison of wood density and water content between dry evergreen and dry deciduous forest trees in Central Cambodia. *Jpn Agric Res Q* 51:363–374
- King DA, Davies SJ, Tan S, Noor NSM (2006) The role of wood density and stem support costs in the growth and mortality of tropical trees. *J Ecol* 94:670–680
- Konno K (2011) Plant latex and other exudates as plant defense systems: roles of various defense chemicals and proteins contained therein. *Phytochemistry* 72:1510–1530
- Larjavaara M, Muller-Landau HC (2010) Rethinking the value of high wood density. *Funct Ecol* 24:701–705
- Lebrija-Trejos E, Bongers F, Pérez-García EA, Meave JA (2008) Successional change and resilience of a very dry tropical deciduous forest following shifting agriculture. *Biotropica* 40:422–431
- Lebrija-Trejos E, Meave JA, Poorter L, Pérez-García EA, Bongers F (2010) Pathways, mechanisms and variability of tropical dry forest succession. *Perspect Plant Ecol Evol Syst* 12:267–275
- Lebrija-Trejos E, Pérez-García EA, Meave JA, Poorter L, Bongers F (2011) Environmental changes during secondary succession in a tropical dry forest in southern Mexico. *J Trop Ecol* 27:477–489
- Letcher SG, Lasky JR, Chazdon RL et al (2015) Environmental gradients and the evolution of successional habitat specialization: a test case with 14 neotropical forest sites. *J Ecol* 103:1276–1290
- Markesteijn L, Poorter L, Bongers F, Paz H, Sack L (2011) Hydraulics and life history of tropical dry forest tree species:

- coordination of species' drought and shade tolerance. *New Phytol* 191:480–495
- Martínez-Yrizar A, Sarukhán J, Pérez-Jiménez A, Rincón E, Maass JM, Solís-Magallanes A, Cervantes L (1992) Above-ground phytomass of a tropical deciduous forest on the coast of Jalisco, México. *J Trop Ecol* 8:87–96
- McCulloh KA, Johnson DM, Meinzer FC, Voelker SL, Lachenbruch B, Domec JC (2011) Hydraulic architecture of two species differing in wood density: opposing strategies in co-occurring tropical pioneer trees. *Plant Cell Environ* 35:116–125
- Meave JA, Romero-Romero MA, Salas-Morales SH, Pérez-García EA, Gallardo-Cruz JA (2012) Diversidad, amenazas y oportunidades para la conservación del bosque tropical caducifolio en el estado de Oaxaca, México (Diversity, threatens and opportunities for tropical dry forest conservation in Oaxaca state, Mexico). *Ecosistemas* 21:85–100
- Méndez-Alonzo R, Paz H, Zuluaga RC, Rosell JA, Olson ME (2012) Coordinated evolution of leaf and stem economics in tropical dry forest trees. *Ecology* 93:2397–2406
- Murphy PG, Lugo AE (1986) Ecology of tropical dry forest. *Annu Rev Ecol Syst* 17:67–88
- Nearn WT (1955) Effect of water soluble extractives on the volumetric shrinkage and equilibrium moisture content of eleven tropical and domestic woods. *Bull. 598, Agricultural Experiment Station, Pennsylvania State University, University Park, PA*
- Niklas KJ (1999) The mechanical role of bark. *Am J Bot* 86:465–469
- Nogueira EM, Nelson BW, Fearnside PM (2005) Wood density in dense forest in central Amazonia, Brazil. *For Ecol Manag* 208:261–286
- Oluwadare AO, Ashimiyu OS (2007) The relationship between fiber characteristics and pulp-sheet properties of *Leucaena leucocephala* (Lam.) de wit Middle-East. *J Sci Res* 2:63–68
- Ordóñez JAB, Galicia A, Venegas NJ, Hernández T, Ordóñez MdJ, Dávalos-Sotelo R (2015) Densidad de las maderas mexicanas por tipo de vegetación con base en la clasificación de J. Rzedowski: compilación (Density of mexican woods by vegetation type based on J. Rzedowski classification: compilation). *Madera Bosques* 21:77–126
- Panshin AJ, de Zeeuw C (1980) Textbook of wood technology. McGraw-Hill Inc, New York
- Paz H, Pineda-García F, Pinzón-Pérez LF (2015) Root depth and morphology in response to soil drought: comparing ecological groups along the secondary succession in a tropical dry forest. *Oecologia* 179:551–561
- Pearcy RW, Ehleringer J, Mooney HA, Rundel PW (1991) Plant physiological ecology. Chapman and Hall, London
- Peña-Claros M (2003) Changes in forest structure and species composition during secondary forest succession in the Bolivian Amazon. *Biotropica* 35:450–461
- Pérez-García EA, Meave JA, Villaseñor JL, Gallardo-Cruz JA, Lebrija-Trejos E (2010) Vegetation heterogeneity and life-strategy diversity in the flora of the heterogeneous landscape of Nizanda, Oaxaca, México. *Folia Geobot* 45:143–161
- Pérez-Harguindeguy N et al (2013) New handbook for standardised measurement of plant functional traits worldwide. *Aust J Bot* 61:167–234
- Pineda-García F, Paz H, Meinzer FC (2013) Drought resistance in early and late secondary successional species from a tropical dry forest: the interplay between xylem resistance to embolism, sapwood water storage and leaf shedding. *Plant Cell Environ* 36:405–418
- Pineda-García F, Paz H, Meinzer FC, Angeles G (2015) Exploiting water versus tolerating drought: water-use strategies of trees in a secondary successional tropical dry forest. *Tree Physiol* 36:208–217
- Plavcová L, Jansen S (2015) The role of xylem parenchyma in the storage and utilization of nonstructural carbohydrates. In: Hackett UG (ed) Functional and ecological xylem anatomy. Springer, Cham, pp 209–234
- Poorter L, Wright SJ, Paz H, Ackerly DD et al (2008) Are functional traits good predictors of demographic rates? Evidence from five neotropical forests. *Ecology* 89:1908–1920
- Reva VL, Fonseca JL, Lousada I, Abrantes AR, Figueiredo Viégas DX (2015) Basic density, extractive content and moisture sorption properties of *Pinus pinaster* wood infected with the pinewood nematode, *Bursaphelenchus xylophilus*. *J For Res* 26:233–240
- Rosell JA, Olson ME (2014) The evolution of bark mechanics and storage across habitats in a clade of tropical trees. *Am J Bot* 101:764–777
- Russell AL (2005) Standardization in history: a review essay with an eye to the future. The standards edge: future generations. In: Bolin S (ed) The standards edge: future generations. Sheridan Press, Ann Arbor, pp 247–260
- Ruzin SE (1999) Plant microtechnique and microscopy. Oxford University Press, New York
- Saha S, Howe HF (2003) Species composition and fire in a dry deciduous forest. *Ecology* 84:3118–3123
- Schmidt O, Magel E, Frühwald A, Glukhykh L, Erdt K, Kaschuro S (2016) Influence of sugar and starch content of palm wood on fungal development and prevention of fungal colonization by acid treatment. *Holzforschung* 70:783–791
- Silva-Guzmán JA, Fuentes F, Rodríguez R et al (2010) Fichas de propiedades tecnológicas y usos de maderas nativas de México e importadas (cards of technological properties and uses of native and imported woods of Mexico). Amaya Ediciones, Guadaluajara
- Slik JWF, Bernard CS, Breman FC, Van Beek M, Salim A, Sheil D (2008) Wood density as a conservation tool: quantification of disturbance and identification of conservation-priority areas in tropical forests. *Conserv Biol* 22:1299–1308
- StatSoft, Inc. (2007) STATISTICA (data analysis software system), version 8.0. www.statsoft.com
- Trejo I, Dirzo R (2000) Deforestation of seasonally dry tropical forest: a national and local analysis in Mexico. *Biol Conserv* 94:133–142
- van Gelder HA, Poorter L, Sterck FJ (2006) Wood mechanics, allometry, and life-history variation in a tropical rain forest tree community. *New Phytol* 171:367–378
- Vielle C, Navas ML, Vile D, Kazakou E, Fortunel C, Hummel I, Garnier E (2007) Let the concept of trait be functional! *Oikos* 116:882–892
- Wangaard FF, Granados LA (1967) The effect of extractives on water-vapor sorption by wood. *Wood Sci Technol* 1:253–277
- Wiemann MC, Williamson GB (1989) Wood specific gravity gradients in tropical dry and montane rain forest trees. *Am J Bot* 76:924–928
- William VZ (1983) Tannins: does structure determine function? An ecological perspective. *Am Nat* 121:335–365
- Williamson GB (1975) Studies in secondary succession within forests. Dissertation, Indiana University
- Williamson GB, Wiemann MC (2010a) Age-dependent radial increases in wood specific gravity of tropical pioneers in Costa Rica. *Biotropica* 42:590–597
- Williamson GB, Wiemann MC (2010b) Measuring wood specific gravity... correctly. *Am J Bot* 97:519–524
- Wolfe BT, Kursar TA (2015) Diverse patterns of stored water use among saplings in seasonally dry tropical forests. *Oecologia* 179:925–936

Zanne AE, Westoby M, Falster DS, Ackerly DD, Loarie SR, Arnold SEJ, Coomes DA (2010) Angiosperm wood structure: global patterns in vessel anatomy and their relation to wood density and potential conductivity. *Am J Bot* 97:207–215

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

CAPÍTULO 5

Wood anatomy of 13 species from a tropical dry forest secondary vegetation



Wood anatomy of 13 species from a successional tropical dry forest

Abstract

Species occurring in tropical dry forest (TDF) recovering vegetation represent an interesting group from a water stress adaptations point of view, as they face water scarcity during a well-marked dry season and display different phenological and ecological responses. Some wood anatomical features of their stems may be useful to explore possible hydric stress coping mechanisms. Here, we describe the wood anatomy of 13 frequent species, from seven families, in TDF secondary vegetation. As the studied species grow in a seasonally dry environment, we expected that they shared wood anatomical features such as conspicuous growth marks, or predominance of ring-porosity due to changes in water availability, as well as anatomical features associated with drought resistance, such as paratracheal parenchyma. Most species have diffuse-porosity and various inter-specific wood cell arrangements and sizes. Axial parenchyma is associated with vessels in diverse ways. Simple vessel perforation plates are common to all studied species. Different features delimit poorly defined growth mark boundaries, in agreement with previous reports for other tropical species. Earlywood is difficult to distinguish from latewood, even in the two ring-porous legumes. Main ground tissue components are complex, as they may include non-septate fibres, septate living fibres (in five species), gelatinous fibres, or no fibres. Axial and radial parenchyma arrangement is also diverse, and it may be scarce, abundant, or the main and unlignified ground tissue component. Vessel clusters are common but have a wide range of vessels per group (maximum 3–29). Mean vessel diameter range is ≤ 50 – $200 \mu\text{m}$. The studied species have between less than five vessels per mm^2 and more than 100, as well as very thin to very thick-walled fibres. Taxonomic and phenological diversity observed in TDF successional species and the anatomical features recorded in this study suggest different water stress coping mechanisms resulting from different wood anatomical combinations. The recognition of the complexity and multifunctionality of stem woody

tissue warns us against the oversimplification of the relationship between their anatomical features, functions and ecological performance of TDF species.

Key words

Cactaceae, Fabaceae, gelatinous fibres, growth rings, parenchyma arrangement, septate fibres.

Introduction

Describing wood anatomical features may focus on taxonomic and systematics purposes, but also on shedding light on the relationships between plant structure and function (Baas et al. 2016). Angiosperm wood is a diverse and complex tissue usually conformed by fibres, vessel elements, and axial and radial parenchyma cells. Characteristics of each cell type, cell spatial arrangement, and their degree of inter-connection affect whole-plant functions such as hydraulic safety, water storage and mechanical support (Sperry et al. 2008). TDF species represent an interesting group from the point of view of adaptations to water stress, and some of their stem secondary xylem anatomical features stem may be useful to explore the spectrum of possible hydric stress coping mechanisms in seasonally dry regions (Hasselquist et al. 2010; Fu et al. 2012; Pineda-García et al. 2015; Pivovarovoff et al. 2016; Zhu et al. 2017).

TDF is one of the most extensive tropical vegetation types in Mexico and Central America (Murphy and Lugo, 1995). It is a diverse plant community (Derroire et al. 2016), with Fabaceae having the highest number of tree species (Murphy & Lugo 1986; Gentry 1995). In the study area, *Lysiloma divaricatum* is a structurally important canopy component (Muñoz-Avilés 2015), and there are also conspicuous plant elements which belong to the Cactaceae (Pérez-García et al. 2010), such as *Pachycereus pecten-aboriginum* and *Pilosocereus collinsii*, which are woody species with similar or even higher wood density than other species belonging to Euphorbiaceae and Caricaceae families (Romero et al. 2020). Secondary vegetation derived from TDF covers an important area in the lowland tropics, including Mexico (Janzen 1988; Trejo & Dirzo 2000). Secondary TDF vegetation is

also a diverse plant community, as many mature TDF species persist in recovering vegetation (Lebrija-Trejos et al. 2010; Bhaskar et al. 2014).

In this study we describe the wood anatomy of 13 species present in the canopy of secondary vegetation that grows after tropical dry forest (TDF) is burned and cleared for agricultural or livestock purposes. This vegetation type occurs in regions where temperature is isothermal, but rainfall falls with a clear seasonality. Most TDF species drop their leaves during the dry season (Brown & Lugo 1990), although with a high phenological variation: semi-deciduous to deciduous trees frequently co-occur and show a large variability in their leaf life-span and leaf growth rates (Eamus 1999).

As the studied species coexist in late successional stages under a clear rainfall seasonality, it may be expected that there will be, among those woody species, some tendency or common pattern in their anatomical characteristics, commonly associated with the dry climate where they dwell. But, on the contrary, given the taxonomic, phenological and structural diversity observed in species present in TDF recovering vegetation it may be expected that there will be a high anatomical diversity in their secondary vascular tissue, as well as different possible water stress coping mechanisms. Thus, additionally to the wood description, in this study we also aim to discuss the potential impact that some wood anatomical features could have on water stress resistance.

Methods

Study area

The study was conducted in Nizanda, Oaxaca, southern Mexico (16° 39' 30" N, 95° 00' 40" W). Derived from agriculture and grazing activities, there are secondary vegetation patches of different ages across the region (Gallardo-Cruz et al. 2012). Mean annual temperature is 27.6 °C and average total annual rainfall is 902.6 ± 355.4 mm (± SD), with a strong seasonality: dry season from November to April and rainy season from the end of May to mid-October. TDF is the main vegetation type of the region (Pérez-García et al. 2010). At least 50 woody species occur in mature TDF of the study region and also in secondary

vegetation (Lebrija-Trejos et al. 2010). Only seven woody species occur exclusively in secondary vegetation, i.e. have not been recorded in mature forest vegetation of the region (Pérez-García et al. 2010).

Species selection and some ecological features

We selected the 13 most frequent species that occur in secondary vegetation (*i.e.* successional species; Table 1) and coexist in late-successional stages, based on previous studies (Lebrija-Trejos et al. 2008; Romero-Pérez unpublished results) and field observations. These species belong to 7 families and 12 genera. Most of the species are deciduous (11), although they differ in phenology (see details in Table 1). Three of the species are exclusive of secondary vegetation (Table 1), highly abundant in early successional stages, but persist in late successional stages, although with less frequency. The other 10 selected species occur in both secondary and mature forest (Table 1; see details in Romero et al. 2020 Materials and Methods).

Wood sample collection and procedure

Three to six adult, healthy plants with straight stems of each species were selected (see Table S1 in Supplementary material, in Annexes of Chapter 5 at the end of this thesis) from late successional plots (>50 years of abandonment following anthropogenic disturbance). A wood sample was collected with a saw from the main stem of each individual, and immediately stored in a glycerine-ethanol-water solution (1:1:1), in which they remained for three months until sectioning. Transverse, tangential and radial sections (20 to 30 μm thick) were cut with a sliding microtome (Leica 2000R, Wetzlar, Germany). Half of the sections were bleached and then all dehydrated with ethanol (50 % – 96 %), stained with safranin-fast green, rinsed with alcohol 100 %, cleared in xylol, and mounted with synthetic resin.

Wood anatomical description

Qualitative wood anatomical traits were described following IAWA recommendations (IAWA Committee 1989). Tangential vessel diameter, vessels per square millimetre, number of vessels per group, and fibre diameter and fibre wall thickness were measured or counted with Image analyser Pro v. 7.1 (ImagePro Plus 7.1, Media Cybernetics, Silver Spring, MD, USA) adapted to compound microscope Olympus BX51 (Tokyo, Japan). For each individual, vessels frequency and number of vessels per group were counted in 9 to 12 optical fields of 0.1 mm² (vessel frequency total area added 1 mm²), in the area covering the most recently produced wood tissue, (approximately inside one or two growth rings, depending on the characteristics of each particular wood sample; example in Fig. S1). A mean of 50 fibres was measured per individual. For diffuse porous species a mean of 50 vessels per individual was measured. For ring porous species in individuals with clear growth rings 50 earlywood vessels and 50 latewood vessels were measured; 100 vessels per individual were measured. Mean and standard deviation were calculated; the minimum and maximum are also presented because maximum vessel diameter may be also a relevant feature explaining conductive capacity (Baas et al. 1983).

Results

General wood description

Macroscopically growth marks distinct in all species except in *Lonchocarpus lanceolatus*, and more evident in *Acacia cochliacantha*, *Lysiloma divaricatum*, *Mimosa eurycarpa*, *Cnidoscolus megacanthus*, *Coccoloba liebmannii*, *Bursera simaruba*, *Phyllostylon rhamnoides*, *Pilosocereus collinsii*, than in *Bonellia macrocarpa*, *Jacaratia mexicana*, *Mimosa tenuiflora*, and *Pachycereus pecten-aboriginum*. Microscopically, boundaries mostly poorly defined (Table 2) or marked by radially flattened latewood fibres, changes in fibre and axial parenchyma dimensions, changes in vessel distribution, changes in the occurrence of gelatinous fibres and non-gelatinous fibres and marginal parenchyma with crystals. Wood commonly diffuse-porous and rarely semi-ring and ring-porous (Table 2).

Mean tangential vessel diameter commonly $\leq 50 \mu\text{m}$, but extremes from $4.59 \mu\text{m}$ in *Acacia* to $267 \mu\text{m}$ in *Jacaratia mexicana* (Table 4). Vessels are $41\text{--}100/\text{mm}^2$, varying from 6 vessels/ mm^2 in *Jacaratia mexicana* to $178 \text{ vessels}/\text{mm}^2$ in *Phyllostylon rhamnoides* (Table 5). Vessel solitary, in radial rows of 4 to more cells and occasionally in clusters up to 29 vessels, (Table 3); vessels outline oval to rounded (Table 2). Vessel elements with exclusively simple perforation plates, intervessel pits predominantly alternate, alternate to opposite and pseudoscalariform in both cacti and *Jacaratia mexicana* (Table 2). Vessel-ray pitting similar to intervascular pitting in shape and size, except for *Jacaratia mexicana*, which are apparently pseudoscalariform, and *Cnidoscolus megacanthus*, with part of the vessel-ray pits with reduced borders, and pits of two distinct sizes in the same ray cell (Table 2). Vessel deposits common (Table 2). Fibres exclusively with simple and minute pits, mostly non-septate septate in five species (Table 2) and gelatinous fibres in seven species (Table 6); *Jacaratia mexicana* fibreless. Fibres with thin to very thick-walls (Table 6), with the thinnest in *Cnidoscolus megacanthus* ($1.31 \mu\text{m}$) and the thickest in *Acacia cochliacantha* ($4.32 \mu\text{m}$). Apotracheal axial parenchyma diffuse and paratracheal from scanty to banded, strands 2-8 cells (Table 2) and unligified parenchyma in *Jacaratia mexicana* (Fig. 1M). Uniseriate rays commonly present and more frequent in *Cnidoscolus megacanthus* and *Coccoloba liebmannii*, multiseriate 2-3-seriate but 10-seriate in *Bonellia macrocarpa* and *Jacaratia mexicana* (Table 2). Five species with rays more than 1 mm high and procumbent cells in seven species (Table 2). Storied structure in 2 species (Table 2). Radial canals in *Bursera simaruba*. Prismatic crystals in axial parenchyma or in ray cells common to nine species (Table 2), and silica bodies in *Bonellia macrocarpa*. Marginal axial parenchyma cells have crystals in three legume species (*Acacia cochliacantha*, *Lonchocarpus lanceolatus* and *Lysiloma divaricatum*).

Species wood description

Acacia cochliacantha (Fabaceae; Figs. 1A, 2A and 3A). Growth ring boundaries commonly but not constant (i.e., not in all individuals, and not across the entire tissue) marked by parenchyma bands in earlywood, at the margins of a growth ring, which form a more or less

continuous layer of variable width (1 to 5, and up to 7 layers). Some of these marginal axial parenchyma cells have small crystals, which makes those particular marks more conspicuous (Fig. 4A, B, C); latewood fibres sometimes with reduced radial diameter; some rays locally dilated (Fig. 4B). Earlywood and latewood are undistinguishable. Growth ring boundaries are very conspicuous in individuals where ground tissue is mostly composed by gelatinous fibres mixed with very scarce non-gelatinous fibres (Fig. 4B). Diffuse porous (Fig. 1A). Vessels mostly solitary, partly in small clusters 2-3, or scarce big clusters up to 13 small vessels (Table 3; Fig. 5A). Vessel ray pitting similar to intervessel pits in size and shape throughout the ray cell. Axial parenchyma vasicentric, with short confluences, also in seemingly marginal bands and apotracheal scarce with crystals of different sizes (Figs. 4C and 6A; Table 2); two and four cells per parenchyma strand. Rays homocellular, uni and 2- to 6-seriate, with exclusively procumbent cells.

Lonchocarpus lanceolatus (Fabaceae; Figs. 1B, 2B and 3B). Growth ring boundaries not observed, although rays seem to widen in the region where they coincide with axial parenchyma bands (Fig. 6B, C). Occasionally, a change between gelatinous fibres and non-gelatinous fibres can be seen, particularly in individuals in which gelatinous fibres are the main ground tissue. Diffuse porous (Fig. 1B). Vessels partly solitary (generally the wider vessels), and partly in groups generally conformed by many narrow vessels (Fig. 5B), up to 14 vessels per group (Table 3). Vessel ray pitting similar to intervessel pits in size and shape throughout the ray cell. Frequently ground tissue consists mainly of gelatinous fibres (Fig. 6D), occasionally non-septate fibres, and very rarely septate fibres. Predominantly banded axial parenchyma consisting in 3 and 4 cells wide, occasionally 5 or 6. Fusiform parenchyma cells, and also 2 cells per parenchyma strand. Rays homocellular with exclusively procumbent cells. Rays and axial parenchyma storied (Fig. 2B). Prismatic crystals in axial parenchyma, particularly in both sides of parenchyma bands (Fig. 6B, C).

Lysiloma divaricatum (Fabaceae; Figs. 1C, 2C and 3C). Growth ring boundaries marked by earlywood vessels distinctly larger in diameter than those in latewood (Fig. 4D). Parenchyma in marginal narrow bands, 1 cell thick with crystals commonly defining the boundaries between rings (Fig. 4E, F), which are particularly conspicuous in individuals in

which gelatinous fibres are the main ground tissue. Ring-porous (Figs. 1C, 4D). Apparently, vessel distribution changes in latewood producing less vessels than in earlywood, but transition from earlywood to latewood in the same ring is commonly undistinguishable. Furthermore, it gives the false impression of diffuse porosity when it produces narrow rings. Vessels partly solitary, partly in short radial pattern (2 and 3 vessels per group), and groups with more than 10 common vessels, up to 29 (Fig. 5C). These groups of vessels commonly include many latewood vessels with small diameters and occasionally with earlywood big diameters. Vessel ray pitting similar to intervessel pits in size and shape throughout the ray cell. Axial parenchyma with 2-4 cells per parenchyma strand, in marginal bands sometimes of one-thick cell, paratracheal vasicentric and occasionally aliform. In some individuals ground tissue mainly of bands of gelatinous fibres and occasionally bands of non-gelatinous fibres. Rays homocellular with exclusively procumbent cells (Fig 3C).

Mimosa eurycarpa (Fabaceae; Figs. 1D, 2D and 3D). Growth ring boundaries marked by marginal parenchyma and thicker walled fibres (Figs. 4H-J). Initial earlywood vessels sometimes (i.e. not in every growth ring) surrounded by abundant marginal parenchyma (Figs. 1D, 4I). In some growth rings parenchyma surrounding earlywood vessels changes to smaller diameter vessels, latewood fibres and scarce parenchyma (Fig. 4I, J); sometimes earlywood fibres changes to parenchyma surrounding latewood vessels (Fig. 4H). Occasionally growth marks are more conspicuous when there is a change between latewood gelatinous fibres to earlywood marginal parenchyma followed by non-gelatinous fibres. Ring porous with earlywood vessels distinctly larger in diameter than those in the latewood (Fig. 4G), although in the same growth ring the transition from earlywood to latewood is gradual (Fig. 1D). Ring porous; it gives the false impression of semi-ring porosity when it produces narrow rings (Fig. 4G). Earlywood vessels partly solitary, and partly in short radial multiples of 2-4 vessels. Latewood vessels commonly in groups of many vessels (more than 10 vessels common) up to 21 (Fig. 5D). Vessel ray pitting similar to intervessel pits in size and shape throughout the ray cell. Axial parenchyma predominantly vasicentric, and marginal bands to confluent aliform in earlywood. There are fusiform cells that

occasionally divide into 2 to 4 cells per parenchyma strand. Rays homocellular with exclusively procumbent cells.

Mimosa tenuiflora (Fabaceae; Figs. 1E, 2E and 3E). A band of two to four parenchyma cells define the growth marks, in some of them with tannins, making the growth ring boundaries more conspicuous. This band can be followed by a band of axial parenchyma or by fibres of apparently the same size. Diffuse porous (Fig. 1E). Apparently, it produces fewer vessels in latewood than in earlywood. Vessels solitary, in short radial clusters of 2 vessels, and larger groups of vessels common (up to 17-22 vessels per group). Vessel ray pitting similar to intervessel pits in size and shape throughout the ray cell. Gelatinous fibres are frequent as ground tissue. Axial parenchyma paratracheal confluent, vasicentric and aliform. Rays homocellular with exclusively procumbent cells.

Pachycereus pecten-aboriginum (Cactaceae; Figs. 1F, 2F and 3F). Growth ring boundaries mostly indistinct and earlywood indistinguishable from latewood. When distinct, growth rings delimited non-continuously by earlywood fibres with slightly wider lumen than latewood fibres (Fig. 4K). Diffuse porous (Fig. 1F). Vessels partly solitary, partly in vessel clusters of 2–3 cells (Fig. 5E) and occasionally 4. Vessel outline rounded, occasionally angular. Vessel ray pitting similar to intervessel pits in size and shape throughout the ray cell. In ground tissue septate fibres predominate, some fibres with visible nuclei, and occasionally non-septate fibres. Axial parenchyma vasicentric (Fig. 5E), with 2 cells per parenchyma strand. Multiseriate rays 4 – to 10 seriate, composed of upright and square cells mixed throughout the ray, with predominantly upright cells in the margins.

Pilosocereus collinsii (Cactaceae; Figs. 1G, 2G and 3G). Growth ring boundaries more or less distinct (Figs. 1G, 4L, 4M) and earlywood indistinguishable from latewood. Growth rings apparently delimited by changes in vessel distribution, being more frequent and grouped in earlywood (Fig. 4L, M; Fig. S3), and by earlywood fibres with slightly wider lumen than latewood fibres. Diffuse porous (Fig. 1G). Vessels partly solitary, partly in vessel clusters of 2–3 cells and occasionally up to 4. Vessel outline rounded, occasionally angular. Vessel ray pitting similar to intervessel pits in size and shape throughout the ray cell. Ground tissue composed of septate and non-septate fibres. Axial parenchyma scanty paratracheal and

scarce vasicentric, with 4 cells per parenchyma strand, occasionally 6. Multiseriate rays 4 to 10 seriate, composed of upright, procumbent and square cells mixed throughout the ray, with predominantly upright cells in the margins.

Bonellia macrocarpa (Primulaceae; Figs. 1H, 2H and 3H). Growth ring boundaries distinct (Fig. 4N, O) and earlywood indistinguishable from latewood. In certain specimens, growth rings apparently delimited by grouped vessels (Fig. 1H, and more evident in Fig. 4N), apparently bigger in diameter, that can be or not surrounded by marginal parenchyma, some rays widen in regions coinciding with bigger vessels (Fig. 4N), and occasionally fibres in these regions have wider lumen (Fig. 4O). Semi-ring to diffuse porous (Fig. 1H). Vessels seem to have different radial distribution and sizes throughout the wood: apparently bigger in early wood, and scarce smaller vessels in latewood. Vessels partly solitary, partly in vessel clusters of 2–5 cells. Vessel ray pitting similar to intervessel pits in size and shape throughout the ray cell. In ground tissue fibres are predominantly non-septate but occasionally presents few septate fibres. Axial parenchyma scanty paratracheal and rarely vasicentric, with fusiform parenchyma cells. All rays multiseriate (4 to 10 seriate), predominantly more than 1 mm height, and occasionally shorter rays, composed of predominantly procumbent ray cells, or a mixture of procumbent and square cells in the margins. Silica bodies of different size and shape in ray cells common, and scarce square-prismatic crystals.

Bursera simaruba (Burseraceae; Figs. 1I, 2I and 3I). Growth rings distinct, but the cells that define the boundaries are not constant: in some cases non-continuous layers of radially flattened fibres can be observed (Fig. 4P, Q); some individuals present a change of ground tissue gelatinous fibres to non-gelatinous fibres, and in those cases growth rings boundaries are very conspicuous (Fig. 4Q). Diffuse porous (Fig. 1I). Vessels partially solitary, partly in small clusters of 2 vessels, and occasionally 3 – 4 vessels per group (up to 8). Vessel ray pitting similar to intervessel pits in size and shape throughout the ray cell. Ground tissue fibres septate, frequently gelatinous (Fig. 4Q). Parenchyma scanty paratracheal with four cells per strand. Ray cells procumbent with upright marginal cells. Rays are discontinuous. One or both most external cells of each radius with one crystal.

Cnidocolus megacanthus (Euphorbiaceae; Figs. 1J, 2J and 3J). Occasionally, growth rings distinct at lower optical zoom (Fig. 1J). Cells defining boundaries between growth rings not constant, in some cases non-continuous layers of radially flattened fibres; sometimes gelatinous fibres in bands (Fig. 4V). Diffuse porous (Fig. 1J). Vessels partly solitary, partly in radial multiples of 2 to 4, some up to 8. Vessel ray pits with much reduced borders to apparently simple, with pits of two distinct sizes in the same ray cell. Parenchyma predominantly apotracheal diffuse, and paratracheal vasicentric, with 4 to mostly 8 cells per strand (Fig. 6I). Ground tissue may be composed of gelatinous fibre bands and non-gelatinous bands, or scarce gelatinous fibres in a non-gelatinous matrix (Figs. 4V, 6H). Libriform fibres with pits difficult to distinguish (Fig. 6J). Ray cells upright and square mixed throughout the ray (Fig. 6G). Ray height occasionally > 1 mm.

Coccoloba liebmanni (Polygonaceae; Figs. 1K, 2K and 3K). Growth rings distinct (Fig. 4R, S). Boundaries not always clear or constant, consisting in one discontinuous layer (up to three layers) of radially flattened fibres (Fig. 4S). Diffuse porous (Fig. 1K). Vessels in radial multiples of ≥ 4 common up to 7-25. Vessels predominantly in radial pattern. Parenchyma apotracheal diffuse, predominantly 6 – 8 cells per parenchyma strand. Ground tissue sometimes composed of septate fibres (Fig. 6K, M). Crystals present in apotracheal parenchyma (Fig. 6L).

Phyllostylon rhamnoides (Ulmaceae; Figs. 1L, 2L and 3L). Growth ring boundaries mostly distinct (Fig. 4R, S) and earlywood indistinguishable from latewood. When distinct, growth rings delimited by axial parenchyma in narrow bands up to two cells wide (Fig. 4T, U). Occasionally parenchyma radial cells with crystals coincide with these boundaries (Fig. 4T, U). Diffuse porous (Fig. 1L). Vessels clusters 2-3 common, some in radial multiples of 4 – 8 and up to 13 (Fig. 5G), and some solitary. Axial parenchyma predominantly paratracheal scanty and irregular narrow bands, with 2 – 4 cells per parenchyma strand. Multiseriate rays 1 to 3 seriate, composed of procumbent ray cells.

Jacaratia mexicana (Caricaceae; Figs. 1M, 2M and 3M). Diffuse porous (Fig. 1M). Abundant non-lignified axial parenchyma, and vasicentric paratracheal lignified parenchyma, this latter composed of short cells with wide pits. Some parenchyma fusiform cells storied.

Vessels in tangential bands (Fig. S2), solitary and in short groups up to 3 vessels. Vessel-ray pitting horizontal, pseudoscalariform. Ground tissue without fibres, composed mainly of non-lignified parenchyma. Multiseriate rays, larger than 1 mm, composed of procumbent, square and upright cells mixed (Fig. 3M).

Discussion

Given the taxonomic and phenological diversity of the 13 studied species that occur in late successional stages under a seasonal precipitation regime, we expected that the wood anatomical traits exhibited were also diverse. The only common features to all species were the simple perforation plates and the paratracheal parenchyma, although its arrangement varied greatly, and in some species it was scanty. The wood of *Bonellia macrocarpa*, *Cnidocolus megacanthus*, *Jacaratia mexicana*, and *Lonchocarpus lanceolatus* is described here for the first time. Notably, Carlquist (1998) mentioned that *Jacaratia* wood is fibreless, studying a cultivated tree (1.5 m tall) of *J. hassleriana*, also a member of Caricaceae family. We support this assertion in the six 5 m tall *J. mexicana* trees.

These species present various features delimiting growth marks boundaries, with different degrees of distinctiveness. Although vessel clusters are common in these species, the range of number of vessels per group is extremely variable (3 to a maximum of 29 vessels per group). Tangential vessel diameter range of these species is broad, as the mean values enter in three of the four size categories given by IAWA list features (1989; from ≤ 50 to $200 \mu\text{m}$), and even maximum values observed fall into the fourth and biggest, category size ($> 200 \mu\text{m}$). The number of vessels/ mm^2 range is also broad, as these species may have less than 5 vessels per mm^2 and more than 100. Axial and radial parenchyma arrangement is diverse, and they may be scarce, or conversely the main ground tissue component. Ground tissue component features are heterogeneous, as they may include non-septate fibres, septate fibres, gelatinous fibres, a mixture of them, or no fibres at all. Fibre thickness also presents a very wide range of mean values, ranging from very thin to very thick-walled fibres. Mineral inclusions are also varied, as species can possess crystals, silica bodies and

dark staining deposits. A peculiar wood feature was found: the presence of gelatinous fibres in most of these successional species, in some cases being appreciably abundant.

It was difficult to determine whether fibres were septate or not, as gelatinous fibres were frequent in most of the studied species, and as cellular contents such as tannins and starch were also abundant (Romero et al. 2020), blocking the thin septae observation.

Anatomical features in a functional ecological context

Some qualitative wood anatomical characteristics have been associated with different degrees of resistance to water stress, for example porosity type, parenchyma distribution, vessel arrangement, and vessel perforation plate. Most species are diffuse porous, all studied species have paratracheal parenchyma and simple perforation plates, which are common in TDF (Baas 1976), and clusters commonly have many vessels. This and some other anatomical features described in this study could make possible different water stress coping mechanisms in the studied species and they are discussed in the following sections.

Growth rings marks and porosity type

Indistinct growth rings and diffuse porosity are common features in tropical trees (Boura & De Franceschi 2007; Wheeler et al. 2007). However, it has been suggested that in tropical regions with a clear distinction between dry and wet seasons, deciduous species form distinct growth rings (Segala-Alves & Angyalossy, 2002; Worbes 1995). Ring porosity may also be expected as a result of changes in vessel size associated with seasonal drought, although it has been found that ring porous species are more hydraulically vulnerable than diffuse porous species (Bush et al. 2008; Ogasa et al. 2014). Although the 13 studied species grow in a tropical region, the predominant diffuse porosity type and the non-consistent distinct growth ring boundaries were unexpected findings, as these species occur under a strong precipitation seasonality, and they shed their leaves at least once annually (Maldonado-Romo, 2014). Furthermore, contrary to an isolated TDF in northern Mexico, and to a TDF in the Pacific region (Barajas-Morales & Gómez 1989; Ramírez-Martínez et al. 2017), ring boundaries in the studied successional species are mostly difficult to detect.

Worbes (1995) found that growth periodicity is indicated by the leaf fall behaviour; however, it is likely that some of these species produce wood tissue even during the time they drop their leaves, but periodical sampling is needed to confirm this suggestion.

Diffuse porosity type apparently predominates across Mexican TDFs, as Barajas-Morales & Gómez (1989) report 70% of the studied species as diffuse porous, similar to our results, and Ramírez-Martínez et al. (2007) reported 52% studied species as diffuse porous. Accordingly, most of the studied species show diffuse porosity and a gradient of growth-ring distinctiveness. In the ring-porous species, *Mimosa eurycarpa* and *Lysiloma divaricatum*, some individuals give the false impression of diffuse porosity when it produces narrow rings. Species drought responses to precipitation fluctuations within and between years probably explain these patterns. Ring-porous and diffuse wood type differentiation in temperate deciduous species have been proved to be mediated by continuously moving hormonal signals that promote cambial activity and enable a continuous response to the environment (Aloni 2015). Studies integrating cambial activity and physiology are needed to understand the diffuse vs ring-porous wood in TDF species.

Theoretically, in ring-porous species large differences in vessel diameter allow the distinction between earlywood from latewood, whereas in diffuse porosity species latewood may be recognized by few layers of more lignified fibres, or by marginal parenchyma (IAWA Committee, 1989). In most of the studied species, boundaries are defined by different parenchyma and vessel arrangement patterns, and rays locally dilated associated with an unclear gradual variation in fibre dimensions. Yet, in agreement with Tarelkin et al. (2016) and Silva et al. (2019), we found that growth-ring boundaries distinctness is a highly variable feature, and abrupt changes in vessel diameter, fibre size and cell wall thickness cannot always be observed. Additionally, we recorded gelatinous fibres that in some cases helped identify growth ring boundaries, but this feature needs further and detailed future exploration.

There are environmental, endogenous and genetic causal factors involved in the expression of growth rings with complex relationships among them, therefore, growth rings are not always the result of seasonal changes between favourable and unfavourable

conditions for plant growth (Silva et al. 2019). Worbes (1989) concluded that the number of tropical tree species with annual rings is much larger than generally assumed, and we agreed with him in that studying tropical tree rings is more difficult than in trees of the temperate zones. He reports that in tropical regions with a marked dry season tree species form growth rings, but his study was done in a flooded forest. In our study area mean temperature is isothermal throughout the year, which could explain the lack of conspicuous growth marks, although precipitation throughout the year is highly variable. Future cambium and ecophysiological studies in these and other seasonally dry tropical species are needed to explain the unexpected inconsistency in growth mark distinctiveness, and the prevalence of diffuse-porosity.

Radial and axial parenchyma

The distribution of stem xylem parenchyma in relation with vessels can influence functions such as water transport and storage, as well as cambium reactivation. For example, vessels adjacent to parenchyma cells such as paratracheal axial parenchyma and rays have been viewed as a mechanism preventing and repairing water stress damage in the stem hydraulic system, also involved with stored water mobilization (Brodersen & McElrone, 2013; Ogasa et al. 2013; Carlquist 2015; Morris et al., 2016; Secchi et al. 2017; Morris et al. 2018; Tng et al. 2018). Therefore, we expected to find paratracheal parenchyma in most of the studied species, as this feature may be an advantageous feature during the dry season in agreement with other TDF species (Ramírez-Martínez et al. 2017), all studied species have paratracheal parenchyma.

Axial and radial parenchyma form a continuous network in woods (Carlquist 2015; 2018; Pfautsch et al. 2015), even though connections involving apotracheal and radial parenchyma are not as evident as the ones between paratracheal parenchyma and vessels. Axial parenchyma/ray pitting to vessels are a connecting pathway (Carlquist 2018). Each studied species has two or more combinations of axial parenchyma; five species have apotracheal parenchyma and six species present banded parenchyma (the five legumes studied plus *Phyllostylon rhamnoides*). Confluent and banded parenchyma more than 3 cells

wide occur frequently in tropical regions (Wheeler et al. 2007). The diverse parenchyma arrangement observed in these species may indicate that they produce a well-interconnected parenchyma tissue, which in turn may enhance important stem functions such as water storage and movement. Banded parenchyma can extend connectivity between paratracheal parenchyma directly linked to vessels with other distant vessels (Morris et al. 2018), with ray parenchyma (Morris & Jansen 2016), and with apotracheal parenchyma, which may have storage functions (Carlquist 2015; Secchi et al. 2017).

Another functional contribution of the parenchyma may be embolism repair, as starch stored in parenchyma surrounding vessels may help by generating positive osmotic pressure (Trifilò et al. 2014; Secchi et al. 2017; Morris et al. 2018). This may be happening in species with paratracheal parenchyma and capable of producing vessels with wide diameters, such as the three main pioneer legume species (*Acacia cochliacantha* and the two *Mimosa* species); experimental studies similar to Braun (1984) are needed to test this hypothesis.

Axial parenchyma is directly related to an increased conduction capacity (Zheng & Martínez-Cabrera (2013) and rays to water radial transport, facilitating the coupling of inner bark and xylem (Pfautsch et al. 2015). Hence, connection to large rays can act as pathways for photosynthate transport and storage (Carlquist 2018). There are several radial parenchyma features that may enhance such interconnection as well as storage capacity (Carlquist 2015; Pfautsch et al. 2015). Multiseriate rays may have more contact with vessels than uniseriate rays, taller rays may cover larger stem areas, such as the ones in the two Cactaceae species, *Bonellia macrocarpa*, and *Jacaratia mexicana* (with more than 1 mm height). In addition, *Bonellia macrocarpa* is a peculiar species that produces dense, costly leaves during the dry season (Lebrija-Trejos et al. 2010b). Possibly this species can produce leaves when water is scarce by using water and other resources available in their stem radial parenchyma.

Axial parenchyma may also contribute to the recovery from physical damage (Carlquist 2015), which may be particularly important in early successional stages where most of the studied species occur, as their main stems are logged and burned.

It is worth mentioning that in these tropical species a double staining was used to distinguish in tangential and radial sections septate fibres from axial parenchyma, and that it was a difficult task. Thus, we strongly recommend to take this into account for future functional quantitative studies that include areas of axial parenchyma tissue.

Vessel arrangement

Vessels have been reported to show a tendency towards grouping in dry environments, whereas they are more often solitary and only rarely grouped in humid environments (Carlquist & Hoekman 1985; Barajas-Morales 1985; Lindorf 1994); however, this evidence is controversial. Experimentally drought-affected rainforest species have shown reduced vessel groupings (Tng et al. 2018), and Ewers et al. (2007) found that high vessel number provides xylem safety depending on the probability that an individual vessel is embolized.

Vessel groups are commonly associated with vessel redundancy (Carlquist 1980). In the absence of water in the stem hydraulic system, if a vessel is blocked by an air bubble and is adjacent to another vessel, water transport can continue through the adjacent vessels (Tyree et al. 1994; Cruiziat et al. 2002). Although the percentage of solitary vessels in six of the 13 studied species was higher than 50%, congruently to the vessel redundancy statement, the groups of vessels observed in 11 species frequently showed more than 10 vessels per group (up to 29). Thus, only the two Cactaceae and the Caricaceae species apparently lack a vessel redundancy property, as solitary vessels are common, and the observed clusters are small (up to 4 and 3 vessels respectively). These quantitative patterns may not be so evident in Figure 1, as they display one optical field of one individual of each species, while the proportion of grouped vessels, the maximum vessels per group, and the anatomical description of each species were obtained from six individuals per species and through observing several optical fields per individual. Further quantitative studies are needed to confirm the described vessel grouping patterns.

Fibres roles other than mechanical support

Fibres usually have been associated with stem mechanical support function (Panshin & DeZeeuw 1980), but the presence of living and septate fibres may impact stem functions other than mechanical support such as water storage (Yamada et al. 2011). Septate fibres can be substitutes for axial parenchyma and can be viewed as connecting parts for wood water movement, as well as for supplying carbohydrates during foliation, flowering and fruiting events (Carlquist 2015).

Septate fibres were the main ground tissue in five of the 13 successional species: *Bursera simaruba* and *Coccoloba liebmanni* have exclusively septate fibres, while both Cactaceae species and *Bonellia macrocarpa* have scarce non-septate fibres. This group of five species have scarce paratracheal parenchyma and lack banded parenchyma connecting vessels; additionally, *Phyllostylon rhamnoides* and *Lonchocarpus lanceolatus* have septate fibres, although scarce, but have banded parenchyma. Species with septate fibres (excluding Cactaceae) have either sub-evergreen phenology, produce leaves during dry season (*Bonellia macrocarpa*) or retain leaves during a longer period than the rest of the species (Table 1). The group of five species with septate fibres as the main ground-tissue component have middle to high values of wood water content (Romero et al. 2020). These species have tall rays that apparently are well connected, so ray parenchyma, together with septate fibres may play an important role in stem water storage and leaf production during the dry season, but studies are needed to explore this possibility.

The thin-walled, non-septate fibres of *Cnidocolus megacanthus* are not expected to play an important role in mechanical support. Given that this species has a high wood water content (Romero et al. 2020b), and that it does not have abundant axial parenchyma, probably fibres play an important role in water storage and movement in the axial system. Caution is recommended when conducting functional studies regarding the role of parenchyma, septate fibres, and even non-septate fibres, because they may have analogous functions such as water and starch storage (Yamada et al. 2011). In another Mexican TDF, 23% of important species (*i.e.* with high values of relative importance values) present septate fibres (Ramírez-Martínez et al. 2017), while in this study they were at least 39%.

Gelatinous fibres are commonly reported in reaction wood (Mellerowicz & Gorshkova 2012), but most of the studied species showed gelatinous fibres, although the individuals collected had straight stems. The fibre-ground tissue of some of them, as the dominant species in late successional stages *Lysiloma divaricatum*, seem to be composed mainly of gelatinous fibres. Gelatinous fibres have been reported before, but in commercial species such as *Mimosa tenuiflora* wood, which is used for charcoal (Dias-Leme et al. 2010), and in other genera such as *Acacia* (Warwick et al. 2017). Common functions of gelatinous fibres are related with wood physical properties such as flexibility and stem reorientation (Pilate et al. 2004). The studied species grow under a high mechanical pressure caused by a constant and strong wind characteristic of Tehuantepec Isthmus region (Elliot 2004), but gelatinous fibres have also been reported in other dry regions which lack this peculiar mechanical stress (Sonsin et al. 2012; Warwick et al. 2017). Secondary walls of gelatinous fibres are mainly composed of cellulose, as well as pectic mucilages bound to this almost non-lignified gelatinous layer (Bowling & Vaughn 2008). As cellulose and pectin are hydrophilic, it may be important to explore the role of gelatinous fibres in stem functions such as water storage. It has been hypothesised that hydrophilic polysaccharide deposits in poplar non-gelatinous fibres may contribute to water diffusion and stem water storage (Arend et al. 2008). Yet, experimental studies must be done to explore these possibilities.

Possible mechanisms of water stress resistance in successional TDF species

At the community level, the combinations of wood anatomical features found in the successional species studied may lead to hypothesize the existence of various combinations of wood anatomical responses and coping mechanisms to hydric stress, and probably also different mechanisms of water pulses exploitation for survival and growth. There seem to be important common features such as the presence of axial and radial parenchyma adjacent to vessels, as well as vessel grouping, but cavitation resistance and hydraulic conductivity appear to be controlled by a complex interaction between wood tissue and vessel characteristics (Lens et al. 2011).

A drought-tolerant plant species can resist severe external hydric stress without conserving water, and without suffering tissue damage, or is capable of repairing it, whereas plants with evasive mechanisms can maintain a high water potential when exposed to an external water stress (Levitt 1972). Borchert & Pockman (2005) experimentally found that trees of tropical semi-deciduous forests range from “drought-avoiding” species which maintain high stem water potentials throughout the year, to “drought-tolerant” species which dehydrate during dry season. Probably the studied successional species may have one or a combination of these hydric stress coping mechanisms given through some of their anatomical features. A drought evasive mechanism in species such as *Cnidoscolus megacanthus*, *Jacaratia mexicana*, *Bursera simaruba* and the two cacti may include high stem water storage (Romero et al. 2020) and large vessel diameters, as described for other TDF successional species (Pineda-García et al. 2015).

Pineda-García et al. (2013) found that late-successional TDF species either resist drought through low vulnerability to embolisms, or through a high capacity to store water that delayed the effects of soil drying. Probably the reliance on high wood water content could explain the lack of consistent and well-marked growth marks in *Bursera simaruba*, *Cnidoscolus megacanthus*, *Jacaratia mexicana* and the two cacti. The anatomical features underlying drought evasive mechanism may be given by different cell types. Parenchyma is commonly associated with water storage, but our results suggest that it may play an important role in stem water storage. Jupa et al. (2016) suggest a limited water releasing importance of parenchyma compared to the water released from vessels. Specific studies considering the diversity of cells that could potentially be storing water, such as septate fibres, gelatinous fibres, and vessels are needed.

In the studied species the cell types that can store resources like water and carbohydrates, and their pathways of movement through the secondary tissue, are diverse, as they may include axial parenchyma arranged in different ways, septate fibres, and rays, and maybe gelatinous fibres as well. Additionally, the observed vessel grouping along with the starch content in vessel-associated parenchyma found here and in a previous study (Romero et al. 2020) may play important roles in TDF species responses to drought xylem

cavitation, as found in other species (Trifilò et al. 2014); this may be a possible common tolerance mechanism in this community.

Differences in relative water conduction in ring-porous species (*Lysiloma divaricatum* and *Mimosa eurycarpa*), driven by different vessel arrangement and diameters, likely represent a tolerance mechanism in these water-stressed successional environments (Romero et al. 2020). The other species studied here show diffuse-porous wood with a wide range of vessel grouping and vessel diameters. Water transport mechanisms are different in ring and diffuse-porous species (Boura & De Franceschi 2007; Taneda & Sperry 2008). Probably, these species respond to water pulses through adjustments in vessel arrangement and diameter sizes, but this is not equally clear in diffuse porous species and in ring-porous ones. *Lonchocarpus lanceolatus* is a diffuse porous legume species, with low wood water content (Romero et al. 2020), briefly deciduous, and that did not showed growth marks at all; thus, changes in environmental water availability apparently do not produce evident changes in its wood tissue. Experimental studies and the assessment of root system depth, stomatal behaviour, and bark features may shed light into the understanding of drought resistance mechanisms in this species. Further quantitative studies are needed to explore the functional roles of the observed anatomical features, and to identify the presence of syndromes at a regional level. Anatomical observations may be a basis for experimental studies aimed at testing the hypothesised drought mechanisms.

Conclusions

TDF successional species possess a great diversity of complex features that suggest different mechanisms for coping with the hydric stress that characterizes this seasonal vegetation type. Possibly evasion and tolerance drought resistance mechanisms may result from a variety of combinations and interactions of wood anatomical features in the studied species.

Oversimplification of the relationship between wood tissue types, stem function, and ecological performance must be avoided in the studied tropical species, as the anatomical

features described suggest complexity and multifunctionality of their stem wood tissue. Describing stem wood anatomical features of species in tropical diverse ecosystems can contribute to understanding the relationship between structure and function. Following this first step, specialized methodologies can be developed in order to study wood quantitative features of anatomically complex species, such as those with inconspicuous growth marks, diverse ground tissue cells, diverse vessel and parenchyma space arrangement patterns, and displaying a wide range of diameter sizes.

Acknowledgements

This study is part of the requirements for ER to obtain the Doctor of Science degree from the Posgrado en Ciencias Biológicas (PCB), Universidad Nacional Autónoma de México (UNAM). Funding for this research was provided by the Consejo Nacional de Ciencia y Tecnología (CONACyT), grant no. 270104; and Programa de Apoyo a Proyectos de Investigación e Innovación Tecnológica-Universidad Nacional Autónoma de México (PAPIIT-UNAM); grant no. IN218416 and grant IN217620. We are grateful to the people of Nizanda for their continued hospitality and support. We thank Francisco Mora, Rey David López Mendoza, and Marco Virgilio Alvarado for their assistance in field work, and Alicia Rojas and Marcelo Pace for their technical support in the laboratory.

References

- Aloni, R. (2015). Ecophysiological implications of vascular differentiation and plant evolution. *Trees* **29**, 1–16.
- Alves, E. S. & Angyalossy-Alfonso, V. (2000). Ecological trends in the wood anatomy of some Brazilian species. 1. Growth rings and vessels. *IAWA Journal*, **21**, 3–30.
- Arend, M., Muninger, M. & Fromm, J. (2008). Unique occurrence of pectin-like fibrillar cell wall deposits in xylem fibres of poplar. *Plant Biology* **10**, 763–770.

- Baas P. (1976). Some functional and adaptive aspects of vessel member morphology. In: Baas P, Bolton AJ, Catling DM, eds. Wood structure in biological and technological research. Leiden botanical series 3. Leiden, Germany: Leiden University Press, 157–181.
- Baas, P., E. Werker & Fahn, A. (1983). Some ecological trends in vessel characters. *IAWA Bull. n.s.* **4**, 141–159.
- Baas, P., Beeckman, H., Čufar, K. & Micco, V. D. (2016). Functional traits in wood anatomy. *IAWA Journal*, **37**, 124–126.
- Barajas-Morales, J. (1985). Wood structural differences between trees of two tropical forests in Mexico. *IAWA Journal*, **6**, 355–364.
- Barajas-Morales, J. & Gómez, L. (1989). Anatomía de maderas de México: especies de una selva baja caducifolia. Cuaderno de Divulgación del Instituto de Biología. México, D.F. Universidad Nacional Autónoma de México. 1–163.
- Bhaskar R., Dawson T.E., Balvanera P. (2014). Community assembly and functional diversity along succession post-management. *Functional Ecology*, **28**, 1256–1265.
- Boura, A.s., De Franceschi, D. (2007). Is porous wood structure exclusive of deciduous trees? *Comptes Rendus Palevol*, **6**, 385–391.
- Bowling, A.J. & Vaughn, K.C. (2008). Immunocytochemical characterization of tension wood: gelatinous fibres contain more than just cellulose. *American Journal of Botany* **95**, 655–663.
- Breceda, A., Ortiz, V. & Scrosati, R. (2005). Mauto (*Lysiloma divaricatum*, Fabaceae) allometry as an indicator of cattle grazing pressure in a tropical dry forest in northwestern Mexico. *Rangeland ecology & management*, **58**, 85–88.
- Brodersen, C. & McElrone, A. (2013). Maintenance of xylem network transport capacity: A review of embolism repair in vascular plants. *Frontiers in Plant Science*, **4**, 1–11.
- Braun, H. J. (1984). The significance of the accessory tissues of the hydrosystem for osmotic water shifting as the second principle of water ascent, with some thoughts concerning the evolution of trees. *IAWA Journal*, **5**, 275–294.
- Brown, S. & Lugo, A. E. (1990). Tropical secondary forests. *Journal of Tropical Ecology*, **6**, 1–32.

- Bush S.E., Pataki D.E., Hultine K.R., West A.G., Sperry J.S., Ehleringer J.R. (2008). Wood anatomy constrains stomatal responses to atmospheric vapor pressure deficit in irrigated, urban trees. *Oecologia*, **156**, 13–20.
- Carlquist, S. (1980). Further concepts in ecological wood anatomy, with comments on recent work in wood anatomy and evolution. *Aliso*, **9**, 499–553.
- Carlquist, S. & Hoekman, D. A. (1985). Ecological Wood Anatomy of the Woody Southern Californian Flora. *Iawa Journal*, **6**, 319–347.
- Carlquist, S. (1998). Wood and bark anatomy of caricaceae; correlations with systematics and habit. *IAWA Journal*, **19**, 191–206.
- Carlquist S. (2015). Living cells in wood. 1. Absence, scarcity and histology of axial parenchyma as keys to function. *Bot J Linnean Soc.*, **177**, 291–321.
- Carlquist, S. (2018). Living cells in wood 3. overview; Functional anatomy of the parenchyma network. *The Botanical Review*, **84**, 242–294.
- Centro de Investigación Científica y de Educación Superior de Ensenada (CICESE), (2015). Base de datos climatológica nacional (Sistema CLICOM). <http://clicom-mex.cicese.mx> Accessed May 2018 4.
- Cruiziat, P., Cochard, H. & Améglio, T. (2002). Hydraulic architecture of trees: main concepts and results. *Annals of Forest Science*, **59**, 723–752.
- Derroire, G., Tigabu, M., Odén, P. C. & Healey, J. R. (2016). The effects of established trees on woody regeneration during secondary succession in tropical dry forests. *Biotropica*, n/a-n/a.
- Dias-Leme, C.L., Cartwright, C., & Gasson, P. (2010). Anatomical Changes to the wood of and when charred at different temperatures. *IAWA Journal*, **31**, 333–351.
- Eamus, D. (1999). Ecophysiological traits of deciduous and evergreen woody species in the seasonally dry tropics. *Trends in Ecology & Evolution*, **14**, 11–16.
- Elliot, D., Schwartz, M., Scott, G., Haymes, S., Heimiller, D. & George, R. (2004). Atlas de Recursos Eólicos del Estado de Oaxaca. Laboratorio Nacional de Energía Renovable, Secretaría de Desarrollo Industrial y Comercial del Gobierno del Estado de Oaxaca. Golden, Colorado.

- Ewers, F. W., Ewers, J. M., Jacobsen, A. L. & López-Portillo, J. (2007). Vessel redundancy: Modelling safety in numbers. *IAWA Journal*, **28**, 373–388.
- Fu, P.-L., Jiang, Y.-J., Wang, A.-Y., Brodribb, T. J., Zhang, J.-L., Zhu, S.-D. & Cao, K.-F. (2012). Stem hydraulic traits and leaf water-stress tolerance are co-ordinated with the leaf phenology of angiosperm trees in an Asian tropical dry karst forest. *Annals of Botany*, **110**, 189–199.
- Gallardo-Cruz, J. A., Meave, J. A., González, E. J., Lebrija-Trejos, E. E., Romero-Romero, M. A., Pérez-García, E. A., Gallardo-Cruz, R., Hernández-Stefanoni, J. L. & Martorell, C. (2012). Predicting tropical dry forest successional attributes from space: is the key hidden in image texture? *PLOS ONE*, **7**, e30506.
- Gentry, A.H. (1995). Diversity and floristic composition of neotropical dry forests. Pp. 146–194. In: Bullock, S.H., Mooney, H.A. & Medina, E. (eds) *Seasonally dry tropical forests*. Cambridge University Press, Cambridge.
- Gillespie, T. W., Grijalva, A. & Farris, C. N. (2000). Diversity, composition, and structure of tropical dry forests in Central America. *Plant Ecology*, **147**, 37–47.
- Hasselquist, N. J., Allen, M. F. & Santiago, L. S. (2010). Water relations of evergreen and drought-deciduous trees along a seasonally dry tropical forest chronosequence. *Oecologia*, **164**, 881–890.
- IAWA-Committee (1989). IAWA list of microscopic features for hardwood identification with an appendix on non-anatomical information. *IAWA Journal* **10**, 219–332.
- Janzen, D.H. 1988. Tropical dry forests: The most endangered major tropical ecosystem. Pp. 130–137. In: Wilson, E.O. (ed.), *Biodiversity*. National Academic Press, Washington, D.C.
- Jupa, R., Plavcová, L., Gloser, V. & Jansen, S. (2016). Linking xylem water storage with anatomical parameters in five temperate tree species. *Tree Physiology* **36**, 756–769.
- Lebrija-Trejos, E., Meave, J. A., Poorter, L., Pérez-García, E. A. & Bongers, F. (2010) Pathways, mechanisms and variability of tropical dry forest succession. *Perspectives in Plant Ecology, Evolution and Systematics* **12**, 267–275.

- Lebrija-Trejos, E., Pérez-García, E.A., Meave, J.A., Bongers, F. & Poorter, L. (2010b). Functional traits and environmental filtering drive community assembly species-rich tropical system. *Ecology* **91**, 386–398.
- Lens, F., Sperry, J.S., Christman, M.A., Choat, B., Rabaey, D. & Jansen, S. (2011). Testing hypotheses that link wood anatomy to cavitation resistance and hydraulic conductivity in the genus *Acer*. *New Phytologist* **190**, 709–723.
- Lindorf, H. (1994) Eco-anatomical wood features of species from a very dry tropical forest. *IAWA Journal*, **15**, 361–376.
- Maldonado-Romo, A. F. (2014) *Fenología foliar y reproductiva de la comunidad arbórea del bosque tropical caducifolio en Nizanda, Oaxaca, México*. Bachelor Thesis, Universidad Nacional Autónoma de México, México, D.F., México.
- Martínez-Cabrera, D., Terrazas, T., Ochoterena, H., & López-Mata, L. (2010). Bark and wood anatomy of the Tribe Hamelieae (Rubiaceae). *IAWA Journal* 31, 425.
- Ramírez-Martínez, M., Terrazas, T., Aguilar-Rodríguez, S., Martínez-Ávalos, J.G. (2017). Anatomía de la madera de especies de la selva baja caducifolia de Tamaulipas, México. *Madera y Bosques*, **23**, 21–41.
- Mellerowicz, E.J., Gorshkova, T.A. (2012). Tensional stress generation in gelatinous fibres: a review and possible mechanism based on cell-wall structure and composition. *Journal of Experimental Botany*, **63**, 551–565.
- Morris, H., Plavcová, L., Cvecko, P., Fichtler, E., Gillingham, M. A. F., Martínez-Cabrera, H. I., McGlenn, D. J., Wheeler, E., Zheng, J., Ziemińska, K. & Jansen, S. C. (2016). A global analysis of parenchyma tissue fractions in secondary xylem of seed plants. *New Phytologist*, **209**, 1553–1565.
- Morris, H., Plavcová, L., Gorai, M., Klepsch, M. M., Kotowska, M., Jochen Schenk, H. & Jansen, S. (2018). Vessel-associated cells in angiosperm xylem: Highly specialized living cells at the symplast–apoplast boundary. *American Journal of Botany*, **105**, 151–160.
- Muñoz-Avilés, R. (2015). Dinámica de la estructura y la diversidad de un bosque tropical caducifolio del Istmo de Tehuantepec, Oaxaca, México. Bachelor thesis, Universidad Nacional Autónoma de México, México, D.F., México.

- Murphy, P. G. & Lugo, A. E. (1986). Ecology of tropical dry forest. *Annual review of ecology and systematics*, **17**, 67–88.
- Murphy, P. G. & Lugo, A. E. (1995). Dry forests of Central America and the Caribbean. *Seasonally Dry Tropical Forests* (eds S. H. Bullock, H. A. Mooney & E. Medina), pp. 9–33. Cambridge University Press, Cambridge, UK.
- Panshin, A.J. & Zeeuw, C.d. (1980). Textbook of wood technology. McGraw-Hill, Inc., New York.
- Pérez-García, E. A., Meave, J. A., Villaseñor, J. L., Gallardo-Cruz, J. A. & Lebrija-Trejos, E. (2010). Vegetation heterogeneity and life-strategy diversity in the flora of the heterogeneous landscape of Nizanda, Oaxaca, México. *Folia Geobotanica*, **45**, 143–161.
- Pfautsch, S., Renard, J., Tjoelker, M. G. & Salih, A. (2015) Phloem as capacitor: radial transfer of water into xylem of tree stems occurs via symplastic transport in ray parenchyma. *Plant Physiology*, **167**, 963–971
- Pilate, G., Chabbert, B., Cathala, B., Yoshinaga, A., Leplé, J.-C., Laurans, F., Lapierre, C. & Ruel, K. (2004). Lignification and tension wood. *Comptes Rendus Biologies* **327**, 889–901.
- Pineda-García, F., Paz, H., Meinzer, F. C. & Angeles, G. (2015). Exploiting water versus tolerating drought: water-use strategies of trees in a secondary successional tropical dry forest. *Tree Physiology*, **36**, 208–217.
- Pivovarov, A. L., Pasquini, S. C., Guzman, M. E. D., Alstad, K. P., Stemke, J. S. & Santiago, L. S. (2016). Multiple strategies for drought survival among woody plant species. *Functional Ecology*, **30**, 517–526.
- Ogasa, M., Miki, N.H., Murakami, Y., Yoshikawa, K. (2013). Recovery performance in xylem hydraulic conductivity is correlated with cavitation resistance for temperate deciduous tree species. *Tree Physiology*. **33**, 335–344.
- Ogasa, M., Miki, N.H., Okamoto, M., Yamanaka, N., Yoshikawa, K. (2014). Water loss regulation to soil drought associated with xylem vulnerability to cavitation in temperate ring-porous and diffuse-porous tree seedlings. *Trees* **28**, 461–469.

- Quintanar-Isaías, A., Velázquez-Núñez, M., Solares-Arenas, F., Pérez-Olvera, C.d.I.P., Torre-Blanco, A., (2005). Secondary stem anatomy and uses of four drought-deciduous species of a tropical dry forest in México. *Revista de biología tropical* **53**, 29–48.
- Romero, E., Dávalos-Sotelo, R., Meave, J. A. & Terrazas, T. (2020). Wood density, deposits and mineral inclusions of successional tropical dry forest species. *European Journal of Forest Research*, 1–13.
- Romero, E., González, E.J., Meave, J.A., & Terrazas, T. (2019). Wood anatomy of dominant species with contrasting ecological performance in tropical dry forest succession. *Plant Biosystems*, 1–11.
- Secchi, F., Pagliarani, C. & Zwieniecki, M.A. (2017). The functional role of xylem parenchyma cells and aquaporins during recovery from severe water stress. *Plant, Cell & Environment* **40**, 858–871.
- Segala-Alves, E. & Angyalossy-Alfonso, V. (2002). Ecological trends in the wood anatomy of some Brazilian species. 2. Axial parenchyma, rays and fibres. *IAWA Journal*, **23**, 391–418.
- Silva, M.d.S., Funch, L.S., da Silva, L.B. (2019). The growth ring concept: seeking a broader and unambiguous approach covering tropical species. *Biological Reviews*, **94**, 1161–1178.
- Sonsin, J. O., Gasson, P. E., Barros, C. F., & Marcati, C. R. (2012). A comparison of the wood anatomy of 11 species from two cerrado habitats (cerrado s.s. and adjacent gallery forest). *Botanical Journal of the Linnean Society*, **170**, 257–276.
- Sperry, J.S., Meinzer, F.C., McCulloh, K.A. (2008). Safety and efficiency conflicts in hydraulic architecture: scaling from tissues to trees. *Plant, Cell & Environment* **31**, 632–645.
- Tarelkin, Y., Delvaux, C., De Ridder, M., El Berkani, T., De Cannière, C. & Beeckman, H. (2016). Growth-ring distinctness and boundary anatomy variability in tropical trees. *IAWA Journal*, **37**, 275–S7.
- Taneda, H., Sperry, J.S. (2008). A case-study of water transport in co-occurring ring- versus diffuse-porous trees: contrasts in water-status, conducting capacity, cavitation and vessel refilling. *Tree Physiology*, **28**, 1641–1651.

- Tng, D. Y. P., Apgaua, D. M. G., Ishida, Y. F., Mencuccini, M., Lloyd, J., Laurance, W. F. & Laurance, S. G. W. (2018). Rainforest trees respond to drought by modifying their hydraulic architecture. *Ecology and Evolution*, **8**, 12479–12491.
- Trejo, I. & Dirzo, R. (2000). Deforestation of seasonally dry tropical forest: a national and local analysis in Mexico. *Biological conservation*, **94**, 133–142.
- Trifilò, P., Barbera, P. M., Raimondo, F., Nardini, A. & Gullo, M. A. L. (2014). Coping with drought-induced xylem cavitation: coordination of embolism repair and ionic effects in three Mediterranean evergreens. *Tree Physiology*, **34**, 109–122.
- Tyree, M. T., Davis, S. D. & Cochard, H. (1994). Biophysical perspectives of xylem evolution: is there a tradeoff of hydraulic efficiency for vulnerability to dysfunction? *IAWA Journal*, **15**, 335–360.
- Warwick, N. W. M., Hailey, L., Clarke, K. L., & Gasson, P. E. (2017). Climate trends in the wood anatomy of *Acacia sensu stricto* (Leguminosae: Mimosoideae). *Annals of Botany*, **119**, 1249–1266.
- Wheeler, E.A., Baas, P., & Rodgers, S. (2007). Variations In Dicot Wood Anatomy: A Global Analysis Based on the Insidewood Database, *IAWA Journal*, **28**, 229–258.
- Worbes M. 1995. How to measure growth dynamics in tropical trees: a review. *IAWA Journal*, **16**, 337–351.
- Worbes, M. (1989). Growth rings, increment and age of trees in inundation forests, savannas and a mountain forest in the Neotropics. *IAWA Journal*, **10**, 109.
- Yamada, Y., Awano, T., Fujita, M. & Takabe, K. (2011). Living wood fibres act as large-capacity “single-use” starch storage in black locust (*Robinia pseudoacacia*). *Trees*, **25**, 607–616.
- Zheng, J. & Martínez-Cabrera, H. I. (2013). Wood anatomical correlates with theoretical conductivity and wood density across China: evolutionary evidence of the functional differentiation of axial and radial parenchyma. *Annals of Botany*. **112**, 927–935.
- Zhu, S.-D., Chen, Y.-J., Fu, P.-L. & Cao, K.-F. (2017). Different hydraulic traits of woody plants from tropical forests with contrasting soil water availability. *Tree Physiology*, **37**, 1469–1477.

Table 1. List of 13 woody species occurring in a secondary tropical dry forest (TDF) of Nizanda, Oaxaca, Mexico. Phenology categorization based on Maldonado-Romo (2014).

Species	Family	Leaf phenology	Deciduousness rank
Species present in secondary vegetation and TDF mature forest			
<i>Jacaratia mexicana</i> A.DC	Caricaceae	Largely deciduous	1
<i>Bursera simaruba</i> (L.) Sarg.	Burseraceae	Largely deciduous	2
<i>Cnidoscolus megacanthus</i> Breckon ex Fern.Casas	Euphorbiaceae	Largely deciduous	1, 2
<i>Lysiloma divaricatum</i> (Jacq.) J.F.Macbr.	Leguminosae	Briefly deciduous, brief leaf production	6
<i>Lonchocarpus lanceolatus</i> Benth.	Leguminosae	Briefly deciduous, brief leaf production	7
<i>Phyllostylon rhamnoides</i> (J.Poiss.) Taub.	Ulmaceae	Briefly deciduous, brief leaf production	8
<i>Bonellia macrocarpa</i> (Cav.) B.Ståhl & Källersjö	Primulaceae	Inverse phenology	9
<i>Coccoloba liebmannii</i> Lindau	Polygonaceae	Semi-evergreen	10
<i>Pachycereus pecten- aboriginum</i> (Engelm. ex S.Watson) Britton & Rose	Cactaceae	-	-
<i>Pilosocereus collinsii</i> (Britton & Rose) Byles & G.D. Rowley	Cactaceae	-	-
Species exclusive of secondary vegetation			
<i>Mimosa eurycarpa</i> Herzog	Leguminosae	Briefly deciduous, long leaf production	3
<i>Mimosa tenuiflora</i> (Willd.) Poir.	Leguminosae	Briefly deciduous, long leaf production	5
<i>Acacia cochliacantha</i> Willd.	Leguminosae	Briefly deciduous, long leaf production	4

Species exclusive of secondary vegetation: absent in mature TDF. Deciduousness rank: 1, drops mature leaves earlier; 10, retains mature leaves longer. Species names standardized according to The Plant List (www.theplantlist.org, last accessed March 2019).

Table 2. Anatomical features recorded in the stem of woody species occurring in a successional tropical dry forest. Numbers in each anatomical feature correspond to the IAWA Committee (1989) features. (+) present, (±) weak or variable, (-) does not apply.

Anatomical features	<i>Acacia cochiacantha</i>	<i>Lonchocarpus lanceolatus</i>	<i>Lysiloma divaricatum</i>	<i>Mimosa eurycarpa</i>	<i>Mimosa tenuiflora</i>	<i>Pachycereus pecten-aboriginum</i>	<i>Pilosocereus collinsii</i>	<i>Bonellia macrocarpa</i>	<i>Bursera simaruba</i>	<i>Cnidoscolus megacanthus</i>	<i>Coccoloba liebmannii</i>	<i>Phyllostylon rhamnoides</i>	<i>Jacarata mexicana</i>
Growth rings													
1. Distinct	+	·	+	+	·	·	±	+	±	±	±	±	±
2. Indistinct	·	+	±	±	±	±	·	±	·	·	·	·	±
Vessels													
Porosity													
3. Ring-porous	·	·	±	±	·	·	·	·	·	·	·	·	·
4. Semi-ring-porous	·	·	±	±	·	·	·	±	·	·	·	·	·
5. Diffuse-porous	+	+	·	·	+	+	+	±	+	+	+	+	+
Arrangement													
6. Tangential bands	·	·	·	·	·	·	·	·	·	·	·	±	+
7. Diagonal and/or radial pattern	·	·	·	·	·	·	·	·	·	+	±	·	·
Vessel outline													
12. Angular	·	·	·	·	·	±	±	·	·	·	·	·	·
Perforation plates													
13. Simple	+	+	+	+	+	+	+	+	+	+	+	+	+
Intervessel pits: arrangement													
20. Scalariform	·	·	·	·	·	+	+	·	·	·	·	·	+
21. Opposite	+	·	±	·	·	·	·	+	·	·	·	·	·
22. Alternate	+	+	+	+	+	·	·	+	+	+	+	+	·
Vessel-ray pits													
30. With distinct borders	+	+	+	+	+	+	+	+	+	·	+	+	·
32. With much reduced borders	·	·	·	·	·	·	·	·	·	+	·	·	+
33. Vessel-ray pits of two distinct sizes	·	·	·	·	·	·	·	·	·	+	·	·	·
58. Deposits	+	+	+	+	+	·	·	·	·	·	+	+	+
Fibres													
Ground tissue fibres bordered pits													
61. Simple to minute	+	+	+	+	+	+	+	+	+	+	+	+	-
Septate fibres													
65. Septate fibres present	·	±	·	·	·	+	+	+	+	·	+	+	-
66. Non-septate fibres present	+	+	+	+	+	+	+	±	·	+	·	+	-

Table 2 continued

	<i>Acacia cochliacantha</i>	<i>Lonchocarpus lanceolatus</i>	<i>Lysiloma divaricatum</i>	<i>Mimosa eurycarpa</i>	<i>Mimosa tenuiflora</i>	<i>Pachycereus pecten-aboriginum</i>	<i>Pilosocereus collinsii</i>	<i>Bonellia macrocarpa</i>	<i>Bursera simaruba</i>	<i>Cnidocolus megacanthus</i>	<i>Coccoloba liebmannii</i>	<i>Phyllostylon rhamnoides</i>	<i>Jacaratia mexicana</i>
Anatomical features													
Axial parenchyma													
76. Apotracheal diffuse	±	·	+	·	·	·	·	·	·	+	+	±	-
78. Scanty paratracheal	·	+	·	·	·	+	±	+	+	+	+	±	-
79. Paratracheal vasicentric	+	·	+	+	·	+	±	±	·	±	·	±	+
80. Paratracheal aliform	±	·	±	·	·	·	·	·	·	·	·	·	-
83. Paratracheal confluent	+	·	·	+	+	·	·	·	·	·	·	±	-
84. Unilateral paratracheal	·	·	·	·	·	·	·	·	·	·	·	±	-
Banded parenchyma													
85. Bands more than three cells wide	·	+	·	·	·	·	·	·	·	·	·	·	·
86. In narrow bands (≤ 3 cells wide)	·	+	·	·	·	·	·	·	·	·	·	·	·
89. In marginal bands	+	·	+	+	+	·	·	·	·	·	·	+	·
Cell type/strand length													
90. Fusiform parenchyma cells	·	+	·	+	·	·	·	+	·	·	·	·	+
91. Two cells per parenchyma strand	+	+	+	+	+	+	·	·	·	·	·	+	·
92. Four (3-4) cells per parenchyma strand	+	·	+	+	+	·	±	·	+	+	+	+	·
93. Eight (5-8) cells	·	·	·	·	·	·	·	·	·	+	+	·	·
95. Unlignified parenchyma	·	·	·	·	·	·	·	·	·	·	·	·	+
Rays													
Width													
97. Ray width 1 to 3 cells	+	+	+	+	+	·	·	·	·	·	+	+	·
98. Larger rays commonly 4- to 10-seriate	+	·	·	·	·	+	+	·	+	·	·	·	·
99. Larger rays commonly > 10-seriate	·	·	·	·	·	·	·	+	·	·	·	·	+
100. Multiseriate as wide as uniseriate	·	·	·	·	·	·	·	·	·	+	·	·	·
102. Ray height > 1 mm	·	·	·	·	·	+	+	+	·	±	·	·	+
Cellular composition													
104. All cells procumbent	+	+	+	+	+	·	·	·	·	·	+	+	·
106. Procumbent with upright or squares	·	·	·	·	·	·	·	+	+	·	·	·	·
109. Procumbent, square, upright mixed	·	·	·	·	·	+	+	·	·	+	·	·	+
Storied structure													
118. All rays storied	·	+	·	·	·	·	·	·	·	·	·	·	·
120. Axial parenchyma/vessel elements storied	·	+	·	·	·	·	·	·	·	·	·	·	+

Table 2 *continued*

	<i>Acacia cochliacantha</i>	<i>Lonchocarpus lanceolatus</i>	<i>Lysiloma divaricatum</i>	<i>Mimosa eurycarpa</i>	<i>Mimosa tenuiflora</i>	<i>Pachycereus pecten-aboriginum</i>	<i>Pilosocereus collinsii</i>	<i>Bonellia macrocarpa</i>	<i>Bursera simaruba</i>	<i>Cnidoscolus megacanthus</i>	<i>Coccoloba liebmannii</i>	<i>Phyllostylon rhamnoides</i>	<i>Jacaratia mexicana</i>
Anatomical features													
Secretory elements													
Intercellular canals													
130. Radial canals	+
Prismatic crystals													
136. Present	+	+	+	+	+	.	.	.	+	.	+	+	+
137. In upright and/or square ray cells									+				
139. In procumbent ray cells												+	
141. In axial parenchyma cells	+		+	+	+								
142. In chambered axial parenchyma cells	+	+	+		+						+		
Silica													
159. Present	+
160. In ray cells	+

Table 3. Vessel grouping features observed in the stem of woody species occurring in secondary vegetation derived from a tropical dry forest. Feature number according to the IAWA Committee (1989). (+) present, (\pm) weak or variable.

Species	Vessel groupings Features 10 and 11		Number of vessels per group		Solitary vessel proportion
	≥ 4 common	Clusters common	Mean +/- SD	Maximum	
<i>Acacia cochliacantha</i>	.	\pm	2 \pm 2	13	0.7
<i>Lonchocarpus lanceolatus</i>	.	+	4 \pm 3	14	0.4
<i>Lysiloma divaricatum</i>	.	+	3 \pm 3	29	0.2
<i>Mimosa eurycarpa</i>	.	\pm	2 \pm 2	21	0.6
<i>Mimosa tenuiflora</i>	.	+	4 \pm 3	22	0.3
<i>Pachycereus pecten- aboriginum</i>	.	\pm	1 \pm 1	4	0.7
<i>Pilosocereus collinsii</i>	.	\pm	2 \pm 1	4	0.6
<i>Bonellia macrocarpa</i>	.	+	2 \pm 1	5	0.3
<i>Bursera simaruba</i>	.	\pm	2 \pm 1	8	0.6
<i>Cnidocolus megacanthus</i>	.	\pm	2 \pm 1	8	0.5
<i>Coccoloba liebmannii</i>	+	+	4 \pm 3	25	0.2
<i>Phyllostylon rhamnoides</i>	+	\pm	2 \pm 2	14	0.6
<i>Jacaratia mexicana</i>	.	\pm	2 \pm 1	3	0.5

Table 4. Mean tangential vessel diameter of 13 woody successional species from a tropical dry forest. Mean diameter categories correspond to the IAWA Committee (1989) features 40-44; (+) presence.

Species	Mean diameter (μm)			Mean \pm Standard Deviation (min–max), μm
	≤ 50	50–100	100–200	
<i>Acacia cochliacantha</i>	.	+	.	67.71 \pm 41.98 (4.59–201.22)
<i>Lonchocarpus lanceolatus</i>	+	.	.	49.99 \pm 33.52 (6.74–172.94)
<i>Lysiloma divaricatum</i>	+	.	.	61.97 \pm 42.29 (6.91–191.76)
<i>Lysiloma divaricatum</i> earlywood	.	+	.	93.51 \pm 33.56 (17.35–191.76)
<i>Lysiloma divaricatum</i> latewood	+	.	.	26.64 \pm 12.84 (6.91–74.09)
<i>Mimosa eurycarpa</i>	+	.	.	55.44 \pm 48.13 (4.77–226.46)
<i>Mimosa eurycarpa</i> earlywood	.	.	+	103.73 \pm 43.76 (25.45–226.46)
<i>Mimosa eurycarpa</i> latewood	+	.	.	25.95 \pm 12.99 (6.6–77.97)
<i>Mimosa tenuiflora</i>	+	.	.	59.86 \pm 38.2 (6.47–199.10)
<i>Pachycereus pecten- aboriginum</i>	.	+	.	72.75 \pm 18.94 (18.86–122.44)
<i>Pilosocereus collinsii</i>	+	.	.	47.15 \pm 11.81 (21.86–86.79)
<i>Bonellia macrocarpa</i>	+	.	.	45.06 \pm 15.84 (8.04–100.00)
<i>Bursera simaruba</i>	.	+	.	69.79 \pm 22.98 (19.3–149.24)
<i>Cnidocolus megacanthus</i>	.	+	.	90.63 \pm 35.15 (11.06–163.9)
<i>Coccoloba liebmannii</i>	+	.	.	40.8 \pm 28.81 (5.18–123.47)
<i>Phyllostylon rhamnoides</i>	+	.	.	37.99 \pm 14.51 (9.33–80.42)
<i>Jacaratia mexicana</i>	.	.	+	143.05 \pm 38.92 (30.05–267.29)

Table 5. Vessels per mm² of 13 woody successional species from a tropical dry forest. Mean vessels per mm² categories correspond to the IAWA Committee (1989) features 47-50; (+) presence.

Species	Mean vessels per mm ²				Mean ± Standard Deviation (min–max)
	5–20	21–40	41–100	> 100	
<i>Acacia cochliacantha</i>	.	+	.	.	27.8 ± 12.8 (17–52)
<i>Lonchocarpus lanceolatus</i>	.	.	+	.	42.8 ± 16.5 (27–69)
<i>Lysiloma divaricatum</i>	.	.	+	.	53.0 ± 16.9 (34–79)
<i>Mimosa eurycarpa</i>	.	.	+	.	93.3 ± 21.5 (67–131)
<i>Mimosa tenuiflora</i>	.	.	+	.	52.5 ± 20.7 (25–87)
<i>Pachycereus pecten-aboriginum</i>	+	.	.	.	18.8 ± 4.3 (15–24)
<i>Pilosocereus collinsii</i>	.	.	+	.	44.2 ± 9.9 (30–56)
<i>Bonellia macrocarpa</i>	.	.	+	.	41.8 ± 16.5 (25–64)
<i>Bursera simaruba</i>	.	.	+	.	46.5 ± 7.7 (37–59)
<i>Cnidocolus megacanthus</i>	+	.	.	.	11.4 ± 4.4 (4–16)
<i>Coccoloba liebmannii</i>	.	.	+	.	42.3 ± 19.5 (22–78)
<i>Phyllostylon rhamnoides</i>	.	.	.	+	163.3 ± 22.0 (138–178)
<i>Jacaratia mexicana</i>	+	.	.	.	8.8 ± 2.0 (6–11)

Table 6. Fibre dimensions of 13 woody successional species from a tropical dry forest. The numbers in mean vessels per mm² categories correspond to the IAWA Committee (1989) features; (+) presence.

Species	Fibres				Fibre lumina	Fibre wall thickness
	68. Very thin-walled	69. Thin- to thick-walled	70. Very thick-walled	Gelatinous fibres	Mean ± SD µm	Mean ± SD µm
<i>Acacia cochliacantha</i>	.	.	+	+	3.97 ± 1.12	4.32 ± 0.92
<i>Lonchocarpus lanceolatus</i>	.	.	+	+	3.76 ± 0.92	4.28 ± 0.90
<i>Lysiloma divaricatum</i>	.	.	+	+	4.07 ± 1.50	3.29 ± 0.56
<i>Mimosa eurycarpa</i>	.	+	+	+	5.84 ± 1.77	2.83 ± 0.49
<i>Mimosa tenuiflora</i>	.	.	+	+	5.04 ± 1.81	4.24 ± 0.78
<i>Pachycereus pecten-aboriginum</i>	.	+	+	.	14.64 ± 3.63	4.25 ± 0.95
<i>Pilosocereus collinsii</i>	.	+	+	.	16.59 ± 5.19	3.76 ± 0.71
<i>Bonellia macrocarpa</i>	.	+	+	.	11.38 ± 2.22	2.94 ± 0.50
<i>Bursera simaruba</i>	+	.	.	+	18.39 ± 3.55	1.94 ± 0.34
<i>Cnidoscolus megacanthus</i>	+	.	.	+	24.8 ± 4.64	1.31 ± 0.29
<i>Coccoloba liebmannii</i>	.	+	+	.	11.16 ± 2.24	3.17 ± 0.5
<i>Phyllostylon rhamnoides</i>	.	.	+	.	4.19 ± 1.15	3.47 ± 0.65

Supplementary Information

Figure S1. Area covering the most recently produced wood tissue in the stem of *Mimosa eurycarpa*, approximately inside one or two growth rings.

Table S1. Dendrometric information and details of sample measurements (mean \pm standard deviation) of 13 woody species occurring in late secondary tropical dry forest (more than 50 years of abandonment). Basal diameter is the diameter of the collected stem from which the sample was collected. Height at stem is the height at which sample was collected. AC, *Acacia cochliacantha*; BO, *Bonellia macrocarpa*; BU, *Bursera simaruba*; CO, *Coccoloba liebmannii*; CN, *Cnidoscolus megacanthus*; JA, *Jacaratia mexicana*; LO, *Lonchocarpus lanceolatus*; LY, *Lysiloma divaricatum*; MIE, *Mimosa eurycarpa*; MIT, *Mimosa tenuiflora*; PA, *Pachycereus pecten-aboriginum*; PH, *Phyllostylon rhamnoides*; PI, *Pilosocereus collinsii*.

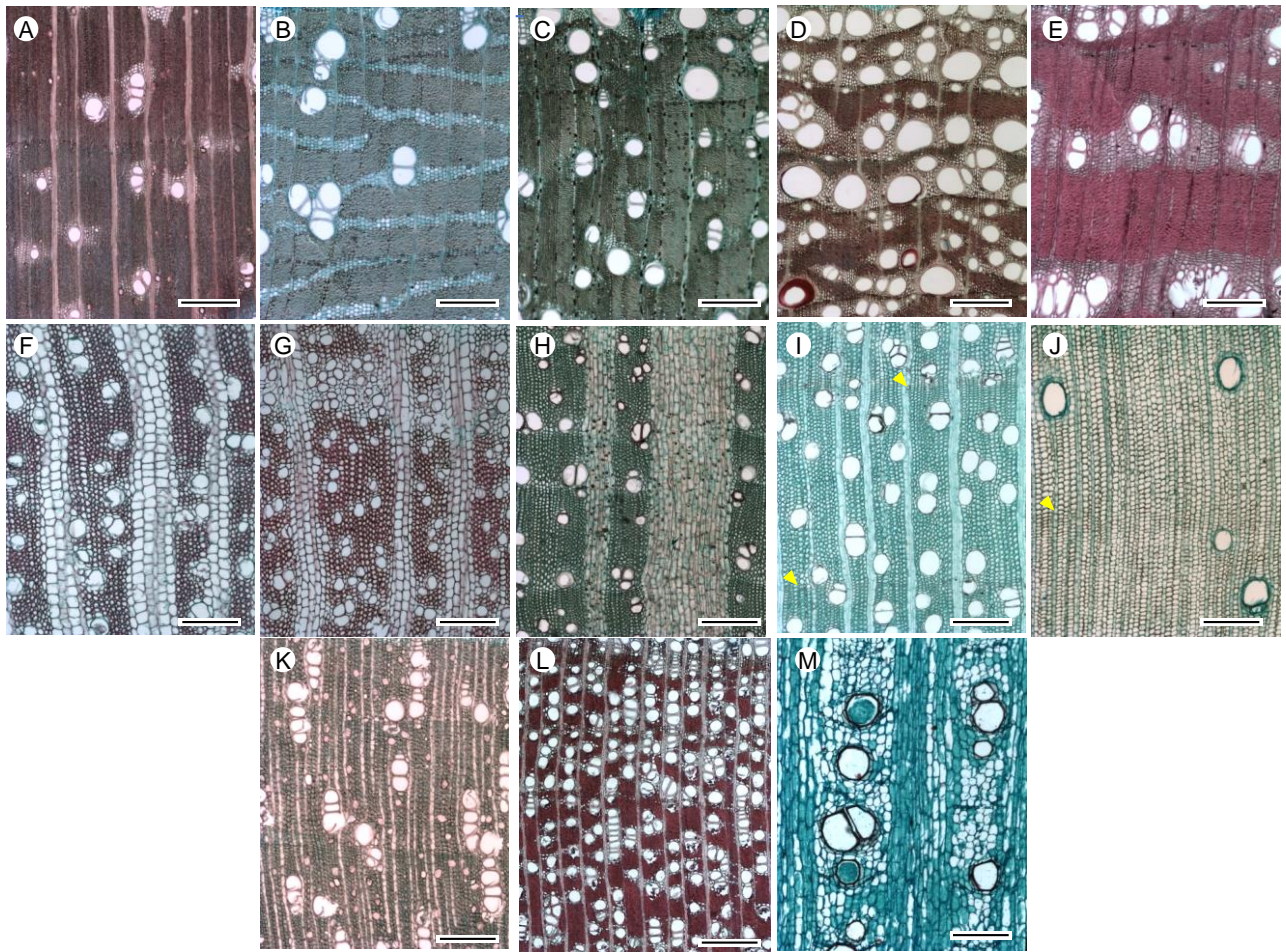


Figure 1. Transverse sections of the stem wood of 13 species present in late tropical dry forest secondary vegetation. A *Acacia cochliacantha*; B *Lonchocarpus lanceolatus*; C *Lysiloma divaricatum*; D *Mimosa eurycarpa*; E *Mimosa tenuiflora*; F *Pachycereus pecten-aboriginum*; G *Pilosocereus collinsii*; H *Bonellia macrocarpa*; I *Bursera simaruba*; J *Cnidoscolus megacanthus*; K *Coccoloba liebmanii*; L *Phyllostylon rhamnoides*; M *Jacaratia mexicana*. Scale bar = 300 μm

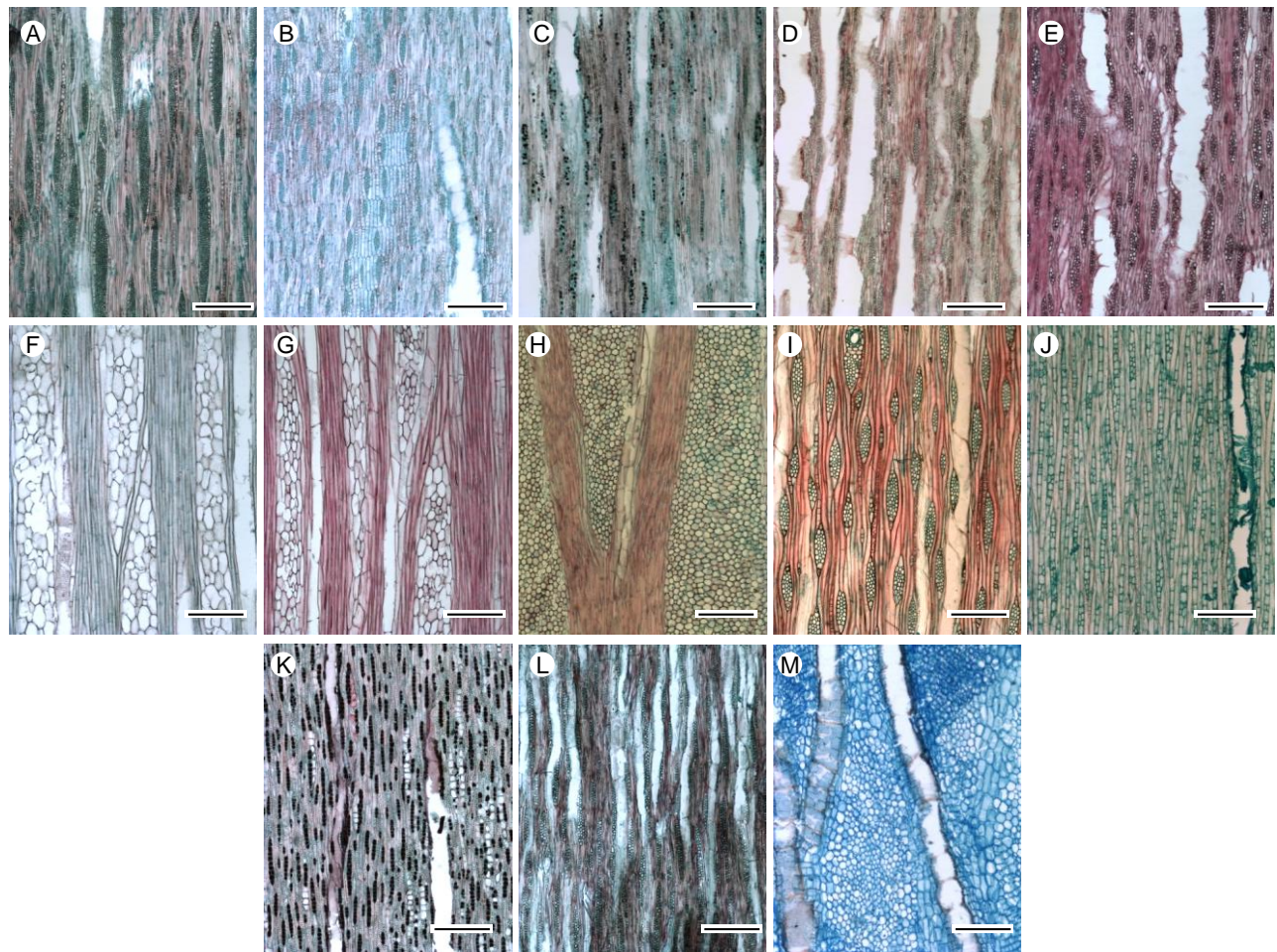


Figure 2. Tangential sections of the stem wood of 13 species present in late tropical dry forest secondary vegetation. A *Acacia cochliacantha*; B *Lonchocarpus lanceolatus*; C *Lysiloma divaricatum*; D *Mimosa eurycarpa*; E *Mimosa tenuiflora*; F *Pachycereus-pecten aboriginum*; G *Pilosocereus collinsii*; H *Bonellia macrocarpa*; I *Bursera simaruba*; J *Cnidoscolus megacanthus*; K *Coccoloba liebmanni*; L *Phyllostylon rhamnoides*; M *Jacaratia mexicana*. Scale bar = 300 μm

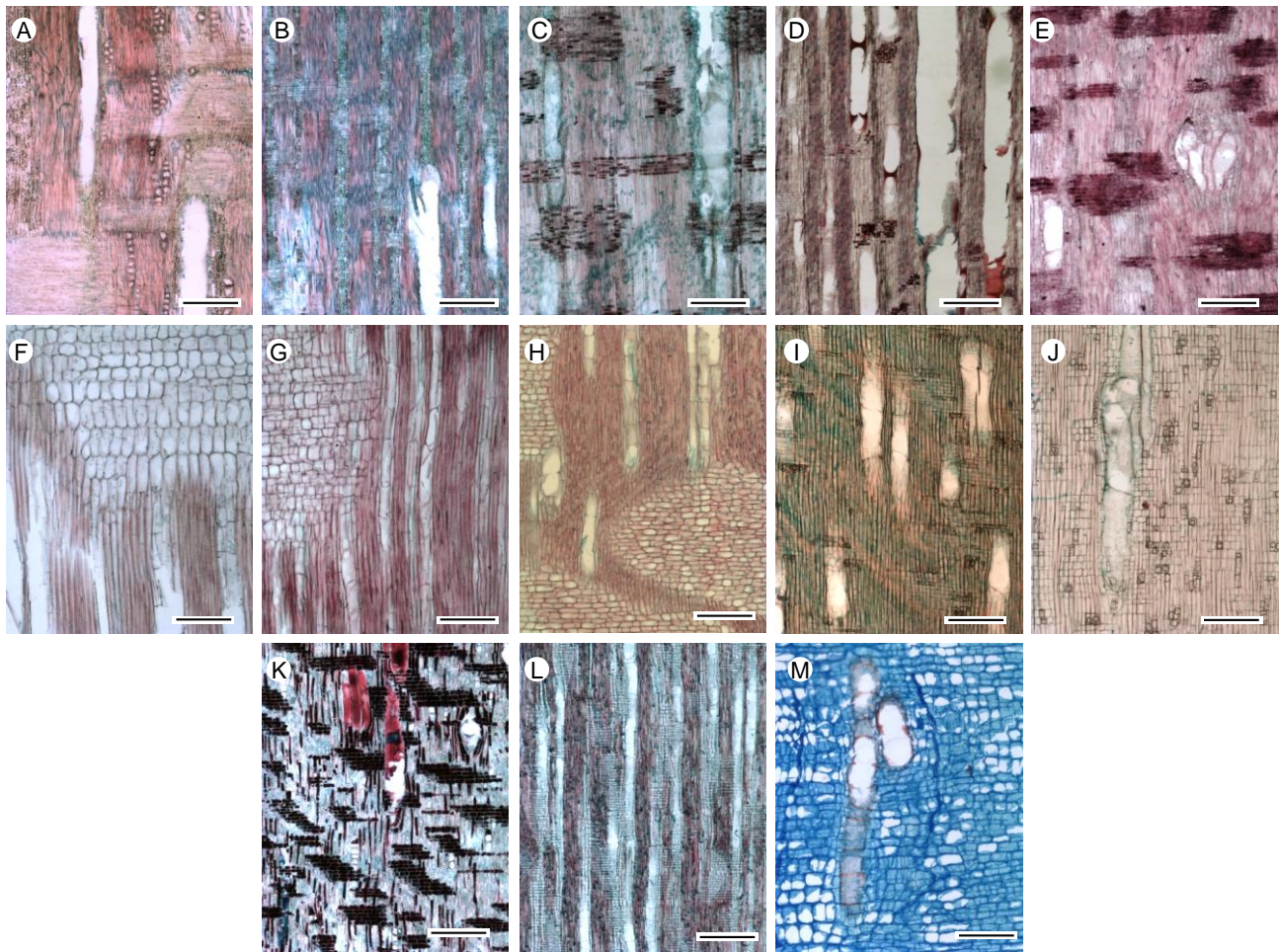


Figure 3. Radial sections of the stem wood of 13 species present in late tropical dry forest secondary vegetation. A *Acacia cochliacantha*; B *Lonchocarpus lanceolatus*; C *Lysiloma divaricatum*; D *Mimosa eurycarpa*; E *Mimosa tenuiflora*; F *Pachycereus pecten-aboriginum*; G *Pilosocereus collinsii*; H *Bonellia macrocarpa*; I *Bursera simaruba*; J *Cnidoscolus megacanthus*; K *Coccoloba liebmannii*; L *Phyllostylon rhamnoides*; M *Jacaratia mexicana*. Scale bar = 300 μ m

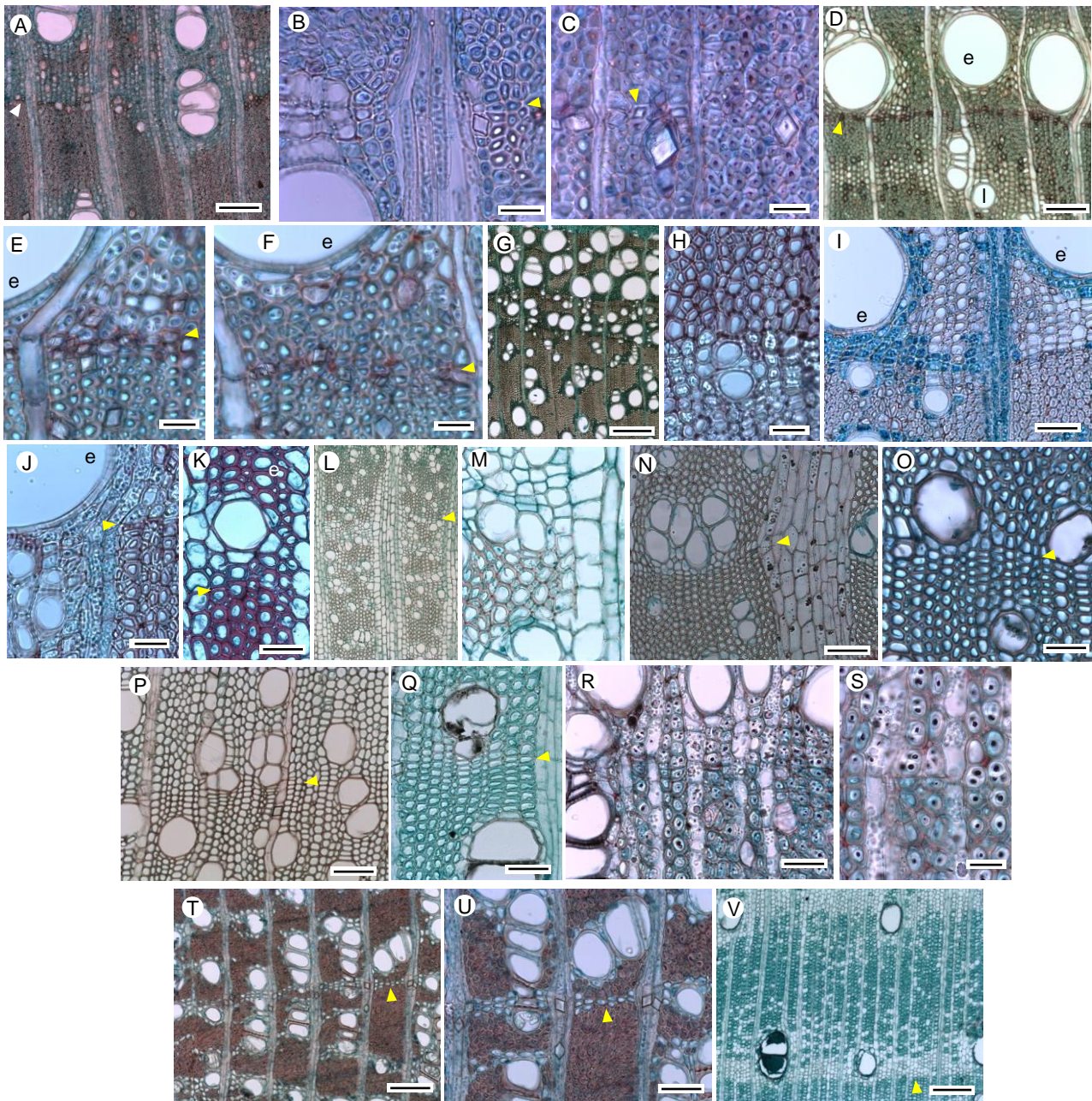


Figure 4. Wood anatomical growth mark details in cross sections of the stem of seven species present in late tropical dry forest secondary vegetation. A, B, C *Acacia cochliacantha* B non-continuous change from gelatinous fibres to non-gelatinous fibres; D-F *Lysiloma divaricatum*, D earlywood (e), latewood vessels (l) and arrow in ring boundary; G-J *Mimosa eurycarpa*, in E earlywood changes from parenchyma to fibres, in F early wood fibres apparently are the same as latewood fibres; K *Pachycereus pecten-aboriginum*, fibres with apparently different wall thickness in earlywood (e) and in latewood (arrow); L, M *Pilosocereus collinsii*, N, O *Bonellia macrocarpa*, P, Q *Bursera simaruba*, R, S *Coccoloba liebmannii*, T, U *Phyllostylon rhamnoides*. V *Cnidoscolus megacanthus*. Scale bar in A, D, N, P, T = 100 μm . Scale bar in B, I, K, M, O, Q, R, U = 50 μm . Scale bar in C, E, F, H, J, S = 20 μm . Scale bar in G, V = 300 μm .

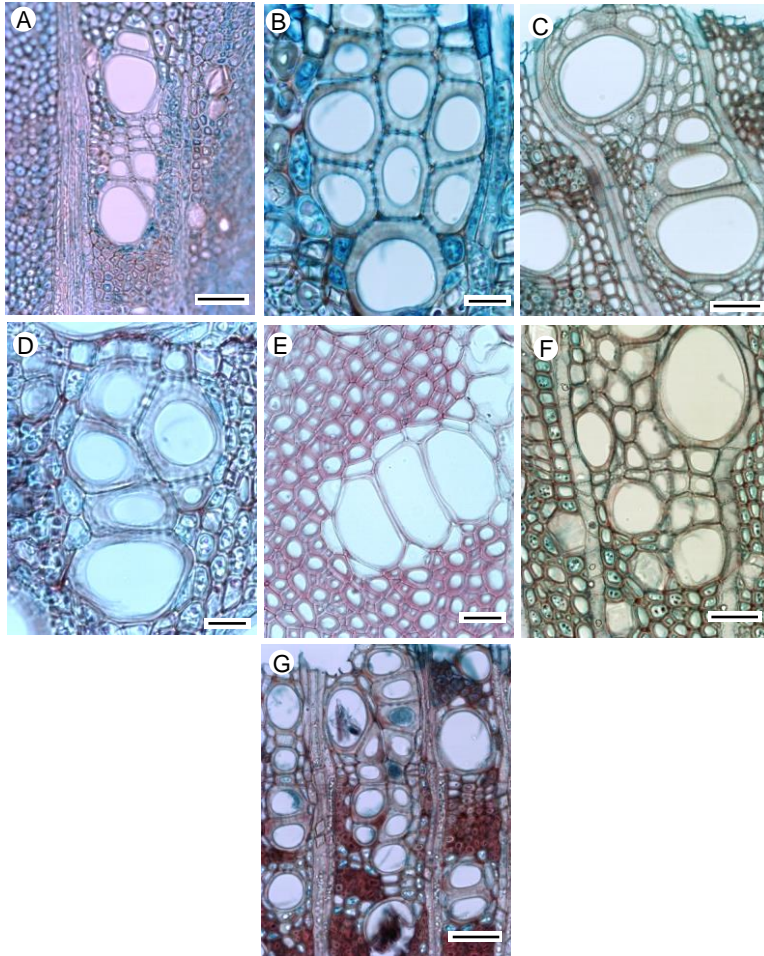


Figure 5. Vessel groups in cross sections of the stem of seven species present in late tropical dry forest secondary vegetation. A, *Acacia cochliacantha*; B *Lonchocarpus lanceolatus*; C *Lysiloma divaricatum*; D *Mimosa eurycarpa*; E *Pachycereus pecten-aboriginum*; F *Cocoloba liebmannii* group of 25 vessels; G *Phyllostylon rhamnoides*, group of 13 vessels. Scale bar in A, C, F, G = 50 μm . Scale bar in B, D, E = 20 μm .

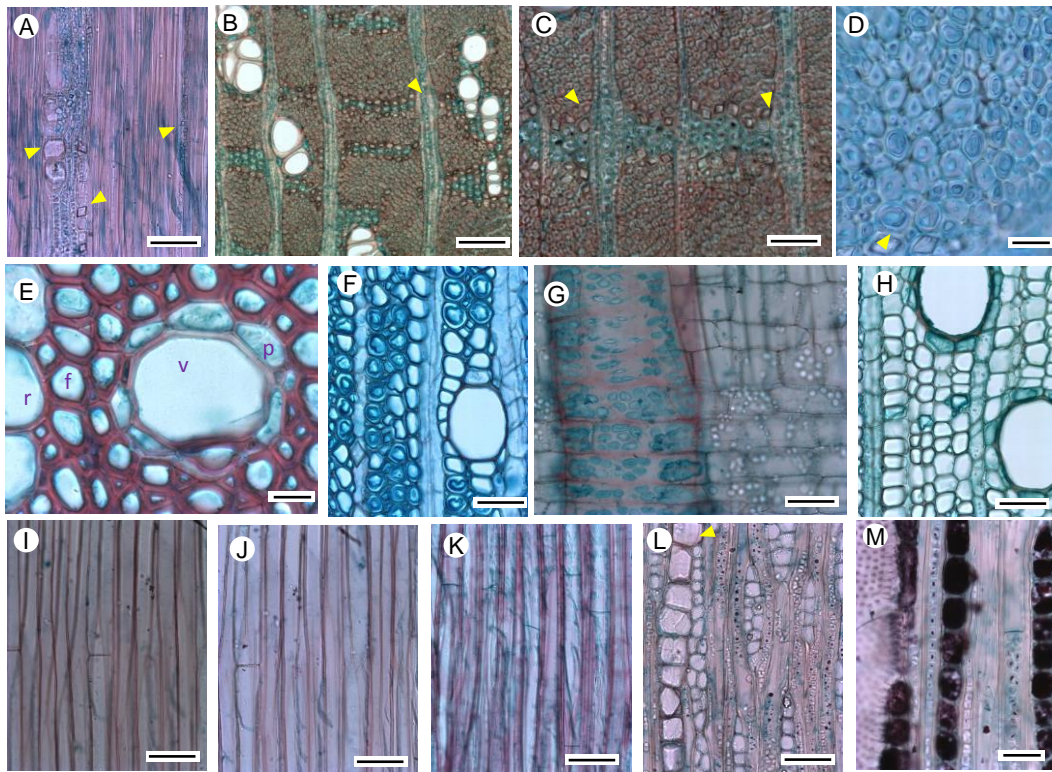


Figure 6. Wood anatomical details of the stem of six species present in late tropical dry forest secondary vegetation. A, *Acacia cochliacantha*, arrows indicate crystals of different sizes in axial parenchyma; B, C, D *Lonchocarpus lanceolatus*, arrows indicate crystals and rays widening in B and C, and gelatinous fibres in D; E *Pachycereus pecten-aboriginum*, radial parenchyma (r), fibres (f), and paratracheal parenchyma (p); F *Bursera simaruba*; G-J *Cnidocolus megacanthus*, K-M *Coccoloba liebmannii*, K ground tissue with septate fibres, L crystals in apotracheal parenchyma, M vessel, rays with tannins, and septate fibre with starch. Scale bar in A, C, F-L = 50 μm . Scale bar in B = 100 μm . Scale bar in D, E, M = 20 μm .

CAPÍTULO 6

Wood anatomical spectrum of early and late-successional tropical dry forest communities



Wood anatomical spectrum of early and late-successional tropical dry forest communities

Abstract

Tropical dry forest secondary vegetation includes a diverse array of species that are subjected to the same seasonal precipitation regime. As wood tissue contains diverse possibilities of functional traits in terms of stem hydraulics and mechanical support, in this study we asked: what is the set of anatomical traits that frequent species co-occurring in early (EC), and co-occurring in late successional communities (LC) exhibit? For 13 important species growing in early and late communities we: (1) quantified vessel and fibre dimensions, vessel density and arrangement, and (2) examined vessel features variability, which may indirectly give insights regarding the degree of xylem adjustment to changes in water availability. Additionally, we analysed if stem wood anatomical features of species growing in both early and late successional communities differ. We constructed generalized linear mixed-effects models to estimate and compare the means and standard deviations of anatomical traits among eight EC and 13 LC coexisting species. Our study revealed high heterogeneity in secondary xylem vessel and fibre features. Vessel features variability suggests a high degree of xylem adjustment to changes in water availability in both EC and LC. The predominance of high vessel redundancy in species coexisting in EC probably indicates that this property is associated with water safety preventing fatal hydraulic system failures. The highly variable dimensions of fibres indicate that species coexisting in LC have different characteristics associated with high mechanical resistance. The high variability of vessel anatomical features along with different type cell combinations may be key to explain the differential ecological performance observed along successional gradients.

Keywords

Vessel dimensions, fibre dimensions, drought-stress resistance, mechanical support.

Introduction

Wood tissue contains diverse possibilities of functional traits in terms of stem hydraulics and mechanical support (Carlquist 1977; Carlquist 2009; Apgaua et al. 2015; 2017; Baas et al. 2016). For example, mean vessel diameter and spatial arrangement may allow to indirectly estimate the conductive capacity of a woody plant, and it may have implications for its hydraulic efficiency and safety. Larger vessel diameters and a higher number of vessels per area are associated with better water transport efficiency, but also with higher risk of embolism (Zimmermann 1983; Hacke et al. 2001).

Anatomical traits exhibited by drought-affected individuals are not always consistent with increasing hydraulic safety. For example, Tng et al. (2018) experimentally found vessels less clustered while inducing drought stress, suggesting that the risk of embolism spreading through adjacent vessels decreases. Contrastingly, von Arx et al. (2013) found in dry sites more clustered vessels and higher number of vessels.

Fibre dimensions may be an indirect indicator of lignin amount and degree of mechanical support. Thick fibre walls are associated with more physical resistance and wider fibre lumina with flexibility, but these relationships are complex rather than direct (Larjavaara et al. 2010). Fibres have also been associated with hydraulic safety, as thicker fibre walls may prevent the risk of implosion under high pressures given by hydric stress (Hacke et al. 2001). Jupa et al. (2016) found for some species that water can be gradually depleted from fibres during drought, so fibre dimensions may also indirectly indicate free space for water storage capacity, although this must be taken with caution, as this has been found to be species dependent. At community level, Aguilar-Rodríguez et al. (2001) found that thick-walled fibre species predominate in dry environments in comparison to more humid ones.

Analysing stem wood anatomical features of species that grow in a particular vegetation type can provide insights on how the anatomical structure responds to ecological stimuli. Secondary vegetation derived from tropical dry forest (TDF) includes a diverse array of species that occur in the same site, and that are regionally subjected to the

same seasonal precipitation regime. TDF secondary succession process is characterized by species turnover over time together with changes in microenvironment (Lebrija-Trejos et al. 2010b). Lebrija-Trejos et al. (2011) found that the seasonal changes in water availability differ between dry and wet seasons: the environmental harshness of the dry season affects the same way both extremes of the successional environmental gradient, while during wet season, soil water availability is higher in late stages than in younger ones. However, TDF successional woody species may differ on their drought resistance mechanisms dealing with the same soil water availability patterns described above (Pineda-García et al. 2015).

The four studied species by Romero et al. (2020a) are dominant components in secondary TDF vegetation, either at early successional stages or late ones. Yet, as secondary TDF communities are typically species-rich (Derroire et al. 2016), we considered necessary a broader anatomical analysis of species present in the recovery vegetation, in order to confirm that some anatomical features do explain the ecological performance, especially the ones associated with water conduction and mechanical properties. In addition, we expected a wide variety of strategies for dealing with environmental filters (Prach et al. 1999; Hasselquist et al. 2010; Pineda-García et al. 2015; Pivovarov et al. 2016).

We hypothesized that the dry season in TDF has acted a selective force that promotes specific adaptive survival strategies, particularly in early successional stages (Murphy & Lugo 1986). We expected homogeneity in characters associated with water conduction that respond to the environment. In early successional stages we expected features associated with water safety, such as high vessel redundancy that allows resilience to cavitation, given by clustered vessels and higher vessel densities (von Arx et al. 2013). Late successional stages are characterized by the presence of individuals bigger in size (height and basal area), which compete for resources such as space. Therefore, we expected to find that the species coexisting in these successional communities had anatomical characteristics associated with high mechanical resistance and high water conduction efficiency.

In this study we asked: what is the set of anatomical traits that frequent species co-occurring in early and co-occurring in late successional communities exhibit? Are there

ecological trends of anatomical features commonly associated with water transport and with biomass production and maintenance? Thus, for 13 important species growing in early and late communities we: (1) quantified vessel and fibre dimensions, and vessel density and arrangement, and (2) examined vessel features variability, which may indirectly give insights into the degree of xylem adjustment to changes in water availability. Additionally, we analysed if stem wood anatomical features of species growing in both early and late successional communities differ.

Methods

Study area

Fieldwork was conducted near Nizanda village, which is in Oaxaca state (16° 39' 30" N, 95° 00' 40" W). Across the region, there are secondary vegetation patches derived from anthropogenic activities (*i.e.*, agriculture and grazing; Gallardo-Cruz et al. 2012). Mean annual temperature is 27.6 °C. Average total annual rainfall is 902.6 ± 355.4 mm (± SD). Precipitation strongly concentrates from the end of May to mid-October. TDF is the main vegetation type in the region (Pérez-García et al. 2010).

In mature TDF forest of the study region, approximately 150 woody species were recorded from which at least 50 woody species occur also in secondary vegetation (Lebrija-Trejos et al. 2010a). Only seven species occur exclusively in secondary vegetation, *i.e.* have not been recorded in mature forest vegetation of the region (Pérez-García et al. 2010).

Species selection

We selected three pioneer species and ten non-pioneer species (13 species in total), because of their high frequency in all TDF successional communities (plots with ages ranging between 2 and > 50 years of abandonment). Wood samples were collected both in early and late successional communities with the following design. Six individuals belonging to

eight species growing on early successional communities (EC) were sampled in three plots (< 5 years of abandonment); the remaining five were absent in EC. Selection of EC individuals was based on size (ca. 30 cm height and 1 cm in diameter). Wood samples from late successional communities (LC) were collected in seven plots (> 50 years of age), for the 13 studied species.

Wood sample collection

For each individual sampled in the EC, a cylinder 1 cm long was cut with a saw near the base of its tallest stem (details in Chapter 4). For individuals in the LC, a section of the main stem 5–6 cm wide was cut with a saw 30 cm above the ground and was fixed in a formaldehyde, alcohol and acetic acid solution (Ruzin 1999) for anatomical analysis. Wood transverse sections were made with a sliding microtome (20–25 μm ; Leica 2000R, Wetzlar, Germany), stained with safranin-fast green and mounted with synthetic resin (Ruzin 1999). Wood sections were examined with an optical microscope (Olympus BX51) and photographs were taken using a digital camera (Evolution LC Color) adapted to the optical microscope.

Anatomical variables were analysed with Image analyser Pro v. 7.1 (ImagePro Plus 7.1, Media Cybernetics, Silver Spring, MD, USA) adapted to compound microscope Olympus BX51 (Tokyo, Japan), in the area covering the most recently produced wood tissue (approximately inside one or two growth rings, depending on the characteristics of each particular wood sample). Tangential and radial vessel diameter, fibre diameter and fibre lumen wall thickness were measured. For diffuse porous species a mean of 50 vessels per individual was measured; for ring porous species in individuals with clear growth rings 50 earlywood vessels and 50 latewood vessels were measured; 100 vessels per individual were measured; a mean of 50 fibres was measured per individual. Vessels per square millimetre and number of vessels per group were counted in 9 to 12 optical fields of 0.1 mm^2 . Vessel area, fibre wall thickness and Runkel ratio ($2 \times \text{mean fibre wall thickness}/\text{mean fibre lumen}$) were calculated.

Statistical analysis

We constructed generalized linear mixed-effects models (GLMM) to estimate and compare the means and standard deviations of anatomical traits among species. For every response variable (vessel tangential diameter, vessel frequency, number of vessels per group, fibre diameter, and fibre lumen) we constructed four models: (1) a model assuming no differences in the means, nor in the standard deviations, between species; (2) a model assuming differences in the means between species, but equal deviations; (3) a model assuming equal means, but different deviations; and (4) a model assuming differences between species both in their means and standard deviations. For each species the whole wood mean was estimated, and where it was possible to distinguish early from late wood, the average was also estimated. Model selection for each response anatomical variable was based on the sample-corrected Akaike Information Criterion (AICc; Burnham and Anderson 2003). Models had similar empirical support whenever ΔAICc was < 2 . Model fitting was performed in R (R Core Team 2015), using the *gamlss* package (Rigby and Stasinopoulos, 2005).

We explored two appropriate probability distributions for each anatomical response variable: for positive continuous variables (i.e., vessel diameter, fibre diameter, and fibre lumen), we used the log-normal and gamma distribution; for vessel frequency, models assumed either a Poisson or a negative binomial distribution; and for the number of vessels per group, the error distribution was either a one-inflated Poisson or a one-inflated negative binomial. One-inflated distributions were used because of the large number of solitary vessels (which were taken as groups containing one vessel element only).

Results

Estimated means of vessel dimensions and distribution in the secondary xylem of eight successional species coexisting in EC and 13 species coexisting in LC are shown in Figures 1 and 2 respectively. Figure 3 shows estimated means of vessel dimensions variation

in EC and LC. Estimated means of fibre features of eight successional species coexisting in EC and 12 species (*Jacaratia mexicana* is a fibreless) coexisting in LC are shown in Figures 4 and 5 respectively. Supplementary material S1 and S2 shows the comparison between intraspecific estimated means of vessel dimensions, vessel distribution and fibre dimensions in the stem wood of species coexisting in EC and LC.

Discussion

Apparently, in early and late TDF successional communities there are some ecological trends of vessel and fibre dimensions, vessel density and arrangement and their variability, which can be associated with water transport and with biomass production and maintenance in the studied species. In general, no discrete groups were recognized: in both cases there is a continuum, with EC being more homogeneous than LC.

Wood anatomical features in early successional communities

In early successional stages we anticipated homogeneous features associated with water safety. In general, mean vessel anatomical features in EC vary almost in a continuum. Mean vessel frequency is particularly homogeneous in EC; the only species differing greatly from the rest in these communities is *Acacia cochliacantha*, as it has few vessels per area. We found a high degree of clustered vessels in six out of the eight early successional species, all of them being legumes with very thick-walled fibres and high wood density, except for *Coccoloba liebmanii* (Romero et al. 2020b). It appears that a main drought-resistance strategy in EC is tolerance of soil drought given by high vessel redundancy, which may confer resilience to cavitation. It is likely that the redundancy property in *Phyllostylon rhamnoides* is given by a different feature, as it is one of the two species with fewer vessels per group in EC, but it has the highest vessel frequency of all. The other species with few vessels per group, *Bonellia macrocarpa*, differs contrastingly from the rest in EC: it is the only species with inverted phenology (i.e., shedding the leaves in the rainy season and bearing foliage in

the dry season), it has the higher wood water content (Romero et al. 2020b), very wide rays (Chapter 5), one of the widest fibre lumen and the lowest variation of vessel area. Probably this species is the only one in EC with a drought evasion mechanism, which relies on having deep roots, as suggested by field observations (Wilfrido pers. comm.).

Mimosa eurycarpa is a dominant species in early succession (Chapter 2), and it has an outstanding mean vessel area in earlywood, suggesting that this species possesses the most efficient water transport system, compared to other species, during the rainy season. Additionally, apparently it has one of the least hydraulically vulnerable secondary xylem during dry season, as its mean latewood-vessel area is one of the smallest in EC.

Mean standard deviation/Mean vessel area variation shows two discrete groups of species: the most variable species are the only three that are exclusive of secondary vegetation (*Mimosa eurycarpa*, *M. tenuiflora* and *Acacia cochliacantha*). These three species, specially *Mimosa* ones, are the early dominant species at least during the first 20 years of secondary succession (Chapter 2). *Lysiloma divaricatum* and *Mimosa eurycarpa* latewoods, as well as *Bonellia macrocarpa* whole-wood, show the lowest variation in EC.

Wood anatomical features in late successional communities

In general, vessel and fibre features were highly variable at the LC level, as well as the intraspecific level. Particularly, vessel area variation was conspicuously high, as intraspecific mean coefficients of variation were above 35%, with a maximum of 145% in *Mimosa eurycarpa*. Although the relative importance of this dominant early species in LC is low (Chapter 2), this species is capable of persisting until more than 70 years of succession, and it faces drastic changes in environmental conditions and resources (Lebrija-Trejos et al. 2011; Lebrija-Trejos et al. 2010b). The high vessel area variation in the tissue produced by *Mimosa eurycarpa* may be key to explain its ecological success along the successional gradient.

As species coexisting in LC also face seasonal drought, we expected to observe features associated with water stress resistance. In theory, if the number of vessels is high, disabling of a given number of vessels by air embolisms formed under water stress would not significantly affect conduction in a plant (Carlquist 1977). *Phyllostylon rhamnoides* and *Mimosa eurycarpa* showed the highest number of vessels per area of LC, which probably are hydraulically safer than other species.

Mimosa tenuiflora and *Acacia cochliacantha* have diffuse porosity and have the same standard deviation as whole wood of *Mimosa eurycarpa*, a ring porous species. These three legume species are conspicuous species in EC, but they are also able to persist in LC. *Mimosa eurycarpa* bears very small latewood vessels and at the same time has the widest vessel diameter of the EC, which are earlywood vessels. Perhaps the ecological success of *Mimosa tenuiflora*, the second is the high variation that was found in its xylem, despite being a diffuse porosity species.

Jacaratia mexicana, followed by *Mimosa eurycarpa* early-wood, *Lysiloma divaricatum* early-wood and *Cnidoscolus megacanthus*, had the widest vessels of LC. Interestingly, both legumes apparently have different strategies in their water economy, as *Jacaratia mexicana* possesses wide vessel diameters and predominantly solitary few vessels, but has the highest wood water content of species coexisting in LC (Romero et al. 2020b). Meanwhile, *Mimosa eurycarpa* has lower intermediate values and *Lysiloma divaricatum* one of the highest values. *Jacaratia mexicana* probably moves water passively only during the rainy season as it loses its leaves; however, probably it may continue transporting water and nutrients on its stem through the living parenchyma that conforms it (Chapter 5).

Anatomical features across successional communities

Pineda-García et al. (2015) found no strong evidence of a functional differentiation between early and late successional species. *Mimosa eurycarpa* is the main pioneer species in EC, but

an unsuccessful one at LC (Lebrija-Trejos et al. 2010a). It has low wood density compared to *Lysiloma divaricatum* (Romero et al. 2020), which is the most successful species in LC and one of the most prominent species in mature forest (Chapter 2). *Lysiloma divaricatum* has wider vessel diameters in earlywood, same as *Mimosa eurycarpa*, although *Lysiloma divaricatum* fibre features indicate more mechanical resistance than the pioneer species has. Apparently, *Mimosa eurycarpa* individuals reach a point where their main stem breaks and the individual dies.

Overall patterns are consistent with Aguilar-Rodríguez et al. (2001), as they found that thick-walled fibres and high specific gravity predominates in dry environments such as in EC, while species medium to low specific gravity and thin walled fibres dominate in environments with higher humidity, such as LC.

Conclusions

Our study revealed high heterogeneity in secondary xylem vessel and fibre features of species coexisting in successional communities derived from a TDF. Vessel features variability suggests a high degree of xylem adjustment to changes in water availability in both EC and LC. The predominance of high vessel redundancy in species coexisting in EC probably indicates that this property is associated with water safety preventing hydraulic system failures. The highly variable fibre dimensions indicate that species coexisting in LC have different characteristics associated with high mechanical resistance.

Co-occurring TDF successional species show stem wood anatomical features that suggest different drought resistance strategies, as well as different biomass production costs. Vessel anatomical features high variability and different type cell combinations may be keys to explain the differential ecological performance observed along successional gradient.

Acknowledgements

Edgar J. González-Liceaga analysed the data. We are grateful to Alicia Rojas and Marcelo Pace for their technical support in laboratory. This study is part of the requirements for ER to obtain the Doctor of Science degree from the Posgrado en Ciencias Biológicas (PCB), Universidad Nacional Autónoma de México (UNAM). Funding for this research was provided by the Consejo Nacional de Ciencia y Tecnología (CONACyT), grant no. 270104; and Programa de Apoyo a Proyectos de Investigación e Innovación Tecnológica-Universidad Nacional Autónoma de México (PAPIIT-UNAM); grant no. IN218416 and grant IN217620.

References

- Aguilar-Rodríguez, S., Abundiz-Bonilla, L., Barajas-Morales, J., 2001. Comparación de la gravedad específica y características anatómicas de la madera de dos comunidades vegetales en México. *Anales del Instituto de Biología, Universidad Autónoma de México, Serie Botánica*, 72, 171-185.
- Apgaua, D.M.G., Ishida, F.o.Y., Tng, D.Y.P., Laidlaw, M.J., Santos, R.M., Rumman, R., Eamus, D., Holtum, J.A.M., Laurance, S.G.W., 2015. Functional traits and water transport strategies in lowland tropical rainforest trees. *PloS one*, 10, e0130799.
- Apgaua, D.M.G., Tng, D.Y.P., Cernusak, L.A., Cheesman, A.W., Santos, R.M., Edwards, W.J., Laurance, S.G.W., 2017. Plant functional groups within a tropical forest exhibit different wood functional anatomy. *Functional Ecology*, 31, 582-591.
- Baas, P., Beeckman, H., Čufar, K., Micco, V.D., 2016. Functional traits in wood anatomy. *IAWA Journal*, 37, 124-126.
- Bates D., Maechler, M., Bolker, B. & Walker, S. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67, 1-48.
- Burnham, K.P. & Anderson, D.R. 2004. Multimodel inference understanding AIC and BIC in model selection. *Sociological Methods and Research*, 33, 261-304.

- Carlquist, S., 1977. Ecological factors in wood evolution: a floristic approach. *American Journal of Botany*, 64, 887-896.
- Carlquist, S., 2009. Non-random vessel distribution in woods: patterns, modes, diversity, correlations. *Aliso*, 27, 39-58.
- Derroire, G., Tigabu, M., Odén, P.C., Healey, J.R., 2016. The effects of established trees on woody regeneration during secondary succession in tropical dry forests. *Biotropica*, 48, 290-300.
- Gallardo-Cruz, J.A., Meave, J.A., González, E.J., Lebrija-Trejos, E.E., Romero-Romero, M.A., Pérez-García, E.A., Gallardo-Cruz, R., Hernández-Stefanoni, J.L., Martorell, C., 2012. Predicting tropical dry forest successional attributes from space: is the key hidden in image texture? *PLOS ONE*, 7, e30506.
- Hacke, U.G., Sperry, J.S., Pockman, W.T., Davis, S.D., McCulloh, K.A., 2001. Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia*, 126, 457-461.
- Hasselquist, N.J., Allen, M.F., Santiago, L.S., 2010. Water relations of evergreen and drought-deciduous trees along a seasonally dry tropical forest chronosequence. *Oecologia*, 164, 881-890.
- Jupa, R., Plavcová, L., Gloser, V., Jansen, S., 2016. Linking xylem water storage with anatomical parameters in five temperate tree species. *Tree Physiology*, 36, 756-769.
- Larjavaara, M., Muller-Landau, H.C., 2010. Rethinking the value of high wood density. *Functional Ecology*, 24, 701-705.
- Lebrija-Trejos, E., Meave, J.A., Poorter, L., Pérez-García, E.A., Bongers, F., 2010a. Pathways, mechanisms and variability of tropical dry forest succession. *Perspectives in Plant Ecology, Evolution and Systematics*, 12, 267-275.
- Lebrija-Trejos, E., Pérez-García, E.A., Meave, J.A., Bongers, F., Poorter, L., 2010b. Functional traits and environmental filtering drive community assembly species-rich tropical system. *Ecology*, 91, 386-398.

- Lebrija-Trejos, E., Pérez-García, E.A., Meave, J.A., Poorter, L., Bongers, F., 2011. Environmental changes during secondary succession in a tropical dry forest in southern Mexico. *Journal of Tropical Ecology*, 27, 477-489.
- Murphy, P.G., Lugo, A.E., 1986. Ecology of tropical dry forest. *Annual Review of Ecology and Systematics*, 17, 67-88.
- Pérez-García, E.A., Meave, J.A., Villaseñor, J.L., Gallardo-Cruz, J.A., Lebrija-Trejos, E., 2010. Vegetation heterogeneity and life-strategy diversity in the flora of the heterogeneous landscape of Nizanda, Oaxaca, México. *Folia Geobotanica*, 45, 143-161.
- Pineda-García, F., Paz, H., Meinzer, F.C., Angeles, G., 2015. Exploiting water versus tolerating drought: water-use strategies of trees in a secondary successional tropical dry forest. *Tree Physiology*, 36, 208-217.
- Pivovarov, A.L., Pasquini, S.C., Guzman, M.E.D., Alstad, K.P., Stemke, J.S., Santiago, L.S., 2016. Multiple strategies for drought survival among woody plant species. *Functional Ecology*, 30, 517-526.
- Prach, K., Pyšek, P., 1999. How do species dominating in succession differ from others? *Journal of Vegetation Science*, 10, 383-392.
- R Core Team 2019, R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Romero, E., González, E.J., Meave, J.A., Terrazas, T. 2020. Wood anatomy of dominant species with contrasting ecological performance in tropical dry forest succession, *Plant Biosystems*, 154, 524-534.
- Romero, E., Dávalos-Sotelo, R., Meave, J.A., Terrazas, T., 2020b. Wood density, deposits and mineral inclusions of successional tropical dry forest species. *European Journal of Forest Research*, 139, 369-381.
- Ruzin S.E. 1999. *Plant microtechnique and microscopy*. Oxford University Press, New York.
- Tng, D.Y.P., Apgaua, D.M.G., Ishida, Y.F., Mencuccini, M., Lloyd, J., Laurance, W.F., Laurance, S.G.W., 2018. Rainforest trees respond to drought by modifying their hydraulic architecture. *Ecology and Evolution*, 8, 12479-12491.

von Arx, G., Kueffer, C., Fonti, P., 2013. Quantifying plasticity in vessel grouping-added value from the image analysis tool ROXAS. *IAWA Journal*, 34, 433-445.

Zimmermann, M. H., 1983. Xylem structure and the ascent of sap. Springer-Verlag, New York.

Supplementary Information

Figure S1. Comparison between estimated means of vessel features in the secondary xylem of species present in early (~ 2 years of abandonment; EC) and late successional communities (> 50 years of abandonment; LC) derived from a tropical dry forest. Asterisks indicate significant differences between means. Vertical lines indicate confidence interval. Species acronyms: AC, *Acacia cochliacantha*; BO, *Bonellia macrocarpa*; BU, *Bursera simaruba*; CO, *Coccoloba liebmanii*; CN, *Cnidoscolus megacanthus*; JA, *Jacaratia mexicana*; LO, *Lonchocarpus lanceolatus*; LY, *Lysiloma divaricatum* (l-latewood, e-earlywood); MIE, *Mimosa eurycarpa* (l-latewood, e-earlywood); MIT, *Mimosa tenuiflora*; PA, *Pachycereus pecten-aboriginum*; PH, *Phylostyllon rhamnoides*; PI, *Pilosocereus colinsii*.

Figure S2. Comparison between estimated means of fibre features in the secondary xylem of species present in late successional communities (> 50 years of abandonment; LC) derived from a tropical dry forest. Asterisks indicate significant differences between means. Vertical lines indicate estimated confidence interval. Species acronyms: AC, *Acacia cochliacantha*; BO, *Bonellia macrocarpa*; BU, *Bursera simaruba*; CO, *Coccoloba liebmanii*; CN, *Cnidoscolus megacanthus*; LO, *Lonchocarpus lanceolatus*; LY, *Lysiloma divaricatum*; MIE, *Mimosa eurycarpa*; MIT, *Mimosa tenuiflora*; PA, *Pachycereus pecten-aboriginum*; PH, *Phylostyllon rhamnoides*; PI, *Pilosocereus colinsii*.

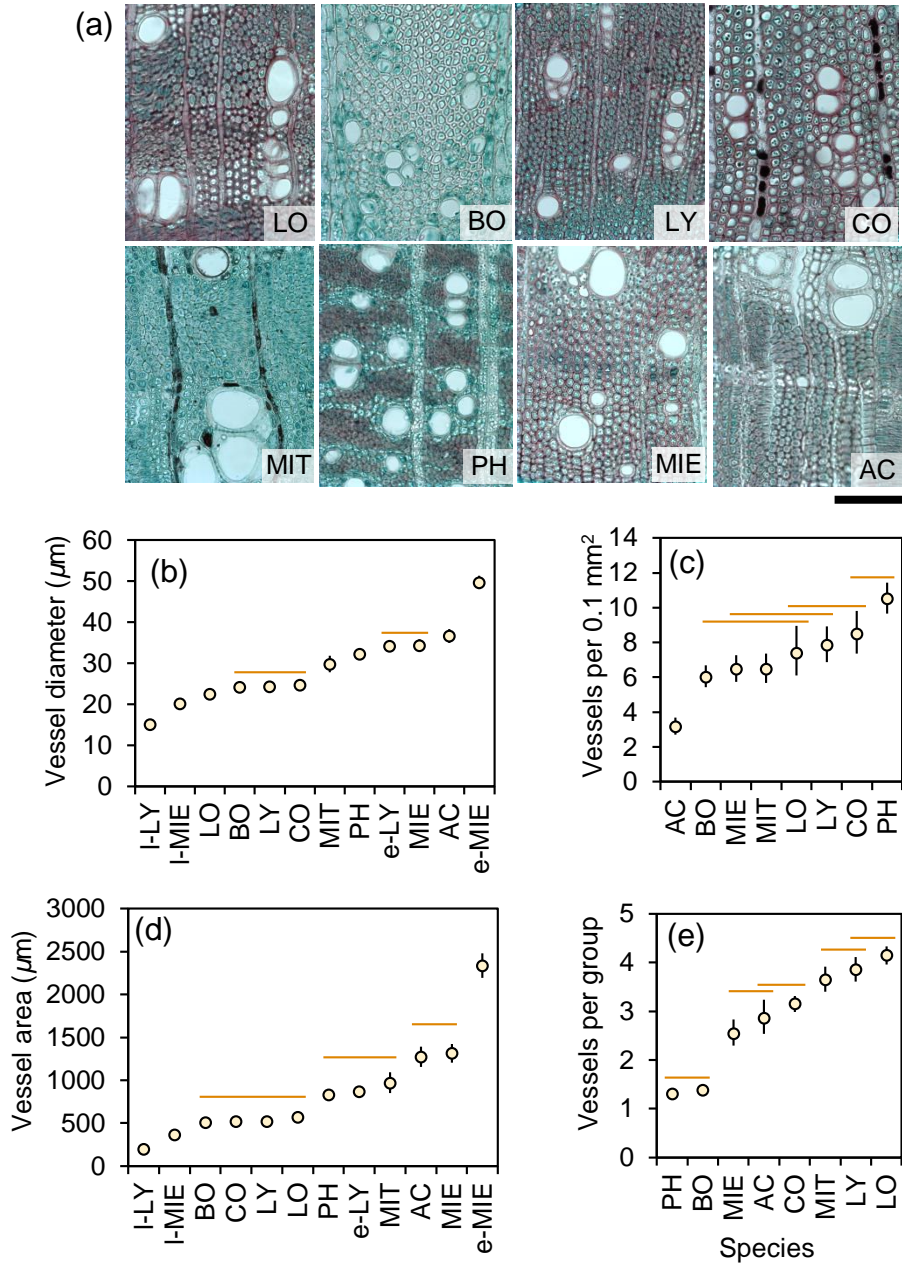


Figure 1. Means of vessel features in the wood of species present in early successional tropical dry forest communities (~ 2 years of abandonment; EC). Brown horizontal bars indicate no significant differences between means. Vertical lines indicate 95% estimated confidence interval. Scale bar in (a) = 100 µm. Species acronyms in (a): AC *Acacia cochliacantha*; BO *Bonellia macrocarpa*; CO *Coccoloba liebmanii*; LO *Lonchocarpus lanceolatus*; MIT *Mimosa tenuiflora*; PH *Phyllostylon rhamnoides*. In ring-porous species: LY *Lysiloma divaricatum* whole-wood; MIE *Mimosa eurycarpa* whole-wood; I- latewood, e-earlywood. Individual height was ≈ 30 cm and stem diameter ≈ 1 cm. Individuals came from resprouts, except for LY.

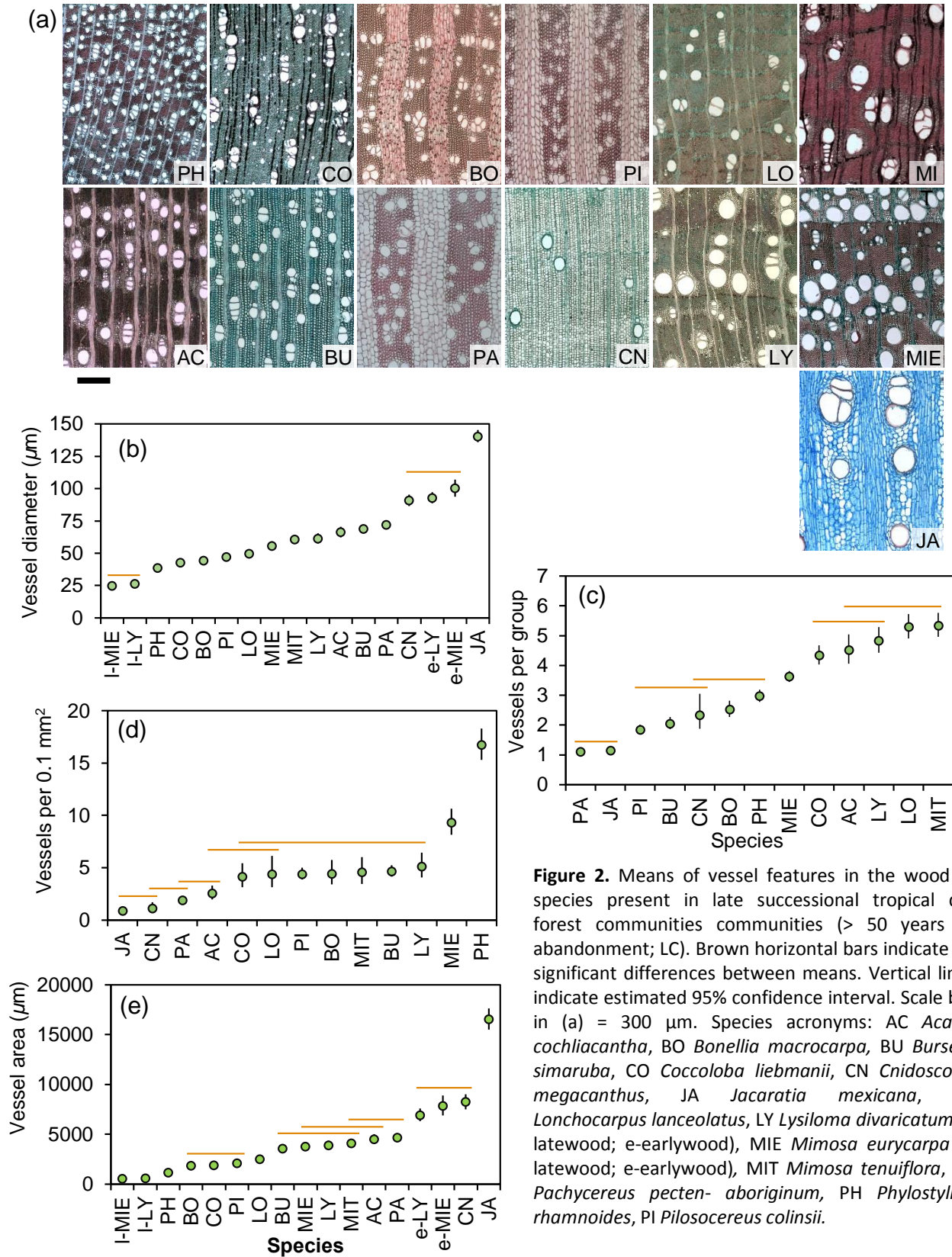


Figure 2. Means of vessel features in the wood of species present in late successional tropical dry forest communities (> 50 years of abandonment; LC). Brown horizontal bars indicate no significant differences between means. Vertical lines indicate estimated 95% confidence interval. Scale bar in (a) = 300 μm . Species acronyms: AC *Acacia cochliacantha*, BO *Bonellia macrocarpa*, BU *Bursera simaruba*, CO *Coccoloba liebmanii*, CN *Cnidocolus megacanthus*, JA *Jacaratia mexicana*, LO *Lonchocarpus lanceolatus*, LY *Lysiloma divaricatum* (l-latewood; e-earlywood), MIE *Mimosa eurycarpa* (l-latewood; e-earlywood), MIT *Mimosa tenuiflora*, PA *Pachycereus pecten- aboriginum*, PH *Phylostyllon rhamnoides*, PI *Pilosocereus colinsii*.

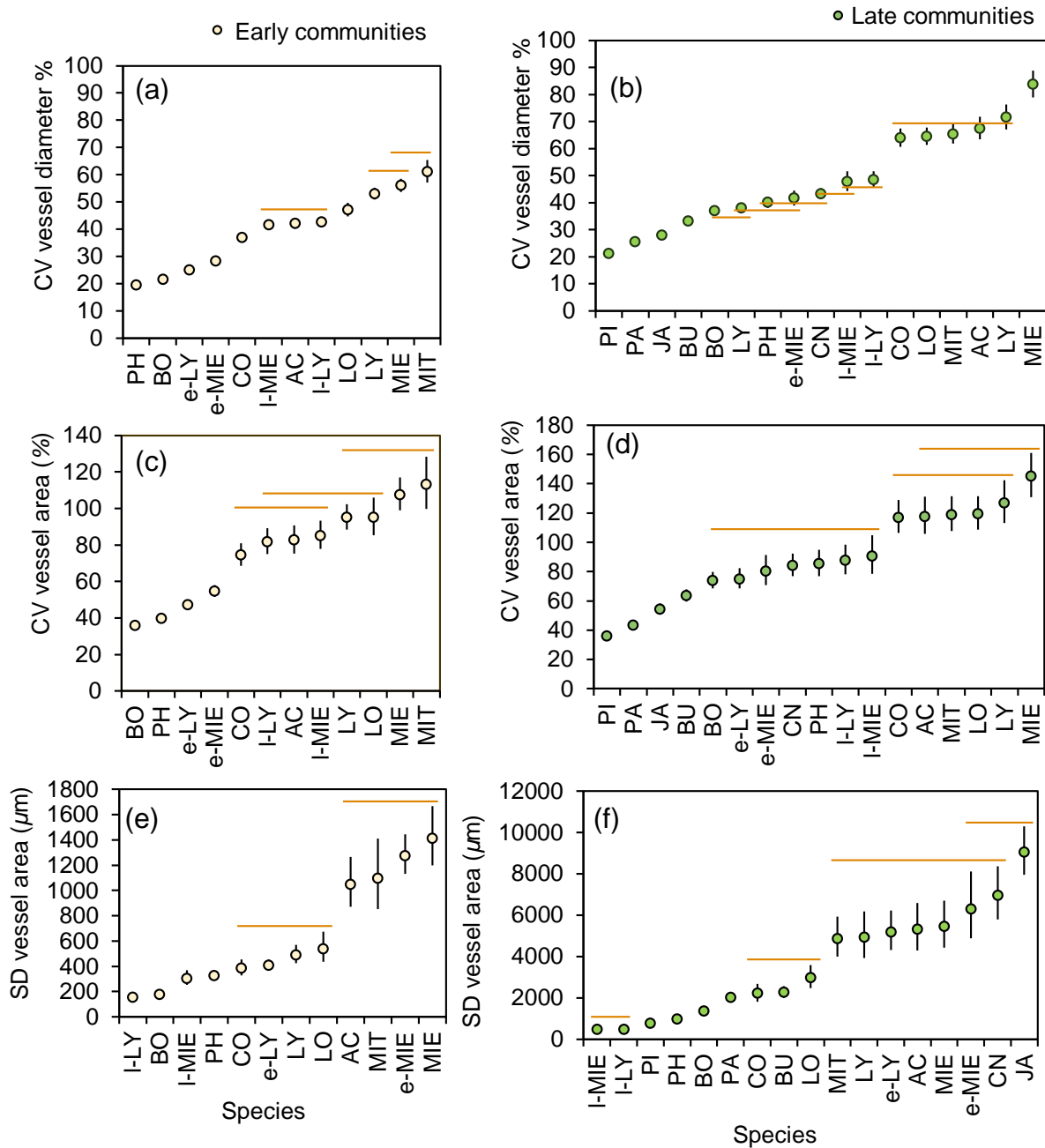


Figure 3. Estimated means of vessel features variation in the wood of species present in early (~ 2 years of abandonment; EC) and late successional tropical dry forest communities (> 50 years of abandonment; LC). Brown horizontal bars indicate no significant differences between means. Vertical lines indicate estimated 95% confidence interval. CV: coefficient of variation. SD standard deviation. Species acronyms: AC *Acacia cochliacantha*, BO *Bonellia macrocarpa*, BU *Bursera simaruba*, CO *Coccoloba liebmanii*, CN *Cnidocolus megacanthus*, JA *Jacaratia mexicana*, LO *Lonchocarpus lanceolatus*, LY *Lysiloma divaricatum* (I-latewood; e-earlywood), MIE *Mimosa eurycarpa* (I-latewood; e-earlywood), MIT *Mimosa tenuiflora*, PA *Pachycereus pecten-aboriginum*, PH *Phyllostylon rhamnoides*, PI *Pilosocereus colinsii*.

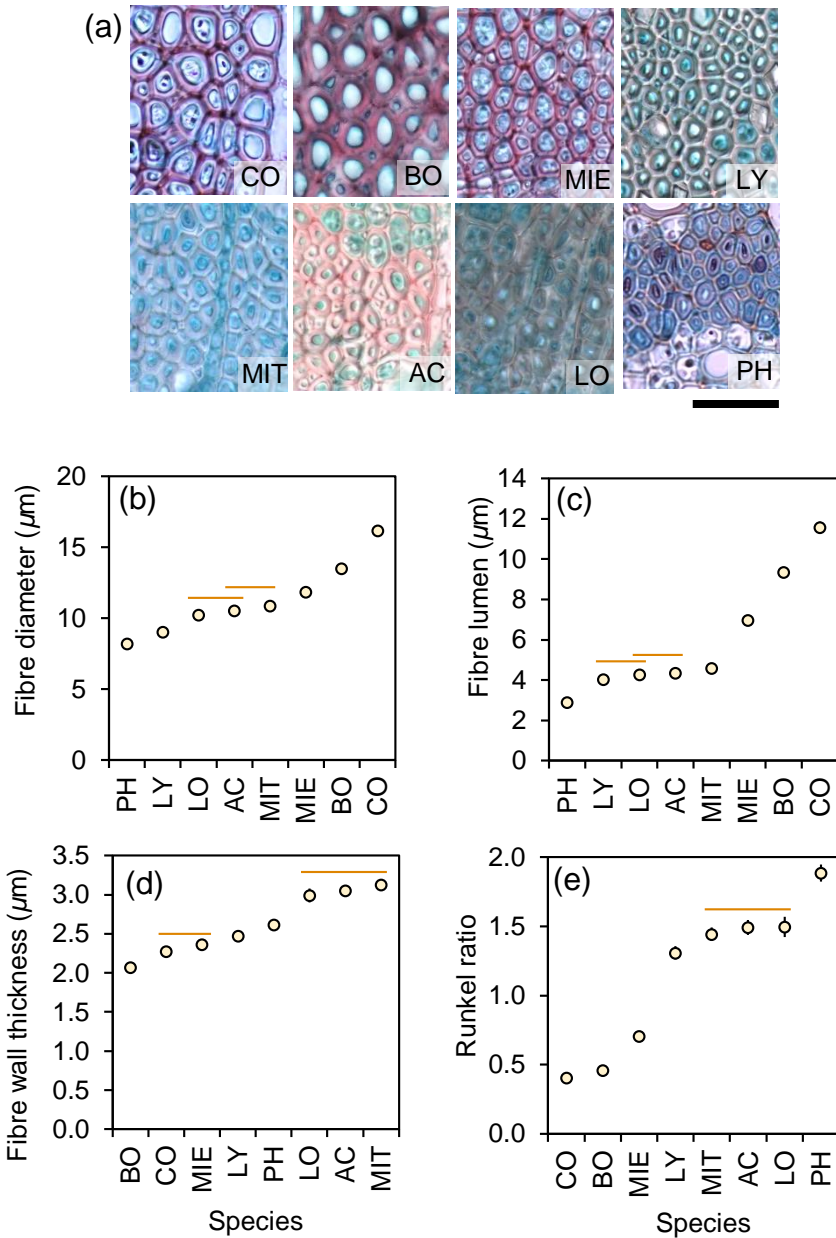


Figure 4. Estimated means of fibre features in the wood of species present in early successional tropical dry forest communities (~ 2 years of abandonment; EC). Brown horizontal bars indicate no significant differences between means. Vertical lines indicate estimated 95% confidence interval. Scale bar in (a) = $40 \mu\text{m}$. Species acronyms in (a): AC *Acacia cochliacantha*; BO *Bonellia macrocarpa*; CO *Coccoloba liebmanii*; LO *Lonchocarpus lanceolatus*; MIT *Mimosa tenuiflora*; PH *Phylostylon rhamnoides*. In ring-porous wood species: LY *Lysiloma divaricatum* whole-wood; MIE *Mimosa eurycarpa* whole-wood; l-latewood, e-earlywood. Individual height was ≈ 30 cm and stem diameter ≈ 1 cm. Individuals came from resprouts, except for LY.

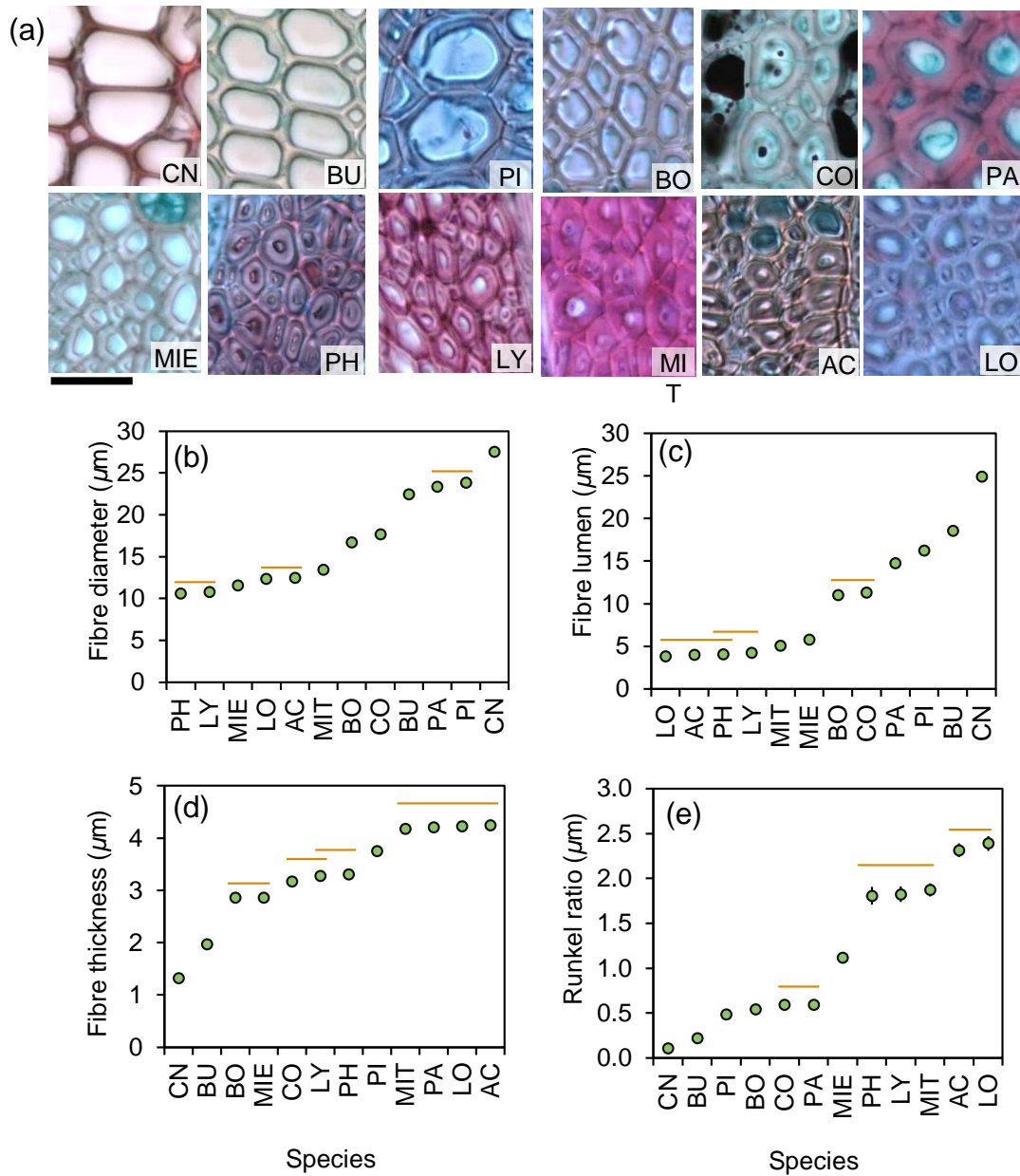


Figure 5. Means of fibre features in the wood of species present in late successional tropical dry forest communities (> 50 years of abandonment; LC). Brown horizontal bars indicate no significant differences between means. Vertical lines indicate estimated 95% confidence interval. Scale bar in (a) = 40 µm. Species acronyms: AC *Acacia cochliacantha*, BO *Bonellia macrocarpa*, BU *Bursera simaruba*, CO *Coccoloba liebmanii*, CN *Cnidocolus megacanthus*, LO *Lonchocarpus lanceolatus*, LY *Lysiloma divaricatum*, MIE *Mimosa eurycarpa*, MIT *Mimosa tenuiflora*, PA *Pachycereus pecten-aboriginum*, PH *Phylostyllum rhamnoides*, PI *Pilosocereus colinsii*.

CAPÍTULO 7

Discusión general y conclusiones



CAPÍTULO 7. DISCUSIÓN GENERAL Y CONCLUSIONES

Las especies que constituyen la vegetación secundaria derivada del bosque tropical caducifolio (BTC) enfrentan escasez de agua durante una estación seca prolongada y distintos filtros ambientales asociados al gradiente sucesional, y presentan diferentes respuestas fenológicas (Lebrija-Trejos *et al.* 2011; Méndez-Alonzo *et al.* 2013; Pineda-García *et al.* 2013; Maldonado-Romo, 2014). El xilema secundario del tallo de las plantas contiene diversas posibilidades de atributos funcionales relacionados con la hidráulica, el soporte mecánico y el almacenamiento de recursos (Carlquist 1977; Carlquist 2009; Apgaua *et al.* 2015, 2017; Baas *et al.* 2016). En este contexto, la premisa inicial de esta investigación era que el análisis de las características del xilema secundario del tallo de las especies sucesionales contribuiría a dilucidar la relación entre el ambiente biótico y abiótico, las funciones del tallo y su desempeño ecológico.

En la fase inicial de esta tesis se analizó el desempeño ecológico de 50 especies sucesionales evaluado a través del área basal con respecto a la edad sucesional (Capítulo 2). Posteriormente, se describieron y analizaron las características anatómicas del xilema de las especies dominantes (Capítulo 3) y de las especies frecuentes en las comunidades sucesionales tempranas (Capítulo 6) y tardías (Capítulos 5 y 6), así como su densidad de la madera y el registro de contenidos celulares e inclusiones minerales (Capítulo 4). En general, el estudio hizo evidente la existencia de una gran complejidad, tanto en la variación del área basal de cada especie con respecto a la edad sucesional, así como en las características anatómicas y físicas estudiadas.

Variación en la acumulación de biomasa en los tallos de las especies a lo largo del gradiente sucesional

La teoría sucesional se enfocó durante años en el bosque tropical perennifolio, mientras que la vegetación sucesional del BTC empezó a recibir atención más recientemente (Bazzaz y Pickett 1980; Murphy y Lugo 1995; Gillespie *et al.* 2000; Quesada *et al.* 2009; Derroire *et*

al. 2016). El primer objetivo particular de esta tesis fue analizar el cambio en el área basal de 50 especies presentes en sitios de bosque secundario de diferentes edades; este análisis aportó información valiosa y novedosa para las especies del bosque secundario derivado de un BTC (Capítulo 2). Integramos dos variables de desempeño ecológico importantes: la presencia de las especies en el sistema y su área basal, siendo esta última un indicador de la acumulación de biomasa en el tallo. Cabe señalar que la presencia de las especies en las parcelas sucesionales es una variable poco analizada en estudios de este tipo. Los resultados sugirieron una capacidad diferencial de las especies para acumular biomasa en sus tallos en condiciones ambientales cambiantes y limitantes asociadas al gradiente sucesional. Además, el procedimiento novedoso utilizado podría ser útil en estudios ecológicos a largo plazo sobre la dinámica direccional de los ecosistemas. Es difícil realizar estos estudios durante períodos muy largos para tener una visión amplia de todo el proceso, por lo que el uso de sitios con distintas edades seguidos en el tiempo es una buena alternativa. Sin embargo, este procedimiento crea problemas analíticos que se abordaron en el Capítulo 2 de esta tesis.

Al evaluar la variación en la presencia y en el área basal de cada una de las especies en función de la edad sucesional (*proxy* de los cambios ambientales sucesionales), se encontró que la edad sucesional explicó la variación en el área basal de la mayoría de éstas. Como se había anticipado, dos especies de *Mimosa* fueron dominantes en etapas tempranas, mientras que otras lo fueron en etapas tardías (incluyendo a *Lysiloma divaricatum* como la especie sucesional dominante tardía). Sin embargo, varias especies mostraron patrones inesperados. Algunos de ellos sugirieron que hay especies que podrían ser sensibles a factores específicos del sitio, como las características edáficas y legado de disturbio, o quizá al efecto de la competencia. La exploración del desempeño de las especies individuales reveló una gran variedad de patrones de cambio sucesional del área basal, lo cual parece indicar que hay una divergencia entre especies en la adquisición de recursos y en la capacidad de resistencia a las condiciones ambientales adversas. Este supuesto anticipaba la gran diversidad de propiedades físicas y de características anatómicas del xilema del tallo que se encontraron en los capítulos posteriores.

Características del xilema secundario del tallo de las especies sucesionales

Las especies seleccionadas y analizadas en los capítulos posteriores incluyeron 13 especies sucesionales, diversas en su taxonomía, fenología y ecología. Pertenecen a 12 géneros y siete familias, incluyendo dos especies leñosas de la familia Cactaceae. Presentan distintos grados de caducifoliedad (Cuadro 1, Capítulo 5; Maldonado-Romo 2014) e incluyen a una especie con fenología invertida (*i.e.*, que produce hojas durante la época de sequía; *Bonellia macrocarpa*). Tres especies son exclusivas de la vegetación secundaria (*Mimosa eurycarpa*, *M. tenuiflora* y *Acacia cochliacantha*), son especies importantes en estadios sucesionales tempranos (Enrique-Vargas *en prep.*), y persisten en estadios sucesionales avanzados, aunque con menor frecuencia (Capítulo 2). El resto de las especies estudiadas están presentes tanto en bosques secundarios como maduros del área de estudio (Capítulo 1) y son componentes estructurales importantes de éstos (Capítulo 2; Muñoz-Avilés 2015).

Las especies estudiadas también son anatómicamente diversas, ya que los intervalos registrados para la media de los diámetros de vasos, el número de vasos por mm², el grosor de las fibras y el número de vasos por grupo son amplios (Capítulos 5 y 6). Además, los coeficientes de variación y las desviaciones estándar de estas variables son altos (Capítulo 6). La cantidad de los parénquimas axial y radial que las especies estudiadas presentan puede ser desde escaso, hasta ser el principal componente del xilema secundario (Capítulo 5). Los componentes del tejido leñoso que constituyen al tallo también son heterogéneos entre las especies: incluyen fibras no septadas, fibras gelatinosas, una mezcla de ambas o incluso no presentan fibras, como en el caso de *Jacaratia mexicana* (Capítulo 5). Los contenidos celulares e inclusiones minerales que presentan las especies sucesionales estudiadas también son variadas, ya que pueden presentar cristales, cuerpos de sílice, gomas y depósitos oscuros que podrían ser taninos (Capítulo 4). Además, se encontró una característica anatómica peculiar: la presencia de fibras gelatinosas en la mayoría de las especies sucesionales, las cuales fueron apreciablemente abundantes en algunas de ellas (Capítulo 5).

Las fibras septadas constituyen una parte importante del xilema secundario del tallo de cinco de las 13 especies sucesionales presentes en comunidades tardías: *Bursera simaruba* y *Coccoloba liebmanni* tienen exclusivamente fibras septadas, mientras que las dos especies de cactus y *Bonellia macrocarpa* tienen fibras no septadas escasas (Capítulo 5). Este grupo de cinco especies presenta parénquima paratraqueal escaso y carece de parénquima en bandas. Por otro lado, *Phyllostylon rhamnoides* y *Lonchocarpus lanceolatus* tienen fibras septadas, aunque escasas, pero ambas especies presentan parénquima en bandas. Las especies con fibras septadas (excluyendo a las cactáceas) tienen fenología subperennifolia, producen hojas durante la estación seca (*Bonellia macrocarpa*) o retienen hojas durante un período más largo que el resto de las especies (Cuadro 1, Capítulo 5).

Los valores promedio de densidad de madera de las especies incluidas en esta tesis tienen una distribución diferencial a lo largo del gradiente sucesional, y va de 0.10 g/cm³ a (*Jacaratia mexicana* en las comunidades tardías) a 0.92 g/cm³ (*Lysiloma divaricatum* en la comunidad sucesional temprana; Capítulo 4). Estos valores de densidad de madera son congruentes con los patrones reportados para vegetación sucesional en sitios estacionalmente secos (Poorter *et al.* 2019); también están dentro del intervalo de valores reportados para las especies de BTC en México, el cual va de 0.16 g/cm³ (*Jacaratia mexicana*) a 1.4 g/cm³ (*Guaiacum sanctum*; Barajas-Morales 1987; Ordóñez *et al.* 2015).

La densidad de la madera, el contenido de agua en la madera, la presencia y abundancia de depósitos celulares y las inclusiones minerales son muy variables entre las especies sucesionales (Capítulo 4). Sin embargo, inesperadamente mostraron una variabilidad intraespecífica baja en la densidad de madera, a pesar de las grandes diferencias en las condiciones ambientales en las comunidades donde crecen. Esto sugiere que la madera, producida por las reiteraciones de tronco de árboles talados (rebrotos a partir de tocones) en la mayoría de las especies frecuentes en comunidades sucesionales tempranas, es ontogenéticamente igual que la madera producida por individuos de la misma especie presentes en las comunidades sucesionales tardías. Nuestros datos confirman los resultados a nivel de comunidad que Zimmermann *et al.* (2019) señalan, ya que ellos no encontraron diferencias significativas en la densidad de la madera del tallo y de las

ramas grandes dentro de un mismo individuo. A partir de este análisis surgieron nuevas preguntas en cuanto al uso de la densidad de la madera como atributo funcional, por lo que sería recomendable estudiar otras variables, como el papel de la superficie que abarca el tallo en la resistencia mecánica (Larjavaara *et al.* 2010) o los componentes anatómicos del xilema del tallo (Poorter *et al.* 2010; Ziemińska *et al.* 2013); los resultados de los capítulos 2, 4 y 6 permitirían hacer los análisis sugeridos en el futuro.

Posibles formas de resistencia a la sequía en las especies en comunidades sucesionales tempranas

Al inicio de la investigación se esperaba encontrar que las especies que coexisten en las etapas sucesionales tempranas presentaran características del xilema del tallo similares asociadas con la resistencia a la sequía. En general, esto fue así, ya que la mayoría de las especies presentó valores altos de densidad de la madera (Capítulo 4) y paredes de las fibras muy gruesas (Capítulo 7). Ambas características se asocian con la resistencia a daños físicos como la implosión de los vasos debido a las presiones negativas generadas por cantidades de agua ambiental bajas. Estos resultados parecen sugerir que siete especies sucesionales en etapas tempranas presentan mecanismos asociados a la tolerancia a la sequía. Sólo una especie de la comunidad temprana, *Bonellia macrocarpa*, parece tener un mecanismo de evasión, dado que presentó un porcentaje alto de contenido de agua en la madera de su tallo en comparación con el resto de las especies (Capítulo 4). Además, esta es la única especie con fenología invertida, por lo que posiblemente mantiene su estatus hídrico durante la época de sequía al utilizar el agua almacenada en sus tallos (posiblemente en los radios; capítulo 5). Además, se ha encontrado que la densidad de la madera se correlaciona negativamente con la cantidad de agua disponible en el suelo (Preston *et al.* 2006), lo cual también puede explicar la predominancia de valores altos de densidad de madera en sitios sucesionales tempranos, donde la cantidad de agua disponible en el suelo es baja (Lebrija-Trejos *et al.* 2011).

Características anatómicas del xilema secundario asociadas con la estacionalidad en la precipitación en especies presentes en comunidades sucesionales tardías

Debido a que las 13 especies sucesionales coexisten en la vegetación secundaria derivada de un BTC, el cual se desarrolla en una región sometida a una marcada estacionalidad en la precipitación (de 4 a 6 meses de sequía cada año), se esperaba que todas las especies presentaran en alguna medida características anatómicas relacionadas con la respuesta a los cambios estacionales en la precipitación. En particular se esperaba observar marcas de crecimiento conspicuas y una distinción evidente entre madera temprana y tardía. Inesperadamente, la mayoría de las especies no presentaron cambios claros y visibles en la distribución, ni en el tamaño de las células que conforman el xilema secundario de sus tallos. Sin embargo, todas ellas presentaron células de parénquima rodeando los elementos conductores de agua, las cuales son características asociadas con la resistencia a la sequía. Por ello, teóricamente las especies que retienen sus hojas en alguna medida durante la época de sequía (Capítulo 5, Cuadro 1) podrían ser capaces de almacenar agua que podría utilizarse en la reparación de embolismos o en mantener el sistema hídrico en funcionamiento.

Un resultado llamativo de esta investigación es que *Mimosa eurycarpa*, especie sucesional temprana dominante, y *Lysiloma divaricatum*, especie dominante tardía, fueron las únicas que presentaron porosidad anular. Los índices de vulnerabilidad bajos en la madera tardía de ambas especies sugieren que presentan una resistencia alta al estrés hídrico (Capítulo 3); probablemente esto, junto con sus altos índices relativos de conducción hídrica (Capítulo 3), explique en parte su capacidad de acumular mayor área basal con respecto al resto de las especies sucesionales (Capítulo 2). Sin embargo, *Mimosa tenuiflora*, la segunda especie dominante en etapas tempranas (Capítulo 2), presentó porosidad difusa y un índice de vulnerabilidad alto (Capítulo 3), aunque quizá la disposición espacial del parénquima (asociado a vasos, en bandas; Capítulo 5) podría estar correlacionado con la prevención de fallas en el transporte hídrico (Morris *et al.* 2016).

Los vasos agrupados se asocian comúnmente con la redundancia en el transporte hídrico: si un vaso está bloqueado por una burbuja de aire, el transporte de agua puede continuar a través de los vasos adyacentes (Carlquist 1980; Tyree *et al.* 1994; Cruiziat *et al.* 2002). Aunque el porcentaje de vasos solitarios en 6 de las 13 especies estudiadas fue superior al 50% (Capítulo 5), los grupos de vasos observados en 11 especies frecuentemente presentaron más de 10 vasos por grupo (hasta 29; Capítulo 5); estas observaciones se reflejan en las medias estimadas para el número de vasos por grupo (2 a 5 vasos por grupo en 11 de las 13 especies estudiadas; Capítulo 6, Fig. 2d). Por lo tanto, solo las dos especies de Cactaceae y una especie de Caricaceae aparentemente carecen de una propiedad de redundancia de vasos, ya que los vasos solitarios son comunes y los grupos observados son pequeños (hasta 4 y 3 vasos, respectivamente).

Las fibras generalmente se asocian con la función de soporte mecánico del tallo (Panshin y DeZeew 1980); sin embargo, la presencia de fibras vivas y septadas puede afectar las funciones del tallo diferentes del soporte mecánico, como el almacenamiento de agua (Yamada *et al.* 2011). Las fibras septadas pueden sustituir al parénquima axial funcionalmente, ya que puede considerarse como un tejido de conexión para el movimiento del agua de la madera, así como para el suministro de carbohidratos durante los eventos de foliación, floración y fructificación (Carlquist 2015). El grupo de cinco especies con fibras septadas como principal componente del xilema del tallo (*Bursera simaruba*, *Coccoloba liebmannii*, *Pachycereus pecten-aboriginum*, *Pilosocereus collinsii* y *Bonellia macrocarpa*) tiene valores medios a altos de contenido de agua de la madera (Capítulo 4). Estas especies tienen radios altos que aparentemente están bien conectados (Capítulo 5), por lo que el parénquima radial, junto con las fibras septadas, podrían tener un papel importante en el almacenamiento de agua del tallo y en la producción de hojas durante la estación seca. Sin embargo, se requieren nuevos estudios para explorar esta posibilidad.

Características del xilema secundario asociadas con la asignación de recursos en el tallo de las especies en comunidades sucesionales tempranas y tardías

La densidad de madera es una variable relacionada con la inversión en la producción de biomasa de una planta; sin embargo, es importante tomar en cuenta que ésta resulta de la interacción que se da entre los componentes anatómicos del xilema (Ziemińska *et al.* 2013). En realidad, todavía estamos lejos de entender bien a bien esta interacción, y por ello hace falta realizar estudios detallados y específicos para averiguar qué características determinan los valores de densidad de madera (Capítulo 4).

Nuestros resultados mostraron que las densidades de la madera de las dos especies de Cactaceae incluidas en esta tesis no difieren significativamente de la densidad de madera de especies de árboles como *Bursera simaruba* y *Cnidoscolus megacanthus* (ambas especies paquicaules; Capítulo 4). La similitud en los valores de densidad de la madera podría indicar que las especies de cactus potencialmente almacenan una cantidad similar de carbono a la almacenada en especies arbóreas. Por esta razón, es realmente importante incluir a las especies leñosas de Cactaceae en las estimaciones de biomasa del dosel del BTC, ya que pueden ser componentes importantes de la estructura de este tipo de vegetación (Capítulo 2). Las dos especies de Cactaceae estudiadas presentan fibras de paredes muy gruesas; incluso las de *Pachycereus pecten-aboriginum* son tan gruesas como las de tres especies leguminosas, aunque difieren tanto en el diámetro total de las fibras, como en el del lumen (Capítulo 6). Sobre este punto en particular, será necesario llevar a cabo nuevas investigaciones que permitan averiguar la capacidad de captura de carbono en las especies sucesionales estudiadas.

Otro resultado muy relevante del estudio es que cinco especies presentan fibras vivas abundantes (Capítulo 5) y un contenido alto de agua en la madera (Capítulo 4) Este tipo de fibras podrían representar el resultado evolutivo de una disyuntiva entre los costos altos de mantenimiento de biomasa y el almacenamiento de agua. En particular, *Bursera simaruba*, *Bonellia macrocarpa* y *Coccoloba liebmanii* presentan fibras de paredes delgadas y lumen amplio (Capítulo 6), lo cual sugiere que el costo de producción de la madera de sus tallos es bajo.

Todas las especies estudiadas, excepto *Jacaratia mexicana*, presentaron almidón almacenado en el parénquima del xilema del tallo (Capítulo 4), por lo que estas especies aparentemente cuentan con una fuente de carbono que podría ser utilizada para la producción de biomasa.

Conclusiones y perspectivas

Aunado a la complejidad estructural y florística de las comunidades sucesionales derivadas del BTC (Lebrija-Trejos *et al.* 2008; Álvarez-Yépiz *et al.* 2008; Chazdon *et al.* 2011; Derroire *et al.* 2016), los hallazgos de esta tesis muestran que las especies sucesionales también tienen una amplia diversidad de patrones de acumulación de área basal con respecto a la edad sucesional, de valores de densidad de la madera, y de características anatómicas del xilema secundario de sus tallos.

En esta investigación se exploraron las posibles implicaciones de las características del xilema secundario de un grupo variado de especies típicas de los bosques secundarios estacionalmente secos, en la resistencia a la sequía. La descripción y el análisis de las características del xilema secundario del tallo de especies sucesionales, que enfrentan distintos filtros ambientales asociados al gradiente sucesional y a la estacionalidad en la precipitación, son dos pasos importantes que preceden la realización de futuros estudios experimentales encaminados a explorar los posibles mecanismos de resistencia al estrés hídrico y las diferentes formas de asignación de recursos, como agua y carbono, así como de producción y mantenimiento de la biomasa. Las características anatómicas de la madera del tallo de las especies estudiadas sugieren la existencia de diferentes mecanismos de resistencia a la sequía, en congruencia con lo descrito para otras especies sucesionales de BTC (Pineda-García *et al.* 2015), así como diferentes costos de producción de biomasa, lo que aparentemente resulta de diferentes combinaciones anatómicas de la madera.

Las especies de plantas presentan distintas estrategias de adquisición de recursos, habilidades competitivas y tolerancias o evasión de ciertas condiciones ambientales asociadas a los gradientes ambientales (Keddy 1992), como el sucesional. En principio, en 7

de las 13 especies estudiadas, se observó en el campo que son capaces de rebrotar después de que su biomasa fue removida por herbívoros o por el fuego. Los mecanismos no fueron estudiados; sin embargo, los componentes anatómicos de la madera del tallo descritos y discutidos en los capítulos 4, 5 y 6 pueden ser la base para futuros estudios. Con base en los resultados de esta tesis, se podrían plantear las siguientes hipótesis: las especies con baja densidad de madera y fibras vivas (p. ej., las dos especies de Cactaceae, *Jacaratia mexicana*, *Bursera simaruba* y la especie de fenología invertida *Bonellia macrocarpa*) podrían constituir un grupo funcional, siendo el almacenamiento de agua en el tallo uno de los mecanismos de evasión de la sequía, como ha sido reportado para otras especies de árboles del BTC (Paz *et al.* 2015), mientras que las especies con contenidos bajos de agua en la madera y con fibras de paredes gruesas con lúmenes reducidos (Capítulos 4 y 6) son tolerantes a la sequía, es decir, son capaces de seguir funcionando con poca agua ambiental.

Los valores de densidad de la madera son el resultado de interacciones complejas entre diferentes variables que caracterizan este tejido (Ziemińska *et al.* 2013). Por lo tanto, antes de seguir utilizando a la densidad de madera como un atributo funcional que nos permite predecir el desempeño ecológico de ciertas especies en un sistema particular, sería conveniente considerar las variables que influyen en los valores de dicha densidad, por ejemplo los depósitos celulares y las inclusiones minerales (Capítulo 4), así como algunas características anatómicas que, en sí, podrían ser atributos funcionales (p. ej., la proporción del área del tallo que ocupan el parénquima, las fibras vivas y los vasos).

Las características anatómicas altamente variables de los vasos, así como las distintas combinaciones de arreglos y tipos celulares en el xilema del tallo podrían ser clave para avanzar en el entendimiento del desempeño ecológico diferencial de las especies (medido a través del área basal) observado a lo largo del gradiente sucesional. El tejido del tallo leñoso de estas especies tropicales parece ser complejo y multifuncional, por lo que se recomienda tomar esto en cuenta al evaluar, en estudios futuros, la relación entre sus características anatómicas, las funciones asociadas en la literatura y su desempeño ecológico.

REFERENCIAS

- Ackerly, D. 2004. Functional strategies of chaparral shrubs in relation to seasonal water deficit and disturbance. *Ecological Monographs*, **74**: 25-44.
- Álvarez-Yépez, J. C., Martínez-Yrizar, A., Búrquez, A. y Lindquist, C. 2008. Variation in vegetation structure and soil properties related to land use history of old-growth and secondary tropical dry forests in northwestern Mexico. *Forest Ecology and Management*, **256**: 355-366.
- Apgaua, D.M.G., Ishida, F.o.Y., Tng, D.Y.P., Laidlaw, M.J., Santos, R.M., Rumman, R., Eamus, D., Holtum, J.A.M., Laurance, S.G.W. 2015. Functional traits and water transport strategies in lowland tropical rainforest trees. *PloS one*, **10**: e0130799.
- Apgaua, D.M.G., Tng, D.Y.P., Cernusak, L.A., Cheesman, A.W., Santos, R.M., Edwards, W.J., Laurance, S.G.W. 2017. Plant functional groups within a tropical forest exhibit different wood functional anatomy. *Functional Ecology*, **31**: 582-591.
- Baas, P., Beeckman, H., Čufar, K., Micco, V.D. 2016. Functional traits in wood anatomy. *IAWA Journal* **37**: 124-126.
- Bazzaz, E.A., Pickett, S.T.A. 1980. Physiological ecology of tropical succession: a comparative review. *Annual Review of Ecology and Systematics* **11**: 287-310.
- Brown, S. y Lugo, A. E. 1990. Tropical secondary forests. *Journal of Tropical Ecology*, **6**: 1-32.
- Carlquist, S. 1977. Ecological factors in wood evolution: A floristic approach. *American Journal of Botany*, **64**: 887-896.
- Carlquist, S. 1980. Further concepts in ecological wood anatomy, with comments on recent work in wood anatomy and evolution. *Aliso*, **9**: 499-553.
- Carlquist, S. 2001. Comparative wood anatomy: Systematic, ecological, and evolutionary aspects of dicotyledon wood. Springer Science y Business Media.
- Carlquist, S. 2009. Non-random vessel distribution in woods: patterns, modes, diversity, correlations. *Aliso: A Journal of Systematic and Evolutionary Botany*, **27**: 39-58.
- Carlquist, S. 2015. Living cells in wood. 1. Absence, scarcity and histology of axial parenchyma as keys to function. *Botanical Journal of the Linnean Society*, **177**: 291-321.
- Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G. y Zanne, A.E. 2009. Towards a worldwide wood economics spectrum. *Ecology Letters*, **12**: 351-366.

- Chazdon, R. L., Finegan, B., Capers, R. S., Salgado-Negret, B., Casanoves, F., Boukili, V. y Norden, N. 2010. Composition and dynamics of functional groups of trees during tropical forest succession in northeastern costa rica. *Biotropica*, **42**: 31-40.
- Chazdon, R. L., Harvey, C. A., Martínez-Ramos, M., Balvanera, P., Stoner, K. E., Schondube, J. E., Avila-Cabadilla, L. D. y Flores-Hidalgo, M. 2011. Seasonally dry tropical forest biodiversity and conservation value in agricultural landscapes of Mesoamerica. Ecology and conservation of neotropical dry forests (eds R. Dirzo, H. A. Mooney, G. Ceballos y H. Young), pp. 195-219. Island Press, Washington, D.C.
- Cochard, H. 2006. Cavitation in trees. *Comptes Rendus Physique*, **7**: 1018-1026.
- Cornwell, W. K., Schwilk, D. W. y Ackerly, D. D. 2006. A trait-based test for habitat filtering: convex hull volume. *Ecology*, **87**: 1465-1471.
- Connell, J.H. y Slatyer, R.O. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist*, **111**, 1119-1144.
- Craven, D., Hall, J. S., Ashton, M. S. y Berlyn, G. P. 2013. Water-use efficiency and whole-plant performance of nine tropical tree species at two sites with contrasting water availability in panama. *Trees*, **27**: 639-653.
- Cruiziat, P., Cochard, H. y Améglio, T. 2002. Hydraulic architecture of trees: Main concepts and results. *Annals of Forest Science*, **59**: 723-752.
- De Micco, V., y Aronne, G. 2012. Morpho-anatomical traits for plant adaptation to drought. In Plant Responses to Drought Stress: From Morphological to Molecular Features. pp. 37–61. Springer-Verlag Berlin Heidelberg.
- Derroire, G., Balvanera, P., Castellanos-Castro, C., Decocq, G., Kennard, D.K., Lebrija-Trejos, E., Leiva, J.A., Odén, P.-C., Powers, J.S., Rico-Grey, V., Tigabu, M. y Healey, J.R. 2016. Resilience of tropical dry forests – a meta-analysis of changes in species diversity and composition during secondary succession. *Oikos*, **125**: 1386-1397.
- Dupuy, J. M., Hernández-Stefanoni, J. L., Hernández-Juárez, R. A., Tetetla-Rangel, E., López-Martínez, J. O., Leyequién-Abarca, E., Tun-Dzul, F. J. y May-Pat, F. 2012. Patterns and correlates of tropical dry forest structure and composition in a highly replicated chronosequence in Yucatan, Mexico. *Biotropica*, **44**: 151-162.
- Durante, M., Maseda, P. H. y Fernández, R. J. 2011. Xylem efficiency vs. Safety: Acclimation to drought

- of seedling root anatomy for six patagonian shrub species. *Journal of Arid Environments*, **75**: 397-402.
- Enriquez-Vargas, M.A. *en prep.* Dinámica sucesional del sotobosque de un bosque tropical caducifolio en Nizanda, Oaxaca, México. Tesis de Licenciatura, Universidad Nacional Autónoma de México, Coyoacán, Ciudad de México., México.
- Ewers, F. W., Ewers, J. M., Jacobsen, A. L. y López-Portillo, J. 2007. Vessel redundancy: Modeling safety in numbers. *IAWA Journal*, **28**: 373-388.
- Finegan, B. 1996. Pattern and process in neotropical secondary rain forests: The first 100 years of succession. *Trends in Ecology and Evolution*, **11**: 119-124.
- Garnier, E., Cortez, J., Billès, G., Navas, M.-L., Roumet, C., Debussche, M., Laurent, G., Blanchard, A., Aubry, D., Bellmann, A., Neill, C. y Toussaint, J.-P. 2004. Plant functional markers capture ecosystem properties during secondary succession. *Ecology*, **85**: 2630-2637.
- Gerhardt, K. y Hytteborn, H. 1992. Natural dynamics and regeneration methods in tropical dry forests - an introduction. *Journal of Vegetation Science*, **3**: 361-364.
- Gillespie, T.W., Grijalva, A. y Farris, C.N. 2000. Diversity, composition, and structure of tropical dry forests in Central America. *Plant Ecology*, **147**: 37-47.
- Guariguata, M. R. y Ostertag, R. 2001. Neotropical secondary forest succession: Changes in structural and functional characteristics. *Forest Ecology and Management*, **148**: 185-206.
- Hacke, U.G., Sperry, J.S., Pockman, W.T., Davis, S.D. y McCulloh, K.A. 2001. Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia*, **126**: 457-461.
- Hoeber, S., Leuschner, C., Köler, L., Arias-Aguilar, D. y Schuldt, B. 2014. The importance of hydraulic conductivity and wood density to growth performance in eight tree species from a tropical semi-dry climate. *Forest Ecology and Management*, **330**: 126-136.
- Holbrook, N. M., Whitebeck, J. L. y Mooney, H. A. 1995. Drought responses of neotropical dry forest trees. *En: Bullock, S. H., Mooney, H. A. y Medina, E. (Eds). Seasonally dry tropical forests.* Cambridge University Press, Cambridge, UK, 243-? pp.
- Keddy, P.A. 1992a. Assembly and response rules: two goals for predictive community ecology. *Journal of Vegetation Science*, **3**: 157-164.
- Keddy, P.A. 1992b. A pragmatic approach to functional ecology. *Functional Ecology*, **6**, 621-626

- Larjavaara, M., y Muller-Landau, H.C. 2010. Rethinking the value of high wood density. *Funct. Ecol.*, **24**: 701-705.
- Lavorel, S., Díaz, S., Cornelissen, J. H. C., Garnier, E., Harrison, S. P., McIntyre, S., ... y Urcelay, C. 2007. Plant functional types: are we getting any closer to the Holy Grail?. *En: Canadell, J. G., Pataki, D. y Pitelka, L. (Eds). Terrestrial ecosystems in a changing world. Springer, Berlin, Heidelberg. Pp. 149-164.*
- Lebrija-Trejos, E., Bongers, F., Pérez-García, E. A. y Meave, J. A. 2008. Successional change and resilience of a very dry tropical deciduous forest following shifting agriculture. *Biotropica*, **40**: 422-431.
- Lebrija-Trejos, E., Meave, J.A., Poorter, L., Pérez-García, E.A. y Bongers, F. 2010a. Pathways, mechanisms and variability of tropical dry forest succession. *Perspect. Plant Ecol. Evol. Syst.*, **12**: 267-275.
- Lebrija-Trejos, E., Pérez-García, E. A., Meave, J.A., Bongers, F. y Poorter, L. 2010b. Functional traits and environmental filtering drive community assembly species-rich tropical system. *Ecology*, **91**: 386-398.
- Lebrija-Trejos, E., Pérez-García, E. A., Meave, J. A., Poorter, L. y Bongers, F. 2011. Environmental changes during secondary succession in a tropical dry forest in southern Mexico. *J. Trop. Ecol.*, **27**: 477-489.
- Lens, F., Sperry, J.S., Christman, M.A., Choat, B., Rabaey, D. y Jansen, S. 2011. Testing hypotheses that link wood anatomy to cavitation resistance and hydraulic conductivity in the genus *Acer*. *New Phytologist*, **190**, 709-723.
- Lens, F., Tixier, A., Cochard, H., Sperry, J.S., Jansen, S. y Herbette, S. 2013. Embolism resistance as a key mechanism to understand adaptive plant strategies. *Curr. Opin. Plant Biol.*, **16**: 287-292.
- Levitt, J. 1980. Responses of Plants to Environmental Stresses. Academic Press
- Lohbeck, M., Poorter, L., Martínez-Ramos, M., Rodríguez-Velázquez, J., van Breugel, M. y Bongers, F. 2014. Changing drivers of species dominance during tropical forest succession. *Functional Ecology*, **28**: 1052-1058.
- Lopez, O. R., Kursar, T. A., Cochard, H. y Tyree, M. T. 2005. Interspecific variation in xylem vulnerability to cavitation among tropical tree and shrub species. *Tree Physiology*, **25**: 1553-1562.
- Maldonado-Romo, A. F. 2014. Fenología foliar y reproductiva de la comunidad arbórea del bosque tropical caducifolio en Nizanda, Oaxaca, México. Tesis de Licenciatura, Universidad Nacional

Autónoma de México, México, D.F., México.

- Madeira, B. G., Espírito-Santo, M. M., Neto, S. D. Â., Nunes, Y. R. F., Arturo Sánchez Azofeifa, G., Wilson Fernandes, G. y Quesada, M. 2009. Changes in tree and liana communities along a successional gradient in a tropical dry forest in south-eastern Brazil. *Plant Ecology*, **201**: 291-304.
- Martínez-Yrizar A., Sarukhán J., Pérez-Jiménez A., Rincón E., Maass J.M., Solís-Magallanes A., Cervantes L. 1992. Above-ground phytomass of a tropical deciduous forest on the coast of Jalisco, México. *Journal of Tropical Ecology*, **8**: 87-96.
- Méndez-Alonzo, R., Pineda-García, F., Paz, H., Rosell, J. A. y Olson, M. E. 2013. Leaf phenology is associated with soil water availability and xylem traits in a tropical dry forest. *Trees*, **27**: 745-754.
- McDowell, N., Pockman, W. T., Allen, C. D., Breshears, D. D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A., Williams, D. G., y Yepez, E. A. (2008). Mechanisms of plant survival and mortality during drought: Why do some plants survive while others succumb to drought? *New Phytologist*, **178**: 719–739.
- Mooney, H. A., Bullock, S. H. y Medina, E. 1995. Introduction. En: Bullock, S. H., Mooney, H. A. y Medina, E. (Eds). *Seasonally dry tropical forests*. Cambridge University Press, Cambridge, UK, 1-8 pp.
- Mora, F., Martínez-Ramos, M., Ibarra-Manríquez, G., Pérez-Jiménez, A., Trilleras, J. y Balvanera, P. 2015. Testing chronosequences through dynamic approaches: Time and site effects on tropical dry forest succession. *Biotropica*, **47**: 38-48.
- Morris, H., Plavcová, L., Cvecko, P., Fichtler, E., Gillingham, M. A. F., Martínez-Cabrera, H. I., McGlenn, D. J., Wheeler, E., Zheng, J., Ziemińska, K. y Jansen, S. C. 2016. A global analysis of parenchyma tissue fractions in secondary xylem of seed plants. *New Phytologist*, **209**: 1553–1565.
- Muñoz-Avilés, R. 2015. Dinámica de la estructura y la diversidad de un bosque tropical caducifolio del Istmo de Tehuantepec, Oaxaca, México. Tesis de Licenciatura, Universidad Nacional Autónoma de México, México, D.F., México.
- Murphy, P. G. y Lugo, A. E. 1995. Dry forests of Central America and the Caribbean. En S. H. Bullock, H. A. Mooney y E. Medina (Eds), *Seasonally dry tropical forests* (pp. 9-33). Cambridge, UK: Cambridge University Press.
- Osunkoya, O. O., Sheng, T. K., Mahmud, N. y Damit, N. 2007. Variation in wood density, wood water content, stem growth and mortality among twenty-seven tree species in a tropical rainforest on Borneo Island. *Austral Ecology*, **32**: 191-201.

- Panshin, A.J. y Zeeuw, C.d. 1980. Textbook of wood technology. McGraw-Hill, Inc., New York.
- Paz H., Pineda-García F., Pinzón-Pérez L.F. 2015. Root depth and morphology in response to soil drought: comparing ecological groups along the secondary succession in a tropical dry forest. *Oecologia*, **179**: 551-561.
- Pérez-García, E.A., Meave, J. y Gallardo, C. 2001. Vegetación y flora de la región de Nizanda, Istmo de Tehuantepec, Oaxaca, México. *Acta Botanica Mexicana*, **56**, 19-88
- Pérez-García, E.A., Meave, J.A., Villaseñor, J.L., Gallardo-Cruz, J.A. y Lebrija-Trejos, E. (2010) Vegetation heterogeneity and life-strategy diversity in the flora of the heterogeneous landscape of Nizanda, Oaxaca, México. *Folia Geobotanica*, **45**, 143-161.
- Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M.S., Cornwell, W.K., Craine, J.M., Gurvich, D.E., Urcelay, C., Veneklaas, E.J., Reich, P.B., Poorter, L., Wright, I.J., Ray, P., Enrico, L., Pausas, J.G., de Vos, A.C., Buchmann, N., Funes, G., Quátier, F., Hodgson, J.G., Thompson, K., Morgan, H.D., ter Steege, H., van der Heijden, M.G.A., Sack, L., Blonder, B., Poschlod, P., Vaieretti, M.V., Conti, G., Staver, A.C., Aquino, S. y Cornelissen, J.H.C. (2013) New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany*, **61**, 167-234.
- Pickett, S.T.A. 1976. Succession: An evolutionary interpretation. *Am. Nat.*, **110**: 107-119.
- Pineda-García, F., Paz, H. y Meinzer, F.C. 2013. Drought resistance in early and late secondary successional species from a tropical dry forest: The interplay between xylem resistance to embolism, sapwood water storage and leaf shedding. *Plant Cell Environ.*, **36**: 405-418.
- Pineda-García, F., Paz, H., Meinzer, F. C. y Angeles, G. 2015. Exploiting water versus tolerating drought: Water-use strategies of trees in a secondary successional tropical dry forest. *Tree Physiology*.
- Poorter, L., McDonald, I., Alarcón, A., Fichtler, E., Licona, J.C., Peña-Claros, M., Sterck, F., Villegas, Z. y Sass-Klaassen, U. 2010. The importance of wood traits and hydraulic conductance for the performance and life history strategies of 42 rainforest tree species. *New Phytol.*, **185**: 481-492.
- Poorter, L., Wright, S. J., Paz, H., Ackerly, D. D., Condit, R., Ibarra-Manríquez, G., Harms, K. E., Licona, J. C., Martínez-Ramos, M., Mazer, S. J., Muller-Landau, H. C., Peña-Claros, M., Webb, C. O. y Wright, I. J. 2008. Are functional traits good predictors of demographic rates? Evidence from five neotropical forests. *Ecology*, **89**: 1908-1920.
- Poorter, L., Rozendaal, D. M., Bongers, F., de Almeida-Cortez, J. S., Zambrano, A. M. A., Álvarez, F. S., ...

- y Bentos, T. V. 2019. Wet and dry tropical forests show opposite successional pathways in wood density but converge over time. *Nature ecology y evolution*, **3**: 928-934.
- Pratt, R. B., Jacobsen, A. L., Ewers, F. W. y Davis, S. D. 2007. Relationships among xylem transport, biomechanics and storage in stems and roots of nine Rhamnaceae species of the California chaparral. *New Phytologist*, **174**: 787-798.
- Preston, K. A., Cornwell, W. K. y DeNoyer, J. L. 2006. Wood density and vessel traits as distinct correlates of ecological strategy in 51 California coast range angiosperms. *New Phytologist*, **170**: 807-818.
- Quesada, M., Sanchez-Azofeifa, G.A., Alvarez-Añorve, M., Stoner, K.E., Avila-Cabadilla, L., Calvo-Alvarado, Castillo, A., Espírito-Santo, M.M., Fagundes, M., Fernandes, G.W., Gamon, J., Lopezaraiza-Mikel, M., Lawrence, D., Morellato, L.P.C., Powers, J.S., Neves, F.S., Rosas-Guerrero, V., Sayago, R. y Sanchez-Montoya, G. 2009. Succession and management of tropical dry forests in the Americas: Review and new perspectives. *Forest Ecology and Management*, **258**: 1014-1024.
- Romero-Duque, L. P., Jaramillo, V. J. y Pérez-Jiménez, A. 2007. Structure and diversity of secondary tropical dry forests in Mexico, differing in their prior land-use history. *Forest Ecology and Management*, **253**: 38-47.
- Romero-Pérez, I.E. 2014. Atributos funcionales y desempeño de especies arbóreas durante la sucesión secundaria de un bosque tropical caducifolio. Tesis de Maestría, Universidad Nacional Autónoma de México, México D.F.
- Ruiz, J., Fandiño, M.C. y Chazdon, R.L. 2005. Vegetation structure, composition, and species richness across a 56-year chronosequence of dry tropical forest on Providencia Island, Colombia. *Biotropica*, **37**, 520-530.
- Rzedowski, J. 1978. Vegetación de México. Limusa, México, D.F.
- Schönbeck, L., Lohbeck, M., Bongers, F., Ramos, M. M. y Sterck, F. 2015. How do light and water acquisition strategies affect species selection during secondary succession in moist tropical forests? *Forests*, **6**: 2047-2065.
- Segala-Alves, E. y Angyalossy-Alfonso, V. 2002. Ecological trends in the wood anatomy of some Brazilian species. 2. Axial parenchyma, rays and fibers. *IAWA Journal*, **23**: 391-418.
- Selaya, N.G., Oomen, R.J., Netten, J.J.C., Werger, M.J.A. y Niels, P.R.A. 2008. Biomass allocation and leaf life span in relation to light interception by tropical forest plants during the first years of secondary succession. *Journal of Ecology*, **96**: 1211-1221.

- SPP (Secretaría de Programación y Presupuesto). 1981. Atlas Nacional del Medio Físico. México, D.F.
- Trejo, I. y Dirzo, R. 2000. Deforestation of seasonally dry tropical forest: A national and local analysis in Mexico. *Biological Conservation*, **94**: 133-142.
- Trifilò, P., Barbera, P. M., Raimondo, F., Nardini, A. y Gullo, M. A. L. 2014. Coping with drought-induced xylem cavitation: Coordination of embolism repair and ionic effects in three Mediterranean evergreens. *Tree Physiology*, **34**: 109-122.
- Tyree, M. T., Davis, S. D. y Cochard, H. 1994. Biophysical perspectives of xylem evolution: is there a tradeoff of hydraulic efficiency for vulnerability to dysfunction? *IAWA Journal*, **15**: 335–360.
- Tyree, M. T. y Zimmermann, M. H., 2002. Xylem Structure and the Ascent of Sap. New York: Springer-Verlag.
- Vieira, D.L.M. y Scariot, A. 2006. Principles of natural regeneration of tropical dry forests for restoration. *Restoration Ecology*, **14**, 11–20.
- Violle, C., Navas, M. L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. y Garnier, E. 2007. Let the concept of trait be functional! *Oikos*, **116**: 882-892.
- Westoby, M., Falster, D.S., Moles, A.T., Vesk, P.A. y Wright, I.J. 2002. Plant ecological strategies: some leading dimensions of variation between species. *Annual Review of Ecology and Systematics*, **33**, 125-159.
- Yamada, Y., Awano, T., Fujita, M. y Takabe, K. 2011. Living wood fibres act as large-capacity “single-use” starch storage in black locust (*Robinia pseudoacacia*). *Trees*, **25**: 607–616.
- Ziemińska, K., Butler, D.W., Gleason, S.M., Wright, I.J. y Westoby, M. 2013. Fibre wall and lumen fractions drive wood density variation across 24 Australian angiosperms. *AoB Plants*, **5**: 1-14.
- Zimmermann, M. H. 1983. Xylem structure and the ascent of sap. Springer-Verlag, New York.
- Zimmermann O. L., Uller, H. F., Klitzke, A. R., Eleotério, J. R. y Vibrans, A. C. 2019. Towards the Fulfillment of a Knowledge Gap: Wood Densities for Species of the Subtropical Atlantic Forest. *Data*, **4**: 104.

ANEXOS

ANEXOS Capítulo 2

Differential performance of 50 canopy tree species through tropical dry forest succession

Supporting Information 1

Table S1. List of species included in the study, along with their family affiliation and acronyms.

Table S2. Models for presence/absence (PA) and basal area (BA) responses to successional age for 50 species of a tropical dry forest.

Table S3. Range of age presence (years of abandonment) in the successional gradient of the 50 species included in the study, the number of plot-age combinations in which they are present (plot-age frequency), and their corresponding ranks.

Figure S1. Diagrams depicting model construction and selection for presence/absence (PA) data. (a) Construction of the PA0 model. (b) Construction of the PA1 model. (c) Model comparison and selection.

Figure S2. Diagrams depicting the model construction and selection for basal area (BA) data. (a) Construction of the BA0 model. (b) Construction of the BA1 model. (c) Model comparison and selection.

Table S1. List of species included in the study, along with their familial affiliation and acronyms. Species names are in agreement with The Plant List (www.theplantlist.org, last accessed on July 28, 2017).

Acronym	Species	Family
ACCO	<i>Acacia cochliacantha</i> Willd.	Leguminosae
ACFA	<i>Acacia farnesiana</i> (L.) Willd.	Leguminosae
ACPI	<i>Acacia picachensis</i> Brandegee	Leguminosae
AECO	<i>Aeschynomene compacta</i> Rose	Leguminosae
AMSI	<i>Amphipterygium simplicifolium</i> (Standl.) Cuevas-Figueroa	Anacardiaceae
APPA	<i>Apoplanesia paniculata</i> C.Presl	Leguminosae
BOMA	<i>Bonellia macrocarpa</i> (Cav.) B.Ståhl & Källersj	Primulaceae
BUEX	<i>Bursera excelsa</i> (Kunth) Engl.	Burseraceae
BUSI	<i>Bursera simaruba</i> (L.) Sarg.	Burseraceae
CAIN	<i>Caesalpinia platyloba</i> S.Watson	Leguminosae
CAOV	<i>Quadrella incana</i> (Kunth) Iltis & Cornejo	Capparaceae
CAPL	<i>Cascabela ovata</i> (Cav.) Lippold	Apocynaceae
CATR	<i>Casearia tremula</i> (Griseb.) Griseb. ex C.Wright	Salicaceae
CEPA	<i>Ceiba aesculifolia</i> (Kunth) Britten & Baker f. subsp. <i>parvifolia</i> (Rose) P.E.Gibbs & Semir	Malvaceae
CHMA	<i>Chloroleucon mangense</i> (Jacq.) Britton & Rose	Leguminosae
CNME	<i>Cnidocolus megacanthus</i> (Jacq.) Britton & Rose	Euphorbiaceae
CODE	<i>Cordia dentata</i> Poir.	Boraginaceae
COLI	<i>Coccoloba liebmannii</i> Lindau	Polygonaceae
CRNI	<i>Croton niveus</i> Jacq.	Euphorbiaceae
EUSC	<i>Euphorbia schlechtendalii</i> Boiss.	Euphorbiaceae
EXCA	<i>Exostema caribaeum</i> (Jacq.) Schult.	Rubiaceae
FOPA	<i>Forchhammeria pallida</i> Liebm.	Capparaceae
GYMO	<i>Gyrocarpus mocinoi</i> Espejo	Hernandiaceae
HACA	<i>Havardia campylacantha</i> (L. Rico & M. Sousa) Barneby & J.W. Grimes	Leguminosae
HAIM	<i>Handroanthus impetiginosus</i> (Mart. ex DC.) Mattos	Bignoniaceae
HEPA	<i>Heliocarpus pallidus</i> Rose	Malvaceae
INLA	<i>Indigofera lancifolia</i> Rydb.	Leguminosae
JAME	<i>Jacaratia mexicana</i> A.DC.	Caricaceae
JAAL	<i>Jatropha alamanii</i> Müll.Arg.	Euphorbiaceae
LELA	<i>Leucaena lanceolata</i> S.Watson	Leguminosae
LOLA	<i>Lonchocarpus lanceolatus</i> Benth.	Leguminosae
LOTO	<i>Lonchocarpus torresiorum</i> M. Sousa	Leguminosae
LYDI	<i>Lysiloma divaricatum</i> (Jacq.) J.F.Macbr.	Leguminosae
MAEM	<i>Malpighia emarginata</i> DC.	Malpighiaceae

Table S1. *Continued.* List of species included in the study, along with their familial affiliation and acronyms. Species names are in agreement with The Plant List (www.theplantlist.org, last accessed on July 28, 2017).

Acronym	Species	Family
MAOX	<i>Manihot oaxacana</i> D.J.Rogers & Appan	Euphorbiaceae
MIAC	<i>Mimosa eurycarpa</i> Robinson	Leguminosae
MIGO	<i>Mimosa goldmanii</i> Robinson	Leguminosae
MITE	<i>Mimosa tenuiflora</i> (Willd.) Poir.	Leguminosae
MYFR	<i>Myrospermum frutescens</i> (Willd.) Poir.	Leguminosae
PAPE	<i>Pachycereus pecten-aboriginum</i> (Engelm. ex S.Watson) Britton & Rose	Cactaceae
PHRA	<i>Phyllostylon rhamnoides</i> (J.Poiss.) Taub.	Ulmaceae
PICO	<i>Pilosocereus collinsii</i> (Britton & Rose) Byles & G.D. Rowley	Cactaceae
RATH	<i>Randia thurberi</i> S.Watson	Rubiaceae
SEAT	<i>Senna atomaria</i> (L.) H.S.Irwin & Barneby	Leguminosae
SEHO	<i>Senna holwayana</i> (Rose) H.S.Irwin & Barneby	Leguminosae
TAOD	<i>Tabernaemontana odontadeniiflora</i> A.O.Simões & M.E.Endress	Apocynaceae
THDE	<i>Thouinidium decandrum</i> (Humb. & Bonpl.) Radlk.	Sapindaceae
THVI	<i>Thouinia villosa</i> DC.	Sapindaceae
SCSC	<i>Schoepfia schreberi</i> J.F.Gmel.	Schoepfiaceae
ZACA	<i>Zanthoxylum caribaeum</i> Lam.	Rutaceae

Table S2. Models for presence/absence (PA) and basal area (BA) responses to successional age for 50 successional species of the tropical dry forest. Φ : temporal autocorrelation estimate for the BA models within plots; R^2_c : correlation conditional on the plot between observed BA values and estimated BA values from the composite model. An asterisk (*) indicates those models for which no AICc could be estimated. NA = not available. Composite model results from the product of the best PA and the best BA model. Model types: GLM, generalized linear mixed models; GAMM, Generalized additive mixed models; logistf, Firth's bias reduced logistic regression; numeric, null model with constant value of 1; GAM, generalized additive model. MIEUwt: *M. eurycarpa* without *M. tenuiflora* plots. MITEwt: *M. tenuiflora* without *M. eurycarpa* plots.

Species	Model construction				Model selection					R^2_c Composite model			
	PA0	PA1	BA0	BA1	Δ AICc PA	Δ AICc BA	Best PA model	Best BA model	Φ	PA0 x BA0	PA0 x BA1	PA1 x BA0	PA1 x BA1
<i>Acacia cochliacantha</i>	GLM	GLM	GAMM	GAMM	41.39	3.61	PA1	BA0 \leq BA1	0.35	-	-	0.42	0.77
<i>Acacia farnesiana</i>	numeric	logistf	GAMM	GAMM	NA	1.74	*PA1	BA0 \leq BA1	0.10	0.38	0.88	0.44	0.87
<i>Acacia picachensis</i>	numeric	logistf	GAMM	GAMM	NA	52.24	*PA1	BA1	0.26	-	0.93	-	0.92
<i>Aeschynomene compacta</i>	GLM	GLM	GAMM	GAMM	22.53	14.27	PA1	BA1	-0.07	-	-	-	0.83
<i>Amphipterygium simplicifolium</i>	numeric	logistf	GAMM	GAMM	NA	27.78	*PA1	BA1	0.47	-	0.98	-	0.97
<i>Apoplanesia paniculata</i>	numeric	logistf	GAMM	GAMM	NA	9.59	*PA1	BA1 \leq BA0	0.13	0.98	0.99	0.98	0.99
<i>Bonellia macrocarpa</i>	numeric	logistf	GAMM	GAMM	NA	4.07	*PA1	BA0 \leq BA1	-0.03	0.99	0.99	0.99	0.99
<i>Bursera excelsa</i>	numeric	logistf	GAMM	GAMM	NA	2.73	*PA1	BA0 \leq BA1	0.77	0.47	0.93	0.48	0.93
<i>Bursera simaruba</i>	numeric	logistf	GAMM	GAMM	NA	26.40	*PA1	BA1	0.79	-	0.89	-	0.89
<i>Capparis incana</i>	numeric	logistf	GAMM	GAMM	NA	10.62	*PA1	BA1	NA	-	0.85	-	0.89
<i>Cascabela ovata</i>	GAMM	GAMM	GAMM	GAMM	2.43	13.98	PA0 \leq PA1	BA1	0.50	-	0.87	-	0.91
<i>Caesalpinia platyloba</i>	numeric	logistf	GAMM	GAMM	NA	7.91	*PA1	BA1 \leq BA0	-0.54	0.84	0.97	0.84	0.97
<i>Casearia tremula</i>	numeric	numeric	GAMM	GAMM	NA	1.48	*PA1	BA1 \leq BA0	-0.37	0.99	0.99	0.99	0.99
<i>Ceiba parvifolia</i>	GLM	GLM	GAMM	GAMM	6.98	18.29	PA1 \leq PA0	BA0	0.20	NA	-	0.30	-
<i>Chloroleucon mangense</i>	numeric	logistf	GAM	GAM	NA	19.05	*PA1	BA1	NA	-	0.54	-	0.74
<i>Cnidocolus megacanthus</i>	GAMM	GAMM	GAMM	GAMM	4.33	13.55	PA1 \leq PA0	BA0	-0.11	0.49	-	0.43	-
<i>Cordia dentata</i>	GLM	GLM	GAMM	GAMM	2.59	10.48	PA1 \leq PA0	BA0	-0.02	0.97	-	0.97	-
<i>Coccoloba liebmannii</i>	numeric	logistf	GAMM	GAMM	NA	31.29	*PA1	BA1	0.16	-	0.95	-	0.88
<i>Croton niveus</i>	GLM	GLM	GAMM	GAMM	14.92	10.18	PA1	BA0	0.19	-	-	0.84	-

Table S2. Continued

Species	Model construction				Model selection					R^2_c Composite model			
	PA0	PA1	AB0	BA1	$\Delta AICc$ PA	$\Delta AICc$ BA	Best PA model	Best BA model	ϕ	PA0 x BA0	PA0 x BA1	PA1 x BA0	PA1 x BA1
<i>Euphorbia schlechtendalii</i>	GLM	GLM	GAMM	GAMM	11.13	19.24	PA1	BA0	NA	-	-	0.48	-
<i>Exostemma caribaeum</i>	numeric	logistf	GAMM	GAMM	NA	20.04	*PA1	BA1	0.10	-	0.90	-	0.89
<i>Forchammeria pallida</i>	numeric	logistf	GAMM	GAMM	NA	17.52	*PA1	BA0	-0.16	0.92	-	0.91	-
<i>Gyrocarpus mocinnoi</i>	GLM	GLM	GAMM	GAMM	3.16	9.13	PA0 ≤ PA1	BA0 ≤ BA1	0.91	0.45	0.81	0.48	0.72
<i>Havardia campylacantha</i>	GLM	GLM	GAMM	GAMM	17.49	1.77	PA1	BA0 ≤ BA1	0.29	-	-	0.67	0.94
<i>Handroanthus impetiginosus</i>	numeric	logistf	GAMM	GAMM	NA	4.16	*PA1	BA0 ≤ BA1	0.39	0.98	0.99	0.98	0.99
<i>Heliolepis pallidus</i>	numeric	logistf	GAMM	GAMM	NA	59.91	*PA1	BA1	0.37	-	0.78	-	0.86
<i>Indigofera lancifolia</i>	numeric	logistf	GAMM	GAMM	NA	1.82	*PA1	BA0 ≤ BA1	NA	0.89	0.99	0.89	0.99
<i>Jatropha alamarii</i>	numeric	numeric	GAMM	GAMM	NA	14.17	*PA1	BA1	-0.8	-	0.74	-	0.70
<i>Jacaratia mexicana</i>	numeric	logistf	GAM	GAM	NA	7.71	*PA1	BA1 ≤ BA0	NA	NA	0.70	0.83	0.92
<i>Leucaena lanceolata</i>	GAMM	GAMM	GAMM	GAMM	0.10	0.35	PA1 ≤ PA0	BA0 ≤ BA1	-0.2	0.97	0.98	0.97	0.99
<i>Lonchocarpus lanceolatus</i>	numeric	logistf	GAMM	GAMM	NA	26.44	*PA1	BA0	0.5	0.89	-	0.79	-
<i>Lonchocarpus torresiorum</i>	numeric	logistf	GAMM	GAMM	NA	6.05	*PA1	BA0 ≤ BA1	-0.59	0.90	0.91	0.90	0.91
<i>Lysiloma divaricatum</i>	numeric	logistf	GAMM	GAMM	NA	64.29	*PA1	BA1	0.47	-	0.84	-	0.85
<i>Malpighia emarginata</i>	numeric	logistf	GAMM	GAMM	NA	27.30	*PA1	BA1	0.19	-	0.99	-	0.99
<i>Manihot oaxacana</i>	GLM	GLM	GAMM	GAMM	4.13	18.88	PA0 ≤ PA1	BA0	NA	0.86	-	0.86	-
<i>Mimosa eurycarpa</i>	numeric	logistf	GAMM	GAMM	NA	25.66	*PA1	BA1	0.23	-	0.90	-	0.90
<i>Mimosa goldmanii</i>	numeric	logistf	GAMM	GAMM	NA	11.20	*PA1	BA1	0.66	-	0.94	-	0.94
<i>Mimosa tenuiflora</i>	numeric	logistf	GAMM	GAMM	NA	30.61	*PA1	BA1	0.52	-	0.64	-	0.64
<i>Myrospermum frutescens</i>	numeric	logistf	GAMM	GAMM	NA	9.34	*PA1	BA0 ≤ BA1	0.35	0.86	0.94	0.88	0.94
<i>Pachycereus pecten-aboriginum</i>	numeric	logistf	GAMM	GAMM	NA	19.29	*PA1	BA0	NA	0.87	-	0.88	-

Table S2. Continued.

Species	Model construction				Model selection					R^2_c Composite model			
	PA0	PA1	BA0	BA1	$\Delta AICc$ PA	$\Delta AICc$ BA	Best PA model	Best BA model	ϕ	PA0 x BA0	PA0 x BA1	PA1 x BA0	PA1 x BA1
<i>Phyllostylon rhamnoides</i>	numeric	logistf	GAMM	GAMM	NA	4.54	*PA1	BA1 \leq BA0	0.52	0.91	0.95	0.92	0.95
<i>Pilosocereus collinsii</i>	numeric	logistf	GAMM	GAMM	NA	43.72	*PA1	BA1	0.28	-	0.96	-	0.96
<i>Randia thurberi</i>	numeric	logistf	GAM	GAM	NA	23.76	*PA1	BA1	NA	-	0.88	-	0.95
<i>Schoepfia schreberi</i>	numeric	numeric	GAM	GAMM	NA	54.80	*PA1	*BA0	-0.83	NA	0.42	NA	0.42
<i>Senna atomaria</i>	GLM	GLM	GAMM	GAMM	12.63	33.66	PA1	BA1	NA	-	-	-	0.75
<i>Senna holwayana</i>	GAMM	GAMM	GAM	GAM	3.16	4.88	PA1 \leq PA0	BA1 \leq BA0	NA	NA	0.25	0.24	0.37
<i>Tabernaemontana odontadeniiflora</i>	numeric	numeric	GAMM	GAMM	NA	17.49	*PA1	BA1	-0.12	-	0.97	-	0.97
<i>Thounidium decandrum</i>	numeric	logistf	GAMM	GAMM	NA	5.62	*PA1	BA1 \leq BA0	-0.47	0.60	0.96	0.52	0.93
<i>Thouinia villosa</i>	numeric	logistf	GAMM	GAMM	NA	12.41	*PA1	BA1	0.16	-	0.98	-	0.97
<i>Zanthoxylum caribaeum</i>	GLM	GLM	GAMM	GAMM	15.81	0.61	PA1	BA1 \leq BA0	-0.11	-	-	0.93	0.97
MIEUw t	numeric	numeric	GAMM	GAMM	NA	39.74	*PA1	BA1	0.89	-	0.86	-	0.86
MITEw t	numeric	numeric	GAMM	GAMM	NA	46.10	*PA1	BA1	0.29	-	0.94	-	0.94

Table S3. Range of age presence (years of abandonment) in the successional gradient of the 50 species included in the study, the number of plot-age combinations in which they are present ($n = 151$), and their corresponding ranks.

Species	Range (years of abandonment)	Plot-age frequency	Frequency rank
<i>Acacia cochliacantha</i>	7 – 57	102	3
<i>Acacia farnesiana</i>	21 – 22	16	35
<i>Acacia picachensis</i>	29 – 50	51	14
<i>Aeschynomene compacta</i>	17 – 70	61	8
<i>Amphipterygium simplicifolium</i>	41 – 61	45	16
<i>Apoplanesia paniculata</i>	35 – 70	54	11
<i>Bonellia macrocarpa</i>	25 – 70	60	9
<i>Bursera excelsa</i>	26 – 70	34	22
<i>Bursera simaruba</i>	26 – 70	52	13
<i>Caesalpinia platyloba</i>	44 – 70	23	30
<i>Cascabela ovata</i>	20 – 46	19	32
<i>Casearia tremula</i>	56 – 70	18	33
<i>Ceiba parvifolia</i>	56 – 61	20	31
<i>Chloroleucon mangense</i>	47 – 50	9	39
<i>Cnidoscolus megacanthus</i>	48 – 70	36	21
<i>Coccoloba liebmannii</i>	34 – 70	82	4
<i>Cordia dentata</i>	18 – 33	16	35
<i>Croton niveus</i>	47 – 61	44	17
<i>Euphorbia schlechtendalii</i>	37 – 61	31	25
<i>Exostemma caribaeum</i>	34 – 39	26	28
<i>Forchammeria pallida</i>	38 – 70	36	21
<i>Gyrocarpus mocinnoi</i>	56 – 70	17	34
<i>Handroanthus impetiginosus</i>	56 – 70	61	8
<i>Havardia campylacantha</i>	29 – 70	53	12
<i>Heliocarpus pallidus</i>	47 – 50	32	24
<i>Indigofera lancifolia</i>	4 – 11	16	35
<i>Jacaratia mexicana</i>	69 – 70	13	36
<i>Jatropha alamanii</i>	56 – 70	18	33
<i>Leucaena lanceolata</i>	21 – 22	25	29

Table S3. Continued.

Species	Range (years of abandonment)	Plot-age frequency	Frequency rank
<i>Lonchocarpus lanceolatus</i>	4 – 70	122	2
<i>Lonchocarpus torresiorum</i>	56 – 70	34	22
<i>Lysiloma divaricatum</i>	34 – 70	75	6
<i>Malpighia emarginata</i>	29 – 61	28	27
<i>Manihot oaxacana</i>	44 – 50	41	18
<i>Mimosa eurycarpa</i>	2 – 61	137	1
<i>Mimosa goldmanii</i>	34 – 70	40	19
<i>Mimosa tenuiflora</i>	3 – 39	79	5
<i>Myrospermum frutescens</i>	56 – 70	37	20
<i>Pachycereus pecten-aboriginum</i>	47 – 70	32	24
<i>Phyllostylon rhamnoides</i>	56 – 70	40	19
<i>Pilosocereus collinsii</i>	41 – 70	48	15
<i>Quadrella incana</i>	15 – 50	75	6
<i>Randia thurberi</i>	48 – 70	12	37
<i>Schoepfia schreberi</i>	47 – 50	11	38
<i>Senna atomaria</i>	26 – 68	68	7
<i>Senna holwayana</i>	34 – 35	29	26
<i>Tabernaemontana odontadeniiflora</i>	41 – 50	34	23
<i>Thouinia villosa</i>	41 – 70	55	10
<i>Thounidium decandrum</i>	14 – 25	17	34
<i>Zanthoxylum caribaeum</i>	49 – 70	26	28

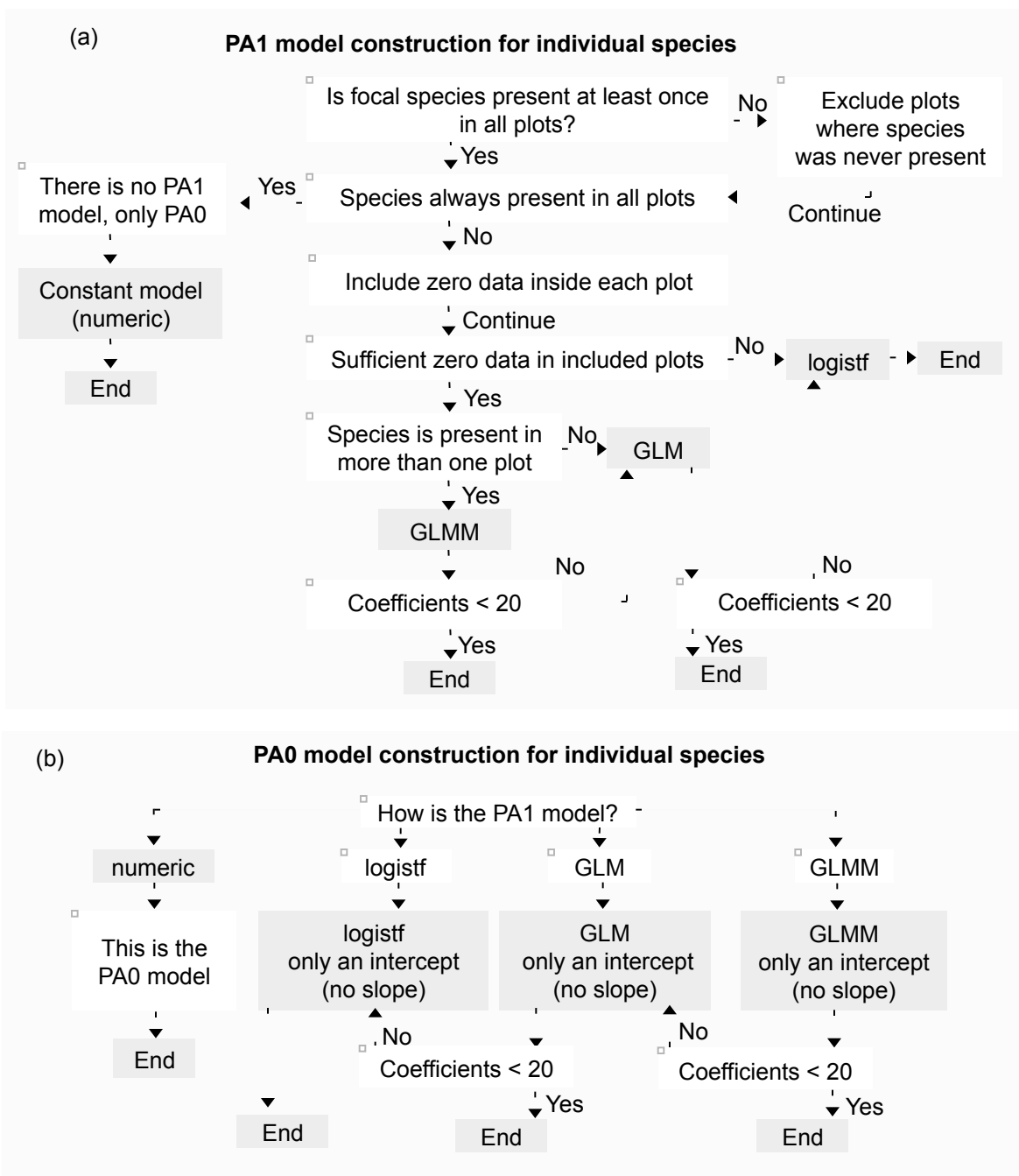


Figure S1. Diagrams depicting the model construction and selection for presence/absence (PA) data. (a) Construction of the PA0 model. (b) Construction of the PA1 model. Model type: numeric, only presence data in those plots where species was recorded; logistf, Firth's bias reduced logistic regression; GLM, generalized linear model; GLMM, generalized linear mixed model. If estimated slope coefficients were > 20 , a logistf model was fitted; for GLMMs, we first attempted to fit a GLM, and proceeded to the logistf model only if the latter was unsuccessful.

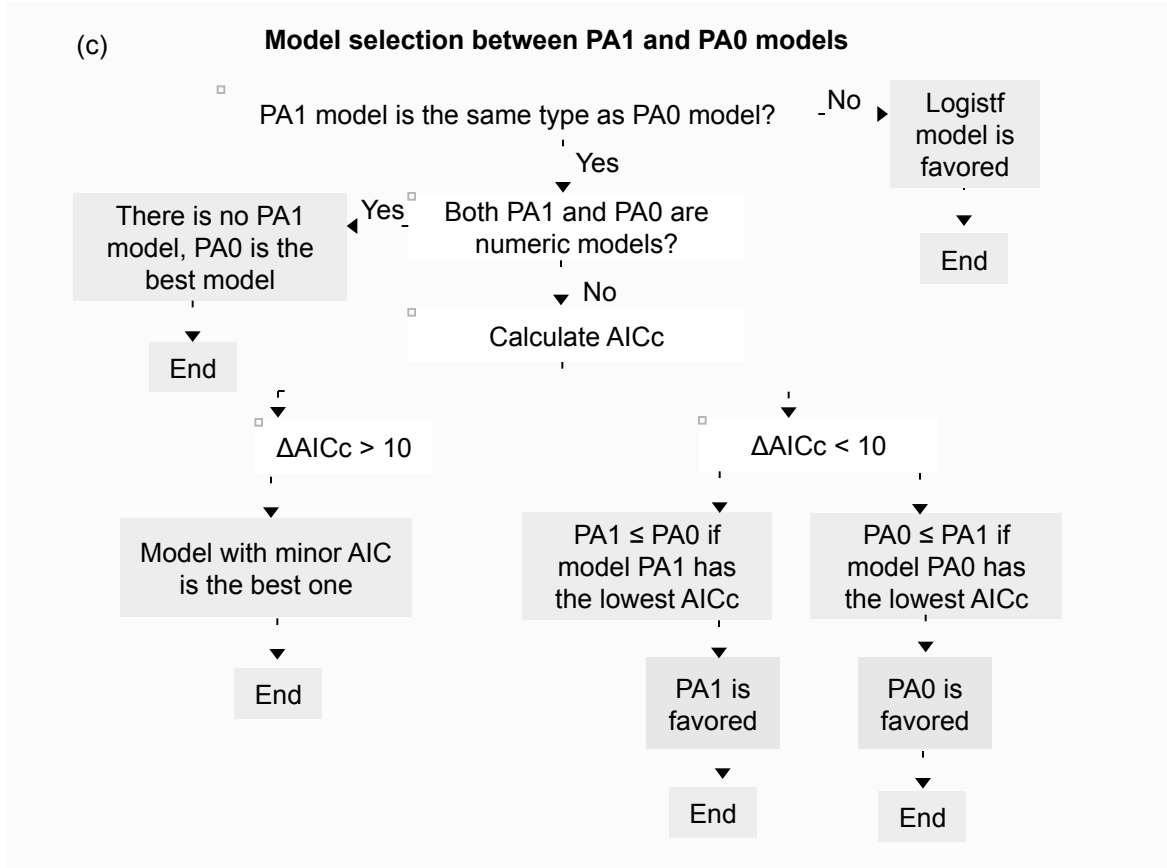


Figure S1. Diagrams depicting the model construction and selection for presence/absence (PA) data. (c) Model comparison and selection. Model type: numeric, only presence data in those plots where species was recorded; logistf, Firth's bias reduced logistic regression; GLM, generalized linear model; GLMM, generalized linear mixed model.

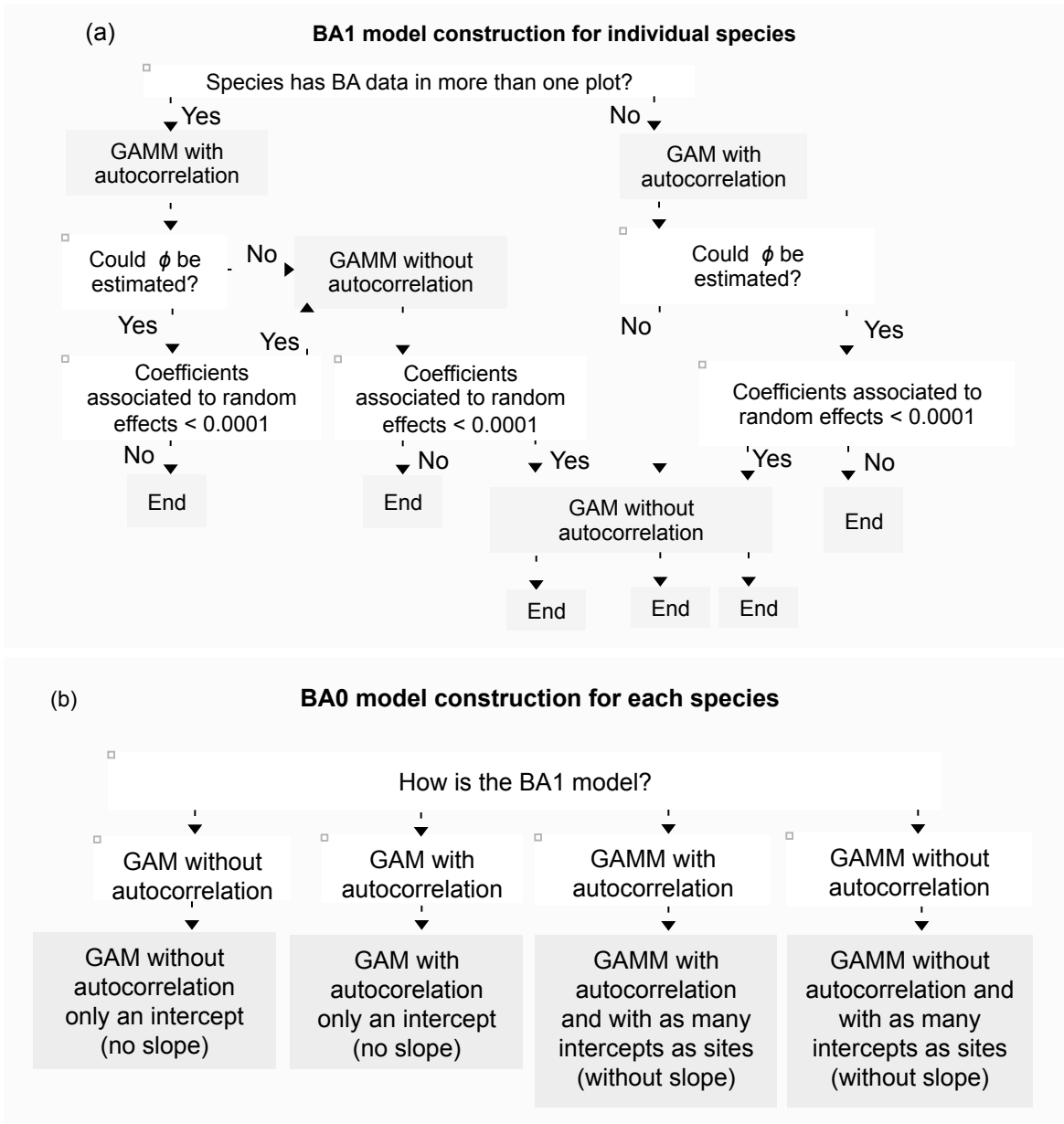


Figure S2. Diagrams depicting the model construction and selection for basal area (BA) data (see main text for explanation). (a) Construction of the BA0 model. (b) Construction of the BA1 model. Model type: GAM, generalized additive model; GAMM, generalized additive mixed model; ϕ : temporal autocorrelation statistic.

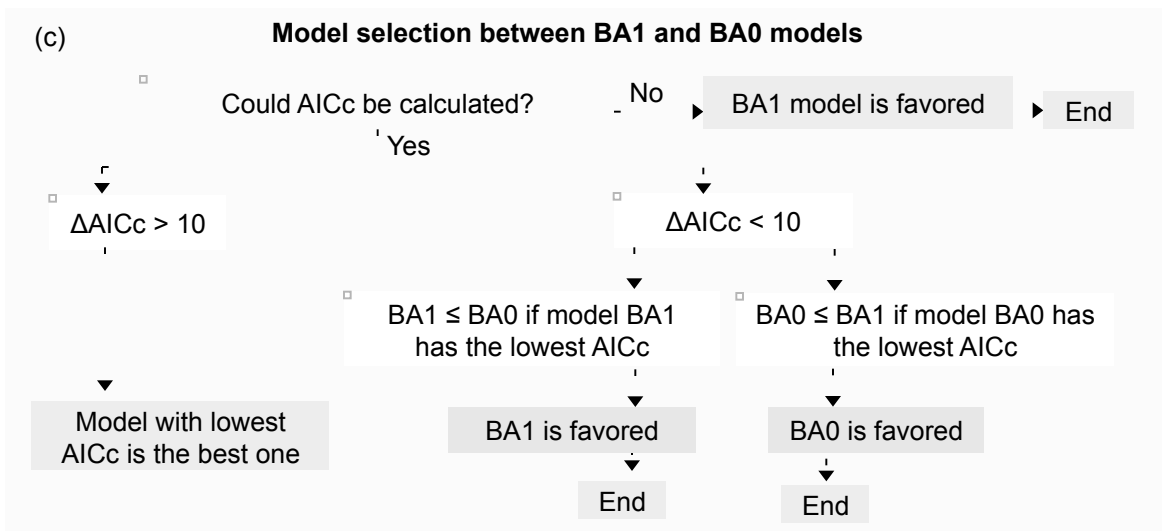


Figure S2. Diagrams depicting the model construction and selection for basal area (BA) data (see main text for explanation). (c) Model comparison and selection. Model type: GAM, generalized additive model; GAMM, generalized additive mixed model; ϕ : temporal autocorrelation statistic. Models can not be compared if BA1 model is not the same type as BA0 model, even though AICc could be estimated; in such cases, model with minor AIC was favored.

ANEXOS Capítulo 2

Differential performance of 50 canopy tree species through tropical dry forest succession

Supporting Information 2

Patterns of basal area changes of canopy tree species during secondary succession in a tropical dry forest in southern Mexico.

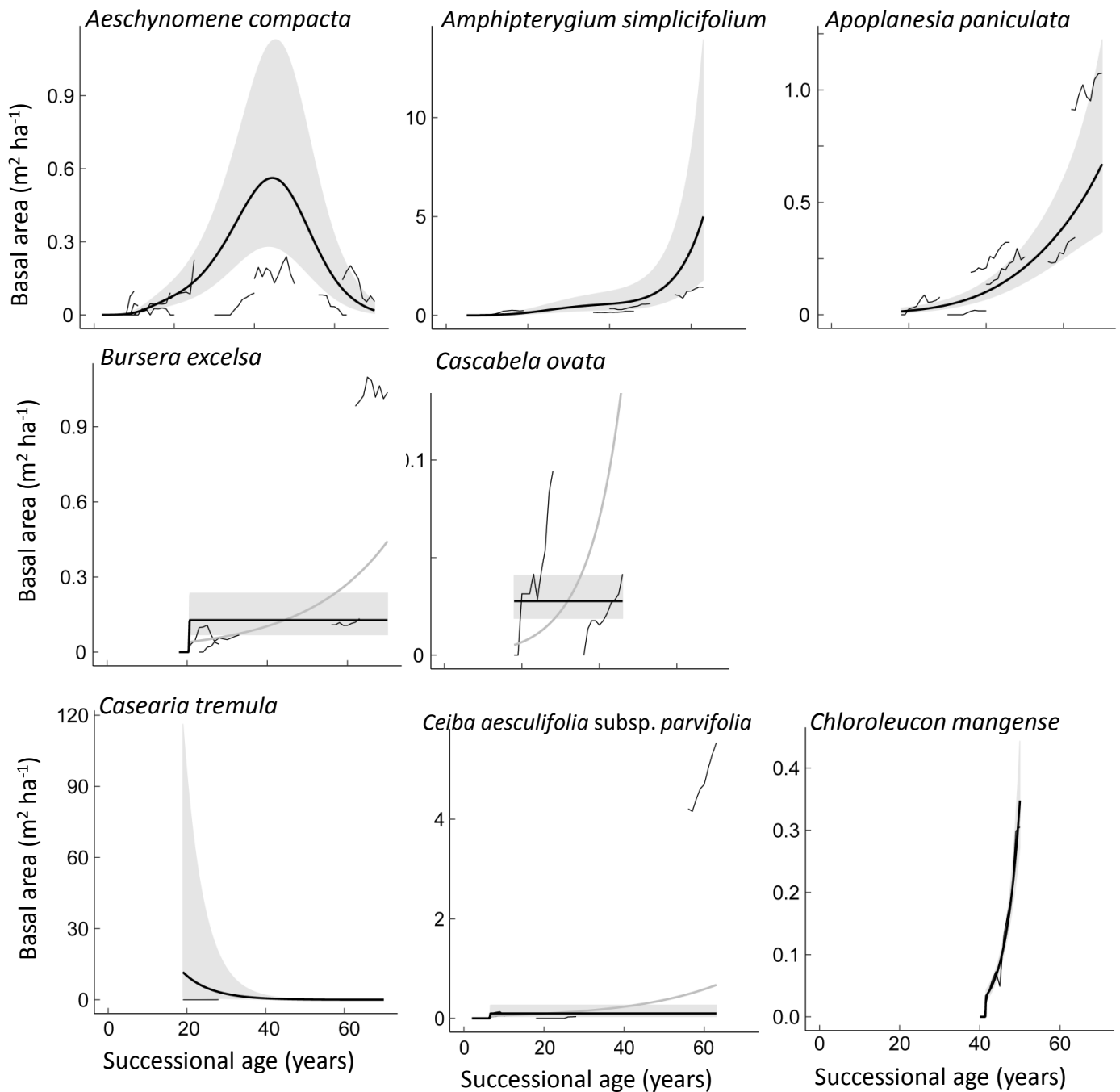


Figure S1. Best-supported presence/absence (left column), basal area (central column) and composite (i.e., resulting from the combination of the first two; right column) models depicting successional changes for 50 tree species from a successional tropical dry forest from southern Mexico (thick black lines). Hairlines are the observed basal area trajectories in individual plots, and thick gray lines represent similarly supported presence/absence, basal area and composite models, respectively. Gray bands are Wald 95 % confidence envelopes. Note that in those presence/absence models with low sample size a step-like model, with a very narrow confidence envelope, is obtained.

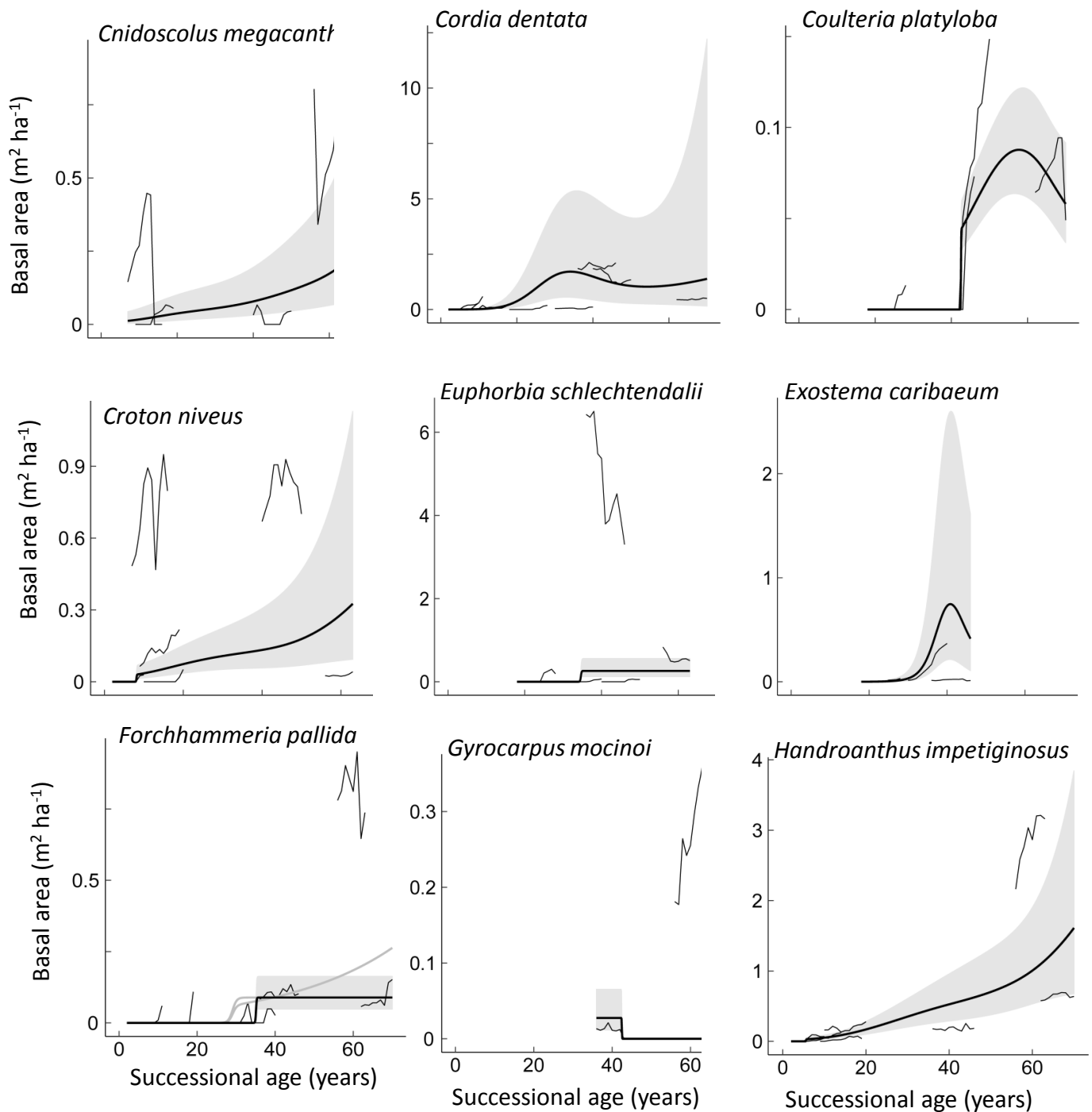


Figure S1. (Continued) Composite models resulting from the combination of the best-supported presence/absence and basal area models depicting successional changes for 50 tree species from a successional tropical dry forest from southern Mexico (thick black lines), with Wald's 95 % confidence envelopes (gray bands). Hairlines are the observed basal area trajectories in individual plots, and thick gray lines represent composite models integrating similarly supported presence/absence and basal area models.

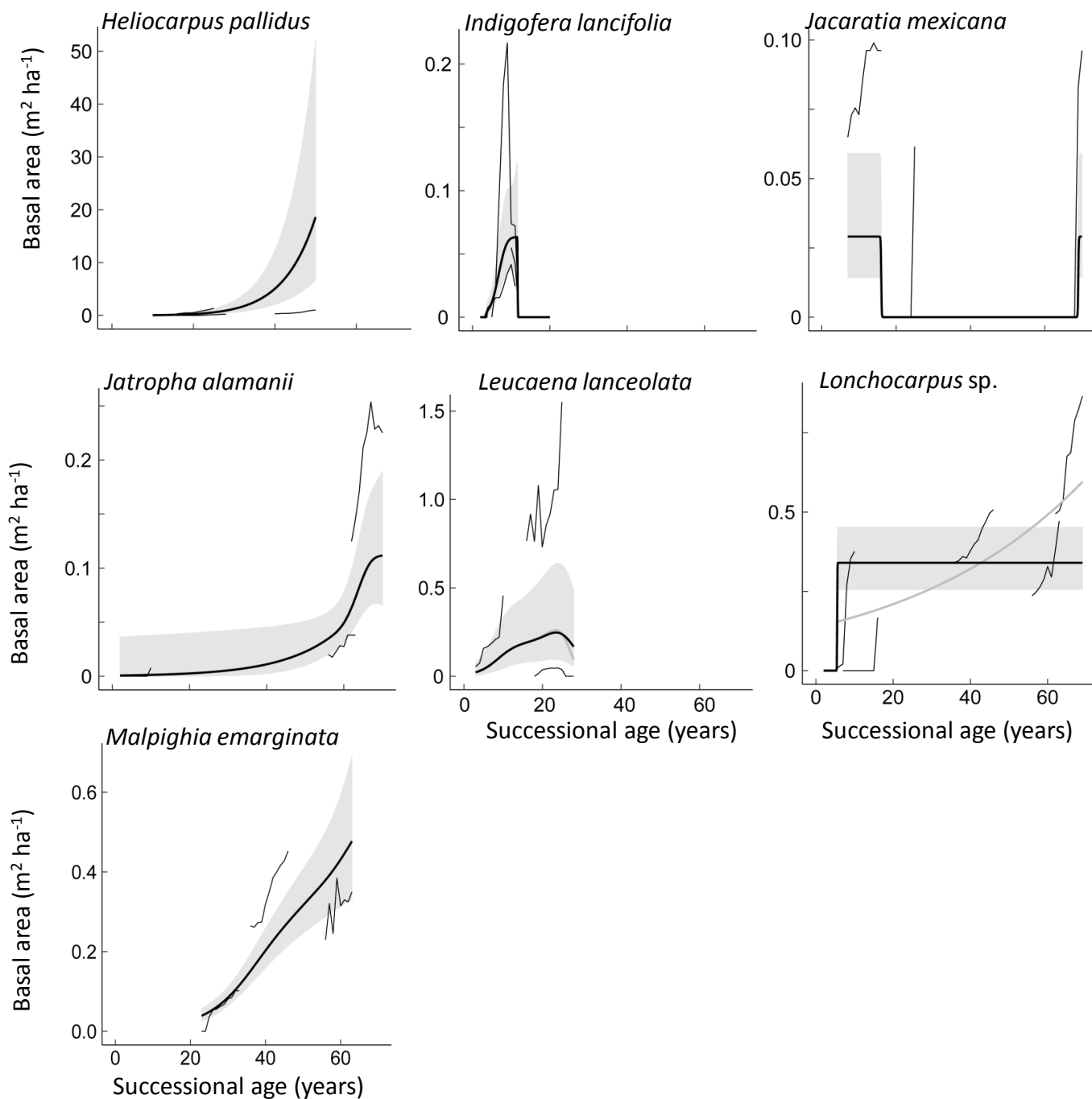


Figure S1. (Continued) Composite models resulting from the combination of the best-supported presence/absence and basal area models depicting successional changes for 50 tree species from a successional tropical dry forest from southern Mexico (thick black lines), with Wald's 95 % confidence envelopes (gray bands). Hairlines are the observed basal area trajectories in individual plots, and thick gray lines represent composite models integrating similarly supported presence/absence and basal area models.

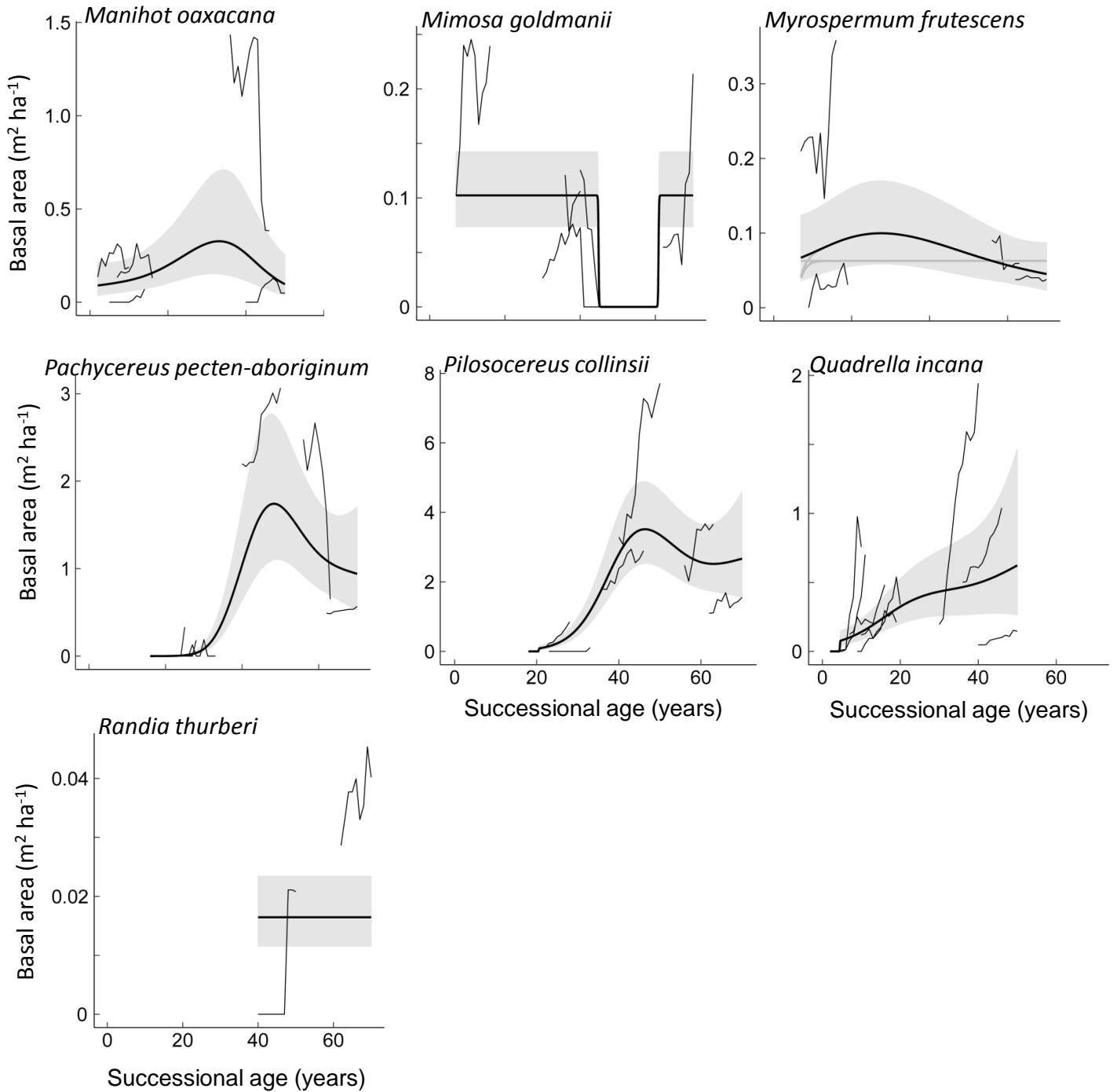


Figure S1. (Continued) Composite models resulting from the combination of the best-supported presence/absence and basal area models depicting successional changes for 50 tree species from a successional tropical dry forest from southern Mexico (thick black lines), with Wald's 95 % confidence envelopes (gray bands). Hairlines are the observed basal area trajectories in individual plots, and thick gray lines represent composite models integrating similarly supported presence/absence and basal area models.

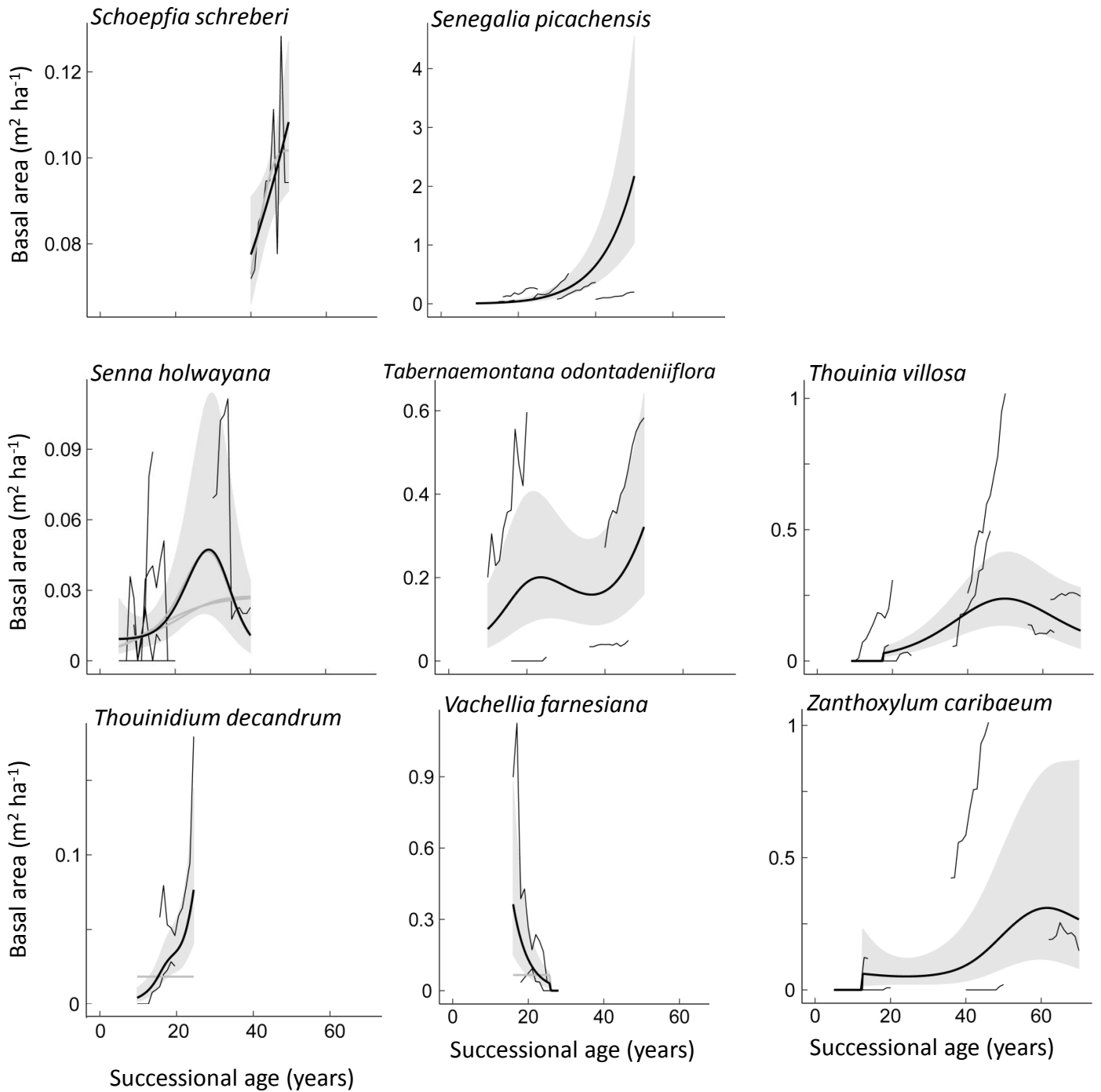


Figure S1. (Continued) Composite models resulting from the combination of the best-supported presence/absence and basal area models depicting successional changes for 50 tree species from a successional tropical dry forest from southern Mexico (thick black lines), with Wald's 95 % confidence envelopes (gray bands). Hairlines are the observed basal area trajectories in individual plots, and thick gray lines represent composite models integrating similarly supported presence/absence and basal area models.

ANEXOS Capítulo 5

Wood anatomy of 13 species from a successional tropical dry forest

Supplementary Information

Figure S1. Area covering the most recently produced wood tissue in the stem of *Mimosa eurycarpa*, approximately inside one or two growth rings.

Table S1. Dendrometric information and details of sample measurements (mean \pm standard deviation) of 13 woody species occurring in late secondary tropical dry forest (more than 50 years of abandonment). Basal diameter is the diameter of the stem from which the sample was collected. Height at stem is the height at which sample was collected. AC, *Acacia cochliacantha*; BO, *Bonellia macrocarpa*; BU, *Bursera simaruba*; CO, *Coccoloba liebmanii*; CN, *Cnidoscolus megacanthus*; JA, *Jacaratia mexicana*; LO, *Lonchocarpus lanceolatus*; LY, *Lysiloma divaricatum*; MIE, *Mimosa eurycarpa*; MIT, *Mimosa tenuiflora*; PA, *Pachycereus pecten-aboriginum*; PH, *Phyllostylon rhamnoides*; PI, *Pilosocereus collinsii*.

Figure S2. Transverse section of *Jacaratia mexicana*

Figure S3. Transverse section of *Pilosocereus colinsii*. Scale bar = 1000 μ m

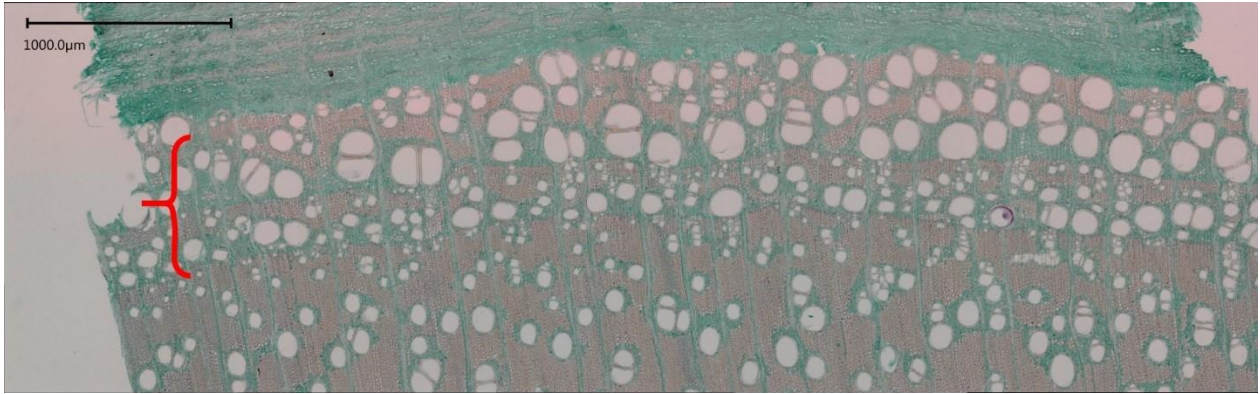


Figure S1. Area covering the most recently produced wood tissue in the stem of *Mimosa eurycarpa*, approximately inside one or two growth rings.

Table S1. Dendrometric information and details of sample measurements (mean \pm standard deviation) of 13 woody species occurring in advanced secondary tropical dry forest (more than 50 years of abandonment). Basal diameter is the diameter of the stem from which the sample was collected. Height at stem is the height at which sample was collected. AC, *Acacia cochliacantha*; BO, *Bonellia macrocarpa*; BU, *Bursera simaruba*; CO, *Coccoloba liebmanii*; CN, *Cnidoscolus megacanthus*; JA, *Jacaratia mexicana*; LO, *Lonchocarpus lanceolatus*; LY, *Lysiloma divaricatum*; MIE, *Mimosa eurycarpa*; MIT, *Mimosa tenuiflora*; PA, *Pachycereus pecten-aboriginum*; PH, *Phyllostylon rhamnoides*; PI, *Pilosocereus collinsii*.

Species	Basal diameter (cm)	Individual height (m)	Height at stem (cm)	Number of individuals
AC	11.1 \pm 2.1	5.4 \pm 0.6	34.2 \pm 6.7	6
BU	20.9 \pm 4.5	7.2 \pm 0.3	46.3 \pm 11.1	6
CN	11 \pm 1.7	5.5 \pm 1.0	26.5 \pm 4.6	5
CO	9.3 \pm 1.9	4.6 \pm 1.0	27.8 \pm 7.3	6
BO	5.6 \pm 0.5	2.3 \pm 0.6	18.8 \pm 5.0	5
JA	35.1 \pm 8.5	5.1 \pm 0.7	33.6 \pm 9.9	6
LO	13 \pm 2.1	6.7 \pm 0.8	34.0 \pm 6.8	5
LY	25.9 \pm 3.8	7.9 \pm 0.9	43.8 \pm 9.3	5
MIA	12.6 \pm 2.1	6.0 \pm 1.4	37.4 \pm 12.1	6
MIT	18.5 \pm 2.9	5.9 \pm 0.8	40.7 \pm 9.4	6
PA	18.4 \pm 1.2	6.7 \pm 0.9	37.7 \pm 2.4	6
PH	16.2 \pm 13.3	5.3 \pm 1.5	36.7 \pm 9.2	3
PI	8.9 \pm 1.8	3.3 \pm 0.9	21.3 \pm 9.3	6
Mean	16.0 \pm 9.0	5.7 \pm 1.8	34.6 \pm 11.4	

Figure S2. Transverse section of *Jacaratia mexicana*.

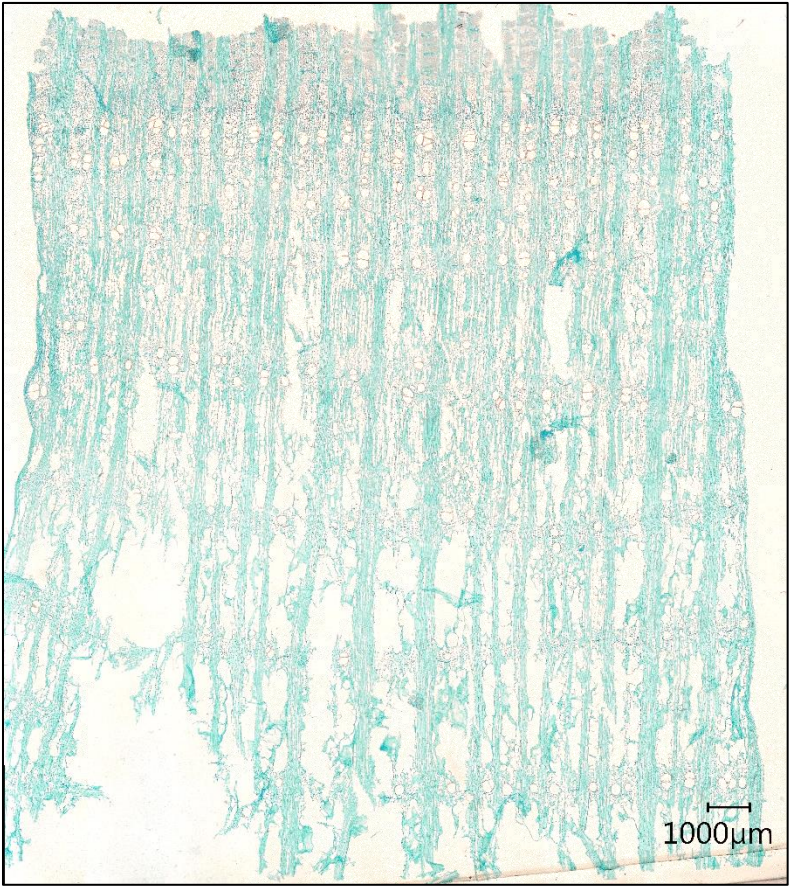
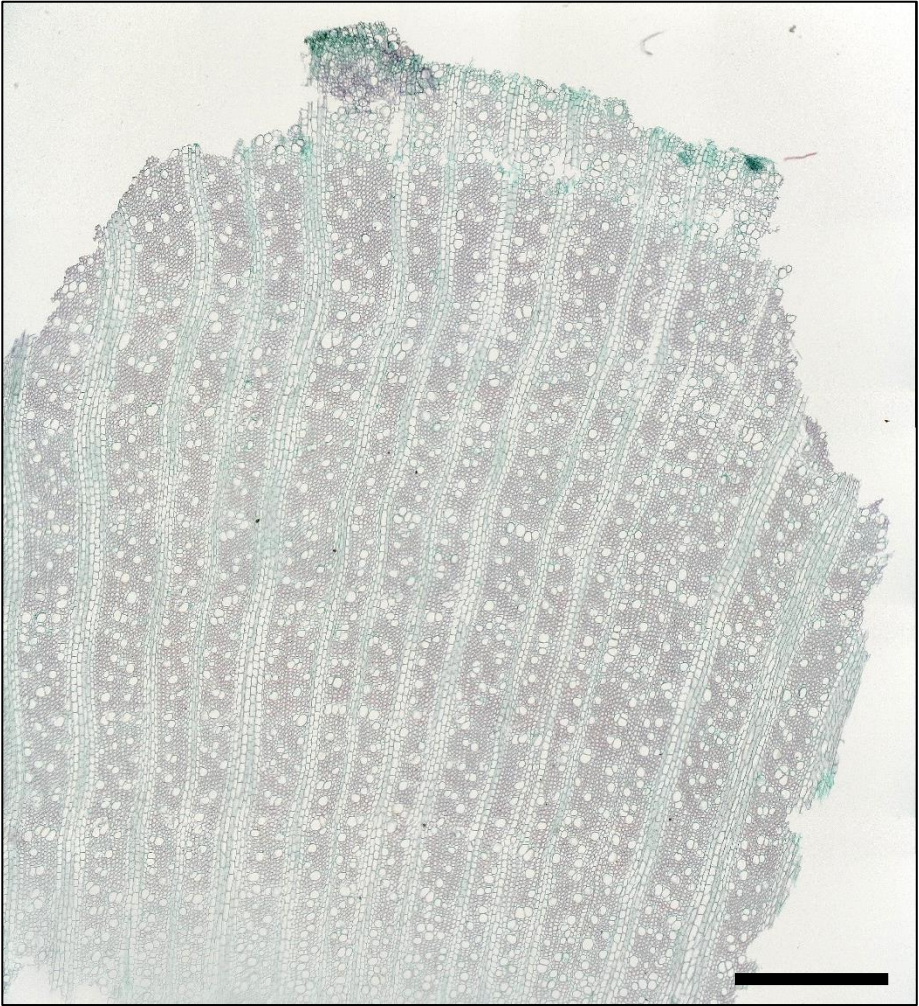


Figure S3. Transverse section of *Pilosocereus colinsii*. Scale bar = 1000 μm



ANEXOS CAPÍTULO 6

Wood anatomical spectrum of early and late-successional tropical dry forest communities

Supplementary Information

Figure S1. Comparison between mean vessel features in the secondary xylem of species present in early (~ 2 years of abandonment; EC) and late successional tropical dry forest communities (> 50 years of abandonment; LC). Brown horizontal bars indicate no significant differences between intraspecific means. Vertical lines indicate estimated 95% confidence interval. Species acronyms: AC *Acacia cochliacantha*, BO *Bonellia macrocarpa*, BU *Bursera simaruba*, CO *Coccoloba liebmanii*, CN *Cnidocolus megacanthus*, JA *Jacaratia mexicana*, LO *Lonchocarpus lanceolatus*, LY *Lysiloma divaricatum* (l-latewood; e-earlywood), MIE *Mimosa eurycarpa* (l-latewood; e-earlywood), MIT *Mimosa tenuiflora*, PA *Pachycereus pecten-aboriginum*, PH *Phylostyllon rhamnoides*, PI *Pilosocereus colinsii*.

Figure S2. Comparison between mean fibre features in the secondary xylem of species present in late tropical dry forest successional communities (> 50 years of abandonment; LC). Brown horizontal bars indicate no significant differences between intraspecific means. Vertical lines indicate estimated 95% confidence interval. Scale bar in (a) = 40 μm . Species acronyms: AC *Acacia cochliacantha*, BO *Bonellia macrocarpa*, BU *Bursera simaruba*, CO *Coccoloba liebmanii*, CN *Cnidocolus megacanthus*, LO *Lonchocarpus lanceolatus*, LY *Lysiloma divaricatum*, MIE *Mimosa eurycarpa*, MIT *Mimosa tenuiflora*, PA *Pachycereus pecten-aboriginum*, PH *Phylostyllon rhamnoides*, PI *Pilosocereus colinsii*.

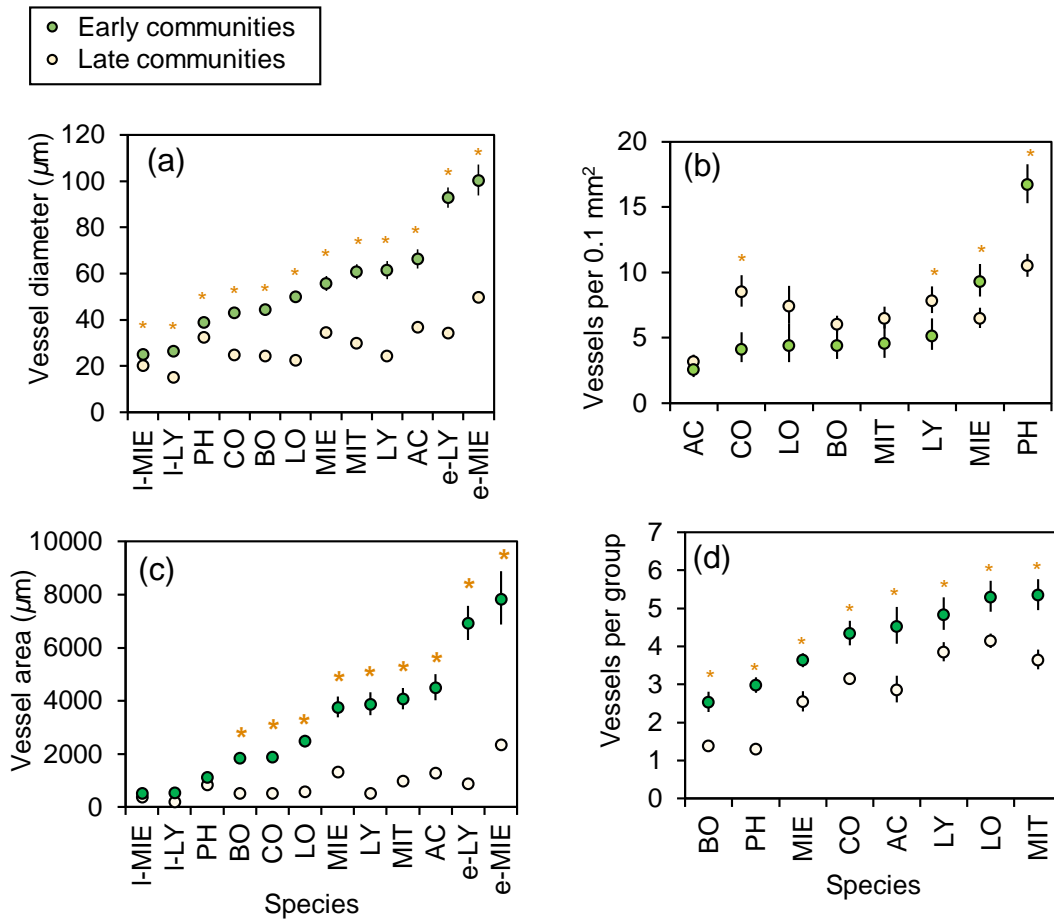


Figure S1. Comparison between estimated means of vessel features in the wood of species present in early (~ 2 years of abandonment; EC) and late tropical dry forest successional communities (> 50 years of abandonment; LC) derived from a tropical dry forest. Brown horizontal bars indicate no significant differences between intraspecific means. Vertical lines indicate estimated 95% confidence interval. Species acronyms: AC *Acacia cochliacantha*, BO *Bonellia macrocarpa*, BU *Bursera simaruba*, CO *Coccoloba liebmanii*, CN *Cnidocolus megacanthus*, JA *Jacaratia mexicana*, LO *Lonchocarpus lanceolatus*, LY *Lysiloma divaricatum* (I-latewood; e-earlywood), MIE *Mimosa eurycarpa* (I-latewood; e-earlywood), MIT *Mimosa tenuiflora*, PA *Pachycereus pecten-aboriginum*, PH *Phylostyllum rhamnoides*, PI *Pilosocereus colinsii*.

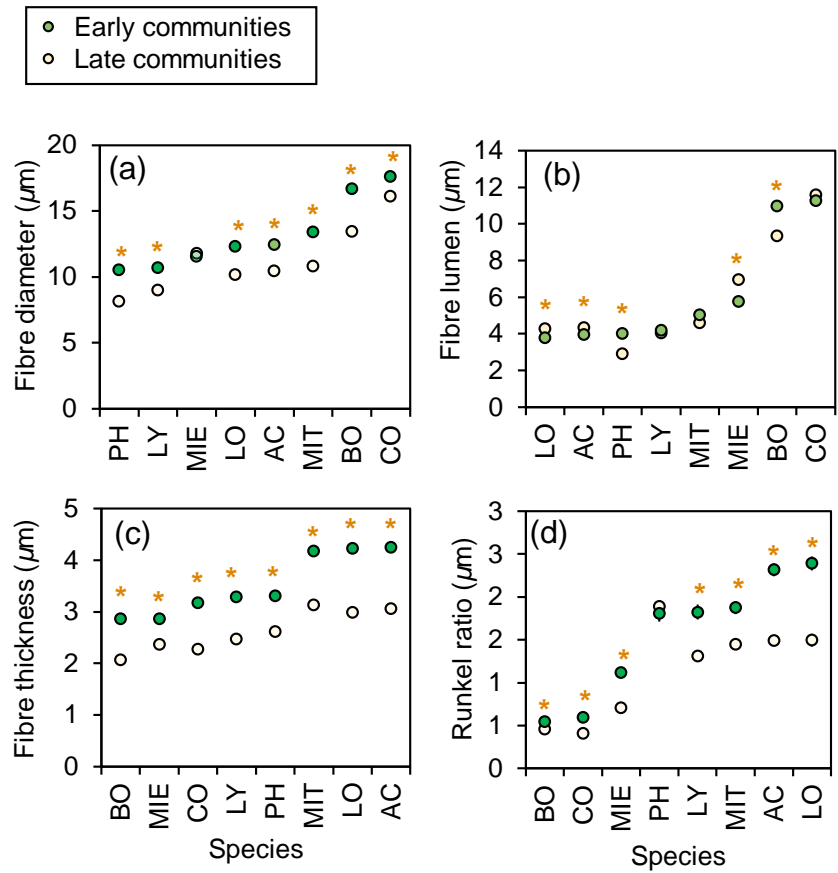


Figure S2. Comparison between estimated means of fibre features in the wood of species present in early (~ 2 years of abandonment; EC) and late tropical dry forest successional communities (> 50 years of abandonment; LC) derived from a tropical dry forest. Asterisks indicate significant differences between means. Vertical lines indicate estimated 95% confidence interval. Species acronyms: AC *Acacia cochliacantha*, BO *Bonellia macrocarpa*, BU *Bursera simaruba*, CO *Coccoloba liebmanii*, CN *Cnidocolus megacanthus*, LO *Lonchocarpus lanceolatus*, LY *Lysiloma divaricatum*, MIE *Mimosa eurycarpa*, MIT *Mimosa tenuiflora*, PA *Pachycereus pecten-aboriginum*, PH *Phylostyllon rhamnoides*, PI *Pilosocereus colinsii*.