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VARIACIÓN REGIONAL DEL CAPITAL DE CARBONO Y CARACTERÍSTICAS FUNCIONALES DEL BOSQUE TROPICAL ESTACIONALMENTE SECO DE YUCATÁN

TESIS

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Introducción

RESUMEN

La variación en la disponibilidad de agua en el bosque tropical estacionalmente seco (BTES) es un factor determinante del funcionamiento del ecosistema. Puede afectar el crecimiento y distribución de las plantas, limitar la tasa de adquisición de nutrientes y la productividad del ecosistema. Entender como el BTES se ajusta a las condiciones erráticas de la disponibilidad de agua y los fenómenos de anomalías que se enfrentan bajo el escenario de cambio climático global, sigue siendo un reto.

Características relacionadas con la distribución del carbono (C) y la asignación de la biomasa por las plantas al compartimento aéreo y/o subterráneo, permiten determinar cuál es la estrategia adoptada por el ecosistema para ajustarse a las condiciones ambientales reinantes. Por otro lado, los atributos foliares están fuertemente relacionados con las propiedades del ecosistema y son sensibles a ser modificados por la disponibilidad de recursos. En sitio con limitada disponibilidad de agua y alta irradiación, como es el caso del BTES, se espera que las especies de árboles ajusten sus características foliares para favorecer un eficiente uso de agua.

Con el objetivo de determinar cómo se ajusta el BTES bajo diferentes condiciones de disponibilidad de agua, fueron seleccionados tres sitios el gradiente natural de precipitación en la península de Yucatán-México. Tres características del BTES fueron estudiadas: (1) la distribución de la biomasa y el capital de carbono C en el piso forestal (mantillo fino, mantillo leñoso, raíces y suelo superficial (0 - 10 cm)), (2) la estrategia de asignación de biomasa vegetal al componente aéreo vs. el componente subterráneo y (3) la variación en las características foliares de especies co-ocurrentes, al igual que la relación entre las características foliares y la tasa de mineralización de N del suelo, todo a lo largo del gradiente de precipitación.

Los resultados muestran el fuerte efecto del régimen de precipitación y la disponibilidad de agua sobre las características del BTES. Mayor limitación por agua favorece mayor almacén de C en los residuos leñosos, raíces y suelo superficial. Por otro lado, la comunidad vegetal sigue un único patrón de asignación de biomasa a lo largo del gradiente de precipitación, con mayor asignación de biomasa al componente aéreo para cada valor del componente subterráneo. Finalmente, las características foliares de las especies caducifolias que co-ocurren a lo largo del gradiente de precipitación varían entre sitios. Al igual que se encontró variación en la relación entre caracteres foliares. Podemos concluir que el régimen de precipitación está ejerciendo un fuerte control sobre las características del ecosistema de BTES.

ABSTRACT

The water availability exerts strong control on the seasonally dry tropical forest (SDTFs) function. It can affect the plants growth and their distribution; limit the rate of nutrient acquisition and ecosystem productivity. Understand how the SDTF is adjusting their characteristics in order to face the erratic conditions of water availability and the anomalies under global climate change scenario, remain being a challenge.

The carbon (C) distribution on the forest floor and the plant biomass allocation to above and belowground compartment are both indicators about what is the ecosystem strategy to adjust to prevailing environmental conditions. Furthermore, foliar attributes are strongly related to the properties of the ecosystem and are sensitive to changes in the resources availability. In limited water availability sites with high irradiation such as is the case SDTFs, it is expected that tree species adjust their foliar traits in favor to an efficient water use.

In order to determine how SDTFs are adjusting to different water availability conditions, we selected three sites along a natural precipitation gradient in the Yucatan Peninsula, Mexico. We were focusing on three characteristics of the BTES: (1) the distribution of biomass and C pools in the forest floor (fine litter, wood debris, roots and soil (0-10 cm)), (2) plants strategy to biomass allocation to above and belowground, and (3) the leaf traits variation in tree species co-occurring, as well as the relationship between leaf characteristics and rate of soil N mineralization, all of three along the rainfall gradient.

Main results showed a strong effect of precipitation regime and water availability on SDTFs characteristics. C pools in wood debris, roots and top soil decrease with the water availability increase. Furthermore, the plant community along the rainfall gradient in SDTF follows a unique pattern of biomass allocation; i.e., more biomass is allocated to aboveground for each value of belowground biomass. Finally, it was found that the foliar traits of deciduous tree species co-occurring along the rainfall gradient vary between species and between sites. As well as it was found variation in the relationship between leaf traits among sites. We conclude that the precipitation regime is exerting strong control over ecosystem characteristics of SDTF.

INTRODUCCIÓN GENERAL

El bosque tropical estacionalmente seco (BTES) ocupa un área importante (42%) de la región tropical y subtropical (Holdridge 1967). Se caracterizada por una temperatura media anual mayor de 17°C, precipitación menor de 1600 mm año^{-1}, con periodos secos con duración de 5 a 6 meses, durante los cuales la precipitación es menor de 100 mm y vegetación caducifolia. Estas características han favorecido la presencia de especies endémicas y/o de rango restringido de distribución (Trejo 1999; Pennington *et al.* 2009).

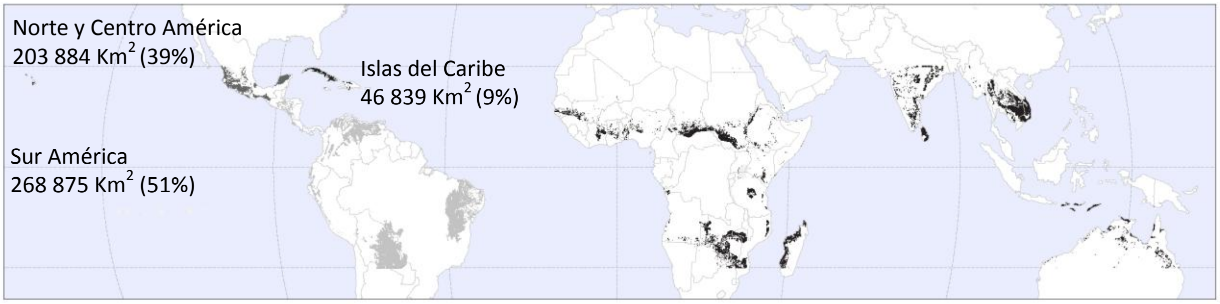
A pesar de su importancia, el BTES sigue siendo uno de los ecosistemas más amenazados de la biosfera (Janzen 1988; Gentry 1992). En México ~10% de la cobertura vegetal corresponde a BTES (Challenger y Soberón 2008). Dicho ecosistema está expuesto a alta presión por el incremento en la agricultura (64% 1977–1992) provocando una transformación de ~98% de su cobertura original (Solís y Campo 2004; Cairns *et al.* 2000). Esto ha generado que los bosques en estado maduro de algunas zonas del país, como es el caso del estado de Yucatán, sean prácticamente inexistentes (Campo y Vázquez-Yanes 2004). Y en general se considera que corresponden a bosques secundarios en diferentes estados de regeneración (Campo y Vázquez-Yanes 2004).

En el marco de las tendencias del cambio climático global, se ha pronosticado un incremento en la temperatura y disminución en la precipitación a lo largo de Centro América y el Caribe (Neelin *et al.* 2006). A escala regional, se he reportado que ~50% de los bosques tropicales caducifolios de México, son sensible al cambio climático (Villers-Ruíz y Trejo 1997). Variación en el régimen de precipitación y en la temperatura tendrán efectos ecológicos que pueden resultar en la expansión de las zonas de desierto en México; sin embargo, aún no conocemos la magnitud y dirección de la respuesta de éste ecosistema (Villers- Ruíz y Trejo-Vázquez 1997). Las expectativas de cambio para la zona del BTES incluyen incremento en la temperatura de hasta 2.5°C y disminución en la precipitación de al menos 50mm año^{-1} (Miles *et al.* 1996). Estudiar la variación de los atributos del las comunidades vegetales, a través del gradiente de precipitación natural a lo largo del cual se distribuye el BTES, nos permitirá contestar preguntas ecológicas a escala ecosistémica. Finalmente, la información así generada resulta de gran utilidad para entender las consecuencias de los cambios esperados en el contexto del cambio climático global y prepararnos para asumir las decisiones de manejo apropiadas para mitigar el impacto (Schwinning *et al.* 2004).

Origen y Distribución del Bosque Tropical Estacionalmente Seco

Dada la historia de uso del BTES ha sido difícil reconocer el área de distribución original de éste ecosistema (Trejo y Dirzo 2000). Según Miles y colaboradores (2006), más de la mitad del bosque tropical seco se encuentra en América (~54%) y ~38% se encuentra ubicado en México (Portillo-Quintero y Sánchez-Azofeifa 2010). La Figura 1., muestra la distribución global del BTES y es claro que más de la mitad se localiza en Sur América y el remante está distribuido igualmente entre Norte y Centro América (12.5%), África (13.1%) y Eurasia (16.4%). Una pequeña proporción ocurren en Australasia y el Sur este de Asia (3.8%). Para un total de remanente de BTES estimado para el año 2000 de 1.048.700 km^2 (Miles *et al.* 2006) (Figura 1).

Figura 1. Patrón global de distribución del bosque tropical estacionalmente seco (BTES). Las zonas coloreadas en grises y negro corresponden a la distribución global. La zona en gris oscuro corresponde al BTES localizado en México (~38%) (Portillo-Quintero y Sánchez-Azofeifa 2010). En conjunto, las zonas gris claro y gris oscuro corresponden a más de la mitad del BTES (~54%) distribuido en América con una extensión total de 519,597 km^2. La figura fue tomada de Miles y colaboradores (2006) y modificada para contrastar los BTES de América y México.



Al menos para el BTES distribuido en el Neotrópico, existe evidencia de conexión histórica entre los parches remanentes, según la distribución actual de las especies (Pennington *et al.* 2000). Por ejemplo, Prado y Gibbs (1993) concluyen que el patrón ampliamente fragmentado de distribución de éste ecosistema es el vestigio de una extensa y continua formación vegetal estacional, que alcanzo su máxima extensión durante el período seco del Pleistoceno (~1.8 a 1.2 Ma), en coincidencia con la contracción del bosque húmedo. Evidencia más actual incluyendo nuevos taxones, apoyan la conclusión de Prado y Gibbs (1993) (Pennington *et al.* 2000). Para el caso de México, poca información ha sido publicada en cuanto al tiempo de origen del BTES. Becerra (2005), siguiendo el tiempo de diversificación del genero *Bursera*, encontró que el BTES de México se originó durante el Oligoceno (~30 a 20 Ma) y se estableció primero en la zona oeste (correspondiente con la provincia del Pacífico) y de ahí, se expandió al sur y centro de México.

En México el BTES se encuentra distribuido a lo largo de la costa del Pacífico (hasta el sur de Sonora en su límite norte), a lo largo de las faldas bajas y los cañones de la vertiente del Pacífico de la Sierra Madre Occidental. Cubre una gran extensión de Sonora y sur este de Chihuahua hasta el sur del estado de Chiapas, continuando en América Central (Becerra y Venable 2008). Al sur este del país, este ecosistema alcanza las planicies, llanuras y otras zonas bajas e inundables de la Península de Yucatán y el sur de Veracruz y Tabasco. Dentro del marco de la clasificación de las provincias biogeografías (CONABIO 1997), los núcleos del BTES en México se distribuyen en las provincias de la Costa del Pacifico, la Depresión del Balsas al oeste del país, y la provincia de Yucatán. Sin embargo, existen varias razones que señalan variación en las condiciones del BTES en los dos núcleos antes mencionados; por un lado, la ubicación geografía de la provincia Yucateca y por otro, su identidad geológica (Espinosa *et al.* 2008). Adicionalmente, algunos autores han encontrado mayor asociación de la flora yucateca con la flora de Cuba y las Antillas Mayores que con ésta ubicada en la zona continental de México (Rzedowski 1978, Morrone 2005; Espinosa *et al.* 2008).

Precipitación y Disponibilidad de Agua

La magnitud y frecuencia de los eventos de precipitación son factores ambientales determinantes del desempeño de los ecosistemas terrestres (Austin *et al.* 2004). Dichos eventos controlan la disponibilidad de agua y gobiernan procesos como la fotosíntesis y los ciclos de los nutrientes, al mismo tiempo que regulan la descomposición de la materia orgánica, producción de hojas, producción de raíces finas y la dinámica de los microorganismos (Dirzo *et al.* 2011). Adicionalmente a la precipitación, otro factor determinante es la estacionalidad de las lluvias, la cual favorece la existencia de ciclos de humedad-sequia que alteran el desempeño de los ecosistemas. La fuerte estacionalidad de las lluvias en el BTES, conlleva a que los procesos ecológicos y la productividad primaria neta sean a su vez, fuertemente estacionales.

Dado el importante impacto de la disponibilidad de agua sobre el ecosistema, es considerada como el factor ambiental más importante que afecta la ocurrencia y crecimiento de árboles en el BTES; además de los procesos a nivel del ecosistema (Krames y Boyer 1995; Austin *et al.* 2004). A nivel ecosistémico se ha documentado que la disponibilidad de agua y en general el régimen de precipitación afectan la ocurrencia y crecimiento de los árboles (Enquist y Leffler 2000, Nath *et al.* 2006), la distribución de la diversidad (Gentry 1982, Hughes y Vitousek 1993), la productividad del ecosistema (Martinez-Yrizar *et al.* 1996, Eamus 2003), la forma como son asignados los recursos por las plantas (Waring y Slesinger 1985, Callaway *et al.* 1994, Bazzaz 1997) y los cambios en los atributos de la hojas (Shulze *et al.* 1998, Reich *et al.* 1999, Eamus 2003), entre otros.

Tendencias De Cambio Climático Global Del Bosque Tropical Estacionalmente Seco

Neelin y colaboradores (2006) muestran una tendencia de cambio hacia mayor sequia a lo largo del centro de América y el Caribe. Por lo que una gran proporción de BTES está en alto riesgo de un cambio climático severo, principalmente en América, con un 39.8% en la región Norte y Centro de América y 37.0% en Sur América (Miles *et al.* 2006). En los BTESs del territorio mexicano, se presentan períodos de precipitación < 100 mm durante 6-8 meses. Datos de precipitación presentado en 2004, por el centro de predicción climática de Estados Unidos (reporte para la nación "*The North American Monsoon"* del centro de predicción climática de Estados Unidos, 2004) muestran que la mayor acumulación de precipitación se da durante los meses de mayo y junio, con mayor depósito de lluvias al oeste de la Sierra Madre Occidental y en la parte sur del golfo de México; tiempo durante el cual la media de precipitación puede exceder 300 mm. La porción oeste de México recibe un 70% de su precipitación anual durante este período. Adicionalmente, la cantidad de precipitación que cae al año en el BTES, está influenciada por la presencia de ciclones tropicales, lo cual produce una alta variabilidad en el régimen y estacionalidad de las lluvias (García-Oliva *et al.* 1991).

Se ha predicho que el BTES experimentará fuertes cambios climáticos en los siguientes años debido al calentamiento global. Se ha proyectado que la media de temperatura incrementará en 3°C hacia finales del siglo, que el régimen de precipitación cambiará (Held y Soden 2006, Neelin *et al.* 2006), lo que se considera tendrá un impacto más severo en la dinámica del ecosistema que los efectos del aumento en el CO_2 y la temperatura combinados, principalmente en sistemas áridos y semiáridos (Welzin *et al.* 2003). Dentro del cambio climático esperado, se ha considerado que eventos climáticos como el fenómeno del Niño llegaran a ser más severos y frecuentes (Timmermann *et al.* 1999, IPCC 2007).

OBJETIVOS

La presente investigación se llevo a cabo con el objetivo de estudiar el efecto del régimen de precipitación como modelador del funcionamiento del ecosistema de bosque tropical estacionalmente seco, tomando como referencia: (1) la distribución de los capitales de carbono en el piso forestal, (2) la estrategia de asignación de biomasa de las comunidades vegetales presentes y (3) la variación en las características foliares.

Objetivos Generales

I. Determinar la distribución espacial del capital de carbono en residuos vegetales depositados en la superficie del suelo, en el suelo mineral y las raíces, a lo largo del gradiente de precipitación del bosque tropical estacionalmente seco de Yucatán.

    a. Cuantificar la biomasa y el capital de C de los residuos leñosos y mantillo fino depositados en el suelo del bosque, las raíces y el suelo mineral superficial a lo largo del gradiente de precipitación enel bosque tropical estacionalmente seco de Yucatán.

    b. Determinar el efecto del gradiente de precipitación sobre los capitales de C del piso foresta.

II. Determinar cuál es la estrategia de asignación de biomasa de las plantas a compartimentos aéreos y subterráneos, dentro del contexto de la hipótesis alométrica o balanceada, a escala ecosistémica en el bosque tropical estacionalmente seco a lo largo del gradiente de precipitación en Yucatán.

    a. Cuantificar la biomasa asignada por las plantas al compartimento aéreo y subterráneo en sitios con diferente régimen de precipitación en el bosque tropical estacionalmente seco de Yucatán.

    b. Establecer cuál es la estrategia de asignación de biomasa, dentro del marco de la hipótesis de asignación alométrica o asignación balanceada, de la comunidad vegetal del bosque tropical estacionalmente seco a lo largo del gradiente de precipitación,.

III. Determinar cómo varían los atributos de la hoja en especies que co-ocurren a lo largo del gradiente precipitación en el bosque tropical estacionalmente seco de Yucatán. A la vez que se busca explorar si los atributos foliares ser relacionan con la transformación de N del suelo.

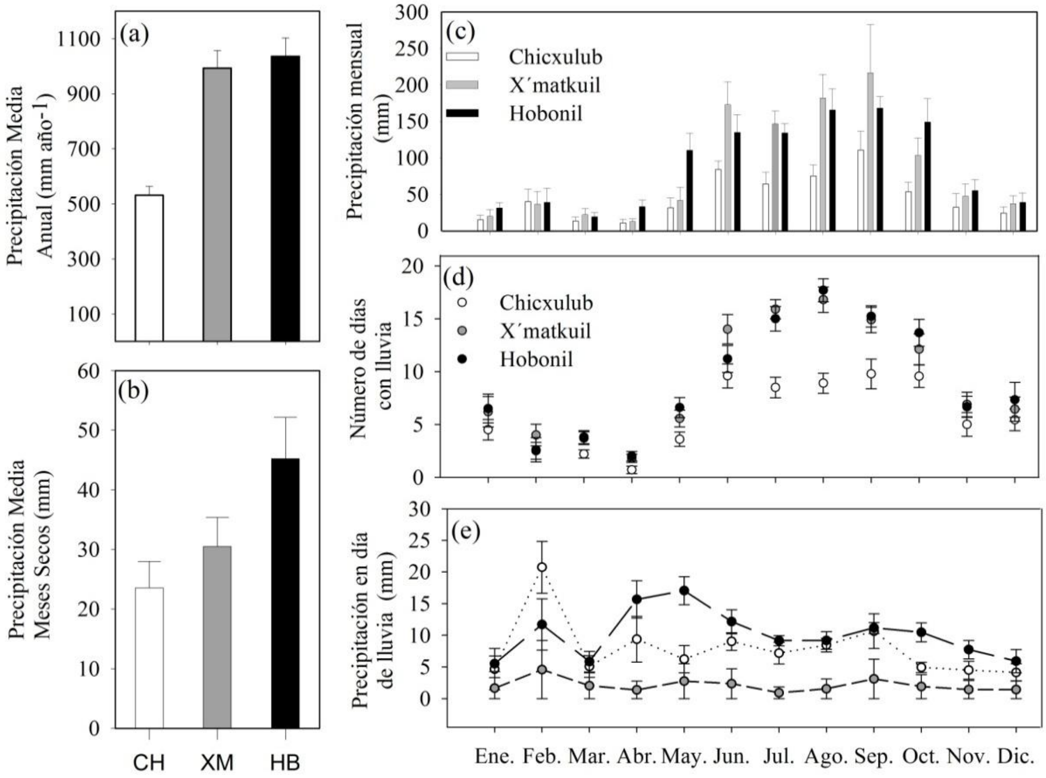
  a. Determinar la variación en los caracteres foliares, morfológicos y químicos, de especies caducifolias que co-ocurren a lo largo del gradiente de n el bosque tropical estacionalmente seco de Yucatán.
  b. Explorar si existe relación significativa entre los caracteres foliares y la tasa de mineralización de nitrógeno del suelo.

SITIO DE ESTUDIO

El sitio de estudio se encuentra localizado en la península de Yucatán, al sur-oeste de México. Se seleccionaron tres sitios, los cuales serán nombrados con claves asociadas al nombre de la localidad así: Chicxulub (CH), 21°14´N – 89°3´O; X´matkuil (XM), 20°51´N – 89°35´O y Hobonil (HB), 19°38´N – 88°59´O. Los tres sitios se desarrollan sobre similar material parental, que corresponde a roca caliza, lo cual ha permitido el desarrollo de suelos someros y ricos en carbonatos. El suelo más representativo para los tres sitios se clasifica como Rendosol lítico. Se caracteriza por ser un suelo superficial, con profundidades de 10 a 100 cm, con un horizonte superficial rico en materia orgánica lo que le confiere alta permeabilidad (Shang y Tiessen 2003). Topográficamente los tres sitios presentan zonas de planicie como la forma geomorfológica más sobresaliente, al igual que algunas zonas de lomeríos especialmente en HB. La vegetación de los tres sitios corresponde a bosque tropical caducifolio del tipo selva mediana caducifolia y selva mediana sub-caducifolia (Rzedowski 1998). Los tres sitios fueron usados para cultivos de agave y hortalizas, la referencia local indica un tiempo de abandono de aproximadamente 50 años. La variación más conspicua de las tres localidades corresponde a su régimen de precipitación (Figura 2). En términos generales, la variación intra-anual de la precipitación es extrema; sin embargo, un análisis detallados del régimen de precipitación para los sitios del presente estudio muestran que dicha variación interanual no es igualmente marcada para todos los sitios y a su vez es compensada con la cantidad de eventos de lluvia y la intensidad de los mismos. La Figura 2., muestra a modo de resumen algunos indicadores del régimen de precipitación en los tres sitios, que corresponden con baja (CH), intermedia (XB) y alta (HB) disponibilidad de agua.

Aunque la media anual de precipitación, no muestra claramente el gradiente de disponibilidad de agua de baja a intermedia a alta precipitación, es importante notar que la precipitación durante los meses más secos (b) sí muestra dicho gradiente entre los tres sitios. La precipitación durante los meses de mayor sequía, ha sido considerada como un determinante del uso anual de agua por los árboles (Eamus *et al.* 2001), afectando así las características del ecosistema. Otro aspecto importante, surge al analizar la Figura 2(d); el número de días con lluvia durante los meses de mayor sequía es igual durante casi todos los meses.

Figura 2. Datos climáticos correspondientes al periodo de 2001 a 2010, de las estaciones meteorológicas: Progreso (21.30°N–89.60´O) para Chicxulub; Mérida Observatorio (21.00°N–89.60´O) para X´matkuil y Tankankin (20.09°N–89.17´O) para Hobonil. (a) Media anual de precipitación, (b) media de precipitación en los meses más secos, (c) media de precipitación mensual a lo largo del año, (d) número de días con lluvias en cada mes y finalmente (e) la intensidad de la lluvia durante los días de lluvia en cada mes.



En contraste, la mayor diferencia se observa durante los mese de lluvias, durante los cuales el sitio que llamamos de menor disponibilidad de agua (Chicxulub), presenta un número significativamente menor de días con lluvia. La última observación mencionada se contrarresta con el hecho que la cantidad de agua que cae por cada evento de lluvia es igual para el Chicxulub y el sitio considerado de mayor disponibilidad de agua (Hobonil). En resumen el número menor de eventos de lluvia se compensa con lluvias más intensas en Chicxulub.

CAPÍTULO I.

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SHORT COMMUNICATION

The effects of precipitation regime on soil carbon pools in Yucatan Peninsula

Running head: Carbon storage across a precipitation gradient

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Resumen

A lo largo del gradiente de precipitación bosque tropical estacionalmente secos de la Península de Yucatán, se estudiaron los almacenes de carbono en la superficie del suelo del bosque (hojarasca fina y desechos de madera) y en el suelo superficial de 0 – 10 cm de profundidad (biomasa de raíces y materia orgánica). Con el objetivo de evaluar cómo diferentes regímenes de precipitación afectan los almacenes de C. Nuestros sitios de estudio fueron bosques localizados en una región seca (relación de evapotranspiración potencial = 3,2 mm^{-1} mm, con una media de precipitación anual = 537 mm), una región más húmeda (2,0 mm^{-1} mm; 993 mm) y una región en la que el agua es relativamente menos limitante (1,3 mm^{-1} mm; 1086 mm). En general, se encontró que principalmente tres almacenes, que son los residuos de madera, las raíces, y el C orgánico del suelo) proporcionan evidencia de la disminución significativa de C en el suelo con el aumento de la precipitación media anual en Península de Yucatán. Una posible explicación para este patrón inesperado es que en la región más seca se da una disminución en el recambio de C debido a la disminución de la precipitación media anual, lo que resulta en mayor acumulación de C por unidad de C que entra en el sistema.

Palabras clave: Piso forestal, suelo cárstico, raíces, bosque tropical estacionalmente seco, residuos de madera, México.

Abstract

Carbon pools in the forest floor (fine litter and wood debris) and in top soil (root biomass and organic matter) were studied in seasonally dry tropical forests in a regional spatial precipitation gradient of the Yucatan Peninsula. The study's objective was to assess how variation in precipitation regimes affects soil C storage. Our study included forest sites in a dry region (potential evapotranspiration ratio = 3.2 mm mm^{-1}; mean annual precipitation = 537 mm), a wetter region (2.0 mm mm^{-1}; 993 mm) and a region, in which water was comparatively less limiting (1.3 mm mm^{-1}; 1086 mm). Overall, we observed that, three pools (wood debris, roots, and soil organic C) provide evidence for the significant decrease in soil C storage with increase in mean annual precipitation in Yucatan Peninsula. A potential explanation for this unexpected pattern includes a decreasing C turnover with decrease in mean annual precipitation, resulting in higher C accumulations per unit of C input in the driest region.

Key Words: forest floor, karstic soils, roots, seasonally dry tropical forest, wood debris, Mexico

Precipitation has long been recognized as a control on plant production on a global scale (Lieth 1973). Empirical studies and models (Del Grosso *et al.* 2008, Luyssaert *et al.* 2007) suggest that in drier ecosystems, plant productivity increases with increases in mean annual precipitation (MAP). On the other hand, precipitation exerts a strong control on the organic matter decomposition (Sanderman & Amundson 2005). It is well known that the activity of soil micro-organisms increases with soil moisture (Davidson *et al.* 1998). This relationship helps drive the decrease in residence time of organic matter with MAP, and the net result of the balance in inputs and losses with precipitation underlies the observed soil C storage patterns with climate.

Tropical forest soils contain large stocks of C (Pan *et al.* 2011), and studies and models indicate that soil C storage may be vulnerable to changes in climate conditions (Cox *et al.* 2000, Jenkinson *et al.* 1991). Knowledge of direct and indirect effects of precipitation on the C cycling and soil C storage of tropical forests has been derived from studies in mesic to wet gradients (Posadas & Schuur 2011, Schuur *et al.* 2001). Measurements on these gradients show that C storage increase with MAP, but this trend is altered by excess precipitation. Despite seasonally dry tropical forests (SDTF) (i.e., forests with a MAP that varied from 250 to 2500 mm) occupying around 40% of the tropical forest area (Miles *et al.* 2006), and consequently their effect on the interactions between land surface and atmosphere being potentially substantial, the potential effect of precipitation variability on biogeochemical processes in these ecosystems have not been studied as extensively as in the tropical moist forests. Here, we quantify the C pools in the forest floor and in topsoil of SDTFs in a regional spatial precipitation gradient of the Yucatan Peninsula, that have the advantage that most site conditions can be assumed relatively similar across the gradient (e.g. mean annual temperature, topography, rock material and soil type, and vegetation type).

The study was carried out in south-eastern Mexico on the Yucatan Peninsula including three regions (Chicxulub, 21º14’N, 89º32’W; X´matkuil, 20º52’N, 89º36’W; and Hobonil, 20º00’N, 89º02’W) with different precipitation regime (Table 1). The climate is hot and subhumid and would support either tropical dry or very dry forest in the Holdridge system (Holdridge *et al.* 1971). Mean temperature across regions is around 26ºC. The averages of annual precipitation (MAP) and of annual potential evapotranspiration (PET), as well as the potential evapotranspiration ratio (i.e. PET/MAP ratio) differ considerably among regions (by a factor of 2 in the case of the MAP, by 39% in the case of the PET, and by 2.4 times in the case of the potential evapotranspiration ratio). The landscape consists of flat areas (7 m asl for Chicxulub; 22 m asl for X´matkuil; and 35 m asl for Hobonil). Soils (lithic rendolls) are mainly shallow and organic-rich and directly overlie weathered calcium carbonate (Shang & Tiessen 2003); bulk density is about 0.8 g cm^{-3}. The predominant vegetation in the Yucatan Peninsula is the SDTF, in which mean canopy height is 3-5 m. Floristically, Leguminosae are the most important family in all studied regions.

Three sites were selected in each region and four plots (144 m^2) per site were established in March 2010. Plots were installed taking into account the similar elevation and slope, and with similar MAP. In addition, plot installation was carried out avoiding large variation in the vegetation structure and composition at the local scale. At each plot dead fallen phytomass was sampled during the dry season (March 2010) and partitioned into fine-litter fraction (includes leaves, flowers, fruits and small twigs), and deadwood debris to include all woody residues deposited in the forest floor. Fine litter was collected in four 0.5-m^2 subplots per plot. Fine litter samples were selected to exclude all wood residues less than 5 mm in diameter. Deadwood debris was sampled using the planar-intersect technique (Kauffman *et al.* 1993), and two planar intersect were established in each plot. The diameter was measured to all wood particles that intersected each sample plane. A subsample of wood was carried to the laboratory to determine the specific density. Four soil cores (5 cm in diameter) from the upper 10 cm of soil (surface horizon) were collected (March 2010) randomly in each plot. When the soil was very shallow (< 10 cm in depth), the soil samples were collected up to rock contact. All soil samples were stored to 4°C until they were processed. Roots in the upper soil profile (0-10 cm) were sampled using one micro-plot (1 m^2) located in a corner of each plot, which was carefully excavated.

Soil samples were hand homogenized and sieved (to pass a 2-mm mesh) in the laboratory and a subsample was dried at constant weight for moisture determination. Fine roots (2 mm or less) were separated from soil samples. The remaining soil was used to measure organic C concentrations. Roots collected from micro-plots were separated on trays, collected with forceps and classified in size classes (diameter 4 mm or less; >4 to 10 mm; >10 to 20 mm, and >20 mm). Samples of fine litter and samples for each size class of wood debris and roots were oven dried at 70°C for 48 h. A subsample of each of these samples was milled and weighed to C determination. Carbon concentrations in litter, wood debris, root and soils were determined using an automated C-analyzer (SHIMADZU 5005A). Soil inorganic C concentration was estimated from carbonate concentration in samples; a subsample of 5 g of each soil sample was ground, sieved (No. 100), mixed with 50 ml of 0.5 N HCl and, heated until boiling over 5 min. The mixture was filtered (No. 2) and the extracts were separated to an aliquot of 5 mL. Aliquots were mixed with two drops of phenolphthalein to titrate the remaining acid with 0.25 N of NaOH (van Reeuwijk 2002). Soil organic C concentration was determined from the difference between the total C concentration and the inorganic C concentration. All analyses were performed in duplicate samples.

One-way ANOVA with Tukey-Kramer HSD test was used to examine the effect of region on C pools in the forest floor, soil and roots. Where necessary, data were log-transformed. Statistical analyses were performed using R 2.13.1 1 Program R Development Core Team 2011.

Mean of C concentration was higher in roots (475 ± 5 mg C g^{-1}) (mean ± 1 SE) than in litter standing crop (408 ± 13 mg C g^{-1} for fine litter, and 437 ± 3 mg C g^{-1} for wood debris) (F = 18.6, $P < 0.001$). Carbon concentration in the forest floor and in roots did not varied among regions (F = 1.76 for fine litter, F = 0.29 to 0.76 for wood debris size classes, and F = 0.24 to 1.73 for root size classes, $P < 0.05$). However, soil organic C concentration decreased following the order Chicxulub > X'matkuil > Hobonil (201 ± 20, 144 ± 13, and 63 ± 2 mg C g^{-1}, respectively) (F = 21.4, $P < 0.001$).

Fine-litter C pool increased with increasing MAP (Table 2). In contrast, C pools in total wood debris decreased with increase in MAP, reflecting large differences across regions in pools associated with lower size classes. Also C pools in total root biomass were larger in the driest, Chicxulub region, than in wetter regions (by 66% relative to C pools in X'matkuil, and by a factor of 2 relative those pools in Hobonil). Differences across regions reflected changes in C pools for size classes lower than 20 mm in diameter. Roots of the largest size class (i.e. > 20 mm in diameter) constituted a statistically homogeneous group across regions ($P > 0.05$). Chicxulub soils also had the highest organic C pools relative to soils from wetter counterparts. Overall, we found a decreasing gradient in the total C pool in Yucatan soils in the direction of Chicxulub > X'matkuil > Hobonil, and the corresponding ANOVA indicated that this gradient is highly significant.

A high proportion of the total C pool (93%-95%) was in the top 10 cm of soil in all forest regions. The smallest C pool was in roots (1.8%-2.4% of the total C), meanwhile the C in the forest floor represented 3%-5% of the total pool. These patterns were observed irrespective of study region. However, distribution of C in the forest floor varied across regions; the proportion of the forest-floor C pool in wood debris decreased from 80% in the driest region, to 51% and 42% in X'matkuil and Hobonil regions, respectively.

The amount of total forest-floor dry mass in the three regions ranged from 7.2 to 11.7 Mg ha^{-1} (data not showed), and is closer to the upper end of the global range for SDTFs (1.5-12.6 Mg ha^{-1}; Martínez-Yrízar 1995). In contrast, the mean organic C concentrations in soils of the Yucatan Peninsula (63-201 mg C g^{-1}) exceed away values reported for others SDTF soils (9.8-47 mg C g^{-1}; García-Oliva & Jaramillo 2011). Total C pools in the Yucatan Peninsula, calculated from Table 1 (for above-ground biomass with a C concentration of 50%; 23.7 Mg C ha^{-1} for Chicxulub, 24.4 Mg C ha^{-1} for X'matkuil, and 32.8 Mg C ha^{-1} for Hobonil) and Table 2, were 154 Mg C ha^{-1} for Chicxulub, 127 Mg C ha^{-1} for X'matkuil, and 96.6 Mg C ha^{-1} for Hobonil. Surface soil C accounted for 85%, 81% and 66% of the total C for Chicxulub, X'matkuil and Hobonil regions, respectively. These C proportions in Yucatan soils are larger than values in others tropical forest soils (soil C accounted for 32% of total C in tropical forests; De Deyn *et al.* 2008, Pan *et al.* 2011). Despite of our data are not enough to support a mechanistic explanation, has been reported that karstic soils and specifically Yucatan's soils have high potential to form aggregates with carbonates and Ca impregnated, favouring C stabilization by slow organic matter decomposition (Shang & Tiessen 2003). Thus, soil C stabilized and the low water availability are driving a low soil metabolic activity preventing C losses by either soil respiration or leaching.

Three pools provide evidence for the significant decrease in soil C storage with increase in MAP in Yucatan Peninsula (wood debris, roots and soil organic C). The consistent trend with precipitation amount in soil C storage that we found seems to contradict findings that C storage in tropical forest soils increase with MAP (Posadas & Schuur 2011, Schuur *et al.* 2001). The differences in precipitation regime between our study (500-1100 mm) and that of Schuur studies (2200-5000 mm and 2500-9500 mm) may explain this big difference in the pattern of the C storage between the two types of forest ecosystem (i.e. SDTFs and tropical rain forests).

Why this pattern occurs can be understood by considering how variation in precipitation may drive the inputs and losses of soil C to and from the soil system. Thus, a potential explanation for this inconsistency includes a decreasing C turnover with decreasing MAP, resulting in higher C accumulation per unit of C input in the driest region. Inter-site experiments conducted throughout the tropics show that rainfall is positively correlated with decay rates in tropical forests (Powers *et al.* 2009). Decomposition rates of leaves from dominant tree species were measured across the local precipitation gradient in Yucatan where other factors (topography, parent material, vegetation, and ecosystem age) were held constant (M. Bejarano unpubl. data). Results of these experiments indicates that decomposition rates of leaves placed on the soil surface increase by 55% with increase precipitation, whereas litterfall increased only by 10% across the gradient (J. Campo pers. obs.).

A major limitation of this study could be introduced by the limited soil depth explored. However, soil C and its response to precipitation regime was focused on surface horizons because higher root biomass and soil C concentrations are usually found in this upper 10 cm of soil. A large proportion of root biomass was found in this upper 10 cm of soil (approximately one third of the total root biomass; Roa-Fuentes *et al.* in prep.). Given that the results of soil C inventory studies in other Yucatan sites across the precipitation gradient have shown that a large fraction (more than 60%) of the total soil organic C is also located in this surface horizon (J. Campo unpl. data), we think this is a robust pattern that should stimulate further research in the dynamic nature of soil C in dry-to-mesic tropical forests.

The new climate relationships observed in Yucatan Peninsula, add to our conceptual understanding of the effect of precipitation regime on soil carbon storage in tropical forests. Patterns observed in carbon storage in Yucatan soils have several implications for how carbon sequestration and turnover in tropical forests may respond to climate change.

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Table 1. General characteristics of the three studied forest sites

	Chicxulub	X'matkuil	Hobonil
Climate[1]			
Mean annual temperature (ºC)	25.8	26.6	26.2
Mean annual precipitation (mmyr^{-1})	537	993	1086
Potential evapotranspiration (mmyr^{-1})	1723	2023	1457
Potential evapotranspiration ratio(mm mm^{-1})	3.21	2.04	1.34
Bulk density(gcm^{-3})	0.70	0.78	0.91
Soil[2]			
pH	7.4	7.5	7.4
Sand (%)	74.1	64.3	57.6
Silt (%)	4.2	7.5	4.3
Clay (%)	21.7	28.2	38.1
Vegetation[3]			
Tree density(stem ha^{-1})	37.4	104.3	56.4
Tree height (m)	3.3	3.3	5.4
Aboveground biomass (Mg ha^{-1})	47.4	48.8	65.6

[1] Climate data (Servicio Meteorológico Nacional, personal communication

[2] Soil data (Roa-Fuentes *et al.* unpublished data)

[3] Vegetation data (Roa-Fuentes *et al.* 2012)

Table 2. Soil carbon pools in three study regions of Yucatán Peninsula.

Pool	Chicxulub	X´matkuil	Hobonil	*F*-value
		(Mg C ha^{-1})		
Fine litter	0.83b ±0.03	1.87a ±0.22	1.73a ±0.23	0.83**
Wood debris				
Diameter (mm)				
0.65-2.54	1.75a ±0.28	0.95ab ±0.08	0.48b ±0.19	10.33*
2.55-7.62	1.90a ±0.19	0.63b ±0.03	0.61b ±0.28	13.67**
> 7.63	0.37a ±0.19	0.05a ±0.03	0.19a ±0.10	1.67^{NS}
Total DWD	4.23a ±0.69	1.71b ±0.17	1.32b ±0.59	5.52**
Roots to 10 cm				
Diameter (mm)				
≤ 4	1.58a ± 0.12	0.98b ±0.12	0.73b ±0.08	15.7**
> 4-10	0.92a ± 0.15	0.45b ±0.05	0.31b ±0.04	11.77**
> 10-20	0.51a ± 0.08	0.32ab ±0.05	0.24b ±0.01	6.17*
> 20	0.07a ± 0.04	0.10a ±0.01	0.13a ±0.02	1.0.1^{NS}
Total Roots C	3.08a ± 0.39	1.85b ± 0.23	1.41b ± 0.15	16.19**
Soil to 10 cm	122.6a ±7	97.8b ±9.9	59.3c ±4.8	21.2***
Total	130.6a ±6.4	102.8b ±10.6	63.8 ±6.2c	20.3***

Data are mean ± SE of three forest sites. Different lower case letters (a,b) indicate means are significantly different, when testing for differences among regions. NS, $P \geq 0.05$; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

CAPÍTULO II

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Plant Biomass Allocation across a Precipitation Gradient: An Approach to Seasonally Dry Tropical Forest at Yucatán, Mexico

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Resumen

Se ha sugerido que la asignación de biomasa en plantas a tallos y raíces a nivel ecosistémico sigue una única estrategia, según la cual la biomasa de los tallos escala isométricamente con la biomasa de las raíces, una hipótesis conocida como "escalamiento isométrico". En este estudio, se examinó una teoría, según la cual la biomasa de las plantas se asigna preferentemente al órgano que cosechas el recurso limitante del crecimiento, una teoría conocida como la "hipótesis de crecimiento balanceado". Nuestro objetivo fue poner a prueba estas dos hipótesis alternativas a nivel de ecosistema a lo largo del gradiente de disponibilidad de agua. Se cuantificó la biomasa total del tallo y de las raíces en tres sitios de bosque tropical estacionalmente seco en tres localizados en la península de Yucatán, a lo largo de un gradiente de precipitación. El análisis de eje mayor reducido (RMA, por sus siglas en ingles), mostró que las pendientes de la relación entre la biomasa del tallo y la raíz a lo largo del gradiente de estudio son estadísticamente similar y significativamente diferente de 1.0 (pendiente común = 2.5), lo que contrasta con la hipótesis del "escalamiento isométrico". El coeficiente alométrico fue diferente entre las regiones a lo largo del gradiente de precipitación, lo que demuestra que la asignación de biomasa por las plantas al componente aéreo es mayor en el sitio de mayor precipitación comparado con el sitio de menor precipitación, donde la biomasa es asignada en mayor proporción a las raíces. La proporción tallo: raíz aumenta a raíz de menor a mayor disponibilidad de agua. Nuestros resultados mostraron que la asignación de biomasa en plantas del BTES sigue una estrategia alométrica simple en la que mayor biomasa se asigna a los tallos independientemente de la disponibilidad de agua, lo que sugiere que a nivel ecosistémico la asignación de biomasa es invariante a través del gradiente de disponibilidad de agua.

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ECOSYSTEMS

Plant Biomass Allocation across a Precipitation Gradient: An Approach to Seasonally Dry Tropical Forest at Yucatán, Mexico

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ABSTRACT

It has been assumed that plant biomass partitioning to stems and roots at the ecosystem level follows a single strategy according to which the stem biomass scales isometrically with root biomass, a hypothesis known as 'isometric scaling'. In this study, we examined an alternative theory used for plants: plant biomass is allocated preferentially to the plant organ that harvests the limiting growth resource, a theory known as the 'balanced growth hypothesis'. Our objective was to test these two alternative hypotheses across a water availability gradient. We quantified the stem and root biomass in a seasonally dry tropical forest (SDTF) in three regions of the Yucatán peninsula along a precipitation gradient. Reduced major axis analysis showed that the slopes of the relationship between stem and root biomass across the study regions were statistically similar and significantly different from 1.0 (common slope = 2.5), which contrasts with the 'isometric scaling' hypothesis. The allometric coefficient was different between regions along the precipitation gradient, which showed that plant biomass allocation to stems is higher in high than in low water availability regions where biomass is allocated in greater proportions to roots. The stem:root ratio increases following the low to high water availability gradient. Our results showed that plant biomass allocation in the SDTF follows a simple allometric strategy in which greater plant biomass is allocated to stems irrespective of water availability, suggesting to the forest level that plant biomass allocation strategy is invariant across the water availability gradient.

Key words: Allometry; Isometric scaling; Root biomass; Stem biomass; Stem:root ratio; Water availability gradient.

INTRODUCTION

The plant biomass allocation pattern is an important topic in ecology because of the implications for plant growth, which involves a trade off in the plant life history (Müller and Schmid 2000; Shipley and Meziane 2002; Weiner 2004). Biomass allocation is considered the main process governing differentiation and structure in forest ecosystems (Seidl and others 2010). At the forest community

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level, plant biomass allocation strategies are linked to the plant community's adaptive response to environmental changes and performance (Poorter 2001; Binkley and others 2004; Niklas 2005).

Different models of plant biomass allocation have been proposed. According to the allometric allocation hypothesis, the most parsimonious plant biomass allocation strategy follows a simple allometric strategy instead of adjusting to particular resource availabilities (Müller and Schmid 2000 Poorter and Nagel 2000). According to this model, plant biomass allocation is rarely affected by the supply of water or nutrients (Müller and Schmid 2000). Enquist and Niklas (2002) argued that a simple allometric strategy is isometric scaling, according to which the standing stem biomass (S_M) scales nearly isometrically with respect to the standing root biomass (R_M) (Enquist and Niklas 2002). Isometric scaling has been observed in individual plants (Niklas 2005) and at the forest ecosystem scale (Cheng and Niklas 2007; Yang and Luo 2011); in both cases, there were no significant changes in isometric scaling with environmental factors (Yang and Luo 2011) following the prediction of a general strategy, in monospecific or mixed stands, despite differences in species composition and structural stand traits (Cheng and Niklas 2007). An alternative is the balanced growth hypothesis, according to which plant biomass is allocated preferentially to the plant organ that harvests the limiting growth resource (Bloom and others 1985; Shipley and Meziane 2002). Because nutrients and water are captured by the roots, biomass is allocated to roots if water or mineral nutrients become limiting. According to this hypothesis, plants should allocate more resources to the roots on infertile sites to increase the nutrient uptake (Bloom and others 1985). A variation is the response to differential selection for adaptations to different environmental conditions (Bazzaz and Grace 1997; Reich 2002; Cheng and Niklas 2007).

Despite the importance of plant biomass allocation for global carbon cycling (Houghton and others 2009), how the plant allocates biomass above- and below-ground remains unclear (Bazzaz and Grace 1997). In recent years, ecologists have sought to understand plant biomass allocation strategies at the ecosystem level (Yang and others 2010; Yang and Luo 2011). However, when different types of forest ecosystems are included, the results have not been consistent (for example, 10 out of 16 studies showed the expected isometric slope between the above- and below-ground organs, Yang and Luo 2011); for instance, the forest with mean annual precipitation (MAP) below 1,500 mm showed slope values higher than 1.0.

The seasonally dry tropical forest (SDTF) in Mexico is characterized by marked seasonal precipitation with five to six dry months of precipitation lower than 100 mm (Trejo 1998). Aside from regular periods of water limitation, the vegetation in SDTF shows potential for multiple limiting nutrients either directly by the effect of water availability on organisms or indirectly by the effects of soil water on nutrient availability (Austin and Vitousek 1998; Campo and others 2007). Although SDTF vegetation has developed strategies to cope with the heterogeneity in water availability (Niinemets 1997; Wright and others 2001; Pennington and others 2009), the effect of environmental conditions on biomass allocation to stems or roots is unclear.

Plant species adapted to dry and hot conditions tend to have reduced biomass allocated to leaves compared to stems or roots (Callaway and others 1994; Bazzaz and Grace 1997). Murphy and Lugo (1986) found higher root biomass (as a percentage of the total biomass) in SDTFs than in wet tropical forests (8–50% and <5–33% of the total biomass, respectively). These results were in line with the generally accepted idea that root biomass allocation is strongly correlated with available soil moisture and the common prediction that the root:stem ratio increases with decreases in MAP (Chapin and others 1993). At first glance, soil water stress causes greater biomass allocation to roots (Kramer and Kozlowski 1979; Murphy and Lugo 1986; Sanford RL and Cuevas 1996). On the other hand, the negative relationship between the root:stem ratio with soil nutrient availability at the ecosystem scale has been documented for tropical (Vitousek and Sanford 1986) and Mediterranean ecosystems (Wright and others 2001), suggesting elevated root:shoot ratios in nutrient-poor sites (Vitousek and Sanford 1986).

To test the biomass allocation hypotheses discussed above, we explored the plant biomass allocation pattern between the stem and root compartments in a Mexican SDTF across a natural precipitation gradient. The leaf biomass was not included in this study due to the increased deciduousness with declining rainfall in our study sites (Pennington and others 2009) and based on results from previous studies showing that the small leaf fraction of the plant in the field implies that the strong differentiation of biomass allocation seems to be between stems and roots (Poorter and others 2011). This observation led us to use the stem biomass as an indicator of the total aboveground biomass compared with the belowground biomass. In addition, we used soil total and inorganic N as well as net N mineralization to explore the relationship between N availability and biomass allocation patterns. According to the balanced growth hypothesis we expected that: (i) the slope of the stem versus root biomass allometric trajectory changes with water availability between sites (that is, lower slope value in the site with lower water availability); (ii) greater biomass would be allocated to roots proportionally to stems in sites with lower water availability.

Study Sites

This research was conducted in the western Yucatán peninsula, in three regions (Chicxulub, CH; X'matkuil, XM; and Hobonil, HB) located along a natural precipitation gradient (from ~530–1,035 mm of MAP) (Table 1). Precipitation during the dry season was included (Table 1) to address the idea that dry season conditions may limit tree water use during the wet season (Eamus and others 2001). Across the region, the climate is characterized by a mean annual temperature of 25°C and highly variable precipitation on both seasonal and annual time scales (Whigham and others 1990; Harmon and others 1995). The landscape consists of flat areas (less than 90 m asl). The available meteorological data (years 2001–2010) for the study regions show that precipitation peaks in September, whereas a dry season occurs from December to April (García 2004). In addition to the precipitation gradient, the study regions follow a soil water plant availability gradient according to which the driest region has the lowest soil water retention capacity (Tables 1, 2). The soils are shallow, calcareous, and highly permeable due to high organic matter content (Solís and Campo 2004) and underlying limestone fractured bedrock (Whigham and others 1990). A slow turnover time of soil organic matter (Shang and Tiessen 2003) limits the nutrient release and forest primary production (Campo and Vázquez-Yanes 2004).

We did not enumerate the species composition in this study, but it is known that the predominant vegetation along of the Yucatán peninsula is the tropical deciduous forest (Miranda 1958) with floristic composition similar to that found on limestone substrates throughout the dry tropics of the Caribbean and Middle America (White and Hood 2004). Floristically, Leguminosae is the most important family in the three studied forests and the most important species reported at each study region are: in CH, *Thouinia paucidentata* Radlk., *Lysiloma latisiliquum* (L.) Benth., *Gymnopodium floribundum* Rolfe, *Acacia gaumeri* S.F. Blake, *Caesalpinia gaumeri* Greenm, *Leucaena leucocephala* (Lam.) de Wit (González-Iturbe and others 2002); in XM, *Cordia alliodora* (Ruiz & Pav.) Cham., *C. gaumeri*, *Bunchosia glandulosa* (Cav.) DC., *Bursera simaruba* (L.) Sarg., *A. gaumeri*, *Lonchocarpus yucatanensis* Pittier (Mizrahi and other 1997); and in HB, *B. simaruba*, *Piscidia piscipula* (L.) Sarg., *G. floribundum*, *C. gaumeri*, *Eugenia axillaris* Vell., *L. yucatanensis*, *Vitex gaumeri* Greenm. (White and Hood 2004). The common species along the three regions are *C. gaumeri*, *B. simaruba*, *A. gaumeri*, *G. floribundum* *L. yucatanensis*, *L. latisiliquum* and *P. piscipula.*

The three study regions were previously used for henequén (*Agave fourcroydes* Lem.) cultivation in CH, and for corn and vegetable cultivation in XM and HB. The three regions were abandoned approximately 50 years ago (González-Iturbe and others 2002; White and Hood 2004) and have not been used for agriculture or grazing in recent history. All selected sites represent late successional forest according to the Mayan forest succession nomenclature (Gomez-Pompa 1987), which is a common forest succession stage in the study region.

At each study region, after determining the low to high water availability gradient (Table 2), we selected three localities and installed four replicate

Table 1. Characteristic of Three Regions in Yucatán, Mexico

	Chicxulub (CH)	**X'matkuil** (XM)	**Hobonil** (HB)
Location	24°14′N–89°3′W	20°51′N–89°35′W	19°38′N–88°59′W
Altitude (m)	4	12	89
Clime type*	BS1	Aw0	Aw1
Mean annual precipitation (mm y^{-1})	531b ± 32	993a ± 64	1036a ± 67
Water stress months	November–May	December-May	December–April
Mean month precipitation in water stress months (mm month^{-1})	23.6c ± 4.4	30.5b ± 4.8	45.2a ± 6.9

Climatic data (years 2001–2010) were taken at the meteorological stations: Progreso (21.30′N–89.60′W) for Chicxulub; Mérida Observatorio (21.00′N–89.60′W) for X'matkuil; Tankankin (20.09′N–89.17′W) for Hobonil. Within rows, different letters indicate means are significantly different (P < 0.05) among regions.

** Clime type, according to García (2004).*

Table 2. Soil Characteristics in Three Regions of Yucatán, Mexico

Soil attributes	Regions			Model
	Chicxulub (CH)	X′matkuil (XM)	Hobonil (HB)	*F* value
Bulk density (Mg m^{-3})	0.70b ± 0.06	0.78ab ± 0.04	0.91a ± 0.05	5.45**
Soil texture (%)				
Sand	57.0a ± 8.2	27.8b ± 1.7	35.6b ± 1.5	9.28**
Silt	5.6a ± 1.1	7.0a ± 0.8	4.1a ± 0.3	2.90
Clays	31.7b ± 6.1	58.2a ± 0.5	56.1a ± 1.5	16.3***
Field capacity (% soil moisture)	65.6	43.0	33.1	
Permanent wilting point (% soil moisture)	57.7	35.6	26.5	

*Data are mean ± SE of 12 plots. Within rows, different letters indicate means are significantly different among regions. ** $P < 0.01$, *** $P < 0.001$.*

144 m^2 (12 × 12 m) plots per locality. Plots were installed taking into account the similar elevation and slope, and with similar MAP amounts. In addition, plot installation was carried out avoiding large variation in the vegetation structure and composition at the local scale.

METHODS

Stem and Root Biomass

During the dry season (March 2010) the above and belowground plant biomass were sampled at the three regions. To avoid the common above-ground biomass calculation error of including only a few individuals (Cheng and Niklas 2007), diameter at breast height (dbh, 1.4 m above-ground) and height for all tree trunks with dbh at least 3 cm were measured.

Seventy percent of the trees in each region were sampled for wood density determinations and a regional dbh-wood density was generated for later use in scaling up the measured diameters to estimate tree wood density in the remaining 30% of trees that were not sampled. The data points of wood density measured in the field were used to validate the regressions relating tree dbh to wood density (Table 3). To sample the wood density, we used an incremented borer to extract a stem wood core ranging from 5 to 10 cm depth into the trunk and large individual sections of branches from smaller individuals.

The Swenson and Enquist's (2008) method was used for shrubs, collecting a basal stem section and a basal wood branch section from fifty individuals near the plots. The wood density data on the basal stem and branches were used to determine the conversion equation to correct the wood density in the branch, thus avoiding extrapolation of Swenson and Enquist's (2008) equation to tropical rain forests. Wood density data on all other shrubs inside the plots were collected by sampling a branch section. Finally, for all cores and branch sections, length and diameter were measured immediately in the field after removal of the cortex. The wood density was estimated as the ratio of the oven-dried mass of a wood sample divided by its green volume (Chave and others 2006). The green volume was measured from the geometrical dimensions of the wood cores. The wood cores and branch sections were oven-dried at 70°C until they achieved a constant weight (48 h). Stem biomass ($\geq$3 cm) was estimated using the multiple regression equation for a SDTF at the Chamela Biological Station (Jalisco, Mexico; Martínez-Yrizar and others 1992) as follows: $\log_{10}$ (mass) = −0.7595 + 0.9011 $\log_{10}$ (basal area) + 0.5715 $\log_{10}$ (wood density) + 0.5654 $\log_{10}$ (height).

We used a second above-ground plant sampling to include plants with dbh below 3 cm; four microplots (1 × 1 m) into each plot were demarcated

Table 3. Equations Used to Calculate Tree Wood Density

Region	*n*	Parameter/equation	R^2_{adj}	*F* value
Chicxulub (CH)	391	Log (WD) = −0.53 − 0.04 (log BA)	0.71	933***
X′matkuil (XM)	872	Ln (WD) = −0.90 + 0.09 (ln BA)	0.44	901***
Hobonil (HB)	474	Ln (WD) = −1.60 − 0.27 (ln BA)	0.45	875***

WD wood density (g cm^{-3}), BA basal area (cm^2 $tree^{-1}$).
*** $P < 0.001$.*

and the total biomass in each micro-plot was harvested. The aboveground biomass harvested was oven-dried at 70°C until constant weight (48 h). Total aboveground biomass was calculated using the results of the multiple regression equation ($\geq$3 cm) plus the biomass harvested in the micro-plots ($<$3 cm).

Root samples were collected following Jaramillo and others (2003). One micro-plot (1 × 1 m) was established in the same plots where stem biomass was measured (that is, stem wood cores, dbh and height). Root micro-plots were carefully excavated to reach the lithic contact (~50 cm), and when necessary, roots were sampled following their route into the fractured limestone to be sure we included all of the root biomass present. The root biomass sampled and quantified was used to avoid the inconvenience of using the same regression equations in the stem and root biomass estimation. In the laboratory, roots were carefully washed and weighed. In addition, the fine roots ($\leq$ 1 mm in diameter) were sampled separately in soil cores (5 cm × 10 cm; four per plot). Roots were placed in paper bags and oven-dried at 70°C to a constant weight; the total root biomass used for allometric and ratio analyses was calculated as the sum of all diameter classes. For the allometric analysis, the stem biomass was denoted as S_M and the root biomass as R_M.

Soil Sampling and Analytical Methods

Total N and inorganic N concentration, and soil N transformation were determined in soil samples taken from the same plots as those from which the stem and root biomass were sampled. The mineral soil was sampled on March 2010 using a 5-cm diameter soil bulk density sampler (0–10 cm in depth). Four soil cores from each plot were collected randomly and stored to 4°C until they were processed. When the soil was very shallow ($<$10 cm in depth), the soil samples were collected up to rock contact. To determine net N mineralization soil was sampled by using PVC (polyvinylchloride) tube cores (5 × 10 cm) with a plastic mesh at the bottom.

Total N concentration in the soil was determined from acid digestion in H_2SO_4 concentrated for total Kjeldahl N (Anderson and Ingram 1993) and analyzed colorimetrically on a Braun Luebbe autoanalyzer system. Inorganic N (NH_4^+ and NO_3^-) concentration was determined by extraction from fresh sub-sample soil with 2 M KCl, shaken for 60 min, filtered through a Whatman No. 1 paper filter (Robertson and others 1999), and determined colorimetrically on a Braun Luebbe autoanalyzer system. Net N mineralization was measured as an indicator of N availability for plants from 14-day laboratory aerobic incubations. Before soil incubation, both ammonium (NH_4^+-N mg N g^{-1}) and nitrate (NO_3-N mg N g^{-1}) were determined by extracting with 2 M KCl. Each sample was wetted to field water holding capacity and incubated at 25°C. Net N mineralization (μg N g^{-1} day^{-1}) was estimated as the difference between initial (time = 0, before incubation) and final (t = 14 days) inorganic N concentrations. The inorganic N is reported like the NH_4^+ - N plus NO_3^- - N.

Data Analysis

All variables were log transformed prior to analysis to meet the ANOVA assumption and to make the proportional deviations consistently independent of the scale and units measurement. The Pearson correlation coefficient was calculated to explore correlations between S_M and R_M with the soil total N and inorganic N concentrations, or net N mineralization. One-way ANOVA was used to examine the effect of MAP on soil N concentrations, and net N mineralization among regions. Model Type II (RMA) regression was used to explore the slope (allometric exponent) and y-intercept (allometric coefficient) of the S_M versus R_M linear function across regions. The biomass measurements made on all 36 plots (12 per region) were used to establish the allometric function between S_M and R_M across three regions. The regression of the form $\log y = \log \alpha + \beta (\log x)$ was used to describe the allometric relationship between S_M and R_M, where x is R_M (Mg ha^{-1}), y is S_M (Mg ha^{-1}), α is the intercept, and β is the scaling slope. The adjusted R^2 was used to quantify goodness of the fitting model. The package 'smatr 3.2.2' (Warton and others 2011) for R 2.13.1 (R Development Core Team 2011) was used to determine whether the numerical values of the allometric exponent and coefficient differed. All statistical analyses were carried out using the R 2.13.1 1 program (R Development Core Team 2011).

RESULTS

Stem and Root Biomass

We found that branch wood density is a good predictor of stem wood density using a regression analysis (dbh ≥ 3: $R^2_{adj} = 0.82$; $P < 0.001$). This significant relationship suggests that stem wood density could be estimated for the trees in our study region using branch sections without having to

Table 4. Structural Characteristics and Biomass of Seasonally Dry Tropical Forest

Parameters	Chicxulub (CH)	X'matkuil (XM)	Hobonil (HB)	*F* value
Forest structure				
Tree height (m)	3.30b ± 0.22	3.34b ± 0.06	5.35a ± 0.19	43.6***
Basal area (m^2 ha^{-1})	30.1a ± 5.2	33.7a ± 3.7	30.9a ± 4.9	0.16
Tree density (stem ha^{-1})	2598b ± 338	7210a ± 391	3923b ± 441	8.38**
Stem biomass S_M (Mg ha^{-1})				
dbh $\geq$3 cm	42.19a ± 7.59	45.31a ± 5.35	62.21a ± 9.80	1.99
dbh $<$3 cm	5.24a ± 1.33	3.44a ± 0.92	3.37a ± 0.27	2.37
Total S_M	47.44a ± 7.23	48.76a ± 5.4	65.59a ± 9.70	1.68
Root biomass R_M (Mg ha^{-1})				
Diameter $\leq$1 mm	3.55a ± 0.35	3.15a ± 0.24	2.72a ± 0.33	2.09
Diameter 1–4 mm	5.11b ± 0.26	6.66a ± 0.50	4.86b ± 0.37	5.68**
Diameter $>$4–10 mm	6.03a ± 0.63	6.17a ± 0.40	3.78b ± 0.39	8.51**
Diameter $>$10–20 mm	5.81a ± 0.61	4.44 a ± 0.57	4.39a ± 0.48	2.11
Diameter $>$20 mm	1.62ab ± 0.60	0.63b ± 0.20	3.51a ± 1.07	4.05*
Total R_M	22.12a ± 1.15	21.04a ± 1.48	19.27a ± 0.17	1.26

dbh diameter at breast height.

Data are mean ± SE of 12 plots. Within rows, different letters indicate means are significantly different among regions. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

core the main stem. The equation was: $y = 0.336 + 0.964(x)$.

The total of stems (dbh ≥ 3 cm) sampled was 2,378. The total stems sampled per site decreased following the order: XM > HB > CH (Table 3). Stem height increases with MAP, and stem density was higher in the site with median precipitation (XM) compared to the sites with low and high precipitation (CH and HB, respectively) (Table 4). In contrast, basal area per unit of surface did not vary with MAP. Consistently across regions larger trees (that is, with dbh ≥3 cm) accounted for 90% of the total S_M (CH = 88.9%, XM = 95.4%, and HB = 94.7%). Due to considerable variability in S_M among the three study localities within each region, there were no statistically significant differences in S_M in absolute terms across the three regions. Also, the total R_M did not change across regions; however, inconsistent patterns across regions were observed in the biomass of different diameter roots. A remarkable contrast was observed in the proportion of large root (>20 mm in diameter) biomass to total root biomass between the wettest region and drier regions; large roots represented 7 and 3% of total root biomass in CH and XM, respectively, this proportion increased by 2–6 times in HB (to 18% of the total root biomass) showing a high proportion of larger roots in the most humid region.

Soil N Concentrations and Mineralization

Soil total N and inorganic N concentrations were higher in the driest region (that is, CH) than in the wettest region (that is, HB) (by four times for total N, and by 68% for inorganic N) (Table 5). In contrast, net N mineralization was significantly higher in HB than in XM.

Soil total N concentrations showed a significant relationship with R_M ($R^2_{adj} = 0.54$; $P = 0.005$) when the two extreme environment regions (CH and HB) were included in the model. The biomass allocated to roots at a certain soil total N concentration was higher in CH than in HB ($P < 0.001$). Soil inorganic N concentration showed the same pattern of relationship with the R_M ($R^2_{adj} = 0.36$; $P = 0.004$). At each region, the correlation between soil total N and inorganic N concentrations with R_M were as follows: CH, $r = -0.54$ and -0.62; HB, $r = -0.65$ and -0.64, respectively; $P < 0.01$). Net N mineralization did not show relationships with root biomass ($F = 0.01$; $P = 0.90$).

Patterns of Plant Biomass Allocation

The test of slope heterogeneity with combined data showed homogeneity between S_M versus R_M regression slopes across the three study regions ($P = 0.28$). The commonly computed S_M versus R_M regression slope across regions was $\beta_{RMA} = 2.52$ with 95% CIs of 1.85, 3.43 (Figure 1). The mean $\beta_{RMA} \pm$ SE was 2.59 ± 0.05, which is statistically different than the isometric ($P = 1.16e^{-0.06}$). The amount of biomass allocated to roots increased significantly less than the amount allocated to stems ($\beta_{RMA} > 1$).

Variations in the allometric coefficient (α) were observed across the S_M versus R_M regression curves

Table 5. Soil N in Three Regions of Yucatán, Mexico

Soil parameter	Regions			Model
	Chicxulub (CH)	X'matkuil (XM)	Hobonil (HB)	*F* value
Total N (%)	6.91a ± 0.13	3.79 b ± 0.27	1.83c ± 0.13	54.8***
Inorganic N (mg N g^{-1})	0.47a ± 0.01	0.47ab ± 0.06	0.28b ± 0.01	7.35**
Net N mineralization (mg N g^{-1} d^{-1})	0.65ab ± 0.24	0.09b ± 0.01	1.35a ± 0.36	5.68**

Inorganic N (NO_3^- plus NH_4^+). Data are mean ± SE of 12 plots. Within rows, different letters indicate means are significantly different among regions.
*** P < 0.01, *** P < 0.001.*

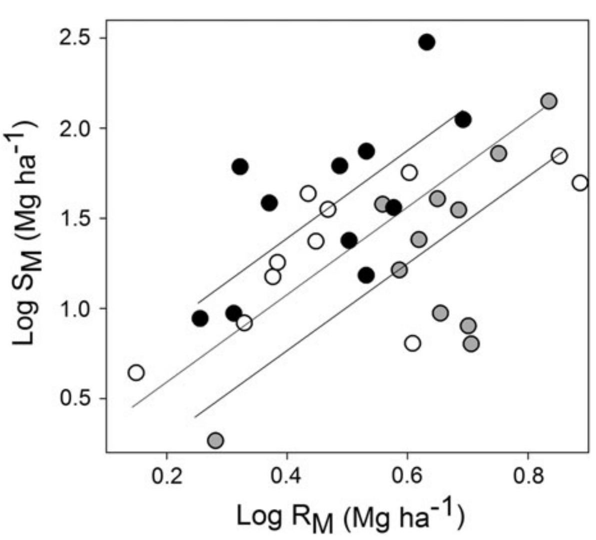

Figure 1. Reduced major axis (RMA) regression between stem biomass (S_M) and root biomass (R_M) in three regions of Yucatán, Mexico: Chicxulub, MAP = 531 mm (*gray circles*); X'matkuil, MAP = 993 mm (*empty circles*); and Hobonil MAP = 1036 mm (*solid circle*).

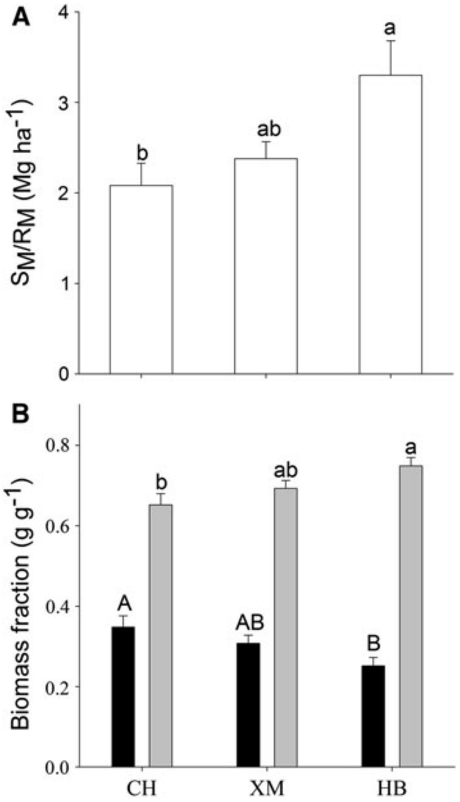

Figure 2. a Stem/root biomass (S_M/R_M) ratio and **b** biomass fractions of roots (*black bars*) and stems (*gray bars*) in three regions of Yucatán, Mexico: Chicxulub, MAP = 531 mm (CH); X'matkuil, MAP = 993 mm (XM); and Hobonil, MAP = 1036 mm (HB). The *lowercase letters* (*a*, *b*) indicate that means are significantly different ($P < 0.05$) among regions for S_M/R_M ratio or stem biomass fraction, and the *uppercase letters* (*A*, *B*) indicate that means are significantly different ($P < 0.05$) among regions for root biomass fraction.

between driest and wettest regions ($W = 14.36$; $P = 0.0006$), indicating that the values of S_M vary with respect to R_M across different water availability conditions. Less biomass was allocated to stems in the low-MAP region than in the high-MAP region for any given amount of biomass allocated to roots.

The influence of region on biomass allocation patterns (represented by the biomass ratio, S_M:R_M) was statistically significant (Figure 2a; $F = 4.58$; $P = 0.01$). The stem biomass fraction increased and the root fraction decreased with MAP (Figure 2b). Thus, the S_M:R_M ratio increased with increase in the MAP.

The correlation analyses showed a negative relationship between the S_M:R_M ratio and soil total N and inorganic N concentrations (Figure 3). Thus, the fraction of biomass allocated to roots increased and the fraction allocated to stems decreased as soil N availability increased. On the other hand, the results did not show a significant relationship between the S_M:R_M ratio and soil net N mineralization ($F = 0.07$; $P = 0.78$).

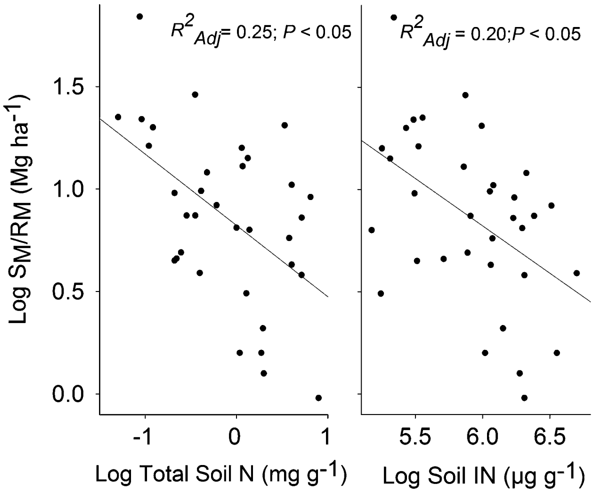

Figure 3. Log stem/root biomass (S_M/R_M) ratio as a function of total soil N and inorganic N (soil IN) concentrations in Yucatán, Mexico.

DISCUSSION

Stem and Root Biomass Across the Precipitation Gradient

The range of values for stem biomass estimated in our study is lower than the range found in other studies that were carried out in other SDTFs in the Yucatán (Lawrence and Foster 2002; Cairns and others 2003; Vargas and others 2008). Our stem biomass data are at the lower end of the range reported for SDTFs (35–140 Mg ha^{-1}; Jaramillo and 2011), and are comparable with the aboveground biomass estimate by the MODIS model for SDTFs in Central America ($<$100 Mg ha^{-1}; Saatchi and others 2011). The low quantity of aboveground biomass observed in our study may be due to the timing of the sampling, which was late in the dry season after the plants achieved dry acclimation which is likely to lead to underestimating aboveground plant biomass of the smaller-than-3 cm dbh category (Bazzaz and Grace 1997). In addition, in the Yucatán peninsula anthropogenic disturbance is recognized as an important determinant of the aboveground biomass variation (Chave and others 2001; Urquiza-Haas and others 2007); in this way, although anthropogenic disturbances have not been reported in our study areas for at least 30–50 years before present, logging and other disturbances that affect the aboveground biomass cannot be ruled out in our study sites (White and Hood 2004; Urquiza-Haas and others 2007).

Also root biomass in Yucatán forests is comparable with the reported data for other SDTFs in Mexico (16–35 Mg ha^{-1}; Jaramillo and 2011) and falls into the expected value of 22.7–31.8% (as a percentage of the total biomass) reported by Murphy and Lugo (1986; 8–50%) in SDTFs. However, in absolute terms, our results contrast with other studies reporting that root biomass is correlated with soil water availability; according to which, the water stress causes greater root biomass allocation (Sanford RL and Cuevas 1996). The last mentioned pattern and the lack of a relationship between soil total N and soil inorganic N concentrations with total root biomass suggests that biomass allocation to roots in the SDTF is not responding to soil resource availability as was suggested by Cairns and others (1997) in the world's upland forest. The lack of relationships observed in the Yucatán could be an indication that water stress conditions could be resolved by other ways that do not include readjustment of either total root biomass or fine roots ($\leq$1 mm in diameter).

Patterns of Biomass Allocation

In contrast to our expectations, the RMA analyses showed that plant biomass allocation follows the same rule of plant biomass allocation to S_M and R_M across the three regions with different water availabilities; that is, the slope of S_M versus R_M was statistically equal across the regions. This result is consistent with the idea of *conservative* plant biomass allocation (Müller and Schmid 2000; Poorter and Nagel 2000), according to which the strategy of plant biomass allocation does not change with resource availabilities.

The log–log S_M and R_M regression showed slope values different from 1.0 ($\beta_{\text{stem–root}} > 1$); which is in contrast to the isometric prediction (Enquist and Niklas 2002) and showed that biomass allocated to stems will increase disproportionally with biomass allocated to roots across the regional variation in the SDTF. Despite the non-isometric stem to root scaling pattern observed in regions with MAP lower than 1,500 mm (Yang and Luo 2011), the generality of isometric scaling has been favored over an allometric explanation (Yang and Luo 2011) mainly based on factors that led to underestimating root biomass (for example, Cheng and Niklas 2007). Nevertheless, the last argument could well apply to all regions, and therefore still be useful to determine how biomass allocation differs among biomes (Poorter and others 2011), without ignoring the difficulty of root biomass estimation. However, it has been pointed out that woody species (the dominant form of forest stands in the SDTF) showed an increased investment in stems biomass (Poorter and others 2011). On the other hand, it may be more parsimonious for plants to have a simple allometric strategy—different from the isometric one—than to adjust their biomass allocation to particular resource availabilities (Müller and Schmid 2000). In addition, the different *y*-intercept between the allometric trajectories showed the expected pattern, according to which the plants are usually small under low resource conditions and large under high resource conditions (Müller and Schmid 2000). The increased allometric coefficient for allocation to stems versus roots by water availability observed in the Yucatán shows that plants at the ecosystem scale, in the same way as at the species scale, allocate more biomass to stems regardless of the plant size when water resources increase (Müller and Schmid 2000).

The environmental effect missing in allometric analyses is obvious in the ratio analysis although the allometric analyses have a better fit ($R^2_{\mathrm{adj}} = 0.50$) than the ratio analyses ($R^2_{\mathrm{adj}} = 0.26$), which is in agreement with the result reported by (Müller and Schmid 2000). The increasing $S_\mathrm{M}/R_\mathrm{M}$ ratio with MAP increases observed in our study has been reported for other forests as evidence that $S_\mathrm{M}/R_\mathrm{M}$ ratios become higher as moisture availability increases (Cairns and others 1997; Schenk and Jackson 2002; Mokany and others 2006) in spite of the lack of water availability effect on the absolute S_M and R_M values.

The expectation that biomass allocation to R_M increases when soil nutrient availability decreases (Bloom and others 1985; Shipley and Meziane 2002) was not supported by our data. In absolute terms, $\mathrm{R_M}$ did not show any significant trend in relation to soil N (both total and inorganic concentrations). The inverse relationship between soil N and root biomass reported for nutrient poor soils (Vitousek and Sanford 1986; Vogt and others 1995) was not corroborated in our study. In contrast, our results showed a negative correlation between the $S_\mathrm{M}/R_\mathrm{M}$ ratio and soil total N and inorganic N concentrations. We cannot determine whether such a decrease in $S_\mathrm{M}/R_\mathrm{M}$ ratio resulted from the observed increase of soil N content itself (thus relaxing a possible direct N limitation to plants) (for example, Campo and Vázquez-Yanes 2004), or whether it reflects decreased nutrient stress (an indirect consequence of increase in MAP), or both.

In summary, we conclude that the particular properties of SDTFs (with a markedly seasonal rainfall regime, soil N variation, and soil water retention capability) could leave a mark on plant biomass allocation, in addition to other ecosystem attributes (compare Schwinning and others 2004). In our case, plant biomass allocation moves to S_M over R_M and the slope value moves away from 1. Given that aboveground biomass is most vulnerable to events such as fire, logging, land conversion, storms, and pests (Houghton and others 2009), our results demonstrate the vulnerability of the carbon stock in SDTF ecosystems given the trend for aboveground biomass away from belowground biomass allocation. The potential for carbon release to the atmosphere with disturbance to the SDTF is high and requires measures to avoid forest degradation.

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CAPÍTULO III

Shifting in foliar traits and their correlationship along the water availability gradient

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Resumen

Los caracteres foliares y la relación entre ellos tienen implicación importante no solo para el rendimiento de la planta sino para el funcionamiento del ecosistema. Dichos rasgos están estrechamente asociados con el uso de los nutrientes por las plantas y podrían mostrar el estado de los nutrientes del suelo. Los rasgos foliares así como el ciclo de los nutrientes en el suelo se ven afectados por las condiciones climáticas. Plantas que viven en sitios secos tienen hojas gruesas con alto contenido de nitrógeno lo que puedan promover el recambio del nitrógeno. Nosotros estudiamos la variación de los rasgos foliares, su relación y la relación entre el componente de rasgos foliar y la mineralización del nitrógeno del suelo a lo largo del gradiente de precipitación en el bosque tropical estacionalmente seco en Yucatán, México. Se llevo a cabo un análisis para cada rasgo foliar y se exploro la relación entre ellos. Además, se llevó a cabo un análisis multivariado de los rasgos foliares y su variación a lo largo del gradiente de precipitación. Finalmente, se exploró la correlación entre el componente de los rasgos foliares y la mineralización de nitrógeno en el suelo. La mayoría de los rasgos foliares variar significativamente de una manera diferente entre las especies a lo largo del gradiente de precipitación. La relación rasgo a rasgo está lejos de ser invariantes para las especies y para los sitios de precipitación diferente. Un importante resultado muestra que el área foliar específica y la relación nutriente foliar no fue significativa para todos los sitios y esa relación fue negativa. El primer componente principal de los caracteres foliares se correlaciona significativamente con la mineralización del nitrógeno del suelo.

Palabras clave: bosque caducifolio, δ^{15}N foliar, paisaje kárstico, nutrientes foliares, ciclo del N, bosque tropical caducifolio, SLA.

Abstract

The foliar traits and the relationship between them have important implication on plant performance and beyond, on the ecosystem function. Since those foliar traits are closely associated with plants nutrient use, they could show the soil nutrient status. Foliar traits as well as soil nutrients cycles are affected by the clime conditions. Plants living in dry sites have thick leaves with high nitrogen content which can promote high nitrogen turnover. In order to explore the leaf trait variation, their relationship and the relationship between the foliar traits component and soil nitrogen mineralization, we measured the soil nitrogen mineralization and six leaf traits from four co-occurring deciduous species in seasonally dry tropical forest in Yucatán, Mexico along the precipitation gradient. We carried out analysis for each foliar trait and explored the trait to trait relationship, and it was carried out a multivariate analysis of foliar traits and their variation along the precipitation gradient. Finally, it was explored the correlationship between the leaf trait component and the soil nitrogen mineralization. Most of the foliar traits vary significantly in a different way among species along the precipitation gradient. The trait-to-trait relationship is away to be invariant for species and for the different precipitation sites. An important result shows that specific leaf area and leaf nutrient relationship was not significant to all sites and such relationship was negative. The first principal component from the six leaf traits was statistically significant correlated with the soil nitrogen mineralization.

Key words: Deciduous forest, foliar δ^{15}N, leaf nutrients, N cycle, seasonally dry tropical forest, specific leaf area.

Introduction

Foliar traits play an important role beyond plant performance. They are closely related to carbon assimilation; N uptake and water use and, thus, drive the biogeochemical cycles and energy balance of terrestrial ecosystems (Ackerly *et al.* 2002; Wright *et al.* 2004). Foliar traits changes along the environmental gradient have important implication not only on plants performance but on the ecosystem functioning (Ackerly *et al.* 2002; Laughlin *et al.* 2011). There are a general trend occurring across a wide range of species; for instance, species inhabiting dry sites have low specific area (SLA) and high nutrient content, in order to reduce water loss (Wright *et al.* 2001;

2002). Together with another leaf attributes such leaf dry matter content (LDMC) it has been possible to infer the plant strategy to resource-use and beyond the species, the relationship with soil resources to ecosystem scale (Garnier *et al.* 2001; 2011; Li et al 2005). This is particularly true for soil nitrogen (N) which accounts for about 88% of the global N to plant nutrition (Schlesinger 1997). Species with high leaf N content by mass ($\mathrm{LNC_{mass}}$) and SLA produce high-quality litter with highest decomposition rates both associated with increased rates of soil N transformations (Laughlin *et al.* 2010; Orwin *et al.* 2010). Since the soil N cycle and foliar traits change with the water availability (Aranibar *et al.* 2004; Wright *et al.* 2001), likewise the proportionality of their relationship differs along the water availability gradient too. However few studies have examined such relationship taking into account the water availability.

Water limitation is common across a wide set of forest ecosystems, as in seasonally dry tropical forests (SDTF), which are characterized several months of drought during which precipitation is lower than 100 mm per month (Pennington *et al.* 2009). The extreme drought, occurring at least five months each year, may control plant growing strategies (Prior *et al.* 2003), directly by the effect of water availability on organisms or indirectly by the effects of soil water on nutrient availability (Austin and Vitousek 1998). Here we explored how the foliar traits vary along a precipitation gradient, as well as how the relationship between the foliar traits and soil N mineralization vary between different forests exposure to different precipitation regime in seasonally dry tropical forest (SDTF). We also included additional analysis to explorer the leaf trait relationships along the precipitation gradient. SDTFs cover the largest area (12.5%) of North and Central America and have a high risk (39.8%) of climate change, with a trend toward substantial rainfall reduction per at least 50 mm $\mathrm{year^{-1}}$ (Miles *et al.* 2006; Neelin *et al.* 2006). Perhaps the most conspicuous characteristic of SDTFs are the pronounced seasonality in rainfall distribution resulting in several months of drought (Pennington *et al.* 2009), which exert control on leaf traits directly by the effect of water availability on organisms or indirectly by the effects of soil water on nutrient availability (Prior *et al.* 2003; Austin and Vitousek 1998).

We measure a core of six foliar traits in four deciduous species from three sites (low, intermediate and high precipitation); focusing on the shifts in the foliar attributes and the proportionality among SLA and $\mathrm{LNC_{mass}}$, leaf phosphorus content ($\mathrm{LPC_{mass}}$), LDMC and leaf thickness relationship along the water availability gradient. Simultaneously, we evaluated the usefully of the leaf traits as indices of soil nutrient status by including measured of soil net N mineralization. Previously, it has been pointed that the leaf traits relationship are *invariant* across all species and environments (Reich *et al.*1997); however, recent research has shown contrasting results (Chen *et al.* 2011). Our expectation were as follows: (1) leaf traits shift among sites, conserving the species ranking (2) the relationships between foliar traits vary independently among different species and among sites and finally (3) leaf traits component reflect the soil N mineralization.

Methods

Study site and species selection

We selected three sites in the Yucatán peninsula in south eastern-Mexico, located within the limestone karsts landscape with deciduous and semi-deciduous forests (Miranda 1958; Challenger and Soberón, 2008). Leguminosae is the most abundant family (Ceccon *et al.* 2002; Zamora *et al.* 2008) and the canopy typically reaches heights of 3 to 10 m, sometimes reaching 15 m. The climate is hot and sub-humid and supports either tropical dry or very dry forest in the Holdridge *et al.* (1971) system. Soils are shallow, calcareous, and highly permeable (Solís and Campo, 2004) and underlying limestone fractured bedrock (Whigham *et al.* 1990).

Sites are located along a gradient of mean annual precipitations (MAP; ~530 to 1036 mm yr^{-1}) that include a marked dry mean monthly precipitation gradient. Our study sites follow a gradient of soil water retention according to which the site with low precipitation show the high soil water retention capacity (Roa-Fuentes *et al.* 2012). Sites represent low, intermediate and high water availability conditions as follow: Chicxulub (thereafter CH), X'matkuil (XM) and Hobonil (HB).

Four deciduous tree species were included into our study, which are the most common co-occurring tree species in the three sites. Two most common legumes species *Piscidia piscipula* (L.) Sarg., and *Lysiloma latisiliquum* (L.) Benth. And the other two are the most common non-legume species (*Busera simaruba* (L.) Sarg. and *Gymnopodium floribunda* Rolfe). We examined six replicate trees per site (diameter breast height, DBH to 1.30 m > 10 cm) of each of the four target tree species (n = 24 trees per site). Mature (*i.e.*, breeding age) trees were randomly chosen within each mixed species stand.

Leaf and soil sampling

We measured SLA (cm^2 g^{-1}), leaf thickness (µm), LDMC (mg dry mass g^{-1} fresh mass), LNC$_{mass}$ (mg N g^{-1} dry leaf mass), leaf P content mass (LPC$_{mass}$, mg P g^{-1} dry leaf mass) and natural abundance foliar ^{15}N (hereafter referred as δ^{15}N). Twenty to thirty sun-lit foliage samples were collected from the upper canopy in the wet season (September) of 2010 and 2011. Only mature and fully expanded leaves were selected and were kept in water-saturated conditions following the protocol proposed by Garnier *et al.* (2001). Surface area was measured using a leaf area meter (LI 3100C), fresh mass was measured immediately, and these leaves were oven-dried at 70°C to constant weight. SLA was calculated as the quotient of leaf area and average leaf dry mass, excluding the petioles. The rachis was included for compound-leaved species. LDMC was calculated as the ratio of leaf dry mass and fresh mass. Leaf thickness was measured using a digital micrometer (Mitutoyo 293). Remainder leaves were dried and processed for foliar N and P content. Foliar LNC$_{mass}$ and LPC$_{mass}$ were determined by acid digestion using Kjeldahl method (Anderson and Ingram, 1993). Natural abundance N isotope analysis was carried out in the Stable Isotope Laboratory of Boston University. Leaves were combusted in a Euro EA Elemental Analyzer and the combustion gases were separated on a GC column, passed through a GV Instruments diluter and reference gas box, and analyzed for ^{15}N content on a GVI IsoPrime isotope ratio mass spectrometer. Continuous flow analysis also reported N content of each sample. Additionally we collected soil (0 - 10 cm depth) in the same dates as leaves to determine the rates of net N mineralization; which was evaluate in 14 day laboratory aerobic incubations (Robertson *et al.* 1999); each sample was wetted to field water holding capacity with deionized water and incubated at 26°C.

Statistical analyses

All data were log transformed prior to analysis to meet the assumption of normality. Values for leaf traits were averaged across the two years (2010 and 2011) because they were not significantly different among the two years ($P > 0.05$). The effect of species identity and water availability on the leaf traits were analysed using two-way analysis of variance (ANOVA) and Tukey HSD method was used to make pairwise comparisons when the effect of factor was statistically significant ($P \leq 0.05$). Student's t-test was used to determine whether δ^{15}N mean for each species was significantly different from 0‰. We interpreted foliar $\delta^{15}N$ values close to 0‰ as an indicator of plants with access to N_2; in contrast, we interpreted $\delta^{15}N$ values different from 0‰ as plants having a majority of their N come from other sources (Robinson, 2001). Pearson´s tests were used for comparing the significance of correlations among SLA and leaf structural and nutrient traits. Standardized major axis (SMA) slopes with 95% confidence intervals were fitted for describing the bivariate relationship when the proportional relationship between variables across the species and sites was required. The package 'smatr 3.2.2' (Warton *et al.* 2011) was used with R to determinate whether the numerical values of allometric exponent and coefficient differed. We also analysed standardized data using principal components analysis (PCA) to account total leaf trait spectrum variation into a component. The principal component derived from the PCA and soil net N mineralization was used to obtain the bivariate relationship. We used the package "vegan 2.0-3" (Oksanen *et al.* 2011) to carry out the PCA. All statistical analyses were carried out using the R 2.13.1 1 program (R Development Core Team 2011).

Results

Foliar attributes variation

All leaf attributes showed significant differences among tree species and except for LDMC, all leaf attributes showed a significant site effect (Tables 1 and 2). There was also a statistically significant interaction between the effects of species and site on SLA, thickness, LNC_{mass} and LPC_{mass} values with distinct patterns between species by site. Species ranking for leaf traits among different environments was not maintained (Fig 1); except by species ranking for LDMC. The four tree species had a consistent pattern of LDMC across the three sites, from high to low as follows: *L. latisiliquum*, *G. floribundum*, *P. piscipula* and *B. simaruba* (Table 1). Foliar $\delta^{15}N$ values of *P. piscipula* were the lowest across the three sites (CH: 2.56 ± 0.29‰; XM: 0.21 ± 0.24 ‰; HB: 0.53 ± 0.38 ‰) and natural abundance ^{15}N in foliage in this was not statistically different from 0‰ (t = 14.88; P = 0.42 and t = 1.37; P = 0.22) in XM and HB. *G. floribundum* had significantly higher $\delta^{15}N$ values across three sites (Fig 1) compared to *B. simaruba* and *L. latisiliquum*. $\delta^{15}N$ values decreased with increasing the water availability for all four tree species (CH > XM = HB).

SLA varied 1.5 fold (103.45 – 162.90 $cm^2\ g^{-1}$) among species following the ranking from high in

B. simaruba and *G. floribundum* (no-legumes species) to low in *L. latisiliquum* and *P. piscipula* (legumes species) in the two sites with lowest (CH) and highest water availability (HB; $F = 6.30$, $P = 0.002$) (Table 1).There was no significant difference in SLA among the four tree species at the intermediate water availability site, XM (Table 1). Leaf thickness did not show consistent trends between species and site except by the lower leaf thickness values for *G. floribundum* across all three sites ($F = 11.31$; $P < 0.0001$; Fig 1). Legumes and no-legumes from all sites showed a general ranking of lower $\mathrm{LNC}_{\mathrm{mass}}$ for *B. simaruba* (13.8 mg N g^{-1} ± 0.8) and *G. floribundum* (18.5 ± 0.5) compared to *L. latisiliquum* (24.7 ± 0.8) and *P. piscipula* (23.2 ± 0.5). $\mathrm{LPC}_{\mathrm{mass}}$ values showed a similar trend for species and sites.

Pairwise comparisons between leaf area and leaf dry mass across all tree species showed a common slope ($P = 0.69$) indistinguishable from 1 ($R^2 = 0.95$; $P = 0.59$; 95% CI = 0.93 – 1.32); *i.e.*, to the four tree species the lamina surface area scale isometrically with foliar dry mass. Slope for individual species ranged between 0.94 for *B. simaruba* ($R^2 = 0.55$; $P = 0.0005$), 0.85 for *G. floribundum* ($R^2 = 0.66$; $P = 0.00004$), 0.77 for *L. latisiliquum* ($R^2 = 0.40$; $P = 0.005$) and 1.03 for *P. piscipula* ($R^2 = 0.52$; $P = 0.0007$). Numerical *y*-intercept value was different ($P < 0.0001$) between species; Tukey multiple comparisons between *y*-intercept values showed significant differences when *B. simaruba* was compared with the remained tree species (*P. piscipula*, *L. latisiliquum* and *G. floribundum*). The last mentioned results are consistent across three sites ($P = 0.93$).There was a significant negative relationship between SLA and leaf thickness across all plant species and within each site (Table 3). In the same way, the relationship between SLA and LDMC was negative; however, the correlation was not statistically significant in the intermediate water availability site (XM) and for the legume species (*L. latisiliquum* and *P. piscipula*). The relationships between SLA and $\mathrm{LNC}_{\mathrm{mass}}$ or $\mathrm{LPC}_{\mathrm{mass}}$ relationship were not statistically significant for three species and it was negatively correlated in the lowest and highest water availability sites (CH and HB).

We found a common slope of -0.57 for fitting SLA-$\mathrm{LNC}_{\mathrm{mass}}$ for each site ($P = 0.27$; CI = -0.71 to -0.47); showing that $\mathrm{LNC}_{\mathrm{mass}}$ decreased slowly than proportionally with SLA. The SLA-$\mathrm{LNC}_{\mathrm{mass}}$ relationship was not significantly ($P = 0.49$; $R^2_{Adj} = 0.02$) when the fitting slope was analysed via SMA in intermediate water availability site (XM) (Fig. 2). Individual SLA-$\mathrm{LNC}_{\mathrm{mass}}$ slopes by species were heterogeneous ($P = 0.042$), and the bivariate relationship was significantly only to

G. floribundum (-0.83, R^2_{Adj} = 0.32; *P* = 0.016). Slope common test showed that SLA-LPC_{mass} bivariate relationship to each site showed common slope of -0.76 (*P* = 0.20). The elevation test showed a marginal significantly differences between XM and HB (*P* = 0.04). The bivariate relationship SLA and LPC_{mass} was not significant to each specie (*B. simaruba*, *P* = 0.09; G. *floribundum*, *P* = 0.08; *L. latisiliquum*, *P* = 0.90 and *P. piscipula*, *P* = 0.17).

Link between foliar traits and soil N mineralization

The multivariate leaf traits analyses showed a first principal component (PC1) accounted for 47% of the total variance (Fig. 3). This PC1 presented high loadings for SLA (eigenvector = -0.50) and LNC_{mass} or LPC_{mass} (eigenvectors = 0.49 and 0.48, respectively). The second principal component (PC2), accounted for 12.27% of the total variation, presented contrasting high loadings for LDMC and leaf thickness. Species found at the negative end of the PC1 exhibited high SLA values (no-legumes: G. floribundum and B. simaruba). In contrast with the species found at the positive end of this spectrum (Legumes: L. latisiliquum *and* P. piscipula*) who exhibited the high* LNC_{mass} *and* LPC_{mass}*.*

Additional analysis showed a significant positive relationship between rates of net N mineralization and leaf trait spectrum at all sites. Linear bivariate relationship between net N mineralization and leaf traits spectrum across sites showed a common slope of 0.18 (*P* = 0.10; CI: 0.15 to 0.24). There were clear difference between the numerical value of *y*-intercept, with lower soil N mineralization at a given point of leaf trait spectrum for low water availability site (CH, 2.46) and there were no differences between intermediate and high water availability sites (XM, 3.16 and HB, 3.10).

Discussion

Shift in Leaf trait between species and site

In contrast with our prediction (1), the pattern of foliar traits responds in a different way among species and sites with different water availability**.** Almost all foliar traits (except LDMC) varied between co-occurring deciduous species with distinct ranking among sites. The last results suggest flexibility in leaf trait adjustment in response to water availability. Thus, the pattern of species' response to water availability is not maintained when comparing co-occurring deciduous tree species in SDTF. LDMC was the most stable leaf traits conserving the species hierarchy, suggesting less sensitivity to variation in water availability compared to other leaf traits. A similar conclusion was reached by Li *et al.* (2005) in plants growing in sand dunes; they found that LDMC is relatively insensitive to variation in soil resources.

Our results support the inverse relationship of foliar $\delta^{15}N$ and precipitation gradient (Table 1) that has been widely documented (Austin and Vitousek, 1998; Amudson *et al.* 2003). $\delta^{15}N$ values indistinguishable from 0‰ for *P. piscipula* in the intermediate and high water availability sites suggest that this tree species has access to N_2 when water is most available. Inhibition of nitrogenasa activity and *Rhizobium* nodulation could have occurred at the driest site (CH) as a response to drought stress and high availability of alternative inorganic N sources (NO_3^- and NH_4^+) as was documented for Schubert (1995).

Unlike past studies (Reich *et al.* 1999; Wright *et al.* 2001), we did not observe increasing of SLA in the site with the most water availability. Since that SLA is most determiners in the foliar adaptation to irradiance (Hodgson *et al.* 2011), the lack of the SLA's response to precipitation in our tropical ecosystem with high irradiation is in concordance with the weak global control of precipitation on the SLA reported by Wright *et al.* (2004). The mean values of SLA (132.03 cm^2 g^{-1}) falls into the range reported recently by Pringle *et al.* (2011) for deciduous species in a SDTF of Chamela-Mexico (MAP = 735 mm y^{-1}) and is greater compared to those reported by Powers and Tiffin (2010) for a SDTF of Costa Rica (MAP = 1500 to 1700 mm $year^{-1}$).

Lower SLA values of legumes tree species (*L. latisiliquum* and *P. piscipula*) compared to non-legumes tree species (*B. simaruba* and *G. floribundum*), are in concordance with results reported by Powers and Tiffin (2010) and suggesting that leguminous species are reducing water loss and susceptibility to desiccation or other biotic factors such herbivory, by construct thick leaves (Lambers and Poorter, 1992).

LNC_{mass} shows a trend to decline in sites with increased in water availability, changes of LNC_{mass} has been considered in other studies at the global scale (Reich and Oleskin, 2004; Wright *et al.* 2001; 2005). High LNC_{mass} in legumes tree species indicated a high N demanding to allow keep high levels of N in their leaf tissue along the precipitation gradient (Crews, 1999; Campo and Dirzo, 2003). The high leaf quality of legumes species in our study has been considered independent of their capacity to fixing atmospheric N, and the N fixation cannot be assumed (Sprent 1995). The observed variation in almost all leaf traits, along the water availability gradient, may be attributable to genotypic differences in addition to phenotypic plasticity in response to water availability. Regardless the explanation for intraspecific variability it is important highlight that leaf trait variation is not associated invariantly with species identity and with the sites in the SDTF.

Leaf trait relationship

In concordance with our expectation (2), similar the leaf traits correlationship varied independently between species and sites. Our results do not show the positive and invariant relationship between SLA and LNC_{mass} as was found per Chen *et al.* (2011). SLA and LNC_{mass} relationship has been considered spurious (Shipley *et al.* 2005), since LNC_{mass} is causally independent of SLA. Our results have important implications, since the relationship SLA-LNC_{mass} has been considered as a plant response to physical and evolutionary constrains. They are in concordance with the Shipley *et al.* (2005) proposition about of such constrictions are not absolute. Since our target tree species are growing in high light and N availability environments, we suggest that thick leaves (low SLA), and increased leaf N per mass unity are indicating a suboptimal LNC_{mass} at a given SLA. Given that SLA does not affect the whole leaf efficiency on light capture (Evans and Poorter, 2001) we can suppose that the slight change of LNC_{mass} along the water availability gradient are driving the leaf response to environmental changes to keep high photosynthetic rates.

Finally in concordance with our expectation (3) our result reflects the positive relationship of leaf quality with increases in net N mineralization, by the positive relationships with PCA1. Such relationship is influenced by legumes species (*L. latisiliquum* and *P. piscipula*) which showed the highest leaf N and P content. Thus, leaf trait spectrum show to be effective as indicator of soil net N mineralization; which highlights the effect of leaf traits on belowground ecosystem process, such as N cycling. Similar results have been reported in Ponderosa pine forest by Laughlin *et al.*, (2011). The mechanistic interpretation of this positive correlationship was explored by Orwin *et al.* (2010), who found a promotion in bacteria communities favoring fast rates of soil N cycling, in soil beneath species with increased leaf quality. The common slope in the bivariate analysis net

N mineralization and leaf trait spectrum suggest equivalence in the predictive power of leaf trait spectrum on net N mineralization along the water availability gradient in SDTF.

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Table 1. Mean ± standard error of leaf traits of co-occurring tree species across three sites in seasonally dry tropical forest at Yucatán, Mexico. Different lowercase letters indicate that means are significantly different ($P \leq 0.05$) among co-occurring species within each site. Different uppercase letters indicate that means are significantly different ($P \leq 0.05$) among sites for each tree species.

Foliar traits	Sites		
	Chicxulub	X´matkuil	Hobonil
	SLA (cm^2 g^{-1})		
B. simaruba	153.13^{aA} ± 9.02	114.13^{aA} ± 5.31	156.98^{abA} ± 18.66
G. floribundum	130.93^{aB} ± 4.55	149.50^{aAB} ± 15.86	201.60^{aA} ± 19.04
L. latisiliquum	94.72^{bA} ± 11.1	140.55^{aA} ± 27.99	99.15^{cA} ± 11.04
P. piscipula	86.06^{bB} ± 3.88	103.30^{aAB} ± 6.05	125.53b^{bA} ± 9.61
	Thickness (µm)		
B. simaruba	239.94^{bB} ± 11.67	277.31^{aA} ± 6.35	224.51^{aB} ± 8.77
G. floribundum	195.30^{bA} ± 8.44	186.25^{cA} ± 11.14	125.75^{bB} ± 7.94
L. latisiliquum	258.33^{bA} ± 34.03	220.62^{bcA} ± 19.04	233.77^{aA} ± 22.31
P. piscipula	353.82^{aA} ± 16.57	281.17^{abAB} ± 14.57	231.20^{aB} ± 19.37
	LDMC (mg g^{-1})		
B. simaruba	280.88^{cA} ± 22.13	318.92^{cA} ± 10.27	297.34^{cA} ± 23.90
G. floribundum	394.70^{abA} ± 10.86	377.55^{abA} ± 21.02	400.75^{abA} ± 37.41
L. latisiliquum	446.74^{aA} ± 26.17	418.83^{aA} ± 4.90	457.86^{aA} ± 15.82
P. piscipula	326.49^{bcA} ± 14.23	350.87^{bcA} ± 14.28	351.23^{bcA} ± 17.81
	LNC$_{mass}$ (mg N g^{-1})		
B. simaruba	18.83^{cA} ± 0.93	21.07^{bcA} ± 0.30	16.42^{bB} ± 0.52
G. floribundum	19.24^{bcA} ± 0.66	20.31^{cA} ± 0.66	13.09^{cB} ± 0.52
L. latisiliquum	26.33^{aA} ± 1.14	26.51^{aA} ± 1.06	21.84^{aB} ± 0.99
P. piscipula	21.92^{bA} ± 0.58	23.40^{bA} ± 0.42	23.81^{aA} ± 1.21

	LPC$_{mass}$ (mg P g^{-1})		
B. simaruba	$1.44^{cB} \pm 0.11$	$1.85^{bA} \pm 0.06$	$1.58^{bAB} \pm 0.05$
G. floribundum	$1.59^{bcA} \pm 0.18$	$1.59^{cA} \pm 0.05$	$1.10^{cB} \pm 0.07$
L. latisiliquum	$2.59^{aA} \pm 0.11$	$2.25^{aA} \pm 0.06$	$1.83^{aB} \pm 0.12$
P. piscipula	$2.04^{abA} \pm 0.06$	$2.10^{aA} \pm 0.03$	$1.82^{aB} \pm 0.08$
	$\delta^{15}N$ (‰)		
B. simaruba	$5.21^{aA} \pm 0.19$	$0.98^{bC} \pm 0.20$	$2.07^{aB} \pm 0.25$
G. floribundum	$5.35^{aA} \pm 0.47$	$3.17^{aA} \pm 1.06$	$2.07^{aA} \pm 0.52$
L. latisiliquum	$5.68^{aA} \pm 0.49$	$1.51^{abB} \pm 0.10$	$1.23^{abB} \pm 0.11$
P. piscipula	$2.56^{bA} \pm 0.29$	$0.21^{bB} \pm 0.24$	$0.53^{bB} \pm 0.38$

No-legumes: *B. simaruba* (*Bursera simaruba*) and *G. floribundum* (*Gymnopodium floribundum*). Legumes: *L. latisiliquum* (*Lysiloma latisiliquum*) and *P. piscipula* (*Piscidia piscipula*). SLA, specific leaf area; LDMC, leaf dry matter content; LNC$_{mass}$, leaf nitrogen content mass; LPC$_{mass}$, leaf phosphorus content mass.

Table 2. *F*-ratios and significant levels of two ways ANOVA for leaf traits of the co-occurring tree species across the three sites in a seasonally dry tropical forest of the Yucatán, Mexico. ($P \leq 0.05$; $n = 6$).

Leaf traits	Effect tests			Total Model	
	Species	Site	Species * Site	F	R^2_{Adj}
SLA	13.26 ***	4.47 **	3.43 **	6.30 ***	0.45
Thickness	29.12 ***	13.43 ***	3.44 *	12.51 ***	0.64
LDMC	29.87 ***	0.87 NS	0.88 NS	8.47 ***	0.53
LNC_{mass}	64.34 ***	37.12 ***	8.42 **	28.89 ***	0.81
LPC_{mass}	40.17 **	17.66 ***	4.54 ***	16.65 ***	0.71
$\delta^{15}N$	6.63 ***	22.47 ***	1.40 NS	6.83 ***	0.48

NS = not significant. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. SLA, specific leaf area; LDMC, leaf dry matter content; LNC_{mass}, leaf nitrogen content mass; LPC_{mass}, leaf phosphorus content mass.

Table 3. Pearson correlation coefficients for specific leaf area and leaf structural and nutrient traits in three sites (CH, Chicxulub; XM, X´matkuil and HB, Hobonil) in a seasonally dry tropical forest of the Yucatán, Mexico.

Leaf traits	Specific leaf area							
	Total (*n* = 72)	Sites			Species			
		CH (*n* = 24)	XM (*n* = 24)	HB (*n* = 24)	*B. simaruba* (*n* = 18)	*G. floribundum* (*n* =18)	*L. latisiliquum* (*n* = 18)	*P. piscipula* (*n* = 18)
Thickness	-0.74 ***	-0.70 **	-0.74 ***	-0.74 **	-0.70 **	-0.77 ***	-0.77 ***	-0.82 ***
LDMC	-0.36 **	-0.42 *	-0.28 $^{\mathrm{NS}}$	-0.55 **	-0.84 ***	-0.49 *	-0.38 $^{\mathrm{NS}}$	-0.13 $^{\mathrm{NS}}$
Leaf δ^{15}N	0.11 $^{\mathrm{NS}}$	-0.34 $^{\mathrm{NS}}$	0.16 $^{\mathrm{NS}}$	0.34 $^{\mathrm{NS}}$	0.34 $^{\mathrm{NS}}$	-0.29 $^{\mathrm{NS}}$	-0.33 $^{\mathrm{NS}}$	-0.17 *
$\mathrm{LNC}_{\mathrm{mass}}$	-0.51 **	-0.63 **	-0.15 $^{\mathrm{NS}}$	-0.56 **	0.31 $^{\mathrm{NS}}$	-0.56 *	-0.26 $^{\mathrm{NS}}$	-0.39 $^{\mathrm{NS}}$
$\mathrm{LPC}_{\mathrm{mass}}$	-0.53 ***	0.54 **	-0.29 $^{\mathrm{NS}}$	-0.59 **	0.40 $^{\mathrm{NS}}$	-0.41 $^{\mathrm{NS}}$	0.12 $^{\mathrm{NS}}$	-0.33 $^{\mathrm{NS}}$

NS = not significant. * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$. No-legumes: *B. simaruba* (*Bursera simaruba*) and G. floribundum (*Gymnopodium floribundum*). Legumes: *L. latisiliquum* (*Lysiloma latisiliquum*) and *P. piscipula* (*Piscidia piscipula*). SLA, specific leaf area; LDMC, leaf dry matter content; $\mathrm{LNC}_{\mathrm{mass}}$, leaf nitrogen content mass; $\mathrm{LPC}_{\mathrm{mass}}$, leaf phosphorus content mass.

Figure list

Fig. 1. Patterns of spatial variation in (a) specific leaf area (SLA); (b) leaf thickness; (c) leaf dry matter content (LDMC); (d) leaf N content per mass unit (LNC_{mass}); (e) leaf phosphorus content per mass unit (LPC_{mass}) and (f) natural abundance ^{15}N ($\delta^{15}N$) of four co-occurring tree species across a water availability gradient in a seasonally dry tropical forest at Yucatán, Mexico. Triangles are no-legumes (empty: *Bursera simaruba*; black: *Gymnopodium floribundum*) and circles are legumes species (empty: *Piscidia piscipula*; black: *Lysiloma latisiliquum*.

Fig. 2. Reduced major axis (RMA) regression between specific leaf area (SLA) and leaf nitrogen content by mass unity (LNC_{mass}) in three regions of Yucatán, Mexico: Chicxulub, MAP = 531 mm (gray circles); X'matkuil, MAP = 993 mm (empty circles); and Hobonil MAP = 1036 mm (solid circle).

Fig. 3. Principal components analyses (PCA) of the tree species-leaf trait matrix (72 trees x 6 leaf traits)**.** The first principal component (PC1) represented a contrast between the leaf nutrients and SLA. Principal component 2 (PC2) represent a contrast between LDMC and leaf thickness. Triangles are no-legumes (empty: *Bursera simaruba*; black: *Gymnopodium floribundum*) and circles are legumes species (empty: *Piscidia piscipula*; black: *Lysiloma latisiliquum*.

Fig 1

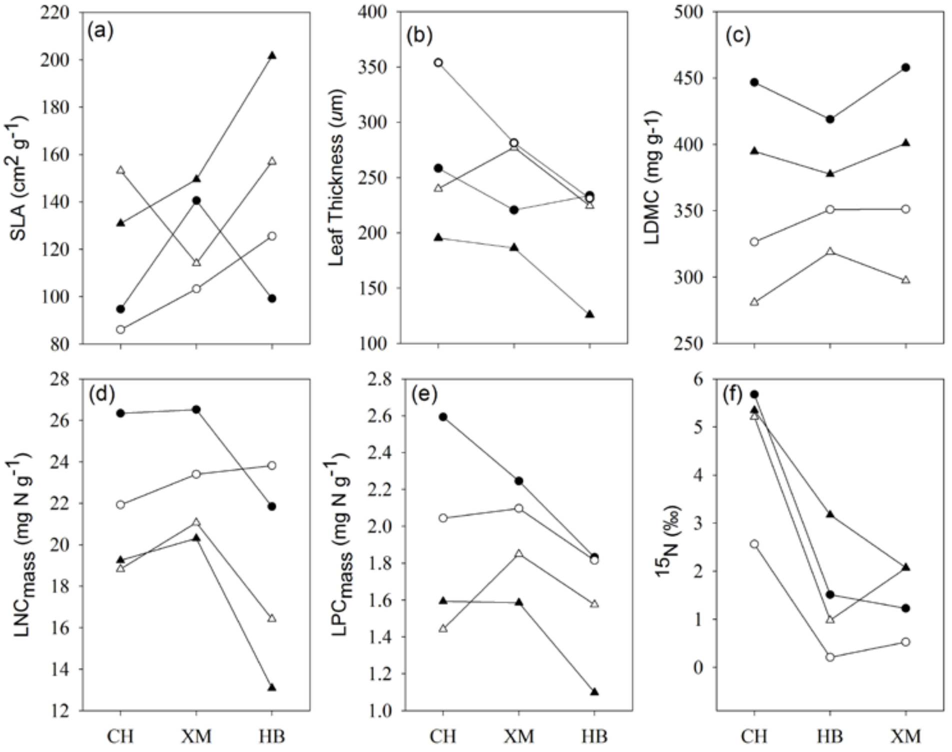

(a)
SLA (cm^2 g^{-1})
220
200
180
160
140
120
100
80
(b)
Leaf Thickness (*u*m)
400
350
300
250
200
150
100
(c)
LDMC (mg g-1)
500
450
400
350
300
250
(d)
LNC$_{mass}$ (mg N g^{-1})
28
26
24
22
20
18
16
14
12
(e)
LPC$_{mass}$ (mg N g^{-1})
2.8
2.6
2.4
2.2
2.0
1.8
1.6
1.4
1.2
1.0
(f)
^{15}N (‰)
6
5
4
3
2
1
0
CH
XM
HB
CH
XM
HB
CH
HB
XM

Fig 2

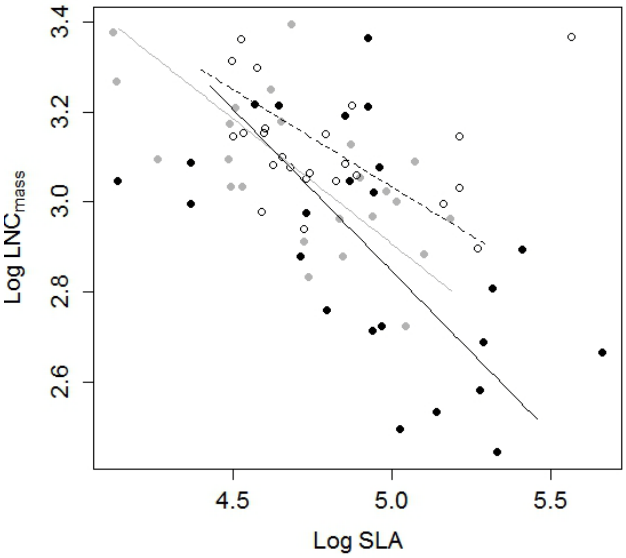
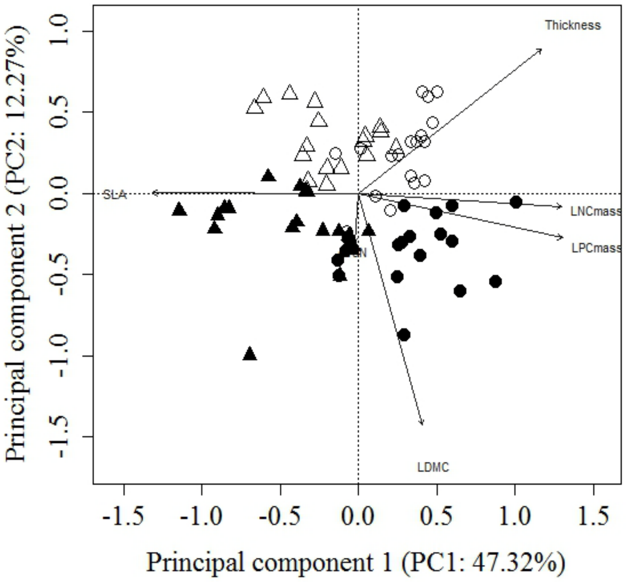


Fig 3


Thickness
SLA
LNCmass
LPCmass
LDMC
Principal component 2 (PC2: 12.27%)
1.0
0.5
0.0
-0.5
-1.0
-1.5
-1.5
-1.0
-0.5
0.0
0.5
1.0
1.5
Principal component 1 (PC1: 47.32%)

DISCUSIÓN Y CONCLUSIONES

Nuestros resultados muestran que la disponibilidad de agua en el bosque tropical estacionalmente seco, juega un importante papel modelador, tanto en los patrones de distribución de la biomasa vegetal viva (Capítulo II) y la biomasa muerta (Capítulo I), como en la magnitud y dirección en la que varían los caracteres foliares, su relación y el efecto de éstos con la mineralización de nitrógeno (N) en el suelo (Capítulo III). A continuación serán enumeradas las principales conclusiones de la presente investigación, las cuales serán discutidas a la luz de los patrones propuestos, tanto para otros bosques tropicales estacionalmente secos como para datos globales, en el caso que estén disponibles. Con esto, serán discutidos los aspectos funcionales que pueden estar dirigiendo los patrones encontrados, resaltando aspectos que no fueron mencionados o solo fueron comentados en la discusión de cada capítulo en particular.

Conclusión 1: *"Menor precipitación y disponibilidad de agua favorece mayor acumulación de necromasa total en el piso del bosque"*

El patrón observado a lo largo del gradiente de precipitación es inconsistente con el patrón reportado a escala regional para otros ecosistemas (Austin 2002; Zhou *et al.* 2009); según el cual, menor precipitación favorece menor acumulación de necromasa vegetal (será usado ***necromasa*** para hacer referencia al mantillo fino y grueso que está depositado sobre la superficie del suelo). La acumulación de necromasa es el resultado de la interacción entre la producción y la descomposición; por lo que el patrón general observado ha sido argumentado sobre la base que a baja precipitación se da una menor producción y en consecuencia baja acumulación de necromasa (*e.j.*, Martínez-Yrizar *et al.* 1995, Lawrence 2005); por otro lado, se asume que en sitios de menor precipitación el proceso de descomposición del mantillo es más lento, lo que sería favorable para una mayor acumulación. En la presente investigación no se llevaron a cabo medidas de la productividad y la descomposición; sin embargo, evidencia adicional indica que en el gradiente de menor a mayor precipitación y disponibilidad de agua, representado por los tres sitios, se encuentra una tendencia de incremento de la productividad con el aumento en la precipitación (J. Campo, *comunicación personal*), al igual que ocurre con el proceso de descomposición de la necromasa (Bejarano-Castillo, *comunicación personal*).

El patrón de acumulación de necromasa a lo largo del gradiente de precipitación es un indicador de que la tasa de descomposición es insuficiente para contrarrestar la producción; es decir, la producción excede las pérdidas. Por lo que es de esperar que la necromasa producida en el sitio de menor precipitación muestre mayor tiempo de residencia sobre la superficie del suelo y entonces, se acumule de un periodo de producción a otro. Resultados de descomposición de mantillo para nuestra región de estudio apoyan ésta hipótesis (Bejarano-Castillo, *comunicación personal*). Otro punto importante tiene que ver con que el patrón de mayor necromasa en el sitio de menor precipitación es impulsado en mayor medida por la presencia de necromasa correspondiente a leño, la cual ofrece mayor resistencia para la descomposición (Kauffman *et al.* 1993).

Conclusión 2*: "El gradiente de precipitación y disponibilidad de agua no afecta la biomasa total de raíces, distribuida a lo largo de todo el perfil del suelo; en contraste, la biomasa de raíces distribuidas en el suelo superficial (0 - 10 cm) responde a la disponibilidad de agua siguiendo un patrón inverso de mayor a menor biomasa de raíces con el incremento en la precipitación y disponibilidad de agua"*

La variación en la disponibilidad de agua es un factor que influencia fuertemente la distribución de las raíces. Así, se ha considerado que las plantas responden al estrés hídrico aumentando la biomasa en raíces, para maximizar el área de absorción de agua y un mayor alcance de forrajeo (Kramer y Kozlowski 1979; Murphy y Lugo 1986; Sanford y Cuevas 1996). Como lo menciona el enunciado, solo las raíces distribuidas en el suelo superficial, esto es, en los primero 10 cm, responden siguiendo el patrón inverso esperado entre la biomasa de raíces y la disponibilidad de agua. En términos generales para bosques tropicales se ha encontrado que la distribución de raíces varía a lo largo del perfil de suelo, con una alta proporción distribuida en los primero centímetros (Jaramillo *et al.* 2003a; 2003b). En ésta investigación se encontró que el ~ 30%, 18% y 15% de raíces está distribuida en el suelo superficial en los sitios de menor a mayor precipitación respectivamente. Dicho compartimento es más sensible a los cambios en la precipitación y disponibilidad de agua, comparados con la biomasa de raíces que se distribuye a lo largo de todo el perfil del suelo (Ro-Fuentes *et al.* 2012). Esta variación en la estrategia de forrajeo puede estar asociada con la dinámica del agua y los nutrientes a lo largo del perfil del suelo. Knapp y colaboradores (2008) en una revisión de la dinámica del agua del suelo ante los cambiantes regímenes de precipitación, describen el mecanismo que favorece la acumulación de mayor contenido de raíces en el suelo superficial. Pocos eventos de lluvia y alta irradiación característica de ambientes xericos, provoca que el agua que alcanza las capas superiores del suelo este expuesta a una rápida evaporación, conduciendo a una reducción significativa en la disponibilidad de agua e impidiendo infiltración de agua a mayor profundidad (Fischer y Turner 1978). Asumiendo que éste sea el fenómeno que gobierna la distribución de agua en el suelo de Chicxulub, el sitio de menor precipitación y menor disponibilidad de agua, mayor biomasa de raíces superficiales será necesaria para "capturar" el agua disponible para el funcionamiento de la comunidad vegetal. Lo cual es evidente según los datos reportados en la presente investigación. En los sitios más mésicos, el suelo usualmente presenta mayor humedad, por lo que los eventos de lluvia pueden incrementar el agua que percola a capas más profundas del suelo (Knapp *et al.* 2008), favoreciendo que haya mayor forrajeo a horizontes más profundos.

Otro factor que influencia la distribución de la biomasa de raíces es la profundidad del suelo. El suelo en los tres sitios alcanza profundidades que varían de 10-50 cm en Chicxulub y X´matkuil y 15-75 cm en Hobonil. Mayor profundidad del suelo en Hobonil, puede estar favoreciendo que las raíces se distribuyan a mayor profundidad. Ya sea por la dinámica del agua en el suelo o por la profundidad del mismo, la presencia de mayor cantidad de raíces superficiales tiene importantes implicaciones sobre la vulnerabilidad del sistema a perturbación; por ejemplo, el sitio de menor precipitación es entonces más susceptible a eventos de fuego, que pueden alcanzar el suelo superficial liberando el carbono orgánico y alterando la dinámica de una posterior regeneración (Jaramillo *et al.* 2003b).

Conclusión 3: *"Menor precipitación y disponibilidad de agua favorece mayor concentración del contenido de carbono orgánico del suelo superficial (0 -10 cm)"*

Nuestros resultados no muestran el patrón de acumulación de carbono orgánico del suelo (COS) a lo largo del gradiente de precipitación, generalmente aceptado; según el cual, el COS incrementa con el aumento en la precipitación media anual (Jobbágy y Jackson 2000; Schuur *et al.* 2001). Los mecanismos que explican dicho patrón están asociados a que la mayor disponibilidad de agua es un factor clave en el control de los procesos que componen el balance de las entradas (producción de plantas) y salidas (descomposición) de COS (Jenny 1941, Schlesinger 1977). Aunque no tenemos evidencia para los sitios de estudio, en bosques tropicales estacionalmente secos, la baja disponibilidad de agua, extrema durante la temporada de sequia, puede limitar la tasa de producción y descomposición de materia orgánica (Webb *et al.* 1978, Sala *et al.* 1988, Amundson *et al.* 1989). Es decir, podemos esperar que el sitio con mayor precipitación y así, mayor disponibilidad de agua muestre mayor productividad, favoreciendo mayor entrada de materia orgánica al suelo. En la misma dirección, podemos esperar que el proceso de descomposición y mineralización de la materia orgánica en el suelo sea favorecido por la mayor disponibilidad de agua. Dicho patrón fue corroborado por los resultados de Bejarano-Castillo (comunicación personal) y de la presente investigación, que muestran que en Hobonil el sitio de mayor disponibilidad de agua, se da mayor tasa de descomposición y una significativamente mayor tasa de mineralización (Ver capítulo IV).

Hay dos vías por las cuales explicar los resultados encontrados. En primer lugar, se puede sugerir una compensación entre la mayor productividad esperada en el sitio de mayor precipitación y al mismo tiempo, una mayor tasa de mineralización de la materia orgánica que favorece la pérdida de COS, ya sea a la atmósfera en forma de CO_2 o el movimiento del COS a horizontes más profundos del suelo, favorecidos por la percolación de agua. En el extremo contario, menor productividad, aunado a una menor tasa de descomposición y mineralización de la materia orgánica puede provocar que mayor contenido de COS se encuentre en el suelo superficial. Una vía alternativa y claramente asociada con las particularidades del paisaje kárstico del estudio, tiene que ver con el alto potencial del suelo para formar agregados con carbonatos y Ca impregnado, lo que favorece la estabilización del C por una lenta descomposición de la materia orgánica (Shang y Tiessen 2003; Gamboa *et al.* 2010). Resultados no reportados en la presente investigación, muestran que el suelo del sitio de menor precipitación (Chicxulub) presenta un mayor contenido de carbono inorgánico (% CaCO3; Chicxulub: 24.01±0.69; X´matkuil 10.34 ± 3.14 and Hobonil 2.37 ± 0.47. Método volumétrico, DAEVA), lo que sugiere una mayor probabilidad de formar dichos agregados que favorecen la estabilización del COS.

Conclusión 4: *"El patrón de asignación de biomasa del bosque tropical estacionalmente seco sigue una estrategia alométrica no isométrica, invariante a lo largo del gradiente de precipitación"*

No se encontró evidencia de un re-ajuste de la asignación de biomasa a compartimientos aéreos vs. raíces en respuesta a la disponibilidad de agua, a lo largo del gradiente de precipitación estudiado. El bosque tropical estacionalmente seco sigue un único patrón alométrico de asignación de biomasa, según el cual mayor biomasa es asignada al componente aéreo para cada valor dado de biomasa de raíces. Resultados similares son reportados por Yang y Luo (2011) para 5 de los 16 estudios que incluyeron en su análisis, en donde la pendiente fue mayor a uno. De los 16 estudios incluidos en la revisión de Yang y Luo (2011), uno es un ecosistema boreal, diez son templados y 5 son tropicales; de estos últimos, tres sitios presentan precipitación superior a los 3000 mm anuales uno es amazónico y uno es un bosque tropical estacionalmente seco con vegetación semi-caducifolia y precipitación de 1650 mm anuales. Los datos anteriores son mencionados para resaltar el hecho que el patrón reportado por Yang y Luo (20011) a escala ecosistémica, según el cual la asignación de biomasa es isométrica, incluye un sesgo importante en la representatividad de los diferentes ecosistemas, entre los cuales se encuentra el bosque tropical estacionalmente seco de interés en la presente investigación.

Müller y colaboradores (2000) resumen la falta de variación en la asignación aérea y subterránea en respuesta a la disponibilidad de recursos diciendo: "Puede ser más parsimonioso que las plantas hayan evolucionado una estrategia alométrica simple, que un mecanismo que le permita ajustar su asignación a la disponibilidad de recursos". Para el caso del presente estudio, nuestros resultados muestran que se ha seguido por una estrategia óptima, donde mayor biomasa es asignada al componente aéreo.

Conclusión 5: *"El gradiente de precipitación y disponibilidad de agua tiene un efecto significativo sobre el ranking de las especies caducifolias que co-ocurren a lo largo del bosque tropical estacionalmente seco de Yucatán, basado en los caracteres foliares"*

Garnier y colaboradores (2001) se refieren al caso que nosotros encontramos; es decir, que el ranking de las especies no se mantiene en los diferentes ambientes, explicando que las especies muestreadas en sitios diferentes son genéticamente diferentes. Aunque no tenemos evidencia genotípica para las especies estudiadas a lo largo del gradiente, es de esperar que hagan parte de poblaciones diferentes. Por otro lado, aún siendo diferentes poblaciones o parte de una misma población la variación en la respuesta de los caracteres foliares a lo largo del gradiente refleja plasticidad fenotípica del carácter para ajustarse a las condiciones ambientales reinantes. Sea cual sea la mejor explicación a la variación intra-especifica de los caracteres foliares, debemos resaltar que estos caracteres no están asociados invariantemente con la identidad de la especie a lo largo del gradiente de precipitación. Estos resultados contradicen los patrones encontrados usando bases de datos globales, donde se incluye un amplio rango de especies y biomas (Wright *et al.* 2004).

Sin embargo, la disponibilidad desigual de datos para todos los biomas (Wright *et al.* 2004: Total de estudios: 175; estudios en el rango de precipitación del SDTF = 24 (13.7%); estudios con bosque caducifolio: 4 (2.29%)), debilita el alcance global de dichos patrones. Por lo que es necesaria una revisión minuciosa de cómo está representado el sitio de interés, para evitar sesgos en la interpretación.

***Conclusión 6**: "La correlación entre el área específica de la hoja y el contenido de nitrógeno y fosforo, está lejos de ser invariante a través de los sitios y entre las especies caducifolias que co-ocurren a lo largo del gradiente de disponibilidad de agua".*

La correlación positiva entre el SLA y los nutrientes de la hoja, principalmente el nitrógeno, ha sido acuñada a una constricción física y funcional sobre la forma y función de la hoja (Reich *et al.* 1999); e incluso, dado que dicha relación ha sido reportada ampliamente, se ha sugerido que representa una convergencia evolutiva (Reich *et al.* 1999). El mecanismo que gobierna dicha correlación, ha sido explicado por la presunta conexión causa efecto entre los atributos foliares, tendientes a maximizar la tasa fotosintética (Evans y Poorter 2001). Sin embargo, recientemente se ha sugerido que dicha conexión no es causal y que los caracteres foliares implicados pueden variar independientemente, por lo que la constricción física y evolutiva a la cual se arguye dicha correlación no es absoluta (Shipley *et al.* 2005). Nuestros resultados, muestran que la correlación no se mantiene a lo largo del gradiente de disponibilidad de agua ni entre especies, soportando la idea antes mencionada de la falta de causalidad entre el SLA y el contenido de nitrógeno de la hoja. Por otro lado, nuestros datos mostraron correlación negativa entre estos dos caracteres foliares, siempre que fue significativa. Resultados similares se han reportado para bosques templados de china, para diferentes grupos funcionales en sitios secos y húmedos (Chen *et al.* 2011). Es así, que hojas gruesas con alto contenido de nitrógeno por unidad de masa (la estrategia dominante en las especies estudiadas en la presente investigación) suponen la presencia de un contenido sub-óptimo de nitrógeno para un valor de SLA. Adicionalmente, la interpretación de los resultados aquí reportados debe considerar que las especies estudiadas crecen en un ambiente de alta disponibilidad de luz y dado que el SLA no afecta la eficiencia total de captura de luz (Evans y Poorter 2001), se sugiere que el ligero cambio en el contenido de nitrógeno de la hoja a lo largo del gradiente de disponibilidad de agua está conduciendo la respuesta de la hoja a los cambios ambientales para mantener el metabolismo foliar.

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