El Colegio de la Frontera Sur

Dinámica de carbono en diferentes etapas sucesionales

de la selva mediana sub-perennifolia en Calakmul,

Campeche

TESIS

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DEDICATORIA

A mi madre **Ana Kumari Aryal**,

por educarme de tener fe y determinación en la vida, también por su paciencia y valor de estar lejos de su hijo más de cuatro años.

समर्पण

मेरी आमा **ण कुमारी अर्याल** मा,
जीवनमा आफूप्रति विश्वास र अठोट लिन सिकाउने तथा चार बर्ष भन्दा लामो समय सम्म आफनो छोरोबाट टाढा रहनसक्ने वहाको धैर्यता र मुल्य प्रति समर्पित ।

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CAPÍTULO I

Introducción general

Carbono y sistema climática

El Carbono se mueve naturalmente entre formas bióticas y abióticas de la biosfera y atmósfera. Las actividades humanas han alterado el equilibrio natural del ciclo del carbono, así en los últimos 200 años, se han agregado a la atmósfera cerca de 400 petagramos (1 Pg = 10^{15} gramos = 10^9 toneladas) de carbono en forma de dióxido de carbono (CO_2) por la quema de combustibles fósiles y deforestación (Sabine et al., 2004; Stocker et al., 2013). Aunque la mayor parte de adición de CO_2 en la atmósfera con el tiempo vuelve a los sumideros del mar y la tierra, éste tiene un tiempo de residencia relativamente largo. Alrededor del 50% de un sólo pulso de CO_2 se elimina al cabo de 30 años, 30% en unos siglos, y el restante 20% puede persistir en la atmósfera durante miles de años (Stocker et al., 2013). CO_2 es uno de los principales gases de efecto invernadero (GEI) por su naturaleza de atrapar el calor y contribución al calentamiento del planeta (Bonan, 2008; Stocker et al., 2013).

La cuantificación de las fuentes y sumideros de carbono, su distribución espacial y evolución en el tiempo son áreas críticas de investigación, ya que debe entenderse y evaluarse cuantitativamente la magnitud y dinámica de la perturbación humana y natural sobre los flujos y los sumideros de carbono para proponer acciones de mitigación del cambio climático (Canadell et al., 2010; Le Quéré et al., 2014).

Carbono y ecosistemas forestales

Los ecosistemas forestales del mundo intervienen en el clima influyendo procesos físicos, químicos y biológicos que afectan la dinámica energética del planeta, el ciclo hidrológico, y la composición atmosférica. Las plantas absorben carbono a través de la fotosíntesis y lo liberan a la atmósfera cuando respiran, se queman o se descomponen; esto se acrecienta en los ecosistemas forestales (Bonan, 2008; FAO, 2010a). Las tasas de acumulación en biomasa, descomposición de materia orgánica y oxidación de carbono por incendios en ecosistemas forestales pueden alterar la

concentración de CO_2 en la atmósfera por dos vías (Bonan, 2008; Schlesinger y Bernhardt, 2013). Por lo anterior, es importante entender el papel de los ecosistemas boscosos como sumideros y fuentes de carbono (Houghton, 2010; Pan et al., 2011).

Los ecosistemas forestales a nivel mundial cubren aproximadamente 41.6 x 10^6 km^2 de la superficie de la tierra, de los cuales el 42% se ubica en zonas tropicales (Sabine et al., 2004; Stocker et al., 2013). Un estudio reciente indica que el cambio en uso y cobertura de suelo emite aproximadamente 1.2 Pg $año^{-1}$ de carbono , lo cual equivale a 13% de las emisiones globales de carbono (Houghton et al., 2012). La deforestación y degradación de bosques en México emiten anualmente alrededor de 17 Tg de carbono a la atmósfera (De Jong et al., 2010). La emisión de carbono es mayor en los bosques tropicales (aprox. 10.5 Tg $año^{-1}$) con tasas relativamente más altas en la Península de Yucatán, en el sur (Oaxaca, Chiapas y Tabasco), y el oeste de México (Jalisco y Guerrero) (De Jong et al., 2010; Soto-Pinto et al., 2010; Vester et al., 2007).

En la región sur de la Península de Yucatán, donde se asienta la reserva de Calakmul, aproximadamente 8.8% (97400 ha) del área boscosa (selva alta y selva baja) se ha transformado a otros usos del suelo entre 1969 y 1997 (Turner et al., 2004). Sin embargo, hay evidencias de que la tasa de deforestación en la región ha disminuido en los últimos diez años con la regeneración de bosques secundarios en distintas etapas (Rueda, 2010; Turner, 2010). La pérdida de bosques y los cambios en el uso de suelo en la Península de Yucatán generan atención especial debido al papel fundamental de la Península en el Corredor Biológico Mesoamericano y su contribución al balance regional de carbono (Eaton y Lawrence, 2009; Vargas et al., 2008).

Reservorios y flujos de carbono en ecosistemas forestales
Existen cinco principales reservorios de carbono en un ecosistema forestal (Gibbs et al., 2007; Girardin et al., 2014). Ellos son: 1) biomasa viva aérea, 2) biomasa de raíces, 3) mantillo, 4) madera muerta, y 5) carbono orgánico del suelo (Fig. 1).
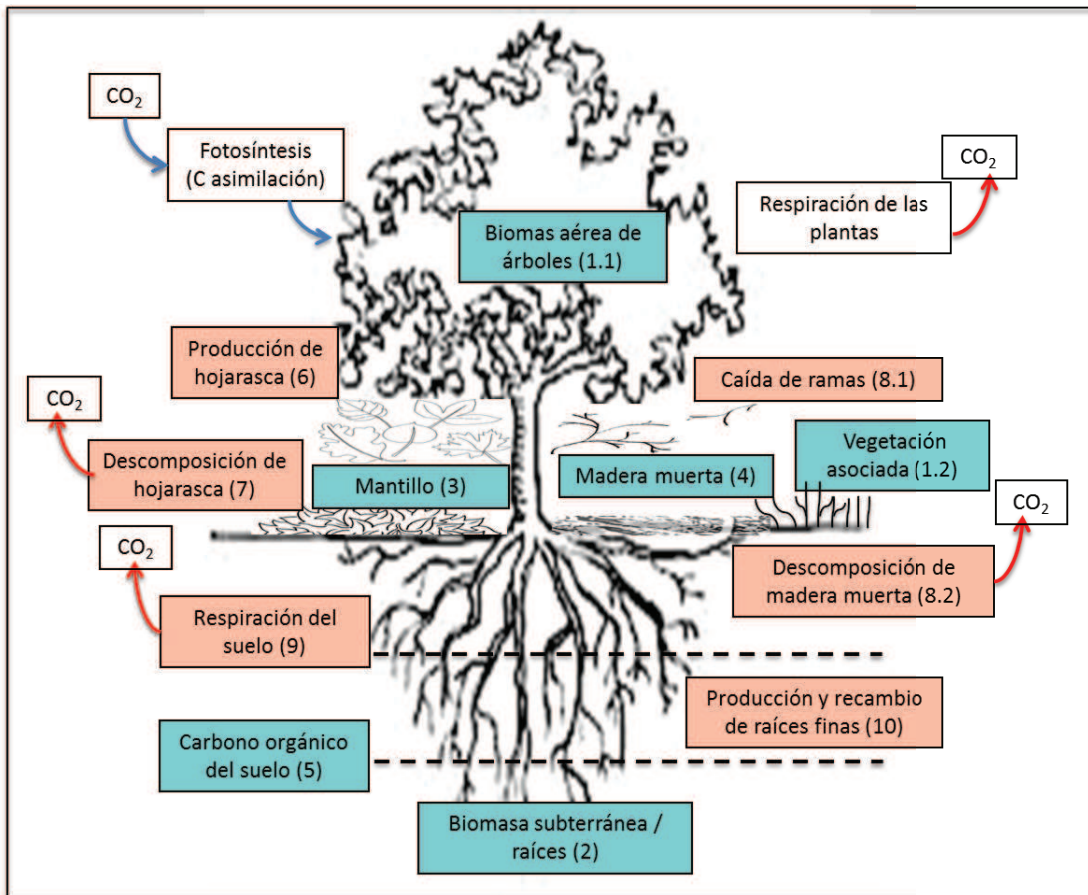
Figura 1: Representación de los reservorios y flujos de carbono en ecosistemas forestales. Los números 1 a 5 en paréntesis dentro de las cajas representan los reservorios y 6 a 10 indican los procesos del flujo / transferencia de carbono. Fotosíntesis y respiración autotrófica de las plantas no están numeradas (elaboración propia)

Biomasa aérea incluye la biomasa de los árboles y de la vegetación asociada. Biomasa de raíces es la biomasa viva de los raíces bajo la tierra tanto de los árboles como de la vegetación asociada. Por la dificultad en las mediciones directas, la biomasa de raíces normalmente se estima con el dato de biomasa aérea usando la ecuación alométrica. Mantillo es la masa de hojarasca acumulada en el piso forestal. Mantillo incluye la hojarasca fresca, fragmentada y la capa de humus sobre suelo. Madera muerta es la masa de todos los detritos leñosos que se encuentran en pie o en piso forestal. Carbono orgánico del suelo (COS) es la cantidad de carbono en

suelo del origen orgánico a una profundad dada. COS no incluye carbono de los carbonatos de suelo.

Las transferencias de carbono de un reservorio a otro dentro de un ecosistema forestal ocurren por procesos como: la caída de hojarasca y ramas, mortalidad de árboles, y renovación de raíces finas (Fig. 1). El flujo de carbono de los ecosistemas forestales hacia la atmósfera ocurre por procesos como descomposición de materia orgánica (fuste y ramas, hojarasca, raíces y materia orgánica del suelo), respiración de las plantas (autotróficos), y la quema (oxidación espontánea) (Schlesinger y Bernhardt, 2013). La caída de hojarasca y mortalidad de raíces finas de la planta son las vías dominantes del retorno de nutrientes al suelo (Jourdan et al., 2008; Schlesinger y Bernhardt, 2013). La hojarasca se compone de hojas, ramas finas (<1 cm diámetro), inflorescencias, frutos y otras estructuras de las plantas, de estos las hojas constituyen la mayor parte de la producción anual y la entrada de nutrientes a los suelos forestales (Ostertag et al., 2008; Pérez-Suárez et al., 2009).

Las raíces finas (<2 cm de diámetro) son los componentes más importantes que contribuyen a los flujos de carbono en el suelo y son una fuente importante de entrada de carbono y otros nutrientes (Finér et al., 2011). La producción de raíces finas puede contribuir de 30% a 60% a la producción primaria neta (PPN) anual en los ecosistemas forestales (Brunner et al., 2013; Jourdan et al., 2008). Debido a las dificultades metodológicas y la amplia gama de factores internos y externos que afectan la dinámica de raíces finas, los estudios de la contribución de estas al ciclo de carbono del ecosistema son aún limitados (Finér et al., 2011; Xiao et al., 2008). La descomposición de hojarasca y madera son flujos importantes de carbono y pueden variar dependiendo de la composición de especies, clima y micro-ambiente (Forrester et al., 2012). La conversión del carbono orgánico a CO_2 por los descomponedores (principalmente macro fauna, bacterias y hongos) en el suelo se llama respiración heterotrófica de suelo. La respiración de suelo es otro flujo más importante de CO_2 de los ecosistemas terrestres a la atmósfera (Knohl et al., 2008). Los ecosistemas forestales del sur de la Península de Yucatán, aún carecen de

estudios sobre el flujo de carbono por respiración del suelo y su contribución al balance regional del carbono. Es importante evaluar todos los almacenes y los procesos de transferencias de carbono para determinar en qué etapa de sucesión ecosistemas forestales actúan como una fuente o un sumidero de carbono (Fig. 2).
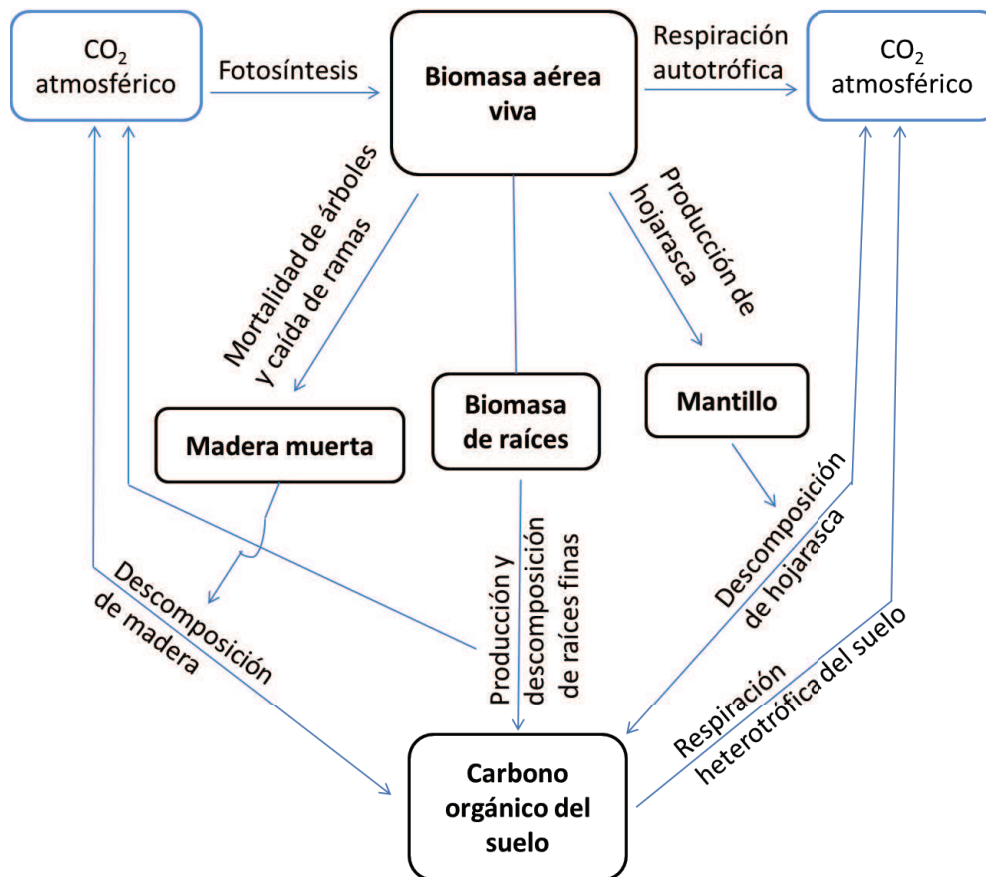
Figura 2: Diagrama representativa de direcciones de los flujos de carbono en un ecosistema forestal. El balance de carbono, en un tiempo dado, es la función de todos los flujos tanto hacia al ecosistema como hacia a la atmosfera. Un ecosistema forestal puede considerar como un sumidero cuando la ganancia de carbono por la acumulación es mayor a la perdida por los procesos de descomposición y respiración. Se considera fuente cuando la pérdida es mayor que la ganancia (elaboración propia).

Los almacenes de carbono (Mg C ha^{-1}) cambian, con el tiempo, ya que el carbono se transfiere de un reservorio a otro dentro del sistema o a la atmosfera por diferentes procesos de transferencias (Mg C ha^{-1} año^{-1}) que ocurren en un ecosistema forestal (Fig. 2). Los ecosistemas forestales que capturan más carbono de lo que emiten a la

atmosfera están considerados como sumideros y los que emiten más que captura son las fuentes. Normalmente, carbono orgánico de suelo es el reservorio más grande pero también existen ecosistemas forestales donde biomasa viva es el reservorio más grande.

Sucesión forestal y dinámica de carbono

La sucesión es el cambio secuencial en la estructura y composición de un grupo de especies a través de tiempo en un sitio dado (Pickett et al., 1987; Prach y Walker, 2011). En este estudio, la sucesión forestal se refiere al estado de recuperación, en el cual, la vegetación leñosa vuelve a crecer a través de tiempo después de la tala de bosque para la agricultura u otros usos (Brown y Lugo, 1990; Guariguata y Ostertag, 2001a; Marín-Spiotta et al., 2007). Actualmente, la superficie de bosques en distintas etapas de sucesión está aumentando y actualmente representan ~57% del total de los bosques mundiales (de Jong, 2013; Gibbs et al., 2007; Vargas et al., 2013). En México, los bosques secundarios y degradados comprenden aproximadamente el 64% del total de los bosques tropicales (De Jong et al., 2010; FAO, 2010b; Kauffman et al., 2009).

Las tasas de captura de carbono y descomposición cambia en magnitud a medida que el ecosistema forestal atraviesa por diferentes etapas de crecimiento (Gower, 2003; Peichl et al., 2012). Se reporta un aumento gradual en la productividad de los bosques tropicales durante las primeras 2 - 3 décadas del desarrollo, llegando a su máximo entre los 30 y 80 años, seguido por una disminución paulatina (Schimel et al., 2001; Schwalm et al., 2007). Sin embargo, el momento de la máxima productividad varía dependiendo de varios factores (Brown yLugo, 1990; Peichl et al., 2012), entre ellos las transiciones en estructura, dinámica de poblaciones de especies, composición de especies, calidad del sitio, los antecedentes del uso del suelo y tipo e intensidad del disturbio (de Jong, 2013; Esparza-Olguín et al., 2002; García-Licona et al., 2014; Mendoza-Vega and Messing, 2005; Ochoa-Gaona et al., 2007). La tasa de acumulación de carbono varía con la edad durante la trayectoria sucesional en ecosistemas forestales secundarias por el crecimiento de especies leñosas y pueden cambiar los flujos de CO_2 convirtiéndose de una fuente de CO_2 a

un sumidero neto (Ferlan et al., 2011; Fonseca et al., 2011; Kenzo et al., 2010). Algunos reportes indican que los bosques secundarios acumulan rápidamente la biomasa después de la agricultura y alcanzan el 80% del área basal de los bosques maduros en 40-50 años (Klepeis y Turner II, 2001). Pero, la tasa de acumulación de biomasa puede disminuir paulatinamente con la edad debido a la mortalidad de las especies heliófilas o pioneras y la tasa se estabiliza cuando alcanzan estadios intermedios o avanzados, con un mayor número de heliófilas tardías y especies esciófilas (Fonseca et al., 2011).

La cantidad de nutrientes en el suelo también puede cambiar en el curso de la sucesión (Brown y Lugo, 1990). Se ha reportado un aumento en carbono orgánico del suelo (COS) con la edad en bosques tropicales (Guariguata y Ostertag, 2001a; Mendoza-Vega et al., 2003) pero también hay evidencias que COS no aumenta significativamente con la edad (Orihuela-Belmonte et al., 2013; Ostertag et al., 2008). Además de la edad de sucesión, tanto la calidad del sitio como la intensidad de uso de suelo pueden afectar la tasa de recuperación de la biomasa, producción de hojarasca y acumulación de carbono en el suelo para los bosques tropicales que están en diferentes etapas sucesionales (Eaton y Lawrence, 2009; Ochoa-Gaona y González-Espinosa, 2000; Schmook, 2010).

Planteamiento del problema
La edad sucesional de los ecosistemas forestales tiene profundas implicaciones en el flujo de carbono a nivel local y regional y es una de las fuentes importantes de incertidumbre en las estimaciones de flujos de GEI (De Jong et al., 2010). En las estimaciones de las tasas de recambio en ecosistemas forestales secundarios, el nivel de incertidumbre es mayor por la escasez de información de la dinámica de carbono, especialmente de raíces y componentes no-arbóreos (Fonseca et al., 2011; Kauffman et al., 2009). Recientemente, se ha reportado que la tasa de deforestación en el sur de la Península de Yucatán ha disminuido y que actualmente el paisaje en la región se conforma principalmente de un mosaico de rodales forestales secundarios de diferente edad con algunas áreas de bosques no perturbados

(Rueda, 2010; Vester et al., 2007). La composición de especies, biomasa y productividad de rodales forestales secundarios varían según su etapa de recuperación (Connell y Slatyer, 1977; García-Licona et al., 2014; Marín-Spiotta et al., 2007). Los bosques jóvenes suelen estar dominados por las especies pioneras y los maduros por especies leñosas tardías (Chazdon et al., 2007; Fonseca et al., 2011; Guariguata y Ostertag, 2001b). Debido a la transición en la dominancia de especies, se espera que la acumulación de biomasa y descomposición de materia orgánica es más rápido en los bosques jóvenes y disminuye en la medida que los bosques llegan a las fases maduros (Chazdon, 2014; Marín-Spiotta et al., 2007). Por lo tanto, la cantidad de carbono acumulado y las tasas de transferencia de un reservorio a otro varía a lo largo de la sucesión secundaria (Brown y Lugo, 1990; Ostertag et al., 2008). Por lo anterior, es necesario tomar en cuenta la estructura de edades del paisaje para mejorar la estimación de los balances regionales de carbono de los ecosistemas forestales (Turner, 2010). Evaluar el cambio en reservorios y transferencias de carbono durante la trayectoria de regeneración es fundamental para proponer acciones de conservación de ecosistemas forestales y mitigación de GEI. La dinámica del carbono de un ecosistema forestal solo puede entender o modelar adecuadamente por medio de los estudios que integran y acoplan todos los almacenes y transferencias de carbono entre los reservorios en una unidad espacio-temporal. Por ello, se requiere llevar a cabo un estudio holístico que analice los almacenes y tasa de transferencias de carbono a lo largo de un gradiente de perturbación y recuperación de la vegetación, considerando los factores como la edad de la sucesión, cambio en la composición de especies, historia del disturbio y calidad del sitio. El propósito de éste estudio es estimar el cambio en los cinco reservorios y los procesos de transferencias de carbono entre ellos y la atmósfera tomando en cuenta el crecimiento de los árboles, las tasas de mortalidad, producción y descomposición de materia orgánica en diferentes etapas de sucesión de la selva sub-perennifolia de Calakmul, Campeche. Los resultados podrían servir como base para la toma de decisiones locales o regionales para generar acciones de mitigación de emisiones de GEI.

Objetivos

Objetivo general

Analizar los almacenes y transferencias de carbono para generar las trayectorias de acumulación en diferentes etapas de sucesión de la selva mediana sub-perennifolia de Calakmul, Campeche, México

Objetivos específicos

- Evaluar el cambio en el reservorio de carbono por reclutamiento, crecimiento y mortalidad de los árboles en relación a la edad de sucesión e intensidad de uso anterior de suelo.
- Determinar el efecto de edad de sucesión y estacionalidad en la producción de hojarasca.
- Evaluar si hay efecto de la edad de sucesión en la tasa de caída de materia leñosa (ramas) y su descomposición.
- Analizar el balance de carbono considerando todos los procesos de transferencias en diferentes etapas de sucesión.

Estructura de tesis

La tesis contiene seis capítulos: introducción general (capítulo I), reservorios de carbono y cambios (capítulo II), producción de hojarasca y transferencia de nutrientes (capítulo III), producción y descomposición de materia leñosa (capítulo IV), balance de carbono (capítulo V) y conclusión general (capítulo VI). Las hipótesis, los métodos relacionados a cada uno de los objetivos específicos están presentados en los capítulos respectivos. En caso requerido, se ha presentado los alcances y limitaciones del estudio en los capítulos correspondientes.

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CAPÍTULO II

Carbon stocks and changes in tropical secondary forests of southern Mexico

Carbon stocks and changes in tropical secondary forests of southern Mexico

Deb R. Aryal[1], Bernardus H.J. De Jong[1]*, Susana Ochoa-Gaona[1], Ligia Esparza-Olguin[1], Jorge Mendoza-Vega[1]

[1]El Colegio de la Frontera Sur, Unidad Campeche, Av. Rancho Polígono 2A, Parque Industrial Lerma,

Campeche, Campeche CP 24500, Mexico

*Corresponding author

Abstract

The role of tropical secondary forests in carbon accumulation has been widely acknowledged, but the rates of changes in carbon stocks still remain uncertain. The aim of this study was to analyze the changes in carbon pool sizes and accumulation rates associated with growth, recruitment and mortality of trees at different ages of forest succession in semi-evergreen tropical forests and relate these to the age of the secondary vegetation and prior land use intensity. The study was carried out in a chronosequence of secondary and mature forests around Calakmul Biosphere Reserve in southern Yucatan Peninsula, Mexico. Permanent monitoring plots were established and measured in 2011 and 2012 to account all carbon stocks and changes due to tree increments, establishment of new trees and tree mortality in different age classes of secondary forests.

We found that carbon stocks in living tree biomass increased rapidly in the early stages and decreased in the older secondary forests. The annual carbon dynamics of trees was higher in younger secondary forest compared to older forests, due to higher tree growth and recruitment. Growth functions predict that secondary forests recover live aboveground biomass carbon stocks to pre-disturbance levels (99.56 Mg C ha^{-1}) at the age of about 125 years or more, while the basal area (33.2 m^2 ha^{-1}) regain this level at the age of about 85 years. The longer carbon recovery time can be explained by the fact that mature forests are dominated by hardwood species whereas secondary forests are composed of softwood species and that species composition turnover during succession is relatively slow. Secondary forests of 35 years look

similar to mature forests in terms basal area, but this is located in large number of small and medium sized trees, whereas in mature forests most of the basal area is in trees of > 20 cm diameter. In addition, the intensity of slash and burn agriculture can negatively alter the velocity of carbon accumulation. These findings have important implications for national forest carbon monitoring systems, greenhouse gas emission inventories and regional level REDD+ strategies.

Introduction

Tropical secondary forests play an important role in global carbon cycle (Canadell et al., 2010; De Jong et al., 2010; Pan et al., 2011) because of their fast growing nature and accumulation of atmospheric carbon (Bonan, 2008; 2010; Chazdon et al., 2007, 2005; Raupach et al., 2007). Successional mosaics of secondary forest have been increasing rapidly in the tropics due to shifting cultivation and abandonment of agricultural lands or grasslands, which currently cover about 57% of world´s tropical forest area (Brown and Lugo, 1990; FAO, 2010a; Guariguata and Ostertag, 2001; Ostertag et al., 2008). In Mexico, secondary and degraded forests occupy about 64% of total lowland forest cover (FAO, 2010b).

Understanding the carbon dynamics of successional forests is becoming critical for the development of tropical forest conservation and management strategies as well as for REDD+ intervention potentials (Asner, 2011; Edwards et al., 2010; Pan et al., 201, Purves et al., 2008; Wright, 2005). The current estimations of carbon stocks and stock change of tropical secondary forests still have a high level of uncertainty (Asner, 2011; De Jong et al., 2010; Houghton, 2010, Chazdon et al., 2005; Drake et al., 2011; Pregitzer and Euskirchen, 2004). Although there are some studies related to carbon stocks in Yucatan peninsula of Mexico (Eaton and Lawrence, 2009, Cairns et al 2003, Urquiza-Haas et al 2007), carbon dynamics derived from tree recruitment, growth and mortality has not yet understood.

Carbon stock changes in live tree biomass within a certain period of time after abandoning cultivation is the aggregated outcome of growth of existing trees plus recruitment of new individuals minus mortality (Chazdon et al., 2005; Lebrija-Trejos et al., 2010; Prach and Walker, 2011; Van Breugel et al., 2006). Tree establishment, growth, mortality, and longevity vary according to the species and stage of forest succession, which in turn also influences carbon dynamics (Huston and Smith, 1987; Martínez-Ramos and García-Orth, 2007; Mascaro et al., 2011; Noble and Slatyer, 1980; Pickett et al., 1987; Tilman, 1985).

Dramatic changes in vegetation structure and composition occur during the first few years of succession in tropical regions, as woody species rapidly colonize abandoned fields (DeWalt et al., 2003; Guariguata and Ostertag, 2001; Marín-Spiotta et al., 2008; Oliver and Larson, 1990). Due to transition in canopy dominance from light-demanding pioneer trees to shade tolerant species, secondary forests are expected to exhibit rapid changes compared to mature forests (Brown and Lugo, 1990; Chazdon et al., 2005; Purves et al., 2008). Considering the asymptotic behavior of most successional trends, we would predict a decreasing rate of carbon turnover with successional age, i.e. community dynamics decrease with forest age (Lebrija-Trejos et al., 2010; Van Breugel et al., 2007; Vargas et al., 2008). We also expect that under asymmetric competition, growth concentrates in the larger individuals and smaller individuals suffer higher mortality rates, resulting in declining tree density and an increasing average carbon stock per tree (Huston and DeAngelis, 1994; Van Breugel et al., 2006) although variations between species responses may be high.

Tropical forests in southern México have suffered from different cycles of anthropogenic and natural disturbances such as slash and burn agriculture, selective logging, clearance for pasture establishment, forest fires and hurricanes (Klepeis et al., 2004; Ochoa-Gaona et al., 2007; Schmook, 2010; Turner II et al., 2001). The recovery rates of successional forests after abandonment may also vary according to the age and the former intensity of land use in terms of frequency and duration of

previous fallow periods versus cultivation cycles (Levy-Tacher and Rivera, 2005; Ochoa-Gaona et al., 2007; Schmook, 2010). Despite the attempts to develop ecological succession models that formulate generalized interpretation for any ecosystem, there is still a need for theoretical modelling based on long-term monitoring of recruitment, growth and mortality of trees in successional stages of tropical forest ecosystems to understand the vegetation dynamics in these forests along the whole succession gradient (Lebrija-Trejos et al., 2010; Rees et al., 2001). In this study, we aim to analyze the effect of successional age and shifting cultivation intensity on all carbon pool sizes and accumulation rates that occur from tree growth, mortality and recruitment in semi-evergreen tropical secondary forests of southern Mexico. In this paper we examine the following research questions: i) Carbon stocks changes evenly among the C pools with forest age?; ii) how do tree recruitment and mortality influence carbon dynamics during secondary forest succession?; iii) does previous land use intensity affect carbon accumulation in secondary forest after slash and burn agriculture?; and iv) how long does it take for secondary forests to recover forest structure and carbon stocks of mature forests after slash and burn agriculture? Based on the research questions we tested the following hypotheses: i) carbon stocks changes differently among pools during secondary forest succession; ii) carbon stock changes due to tree growth, recruitment and mortality are relatively higher in younger stages of forest succession than in older stages; iii) increasing land use intensity (in terms of number of cultivation years and frequency of cropping cycles) reduces carbon accumulation rates in secondary forests and iv) carbon stocks in live biomass recover slower than forest structure (expressed in basal area) during forest succession.

Methods
Study sites
The study was conducted in four localities around Calakmul Biosphere Reserve, situated in the south of Yucatan Peninsula, Mexico. Sampling sites were located in four communities: Cristóbal Colon, El Carmen II, Narciso Mendoza and Nuevo Conhuas (Fig 1). The region is composed of rolling limestone hills and ridges of

karstic origin that ranges from 100 to 380 m above sea level (Bautista et al., 2011; García and March, 1990; Vester et al., 2007). The dominating soil type in the region is rendzic leptosols, mixed with vertisols where lands are inundated in the rainy season (so called *bajos*, Bautista et al., 2011; INEGI 2011; IUSS Working Group WRB, 2006). The region is characterized by a sub-humid tropical climate with an average precipitation of about 950 mm per year (with major portions of the rainfall within the months from July to October) and mean annual temperature of about 22°C (García, 1973; Xuluc-Tolosa et al., 2003). Semi-evergreen tropical forest is the dominant ecosystem in the region (Miranda and Hernández-Xolocotzi, 1963; Pérez-Salicrup, 2004), of which large tracts have been converted to slash-and-burn agriculture that created a mosaic of agricultural lands mixed with secondary forests in various stages of development. The characteristic species of mature forests are *Manilkara zapota* (L.) van Royen*, Pouteria reticulata reticulata* (Engl.) Eyma*, Gymnanthes lucida* Swartz., *Vitex gaumeri* Greenman*, Metopium brownie* (Jacq.)*, Lonchocarpus castilloi* Standl.*, Brosimum alicastrum* Swartz and *Talisia oliviformis* (Kunth) Radlk., whereas, common species in secondary forests are *Lonchocarpus xuul* Lundell., *Lysiloma latisiliqua* (L.) Benth., *Croton arboreus* Millsp., *Bursera simaruba* (L.) Sarg., *Hampea trilobata* Standl.*, Piscidia piscipula* (L.) Sarg., and *Chysophyllum mexicanum* Brandegee ex Standl. (Martínez et al., 2001; Torrescano and Islebe, 2006).

Age	CC	EC	NM	NC
4	2	2	0	4
10	3	3	0	1
20	3	2	0	3
35	0	1	3	0
MF	2	2	0	1

CC: Cristobal Colon; EC: El Carmen II; NM: Narcizo Mendoza; NC: Nuevo Conhuas; MF: Mature Forest
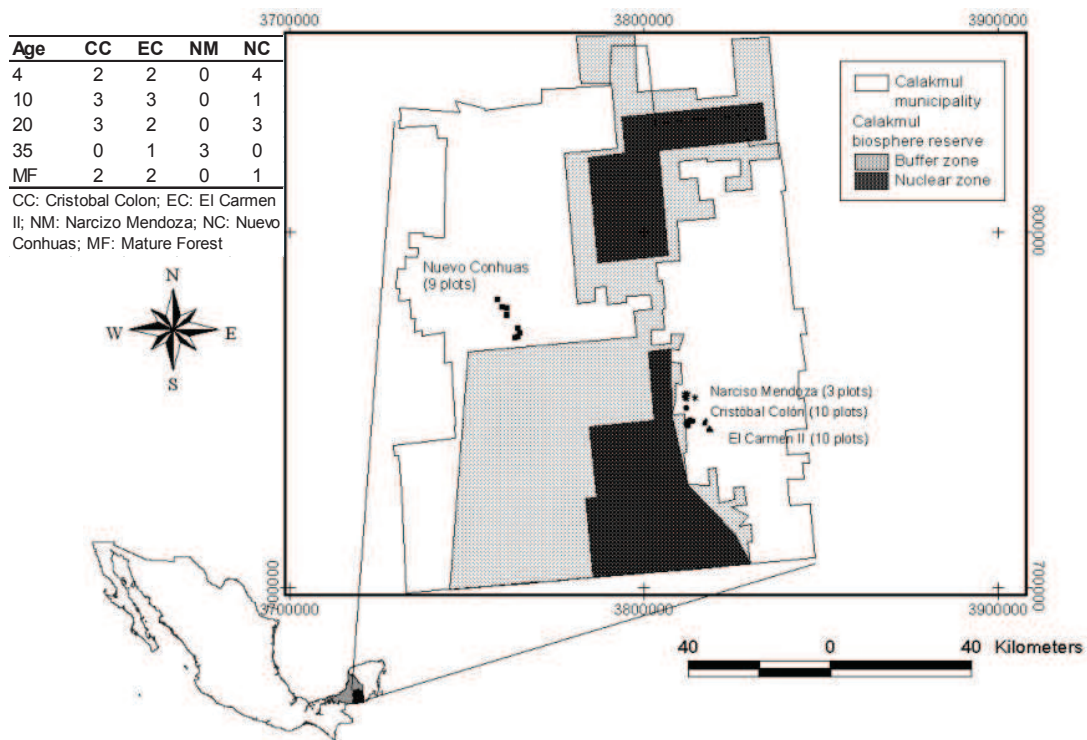
Figure 1. Location of study area and sampling plots in Campeche, Mexico

Sampling plots and measurements

We established and measured 28 carbon monitoring plots of 1000 m^2 size (50 x 20 m) in five age classes of forest succession in 2011 and re-measured these after one year (See Figure 1 for the plot distribution). The age classes correspond to the time after abandonment of the slash-and-burn plot until 2012. Eight plots were established in 4-years old secondary forest stands, seven plots in 10 year old stands, eight in 20 years old stands, and five plots in non-slashed mature forest stands, considered more than 85 years old. In 2012, four additional plots of 35 year old stands were measured. We determined stand ages by means of interviews with land-owners, cross-checking by participatory community appraisal and field observations by experts. Separate measurement and estimation protocols were applied to calculate the stocks and stock change in the five carbon pools: aboveground live biomass (tree and non-tree), belowground live biomass (roots), woody debris (standing dead trees and fallen trunks and branches), litter, and soil organic carbon.

Measurement, counting and labeling of trees of ≥1 cm diameter at breast height (DBH, 1.3 m above ground level) were carried out in 400 m^2 nested plot and trees of ≥10 cm DBH in 1000 m^2 plot. All trees were identified, individually marked, and DBH and total height were measured in 2011 and 2012. Recruitment and mortality of trees were recorded in 2012. All stems of ≥1 cm DBH within each plot were marked with an aluminum tag secured to the tree with an aluminum nail at approximately 1.20 meters above the ground. The diameter of each tree (both live and dead) was measured with a diameter tape at 1.30 m. The sampling plots of 35 years were measured only in 2012, thus, we couldn´t calculate current annual increment (CAI), tree growth, recruitment and mortality for this age group. Carbon stocks and mean annual increment (MAI) values presented in the results, if not specified, were obtained from 2012 measurements. Since there is little time between the two measurements, the error of DBH measurement may be greater than the diameter increase during this period. We therefore estimated the error in DBH measurement, remeasuring a series of 21 trees of varying size independently 10 times by each crew member. The standard error of these measurements was calculated for three DBH groups (<10cm; 10-20 cm; > 20 cm). We calculated the measurement error in live biomass and biomass change rates, applying the 95% confidence interval (95%CI) of the error in the measurement of each tree and summed these separately for each measurement year and plot. The average growth was calculated and also the conservative difference (minimum growth), subtracting the lower 95%CI of 2012 (2012_{min}) with the higher 95% CI of 2011 (2011_{max}).

All diameters of individuals with more than one stem of ≥1 cm DBH were recorded separately, and converted to one tree diameter based on the sum of the basal areas of all stems. Aboveground live biomass of each individual tree was calculated using published allometric equations. Equation 1 (Cairns et al., 2003; Urquiza-Haas et al., 2007) was applied for trees with DBH ≥ 10 cm, equation 2 (Chave et al., 2005) for trees with DBH between 5 and 9.9 cm and equation 3 (Hughes et al., 1999) for trees with DBH<5 cm.

$$AGB = ((\exp(-2.12605 + 0.868 \ln(D^2H))\, \rho/\,\rho_m)/10^3 \ \ldots\ldots\ldots\ldots \text{(eq. 1)}$$
$$AGB = (\exp(-2.187 + 0.916 \ln(\rho D^2H))/10^3 \ \ldots\ldots\ldots\ldots\ldots\ldots \text{(eq. 2)}$$
$$AGB = (\exp(4.9375 + 1.0583 \ln(D^2))1.14/10^6 \ \ldots\ldots\ldots\ldots\ldots \text{(eq. 3)}$$

Where, AGB is aboveground biomass of the tree (Mg dry weight), D is the diameter at breast height (cm), H is the total height of the tree (m), ρ is the wood density of each individual tree species (g cm^{-3}), ρ_m is the mean wood density of the trees used to generate the equation (0.75 g cm^{-3}).

Species specific wood density data were obtained by averaging the reported values (Chave et al., 2009; Fearnside, 1997; Nogueira et al., 2005; Torelli and Željko, 1994; Valdez-Hernández et al., 2010; Vandecar et al., 2011; Zanne et al., 2009). Basal area weighted wood density of each stand was calculated by equation 4 (Urquiza-Haas et al., 2007).

$$WD_{st} = \frac{\sum_{i=1}^{n}(WD_i \times BA_i)}{\sum_{i=1}^{n} BA_i} \ \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \text{(eq. 4)}$$

Where, WD_{st} is stand level wood density (g cm^{-3}), WD_i is the wood density of tree i (g cm^{-3}) and BA_i is the basal area of tree i (m^2 ha^{-1}).

Aboveground non-tree biomass was harvested at ground level in four 1 m^2 subplots, randomly distributed within the 1000 m^2 plot. All the collected biomass was oven-dried at 70°C for 72 hours to obtain dry weight. Aboveground tree biomass and non-tree biomass were combined to obtain total aboveground live biomass. Belowground live biomass was estimated using the allometric equation 5 (Cairns et al., 1997).

$$RB = \exp(-1.085 + 0.926 \ln(AGLB)) \ \ldots\ldots\ldots\ldots\ldots \text{(eq. 5)}$$
Where, RB is root biomass (kg dry weight), and AGLB is aboveground live biomass (kg dry weight).

A factor of 0.47 was used to convert all live biomass pools to carbon (Fonseca et al., 2011). Forest floor litter was sampled in four random subplots of 0.25 m^2 within the monitoring plots. Freshly fallen litter, fragmented dry litter and decomposed litter (humus) layers were collected separately and oven dried at 70°C for 72 hours. Litter biomass of the three layers were converted to carbon using different C fractions, 0.39 for fresh, 0.36 for dry and 0.27 for humus (Orihuela-Belmonte et al., 2013). Downed dead wood of ≥1 cm diameter were sampled using the line intersect method (Van Wagner, 1968) in four 25-meter straight lines moving outward from each corner of the 1000 m^2 rectangular plots. Deadwood volume was calculated using equation 6 (Brown and Roussopoulos, 1974; Van Wagner, 1968).

$$V = \frac{\pi^2}{8L} \sum_{i=1}^{n} d_i^2 \dots\dots\dots\dots\dots\dots\dots\dots(eq.\ 6)$$

Where, V is the deadwood volume (m^3 ha^{-1}), L is the length of sampling line (m), and d$_i$ are the deadwood diameters in intersection (cm).

Dry weight of the deadwood was calculated applying wood density according to the state of decomposition. We applied wood densities of 0.74 g cm^{-3}, 0.78 g cm^{-3}, 0.62 g cm^{-3} and 0.27 g cm^{-3} respectively for fresh, hard dry, soft dry and decomposed deadwood (Eaton and Lawrence, 2006). Carbon content of deadwood biomass was calculated by using a factor of 0.50 (Fonseca et al., 2011). Land use intensity index was calculated using the equation 7 (Young, 1997).

$$LUI\ index = \sum \left(\frac{C}{C+F}\right) \dots\dots\dots\dots\dots\dots\dots\dots (eq.\ 7)$$

Where, LUI index: land use intensity index, C: number of continuous cultivation years in a slash and burn cultivation cycle, F: number of fallow years after each cultivation period. The land-use history was obtained through detailed interviews with the landowner.

Current annual increment (CAI) indicate the rate of carbon accumulation due to plant growth in a particular year and was calculated by using equation 8 (Djomo et al., 2011).

$$CAI = \frac{C2 - C1}{T} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots. \text{ (eq. 8)}$$

Where, CAI is the net (growth + recruitment – mortality) current annual increment (Mg C ha^{-1} yr^{-1}), C1 and C2 are the carbon stocks (Mg C ha^{-1}) in two different years, T is the time interval between the two measurements (years). Another parameter used to demonstrate the carbon accumulation rate was the mean annual increment (MAI) that was calculated, dividing the accumulated carbon stock in live biomass by the corresponding age of the forest ecosystem (Fearnside and Guimarães, 1996; Vargas et al., 2008).

The amount of carbon accumulated in newly grown trees (of ≥1 cm DBH) in the 2012 measurements are considered as recruitment and the amount of carbon converted from live to dead biomass due to tree mortality during the period between two measurements is considered as mortality. The amount of carbon added to a living tree due to increase in tree size (DBH) between the two measurements is called growth.

Statistical analysis

All data were tested for normality using Kolmogorov-Smirnov goodness-of-fit test. Since deadwood carbon stock data did not meet the assumptions of parametric tests, we applied the log10 transformation before analysis. Carbon stocks and accumulation rate data were analyzed statistically using analysis of variance (ANOVA; $\rho < 0.05$) to evaluate the significant differences among successional age groups. A repeated measures ANOVA was used to test for significant differences in changes due to growth, recruitment and mortality between the two measurement years. Tukey's significant difference test ($\rho < 0.05$) was used as a post-hoc test to separate homogeneous groups of age classes in relation to each C pool and accumulation rate. Pearson's correlation and stepwise multivariate regression analysis were

performed to evaluate the effect of forest age and land use intensity on carbon stocks as well as accumulation rates. The Chapman-Richard function (eq. 9) was used to estimate the recovery time of biomass carbon stock and basal area, taking the average basal area and biomass density of the mature forest plots as the upper limits of the equation (Zeide 1993).

$$Y = Y_{max} (1- \exp (a.Age))^b \dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots \text{(eq. 9)}$$

Where, Y is basal area or aboveground live biomass, Y_{max} is the upper asymptotic limit, using 99 Mg C ha^{-1} as the upper limit for live biomass and 33 m^2 ha^{-1} as the limit for basal area.

Results
Carbon stocks and accumulation rates by forest age
Carbon stocks in three out of five carbon pools showed significant differences between successional stages of tropical semi-evergreen forest except for deadwood carbon and soil organic carbon. Mature forests showed higher carbon stocks in all pools, compared to secondary forests. Average carbon stocks in live aboveground biomass varied from 11.72 Mg C ha^{-1} in secondary forest of 4 years old to 99.56 Mg C ha^{-1} in mature forests (Table 1).

Litter carbon stocks was significantly lower in 5-year old secondary forests (3.70 Mg C ha^{-1}) compared to mature forests (5.62 Mg C ha^{-1}), but not in other age classes. Carbon stocks in deadwood and soil organic carbon did not show any significant differences among age groups (Table 1). Mature forests reserve a total of 165.12 Mg C ha^{-1} in combined live and dead biomass whereas 4-year old forests retain 36.90 Mg C ha^{-1} in these pools. Carbon stocks in dead biomass (forest litter + deadwood) showed no trend (Fig 2).

Table 1: Average wood density and carbon stocks (Mg C ha^{-1}) at different stages of succession (estimated from 2012 measurements). Values in parenthesis indicate standard deviation. Different letters show significant differences among age groups within a pool (α=0.05).

Forest age (Yrs)	Sample size (N)	Stand WD (g cm^{-3})	Carbon stocks in five different pools (Mg C ha^{-1})					
			AGLB	RB	Litter	DW	SOC	Total
4	8	0.60[a] (0.05)	11.72[a] (4.92)	3.28[a] (1.23)	3.33[a] (0.62)	18.57 (7.85)	54.86 (24.53)	91.77[a] (26.98)
10	7	0.65[a] (0.05)	28.92[ab] (12.49)	7.56[ab] (3.09)	3.57[ab] (1.09)	12.03 (4.86)	53.26 (15.10)	105.33[ab] (22.55)
20	8	0.66[a] (0.04)	40.89[b] (11.99)	10.46[b] (2.84)	5.07[ab] (1.12)	19.18 (18.36)	50.30 (33.20)	125.90[ab] (38.02)
35	4	0.69[a] (0.09)	55.52[c] (2.52)	13.91[c] (0.58)	5.34[ab] (1.48)	12.25 (7.50)	68.42 (29.81)	155.44[b] (30.54)
MF	5	0.81[b] (0.06)	99.56[d] (20.83)	23.83[d] (5.32)	5.62[b] (1.47)	35.87 (8.97)	66.79 (34.70)	231.67[c] (43.34)

MF = mature forest, WD = wood density, AGLB = aboveground live biomass, RB = root biomass, DW = dead wood, and SOC = soil organic carbon.

Combining all pools, a gradual increase in total carbon stock could be observed according to the age, with significant differences between age groups. We also found that stand level wood density of mature forest was significantly higher compared to all age classes of secondary forests, whereas we didn´t find any differences among the age classes (Table 1).

Secondary forests of 4 and 10 years accumulated on average 4.7 Mg C ha^{-1}yr^{-1} and 4.4 Mg C ha^{-1} yr^{-1} respectively in aboveground live biomass (AGLB), where 20-year old secondary forests accumulated 2.44 Mg C ha^{-1} yr^{-1} from 2011 to 2012 (Table 2). The mean current annual accumulation rate showed a similar trend with high rates (2.9 – 3.0 Mg C ha^{-1} yr^{-1}) in the younger forests and lower rates in 35-year old and mature forests (1.1 – 1.6 Mg C ha^{-1} yr^{-1}).
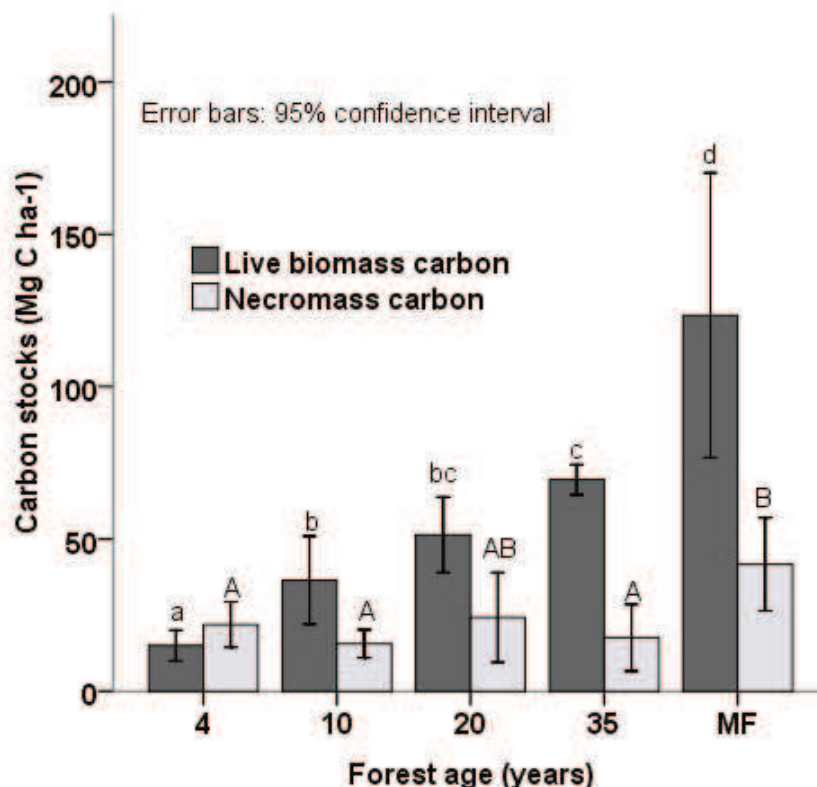
Figure 2. Carbon stocks in live and dead biomass by age groups (2012 measurement). Different letters above bars show significant differences among age groups (α=0.05). MF is mature forest.

Table 2: Average annual increment rates in aboveground living biomass (Mg C ha^{-1} yr^{-1}) and basal area (m^{2}ha^{-1}yr^{-1}) at different stages of forest succession. Values in parenthesis indicate standard deviation. Different letters in exponent show significant differences among age groups (α=0.05).

AIR	Forest age (years)				
	4	**10**	**20**	**35**	**MF**
CAI $_{AGLB}$	4.7(1.3)[a]	4.4(1.8)[ab]	2.4(0.7)[bc]	nd	0.3(2.6)[c]
CAI $_{BA}$	2.9(0.8)[a]	1.9(0.6)[b]	1.0(0.6)[bc]	nd	0.4(0.5)[c]
MAI $_{AGLB}$	3.0(1.1)[a]	2.9(1.3)[a]	2.0(0.6)[ab]	1.6(0.1)[ab]	1.1 (0.2)[b]
MAI $_{BA}$	2.2(0.5)[a]	1.6(0.6)[ab]	1.0(0.2)[bc]	0.8(0.0)[c]	0.4 (0.1)[c]

AIR= Annual increment rates, CAI = current annual increment, MAI= mean annual increment (2012 measurement), AGLB = aboveground living biomass, BA =basal areas, MF = mature forests (here considered 85 years old), nd = no data

Carbon stocks change due to tree growth, recruitment and mortality

The species composition and tree density of forest ecosystem changed with age because of the mortality of some trees and recruitment of others. Younger 4-year old secondary forest showed the highest relative rate of tree growth (87% of initial C stock) followed by 10-year old secondary forest (25% of its initial C stock) (Table 3), whereas 20-year old secondary forest and mature forest showed lower rates of tree growth (9% and 2% of their initial C stock respectively) between 2011 and 2012 (Table 3). The minimum detectable change in growth (to compensate for possible errors in repeated measurements) for all age groups was positive. The relative rate of tree recruitment was high in 4-year old forests (13.2% of initial C stock), and decreased sharply with forest age. Tree mortality ranged from 1.4% of initial C stocks in mature forest to 3.3% in 4-year old forest, without significant differences between age groups. The net changes in carbon stocks were positive in all age groups but decreased sharply with increasing forest age (Tables 2 and 3). The differences in carbon stocks between the two measurements were significant ($p<0.05$) in the 4- and 10-year old forests, whereas the 20-year old and mature forests did not show significant difference between the two measurements (Table 3).

Aboveground tree biomass carbon and basal area distribution by diameter class

The largest amount of carbon in AGLB was concentrated in smaller trees in the early stages of succession and gradually changed to larger trees in the older plots, as expected. Young 4-year old forests accumulated 58% of its C stocks in trees with DBH<5 cm (6.6 Mg C ha^{-1}; Table 4), 31% in trees with DBH of 5-10 cm and only about 12% in trees with DBH≥10 cm, whereas in 10-year old forests accumulated only 33% of its stock in trees with DBH<5 cm, 47% in trees with DBH between 5-10 cm (13.4 Mg C ha^{-1}) and 20% in trees with DBH≥10 cm. In 35-year old secondary forests about 49% of the C stock was stored in trees with DBH between 10 and 20 cm, with only about 11% in trees with DBH>20 cm, whereas in mature forest more than 56% was located in trees with DBH ≥20 cm (55.8 Mg C ha^{-1}). Although the 35-

old forests recovered about 85% of BA of mature forests, this is mainly due to the relatively high number of small to medium sized trees (5-20 cm; Table 4).

Table 3: Annual change in aboveground tree biomass carbon stock due to tree growth, recruitment and mortality at different ages of forest succession Different letters in exponent show significant differences among age groups while asterisks show significant differences between two measurement years (α=0.05). Reported percentages are of respective initial stocks. Values in parenthesis represent standard deviation.

Forest age →	4 yrs	10 yrs	20 yrs	MF
Sample size	7	7	8	4
Initial stock in 2011				
C (Mg C ha^{-1})	6.72 (4.24)^{a*}	24.19(11.91)^{ab*}	38.12(11.56)^{b}	98.75(26.51)^{c}
ME (95%CI)	±0.05	+0.14, -0.13	±0.19	±0.29
N (Trees ha^{-1})	5985 (2653)	8375 (4761)	8601 (2227)	5033 (1568)
Tree growth				
C (Mg C ha^{-1}yr^{-1})	4.58 (1.55)^{a}	4.47 (1.62)^{a}	3.15(1.05)^{ab}	1.88 (0.71)^{b}
%	87.6 (44.0)^{a}	25.1 (17.5)^{b}	9.3 (5.3)^{b}	2.0 (0.9)^{b}
CD (Mg C ha^{-1}yr^{-1})	3.98	4.45	2.91	1.46
N (Trees ha^{-1})	5782 (2595)	8000 (4956)	8089 (2286)	4858 (1463)
%	96.6 (2.62)	91.9 (8.01)	93.6 (4.28)	96.8 (1.36)
Tree recruitment				
C (Mg C ha^{-1} yr^{-1})	0.39 (0.41)^{a}	0.09 (0.08)^{b}	0.06 (0.04)^{b}	0.14 (0.21)^{b}
%	13.2 (22.2)^{a}	0.7 (0.9)^{b}	0.2 (0.1)^{b}	0.2 (0.2)^{b}
N (Trees ha^{-1})	1694(1806)^{a}	433 (188)^{b}	296 (142)^{b}	170 (100)^{b}
%	33.0 (40.9)^{a}	7.38 (5.4)^{b}	3.5 (2.0)^{b}	3.3 (1.1)^{b}
Tree mortality				
C (Mg C ha^{-1} yr^{-1})	0.23 (0.35)	0.53 (0.59)	0.90 (0.84)	1.70 (2.22)
%	3.3 (4.3)	3.1 (3.2)	2.9 (3.4)	1.4 (1.5)
N (Trees ha^{-1})	204 (187)^{b}	375 (222)^{ab}	513 (285)^{a}	175(109)^{b}
%	3.4 (2.6)	8.1 (8.0)	6.4 (4.2)	3.2 (1.3)
Net change				
C (Mg C ha^{-1} yr^{-1})	4.7(1.3)^{a}	4.4(1.8)^{ab}	2.4(0.7)^{bc}	0.3(2.6)^{c}
%	97.5 (60.3)^{a}	24.7 (17.2)^{b}	6.9 (2.5)^{c}	0.8 (2.3)^{d}
Final stock in 2012				
C (Mg C ha^{-1} yr^{-1})	11.45(5.16)^{a*}	28.59(12.69)^{ab*}	40.56(11.84)^{b}	99.08(24.16)^{c}
ME (95%CI)	±0.08	+0.19, -0.14	+0.20, -0.19	±0.29
N (Trees ha^{-1})	7476 (3007)	8432 (4904)	8384 (2319)	5028 (1548)

MF = mature forest, ME = measurement error expressed in 95% confidence interval, CD = conservative difference (2012$_{min}$ – 2011$_{max}$).

Table 4: Distribution of aboveground live (tree) biomass carbon stocks (Mg C ha^{-1}), tree density and basal area according to diameter size at different age classes. Different letters in exponent in total values show significant differences among age classes (α=0.05).

Diameter clases / Parameters	Forest age (number of plots)				
	4 yrs (8)	10 yrs (7)	20 yrs (8)	35 yrs (4)	MF (5)
1.0 - 4.9 cm					
AGLB (SD)	6.6 (2.2)	9.6 (6.2)	8.8 (3.9)	4.0 (1.8)	2.0 (0.9)
% AGLB	58%	33%	22%	7%	2%
N trees	7089	7151	6698	4019	3259
BA	5.6 (1.7)	6.5 (4.1)	6.2 (2.5)	3.3 (1.3)	1.8 (0.7)
5.0 - 9.9 cm					
AGLB (SD)	3.6 (2.6)	13.4 (7.4)	19.1 (8.3)	18.3 (4.7)	10.5 (3.9)
% AGLB	31%	47%	47%	33%	11%
N trees	383	1134	1440	1733	956
BA	2.3 (1.3)	6.5 (3.0)	8.6 (3.4)	8.3 (2.4)	3.9 (1.7)
10.0 - 14.9 cm					
AGLB (SD)	1.2 (1.8)	4.7 (5.6)	8.3 (5.2)	16.1 (1.1)	17.2 (6.4)
% AGLB	10%	17%	21%	29%	17%
N trees	43	131	224	568	412
BA	0.7 (0.9)	2.4 (2.6)	3.8 (2.4)	7.3 (0.9)	5.2 (1.5)
15.0 - 19.9 cm					
AGLB (SD)	0.1 (0.2)	0.6 (0.5)	2.9 (2.3)	10.7 (5.0)	13.6 (3.6)
% AGLB	1%	2%	7%	19%	14%
N trees	3	14	44	200	160
BA	0.1 (0.1)	0.4 (0.2)	1.5 (1.1)	4.9 (2.0)	3.9 (0.8)
>20.0 cm					
AGLB (SD)	0.1 (0.1)	0.4 (0.8)	1.5 (2.1)	6.1 (4.0)	55.8 (16.3)
% AGLB	1%	1%	4%	11%	56%
N trees	1	6	13	60	228
BA	0.1 (0.1)	0.4 (0.8)	0.8 (0.9)	3.4 (2.1)	18.5 (4.2)
Total					
AGLB (SD)	11.5 (5.2)[a]	28.6 (12.7)[ab]	40.6 (11.8)[b]	55.2 (2.4)[c]	99.1 (24.2)[d]
% AGLB	100%	100%	100%	100%	100%
N trees	7519	8436	8418	6579	5015
BA	8.7 (2.3)[a]	16.2 (6.4)[b]	20.9 (4.9)[bc]	27.2(1.2)[cd]	33.2 (5.8)[d]

AGLB = mean aboveground live biomass (Mg C ha^{-1}), SD = standard deviation, % AGLB = the percentage of live aboveground biomass, N trees = the number of trees per hectare, BA = the mean basal area (m^2 ha^{-1}), MF = mature forest.

Effect of land-use intensity on carbon accumulation

Repeated shifting cultivation cycles with shorter fallow and continuous longer cultivation periods affected carbon accumulation after abandonment. The older secondary forests of 35 years only experienced one cultivation cycle resulting in lower LUI indices (close to 0), whereas younger secondary forests had been slashed more than once with varied cycles of cultivation and fallow, resulting to higher land-use intensity indices (up to 1.44). Combined (live + dead) biomass carbon accumulation was positively correlated with forest age (r = 0.77, ρ<0.01) and negatively correlated with LUI (r = - 0.61, ρ<0.05) (Fig. 3). Stepwise multivariate regression analysis showed that both forest age and LUI were significant predictors of the variation in total carbon stock. The partial correlation analysis indicate that forest age and LUI are not correlated (Partial correlation coefficient of carbon stock with forest age, controlling for LUI = 0.678; and LUI, controlling for age = -0.423; tolerance = 0.760; VIF = 1.316).
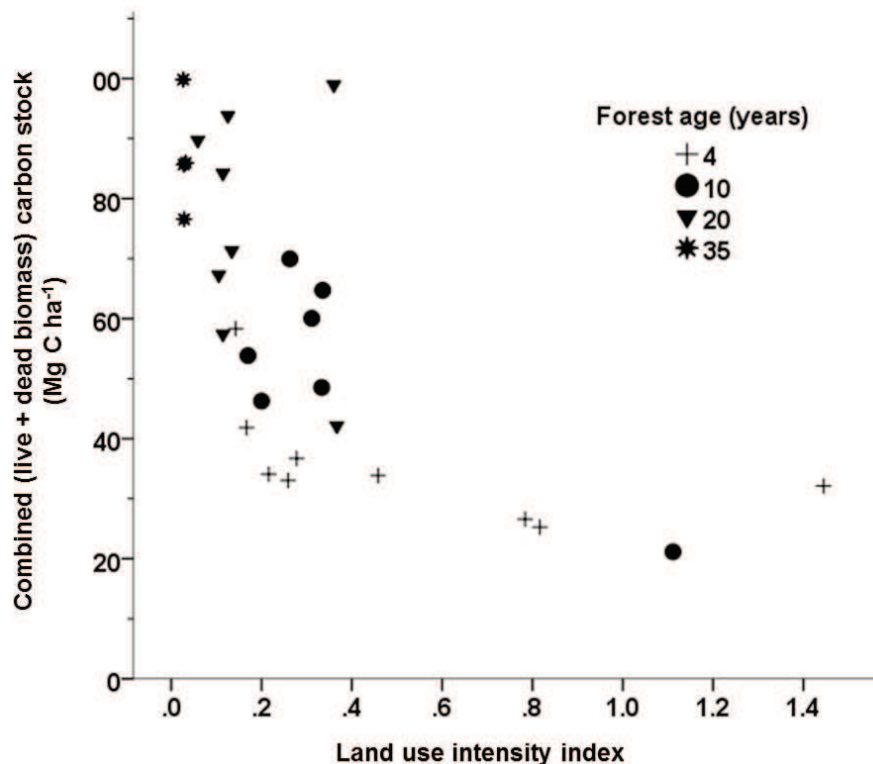
Figure 3. Effect of land use intensity in total biomass carbon stocks. TC is total carbon; LUI is land use intensity index

Time to recover pre-disturbance carbon densities

We applied the Chapman-Richard growth function to estimate the recovery time for BA and AGLB (Zeide1993). To compare both functions, we assumed for both cases the age of mature forests at 85 years (Fig 4).

Figure 4 Panel A: Basal Area = 33 * (1 - exp(a * Age))^b; a = -0.044 ± 0.012; b = 0.79 ± 0.19; p<0.01; variance explained: 78%. Y-axis: Basal Area (m²/ha). X-axis: Age.

Figure 4 Panel B: Living Biomass = 99 * (1 - exp(a * Age))^b; a = -0.03 ± 0.007; b = 1.05 ± 0.21; p<0.001; variance explained: 84%. Y-axis: Living Biomass (Mg C/ha). X-axis: Age.

Figure 4. Chapman-Richard growth functions for basal area (A) and aboveground living biomass (B), assuming mature forest at 85 years. Asymptotic limits of basal area = 33 m^2 ha^{-1} and AGLB = 99 Mg C ha^{-1}.

We used the average BA and AGLB of the mature forests as the asymptotic upper limit in the equation, 33 m^2 ha^{-1} and 99 Mg C ha^{-1} respectively. The estimated carbon recovery time for BA is about 85 years, whereas the 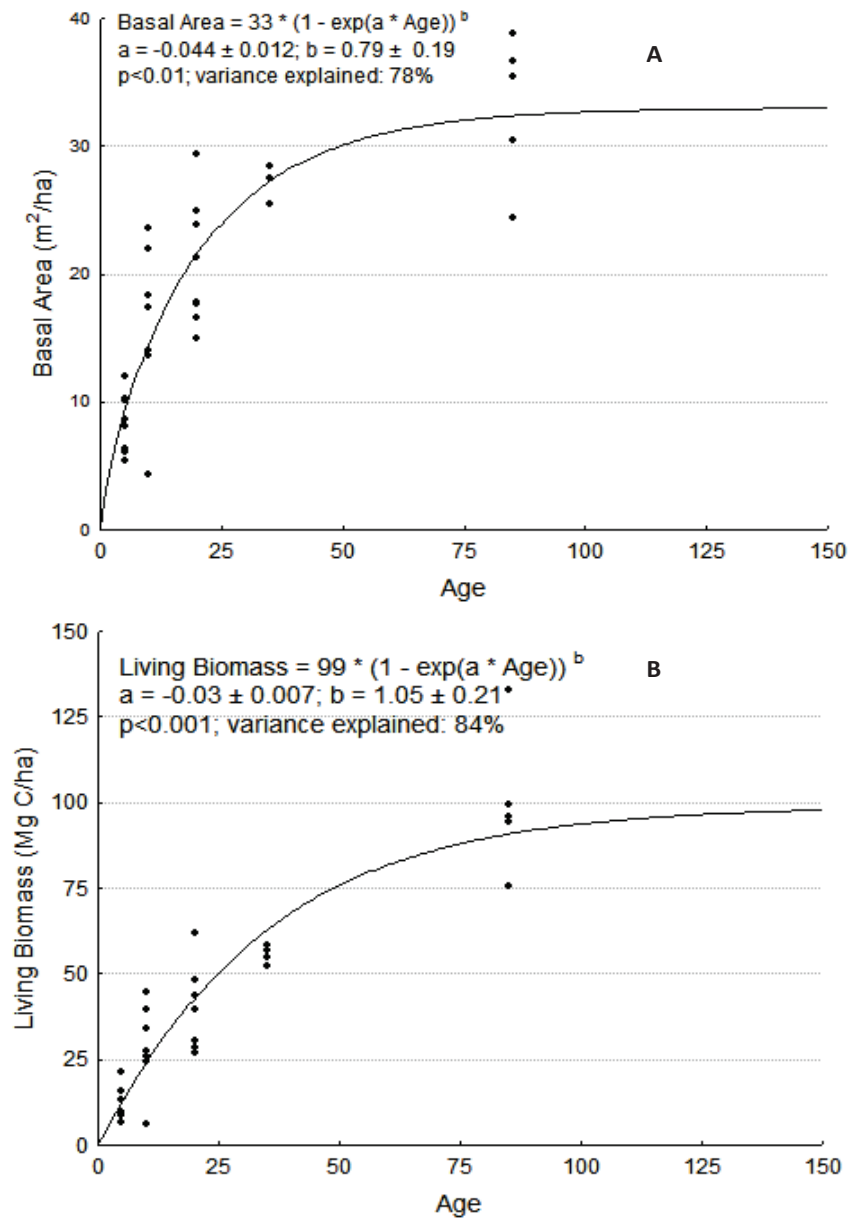time to recover pre-disturbance biomass densities would take more than 125 years after abandonment of the agricultural practice (Fig 4A and B). The difference in recovery time between BA and AGLB is mainly due to the higher wood density of the species in mature forest compared to all secondary stages (Table 1).

Discussion

During the stages of succession, the forest ecosystems go through important processes like tree establishment, canopy closure, competition, nutrient cycling and stabilization (Clements, 1916; Gómez-Pompa and Vázquez-Yanes, 1981; Macario-Mendoza, 2003; Prach and Walker, 2011). Although different studies use different age categories to define successional stages, in general younger secondary forests are considered more productive than older ones (Brown and Lugo, 1990; Drake et al., 2011; Pregitzer and Euskirchen, 2004). In our study the annual rate of carbon accumulation was higher in younger stages of succession and decreased with age, which is in accordance with other studies (Chazdon et al., 2007; Lebrija-Trejos et al., 2010; Purves et al., 2008; Vargas et al., 2008). Brown and Lugo (1990) reported that aboveground biomass carbon increases by 3.1 Mg ha^{-1} yr^{-1} during the first 20 years of succession and 0.9 Mg ha^{-1} yr^{-1} in the following 60 years of re-growth in tropical forest ecosystems. Pan et al. (2011) reported total live and dead biomass carbon accumulation rate of 4.56 Mg C ha^{-1} yr^{-1} in secondary forests of tropical America. Both CAI and MAI estimates in our study are similar to these studies but much higher than the 1.5 Mg C ha^{-1} yr^{-1}, reported by Read and Lawrence (2003) for young secondary forests of the Yucatán Peninsula.

Litter carbon stocks increased with forest age and reached mature forest level (5.62 Mg C ha^{-1}) at the age of 20 years (5.07 Mg C ha^{-1}) and is within the range reported in other studies of similar tropical forests (Fonseca et al., 2011; Hughes et al., 1999; Jaramillo et al., 2003). No significant trends could be observed in the dead wood biomass between the age classes. Reported woody debris carbon stocks for tropical forests ranged from 2.4 Mg C ha^{-1} in dry forest to 61.4 Mg C ha^{-1} in humid evergreen

forests (Eaton and Lawrence, 2006; Keller et al., 2004; Orihuela-Belmonte et al., 2013) and may fluctuate particularly due to disturbance history, such as fires and hurricanes, and variation in decomposition rates (Harmon et al., 1995) . Particularly softwoods that predominate in the secondary forests have in general faster decomposition rates (Harmon et al. 1995), which may explain in part the higher necromass stock in mature forests, where slow decomposing hardwood species dominate.

Carbon stocks change due to growth, recruitment and mortality of trees

The forest structure, species composition and primary productivity change as the vegetation grow (Drake et al., 2011; Hartter et al., 2008; Lebrija-Trejos et al., 2010). The velocities of such changes also vary in different stages of forest succession (Hughes et al., 1999; Lebrija-Trejos et al., 2010; Marín-Spiotta et al., 2008). This variation may be attributed to mechanisms like species establishment, variable growth, competition, disturbance history and the environment (Marín-Spiotta et al., 2008; Mendoza-Vega and Messing, 2005; Ochoa-Gaona et al., 2007; Prach and Walker, 2011), or degree of human interference. Thus, the dynamic changes in carbon flux and balance are strongly linked to successional phases of vegetation growth after abandonment (Chazdon et al., 2007; Lebrija-Trejos et al., 2010; Marín-Spiotta et al., 2008). Carbon stocks and mean annual increment rates have been documented (Eaton and Lawrence, 2009; Hughes et al., 1999; Jaramillo et al., 2003; Orihuela-Belmonte et al., 2013; Urquiza-Haas et al., 2007), but variation in growth, recruitment and mortality of trees along the successional gradient of young secondary to mature forests and their relations to carbon dynamics has not been reported elsewhere. Our findings demonstrate that younger secondary forests can be characterized as forests at establishment phase as tree recruitment was very high at this stage and got near to zero in the older secondary forests. The gradual decrease in tree growth and fairly constant rate of tree mortality in proportion to live biomass result in a decrease of net carbon accumulation with forest age (Chazdon et al., 2005; Marín-Spiotta et al., 2008; Willig and Scheiner, 2011). The average net change in carbon stocks is positive in all phases of forest succession but decreased with age reaching nearly zero in mature forests, which in turn, demonstrate that tropical

secondary forests act for many years as an important sink of atmospheric carbon dioxide (Bonan, 2008; De Jong et al., 2010; Le Quéré et al., 2013; Pan et al., 2011). Thus, our hypothesis of higher carbon turnover in younger phases of succession compared to older phases was accepted in terms of percentage of carbon stock change in all processes and also in absolute terms for tree recruitment and growth, only tree mortality increased with age, as larger trees died in these stages.

Time of recovery of pre-disturbance biomass densities

Our study reveals that the estimation of the time of recovery of secondary forests to pre-disturbed conditions take much longer than previously reported. In our case 35-year old secondary forests stored only about 56% of AGLB found in mature forests, which is similar to those reported by Urquiza-Haas et al. (2007), who found that 25-year old secondary forests only recovered about 40% of live biomass, but is much lower than Turner et al (2001), who report that 25-year old fallow already contained about 80% of the biomass of mature forests in the same type of forest or in semi-evergreen forests of Chiapas, where forests at the age of 31 – 40 years recovered almost 79% of the biomass (Orihuela-Belmonte et al., 2013). Looking at forest structural traits, we noticed that forests recover total basal area fast, mainly due to high densities of relatively small trees, compared to mature forests, where 56% of BA is due to trees > 20 cm DBH. Also, the trees in secondary forests are dominated by softwood species, which are very slowly substituted by slow-growing hardwood species. Even the 35-year old plots were still dominated by softwood species, as can be derived from the average wood density of the trees. We therefore adjusted the applied general allometric equations according to the wood density of each tree present in the plots, as suggested by Urquiza-Haas et al. (2007). Estimating the recovery time of forests with the Chapman-Richard function, indicate that it will take more than 125 years to recover pre-disturbance biomass densities, which is much longer than the 55-95 years reported for similar forest types by Read and Lawrence (2003) and Vargas et al. (2008, applying a similar Chapman-Richard function), or Orihuela et al. (2013) for semi-evergreen forests of Chiapas and Hughes et al. (1999) for wet tropical forests in Veracruz. The change in species composition from

dominance of softwood species to hardwood species and the increase in DBH of these hardwood trees to pre-disturbance sizes may explain this long time span.

The gradual decrease of current and mean annual increment of live biomass with age, reaching near to zero in mature forests, is modeled in this study with an asymptotic function of biomass accumulation (Clements, 1916; Gómez-Pompa and Vázquez-Yanes, 1981; Prach and Walker, 2011; Van Breugel et al., 2007; Vargas et al. 2008). However, the accumulation of live biomass may be negative in some years due to mortality of one or more large trees that momentary decreases the amount of live biomass, as occurred in one of our monitoring plots of mature forests, which coincides with the dynamic equilibrium model of forest succession (Drake et al., 2011; Feet, 1992; Mascaro et al., 2011).

Effect of land use intensity on carbon accumulation

Although forest age was the principal predictor of carbon stocks and accumulation rates (Bradford et al., 2008; Brown and Lugo, 1990; Vargas et al., 2008), LU-intensity also affected significantly carbon accumulation, particularly in the younger age classes where a high variation in LU-intensity was observed. The type, intensity and duration of previous land use have strong effect in the growth and carbon recovery trajectory of secondary forests (Chai and Tanner, 2011; Chazdon et al., 2005; Klepeis et al., 2004; Marín-Spiotta et al., 2008; Ochoa-Gaona et al., 2007; Ostertag et al., 2008). The LU-intensity index applied in this study, not only considered the number of cycles of cultivation, but also accounted for the crop and fallow duration. The accumulated carbon stock in live and dead biomass pools showed a negative correlation with LU- intensity in all age classes of forest succession, as has been reported by Caspersen et al. (2000). However, it was more pronounced in younger forests that have passed either through more cycles of slash and burn agriculture or longer duration cultivation.

Shifting cultivation is often considered as a biodiversity-friendly agricultural system, where short cultivation periods, long fallows and the mosaic feature of the traditional system maintain seed pools that allow the regeneration of diverse secondary forests (Padoch and Pinedo-Vásquez 2010, Rerkasem et al. 2009). However, our results

showed that landowners do not always leave their plots for sufficient periods of fallow and cultivate repeatedly the same plots for years. In addition, burning the slashed residues (deadwood, litter and non-tree vegetation) every year before seed sowing is the common practice in shifting cultivation, which reduces the carbon stocks in live as well as dead biomass on the soil surface. More intensive burning and cropping reduce the seed and propagule pools of original trees species and foster invasive species like bracken ferns (*Pteridium aquilinum* L. Kuhn) after land abandonment (Schneider and Fernando 2010). However, conservation incentives and remittance from relatives abroad have partially controlled the expansion of slash and burn agriculture in some households (Schmook et al 2013). Introduction of land-efficient sustainable production systems, off-farm income diversification and incentives for carbon stock conservation and enhancements could be considered as some of the alternatives in sustaining both farmers and forests in the region.

Soil organic carbon

Our estimates of soil organic carbon (50 – 68 Mg C ha^{-1}) is similar to the amount reported by Orihuela et al. (2013; 62 – 92 Mg C ha^{-1}) and Vargas et al. (2008; 22 – 85 Mg C ha^{-1}). The region of our study was dominated by shallow soil horizon with average soil depth of <20 cm as reported by Vargas et al. 2008. In the plots where soil depth was more than 20 cm, the SOC fraction was low (0 – 3.3%) compared to shallow soils (3.1 % to 11.6% at 0-10 cm and 0.1 – 7.3% at 10-20 cm depth, data not presented). The soils with high organic carbon levels were characterized by lower bulk densities (0.59 Mg m^{-3} at 0 - 10 cm). These characteristics give rise less soil material and thus lower soil organic carbon densities expressed in Mg C ha^{-1}. It has been reported that increased leaf litter inputs and fine roots turnover commonly associated with secondary forest development lead to an increase in SOC stocks (Brown and Lugo 1990, Guariguata and Ostertag 2001). In contrast, SOC stocks in our study did not vary significantly among the age groups indicating a more stable nature of SOC compared to the above ground biomass carbon. Other factors that may have influenced to rather stable SOC contents along the age classes are related to the relatively slow processes of change that occur in soil organic matter in forest-

agriculture transitions where farming systems are low-input and non-mechanized (Hughes et al. 1999, Mendoza-Vega and Messing 2005, Soto-Pinto et al. 2010). Soil mineralogical processes like impregnation with fine particle-sized carbonates have explained the stability of organic carbon in these types of soils (Oades 1988, Shang and Tiessen 2003). These authors mentioned that the basic environment accelerates the initial stages of decomposition of volatile carbons, but the intimate mixing with soil components slows down the later stages of decomposition of more stable organic matter. In addition, we didn´t find any significant correlation between aboveground biomass and SOC (results not presented), which is similar to the findings of Schedlbauer and Kavanagh (2008) in a secondary forest chronosequence of north eastern Costa Rica.

Sources of uncertainty.

Any unique or repeated measurement of carbon densities and dynamics in natural ecosystems has associated sources of error and uncertainty. The main sources of uncertainty that explain the variation in carbon stocks and change rates among plots within the same age group and land-use intensity are linked to uncertainties in determining the exact age of the plots and trees within the plots and the spatial variation of ecological conditions between the plots, such as soil and climate. Although we have assigned a particular age to each group, these may vary one or two years in the younger age classes and probably increases to about 5 years in the older classes. In terms of ecological conditions, the plots in Nuevo Conhuas are located further away those in the other three communities and therefore may present slightly different rainfall patterns and soil conditions. Particularly rainfall may be a constraining factor in carbon accumulation rates, as pointed out by Orihuela et al (2013). However, climate data are not available to detect spatial differences in rainfall or temperature and the number of plots was too small to detect significant differences in soil conditions. The exact carbon density and change rate may have errors due to the sampling design to estimate the various pools and measurement practices. Since the repeated measurement of DBH over a short time period is prone to a measurement error that in total may be larger than the estimated increment. We

therefore calculated the minimum detectable difference between the two measurements taking into account the measurement error. As such, the gross increment of the living trees in all age classes including mature forests was positive.

Conclusion

This study focused on tracing the successional trajectories of carbon sequestration and underlying processes that occur during secondary forest growth. Analysis of tree community dynamics like tree recruitment, growth and mortality provided us a better understanding on how these processes influence part of the carbon dynamics at different stages of forest regrowth. Our results clearly indicated that very high carbon accumulation rates (nearly hundred percent annual carbon addition in live biomass) in the first five years of succession was explained by high relative tree growth and high recruitment rates. The net positive carbon accumulation rates in older secondary and mature forests were the results of tree growth, whereas recruitment did not play a significant role anymore. Lower recruitment rates and slower growth of trees in later stages of succession may explain part of the long period of carbon recovery. Changes in species composition during succession show a pattern of dominance of softwood species in the early stages, gradually changing to dominance of hardwood species, which may explain the long time required to recover pre-disturbance carbon densities. There was no significant difference in stand level wood density in secondary forest of 4 to 35 years, however, the mature forest showed significantly higher average stand level wood density compared to all the secondary forests in this study. This, in turn, resulted to significantly higher carbon density in mature forest biomass than older secondary forest despite the fact that there was no significant difference in basal area between the secondary forest and mature forests. Converting one hectare of mature forest to slash and burn agriculture would mean the loss of about 165 Mg of live and dead biomass carbon equivalent to 605 tons of CO_2 flux to the atmosphere. This in turn, may take more than a century to re-capture the lost carbon if this land is abandoned after cultivation.

The principal predictor of carbon stocks and accumulation rates of secondary forests is age after abandonment. Younger forests accumulate carbon more rapidly

compared to older secondary forests. Tree establishment, growth and mortality dynamics was also higher in younger forests. Repeated burning and more intensive cultivation may prolong the time taken for carbon recovery. This study not only highlighted the role of younger forest in carbon cycling but also emphasized the importance of conserving old-growth mature forests for carbon retention. The area covered by similar secondary forest mosaics in Mexico is about 8.7×10^6 hectares (FAO 2010b) which is considered vulnerable as landowners can readily convert these to treeless land use systems to meet their basic needs. Community participation in REDD+ actions and strategies would significantly enhance sustainable land use and conservation of these important carbon reserves in Mexico. The methods and results of the present study provide a sound and consistent basis on the issues related to the estimation of carbon stocks, emissions, and removals arising from the changes that commonly occur in tropical forest-agriculture continuum and modeling the carbon loss and gain from successional dynamics of tropical forests.

Limitations and recommendations

The data used to estimate the carbon stock changes in this study were obtained from measurements in two subsequent years in a chronosequence. As a result, we couldn´t analyze the possible year to year variation in growth rates, recruitment and mortality within each age class.. This question will be resolved once we have more data available in subsequent years.

Another limitation is we couldn´t obtain the secondary forests plots of more than 35 years. The oldest secondary forests considered in the study were of 35 years after abandonment of slash and burn agriculture. It was difficult obtain the sampling plots older than 35 years as the current human settlements in the study area has a history of about 30 to 40 years. Therefore, we couldn´t have more field information about the changes that can occur in older phases secondary forest succession before they get to mature forests. The trajectories of carbon accumulations were derived from regression models based on the information obtained from secondary forests of up to 35 years and mature forests. The establishment sampling plots for 35 years age only in the second measurement year precluded to calculate the growth, recruitment and

mortality for this age class. The changes that occur in this age class can be obtained by the subsequent measurement.

Acknowledgements

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CAPÍTULO III

Successional and seasonal variation of litterfall and associated nutrient transfer in semi-evergreen tropical forests of SE Mexico

Successional and seasonal variation of litterfall and associated nutrient transfer in semi-evergreen tropical forests of SE Mexico

Deb Raj Aryal[1], Bernardus HJ De Jong[1*], Susana Ochoa-Gaona[1], Jorge Mendoza-Vega[1], Ligia Esparza-Olguin[1]

[1]El Colegio de la Frontera Sur (ECOSUR), Av. Rancho Polígono 2-A, Ciudad Industrial, Lerma, C.P. 24500, Campeche, México

*Corresponding author

Abstract

Forest conversion to agriculture and grassland has been widespread in the late twentieth century in SE Mexico. The productivity, functioning and carbon dynamics of the secondary forests growing after abandonment of agricultural fields are expected to be different from mature primary forests. In this study, we analyzed whether forest age and seasonal variation affect the amount and temporal distribution of litter production and associated nutrient transfers from vegetation to soil in secondary forests grown after slash and burn agriculture and compared these with corresponding transfers in mature forests. The experiment was conducted across a chronosequence of semi-evergreen tropical forest of Calakmul, located in the southern part of the Yucatan peninsula, Mexico. Total litterfall ranged from 4.1±0.7 to 7.1±0.5 Mg ha^{-1}yr^{-1} with leaf contribution between 84 to 90%. The associated carbon transfer ranged from 1.9±0.3 to 3.2±0.2 Mg ha^{-1}yr^{-1} while nitrogen transfer ranged from 49±9 to 83±6 kg ha^{-1}yr^{-1}. Secondary forests recovered the litter production to mature forests level within 5 years. We found that secondary forests between 10 to 20 years old produce more litter than earlier stages or mature forests. However, the accumulated forest floor litter mass increased gradually with age and was highest in mature forest. Peaks in monthly litterfall coincide with dry season, while the proportion of dry season litterfall was larger in secondary forests compared to mature forests. Aboveground net primary productivity (ANPP) decreased after 10 years with forest age. Land-use intensity affected litter production. Soil quality did not influence litterfall or litterfall distribution.

Introduction

Secondary and primary forests in the tropics are undergoing rapid change in their function, composition and carbon cycling because of different types and degrees of human intervention (Brown and Lugo 1990; Malhi 2012; Aryal et al 2014). Most forests were converted to extensive pasturelands and agricultural fields during the decades of late twentieth century in southern Mexico due to large scale incentives for animal production and agriculture plans (De Jong et al 2000; Turner et al 2004; Isaac-Márquez et al 2008; Aryal et al 2012). Such anthropogenic interventions created gradients of secondary forests at varies stages of succession, mixed with pasture land and patches of slash and burn agriculture (Ochoa-Gaona et al 2007; Rueda 2010). Slash and burn agriculture is still one of the major land use of the Mayan farmers in south eastern Mexico (Schmook et al 2013). One of the key challenges of modern ecologists is to understand the patterns, processes and pathways of carbon cycling of those transitional forests in fine spatial and temporal scales (Thuille and Schulze 2006; Malhi 2012).

Litterfall is one of the fundamental processes of nutrient cycling in forest ecosystems (Cuevas and Medina 1986; Takyu et al 2003; Dent et al 2006; Negash and Starr 2013) and an important pathway of carbon and energy transfer from vegetation to soil (Bray and Gorham 1964; Vogt et al 1986; Zhou et al 2014). Litter production is an important part of the net primary production (NPP), that is the net amount of carbon captured by plants through photosynthesis (Melillo et al 1993) and represents a link between carbon capture through photosynthesis and emission through litter decomposition (Meentemeyer et al 1982). As most of the leaf, flower and fruit production in the sub-humid tropics is recycled every year, the quantification of litterfall is important to understand productivity, phenology, carbon dynamics and the capacity of the forest ecosystems to recover from human and natural disturbances (Ewel 1976; Vitousek 1984; de Jong 2013) . Litterfall studies can also provide the analogy to detect synchronies between biological and meteorological cycles (Chapin

III and Eviner 2005). A better understanding of the temporal patterns and processes of forest litterfall dynamics provide a basis of modelling responses of forest ecosystems to climate change (Martinez-Yrizar and Sarukhan 1990; Thuille and Schulze 2006; Scheer et al 2011).

Globally, there are studies related to litterfall and forest production (Ewel 1976; Chapin III and Eviner 2005; Scheer et al 2011; Zhou et al 2014). However, the pattern of litterfall and associated carbon and nutrient flows during the successional stages and the effect of land use history have not been well understood in tropical secondary forest ecosystems. In this study, we applied field based experiment on litter production and associated nutrient flux in a chronosequence of tropical secondary and mature forests. We hypothesized that: i) annual litter production increases with forest age rapidly to reach a dynamic equilibrium in early stages of secondary forests, and ii) stands with more intensive land use before abandonment has lower litter production in the same successional stages than stands with less intensive land use.

Methods

Study sites

The study was conducted in two localities around Calakmul Biosphere Reserve, situated in the south of Yucatan Peninsula, Mexico. Sampling sites were located in communities (ejidos): El Carmen II and Cristóbal Colon of the municipality of Calakmul (Fig. 1). The region is composed of rolling limestone hills and ridges of karstic origin that ranges from 100 to 380 m above sea level (Bautista et al. 2011). The dominating soil types in the region are rendzic leptosols and vertisols (Bautista et al. 2011). The region is characterized by a sub-humid tropical climate (García 1973; Xuluc-Tolosa et al 2003) with an average precipitation of about 1000 mm per year (with major portions of the rainfall from June to October, Fig 2) and mean annual temperature of about 26°C. Semi-evergreen tropical forest is the dominant forest type in the region (Rzedowski 1981; Pérez-Salicrup 2004), of which large portions have been converted to slash-and-burn agriculture that created a mosaic of agricultural lands mixed with secondary forests in various stages of development (Table 1).
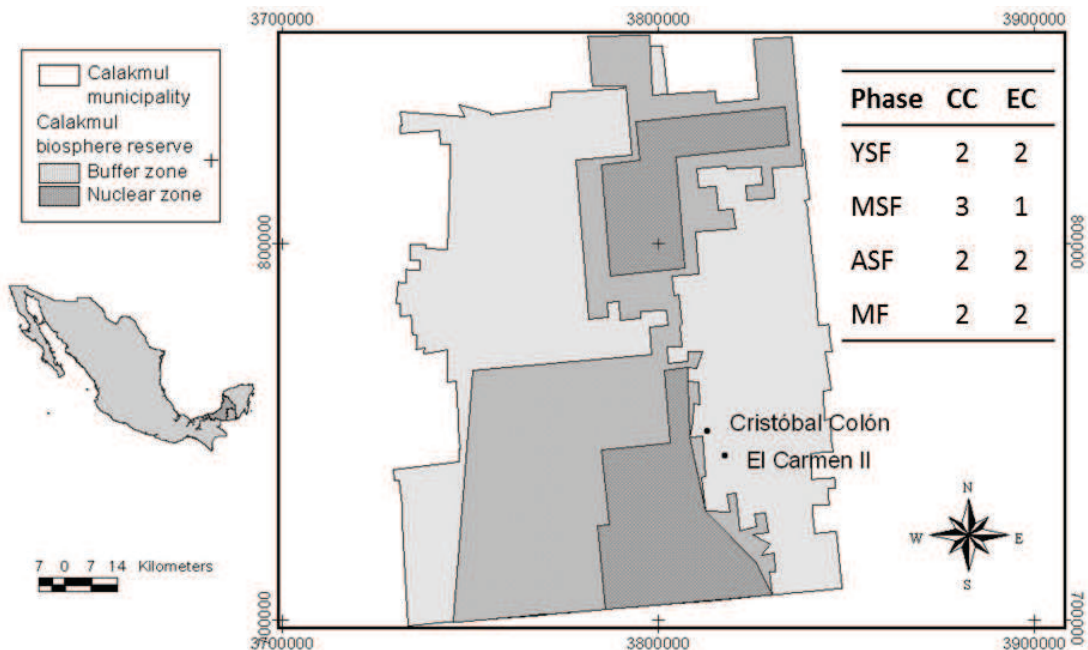
Figure 1: Location of study site and distribution of experimental plots in two localities. CC = Cristobal Colon, EC = El Carmen II. YSF = young secondary forests, MSF = medium secondary forests, ASF = advanced secondary forests and PF = primary forests
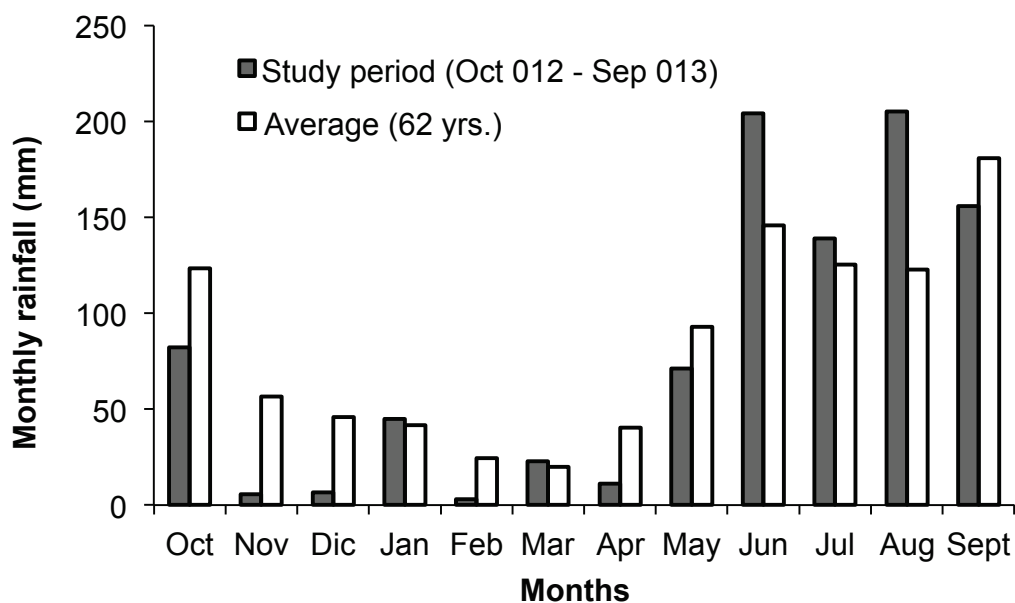

Figure 2: Monthly precipitation for the study region obtained from Meteorological station, Zoh Laguna, Calakmul (89°25'32"W, 18°35'02"N). Data courtesy: Comisión Nacional de Agua (CONAGUA), Campeche.

These are forests with trees reaching 15–25 m in height in mature stands, 25%–50% of which lose their leaves during the dry season(Martínez and Galindo-Leal 2002; Román-Dañobeytia et al 2014).

Litter sampling

Forest stands of four different phases of succession (young, medium and advanced secondary forests and mature forests) were selected for the experiment (Table 1). A total of 16 carbon monitoring plots of 1000 m^2 were established (four plots in each successional stage). Age was referred to the number of years after abandonment of cultivation.

Litterfall was collected at fortnightly intervals during a whole year (from October 2012 to September 2013) with 12 circular litter traps of 0.5 m^2 (Cuevas and Medina 1986; Takyu et al 2003) placed around each carbon monitoring plot. All the traps were placed at a height of about 1 m from the ground surface with the support of triple iron stands. The collected samples were put in paper bags and transported to laboratory for processing. The samples were oven dried at 70°C for 3 days to obtain stable dry weight and separated in to: leaves, twigs and cortex, fruits and flowers and a rest group. These components were weighted separately and sub sampled for laboratory analysis.   Carbon (C), nitrogen (N), phosphorus (P) and potassium (K) content of each component were analyzed to evaluate the nutrient flux associated with litterfall.
Forest floor litter samples (O horizon) and mineral soil samples up to 30 cm depth (0 – 10 cm, 10 - 20 cm and 20 – 30 cm separately) were collected from four random locations from each plot using standard procedures (Etchevers Barra 1992; Aryal et al 2014). Litter and soil samples were analyzed for carbon fraction using a Shimadzu A500 organic carbon analyzer (Shimadzu 2001) and nitrogen analysis were done by semi-micro Kjeldahl method (Bremner and Mulvaney 1982). Available phosphorus were analyzed by Olsen´s method of extraction with sodium bicarbonate (Olsen 1954) and exchangeable potassium by atomic-absorption spectrophotometry (David 1960). We estimated the amount of carbon and nutrient stocks per hectare using the nutrient fractions obtained from the laboratory analysis. These estimates of carbon and

nutrients (kg ha^{-1} or Mg ha^{-1}) were made separately for litterfall, forest floor litter mass and soil up to 30 cm depth.

Table 1: General characteristics of each phases of forest succession

Characteristic features	Successional phases			
	YSF	MSF	ASF	MF
Age yrs.	5	10	20	Non slashed
SQ index	17.7±*1.1*	18.1±*0.8*	18.4±*1.2*	17.5±*0.8*
Trees per hectare	7519±1137	8436±1854	8418±820	5015±774
Basal area m^{2}ha^{-1}	8.7±*0.8*[a]	16.2±*2.4*[b]	20.8±*1.7*[b]	33.2±*2.6*[c]
Stand height m.	≤5	5 - 10	10 -15	15 - 25
Diversity index	*2.6±0.09*	*2.8±0.11*	*2.9±0.10*	*2.9±0.13*
Characteristic species (Aryal et al 2014)	*Hampea trilobata* Standl.*, Piscidia piscipula* (L.) Sarg., and *Chrysophyllum mexicanum* Brandegee ex Standl., *Thevetia gaumeri* Hemsl., *Diospyros salicifolia* Humb. & Bonpl. ex Willd., *Trema micrantha* (L.) Blume, *Thevetia ahouai* (L.), *Lonchocarpus xuul* Lundell, *Bursera simaruba* (L.) Sarg.	*Lonchocarpus xuul* Lundell, *Croton icche* Lundell, *Coccoloba reflexiflora* Standl.*, Croton arboreus* Millsp., *Neomillspaughia emarginata* (H. Gross) S.F. Blake, *Eugenia winzerlingii* Standl., *Guettarda combsii* Urb, *Hampea trilobata* Standl.	*Lysiloma latisiliquum* (L.) Benth., *Bursera simaruba* (L.) Sarg., *Trophis racemosa* (L.) Urb., *Lonchocarpus castilloi* Standl., *Nectandra salicifolia* (Kunth) Nees. *Eugenia ibarrae* Lundell, *Guettarda combsii* Urb., *Myrciaria floribunda* H. West ex Willd.	*Manilkara zapota* (L.) van Royen, *Pouteria reticulata reticulata* (Engl.) Eyma*, Gymnanthes lucida* Swartz., *Metopium brownie* (Jacq.)*, Brosimum alicastrum* Swartz and *Talisia oliviformis* (Kunth) Radlk., *Piper yucatanense* C. DC., *Myrciaria floribunda* H. West ex Willd., *Vitex gaumeri* Greenm.*, Lonchocarpus yucatanensis* Pittier

YSF: young secondary forests, MSF: medium secondary forests, ASF: advanced secondary forests, MF: mature forests, SQ index: soil quality index, tree density (individual ha^{-1}) considers all the trees of ≥1 cm DBH. Diversity index: Shannon index of biodiversity for trees ≥1cm. The values are mean ± standard error where presented. Different letters in the exponent denote significant differences among successional phases.

Annual aboveground primary productivity (ANPP) was estimated as current annual increment in AGB of live trees between 2011 and 2012 (Aryal et al 2014) plus mean annual litterfall from October 2012 to September 2013. We developed a land use intensity (LUI) index (eq. 1) and soil quality (SQ) index to analyze the effect and order

of importance of predictor variables on litter production, forest floor litter and soil organic carbon. The LUI index was calculated using the equation 1 (Young 1997).

$$LUI\ index = \sum \left(\frac{C}{C+F}\right) \dots\dots\dots\dots\dots\dots\dots\dots\ (eq.\ 1)$$

Where, C: cultivation years in a slash and burn cultivation cycle, F: fallow years after each cultivation period.

The land-use history was obtained through landowner interviews. The SQ index was developed by scaling the values of different soil fertility parameters considering the critical ranges that affect plant nutrient uptake and the ranges obtained from soil sample analysis (Table 2).

Table 2: Parameters, scales and ranges of soil quality indices

Parameters	Scale values				Reference comments
	1	2	3	4	
Soil pH	<5.5 y >8.1	5.6 – 6.0	7.4 -8.0	6.1 – 7.3	most plant nutrients are more available in a neutral pH (Landon 2014)
Cation exchange capacity, cmol kg^{-1}	<5	5.1 – 40.0	40.1 -60	>60	< 5.0 cmol kg^{-1}: degree of infertility, higher: more availability of nutrients (Doran and Parkin 1994; Landon 2014)
Total nitrogen, %	<0.1	0.1 - 0.3	0.3 – 0.5	>0.5	lower: deficient, higher: better nutrient response
Available phosphorous, ppm	trace	1 - 5	5-15	>15	lower: deficient, higher: better nutrient response (Doran and Parkin 1994)
Exchangeable potassium, cmol kg^{-1}	<0.5	0.5 – 1.0	1.0 – 2.0	>2.0	lower: deficient, higher: better nutrient response (Landon 2014)
Calcium carbonate, %	>15	0 -5	5 -15		exchangeable Ca in carbonate clay complex: favourable soil physical conditions, but >15% Ca lead to deficiencies of minor elements (Landon 2014)
Texture	Sand	Clay, sandy clay	Silt, sandy loam, clay loam	loam	loam considered the best for higher nutrient and water availability, sand: poor structure, low water availability, clay: poor structure, impeded drainage (Doran and Parkin 1994; Landon 2014)
SQ range*	Min=7			Max=27	

*Since SQ indices were calculated separately for three depth classes (0-10 cm, 10-20 cm and 20-30 cm), the value obtained for each depth class was weighted by available soil depth to get an average plot level SQ index.

The SQ indices were also used to verify whether soil heterogeneity affect our hypothesis on successional pattern of litter production, accumulation and above-ground primary productivity.

We analyzed the seasonal variation of litterfall using repeated measures analysis of variance (ANOVA) with the data from 12 sampling months as repeated measures. Data were also analyzed to evaluate the significant differences between successional phases with Tukey HSD ($\rho=0.05$). Multiple regression analyses were performed to evaluate the effects of age, slash and burn cultivation intensity and soil quality on annual litter production, aboveground primary productivity, litter accumulation and soil organic carbon content. Backward and forward procedures were applied to see whether the variables respond equally or not. Since the positions of the variables were not changed, multiple regression coefficients (beta values) from forward analysis with respective standard error and probability of error are presented in the results.

Results

Litterfall and nutrient transfer at different successional phases

The average annual litterfall ranged from 4.1 to 7.0 Mg ha-1 with maximum in ASF followed by MSF. Leaf litter comprised of about 90% in secondary forests and 84% in mature forests while small branches (twigs of <1 cm diameter and stem cortex) comprised 5-7% in secondary forests and 10% in mature forests. The highest twig-fall was observed in mature forests while there were no significant differences in reproductive parts (flowers and fruits) fall (Table 3).

Carbon and other nutrients like nitrogen (N), phosphorus (P) and potassium (K) transfer from vegetation to soil follow the pattern of total litterfall being higher in medium and advanced aged secondary forests compared to young secondary and mature forests, as CNPK fraction in litter did not vary. Our estimates show that nutrient transfer vary between 49±9 to 83±6 kg of N, 1.0±0.2 to 1.7±0.1 kg of P and 28±5 to 48±3 kg of K per hectare per year through litterfall (Table 3).

Table 3: Annual litter and nutrient flux from vegetation to soil surface in different phases of forest succession in Calakmul, Mexico. Values in parenthesis indicate the percentage of total litterfall. Different letters in exponent show significant differences between successional phases ($p<0.05$, Tukey HSD).

Components of litterfall	YSF (n=4)		MSF (n=4)		ASF (n=4)		MF (n=4)	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Leaf litter, kg ha^{-1} yr^{-1}	3726.9^a (91%)	615.8	6121.3^b (90%)	438.5	6297.3^b (89%)	497.0	4408.6^{ab} (84%)	254.7
Twigs and cortex, kg ha^{-1} yr^{-1}	216.3^a (5%)	76.1	387.3^{ab} (6%)	39.8	493.6^b (7%)	43.4	541.4^b (10%)	73.2
Reproductive parts, kg ha^{-1} yr^{-1}	170.6^a (4%)	55.1	270.8^a (4%)	43.2	251.6^a (4%)	27.3	299.3^a (6%)	40.3
Total litter fall, kg ha^{-1} yr^{-1}	4113.8^a	722.8	6779.4^b	452.7	7074.5^b	488	5249.3^{ab}	269.1
Nutrient flux								
Carbon, kg ha^{-1} yr^{-1}	1851.2^a	325.2	3050.7^b	203.7	3169.1^b	219.6	2362.2^{ab}	121.1
Nitrogen, kg ha^{-1} yr^{-1}	49.2^a	8.9	80.8^b	5.9	83.1^b	6.0	63.1^{ab}	3.7
Phosphorus, kg ha^{-1} yr^{-1}	1.0^a	0.2	1.7^b	0.1	1.7^b	0.1	1.4^{ab}	0.1
Potassium, kg ha^{-1} yr^{-1}	28.3^a	5.0	46.6^b	3.2	48.3^b	3.4	36.6^{ab}	1.9

YSF: young secondary forests of 5 years, MSF: medium secondary forests of 10 years, ASF: advanced secondary forests of 20 years, MF: mature forests, SE: standard error of the mean

We found that aboveground net primary productivity (ANPP) show a peak at around 10 year old forest and decreases gradually with age afterwards (Fig 3). Initially biomass accumulation is higher than litter production but it slows down and intersects with litter production between 10 to 20 years. As net biomass accumulation (growth + recruitment – mortality of trees) decreases with forest age, ANPP in mature forests is mainly due to annual litter production while in younger secondary forests, live biomass increment contribution to ANPP were higher than litter production (Fig 3).
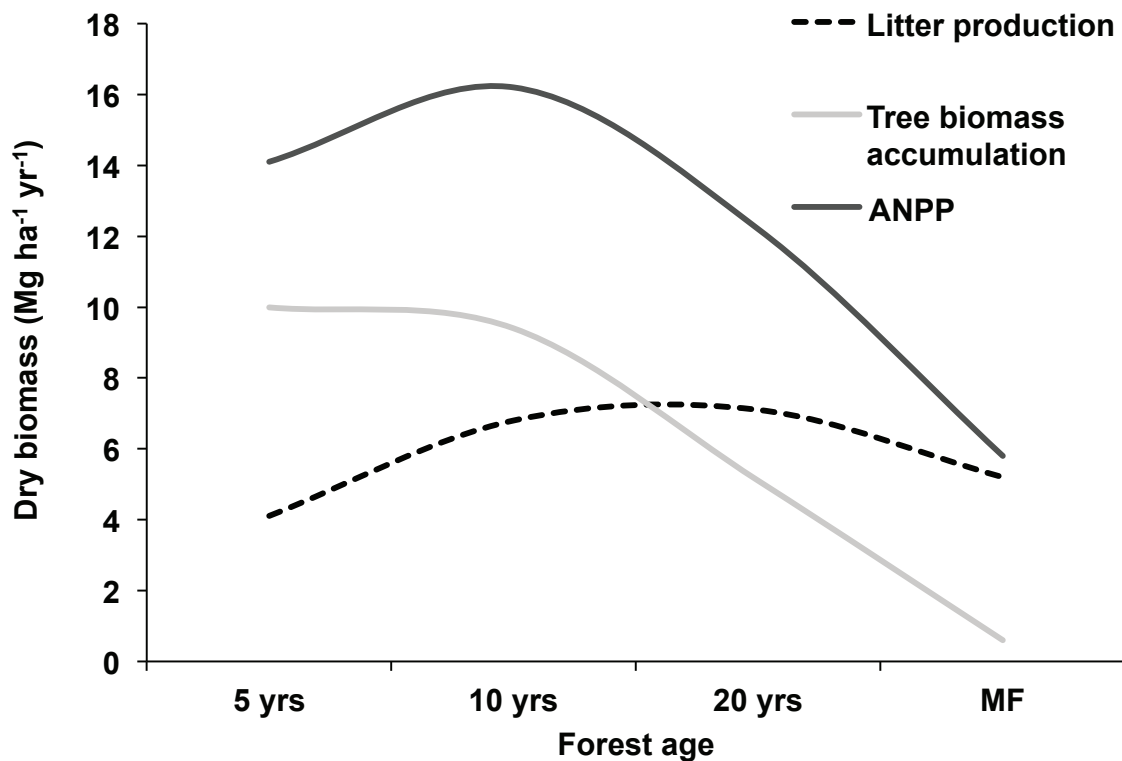
Fig 3: General trends of litter production, aboveground tree biomass accumulation and aboveground net primary productivity (ANPP) with successional age of forests. MF = mature forest.

Total litter mass in organic horizon (O) increased gradually with age and was the highest in mature forests, mainly due to the gradual increase in the accumulated humus layer (O_a horizon). There were no significant differences between successional phases in the amount of fresh (O_i horizon) and dry (O_e horizon) litter. Mature forests accumulate about 12±1 Mg of litter mass per hectare while young secondary forests accumulate about 7±0.8 Mg per hectare. Similarly, we found the same gradual increase in the total amount of accumulated CNPK in forest floor organic mass along the age gradient as the nutrient content in litter did not change. Mature forests of the region accumulate about 162 kg of N, 3 Kg of P and 44 kg of K per hectare in forest floor litter mass (Table 4).

Table 4: Accumulated litter mass on forest floor sampled at the beginning of the experiment. Different letters in the exponent indicate significant differences (ρ<0.05, Tukey HSD) among successional phases. Values in parenthesis indicate the percentage of total mass of respective group.

Forest floor mass in different horizons	YSF Mean	SE	MSF Mean	SE	ASF Mean	SE	MF Mean	SE
O_i horizon (fresh), kg ha^{-1}	1273^a	328	1857^a	351	1494^a	328	1568^a	415
	18%		24%		14%		13%	
O_e horizon (dry), kg ha^{-1}	3197^a	313	2731^a	335	4053^a	313	2900^a	396
	45%		36%		37%		24%	
O_a horizon (humus), kg ha^{-1}	2613^a	608	3015^{ab}	650	5241^{bc}	608	7499^c	770
	37%		40%		49%		63%	
Total, kg ha^{-1}	7083^a	847	7603^{ab}	905	10789^{bc}	847	11967^c	1071
Total nutrients								
Carbon, kg ha^{-1}	2253^a	152	2424^{ab}	286	3354^b	240	3635^b	410
Nitrogen, kg ha^{-1}	97.1^a	6.8	103.1^{ab}	11.6	147.7^{bc}	11.7	162.4^c	18.7
Phosphorus, kg ha^{-1}	1.7^a	0.1	1.8^{ab}	0.2	2.7^{bc}	0.2	3.0^c	0.4
Potassium, kg ha^{-1}	22.5^a	1.7	25.0^{ab}	2.9	36.5^{bc}	3.2	43.8^c	5.7

YSF: young secondary forests of 5 years, MSF: medium secondary forests of 10 years, ASF: advanced secondary forests of 20 years, MF: mature forests, SE: standard error of the mean

The amount of soil organic carbon showed no significant differences among different phases of forest growth. The top soils of 0-10 cm depth accumulate more carbon than deeper horizons in all phases. The average accumulated soil organic carbon ranged from 31 to 42 Mg ha^{-1} in the 0-10 cm layer, 17 to 22 Mg ha^{-1} between 10-20 cm and 5 to 9 Mg ha^{-1} in 20-30 cm layer. Similar trend was observed in total N, available P and exchangeable K (Table 5).

Table 5: Estimation of the amount of carbon and primary nutrients deposited in the soil to a depth of 30 cm. Different letters in exponent indicate statistical difference among depth classes ($\rho<0.05$, Tukey HSD).

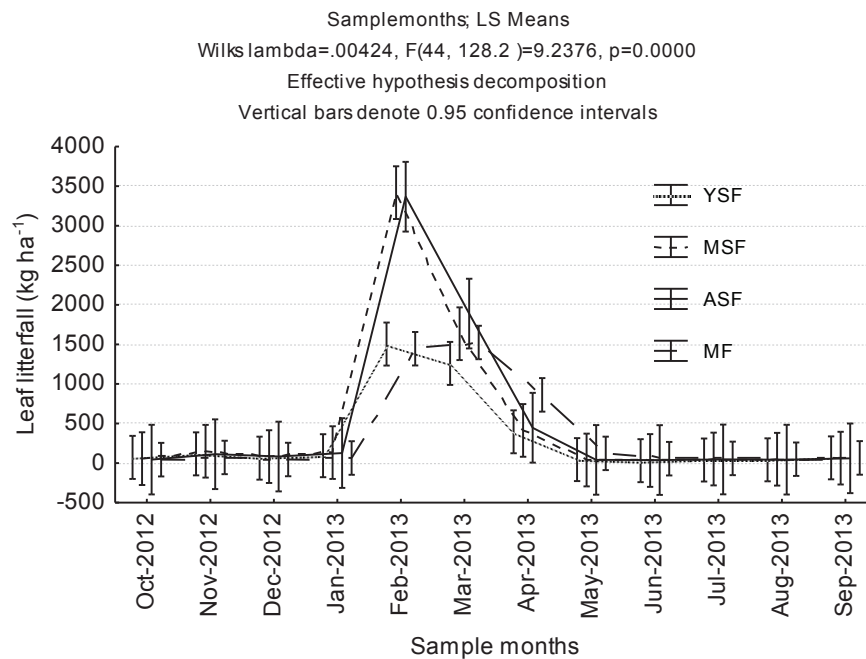| Nutrients in the soil	YSF Mean	SE	MSF Mean	SE	ASF Mean	SE	MF Mean	SE
Soil organic carbon, Mg ha^{-1}								
0-10 cm	31.5^a	5.6	31.3^a	4.1	40.6^a	13.0	41.7^a	9.7
10-20 cm	20.8^b	6.8	16.5^b	4.7	17.8^b	6.0	21.9^b	7.0
20-30 cm	9.3^c	4.8	7.1^c	2.5	5.5^c	3.3	6.2^c	3.5
Total nitrogen, kg ha^{-1}								
0-10 cm	3193^a	301	3128^a	456	3497^a	278	3663^a	1001
10-20 cm	2725^a	239	1968^b	254	3057^a	194	2921^b	614
20- 30 cm	2079^b	280	1664^b	358	1874^b	128	2672^b	608
Available phosphorus, kg ha^{-1}								
0-10 cm	1.6^a	0.5	1.1^a	0.7	1.3^a	0.8	1.8^b	1.0
10-20 cm	1.3^a	0.5	1.2^a	0.6	0.3^b	0.2	2.3^a	0.6
20-30 cm	0.3^b	0.2	0.7^b	0.4	0.3^b	0.2	1.5^b	1.0
Exchangeable potassium, kg ha^{-1}								
0-10 cm	462^a	37	391^a	86	318^a	85	333^a	36
10-20 cm	357^b	40	270^{ab}	56	342^a	99	325^a	45
20-30 cm	349^b	67	229^b	47	277^b	85	289^b	48

YSF: young secondary forests of 5 years, MSF: medium secondary forests of 10 years, ASF: advanced secondary forests of 20 years, MF: mature forests, SE: standard error of the mean, note: since we did not find significant differences among successional phases, indications of statistical differences are not presented.

Seasonal pattern of litterfall

Monthly leaf litterfall ranged from 31±2 kg to 3418±544 kg month^{-1} ha^{-1}. The highest monthly litterfall was observed in MSF during the month of February 2012 and the lowest in YSF during June 2013. Monthly variation showed a uni-modal pattern of leaf fall with the peak during February and March (Fig 4A). Monthly litterfall was inversely related to monthly rainfall (Fig 2, 4A, 4C). Since the monthly variation in average ambient temperature and photoperiod did not vary much during the year, no

significant relationship was observed between these variable and litterfall. However, high leaf fall during February and March coincides with the onset of a warmer and drier period. Unlike leaf fall, reproductive parts (flowers + fruits) fall showed two significant peaks, one during December and the other during April (Fig 4B). Although we did not separate flowers and fruits, April is considered as flowering month (Ochoa-Gaona et al 2008). Therefore, the December peak may be the result of increased fruit production. However, the heights of those peaks differ among successional phases indicating the difference in composition of species. December peak seem to be higher in MSF and ASF while YSF and MF showed relatively equal discharge of reproductive parts during the two peaks (Fig 4B). Twig fall peak was observed during February and March and was highest in mature forests. Almost 70% of annual litterfall was concentrated during two dry months in secondary forests while only 55% of annual litterfall was observed in mature forests during the same period.

4A

Samplemonths; LS Means
Wilks lambda=.00424, F(44, 128.2)=9.2376, p=0.0000
Effective hypothesis decomposition
Vertical bars denote 0.95 confidence intervals

4B

Sample months; LS Means
Wilks lambda=.09892, F(44, 128.2)=2.4204, p=.00007
Effective hypothesis decomposition
Vertical bars denote 0.95 confidence intervals

4C

Samplemonths; LS Means
Wilks lambda=.05670, F(44, 128.2)=3.2556, p=0.0000
Effective hypothesis decomposition
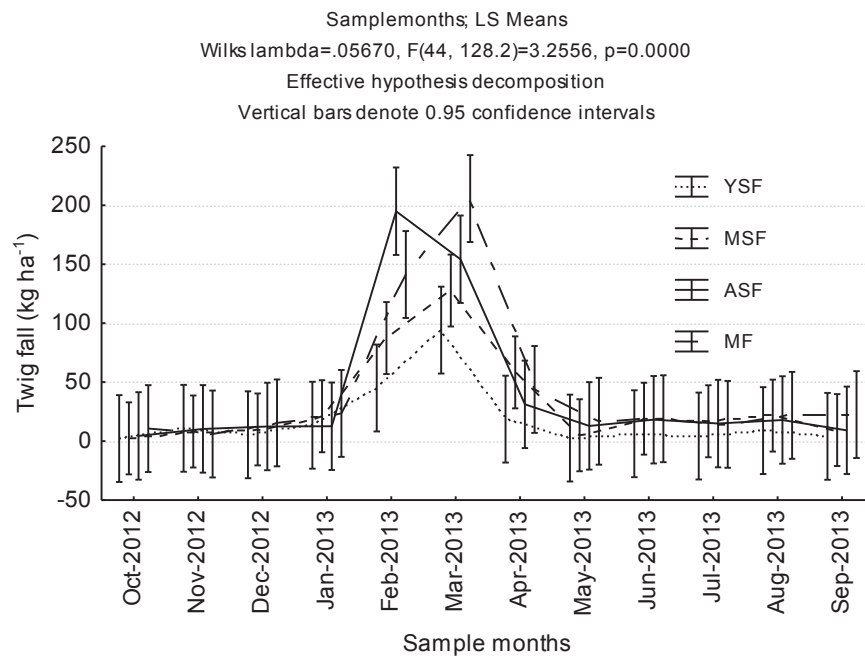Vertical bars denote 0.95 confidence intervals

Figure 4: (A) Monthly leaf litterfall (kg ha^{-1} yr^{-1}), (B) fruits and flower fall; and (C) twig fall in four different phases of forest succession measured from October 2012 to September 2013. YSF = young secondary forests, MSF = medium secondary forests, ASF = advanced secondary forests, MF = mature forests

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Effect of forest age, land use intensity and soil quality on annual litter production and associated carbon transfer

Multivariate regression analysis showed that forest age and land use intensity were significant predictors of annual litterfall and aboveground net primary productivity while soil quality was not a significant predictor (Table 6). It was interesting to note that the land use intensity index was the principal predictor of annual litter production (beta = -0.93, ρ = 0.002) while forest age explained more variance in the case of ANPP (table 6). Only forest age was the significant predictor of forest floor litter (beta = 0.58, ρ = 0.05). Forest age and land use intensity have no significant effect on soil organic carbon accumulation but the SQ index is significantly correlated to SOC-30 (Table 6).

Table 6: Multivariate regression analysis between litter production and carbon accumulation with independent variables like forest age, land use intensity and soil quality

| Dependent variables | Independent variables | | | | | |
| | Forest age | | LUI index | | SQ index | |
	Beta ± SE	ρ-level	Beta ± SE	ρ-level	Beta ± SE	ρ-level
ALP	-0.61±0.23	0.02	-0.93±0.24	0.002	0.06±0.20	0.74
ANPP	-0.97±0.19	0.00	-0.55±0.20	0.01	0.07±0.17	0.67
LM	0.58±0.28	0.05	-0.02±0.03	0.94	-0.15±0.25	0.57
SOC-30	0.27±0.26	0.32	0.09±0.27	0.73	0.92±0.03	0.01

LUI = land use intensity, SQ = soil quality, ALP = annual litter production, ANPP = aboveground net primary productivity, LM = litter mass, SOC = soil organic carbon to a depth of 30 cm, SE = standard error, ρ= probability of error.

Discussion
Annual litter production and accumulation

The quantity of annual litter production in our study was within the reported range in similar forest ecosystems (Table 7). The amount of litter accumulation and nutrient return does not only depend on   litter production but also on the rate of litter

decomposition (Dent et al 2006; Wang et al 2007). Litter decomposition is a function of environmental conditions, species composition, the presence of micro- and macro-organisms and substrate quality (Dickinson 2012; Keiser et al 2013; Norris et al 2013). Studies carried out in the region report that litter decomposition is faster for early successional species compared to older secondary and mature forest species (Read and Lawrence 2003; Xuluc-Tolosa et al 2003; Bejarano et al 2014). They also mentioned that collected leaf litter directly collected from trees decomposes within a year but that decomposition of senesced leaves may take longer. The gradual accumulation of forest floor litter with the increase in forest age, as observed in our study, can thus be explained by the slower leaf decomposition in older forests. The gradual increase in twig-fall and their slower rate of decomposition may be another important factor that can explain the accumulation of forest floor litter mass (Harmon et al 1995).

Table 7: Site, vegetation and quantity of reported litterfall collected from published literatures

Study Location	Vegetation type	Total litterfall (Mg ha^{-1} yr^{-1})	References
Southern Yucatan, Mexico	Tropical semi-evergreen forest	4.1 - 7.1	This study
Chamela Jalisco, Mexico	Tropical deciduous forest	6.5 - 8	Martinez-Yrizar and Sarukhan 1990
Yucatan Peninsula, Mexico	Tropical dry forest	5.0 – 7.7	Whigham et al. 1990
Costa Rica	Forestry plantations	8.2 - 12.6	Montagnini et al 1993
Amazon forest, Venezuela	Caatinga alta and Terra firme	4 - 7	Cuevas and Medina 1986
Southern Yucatan, Mexico	Dry tropical forest	3.8 – 6.8	Lawrence 2005
Guangdong, China	Broadleaf monsoon forest	8.5	Zhou et al 2007
Puerto Rico	Lower montane evergreen forest	8 - 13	Ostertag et al 2008
Chiapas, Mexico	Deciduous secondary forest	3.4 – 5.1	Rivera-Vázquez et al 2013

Seasonality of litterfall and species assemblages of secondary forests

Previous studies in the region show that there is a gradual shift in species composition and dominance during the successional stages of the forest that is growing after abandonment of agricultural land (Ochoa-Gaona et al 2007; Aryal et al 2014; Chazdon 2014). This is also reflected in the phenological characteristics in our study. Our findings demonstrated that secondary forests, grown after slash and burn agriculture, are different in species composition as that of original mature forests in terms of phenological characteristics. Secondary forests at all phases of succession showed higher peaks of litterfall during the dry season compared to mature forests, with about 70% of the annual litterfall concentrated in two dry months compared to 55% in the case of mature forest. Some studies reported that the deciduous intensity range from 25% - 100% during the dry season in the Yucatan peninsula as a whole (Lawrence 2005; Cuba et al 2013) but in the semi-evergreen forests similar to our study site, the reported range vary from 25% to 50% (Martínez and Galindo-Leal 2002).

This alteration in forest phenology may be explained by the changes in environmental conditions associated with land conversion, favoring the establishment of more deciduous species. Another reason may be the reduced availability of seed and propagule of original mature forest species and the higher reproduction capacity of early successional tree species (Moheno 2008). Although, such changes from pioneer to persistent and late successional species are considered natural in tropical forest succession, it may take more than a century for those secondary forests to recover their original composition and dominance of mature forest species (Aryal et al 2014). Such alterations in floristic composition, structure, productivity and functioning of forest ecosystems after land use change, if not addressed properly in policy issues, can adversely affect the conservation efforts in transitional tropical forests (Román-Dañobeytia et al 2014). The transformation of species assemblages may change the nutrient input to soil as well. Increased deciduousness increases understory insolation and susceptibility to forest fires leading to potential emissions of sequestered carbon to the atmosphere (Chapin III et al 2011; Cuba et al 2013). Alteration of seasonal

phenology and species composition of Yucatan forests can also negatively affect the habitat of forest fauna like white-lipped peccary (*Tayassu pecari*) by changing food sources and appropriate shelter (Reyna-Hurtado et al 2009).

Predictor variables of litterfall and forest productivity

None of the individual parameters related to soil fertility had significant effect on litter production. A soil quality index that combines the soil fertility parameters as one independent variable, was also not correlated to litter production, indicating that soil characteristics do not influence the amount of litter produced in one year, which is in contrast with other studies reporting higher litterfall in more fertile soil (Balvanera and Aguirre 2006; Ostertag et al 2008). We also did not find any significant correlation between litterfall and ambient temperature ($r = 0.16$, $\rho = 0.14$) but there was a significant negative correlation between litterfall distribution and monthly precipitation ($r = 0.63$, $\rho = 0.02$) showing that litterfall was significantly higher in the drier months and lower in rainy months, which coincides with other studies in dry or sub-humid the tropics (Moraes et al 1999; Martius et al 2004). February was the driest month in our study period with the highest litterfall in secondary forests. In mature forest, litterfall peaks appeared in March. We assume that mature forests create a micro-climate that reduce evapotranspiration and may maintain soil moisture longer, which, as a result, made them less sensitive to hydrological stress and dry season foliage senescence. Previous studies in the region reported March as the month of the highest litterfall in secondary as well as mature forests (Lawrence 2005). This small shift in litterfall peak may be due to the variation in previous rainfall or variation in the dry period. In our case, the winter rainfall was less than normal, which may have triggered the litterfall earlier in the season.

Forest age and land use intensity were considered as significant predictors of annual litter production and aboveground net primary productivity. The effect of prior disturbance and management legacies like fire, land-use intensification, logging on carbon exchange has been reported in mid latitude forests (Ochoa-Gaona et al 2007; Bradford et al 2008; Aryal et al 2014). A study in tropical secondary forest chronosequence in Puerto Rico reported that site quality has significant effect on litter

production and decomposition (Ostertag et al 2008). In our case, site quality index affected only on soil organic carbon accumulation, indicating that better quality soil can hold more organic carbon. Our results showed that forest litter production as well and aboveground net primary productivity of secondary forests decreased with increasing intensity of slash and burn agriculture before land abandonment. It is interesting to note that land use intensity did not play any significant role in soil organic carbon accumulation along the successional gradient. However, more intensive agriculture with frequent burning during the cultivation period may foster invasive species and pests, making secondary forests less productive (Schneider and Fernando 2010).

Conclusion and recommendation

The study portrayed the litter carbon and nutrient transfer trajectory of successional forests and point out the effect of pre-abandonment cultivation intensity on carbon cycling in tropical forest ecosystems. We found that the secondary forests recover the litter production capacity of mature forest already in early stages of succession. We also observed that carbon and nutrient accumulation in forest floor litter (O horizon) increases gradually with forest age. Litter production do not show any correlation with soil quality but higher previous land use intensity reduced the carbon and nutrient transfer capacity of secondary forests. Due to the seasonal variation in rainfall, litterfall also show a seasonal pattern. The highest litterfall peaks were observed in the dry season and the peak started earlier in secondary forests compared to mature forest. The medium-aged secondary forests seem to be more productive than mature forests in terms of litter production, and also the seasonal pattern of litterfall was slightly different. Secondary forests seem to be more deciduous compared to mature forests. This difference in deciduousness may be due to the difference in species composition and the capacity to tolerate water stress between secondary forests and mature forests. However, further study is required to evaluate this pattern of forest functioning. It takes a long time for secondary forests to recover the original species composition of non-disturbed mature forests. Forest governance strategies in Mexico usually consider only structural parameters of forests. These results are important to

take in to consideration the dynamic processes and functioning of forest succession, define forest terms appropriately, such as secondary and mature forests and redesign forest governance strategies in Mexico.

We recommend a longer term monitoring to analyze the possible inter-annual variation and climate effect. Future research should include litter decomposition experiments to better understand the total nutrient flow and carbon balance of such tropical forests. A detailed analysis of species composition and forest structure could help in interpreting our results.

Acknowledgements

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Carbon flux from woodfall and decomposition in a tropical forest succession

Carbon flux from branch fall and wood decomposition in a tropical forest succession

Deb Raj Aryal[1], Bernardus H J De jong[2], Jorge Mendoza-Vega, Susana Ochoa-Gaona, Ligia Esparza-Olguín

El Colegio de la Frontera Sur, Av. Rancho Polígono 2-A, Ciudad Industrial, Lerma, Campeche, C.P. 24500, México

Correo electrónico: [1] debraj.aryal@hotmail.com, [2] bjong@ecosur.mx

Abstract

Production and decomposition of woody detritus in tropical forest are strongly linked to terrestrial carbon cycle but still pose significant level of uncertainty due to lack of information. In this study we tested the hypothesis that dead wood carbon accumulation from branch fall increases with forest age while wood decomposition rates decreases with the increasing age of successional forests regenerated after swidden agriculture. We also tested the hypothesis that wood decomposition is affected by interspecific variation in wood characteristics. Wood decomposition experiment was set in 16 stands representing four phases of succession in a tropical semi-evergreen forest of southern Mexico. Branch segments of 1 cm -7.5 cm diameter from 30 selected species were placed in a time-series experiment during two years period. The results showed that wood decomposition rate constant, k per year decreased gradually with forest age. The average decomposition rate constants k ranged from 0.13 to 1.09 per year and varied greatly among species. Tree species like *Bursera simaruba*, and *Thevetia gaumeri* decomposed faster while *Eugenia ibarrae*, *Pouteria reticulata* and *Manilkara zapota* decomposed slower. The amount of woody detritus production from branch fall (>1 cm diameter) increased with forest age. Average annual branch fall value ranged 0.6 to 1.7 Mg C ha^{-1} yr^{-1} but the net annual addition was found about 23 - 33% lower than annual sum of branch fall because of the carbon loss within the same year due to continuous decomposition. Higher branch fall and lower decomposition rates in mature forest stands indicate the probability of accumulating more carbon in woody detritus compared to younger secondary forests. Literature review revealed that this study is one of the few

antecedents of deadwood carbon dynamics in tropical secondary forest succession and the information can be applied in continuous carbon monitoring, reporting and verification processes as proposed in REDD+ initiatives.

Keywords: decomposition constant, woody detritus production, forest age, wood density, Yucatan Peninsula

Introduction

Since tropical secondary forests are considered potentially important in mitigating greenhouse gases, better understanding of the patterns and processes of carbon influx and out flux of these ecosystems is essential. Carbon flux from woody material decomposition in successional tropical forests has significant contribution to global carbon cycle. Standing and fallen deadwood material comprise about 20% to 50% of total biomass carbon stocks in tropical successional forests (Delaney et al 1998; Eaton and Lawrence 2006; Aryal et al 2014) and may generate up to 22% of annual carbon emissions from heterotrophic respiration (Chambers et al 2001; Chambers et al 2004). Understanding the accumulation and decomposition of such woody material is, thus, important for accounting and modelling of regional carbon dynamics (Harmon et al 1995; Janisch and Harmon 2002). Studies on wood decomposition are not so common, probably because of longer time period required due to the slow nature of the decomposition process (Bond-Lamberty and Gower 2008). Although tropical forests seem to be faster in carbon cycling, fewer studies on wood decomposition are found in tropical forests compared to temperate and boreal forests (Harmon et al 1995; Janisch et al 2005; Mukhin and Voronin 2007; Bond-Lamberty and Gower 2008; Van Geffen et al 2010).

It has been reported that wood decomposition is simultaneously affected by climate, site, diameter and species-based variation in wood quality, like wood density and lignin content (de Toledo et al 2009; Weedon et al 2009; Van Geffen et al 2010). Seasonal weather conditions can also affect decomposition due to variation in temperature, precipitation and humidity in different period of the year (Harmon and Sexton 1996). Interspecific variation in wood density was found highly related to

successional stages and growth of forest ecosystems in some Australian and Mexican tropical forests (Falster and Westoby 2005; Aryal et al 2014). However, the velocity and patterns of wood decomposition related to forest succession in the tropics has not been fully understood (Harmon et al 1995).

Hypothesis

In this study we tested the following two hypotheses: i) carbon flux through wood decomposition vary among successional phases of forest growth and are faster in younger phases than in older or mature forests in the tropics; ii) Interspecific variation in wood density affect wood decomposition patterns in tropical forests.

Methods
Study area

The study was conducted in successional semi-evergreen tropical forests of south eastern Mexico. These are forests with trees reaching 15 – 25 m height in mature stands, 25% – 50% of which lose their leaves during the dry season (Miranda and Hernández-Xolocotzi 1963; Martínez and Galindo-Leal 2002). Two localities (Cristobal Colon and El Carmen II) of Calakmul municipality situated to the south east of Calakmul Biosphere Reserve, in the Peninsula of Yucatan were selected for the experiment (Fig. 1). The region is characterized by a sub-humid tropical climate (García 1973) with an average precipitation of 1000-1500 mm per year (with major portions of the rainfall from July to October) and mean annual temperature of 22 - 26°C (García Gil et al 2002). The Peninsula of Yucatan is composed of rolling hills and ridges derived from Miocene and Pliocene limestones that ranges from 100 to 380 m above sea level (García and March 1990; Vester et al 2007; Bautista et al 2011). Rendzic leptosols and vertisols are the dominating soil type in the region. The great portion of the original semi-evergreen tropical forest in the region has been converted to slash-and-burn agriculture that created a mosaic of agricultural lands mixed with secondary forests in various stages of development and some patches of primary forests.

Figure 1: Location of study site and distribution of experimental plots in two localities. CC = Cristobal Colon, EC = El Carmen II. YSF = young secondary forests, MSF = medium secondary forests, ASF = advanced secondary forests and PF = primary forests

Wood decomposition experiment

We established 16 carbon monitoring plots representing stands of four different phases of forest succession (Fig. 1). Twelve out of sixteen plots were in secondary forests of three age classes (5, 10 and 20 years after abandonment of slash and burn agriculture) and four in non-slashed primary forests. We selected three species of higher relative importance value (RIV) from each of the 16 experimental plots. RIV was estimated as the average of relative abundance and relative area basal of the species as suggested by Pérez-Salicrup (2004). Some of the species were repeated in various plots. For the sake of having higher representation from more species and reducing repetition of same species in the same phase, we selected some species of lower RIV value too. Thus, a total of 30 species were considered for the experiment.

We collected 108 fresh branch segments of three size categories (36 segments of 55 cm long with about 5 -7.5 cm diameter, 36 segments of 25 cm long with 2.5 - 5 cm diameter and 36 segments of 25 cm long with about 1- 2.5 cm diameter) of each selected species from outside of the plots (Harmon and Sexton 1996). We separated a 5 cm long disc from each wood piece for wood density measurement and dry mass estimation. All 5 cm long discs were transported to ECOSUR forest laboratory where wood volume was calculated by water displacement method, oven dried (70^oC for 72 hours) and weighted (0.01 g precision) to calculate the dry wood mass. Wood density was calculated as a ratio of dry mass to volume.

Another segment of each wood piece was measured its length and diameters at three points (two extremes and midpoint), weighted, labelled with aluminium tags and put inside the semi-elastic cylindrical nylon mesh bag (4 mm mesh size). A total of 1680 prepared wood segments representing four stages of succession and 30 species were placed again in the respective experimental plots beneath the respective tree species on the ground surface in contact with litter layer. To avoid misallocations, wood segments were tied to each other as a chain with sufficient interval in between. Following the time series experimental method, three pieces of wood from each species from all the experimental plots were collected at intervals of one month for initial three months period, then at intervals of two months for next six months and at intervals of three months afterwards during a period of two years in total. Collected wood pieces were then transported to ECOSUR forest laboratory for processing. Soil and fungal mass attached to the wood surface were removed carefully. Wood segments were taken out from the nylon meshes and their remaining lengths and diameters were measured in three points (middle and two ends), oven dried (70^oC for 72 hours) and weighted (0.01 g precision) for remaining current mass.

Branchfall experiment

Two 5 X 5 (25 m^2) subplots were established at a distance of about 50 m in each carbon monitoring plots. Fallen branches (>1 cm diameter) were collected in an approximate interval of 2-3 months from August 2012 to March 2014. Collected branches were weighted and subsamples were taken to laboratory to obtain dry

weight. After 72 hours of oven drying (65°C), subsamples were again weighted to calculate the dry weight of total collected sample. A factor of 0.47 was used to convert dry biomass to carbon fraction (Fonseca et al 2011).

Data analysis

The current wood mass of each wood piece was compared with its initial mass to determine the decomposition rates. Decomposition rate constants (mass loss per year) at each collection interval were calculated using an exponential decay model (Olson 1963) (eq. 1).

$$k = \frac{-\ln\left(\frac{Xt}{Xo}\right)}{t}$$ …………………………………………… (eq. 1)

Where, k is the decomposition rate constant per year, Xt is the current wood mass at time t, Xo is the initial wood mass, and t is the time in years. Since the number of days that the wood segments remained in the field for decomposition varied in different collections, we converted them to years to apply in the model. Decomposition rates constants of the samples obtained at different collections intervals were then averaged to estimate the mean annual constants for each species, sampling plot and successional phase.

To estimate the annual branch fall (absolute sum) we summed up the branch fall amounts from all collection dates and divided by the number of days during the collection period and standardized to 365 days. The amount of carbon added annually from branch fall (net addition) was estimated by deducting decomposition loss from branch fall that occur during the collection period (eq.2).

Net addition = $\sum(BF_{T-1} (1- k) + BF_T)$ …………………… (eq. 2)

Where, BF_T = Amount of branch fall collected at a time T, k = decomposition rate constant, BF_{T-1} = Accumulated branch fall amount from preceding collection time T-1. The values were weighted by the time period to obtain net annual addition.

All the data were first checked for normality. In case where the data did not meet the assumptions of ANOVA, necessary data conversions were applied before analysis. Back-transformed results are presented in the results. One-way ANOVA was used to find the significant differences in wood density, decomposition rates and branch-fall among different phases of forest succession and among species. Homogenous groups among species were determined by Tukey post-hoc test ($\alpha = 0.05$). Stepwise multiple regression analysis (forward and backward) was performed to analyze the relationship between decomposition rate, wood density, forest age and diameter of the wood segments. Beta values with lower than 0.05 level of error probability were considered to determine the variables as significant predictors.

Results

Wood density

Interspecific variation in wood density ranged from 0.34±0.02 to 0.83±0.04 (mean ± 0.95 CI) g cm^{-3} (Table 1). Species like *Gymnanthes lucida*, *Manilkara zapota* and *Eugenia ibarrae* were of higher wood density while *Bursera simaruba*, *Trema micrantha* and *Hampea trilobata* were found as species with lower wood density. Most of the hardwood species were found in mature forests and older secondary forests compared to younger secondary forests. However, we found some softwood species like *Dendropanax arboreus* and *Protium copal* in mature forests as well (Table 1). Some of the species like *Bursera simaruba*, *Croton icche*, *Piscidia piscipula* and *Lonchocarpus castelloi* are found in young and medium aged secondary forests and in cases up to advanced aged secondary forests. Interestingly, the dominant species of mature forests were not found in secondary forests. In general term, wood density of mature forests species are higher compared to secondary forest species.

Table 1: Initial wood density (g cm^{-3}) of selected species collected from four different phases of forest succession. YSF = young secondary forests, MSF = medium secondary forests, ASF = advanced secondary forests and PF = primary forests. N = sample size, WD = wood density, CI = confidence interval.

Species	Family	N	Mean WD	95% CI	Phase
Allophylus cominia (L.) Sw.	Sapindaceae	36	0.58	0.03	YSF
Bravaisia berlandieriana (Nees) T.F. Daniel.	Acanthaceae	36	0.58	0.04	PF
Bursera simaruba (L) Sarg.	Burseraceae	72	0.34	0.02	YSF, MSF
Chrysophyllum mexicanum Brandegee ex Standl.	Sapotaceae	36	0.65	0.01	YSF
Coccoloba reflexiflora Standl.	Polygonaceae	36	0.61	0.02	ASF
Croton arboreus Millsp	Euphorbiaceae	72	0.75	0.02	MSF, ASF
Croton icche Lundell	Euphorbiaceae	108	0.69	0.01	MSF, ASF
Dendropanax arboreus (L.) Decne. & Planch.	Araliaceae	36	0.48	0.02	PF
Diospyros salicifolia Humb. & Bonpl. Ex Willd.	Ebenaceae	36	0.64	0.04	YSF
Eugenia ibarrae Lundell	Myrtaceae	36	0.78	0.02	MSF
Eugenia winzerlingii Standl.	Myrtaceae	36	0.80	0.03	PF
Guettarda combsii Urb	Rubiaceae	72	0.61	0.02	MSF, ASF
Gymnanthes lucida Swartz.	Euphorbiaceae	72	0.83	0.04	PF
Hampea trilobata Standl.	Malvaceae	108	0.48	0.02	YSF, MSF
Lonchocarpus castilloi Standl.	Leguminosae	36	0.70	0.04	ASF
Lonchocarpus xuul Lundell	Leguminosae	180	0.70	0.02	YSF, MSF, ASF
Lonchocarpus yucatanensis Pittier	Leguminosae	35	0.76	0.03	PF
Lysiloma latisiliquum (L) Benth.	Leguminosae	72	0.58	0.03	ASF
Manilkara zapota (L.) P. Royen	Sapotaceae	36	0.78	0.03	PF
Nectandra salicifolia (Kunth) Nees	Lauraceae	36	0.62	0.05	MSF
Neomillspaughia emarginata (H. Gross) S.F. Blake	Polygonaceae	72	0.72	0.03	MSF, ASF
Piper yucatanense C. DC.	Piperaceae	36	0.63	0.02	PF
Piscidia piscipula L. Sarg.	Leguminosae	72	0.59	0.02	YSF, ASF
Pouteria reticulata (Engl.) Eyma	Sapotaceae	73	0.73	0.03	PF
Protium copal (Schltdl.& Cham.) Engl.	Burseraceae	36	0.48	0.03	PF
Talisia oliviformis (Kunth) Radlk.	Sapindaceae	36	0.71	0.03	PF
Thevetia gaumeri Hemsl.	Apocynaceae	36	0.56	0.02	YSF
Trema micrantha (L.) Blume	Ulmaceae	36	0.40	0.04	YSF
Trophis racemosa (L.) Urb.	Moraceae	36	0.56	0.03	ASF
Zuelania guidonia (Sw.) Britton & Millsp.	Salicaceae	36	0.58	0.02	MSF
Total		**1680**	**0.63**	**0.01**	

Wood decomposition rates

The decomposition rate varied strongly among species (Fig. 2). The annual mass loss (decomposition rate constant, k) ranged from 0.13 to 1.09 year^{-1}. Higher decomposition rates were found in species like *Bursera simaruba*, *Thevetia gaumeri* and *Trema micrantha* which are low density species, while *Eugenia ibarrae*, *Eugenia winzerlingii*, *Pouteria reticulata* and *Manilkara zapota* were found as decay resistant species and are high density species (Fig. 2). Homogenous grouping of species according to Tukey HSD test ($\alpha = 0.05$) are presented in Annex 2. Species like *Croton arboreus*, *Lysiloma latisiliquum*, *Piscidia piscipula* and *Lonchocarpus castilloi* showed intermediate decomposition rates (Fig. 2).
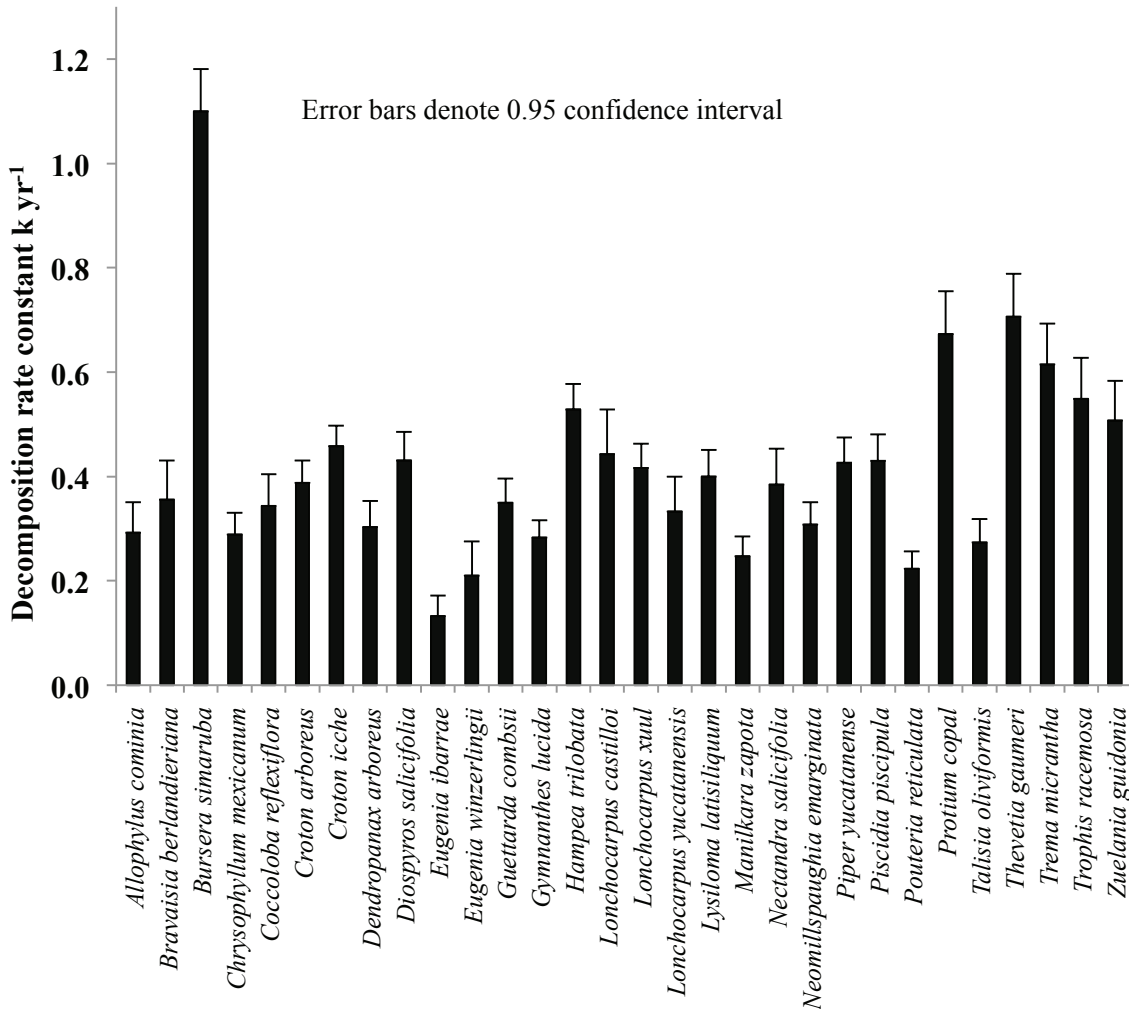

Figure 2: Interspecific variation in wood decomposition rate constant, k yr^{-1}

Most of the decay resistant species were found in mature forest and older secondary forests. However, some mature forest species like *Protium copal* and *Piper yucatanense* decomposed relatively faster.

Wood decomposition relationship with wood density and diameter

Multiple regression analysis showed that wood density and forest age were significantly correlated to wood decomposition rates. Decomposition rate constant (k yr^{-1}) was inversely correlated (β = - 38, $\rho<0.05$) to wood density indicating that the harder the wood the lower the rate of decomposition (Fig. 3 A). Diameter (size) of the wood segment did not show any significant correlation with decomposition rate constant (Fig. 3 B).
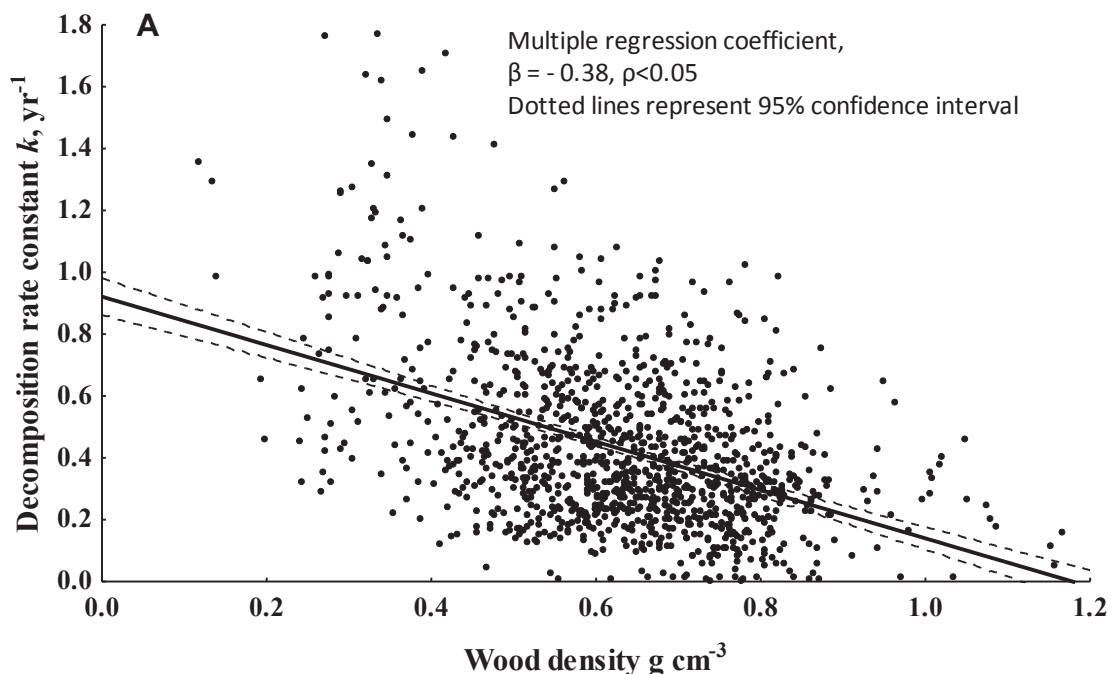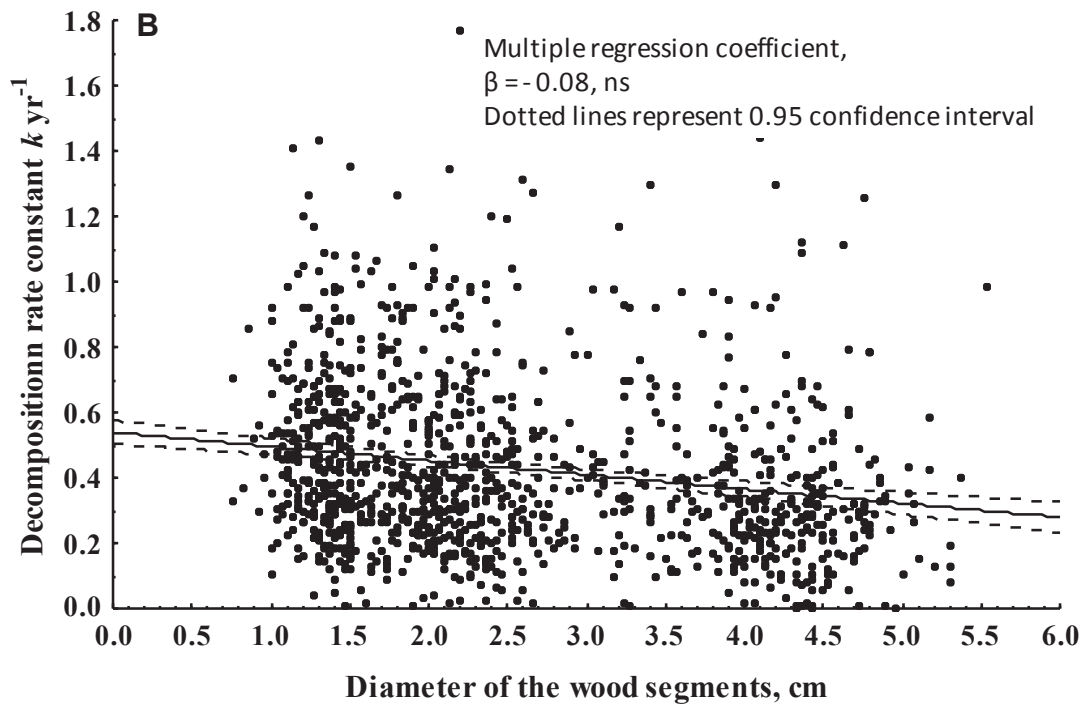
Figure 3: Regression analysis between: A. wood density (g cm^{-3}) and decomposition rate constant (k yr^{-1}); and B. diameter of the wood segment (cm) and decomposition rate constant (k yr^{-1})

In addition to wood density, forest age was also the significant predictors of wood decomposition rates (β = -0.19, ρ<0.05).

Wood decomposition in different phases of forest growth

We observed a decreasing trend of wood decomposition rates with increasing forest age (Fig. 4). The average decomposition rate constant was found highest in youngest secondary forest while primary forest showed the lower rates of wood decomposition.
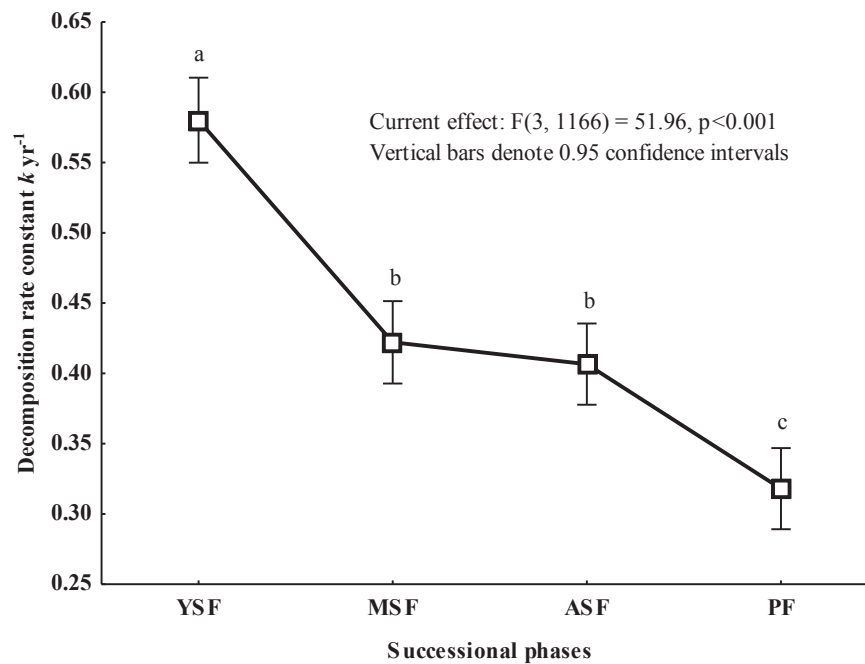
Figure 4: Variation of wood decomposition rate (k yr⁻¹) among four different phases of forest succession. YSF = young secondary forests, MSF = medium secondary forest, ASF = advanced secondary forests, and PF = primary forests. Different letters above the points denote significant differences.

These indicated that the pioneer species, which are dominant in younger phases of succession, decompose faster than older secondary and primary forest species. One-way ANOVA showed significant differences in wood decomposition rates among four different phases of forest succession. Tukey HSD post-hoc test showed that the differences were significant in YSF and PF while MSF and ASF were statistically similar (Fig 4). The average decomposition rates in young secondary forests was nearly double ($k = 0.58+0.02$ yr⁻¹) when compared to primary forests ($k = 0.32+0.01$ yr⁻¹).

Branchfall

We found that woody detritus production from branch fall (>1 cm in diameter) increased gradually with the forest age (Fig. 5).
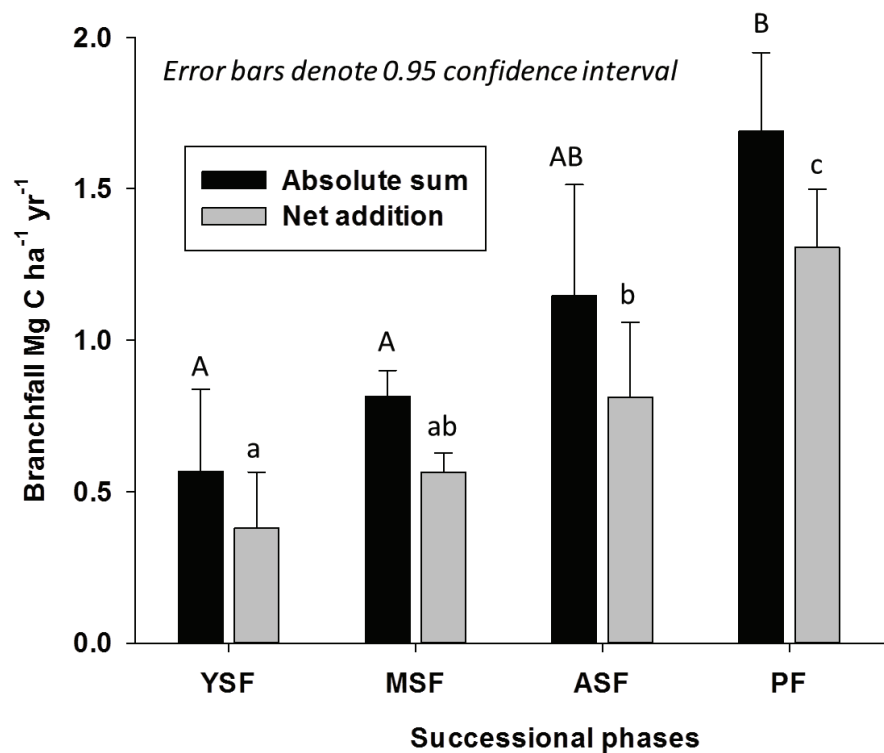
Figure 5: Annual branch-fall (Mg C ha^{-1} yr^{-1}) in four different phases of forest succession. YSF = young secondary forest, MSF = medium secondary forest, ASF = advanced secondary forest, PF = primary forest. Different letters above the bars denote significant differences between successional phases.

Average branch fall (absolute sum) ranged from 0.57 to 1.69 Mg C ha^{-1} yr^{-1} while the average net addition ranged from 0.38 to 1.30 Mg C ha^{-1} yr^{-1}. The highest values were obtained in primary forest in both estimations. These results showed that about 23% of carbon from branch fall was lost by decomposition within the same year of production in PF. This value was 29% in ASF, 31% in MSF and 33% in YSF.

Discussion

Wood growth and decomposition dynamics are theoretically faster in tropical forests than temperate and boreal forests. However, more research reports on wood decomposition are available from temperate and boreal forests than tropical forests (Yatskov et al 2003; Bond-Lamberty and Gower 2008; Freschet et al 2012). Although

efforts have been carried out in recent years to understand the wood decomposition in tropical forests, most of the studies consider a few species in their experiment. We assume that lower the number of species in the experiment, more limited is our understanding on system approach of forest carbon cycling. A recent study in Bolivia considered 15 Neotropical species in its decomposition experiment (Van Geffen et al 2010). In this study, we took in to account 30 species representing four phases of semi-evergreen tropical forest succession. This helped us develop the successional trajectory of wood decomposition rates while secondary forest advances after the abandonment of slash and burn agriculture. In an experiment with four tree species in southern Yucatan peninsula, decomposition rate constants were reported to a range of 0.12 to 0.89 per year (Eaton and Lawrence 2006). These values are relatively similar to our estimates (0.13 - 1.09 yr^{-1}). However, the range in our experiment was slightly wider because of the larger number of species and forest age gradients.

As per our hypothesis wood decomposition rates varied among different phases of forest succession and decreased with the increase in forest age. Younger forests showed higher decomposition rates which can be attributed to the higher abundance and dominance of pioneer species. Higher decomposition in younger secondary forest can reduce the carbon accumulation potential in deadwood pool. However, faster turnover of woody material can help recover soil organic matter in early phases of secondary succession in those forests grown after abandonment of shifting cultivation(Aryal et al 2014). Mature primary forest showed the lowest rates of wood decomposition indicating that carbon turnover is slower in those ecosystems. Slower wood decomposition may contribute to higher carbon reserve in woody detritus in such primary forests. Slower rate of wood decomposition in older secondary and primary forests compared to younger secondary forests can be explained by the differences in wood density between early and late successional species. Another reason of variation in wood decomposition might be the effect of micro-environment. Some reports mentioned that wood decomposition rates in open canopy forest stands were higher compared to intact canopy forest stands because of the alteration of humidity and temperature (Forrester et al 2012). Primary forest stands in our study were found more intact than secondary forests in their canopy cover. However,

further experiment is needed to test the effect of micro-environment putting the same species to decompose in different environmental conditions, which we did not focus in this experiment.

Wood density and decomposition rates

Forest functioning and structure changes rapidly when secondary forests in the tropics get older. One of the parameters that changes in such successional forests is the wood density led by the changes in species composition. It has already been reported that mature forests are dominated by hardwood species compared to younger secondary forests (Aryal et al 2014). The results of this study pointed that wood density significantly affects the rate of wood decomposition in successional tropical forests. Softwood species decomposed faster than hardwood species. This contradicts with some previous studies reporting that wood density do not affect wood decomposition (Van Geffen et al 2010). However, there are studies which mentioned that wood density is one of the predicting variables of wood decomposition rates (Harmon et al 1995; Janisch et al 2005). It is important to note that the effect of other traits of woody species, environment and decomposer community interactions are subject to further investigation in the region (Freschet et al 2012).

Branch fall and woody detritus accumulation

Many studies in tropical forests report only accumulated carbon stocks in deadwood material; and it is not so common to find studies reporting changes in woody detritus production from branch fall in tropical secondary forests. Some studies report production of only fine twigs along with foliar litterfall (Köhler et al 2008). In old growth forest stands of Costa Rica, woody detritus production was reported 2.4 Mg C ha^{-1}yr^{-1} (Clark et al 2002). This value is about 50% higher than our estimates in primary forest stands. This discrepancy can be attributed to the differences in productivity and forest structure. Our results suggested that carbon accumulation rates by woody detritus production increases with forest age while decomposition rates decreases. This in turn led to higher accumulation of carbon in woody detritus when a secondary forest age increases with higher probability of woody detritus carbon accumulation in mature

stands (Janisch and Harmon 2002). Another source of dead wood carbon accumulation in forest ecosystem is the mortality of trees. The relative amount of carbon transfer from live biomass to dead wood material by tree mortality did not change significantly with increase in forest age (Aryal et al 2014). This indicated that the major source of dead wood carbon deposition in older forest stands was derived from branch fall.

Conclusion

This study demonstrated that wood decomposition rates in tropical forests vary strongly among species. Interspecific traits like wood density also affect the rate of wood decomposition. In addition, our results indicated that wood decomposition decreased with forest age while dead woody material production increased in older forests. This, in turn, indicated that woody debris carbon retention in primary forests can prolong because of slower rates of wood decomposition. Although primary forests are considered less efficient in capturing live biomass carbon, slower wood decomposition rates in those forests may still have positive implications in reducing carbon emissions to the atmosphere. Thus, forest conversion to agriculture and grassland can lead to possible feedback to atmospheric CO_2 not only from slashing and burning of live biomass but also by changing the rate of wood decomposition in the secondary forests grown after land abandonment.

One of the major constraints in wood decomposition studies is the requirement of longer time interval to complete the experiment. Thus, only the fine wood segments (<7.5 cm diameter) were considered in our experiment. Even though, the time interval of our study was not so long to trace the whole trajectory of wood decomposition of some decay resistant species, this will, hopefully be better elaborated by continued experiments in these experimental plots. However, we consider it as one the important antecedents in the field of wood decomposition studies in tropical forests. Future investigations should consider the analysis of wood anatomical traits and chemical characteristics like lignin, phenolic extractives and macronutrient composition. Including older secondary forest plots in the chronosequence can also contribute to better understand carbon flux pattern through wood decomposition in

changing tropical secondary forests. Further investigation should also focus on the possible changes in soil organic carbon to explore whether the debris entering into the soil in young secondary forest decompose faster than in older forests or not. This could help us understand the pattern of soil organic carbon recovery in secondary forests after slash and burn agriculture. The results of this study can be used in modelling carbon in-flux and out-flux dynamics of tropical secondary forests and in regular monitoring reporting and verification for wider implementation of REDD+ programs to conserve forests in areas of increasing farming pressure.

Acknowledgements

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Annex 1

Tukey HSD test, homogenous groups; variable: wood density, alpha = .05, Error: between MS = 0.009, df = 1139.																	
Species	WD	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Bursera simaruba	0.34	*															
Trema micrantha	0.40	*	*														
Dendropanax arboreus	0.48		*	*		*											
Protium copal	0.48		*	*	*	*											
Hampea trilobata	0.48			*													
Thevetia gaumeri	0.54			*	*	*	*										
Trophis racemosa	0.56			*	*	*	*	*									
Lysiloma latisiliquum	0.57				*		*	*									
Allophylus cominia	0.58				*	*	*	*									
Zuelania guidonia	0.58				*	*	*	*									
Bravaisia berlandieriana	0.58				*		*	*									
Piscidia piscipula	0.59							*	*								
Coccoloba reflexiflora	0.61							*	*	*							
Guettarda combsii	0.61							*	*								
Nectandra salicifolia	0.62							*	*	*	*						
Piper yucatanense	0.63							*	*	*			*				
Lonchocarpus guatemalensis	0.64							*	*	*	*	*					
Diospyros salicifolia	0.64							*	*	*	*	*					
Chrysophyllum mexicanum	0.65							*	*	*	*	*	*				
Croton icche	0.69								*	*	*	*	*	*			
Lonchocarpus castilloi	0.70								*	*	*	*	*	*	*	*	
Lonchocarpus xuul	0.70								*	*	*	*	*	*	*		
Talisia oliviformis	0.71									*	*	*	*	*	*	*	
Neomillspaughia emarginata	0.72									*	*	*	*	*	*		
Pouteria reticulata	0.73												*	*	*	*	
Croton arboreus	0.75													*	*	*	*
Lonchocarpus yucatanensis	0.76													*	*	*	*
Eugenia ibarrae	0.78														*	*	*
Manilkara zapota	0.78														*	*	*
Eugenia winzerlingii	0.81															*	*
Gymnanthes lucida	0.83																*

Annex 2

Tukey HSD test, homogenous groups; variable: decomposition rate constant _k_, alpha = 0.05, Error: between MS = 0.034, df = 1139.

Species	_k_	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Eugenia ibarrae	0.13	*													
Eugenia winzerlingii	0.21	*	*												
Pouteria reticulata	0.22	*	*												
Manilkara zapota	0.25	*	*	*											
Talisia oliviformis	0.27	*	*	*	*	*									
Gymnanthes lucida	0.28	*	*	*		*									
Chrysophyllum mexicanum	0.29	*	*	*	*	*									
Allophylus cominia	0.29	*	*	*	*	*									
Dendropanax arboreus	0.30	*	*	*	*	*	*								
Neomillspaughia emarginata	0.31		*	*	*	*									
Lonchocarpus yucatanensis	0.33		*	*	*	*	*	*							
Coccoloba reflexiflora	0.34		*	*	*	*	*	*							
Guettarda combsii	0.35		*	*	*	*	*	*							
Bravaisia berlandieriana	0.36		*	*	*	*	*	*		*					
Nectandra salicifolia	0.38		*	*	*	*	*	*	*	*					
Croton arboreus	0.39			*	*	*	*	*		*					
Lysiloma latisiliquum	0.40			*	*	*	*	*		*					
Lonchocarpus xuul	0.42			*	*	*	*	*	*	*					
Piper yucatanense	0.43			*	*	*	*	*	*	*	*				
Piscidia piscipula	0.43				*		*	*	*	*					
Diospyros salicifolia	0.43			*	*	*	*	*	*	*	*				
Lonchocarpus castilloi	0.44				*	*	*	*	*	*	*				
Croton icche	0.46						*	*	*	*	*				
Zuelania guidonia	0.51							*	*	*	*	*			
Hampea trilobata	0.53								*		*	*			
Trophis racemosa	0.55								*	*	*	*	*		
Trema micrantha	0.61										*	*	*		
Protium copal	0.67											*	*	*	
Thevetia gaumeri	0.71												*	*	
Bursera simaruba	1.09														*

CAPÍTULO V

Carbon balance of tropical secondary and primary forests in southern Mexico

Carbon balance of tropical secondary and primary forests in southern Mexico

Deb Raj Aryal[1], Bernardus H J De Jong[2], Susana Ochoa-Gaona, Jorge Mendoza-Vega, Ligia Esparza-Olguín

El Colegio de la Frontera sur (ECOSUR), Av. Rancho Polígono 2-A, Ciudad Industrial Lerma, Campeche, CP 24500, México

E-mail: [1] debraj.aryal@hotmail.com, [2] bjong@ecosur.mx

Abstract

Carbon balance of tropical forests varies along temporal and spatial gradients. Our understandings on the dynamics of terrestrial carbon still have a substantial level of uncertainty. In this study, we measured carbon accumulation, transfers among reservoirs and fluxes to estimate the carbon balance along a successional gradient of tropical forests in southern Mexico. We calculated the net ecosystem productivity (NEP) by using stock change approach in 16 carbon monitoring plots along a successional chronosequence in semi-evergreen tropical forests, grown after abandonment of slash and burn agriculture in southern Mexico. We also estimated carbon gain and loss by measuring biomass accumulation, tree mortality, fine and coarse detritus production, fine root turnover, woody detritus and litter decomposition and heterotrophic soil respiration. The mean NEP ranged from 2.1±0.62 to 3.5±1.04 Mg C ha^{-1} yr^{-1} in secondary forests while that of mature forest was 0.8±0.16 Mg C ha^{-1} yr^{-1}. The net carbon balance (NCB) estimated from gain and loss approach were found very similar to NEP. The NCB ranged from 1.5±0.8 to 3.0±1.9 Mg C ha^{-1} yr^{-1} in secondary forests and that of mature forest was 0.6±1.0 Mg C ha^{-1} yr^{-1}. We found that secondary as well as primary forests in the region have positive carbon balance indicating that they acted as net carbon sink during the measurement years. However, these forests are embedded in agriculture forest landscape matrices that still have the substantial threats of conversion to agricultural lands since slash and burn is the main activity for food production in this region. Policy deliberation and implementation of sustainable landscape management strategies with multi-stakeholder participation seems urgent to reconcile farming practices and conservation efforts so that these important carbon sinks remain the carbon sinks in future.

Keywords

Introduction

Tropical forests play a crucial role in earth's carbon balance and have considerable potential for mitigation of greenhouse gas accumulation in the atmosphere (Houghton 2005; Fahey et al 2009). Changes in forest carbon allocation and fluxes affect not only individual plant growth but also terrestrial biogeochemistry (Litton et al 2007). Changes in biomass accumulation, litter production, fine root turnover and organic matter decomposition in tropical forests have a significant role in changing global carbon balance (Litton et al 2007). Despite the considerable advances that are being made in our understanding of the global carbon cycle, terrestrial carbon sinks in the global carbon budget, are still estimated as the residual of the balance between all other sinks and sources (Le Quéré et al 2014). This implies that there are still huge uncertainties in the estimates of the terrestrial carbon balance related to whether regions or forest landscapes are sources or sinks of carbon (Williams et al 2005).

Components of carbon fluxes and transfers like: biomass accumulation; litter production; woody debris production; decomposition of woody and non-woody debris and organic matter decomposition in the soil, in a forest ecosystem are strongly linked. Carbon transfers from one pool to another pool and fluxes to the atmosphere depend to a large extent on the level of primary productivity (Litton et al 2007), which may vary with forest type, resource availability, tree density, stand age, type and intensity of disturbances, site quality and the scale (Bond-Lamberty et al 2004; Mascaro et al 2012; Aryal et al 2014). Net primary productivity is the amount of carbon accumulated from photosynthesis minus plant (autotrophic) respiration.

Tropical secondary forests are usually considered as net carbon sinks but there are varying views on whether mature forests act as carbon sink or source (Phillips et al 1998; Luyssaert et al 2008). Some reports mentioned that a mature forest can be a net carbon source or carbon neutral (Taylor et al 2014) while others report that

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mature forests still act as net carbon sink (Luyssaert et al 2008; Kashian et al 2013). Broadly, three hypothetical trends of net carbon balance can be drawn in a secondary succession of tropical forests (figure 1).
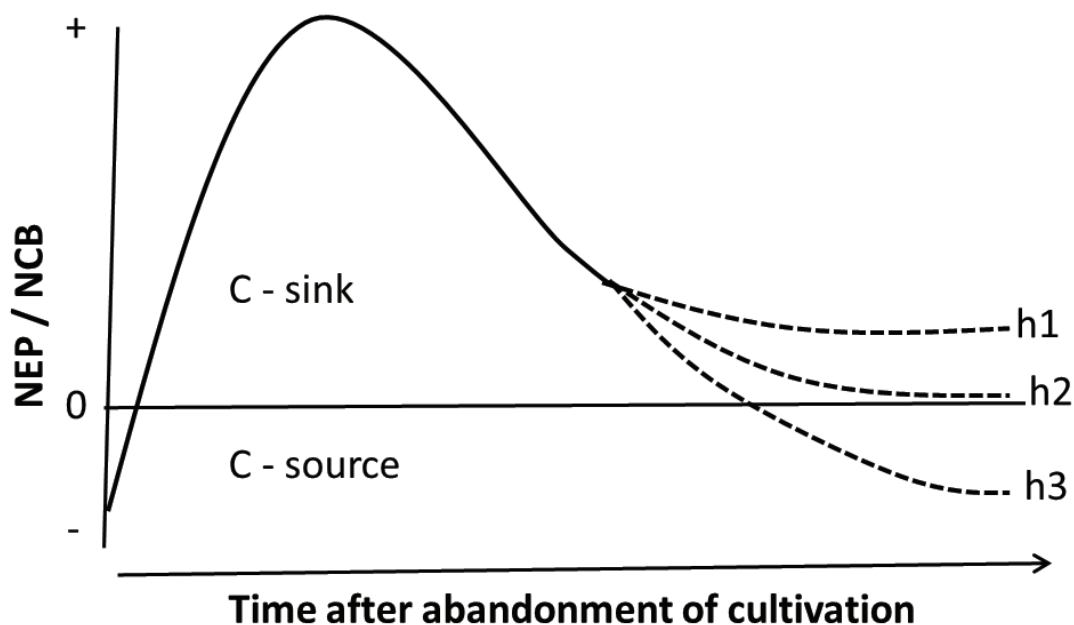

Figure 1: Hypothetical trend of net ecosystem productivity (NEP) / net carbon balance (NCB) related to secondary succession of tropical forests abandoned after slash and burn agriculture. Hypotheses: h1, h2, and h3 represent the three possible trends in mature forest stands. Adapted from Taylor et al (2014).

Forest stands may start as carbon source, and rapidly converting to sink under each hypothesis but after getting to maturity, stands either remain as carbon sink (hypothesis1), follow the carbon neutrality trend or steady state (hypothesis 2) or become the carbon source (hypothesis 3) (Houghton 2005; Taylor et al 2014). There are also two other hypotheses. One hypothesis states that the forest stand reaches a dynamic equilibrium, where they change from sources to sinks and vice versa, mainly due to spatial and temporal variation in the mortality of large trees (Mascaro et al 2012). Another hypothesis states that tropical forests, seen at the landscape scale, are in a continuous turnover process, where the turnover rate (repeated opening of

the same area from time1 and time2) may vary and may be reducing due to climate change. If the turnover rate reduces, this can be considered as a secondarization of the forests and may, thus, decrease the total stock of carbon in the forest at this scale. Some reports illustrate this through the reduction of average wood density of Amazonian forests (Cramer et al 2004; Rice et al 2004; Laurance et al 2009).

There are two principal approaches of quantifying C dynamics in forest landscapes – by measuring changes in carbon stocks over time, or by measuring carbon fluxes directly (Williams et al 2005). In this study, we combined the data from carbon stock changes over time in a forest chronosequence and measurements of biogeochemical processes related to carbon fluxes and transfers among pools. We estimated net ecosystem productivity (NEP) by calculating the changes in total carbon stocks over time and balance of gain, transfer between the components and the loss at different phases of succession in a semi-evergreen tropical forest of southern Mexico. We hypothesized that secondary forests at of all phases of succession act as carbon sink while mature forests are carbon neutral.

Methods

The study was conducted in a chronosequence of semi-evergreen tropical forests succession abandoned after slash and burn agriculture within two localities of Calakmul, Campeche, Mexico. Sampling sites were located in El Carmen II, Cristóbal Colon situated in the southern part of Yucatan Peninsula. The region is characterized by a sub-humid tropical climate (García 1973) with an average precipitation of 1000-1500 mm per year (with major portions of the rainfall from July to October) and mean annual temperature of 22 -26°C (García Gil et al 2002). Rendzic leptosols and vertisols are the dominating soil types (Bautista et al. 2011). The dominant forest type in the region is semi-evergreen tropical forest (Rzedowski 1981; Pérez-Salicrup 2004), of which large portions have been converted to slash-and-burn agriculture that created a mosaic of agricultural lands mixed with secondary forests in various stages of development. A total of 16 carbon monitoring plots (four plots in four age class) were established to evaluate the carbon in 5 pools and transfers and transfer

between these pools and from the pools to the atmosphere (fluxes). We incorporated the results obtained from the experiments on biomass accumulation, litter and wood fall, wood decomposition, fine root turnover and soil respiration to estimate the gain and loss balance of carbon in four phases of forest succession (See chapter II, III and IV of thesis).

Detailed methods and results of living biomass accumulation and tree mortality are presented in (Aryal et al 2014, Chapter II). Description of methods related to litterfall can be found in chapter III. Woody detritus production and decomposition experiments are explained in Chapter IV. The methodology used to measure fine root production and soil respiration are presented in the next sections.

Fine root production

Sixteen ingrowth bags (cylindrical nylon mesh bags) of 8 cm diameter were installed in the soil to a depth of 30 cm in each plot in February 2013 (Fig. 2). Bags were filled with the soil (after eliminating all living and dead roots) from the same hole maintaining approximately the original layer structure and soil density (Jourdan et al 2008). A metal corer of 8 cm diameter was used to dig the hole and take the soil out. Four bags from each plot were collected at three months interval up to one year period and fine roots (≤2 mm diameter) were separated in live and dead classes, washed, oven dried and weighted. Fine root production (Mg C ha^{-1}) was estimated as the sum of dead and live root biomass from positive increments method while fine root turnover (Mg C ha^{-1} yr^{-1}) was estimated as the ratio between positive increments and mean standing live fine root biomass (Neill 1992).

In the positive increments method, we sum up all the positive increments of biomass and necromass between two or more successive sampling dates (Jourdan et al 2008). Mean standing live fine root biomass is the average of live root biomass obtained from different collections during the whole experimental period.

Figure 2: Collected ingrowth bag (left) and fine roots separation (dead and live) from the soil (right).

Soil respiration

PP systems environmental gas monitor (EGM-4) was used to measure the soil CO_2 efflux in different months representing three distinct seasons: summer rainy (June - Oct), winter rainy (Nov - Jan) and dry (Feb –May) of the year. Twelve measurements were made in each carbon monitoring plot during daytime. Soil respiration (CO_2) data were averaged and converted to carbon using a factor of 12/44 (molecular weight of C / molecular weight of CO_2). Heterotrophic soil respiration (Soil respiration-$_{het}$) was estimated as 20% of total soil efflux considering that the rest comes from autotrophic root respiration and dissolved inorganic carbon flows (Hamilton et al 2002).

Carbon balance

We estimated carbon balance using two approaches: i) gain and loss approach; and ii) stock change approach.

Gain and loss approach

We estimated the carbon gains to the forest ecosystems from production and transfers between carbon pools and losses from decomposition of detritus and soil organic matter decomposition. The net carbon balance (NCB) was calculated as the

difference between gain and loss. We did not include the estimates photosynthesis and plant (autotrophic) respiration in our study as we started from measurement of primary productivity.

Gain (production and transfers, Mg C ha^{-1} yr^{-1})

Aboveground net primary productivity (ANPP) was estimated as the sum of annual increases in living aboveground biomass (AGB) of trees (DBH≥1 cm), tree mortality, litterfall and branchfall, while belowground net primary productivity (BNPP) was quantified as the sum of annual increases in root biomass and fine root production (eq. 1 and 2). Total NPP was estimated as the sum of above- and below-ground productivity (Vasconcelos et al 2012) (eq. 3).

ANPP = ALB increment + tree mortality + litterfall + branchfall…….....…. eq. 1

BNPP = BLB increment + root mortality + fine root production……………...eq. 2

Total NPP = ANPP + BNPP ……………………………………………......eq. 3

Loss (decomposition, Mg C ha^{-1} yr^{-1})

We estimated the annual mass loss from decomposition of litter and woody debris using the data from respective production and decomposition rate constants (eq. 4, 5 and 6).

Litter decomposition = (Litter production)* litter decomposition constant, k ……eq. 4

Woody detritus decomposition = (tree mortality + branchfall)* wood decomposition rate constant, k yr^{-1} …………………………………………….. eq. 5

Detrital decomposition = litter decomposition + wood decomposition…………eq. 6

Carbon loss from soil organic matter decomposition and dead root decomposition was considered to be included in heterotrophic soil respiration.

Stock change approach

Net ecosystem productivity (NEP) can be expressed as carbon accumulation rate at the site: net wood, foliage and root increments (growth minus decomposition), net forest floor (fine and coarse litterfall minus litter decomposition) and soil organic C accumulation (Hamilton et al 2002; Alberti et al 2014). We calculated NEP (Mg C ha^{-1} y^{-1}), according to change in observed total C stocks (sequential difference in mean total C between successional ages) divided by the difference in age (Taylor et al 2014) (eq. 7).

$$NEP = (C_i - C_{i-1}) / (T_i - T_{i-1}) \dots\dots\dots\dots\dots\dots\dots\dots\dots \text{eq. 7}$$

Where, NEP = Net ecosystem productivity, C = total carbon, and T = time after abandonment.

Results

Fine root turnover and heterotrophic soil respiration

Mature forest showed higher fine root production compared to secondary forests. However, there were no significant differences in fine root turnover and soil respiration$_{-het}$. The average fine root production ranged from 1.9 to 3.3 Mg C ha^{-1} yr^{-1} while turnover over ranged from 1.3 to 1.5 Mg C ha^{-1} yr^{-1}. Mean values of soil respiration$_{-het}$ ranged from 5.5 to 6.8 Mg C ha^{-1} yr^{-1} (Fig. 3).
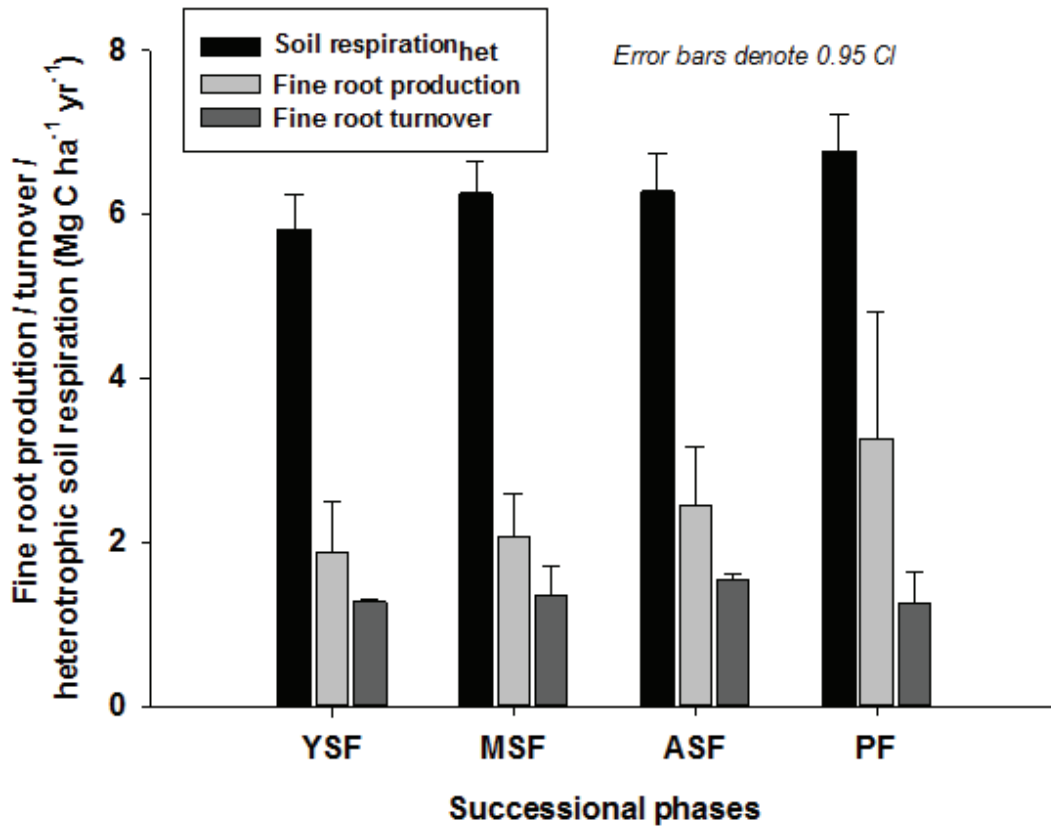
Figure 3: Fine root production, turnover and heterotrophic soil respiration (Mg C ha^{-1} yr^{-1}) among four phases of forest succession. YSF = young secondary forest, MSF = medium secondary forest, ASF = advanced secondary forest, PF = primary forest.

Carbon balance

The absolute amount of carbon fluxes (Mg C ha^{-1} yr^{-1}) in some processes like living biomass C accumulation and detritus decomposition decreased with forest age while other processes like tree mortality, branch fall, fine root production and soil respiration increased with forest age (Table 1). The total NPP increased rapidly for the first 10 years, and started to decrease at subsequent stages of forest succession. Both NEP and NCB decreased gradually with forest age. Interestingly, the difference between two methods NEP a NCB are not big indicating the substantial reliability of process based flux analyses.

Table 1: Analysis of C balance (Mg C ha^{-1} yr^{-1}) using gain-loss approach and stock change approach in tropical secondary and primary forests of SE Mexico. SF = secondary forests, PF = primary forests. The unit (Mg C ha^{-1} yr^{-1}) does not apply for decomposition rate constants (*k*).

Carbon flux / transfer Processes	Amount of C flow (mean±0.95 CI)			
	5 yrs. SF	10 yrs. SF	20 yrs. SF	PF
AGB C accumulation (+)	4.70±0.96	4.40±1.33	2.40±0.52	0.30±1.93
Litter production (+)	1.85±0.64	3.060±0.40	3.17±0.43	2.36±0.24
Tree mortality (+)	0.23±0.26	0.53±0.44	0.90±0.62	1.70±1.64
Branchfall (>1 cm diameter) (+)	0.57±0.27	0.81±0.09	1.16±0.51	1.69±0.26
Wood decomposition rates k yr^{-1}	0.58±0.05	0.42±0.04	0.41±0.05	0.31±0.05
Litter decomposition rates k yr^{-1}[a]	0.87	0.87	0.75	0.64
RB C accumulation (+)	1.26±0.47	1.08±0.47	0.58±0.35	0.08±0.79
Fine root production (+)	1.89±0.62	2.08±0.52	2.44±0.72	3.27±1.54
Fine root turnover rate yr^{-1}	1.28±0.03	1.34±0.35	1.54±0.07	1.29±0.38
Coarse root mortality[b] (+)	0.09±0.04	0.19±0.16	0.31±0.14	0.55±0.64
Detrital decomposition (-)	2.12±0.73	3.35±0.40	3.24±0.50	2.59±0.69
Heterotrophic soil respiration[c] (-)	5.52±1.49	6.25±1.05	6.28±0.89	6.77±0.80
Aboveground NPP	7.40±2.57	8.941.67	7.66±1.06	6.09±0.61
Belowground NPP	3.24±0.95	3.35±0.83	3.33±0.73	3.90±1.45
Total NPP, Mg C ha^{-1} yr^{-1}	10.64±3.44	12.29±2.49	10.99±1.67	9.99±1.52
NEP (Stock change) (+/-)	3.55±1.04	2.71±0.58	2.06±0.62	0.85±0.16
NCB (gain-loss balance) (+/-)	3.00±1.89	2.69±1.48	1.46±0.75	0.64±1.01

[a]Averages obtained from published literatures (Bejarano et al. 2014, Xuluc-tolosa et al. 2003).

[b]Estimated from tree mortality data (Aryal et al. 2014).

[c]Estimated as 20% of total soil efflux considering that the rest come from autotrophic root respiration and dissolved inorganic carbon flow (Hamilton et al. 2002).

We developed the diagrammatic representation of carbon balance between secondary and primary forests (Fig. 4). Carbon stock, transfer and flux data from all successional stages of secondary forests were averaged and compared with those of mature forests. Although the amount of net carbon balance was higher in secondary

forests than primary forests, positive values in both secondary and primary forests indicate that both act as carbon sink. We found higher carbon stocks in primary forest than secondary forest in all carbon pools measured (Fig 4). Primary forests accumulated nearly three times more carbon than secondary forests in live biomass while the difference in soil organic carbon pool was not significant.
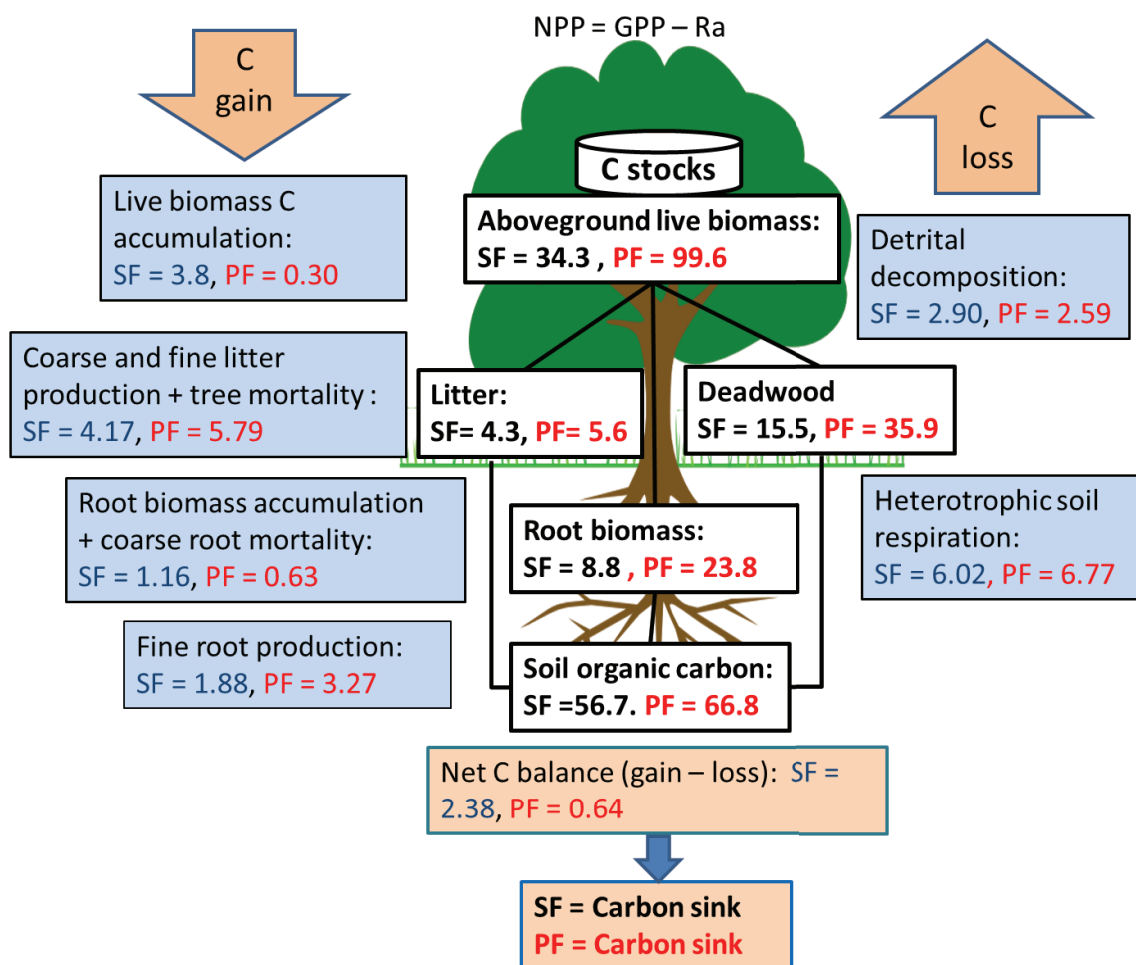

Figure 4: Diagrammatic representation of carbon stocks (Mg C ha^{-1}) and flows between pool and atmosphere (Mg C ha^{-1} yr^{-1}) in tropical secondary and primary forests. SF = secondary forest, PF = primary forest, NPP = net primary productivity, GPP= gross primary productivity, Ra = autotrophic (plant) respiration. The boxes on left represent C in-flows and boxes on the right denote C out-flows. The dark bordered interconnected boxes in the middle represent carbon stocks (Mg C ha^{-1}).

The modeled NEP and NCB potential curves showed rapid decrease in initial stage and slower in the later stages of succession. Both curves follow trajectory of h1 hypothetical trend (Fig. 5). Regarding the stocks, the live + dead biomass curve showed sharp increase in initial phases and slowly afterwards reaching to the primary forest level at an approximate age of 125 years while there was no significant change on soil organic carbon stock with the forest age (Fig 6).
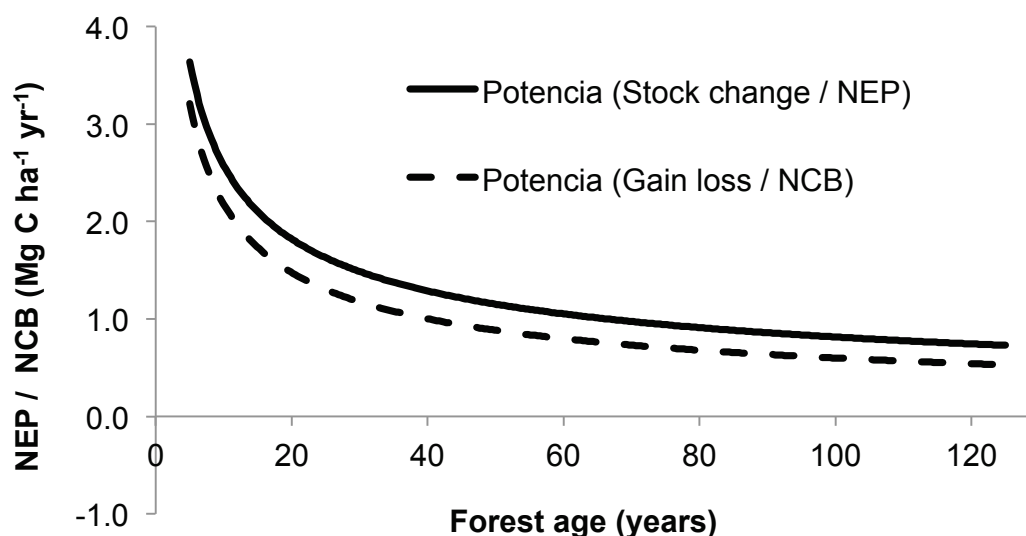

Figure 5: Potential NEP and NCB trajectories during secondary forest succession. NPP = net primary productivity, NCB = net carbon balance.
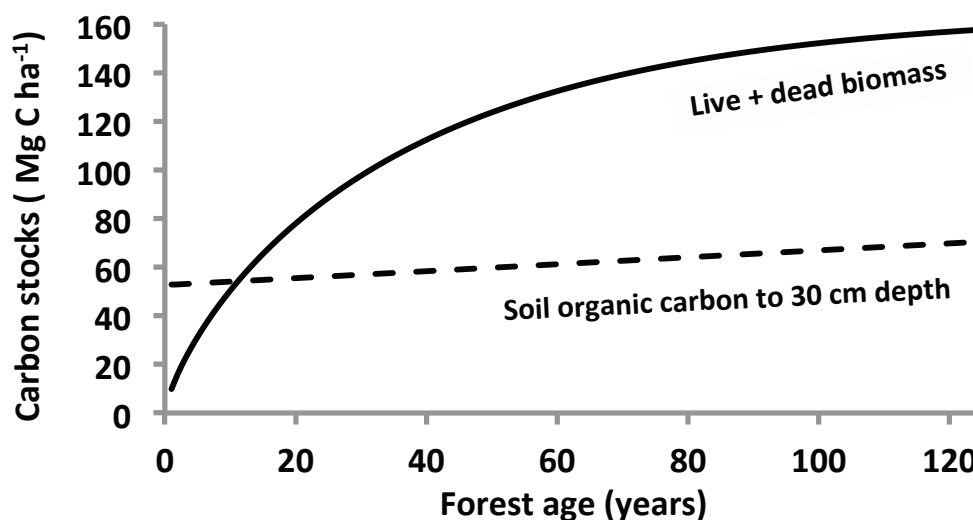

Figure 6: The general trends of carbon stock changes in biomass and soil with the age of secondary forest.

Discussion

Carbon balance in secondary forest succession

Our NEP and NCB estimates lie within the reported ranges in different types of forests (-14.1 to 3.9 Mg C ha^{-1} yr^{-1}) (Janisch and Harmon 2002; Turner et al 2011; Alberti et al 2014; Taylor et al 2014). Both primary and secondary forests of the region have acted as net carbon sink during the experimental period. This demonstrates the importance of conserving these fragile forests frontiers. The amount of carbon that forest ecosystems accumulate in living biomass, forest floor detritus and soil is more than it releases to the atmosphere from detritus (fine litter + coarse woody debris) and soil organic matter decomposition. Contrary to our hypothesis, we found that mature forests are still acting as carbon sink in the tropical forest of southern Mexico, probably not always but at least during the period of our experiment. Our estimates from both methods (TC increment and flux balance) showed that mature forest ecosystems in the region are accumulating carbon. Our finding contradicts with some reports that mentioned that a mature forest can be a net carbon source or carbon neutral (Taylor et al 2014) but supports hypothesis that mature forests still act as net carbon sink (Luyssaert et al 2008; Kashian et al 2013). One of the explanations could be the result of the past disturbance like selective logging of economically important trees from the mature forest that may have opened the gaps and trees grown on those gaps are still increasing. Another explanation could be the stimulation of tree growth due to increased CO_2 fertilization related climate change as suggested by some recent studies (Bugmann and Bigler 2011; Drake et al 2011).

With biomass change estimation data, Phillips et al (1998) suggested that Neotropical forests may be a significant carbon sink. However their estimates only consider live biomass change rates in mature forest stands. Some authors report negative NEP during the initial stage of succession considering that downed deadwood decomposition is the principal source of C loss in this stage (Janisch and Harmon 2002). Initial stage NEP and NCB in our study were found to be positive because most of woody detritus carbon was instantly oxidized in slash and burning activity (Pregitzer and Euskirchen 2004; De Simon et al 2012). Our estimates of carbon

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balance we couldn´t incorporate C export, import, non-biological oxidation like fire, ultraviolet oxidation and dissolution of carbonates (Lovett et al 2006). The contribution of carbonate dissolution in carbon loss (soil CO_2 efflux) could be high because of the presence of carbonate rocks and rendzic soil in Yucatan peninsula. High soil respiration rates observed in our study are probably because of higher carbonate dissolution. Future research should pay attention to estimate carbon flux from carbonate dissolution.

Limitations and sources of uncertainty

We used different methods of estimation of biomass increase, woody and non-woody detritus production, fine root production and turnover. Application of allometric equations in estimating aboveground and belowground biomass increase and direct measurement of litter and branch-fall can have increased the chance of overlap in our estimates of production or gain. We couldn´t separate the contribution of dying trees on litterfall, woody detritus production and fine root turnover estimates, which may have increased the possibility of certain level of double counting. We didn´t consider decomposition of standing dead trees and remnant detritus on carbon loss. Our estimates only focused on the annual production and loss. Some of the fluxes like litter decomposition in our estimates were taken from published reports. Because of the differences in species composition and micro-environment, these rates can have some level of discrepancy from our experimental plots. Future research on the science of forest carbon dynamics in the region should include experiments on those processes of carbon flow.

Another source of uncertainty was the time period of the experiment. Most of our estimates were based on the field experiments of one to two years. Thus, we couldn´t analyze the possible inter-annual variations in carbon capture, transfer and loss. Inter-annual variation in precipitation and other climatic parameters may change the rate and amount of carbon flow from respective biogeochemical processes like photosynthesis, respiration, senescence and decomposition. We recommend that researches in future should consider more than two years of experiment to check the

consistency or discrepancy of the trends and patterns found in short term experiments. Longer term experiments can also help us figure out the sink and source dynamics of mature forests as proposed by dynamic equilibrium or intermediate peak hypothesis (Luyssaert et al 2008; Mascaro et al 2012).

Implications to regional socio-ecological system

Since carbon flux studies have become so important in the context of climate change, understanding carbon fluxes provide a new dimension to the regional socioecological system, creating region-wide information on carbon capture and emission cycle and its interrelationship to other ecosystem services to inform management deliberations (Turner et al 2011). However, the fate of tropical forest ecosystem services are inextricably linked to the broader landscape context, including how the surrounding agricultural matrices are formed and managed (Harvey et al 2008). The size of the carbon pools, NEP and C fluxes are highly sensitive to forest management activities (Fahey et al 2009). At the same time, livelihoods of the people living in these forest-agriculture landscapes depend primarily on agriculture. Although it has been reported that forest loss rate in southern Mexico has been decreased, slash and burn agriculture and extensive livestock farming are the incessant farming practices in the region. The time that those secondary forests remain as carbon sink depend highly on the income and food security of those farming community and their knowledge on land management practices. Complete slash and burn practice or grassland establishment can convert a secondary or mature forest stand from a net carbon sink to a quick carbon source as carbon flux is nearly spontaneous. However, more research needs to be done in the region to evaluate annual carbon flux from slash and burn activity considering the carbon stocks and dynamics of forest stand before slashing. In addition to changing carbon flux pattern, such land conversions have strong implications on other ecosystem services like biodiversity conservation and hydrological balance since forests of southern Mexico is the part of broad Mesoamerican biological corridor. Hence, action agendas incorporating all stakeholders are needed to reconcile farming and biodiversity conservation in such

fragile ecosystems (Harvey et al 2008; Chhatre and Agrawal 2009) as well as to respond to the immediate threats of terrestrial carbon flux to the atmosphere.

Conclusion

This study tried to integrate the evaluation of major biogeochemical processes of carbon flows measured in the same experimental plots. The methods and outcomes can be considered as one of the first antecedents of carbon balance study in the tropical forests of southern Mexico. The results related to carbon fluxes can be applied in larger scale modelling of tropical forest carbon dynamics. The results on carbon balance are plausible both in terms NEP and NCB estimates and are consistent with other studies in the tropical forests. Consideration on extensive time and labor requirements for field as well as laboratory works for all flux measurement should be made in future investigations of this type.

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CAPÍTULO VI

Conclusión general

Este capítulo presenta una síntesis y reafirmación de los resultados, las novedades de la investigación, implicación para las ciencias ecológicas y desarrollo sustentable y la dirección de las investigaciones futuras.

Síntesis de los resultados

El estudio tuvo el propósito de explorar el efecto de la edad de vegetación secundaria e historia de uso de la tierra sobre los reservorios y flujos de carbono en una selva tropical de sureste de México. También se buscó definir las trayectorias de acumulación neta de carbono considerando las variaciones en los procesos biogeoquímicos que ocurren en diferentes etapas sucesionales de la vegetación secundaria y primaria. Esto surgió a partir de que los reportes y antecedentes de los estudios en la vegetación secundaria en los trópicos, especialmente en México, son incompletos y dejan varias cuestiones no resueltos en cuanto a la dinámica de carbono.

Los resultados empíricos están presentados en los cinco capítulos anteriores. El capítulo I explica el contexto de la investigación y como se la aborda en la tesis, el capítulo II demuestra que tanto la edad de la vegetación como la intensidad de uso de suelo afecta a los reservorios de carbono; el capítulo III presenta la variación estacional y sucesional de la producción de hojarasca, el capítulo IV analiza la producción y descomposición de materia leñosa, tomando en consideración el posible efecto de la edad y las características específicas de los árboles, y el capítulo V integra los reservorios, transferencias entre reservorios y flujos hacia la atmosfera de carbono con el fin de estimar la acumulación neta de carbono en diferentes etapas de la sucesión. Con relación a las preguntas principales de la investigación, podemos concluir que el stock de carbono aumenta lentamente con la edad de vegetación secundaria por los cambios en la composición y dominancia de especies y puede tardar más de un siglo para llegar al nivel de la vegetación primaria (Aryal et al., 2014). La historia de uso de suelo es uno de los factores importantes porque los resultados demuestran que a mayor intensidad de uso del suelo, menor es la

velocidad de recuperación de carbono en la vegetación secundaria. Los resultados indican que la vegetación secundaria recupera su capacidad de producción de hojarasca de nivel de la vegetación primaria dentro de cinco años después de abandono de tierra. La producción de hojarasca es alta en la temporada seca. El estudio también demuestra que la tasa de descomposición de materia leñosa es mayor en etapas jóvenes que en las etapas maduras de la vegetación secundaria y selva madura. A demás, el estudio evidencia que tanto la vegetación secundaria como la primaria de la selva mediana sub-perennifolia del SE de México son sumideros netos de carbono demostrado por el balance de ganancia y perdida de carbono, por lo menos durante la fase de experimentación. Las tasas de ganancia y pérdida pueden variar con tiempo, espacio y método de estimación, por lo que se requiere continuar con las mediciones. Este resultado es un paso importante en análisis y entendimiento del estado de las ecosistemas forestales del SE de México en términos de las emisiones y captura de carbono y añade una evidencia en nuestro conocimiento científico sobre la paradigma del balance de carbono de la selva madura en los trópicos (Luyssaert et al., 2008; Taylor et al., 2014). La trayectoria de productividad neta del ecosistema en nuestro estudio no sigue la curva de forma "U invertida" (Janischy Harmon, 2002) y la discrepancia puede explicarse por la diferencia en la cantidad de carbono remante legado del disturbio anterior (Pregitzer y Euskirchen, 2004). El resultado de esta tesis contradice con el hipótesis que considera la selva madura como una fuente neta de carbono (Taylor et al., 2014) pero es consistente con el hipótesis que considera que los ecosistemas forestales maduros pueden ser sumideros netos de carbono por lo menos durante un tiempo dado (Kashian et al., 2013). A demás, la trayectoria de acumulación de carbono en ecosistemas forestales es altamente dependiente a la escala porque puede variar mucho de una escala de rodal a una escala del paisaje (Mascaro et al., 2012). El monitoreo continuo puede comprobar si la acumulación continua durante más tiempo o que la selva madura se convierte en una fuente (temporalmente), de acuerdo con la teoría del equilibrio dinámico.

Novedades y contribución a la ciencia

Esta investigación es uno de los pocos estudios en ecosistemas forestales tropicales que integran los análisis de los almacenes y transferencias de carbono utilizando las mismas parcelas de muestreo. En este sentido, se considera novedoso en sus bases metodológicas porque evalúa diferentes procesos biogeoquímicos relacionados con el flujo y almacenamiento de carbono en la misma unidad espacial. Los resultados exploran varios patrones y procesos de la dinámica de carbono relacionado tanto con la edad de vegetación como la intensidad de uso anterior de suelo. Los resultados demuestran las trayectorias para predecir el estado de acumulación e intercambio de carbono entre ecosistemas forestales y la atmósfera en un futuro próximo considerando el efecto de la intervención humana. Los resultados de los valores de diferentes tasas de los procesos biogeoquímicos que ocurren en una selva secundaria y primaria son de vital importancia en modelación de la dinámica de carbono a una escala mayor. Por ejemplo, las tasas de reclutamiento, crecimiento y mortalidad de árboles, producción de hojarasca, caída y descomposición de ramas, producción y renovación de raíces finas y respiración de suelos son datos cruciales para la modelación del balance de carbono a una escala mayor en espacio y tiempo.

Implicación al desarrollo sustentable y políticas publicas

México tiene una visión de llegar a nivel de cero emisiones en el sector de uso de suelo, cambio de uso de suelo y silvicultura (USCUS) al 2020 (CONAFOR, 2010). Es uno de los países que están preparándose para proyectos de reducción de emisiones por deforestación y degradación que incluye conservación, manejo sustentable y aumento de stock de carbono (REDD+) como parte de la convención marco de naciones unidas sobre cambio climático (CMNUCC). REDD+ es un mecanismo de financiamiento basado en resultados que toma en cuenta la medición, reporte, verificación (MRV) y certificación de la reducción de emisión (Skutsch et al., 2013). Se requiere generar un nivel de referencia y un reporte continúo en cierto intervalo de tiempo (por ejemplo cada dos años) (CONAFOR, 2010). Sin embargo, el costo de medición sobre el beneficio puede ser alto. Los modelos basados en los

procesos biogeoquímicos generados por la medición continua en las parcelas permanentes a nivel sub-nacional pueden ser una alternativa para un sistema de monitoreo de emisión o remoción de Tier 3 (UNFCCC, 2009). Los resultados de nuestro estudio podrían ser útiles para la estimación y modelación de balance de carbono a nivel regional o a nivel de vegetación similar tal y como se ha propuesto en Tier 3 de monitorio de emisión y/o remoción de gases de efecto invernadero. Los resultados de este estudio indican los escenarios de acumulación y emisión de carbono del suelo y renovación de raíces finas (Mendoza-Vega et al., 2003), uno de los experimentos que requiere sustancial cantidad de mano de obra y tiempo para la medición. Además, nuestra estrategia de incorporar las personas locales en diferentes trabajos de campo ha ayudado en fortalecer sustancialmente la capacidad local en el entendimiento y acción sobre la dinámica de carbono de su tierra. La perspectiva de participación comunitaria guiada por los profesionales en mediciones de carbono dentro del marco de MRV es recomendable para generar la información correcta de manera eficiente y sustentable (Palmer Fry, 2011).

Recomendaciones

Aunque el estudio ha intentado integrar todos los flujos de carbono, no ha podido analizar algunos de los flujos por la cuestión de tiempo y recursos económicos. Los experimentos que se deben tomar en cuenta en los futuros investigaciones son: descomposición de hojarasca y raíces finas para reducir el nivel de incertidumbre en estimaciones de las transferencias y flujos de carbono. Considerar las tierras parcialmente-inundables (bajos) y ampliar el estudio a mayor escala podría aumentar el nivel de confianza de los resultados para usar en generación de estrategias y metas alcanzables de políticas públicas relacionadas a la mitigación de gases de efecto invernadero (De Jong et al., 2010). Los resultados presentados en este este estudio son de corto plazo. Se recomienda considerar más de dos años de experimentos para poder analizar la variación interanual de la dinámica de carbono. Al mismo tiempo combinar mediciones directos de los flujos (Eddy covariancia) con los experimentos de campo ayudará a comparar y verificar los resultados medidos por método de inventarios y experimentos en el campo.

Finalmente, en base a los resultados de esta investigación, quiero reiterar que la práctica de roza-tumba y quema es una actividad incesante y es fundamental para la seguridad alimenticia y económica de la gente rural en SE de México(Ochoa-Gaona et al., 2007; Schmook et al., 2013). Por lo cual, los ecosistemas forestales de la región se encuentran en un proceso continuo del cambio en la estructura, composición, función y productividad. Estos cambios influyen significativamente en las tasas de captura, transferencias, flujos y finalmente en el balance de carbono tanto a nivel de rodal como a nivel del paisaje. Reducir la emisión, conservar y aumentar el stock de carbono es prácticamente imposible sin dirigir las necesidades de la gente que vive en y alrededor de los paisajes forestales-agrícolas en los trópicos (Chhatre y Agrawal, 2009). Buscar la sinergia entre la seguridad de sustento de vida de los campesinos y la conservación forestal acoplado con la capacitación y políticas de conservación puede reducir la amenaza de que estos ecosistemas forestales se convierten de sumidero a una fuente neta de carbono.

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Anexos

Anexo 1. Carta de aceptación del artículo: Carbon stocks and changes in tropical secondary forests of southern Mexico.

-----Mensaje original-----

De: ees.agee.0.29d3aa.ebd5d0ca@eesmail.elsevier.com

En nombre de **"Agriculture, Ecosystems & Environment"**
Enviado el: martes, 10 de junio de 2014 21:47
Para: ben-toshiba@hotmail.com; bjong@ecosur.mx
Asunto: AGEE11354R1

Ref.: Ms. No. AGEE11354R1
Carbon stocks and changes in tropical secondary forests of southern Mexico.

Dear Dr. de Jong,

I am pleased to inform you that your paper has now been accepted for publication in **Agriculture, Ecosystems and Environment**. The manuscript will be prepared for press and proofs will be sent to you in due course.

When your paper is published on ScienceDirect, you want to make sure it gets the attention it deserves. To help you get your message across, Elsevier has developed a new, free service called AudioSlides: brief, webcast-style presentations that are shown (publicly available) next to your published article. This format gives you the opportunity to explain your research in your own words and attract interest. You will receive an invitation email to create an AudioSlides presentation shortly.

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With kind regards,

Soundarya S
Journal Manager
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The authors have addressed all the review comments. The revised manuscript is now acceptable for publication in AGEE.
M.R. Carter

Anexo 2. Carta de confirmación de envió del artículo: Successional and seasonal variation of litterfall and associated nutrient transfer in semi-evergreen tropical forests of SE Mexico

-----Mensaje original-----
De: em.fres.0.3e9ae8.e1784180@editorialmanager.com
En nombre de Nutrient Cycling in Agroecosystems (FRES)
Enviado el: lunes, 20 de octubre de 2014 14:00
Para: Ben H.J. de Jong
Asunto: FRES - Submission Confirmation

Dear Ben de Jong,
Thank you for submitting your manuscript, **Successional and seasonal variation of litterfall and associated nutrient transfer in semi-evergreen tropical forests of SE Mexico,** to **Nutrient Cycling in Agroecosystems.**

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Nutrient Cycling in Agroecosystems
Successional and seasonal variation of litterfall and associated nutrient transfer in semi-evergreen tropical forests of SE Mexico
--Manuscript Draft--

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Corresponding Author:	Ben H.J. de Jong, Dr El Colegio de la Frontera Sur Campeche, Campeche MEXICO
Corresponding Author Secondary Information:	
Corresponding Author's Institution:	El Colegio de la Frontera Sur
Corresponding Author's Secondary Institution:	
First Author:	Deb Raj Aryal, MSc
First Author Secondary Information:	
Order of Authors:	Deb Raj Aryal, MSc
	Ben H.J. de Jong, Dr
	Susana Ochoa-Gaona, Dra
	Jorge Mendoza-Vega, Dr
	Ligia Esparza-Olguin, Dra