

**INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA - INPA
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA**

**Topografia e densidade da madeira modulam o crescimento sazonal na
Amazônia Central**

Karina Liana Lisboa Melgaço

Manaus, Amazonas
Maio, 2014

Karina Liana Lisboa Melgaço

**Topografia e densidade da madeira modulam o crescimento sazonal na
Amazônia Central**

Orientador: Dra. Flávia Regina C. Costa

Dissertação apresentada ao Instituto Nacional de Pesquisas da Amazônia como parte dos requisitos para obtenção do título de Mestre em Biologia (Ecologia).

Manaus, Amazonas
Maio, 2014

Banca Examinadora Presencial

Parecer

Dr. Bruce Walker Nelson-
Instituto Nacional de Pesquisas da Amazônia

Aprovado

Dr. Fabien Wagner-
Instituto Nacional de Pesquisas Espaciais

Aprovado

Dr. José Luís Campana Camargo-
Instituto Nacional de Pesquisas da Amazônia

Aprovado

M521 Melgaço, Karina Liana Lisboa
Topografia e densidade da madeira modulam o crescimento na Amazônia Central. --- Manaus : [s.n], 2014.

viii, 50 f. : il.

Dissertação (Mestrado) --- INPA, Manaus, 2014.

Orientador : Flávia Regina C. Costa.

Área de concentração : Ecologia.

1. Ecofisiologia. 2. Topografia. 3. Densidade da madeira
I. Título.

CDD 634.9

Sinopse

Foram monitoradas com dendrômetros 1879 árvores por 12 meses, com intervalos bimestrais, em um gradiente hidro-topográfico de uma floresta de terra-firme na Amazônia Central. Avaliou-se o incremento em circunferência de árvores e palmeiras entre os períodos de monitoramento e os ambientes topográficos. Os maiores valores de incremento em circunferência das árvores ocorreram na transição da estação seca para a estação chuvosa e ao longo do período chuvoso. Em relação à topografia, no final do período chuvoso as árvores das áreas de platôs apresentaram incremento em circunferência maior que as demais áreas, e no período da seca as áreas de baixio tiveram árvores com maior incremento do que as árvores dos platôs e vertentes. Aspectos como nível do lençol freático, precipitação e textura do solo foram avaliados. Considerou-se também a densidade da madeira relacionada às variações de incremento em circunferência entre os períodos de monitoramento e ao longo da topografia.

Palavras-chave: Ecofisiologia, sazonalidade, densidade da madeira, topografia, Amazônia Central.

*À Jair Melgaço, Natalia Lisboa, Lisiane Lisboa , Maria Nair
Lisboa e Bruno Cintra, em retribuição à toda força,
compreensão e amor dedicados nestes anos.*

Agradecimentos

Agradeço ao CNPq pela bolsa de mestrado e à Pós-Graduação em Ecologia do INPA pelos anos de conhecimentos científicos de grande valia profissional, infra-estrutura e a possibilidade de estar em contato com profissionais altamente qualificados e dedicados à Amazônia.

Ao laboratório da Família Vegetal, o qual foi uma escola de aprendizado e convivência. Sem dúvidas, foi o lugar que tive mais contato com pessoas de extrema dedicação ao trabalho. Cresci profissionalmente e pessoalmente um pouco a cada dia de rotina do laboratório.

Agradeço especialmente à minha orientadora Flávia Costa, a qual tenho muita admiração, por todo aprendizado e pela oportunidade de conviver e trabalhar com uma grande pesquisadora. Tenho muito orgulho disso. Por esta convivência fui estimulada a buscar sempre saber mais e isso é coisa que só um bom professor e orientador é capaz de fazer. Por tudo isso, obrigada.

Agradeço a cada um de minha amada família pelo amor incondicional, estímulo, carinho, confiança e compreensão que minimizaram a dificuldade de estar a 4000 km de distância de praia e abraço de pai, de um café-da-manhã e de um denço de mãe, de um desenho animado e uma briga com a irmã, de um aconchego e um bolinho de arroz de vó e da chegada em casa com cachorros. Agradeço por tudo sempre.

Agradeço ao meu companheiro Bruno Cintra, o qual precisei andar os mesmos 4000 km para reencontrar, pelos dias com praias e abraços, cafés-da-manhã e denços, seriados e brigas, aconchegos e chegadas em casa compartilhados com tanto amor desde minha chegada à Manaus.

Aos queridos amigos que estão na beira-do-mar e que só de lembrar o sorriso já brota no rosto: Bruno Godoy, Carol Allage e Joca, Raffa Gonzaga e Manu Reis. Obrigada por todos os pensamentos positivos enviados sempre e pelo carinho.

Às queridas amigas Júlia Valentim e Luíza Figueira, que também fizeram a travessia dos 4000 km de beira do mar para o rio banhar, agradeço por todo companheirismo, risadas e chocolates. Aos amigos feitos aqui e que agora serão levados para todo lugar, independente da quilometragem, que fizeram tudo ser e ficar muito melhor. Agradeço.

RESUMO

Mudanças climáticas são reconhecidas como um dos maiores impactos ambientais sobre o estoque de carbono das florestas tropicais, mas os efeitos e os mecanismos pelos quais o clima afeta o balanço de carbono das florestas tropicais ainda são incertos. A sazonalidade de crescimento tem sido estudada visando compreender isto. Neste estudo foi investigado como o gradiente hidro-topográfico e a densidade da madeira modulam o crescimento intra-anual das árvores em uma floresta de terra-firme na Amazônia Central, Brasil. Foram monitoradas 1879 árvores e palmeiras com dendrômetros, a cada dois meses em nove parcelas de 1ha. O crescimento variou em função da distância vertical da drenagem mais próxima, da textura do solo e densidade da madeira ao longo do tempo. O aumento em circunferência foi principalmente associado com o aumento das chuvas no período de transição da estação seca para chuvosa. No final da estação chuvosa, as árvores situadas em solos argilosos e verticalmente mais distantes do lençol freático tiveram maior crescimento do que as árvores nas vertentes e nos baixios. No entanto, no começo da estação seca, as maiores taxas de crescimento ocorreram nos baixios e nas vertentes com solos arenosos. Além disso, árvores de alta densidade da madeira mantiveram uma baixa variabilidade de crescimento intra-anual em circunferência, com incremento aumentando no período de transição da estação seca para chuvosa, enquanto as árvores de baixa densidade da madeira tiveram alta variabilidade de crescimento. Estas diferenças sugerem que o balanço entre o investimento em crescimento de madeira e a prevenção ao embolismo podem direcionar as respostas fisiológicas ao longo de gradientes hidro-topográficos. O crescimento em circunferência é direcionado pelo aumento de chuvas no período de transição da estação seca para chuvosa, o qual não é o período de maior irradiação e nem com maior quantidade de chuvas, como recentes estudos tem sugerido. Além disso, as condições mais favoráveis para o crescimento variam na topografia ao longo do tempo, de acordo com as melhores condições de água disponível no solo. Os baixios podem ser beneficiados por um período de seca, com o balanço de crescimento em favor destas áreas. Isto poderia significar um menor efeito negativo das secas ao longo da paisagem do que esperado por experimentos, os quais foram conduzidos em áreas distantes do lençol-freático.

Palavras-chave: Dendrômetros, ecofisiologia, alta densidade da madeira, irradiação, baixa densidade da madeira, interações planta-clima, sazonalidade de chuvas, floresta tropical, estação chuvosa.

ABSTRACT

Topography and wood density modulate seasonal growth of central Amazonian forests

Global climatic changes are widely recognized as the greatest current environmental impact, but the effects and mechanisms by which climate affects the carbon balance of tropical forests are uncertain. Growth seasonality has been studied in an attempt to understand this. Here we investigated how hydro-topographic gradients and wood density modulate intra-annual growth of trees in a terra-firme forest in central Amazonian Brazil. A total of 1,879 trees and palms were monitored with dendrometers every two months in nine 1ha plots. Growth varied as a function of terrain height above the nearest drainage, soil texture and wood specific gravity across time. Increases in girth were mostly associated with raising rainfall during the transition from dry to wet season. At the end of the wet season, trees in clayey soils and vertically far from the water table had greater growth increments than trees in slopes and sandy valleys. However, at the start of the dry season, higher growth rates occurred in valleys and slopes with sandy soils. Additionally, trees with high specific gravity woods maintained low intra-annual girth growth variability, with increment increases in the transition period from dry to wet season, while trees with low specific gravity woods had a broad range of growth variability. These differences suggest that a trade-off between wood growth investment and hydraulic safety may be driving physiological responses along topographically-driven hydrological gradients. Tree stem growth is driven by the rainfall increase in the transition from dry to wet seasons, and not by greater irradiation or greater amount of rainfall as recent studies have suggested. Moreover, the most favorable conditions for growth move across the landscape along time, in association with topography, tracking the best conditions of soil-water availability. Valleys around terra-firme streams may benefit from some level of drought, therefore if dry-seasons become longer, the balance of growth may shift in favor of these areas. This would mean a lower net effect of droughts over the landscape than expected from drought experiments, which were conducted in upland areas far from places with a superficial water-table.

Key-words: Dendrometers, ecophysiology, high wood density, irradiation, low wood density, plant-climate interactions, rainfall, seasonality, tropical forest, wet season.

Sumário

Agradecimentos _____	v
Resumo _____	vi
Abstract _____	vii
Introdução _____	1
Objetivos _____	5
Capítulo I _____	6
Referências _____	28
Tabelas _____	35
Figuras _____	36
Informações Suplementares _____	40
Conclusões _____	47
Anexos – Atas e pareceres de qualificação e defesas escrita e oral _____	49

1. Introdução

As mudanças climáticas são reconhecidas como um dos maiores impactos ambientais na atualidade. Estudos recentes indicam que as florestas tropicais são sensíveis ao aumento de dióxido de carbono na atmosfera (Phillips & Gentry 1994; Phillips *et al.* 2004), ao aumento de temperatura (Clark *et al.* 2010), alterações nos padrões de chuva (Phillips *et al.* 2009), ao aumento das secas (Phillips *et al.* 2008; Malhi *et al.* 2008) e alterações na disponibilidade de água no solo (Malhi *et al.* 2008). Alguns autores sugeriram que o maior impacto destas mudanças sobre a biomassa florestal tropical é dado pela fertilização por CO₂ (Körner *et al.* 2006; Huang *et al.*, 2007), causando o aumento da biomassa que tem sido registrada em vários estudos (Phillips *et al.* 1998, Baker *et al.* 2004, Lewis *et al.* 2009, Castilho *et al.* 2010). Entretanto, esta hipótese foi refutada por Clark *et al.* (2010), que mostraram redução do crescimento das árvores com o aumento anual da temperatura noturna em 1°-2°C e diminuição das chuvas na estação seca, sugerindo que a produção de madeira e a mortalidade das árvores podem ser severamente afetadas pelo aquecimento ou resfriamento do clima. De fato, ainda são incertas as causas diretas das mudanças nos padrões de dinâmica e estoque de biomassa observados nas florestas tropicais e se estas estão se comportando como fontes ou sumidouro de carbono (Phillips *et al.* 1998, Clark *et al.* 2004, Pan *et al.* 2011).

O estudo da sazonalidade da fotossíntese e da produção de folhas e madeira pode fornecer pistas para entender a sensibilidade da floresta aos diferentes fatores climáticos (temperatura, precipitação e irradiação) afetados pelas mudanças globais. Na Amazônia, alguns estudos observaram um aumento de 25% no Índice de Vegetação Melhorada – EVI (um proxy para capacidade fotossintética do dossel) com o aumento da irradiância na estação seca (Huete *et al.* 2006) e um aumento de produtividade primária associada às áreas da bacia mais afetadas por um evento de seca extrema ocorrida em 2005, a qual foi atribuída ao aumento de

irradiância e a redução da nebulosidade (Saleska *et al.* 2007, e.g Samanta *et al.* 2010). Estes resultados podem ser associados a mecanismos de aclimatação sazonal das folhas, através da manutenção de sua capacidade fotossintética em períodos secos (Domingues *et al.* 2014). Outros estudos, no entanto, mostraram que a respiração da floresta aumenta e a produtividade primária líquida declina nos períodos secos e/ou com baixa disponibilidade de água no solo (Malhi *et al.* 2004, Bonal *et al.* 2008, Metcalfe *et al.* 2010), bem como o crescimento em diâmetro das árvores (Silva *et al.* 2010; Wagner *et al.* 2012). Em meio a estes resultados aparentemente contraditórios, com medições de campo apresentando um aumento de biomassa e de incremento em diâmetro das árvores na estação chuvosa e dados de satélites e torres de fluxo mostrando flushing de folhas e aumento da produtividade da floresta no período da seca, Wagner *et al.* (2013) demonstraram que há um assincronismo e mudança de alocação de carbono entre a produção de folhas e madeira, indicando que a produção de folhas foi direcionada pela irradiância enquanto a produção de madeira pelas chuvas.

Variações sazonais nas chuvas resultam em grande alteração de água disponível no solo para plantas (Comita *et al.* 2009; Stahl *et al.* 2012). O estoque de água no solo é influenciado pelo regime de precipitação mas também por variações no nível do lençol freático (Tomasella *et al.* 2007) e por propriedades físicas do solo, como textura e porosidade, que determinam a retenção de água. Na Amazônia central o relevo é bem dissecado pela rede de drenagem, resultando em uma paisagem com áreas altas em relação a drenagem (platôs), onde os solos são argilosos, e áreas de vales à beira das drenagens (baixios), onde os solos são arenosos. Na estação seca, as plantas situadas nos platôs podem estar sob estresse hídrico por déficit de água, pois há uma diminuição no aporte de chuvas e o lençol freático está distante da superfície (Hodnett *et al.* 1997). Na estação chuvosa, as plantas dos platôs devem ter as melhores condições de crescimento, tendo em vista a alta disponibilidade de água associada à alta porosidade, boa drenagem e alta capacidade de retenção de água dos solos argilosos. Nas

regiões de baixios, as plantas estão verticalmente mais próximas à drenagem e estão suscetíveis à alta saturação dos solos por água nos períodos chuvosos (Hodnett *et al.* 1997). A saturação e a inundação resultam em supressão do crescimento radial atribuída às condições de anaerobiose no solo (Schöngart *et al.* 2002, 2010, Rodriguez- Gonzalez *et al.* 2010), de forma que a intensidade de chuvas pode se caracterizar como um fator limitante e não um estímulo ao crescimento das plantas no baixio.

As árvores das florestas tropicais apresentam grande variabilidade de respostas fisiológicas frente às mudanças das condições hídricas no ambiente (Stahl *et al.* 2012). Diferentes respostas individuais das árvores à seca dos solos foram observadas, sendo que alguns indivíduos regularam a fotossíntese e a transpiração quando a água disponível no solo foi drasticamente reduzida e outras apresentaram pequenas variações, indicando boa adaptação aos solos secos (Stahl *et al.* 2012). O estudo dos traços funcionais pode trazer grandes contribuições para entendimento desta variação. Por isso a densidade da madeira parece um bom ponto de partida, já que reflete as estratégias de crescimento das árvores assim como relaciona-se com o tamanho e frequência dos vasos, por seguinte à condutividade hidráulica (Poorter *et al.* 2010). Árvores de baixa densidade da madeira são associadas a um rápido crescimento e possuem poucos mas amplos vasos condutores, por outro lado árvores de alta densidade da madeira apresentam baixo crescimento e vasos condutores finos e abundantes. O trade-off entre quantidade e tamanho dos vasos condutores é a razão que direciona a eficiência e segurança da condutividade hidráulica (Baas *et al.* 2004, Poorter *et al.* 2010). Vasos de maior calibre possuem maior condutividade hidráulica, contudo maior risco de embolia e cavitação (Sperry *et al.* 2006), enquanto vasos menores apresentam uma maior segurança hidráulica, apesar de possuírem uma baixa condutividade hidráulica (Baas *et al.* 2004, Santiago *et al.* 2004, Poorter *et al.* 2010, Fan *et al.* 2012).

Dado o conhecimento das variações nas propriedades da madeira, nas taxas de crescimento individuais (Grogan & Schulze 2012) e entre grupos funcionais (Santiago *et al.* 2004) ao longo de gradientes de disponibilidade hídrica (Ferry *et al.* 2010, Baker *et al.* 2003, Bellingam *et al.* 2000), parece lógico esperar que diferentes combinações destes fatores devem levar a diferentes respostas sazonais, indicando diferentes sensibilidades da floresta às mudanças climáticas. O entendimento destas interações pode ajudar a resolver alguns conflitos aparentes nos resultados atuais sobre o balanço de carbono das florestas tropicais.

Neste trabalho procuramos contribuir para compreensão do funcionamento do balanço de carbono e para predições de como a floresta pode responder às mudanças climáticas, avaliando como características ambientais limitam o crescimento secundário intra-anual de árvores em escala local. Visamos responder as seguintes perguntas: (i) como as características hidro-topográficas influenciam o crescimento secundário intra-anual das árvores e palmeiras de uma floresta de terra-firme da Amazônia Central? (ii) Como as características hidro-topográficas modulam o crescimento secundário das árvores e palmeiras, considerando a densidade da madeira? Esperamos que a disponibilidade de água no solo, influenciada pela topografia e a sazonalidade de chuvas, seja o principal preditor para as diferentes respostas de incremento em circunferência das árvores e palmeiras, e que os períodos mais favoráveis ao crescimento variem entre os ambientes topográficos, de acordo com o conteúdo de água no solo. Esperamos ainda que as árvores de alta densidade da madeira apresentem menor variação de crescimento secundário intra-anual, crescimento conservativo, e ao longo da topografia, em função de sua alta densidade de vasos condutores de baixo calibre, enquanto as árvores de baixa densidade da madeira apresentem maior variabilidade de respostas em crescimento secundário ao longo do ano e da topografia, em função de sua anatomia do xilema com poucos vasos condutores, contudo de alto calibre.

2.Objetivos

2.1. Objetivo Geral

O objetivo geral deste trabalho consiste em responder às perguntas: (i) como as características hidro-topográficas influenciam o crescimento secundário intra-anual das árvores e palmeiras de uma floresta de terra-firme da Amazônia Central? (ii) Como as características hidro-topográficas modulam o crescimento secundário das árvores e palmeiras, considerando a densidade da madeira?

2.2. Objetivos Específicos

- Monitorar bimestralmente o crescimento em diâmetro das árvores;

- Relacionar o crescimento em diâmetro das árvores com precipitação acumulada bimestral e radiação fotossinteticamente ativa.

Capítulo I

K. L. L. Melgaço, C. Castilho, J. Schiatti, J.Aquila-Pasquel, H.Santana, F.Costa: Topography and wood density modulate seasonal growth of central Amazonian forests. Manuscrito submetido para *Journal of Ecology*.

Topography and wood density modulate seasonal growth of central Amazonian forests

Karina Melgaço^{1*}, Juliana Schietti¹, Carolina V. Castilho², Jhon del Aquila-Pasquel³, Hellen Santana¹, Flávia R. C. Costa⁴

¹*Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil*, ²*Embrapa Roraima BR 174, Boa Vista-Roraima*, ³*Instituto de Investigaciones de la Amazonia Peruana-IIAP, Iquitos, Peru*, ⁴*Coordenação de Pesquisa em Biodiversidade, Instituto Nacional de Pesquisas da Amazônia – INPA, Manaus, Brazil*.

*Corresponding author, E-mail: kari.melgaco@gmail.com

ABSTRACT

1. Global climatic changes are widely recognized as one of the greatest current environmental impacts, but the effects and mechanisms by which climate affects the carbon balance of tropical forests are uncertain. Growth seasonality has been studied in an attempt to understand this.
2. Here we investigated how hydro-topographic gradients and wood density modulate intra-annual growth of trees in a terra-firme forest in central Amazonian Brazil. A total of 1,879 trees and palms were monitored with dendrometers every two months in nine 1ha plots distributed over 16 km².
3. Growth varied as a function of terrain height above the nearest drainage, soil texture and wood specific gravity across time. Increases in girth were mostly associated with rising rainfall during the transition from dry to wet season. At the end of the wet season, trees in clayey soils and vertically far from the water table had greater growth increments than trees on slopes and in sandy valleys. However, at the start of the dry season, higher growth rates occurred in valleys and slopes with sandy soils.

4. Additionally, trees with high specific gravity woods maintained low intra-annual girth growth variability, with increment increases in the transition period from dry to wet season, while trees with low specific gravity woods had a broad range of growth variability. These differences suggest that a trade-off between wood growth investment and hydraulic safety may be driving physiological responses along topographically-driven hydrological gradients.
5. *Synthesis.* The highest tree stem growth rates are driven by the rainfall inputs in the transition from the dry to wet season, and not by the periods with highest values of irradiation or precipitation. Moreover, the most favorable conditions for growth move across the landscape along time, in association with topography, tracking the best conditions of soil-water availability. Valleys around terra-firme streams may benefit from some level of drought, therefore if dry-seasons become longer, the balance of growth may shift in favor of these areas. This would mean a lower net effect of droughts over the landscape than expected from drought experiments, which were conducted in upland areas far from places with a shallow water-table.

Key-words: Dendrometers, ecophysiology, high wood density, irradiation, low wood density, plant-climate interactions, rainfall, seasonality, tropical forest, wet season.

Introduction

Climate change is recognized as one of the greatest current environmental impact. Recent studies indicate that tropical forests are sensitive to increased atmospheric carbon dioxide (Phillips & Gentry 1994, Huang *et al.* 2007), increased temperature (Clark *et al.* 2010), rainfall pattern changes (Phillips *et al.* 2009; Clark *et al.* 2010) and increased drought (Phillips *et al.* 2009; Malhi & Phillips, 2004). Some authors have suggested that the major impact of

these changes on the tropical forest biomass is due to CO₂ fertilization (Cox *et al.* 2004; Lloyd & Farquhar 2008), causing the increase in biomass recorded by several studies (Phillips *et al.* 1998; Lewis *et al.* 2009; Castilho *et al.* 2010). However, this hypothesis was refuted by Clark *et al.* (2010), who found a reduction of tree growth with an annual 1°-2°C increase in night temperature and decreasing dry season rainfall, suggesting that wood production and tree mortality may be severely affected by either a warming or cooling climate. Overall, the direct causes of the changes in growth patterns and biomass dynamics observed in tropical forests are still uncertain, and it remains unclear if they are behaving as sources or sinks of carbon (Phillips *et al.* 1998, Clark *et al.* 2004; Pan *et al.* 2011).

The study of seasonal variations in photosynthesis and leaf and wood production can provide clues to understand forest sensitivity to those climatic factors (e.g. temperature, precipitation, radiation) affected by global climate changes. Studies in Amazonia have observed a 25% increase in the Enhanced Vegetation Index (a proxy for photosynthetic capacity) with increasing dry season insolation (Huete *et al.* 2006), and the increase in primary productivity that occurred in those parts of the Amazon basin most affected by the extreme drought of 2005 were attributed to increased insolation and reduced cloudiness (e.g. Saleska *et al.* 2007; Samanta *et al.* 2010). Such results may be associated with mechanisms for leaf seasonal acclimation, allowing the maintenance of photosynthetic capacity during dry periods (Domingues *et al.* 2014). Other studies, however, have shown that forest respiration increases and forest net primary productivity declines (Malhi *et al.* 2004; Bonal *et al.* 2008; Metcalfe *et al.* 2010), as well as stem growth (Silva *et al.* 2010; Wagner *et al.* 2012) in dry season and/or periods of low soil water availability. Amid these apparently contradictory results, where field measurements show trees increasing in biomass and diameter in the rainy

season, while satellite data and flux towers showing leaf flushing and increased forest productivity during the dry season, Wagner *et al.* (2013) demonstrated that there is an asynchrony between the carbon allocation to leaf production and to wood, indicating that the former was principally driven by insolation while the later was primarily influenced by rain.

Seasonal variations in rainfall can result in large changes in soil water availability for plants (Stahl *et al.* 2012). The reserve of water in the soil is influenced by rainfall regime but also by variations in water-table level (Tomasella *et al.* 2008), as well as by physical soil properties such as texture and porosity, which determine water retention (Hodnett & Tomasella 2002). In central Amazonia the topography of the landscape is shaped around the drainage network mainly as result of chemical (but also physical to a certain degree) processes of the soil (Chauvel *et al.* 1987). The result is a landscape with high relative drainage areas (plateaus), where the soils are clayey, and valley lowlands (bottomlands) near waterways, where soils are sandy (Chauvel *et al.* 1987). These variations in soil properties and terrain height can result in strongly contrasting seasonal water regimens in plateaus and bottomlands, even when they are horizontally highly proximate. In the dry season rainfall contribution greatly decreases and groundwater is far from the surface (Hodnett *et al.* 1997), therefore plants on plateaus and upper slopes may be under water stress from water deficit (Tomasella *et al.* 2008). In the rainy season, plateaus appear to provide conditions highly favorable to plant growth, with high water availability associated with high porosity and high water retention capacity of clay soils. Rainfall may therefore be expected to be a growth stimulant in such habitats. By contrast, in bottomlands during the rainy season, plant roots are vertically closer to the water-table and susceptible to high soil water saturation and flooding (Hodnett *et al.* 1997). This may give rise to anaerobic conditions which may result in the suppression of radial growth (Schöngart *et al.* 2002, 2005; Rodriguez-González *et al.* 2010).

Hence, for bottomland plants, rain intensity can be characterized as a limiting factor, not a growth stimulus.

Tropical forests trees exhibit great variability in their physiological responses to changing water conditions in the environment (Stahl *et al.* 2012). Different responses between species and within-species to dry soils have been observed, with some individuals regulating photosynthesis and transpiration when soil water availability was drastically reduced, while the response of others have indicated good adaptation to dry soils (Stahl *et al.* 2012). The study of functional traits can greatly aid in understanding this variation. Wood density offers a potentially productive point of entry since, via relationships with hydraulic conductivity, it reflects both the growth strategies of trees and the size and frequency of the vascular tissue components (principally the water-conducting xylem: Poorter *et al.* 2010). Trees with low-density wood are associated with rapid growth and have few but large xylem vessels, while high-density wood trees have slow growth, and xylem vessels that are abundant but narrow. The trade-off between xylem vessel quantity and size is driven by considerations of hydraulic conductivity efficiency and reliability (Baas *et al.* 2004; Poorter *et al.* 2010): larger xylem vessels have a higher hydraulic conductivity, but a higher risk of embolism and cavitation (Sperry *et al.* 2006), while smaller vessels have a higher hydraulic reliability, despite having a low hydraulic conductivity (Baas *et al.* 2004; Santiago *et al.* 2004; Poorter *et al.* 2010; Fan *et al.* 2012).

Given the knowledge of the variations in wood properties and individual growth rates (Grogan & Schulze 2012) and how these differ between functional groups (Santiago *et al.* 2004) along gradients of water availability (Ferry *et al.* 2010; Baker *et al.* 2003; Bellingam *et al.* 2000), it seems logical to expect that different combinations of these factors should lead to different seasonal responses, indicating different sensitivities of the forest to climate change.

Potentially, understanding these interactions offers means to help resolve some of the apparently conflicting results produced by recent studies of tropical forest's carbon balance.

This article aims to contribute to the understanding of the functioning of carbon balance and of how tropical forest might respond to climate change by assessing how environmental characteristics affect the intra-annual secondary growth of trees at a local scale. We aim to answer the following questions: (i) do hydro-topographical features influence the intra-annual secondary growth of trees and palms of a central Amazonian upland forest? (ii) in such forests, do hydro-topographic features modulate trees and palm secondary growth via wood density?

We predict that the availability of soil water, influenced by topography and rainfall seasonality, will be the main explanation for the different responses in tree and palm circumference increase, and that the temporal distribution of most favorable growth period will vary across topographical environments in relation to soil water content. We also expect, over such a topographic gradient, that trees with high wood density will have a lower intra-annual variation of secondary growth and slow growth-rates (due to a conservative, but safer strategy), while trees with low wood density will show greater variability of responses in secondary growth across time and space (year and topography).

Materials and Methods

Study Area

The study was conducted in (Ducke Reserve) the Ducke Forest Reserve (3°5' S, 60°00' W, Amazonas State, northern Brazil), a 10,000 ha (10 x 10 km) area located near the outskirts of Manaus city (Fig. 1), and considered the most intensely scientifically studied site

in central Amazonia (Freire & Azevedo 2010). The vegetation cover is Dense Humid Non-Flooded Lowland Tropical Forest (Brazil 1978), and has a canopy with an average height of 32m (Ribeiro *et al.* 2002), with emergents to 55m. The average annual temperature site is 26° C (Ribeiro & Villa Nova 1979). Regionally, most rainfall occurs between December and May, with a drier period between June and November. Average annual rainfall is 2,421 mm (based on records from 1966-1985), with no year exceeding 3000 mm. However, mean average rainfall at Reserve Ducke has increased in the last 16 years (to 2814 mm), with very high (> 3000 mm) values in 2011 and 2013 (see Figure S1 in Supporting Information). Satyamurti *et al.* (2009) have reported a similar trend for Barcelos, Belém, Manaus, Rio Branco and Soure. As well as Gloor *et al.* 2013 showed this tendency of increasing rainfall has occurred across Amazonia since 1990. Reserve Ducke soil types vary with topography: soils of higher altitude areas (plateaus) are classified as Oxisols rich in yellow clay with low organic C content (Gentry 1990). However, the proportion of sand increases with decreasing altitude, forming red-yellow podzols on the lower slopes, while sand-dominated soils occur in the bottomlands (Mertens 2004).

Sampling regime and environmental variables

A grid with trails spaced every 1 km was installed between 2000 and 2003 as part of the Brazilian Research Program in Biodiversity (PPBio). Nine trails run North-South (N-S) and nine East-West (E-W). Each track is 8 km long, giving a total grid area of 64km². On the E-W tracks there are 72 permanent plots, each 40 x 250 m, whose shape follows local contours to minimize within-plots variations in soil, topography and distance to the water table (Costa & Magnusson 2010). To ensure independence, sample plots are separated by at least 1 km (Fig. 1).

The nine plots selected for this study (Fig. 1) covered the entire range of locally available vertical distances to the water-table, and therefore represent the entirety of variation in hydrologic conditions found in the central Amazonian upland forest study site. The vertical distance to the water table was estimated using the HAND (Height Above Nearest Drainage) algorithm developed by Rennó *et al.* (2008). This algorithm uses a digital elevation model (DEM) to estimate the vertical distance of a chosen point from the local water table surface. A HAND model previously developed for the Ducke Reserve, based on elevation data derived from SRTM (Shuttle Radar Topographic Mission), indicated that the vertical distances to drainage are linked to spatial variations in plant species composition (Schietti *et al.* 2014). Areas with highest HAND values are vertically farther from drainage, and represent plateau areas. Slopes have intermediate, more variable, HAND values, while in bottomlands HAND values are low, reflecting their proximity to the superficial water table. Here surface outcropping of the water table results in areas where soil is fully saturated or lightly flooded. Data on precipitation and photosynthetically active radiation (PAR) for the study period was obtained from the Reserva Ducke meteorological station. Rainfall data were obtained with a rain gauge (daily measurements every hour) and PAR data obtained hourly with a Licor pyranometer. Precipitation values used for the current study are the cumulative rainfall values for the two months preceding each growth recording.

Selection of trees and palms and dendrometer installation

Based on a tree inventory undertaken by C. Castilho (Castilho *et al.* 2006) between 2000-2003 and the most recent re-census in 2007, 1879 trees with diameter at breast height (DBH) ≥ 10 cm were selected. Within each 250 x 40 m plot 200 trees were selected and dendrometers installed. Each plot was sub-divided into 10 x 40 m sections, and eight trees

selected in each, within nine DBH classes of 10 cm intervals. Equal numerical representation for all classes was attempted. However, since there were fewer ($n=47$) individuals in DBH classes ≥ 70 cm, all encountered individuals in these classes were used (Rice *et al.* 2004). When choosing trees the taxonomic identity was not considered, being randomly distributed. The dendrometers were manually-constructed (<http://www.rainfor.org/en/manuals>) and installed between November and early December 2012. To allow each dendrometer to adjust to the stem of its tree, monitoring only began two months after initial installation. For details of the sampling protocol see [http://ppbio.inpa.gov.br /repository/database](http://ppbio.inpa.gov.br/repository/database).

Increment monitoring occurred using analog steel calipers and following the RAINFOR-GEM (Amazon Forest Inventory Network and Global Ecosystem Monitoring network) protocol (available at <http://www.rainfor.org/en/manuals>). Data was collected bimonthly, so between February 2013 and January 2014 six measurements were obtained for each of the 1879 sample individuals (Table 1).

Wood density

Wood density values were obtained from the Global Wood Density Database (Chave *et al.* 2009, Zanne *et al.* 2009: available at <http://datadryad.org/>), following identification of the monitored species used in this study. The density values were available to species level for 969 individuals (~51% of sample), to genus level for 768 individuals (~41% of sample: average value for all species in genus in the database), and to family for 70 individuals (~4% of sample: average value for species in family from database). When the monitored individual was not identified, the average density of all individuals in the plot was used (72 individuals, ~4% of sample).

Monitored individuals were categorized into three levels of wood density (using an adjustment to the definition proposed by Borchert and Pockman (2005): High-density $\geq 0.75\text{g/cm}^3$, Intermediate-density between 0.5 and 0.75g/cm^3 , low-density $\leq 0.5 \text{ g/cm}^3$. However, based on the frequency histogram (see Figure S2) of wood densities from trees monitored with dendrometers at Ducke, the best fit for separating wood density classes in the study sample would be: $\geq 0.70\text{g/cm}^3$ for high density trees, between 0.5 and 0.70g/cm^3 for intermediate density, and $\leq 0.5\text{g/cm}^3$ for low density wood (see Fig. S2).

Data analysis

Increase in trees and palm circumference was summarized as the average increment per individuals of each plot. Analyses for all species pooled together and for wood density categories were conducted. For species with more than 10 individuals (*Brosimum rubescens*, *Caryocar glabrum*, *Ecclinusa guianensis*, *Eperua glabriflora* and *Iryanthera juruensis*), analyses of the increase in circumference were performed at the individual level.

Differences in average circumference increases between monitoring periods for trees and palms, as well as the difference in average increase in circumference for trees by wood density class, were tested with an ANOVA for repeated measures. Simple linear regressions were used to test the relationship between the average increment in circumference for trees and palm and the hydro-topographic gradient (represented by the HAND values for each plot) for each monitoring period.

Results

Photosynthetically Active Radiation and Precipitation

The average monthly photosynthetically active radiation (PAR) and the accumulated monthly rainfall in the Ducke Reserve (Table 1) were negatively correlated ($p = 0.03$ and $r = 0.30$) over the study period (see Figure S3). The annual rainfall was 3386 mm in 2013. No month had less than 100 mm rainfall, and, by the definitions of Sombroek *et al.* (2001), no dry season occurred. However, monthly rainfall in June, August, September and October was less than ~ 30% of the values recorded in previous months, being barely above 100 mm. Additionally, the number of days without rain increased in the period from August to October (16-18 days, compared to 3-9 days in other months).

Average increase in tree circumference

A total of 1879 individual trees and palms were monitored, of which 1795 trees could be identified and represented 452 species from 189 genera in 57 families (see Table S1), 84 being palms from 3 genera and 3 species.

The mean increase in circumference (MIC) for all plots for all trees combined (Table 1), was two-times higher in the period from October to November and three-times higher in the period from December to January, compared with other four periods ($F = 46.08$, $p < 0.01$). These increases in MIC occurred during the transition from wet to dry period (Fig. 2).

Although the average growth in the plots was different only in the transition periods between drier and wetter months, MIC values showed significant differences between the topographic environments (as represented by HAND values) within the wet and dry seasons. At the end of the rainy season (April-May), trees on plateaus showed higher MIC values than those on slopes and in bottomlands ($b_{std} = 0.29$, $r^2 = 0.50$, $p = 0.03$, Fig.3b.). The converse was observed at the beginning of the dry season (June-July), with bottomland trees showing higher MIC values than those on slopes or plateaus ($b_{std} = -0.22$, $r^2 = 0.33$, $p = 0.10$, Fig.3c). In

other periods MIC values did not differ significantly (see Table S2) between the topographic categories (Figs. 3a, c, d, e, f).

Mean circumference increments for different wood density classes

Of the 1795 trees in this study, 948 (~53%) had high wood density ($\geq 0.7\text{g/cm}^3$), 724 (~40%) intermediate wood density (0.5 to 0.7g/cm^3), and 123 (~7%) low wood density ($\leq 0.5\text{g/cm}^3$). The same pattern of enhanced circumference increase in the periods October-November and December-January was found for all trees with high ($F = 10.93$, $p = 0.01$, Fig.2c) and intermediate ($F = 10.93$, $p = 0.01$, Fig.2d) wood density. Trees with low density wood showed highly variable MIC responses between plots and there was no significant differences between the monitoring periods ($F = 1.41$, $p = 0.37$, Fig. 2e), although there was a tendency for greater increment between December-January.

For most periods, there was no difference in MIC at the 5% level of significance between the topographic environments for any of the wood density classes. In the transition periods however, trees of intermediate and high wood density exhibited similar growth increments in relation to topographic environments, which were also the same detected when all trees were pooled together: in April to May, the transition from the rainy to dry seasons (Figs. 3 h,n), individuals of intermediate ($b_{std} = 0.09$, $p = 0.07$, $r^2 = 0.38$) and high wood density ($b_{std} = 0.75$, $p = 0.02$, $r^2 = 0.52$) growing on plateaus displayed greater MIC values than those on slopes and in bottomlands. In the next sample period (June-July), the early dry season, this relationship reversed (Figs. 3i,o), and bottomland trees with intermediate ($b_{std} = -0.06$, $p = 0.004$, $r^2 = 0.84$) and high wood density ($b_{std} = -0.35$, $p = 0.25$, $r^2 = 0.18$) had greater MIC values than those on slopes or plateaus. For low wood-density trees, there was no significant relationship between MIC values and the distance to ground water (see Table S3).

Mean increase in circumference in palms

Across the nine study plots, 84 dendrometers were installed to monitor palms (*Attalea maripa*, n = 2; *Euterpe precatoria*, n = 3; *Oenocarpus bataua*, n = 68; *Oenocarpus bacaba*, n = 11). During the monitoring periods the average annual increase in palm circumference was low (0.16 mm) and no significant differences were recorded between monitoring periods. There was also no relationship between the size increase of palms and the distance to the water table in any monitoring period (see Table S2).

Intra-specific variation in mean increment in circumference

Though nearly all species selected for intra-specific analyses occur in all plots, no significant within-species differences in circumference growth associated to topography were found over the period (see Table S2). Only *Ecclinusa guianensis* species ($b_{std} = 0.58$, $p < 0.1$, $r^2 = 0.40$), a species with one of the largest numbers of sampled individuals (n = 22), showed an association between individual growth and topography: during the rainy season (Dec-Jan) trees of this species on slopes and plateaus showed a greater increase in circumference than those in bottomlands ($b_{std} = 0.63$, $p < 0.01$ to $r^2 = 0.40$, Fig. 4).

Discussion

In this study we found higher mean increase in circumference (MIC) values for trees during periods of transition from dry to wet season, and also recorded that interactions between rainfall, soil texture, vertical distance from the water table and intrinsic characteristics of trees (wood density) can modulate the seasonal growth responses.

Palms, despite not having secondary growth (Tomlinson & Hugget 2012; Renninger *et al.* 2013, Renninger & Phillips 2013), have circumferential deposition of fibers and so can be a good indicator group for estimates of the amount of water retained in the stipe (stem). However, we observed no seasonal patterns of increase in stipe circumference between study periods, nor any changes between topographic environments. This is possibly due to the high within-sample variation, likely caused by waxing and waning of individual stipe circumferences in, respectively, wet and dry periods.

Rainfall seasonality

The results of this study indicate that tree growth may be more sensitive to the amount of rainfall in the transition periods between dry season and rainy season than to the total rainfall volume throughout the rainy season. Unlike patterns predicted for insolation-associated growth (Huete *et al.* 2006; Saleska *et al.* 2007), current results suggest highest rates of increase in circumference are not associated with the dry season (when insolation is highest). They also suggest that patterns of intra-annual tree growth are not simply driven by accumulation of water in the soil. In Iquitos (Peru), a negative relationship was found between increasing rainfall and tree diameter increase (C. Pizango & J. del Aquila Pasquel, unpublished data), while Ishibashi *et al.* (1996) suggested that high precipitation reduces the

amount of Rubisco enzyme: this implies the reduction of photosynthesis and thereby a lessening of carbon assimilation.

In consequence, we believe that increases in circumference recorded in the current study may be associated with two mechanisms: (i) investment in radial growth is stimulated by the onset of the rains and the use of non-structural carbohydrates stored during the dry period. Some studies (e.g., Kitajima *et al.* 1997; Domingues *et al.* 2014) indicate that tropical forest trees have little variation in dry season photosynthetic capacity, which implies that new tissues construction (sink activity) is more limited by the scarcity of water than actually capturing carbon (photosynthesis), which can generate large carbohydrate stores (Würth *et al.* 2005). During the rainy season this stock is consumed and growth is reduced, as recorded here in the final months of the rainy season. Alternatively, (ii) investment in circumferential growth is greater in the transition from dry to wet seasons, when most plants have new leaves, which are photosynthetically more productive (Reich & Borchert 1988; Kitajima *et al.* 1997), and there is still high irradiation despite increasing cloudiness. As the rainy season progresses, the frequency of cloudy days increases and, correspondingly, growth rates decrease. This same pattern of growth has been reported in Bolivia for three tree species and suggested explanations for these results converge with those just described, including the reduction of photosynthetic capacity of older leaves and mobilization of stored carbohydrates for growth (Brienen & Zuidema 2005). These mechanisms are not necessarily mutually exclusive.

Rainfall and soil water availability have been reported as key drivers of growth at a number of study sites (Nepstad *et al.* 2002; Dünisch *et al.* 2003; Brienen & Zuidema 2005; Wagner *et al.* 2012; Grogan & Schulze 2012). However, *Cedrela odorata* studied in Bolivia by Brienen & Zuidema (2005), unpublished data of M. Camargo in the area north of Manaus, and the present study, all show a reduction in growth between the middle and end of the rainy

season, suggesting that large amounts of rainfall do not increase tree growth, and that a substantial volume of rain for an extended period may actually inhibit tree diameter increment.

Soil and hydrology

Variations in tree circumference increments at Reserva Ducke were related not only to seasonality, but also to hydro-topographic gradient, suggesting a variation of tree carbon assimilation behavior linked to interactions between soil texture, rainfall and distance to groundwater.

In the early dry season (June-July), trees in the bottomland areas showed greater increases in circumference than those growing on plateaus, indicating that a combination of reduced rainfall and reduced groundwater level favored plant growth in this environment. For bottomland trees a growth rate decrease was recorded only at the end of the rainy season (April-May), so that only extreme waterlogging (probably due to groundwater upwelling), may lead to this reduction. This may indicate that either anaerobic conditions do not develop throughout the soil profile for most of the rainy season, or that trees may tolerate anaerobic conditions up to some level, to then reduce growth. The rapid switch from low to high growth in the bottomlands between the end of the rainy season and start of the dry season suggests high sensitivity of trees in these areas to changes in rainfall patterns. This may also allow for increased growth if the dry season is longer. However, when considering a similar result along a topographic gradient in Ghana, Baker *et al.* (2003) attributed low growth rates in waterlogged soils to a seasonally low nitrogen availability and not to the anaerobic conditions. Whatever the direct causal factor, drying of waterlogged areas increases growth and therefore these areas can benefit from droughts.

Trees on plateaus, far from the water table, showed smaller circumference increases in the dry season (June-July). This growth reduction early in the dry period was surprising, because the clay soils of the plateaus have good water holding capacity and are slow to dry out: in fact, Tomasella *et al.* (2008) show that only between August and September are these soils effectively dry. These results therefore suggest that either trees on the clay soil plateaus have especially high sensitivity to rainfall reduction, or other factors that change in the transition to the dry season are responsible for determining growth rate.

Trees on slopes, located at the transition between plateaus and lowlands, had MIC values intermediate between those of trees from the plateaus and lowlands at the end of the rainy season (April-May) and early dry season (June-July). Soils on slopes are under the influence of water table fluctuation via capillary action between groundwater and unsaturated soil. Above the limit of water rise by capillarity, water available to plants comes predominantly from direct precipitation. The sum of these processes by which water can enter the soil means that slopes do not dry out in the dry season (Daws *et al.* 2002) and are not inundated in the rainy season, which may well explain why we found trees there to have the most stable growth levels throughout the year.

These results, combined with the observation of a higher average secondary growth in the dry to rainy season transition, and growth decrease at the end of the rainy season, show that a subtle balance between the availability of water and light is needed to promote growth. In Amazonian upland forests, this favorable balance migrates across the landscape as the seasons progress, according to the water conditions given by topographic position and soil type.

Wood density

The results of the current study show how biophysical structures of wood can modulate the seasonal growth responses of trees. Trees with low density wood are associated, in general, with rapid growth, high carbon assimilation and high water storage capacity in xylem cells (Santiago *et al.* 2004; Pockman & Borchert, 2005). Their xylem vessels occur at low density and are of large diameter, which confers higher risk of embolism (Baas *et al.* 2004). In the current study, this group showed great variability in the growth responses to changes in rainfall and between topographical environments. Such variability is likely due to the large diameter of the conducting vessels: though high hydraulic conductivity makes such vessels highly efficient when water is readily available, they are more susceptible to embolism in dry periods, hence the low growth of some individuals during this period.

In terms of comparative growth rates for the three hydro-topographic environments, trees of intermediate wood-density showed very similar behavior to those with high-density wood, in both dry and rainy seasons. Trees of both intermediate and high wood-density had more conservative behavior than trees of low wood-density and their increases in circumference were less susceptible to short-term fluctuations of soil water. Trees of high wood-density generally have slow growth rates. This is associated with low photosynthetic rates (Santiago *et al.* 2004; Fan *et al.* 2012), low capacity for water storage in the more elastic cells of the xylem (Santiago *et al.* 2004) and small but plentiful conducting vessels (Baas *et al.* 2004; Santiago *et al.* 2004; Poorter *et al.* 2010), giving low hydraulic conductivity at the expense of an increased resistance to cavitation and embolism. At the end of the rainy season (April-May) high wood-density trees on plateaus had a greater increase in circumference than those in lowland areas. During this period, the rainfall is high at the Ducke Reserve and groundwater recharge is reaching its peak (Tomasella *et al.* 2008), the surface layers of the

soil in the low-lying areas are under the direct influence of the water table and waterlogged soils are present. These results suggest that, given their low hydraulic conductivity, the best growing conditions for this functional group occur the end of the rainy season on plateaus – when the availability of soil water is high. At the same time, trees in lowlands had a sudden reduction in circumference increase when compared to the previous period (February-March), possibly due to anoxic conditions in waterlogged soil and so unable to invest in growth.

The above-described relationships integrate the distance of the water table, soil texture, and tree wood-density as modulators of growth factors. Trees with low wood-density had great variability of individual responses and therefore no seasonal pattern of increase in circumference. Trees with high and intermediate wood densities showed similar average patterns, with the greatest circumferential increases occurring on plateaus at the end of the rainy season, while bottomlands trees had greater increase in circumference in the dry season.

Intra-specific plasticity in relation to hydro-topographic gradient

The four species examined individually showed little phenotypic plasticity in their growth patterns in relation to hydro-topographical environments. However, individuals of *Ecclinusa guianensis* (intermediate wood-density 0.62g/cm³) growing in plateaus and bottomlands showed quite different patterns of rainy season (December-January) circumference increments. These individuals showed great growth rate variability, with highest values on the plateaus, while those in lowlands were either similar or much lower than those from the plateaus - indicating a high intraspecific variation between the topographical environments (Fig. 4). Individuals of this species growing in different topographical environments vary both in height and in leaf characteristics (Ribeiro *et al.* 2002), and these could be subsequently investigated for better understanding growth plasticity.

It is also worth noting that the only species for which we found intra-specific relationships between seasonal growth and topographic gradient also had the largest number of sampled individuals. The absence of patterns for other species, in this as in other studies, may be simply due to the low number of individuals sampled and not the actual absence of the effect itself.

Conclusions

Predicted scenarios of global climate change include changes in rainfall patterns and water availability in the soil that could affect plant growth, and therefore highlight the importance of a firm understanding of carbon cycle functioning. Contrary to previous studies, which indicated high irradiation or high rainfall as the best conditions for tree growth, we found the highest growth in the transition from dry to wet season, which is not the period of greater irradiation neither of greater water availability to plants. This suggests that the entrance of water in the system at the end of the dry season triggers growth, but accumulation of rainfall towards the end of the wet season can inhibit growth. Moreover, local environmental features, such as soil texture and water-table level, modulate this growth. Growth performance change along the landscape throughout the year, tracking the best conditions of soil water availability – not too dry, not too wet. Growth patterns associated to wood density suggest that a trade-off between investment in wood growth and hydraulic safety may be driving physiological responses along topographically-driven hydrological gradients in central Amazonian terra-firme forests.

The implication of these results is that a large amount of the Amazonian forest, in the valleys around terra-firme streams, may benefit from some level of drought. If dry-seasons become longer, the balance of growth may shift in favor of these areas, which under the

present conditions have lower cumulative growth and hence lower biomass than forests on slopes and plateaus (Castilho et al. 2006). This would mean a lower net effect of droughts over the landscape than expected from drought experiments, which were conducted in upland areas far from places with a superficial water-table.

Acknowledgements

We thank the Brazilian LTER program (Programa de Pesquisa Ecológica de Longa Duração - PELD/CNPq) for funding, Instituto Nacional de Pesquisas da Amazônia-INPA for infrastructure and logistic support, especially the transport section and DSER; the Brazilian Research Program in Biodiversity (PPBio) and PELD for all in-field infrastructure; and the Laboratório de Clima e Recursos Hídricos da Amazônia for climatic data. We thank J.Tavares for editing the Reserva Ducke map, and H. Santana for assistance in the field.

Data Accessibility

- Global Wood Density Database: <http://datadryad.org/resource/doi:10.5061/dryad.234>
- PPBio protocols: <http://ppbio.inpa.gov.br/repository/database>
- Database of Monitoring dendrometers in Reserva Ducke:
<http://peld.inpa.gov.br/knb/metacat?action=read&qformat=peld&sessionid=0&docid=naman.522>.

References

- Baas, P., Ewers, F. W., Davis, S. D., & Wheeler, E. A. (2004). Evolution of xylem physiology. In *The Evolution of Plant Physiology* (eds by A.R. Hemsley & I. Poole, Linnean Society Symposium Series number 21), pp. 273–295, Elsevier Academic Press, London.
- Baker, T. R., Burslem, D. F. R. P., & Swaine, M. D. (2003). Associations between tree growth, soil fertility and water availability at local and regional scales in Ghanaian tropical rain forest. *Journal of Tropical Ecology*, **19**, 109–125.
- Bellingham, P. J., & Tanner, E. V. J. (2000) The Influence of Topography on Tree Growth , Mortality , and Recruitment in a Tropical Montane Forest. *Biotropica*, **32**, 378–384.
- Bonal, D., Bosc, A., Ponton, S., Goret, J.-Y., Burban, B., Gross, P., Bonnefond, Jean-Marc, Elbers, J., Longdoz, B., Epron, D., Guehl, Jean-Marc, Granier, A. (2008). Impact of severe dry season on net ecosystem exchange in the Neotropical rainforest of French Guiana. *Global Change Biology*, **14**, 1917–1933.
- Borchert, R., & Pockman, W. T. (2005). Water storage capacitance and xylem tension in isolated branches of temperate and tropical trees. *Tree Physiology*, **25**, 457–466.
- Brienen, R. J. W., & Zuidema, P. a. (2005) Relating tree growth to rainfall in Bolivian rain forests: a test for six species using tree ring analysis. *Oecologia*, **146**(1), 1–12.
- Castilho, C. V., Magnusson, W. E., de Araújo, R. N. O., Luizão, F. J. (2010). Short-term temporal changes in tree live biomass in a central Amazonian forest, Brazil. *Biotropica*, **42**, 95–103.
- Castilho, C., Magnusson, W., Araújo, N., Luizão, R., Luizão, F., Lima, A., Higuchi, N. (2006) Variation in aboveground tree live biomass in a central Amazonian Forest : Effects of soil and topography. *Forest Ecology and Management*, **234**, 85–96.
- Chauvel A, Lucas Y, Boulet R. (1987) On the genesis of the soil mantle of the region of Manaus, Central Amazonia, Brazil. *Experimentia*, **43**, 234–241.
- Chave, J., Coomes D.A., Jansen, S., Lewis, S.L., Swenson, N.G., Zanne, A.E. (2009) Towards a worldwide wood economics spectrum. *Ecology Letters*, **12**, 351–366.
- Clark, D. A. (2004) Sources or sinks ? The responses of tropical forests to current and future climate and atmospheric composition Sources or sinks ? The responses of tropical forests to current and future climate and atmospheric composition. *Philosophical Transactions of the royal society*, **359**, 477–491.
- Clark, D. B., Clark, D. a., & Oberbauer, S. F. (2010) Annual wood production in a tropical rain forest in NE Costa Rica linked to climatic variation but not to increasing CO₂. *Global Change Biology*, **16**, 747–759.

Costa F.R.C., Magnusson, W.E. (2010) The Need for Large-Scale, Integrated Studies of Biodiversity - the Experience of the Program for Biodiversity Research in Brazilian Amazonia. *Natureza & Conservação*, **08**, 3-12.

Cox, P.M., Betts R.A., Collins M., Harris P.P. (2004) Amazonian forest dieback under climate-carbon cycle projections for the 21st century. *Theoretical and Applied Climatology*, **78**, 137–156.

Daws, M. I., Mullins, C. E., Burslem, D. F., Paton, S. R., & Dalling, J. W. (2002). Topographic position affects the water regime in a semideciduous tropical forest in Panama. *Plant and Soil*, **238**(1), 79-89.

Domingues, T.F., Martinelli,L.A. & Ehleringer,J.R. (2014) Seasonal patterns of leaf-level photosynthetic gas exchange in an eastern Amazonian rain forest. *Plant Ecology and Diversity*, **7**, 189-203.

Dünisch, O.; Montóia, V.R.M., Bauch, J. (2003) Dendroecological investigations on *Swietenia macrophylla* King and *Cedrela odorata* L. (Meliaceae) in the central Amazon. *Trees-Structure and Function*, **17**, 244-250.

Fan, Y., & Miguez-Macho, G. (2010) Potential groundwater contribution to Amazon evapotranspiration. *Hydrology and Earth System Sciences*, **14**(10), 2039–2056.

Fan, Z.X., Zhang, S.B., Hao, G.Y., Ferry Slik, J. W. & Cao, K.F. (2012) Hydraulic conductivity traits predict growth rates and adult stature of 40 Asian tropical tree species better than wood density. *Journal of Ecology*, **100**, 732–741.

Ferry, B., Morneau,F., Bontemps,J., Blanc, L. & Freycon,V. (2010) Higher treefall rates on slopes and waterlogged soils result in lower stand biomass and productivity in a tropical rain forest. *Journal of Ecology*, **98**,106-116.

Freire, E. & Azevedo, R. (2010) Safeguard documentary collection of forest reserve Ducke – Manaus-AM: records of an experience *Ciência da Informação*, **39** (2), 101-114.

Gentry, A. H. (1990) Floristic similarities and differences between Southern Central America and upper and Central Amazonia. In Gentry, A. H., editors. *Four Neotropical rain forests*. Yale University Press, New Haven, CT, 141-157.

Grogan, J., & Schulze, M. (2012). The impact of annual and seasonal rainfall patterns on growth and phenology of emergent tree species in Southeastern Amazonia , Brazil. *Biotropica*, **44**, 331–340.

Hodnett MG, Tomasella J.(2002) Marked differences between van Genuchten soil water-retention parameters for temperate and tropical soils: a new water-retention pedo-transfer functions developed for tropical soils. *Geoderma*, **108**,155-180.

- Hodnett, M. G., Vendrame, I., Marques Filho, A. D. O., Oyama, M. D., & Tomasella, J. (1997). Soil water storage and groundwater behaviour in a catenary sequence beneath forest in Central Amazonia: I. Comparisons between plateau, slope and valley floor. *Hidrology & Earth System Sciences*, **1**, 265–277.
- Huang, Jian-Guo, Bergeron, Yves, Denneler, Bernhard, Berninger, Frank and Tardif, Jacques (2007) Response of Forest Trees to Increased Atmospheric CO₂, *Critical Reviews in Plant Sciences*, **26**, 265 – 283.
- Huete, A. R., Didan, K., Shimabukuro, Y. E., Ratana, P., Saleska, S. R., Hutya, L. R., Yang, W, Remakrsina, R. Namanu, Myneni, R. (2006). Amazon rainforests green-up with sunlight in dry season. *Geophysical Research Letters*, **33**, 1-4 L06405.
- hibashi, M., Usuda, H., & Terashima, I. (1996) The Loss of Ribulose-1, 5-Bisphosphate Carboxylase / Oxygenase Caused by 24-Hour Rain Treatment Fully Explains the Decrease in the Photosynthetic Rate in the Photosynthetic Rate in Bean Leaves. *Plant Physiologist*, **111**, 635–640.
- Kitajima, K., Mulkey, S. S., & Wright, J. S. (1997) Decline of photosynthetic capacity with leaf age in relation to leaf longevities for five canopy tree species. *American Journal of Botany*, **84**(5), 702–708.
- Lewis, S. L., Lopez-Gonzalez, G., Sonké, B., Affum-Baffoe, K., Baker, T. R., Ojo, L. O., Phillips, O., Reitsma, J., White, L., Comiskey, J., Djuikouo, M., Ewango, C., Feldspausch, T., Hamilton, A., Gloor, M., Hart, T., Hladik, A., Lloyd, J., Lovett, J., Makana, J., Malhi, Y., Mbago, F., Ndangalasi, H., Peacock, J., Peh, K., Sheil, D., Sunderland, T., Swaine, M., Taplin, J., Taylor, D., Thomas, S., Votere, R., Wöll, H. (2009) Increasing carbon storage in intact African tropical forests. *Nature*, **457**, 1003–1007.
- Lloyd, J., & Farquhar, G. D. (2008). Effects of rising temperatures and [CO₂] on the physiology of tropical forest trees. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, **363**, 1811–1817.
- Malhi, Y., & Phillips, O. L. (2004) Tropical forests and global atmospheric change : a synthesis Tropical forests and global atmospheric change : a synthesis. *Philosophical Transactions of the Royal Society*, **359**, 549–555.
- Malhi, Y., Baker, T. R., Phillips, O. L., Almeida, S., Alvarez, E., Arroyo, L., Chave, J., Czimczik, C., Di Fiore, A., Higuchi, N., Killeen, T., Laurance, S., Laurance, W., Lewis, S., Montoya, L., Monteagudo, A., Neill, D., Nuñez Vargas, P., Patiño, S., Pitman, N., Quesada, C.A., Salomãos, R., Silva, J.N.M., Lezama, A., Martínez, R., Terborgh, J., Vinceti, B., Lloyd, J. (2004) The above-ground coarse wood productivity of 104 Neotropical forest plots. *Global Change Biology*, **10**, 563–591.
- Mertens, J. (2004) The characterization of selected physical and chemical soil properties of the surface soil layer in the “Reserva Ducke”, Manaus, Brazil, with emphasis on their spatial distribution. Bachelor Thesis, Humboldt University, Berlin.

- Metcalfe, D. B., Meir, P., Aragão, L., Lobo-do-Vale, R., Galbraith, D., Fisher, R. A., Chaves, M. M., Maroco, J. P., Costa, A. C. L., Almeida, S. S., Braga, A. P., Gonçalves, P. H. L., Athaydes, J., Costa, M., Portela, T. T. B., Oliveira, A. A. R., Malhi, Y., Williams, M. (2010) Shifts in plant respiration and carbon use efficiency at a large-scale drought experiment in the eastern Amazon. *New Phytologist*, **187**, 608–621.
- Nepstad, D. C., Moutinho, P., Dias-Filho, M., Davidson, E., Cardinot, G., Markewitz, D., Figueiredo, R., Vianna, N., Chambers, J., Ray, D., Guerreiros, J., Belk, E., Kalif, K., Schwalbe, K. (2002) The effects of partial throughfall exclusion on canopy processes, aboveground production, and biogeochemistry of an Amazon forest. *Journal of Geophysical Research*, **107**(D20), 8085.
- Pan, Y., Birdsey, R., Fang, J., Houghton, R., Kauppi, P. E., Kurz, W., Phillips, O., Shvidenko, A., Lewis, S., Canadell, J., Ciais, P., Jackson, R., Pacala, S., McGuire, A., Piao, S., Rautiainen, A., Sitch, S., Hayes, D. (2011) A large and persistent carbon sink in the world's forests. *Science (New York, N.Y.)*, **333**, 988–93.
- Phillips O.L. & Gentry A.H. (1994) Increasing turnover through time in tropical forests. *Science*, **263**, 954–958.
- Phillips, O. L., Malhi, Y., Higuchi, N., Laurance, W., Nuñez, P., Vásquez, R., Laurance, S., Ferreira, L., Stern, M., Brown, S., Grace, J. (1998) Changes in the carbon balance of Tropical Forests: Evidence from long-term plots. *Science*, **282**, 439–442.
- Phillips, O., Aragão, L., Lewis, S., Fisher, J., Lloyd, J., López-González, G., Malhi, Y., Monteagudo, A., Peacock, J., Quesada, C., Heijden, G., Almeida, S., Amaral, I., Arroyo, L., Aymard, G., Baker, T., Bánki, O., Blanc, L., Bonal, D., Brando, B., Chave, J., Oliveira, A., Cardozo, N., Czimczik, C., Feldpausch, T., Freitas, M. A., Gloor, E., Higuchi, N., Jiménez, E., Lloyd, G., Meir, P., Mendoza, C., Morel, A., Neill, D., Nepstad, D., Patiño, S., Peñuela, M. C., Prieto, A., Ramírez, f., Schwarz, M., Silva, J., Silveira, M., Thomas, A., ter Steege, H., Stropp, J., Vásquez, R., Zelazowski, P., Dávila, E., Andelman, S., Andrade, A., Chao, K., Erwin, T., Di Fiore, A., Eurídice Honorio C., Keeling, H., Killeen, T., Laurance, W., Cruz, A., Pitman, N., Vargas, P., Ramírez-Ângulo, H., Rudas, A., Salamão, R., Silva, N., Terborgh, J., Torres-Lezama, A. (2009). Drought sensitivity of the Amazon Rainforest. *Science*, **323**, 1344–1347.
- Poorter, L., McDonald, I., Alarcón, A., Fichtler, E., Licona, J., Pena-Claros, M., Sterck, F., Villegas, Z., Sass-klaassen, U. (2010). The importance of wood traits and hydraulic conductance for the performance and life history strategies of 42 rainforest tree species. *New Phytologist*, **185**, 481–492.
- Radam-Brasil (1978) Programa de Integração Nacional. Levantamento de Recursos Naturais. V. 18 (Manaus) - RADAM (projeto) DNPM, Ministério das Minas e Energia. Brasil. 626pp.
- Reich, P. B., & Borchert, R. (1988) Changes with leaf age in stomatal function and water status of several tropical tree species. *Biotropica*, **20**, 60–69.

- Renninger, H. J., & Phillips, N. (2012) “Secondary stem lengthening” in the palm *Iriartea deltoidea* (Arecaceae) provides an efficient and novel method for height growth in a tree form. *American Journal of Botany*, **99**, 607–613.
- Renninger, H.J., McCulloh, K., Phillips, N. (2013) A comparison of the hydraulic efficiency of a palm species (*Iriartea deltoidea*) with other wood types. *Tree Physiology*, **33**, 152–160.
- Rennó, C. D., Nobre, A. D., Cuartas, A. L., Soares, J. V., Hodnett, M. G., Tomasella, J., & Waterloo, M. J. (2008) HAND, a new terrain descriptor using SRTM-DEM: Mapping terra-firme rainforest environments in Amazonia. *Remote Sensing of Environment*, **112**, 3469-3481.
- Ribeiro, M. N. G., Villa Nova, N. A. (1979) Estudos climatológicos da Reserva Florestal Ducke, Manaus, AM. III Evapotranspiração. *Acta Amazônica*, **9**, 305-309.
- Ribeiro, J.E., Hopkins, M.J.G., Vicentini, A., Sothers, C., Costa, M.A., Brito, J.M., Souza, M., Martins, H.P., Lohmann, L.G., Assunção, P.A., Pereira, E.C., Silva, C.F., Mesquita, M., Procópio, L. (2002) Flora da Reserva Ducke- Guia de Identificação das plantas vasculares de uma floresta de terra-firme na Amazônia Central. Editora INPA. ISBN: 85-211-0011-6, 816p.
- Rice, A., Hammond, E., Saleska, S., Hutyra, L., Palace, M., Keller, M., Camargo, P., Portilho, K., Marques, D., Wofsy, S. (2004) Carbon balance and vegetation dynamics in an old-growth Amazonian forest. *Ecological Applications*, **14**, 55–71.
- Rodriguez-Gonzalez, P.M., Stella, J.C., Campelo, F., Ferreira, M.T., Albuquerque, A. (2010) Subsidy or stress? Tree structure and growth in wetland forests along a hydrological gradient in Southern Europe. *Forest Ecology and Management*, **259**, 2015-2025.
- Saleska, S., Didan, Kamel, Huete, A, Rocha, H. (2007) Amazon Forests Green-Up During 2005 Drought. *Science*, **318**, 612.
- Samanta, A., Ganguly, S., Hashimoto, H., Devadiga, S., Vermote, E., Knyazikhin, Y., Ramakshrina, R.N., Myneni, R. B. (2010). Amazon forests did not green-up during the 2005 drought. *Geophysical Research Letters*, **37**, LO5401.
- Santiago, L. S., Goldstein, G., Meinzer, F. C., Fisher, J. B., Machado, K., Woodruff, D., & Jones, T. (2004) Leaf photosynthetic traits scale with hydraulic conductivity and wood density in Panamanian forest canopy trees. *Oecologia*, **140**(4), 543–50.
- Santiago, L. S., Goldstein, G., Meinzer, F. C., Fisher, J. B., Machado, K., Woodruff, D., Jones, T. (2004) Leaf photosynthetic traits scale with hydraulic conductivity and wood density in Panamanian forest canopy trees. *Oecologia*, **140**, 543–50.
- Satyamurty, P., Castro, A. A. De, Tota, J., & Eliane, L. (2009) Rainfall trends in the Brazilian Amazon Basin in the past eight decades. *Theoretical and Applied Climatology*.

- Schiatti, J., Emilio, T., Rennó, C., Drucker, D., Costa, F., Nogueira, A., Baccaro, F., Figueiredo, F., Castilho, C., Kinupp, V., Guillaumet, J., Garcia, A., Lima, A. & Magnusson, W. (2014) Vertical distance from drainage drives floristic composition changes in an Amazonian rainforest. *Plant Ecology & Diversity*, **7**, 241-253.
- Schöngart, J., Piedade, M. T. F., Wittmann, F., Junk, W. J., & Worbes, M. (2005) Wood growth patterns of *Macaranga acaciifolia* (Benth.) Benth. (Fabaceae) in Amazonian black-water and white-water floodplain forests. *Oecologia*, **145**, 454–61.
- Schöngart, J., Piedade, M.T.F., Ludwigshausen, S., Horna, V., Worbes, M. (2002) Phenology and stem-growth periodicity of tree species in Amazonian floodplain forests. *Journal of Tropical Ecology*, **18**, 581-597.
- Silva, R., dos Santos, J., Tribuzy, E., Chambers, J., Nakamura, S., & Higuchi, N. (2002). Diameter increment and growth patterns for individual tree growing in Central Amazon, Brazil. *Forest Ecology and Management*, **166**, 295–301.
- Sömbroek, W. (2001) Spatial and temporal patterns of Amazon Rainfall- Consequences for the planning of agricultural occupation and the protection of primary forests. *AMBIO: A Journal of the Human Environment*, **30**, 388-396.
- Sperry, J. S., Meinzer, F. C., & McCulloh, K. A. (2008) Safety and efficiency conflicts in hydraulic architecture : scaling from tissues to trees. *Plant, Cell and Environment*, **31**, 632–645.
- Stahl, C.; Burban, B, Wagner, F.; Goret, J.; Bompuy, F.; Bonal, D. (2012) Influences of seasonal variation in soil water availability on gas exchange of tropical canopy trees. *Biotropica*, **45**, 155-164.
- Tomasella, J., Hodnett, M. G., Cuartas, L. A., Nobre, A. D., Waterloo, M. J., & Oliveira, S. M. (2008) The water balance of an Amazonian micro-catchment: the effect of interannual variability of rainfall on hydrological behaviour, *Hydrological processes*, **22**, 2133–2147.
- Tomlinson, P. B., & Quinn, C. J. (2013) Palms do not undergo secondary stem lengthening: a response to Renninger and Phillips (American Journal of Botany 99: 607-613). *American Journal of Botany*, **100**, 461–464.
- Wagner, F., Rossi, V., Stahl, C., Bonal, D., & Hérault, B. (2012) Water availability is the main climate driver of Neotropical tree growth. *PloS one*, **7**, e34074.
- Wagner, F., Rossi, V., Stahl, C., Bonal, D., & Hérault, B. (2013) Asynchronism in leaf and wood production in tropical forests: a study combining satellite and ground-based measurements. *Biogeosciences Discussions*, **10**, 8247–8281.
- Würth, M., Peláez-Riedl, S., Wright, S. J., & Körner, C. (2005) Non-structural carbohydrate pools in a tropical forest. *Oecologia*, **143**, 11–24.

Zanne, A.E., Lopez-Gonzalez, G., Coomes, D.A., Ilic, J., Jansen, S., Lewis, S.L., Miller, R.B., Swenson, N.G., Wiemann, M.C., and Chave, J. (2009) Global wood density database. Dryad. Identifier: <http://hdl.handle.net/10255/dryad.235>.

Tables

Table 1. Values (mm) for average increase in circumference of trees per plot, accumulated precipitation (mm) and average photosynthetically active radiation (PAR, mol/m²) in each monitoring period, between February 2013 and January 2014.

HAND	Feb	Apr	Jun	Aug	Oct	Dec
	Mar	May	Jul	Sep	Nov	Jan
2.15	0.68	0.59	0.59	0.78	1.23	1.03
3.02	0.79	0.18	0.88	0.32	0.94	1.58
13.62	0.48	0.52	0.37	0.38	1.46	1.61
14.56	0.71	0.42	0.42	0.81	0.84	1.68
17.47	0.48	0.26	0.46	0.57	0.86	2.69
19.31	0.62	0.60	0.59	0.10	0.73	0.97
39.48	0.54	0.59	0.33	0.48	1.33	1.96
40.44	0.74	0.68	0.15	0.78	1.14	1.74
45.57	0.87	0.91	0.56	0.74	1.32	1.72
Cumulative rainfall	881.9	829.6	343.7	249.9	508.3	493.8
PAR	2.8	3.1	3.2	3.1	3.1	2.9

Figures

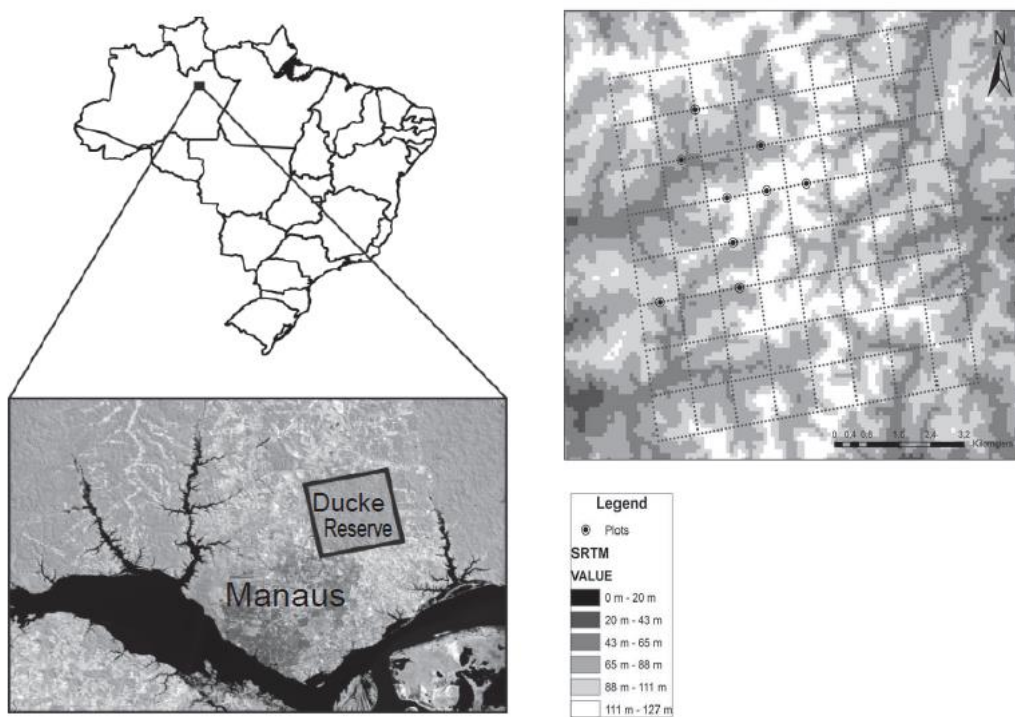


Figure 1. Map of the Ducke Forest Reserve near Manaus, Brazil, showing dendrometer plots.

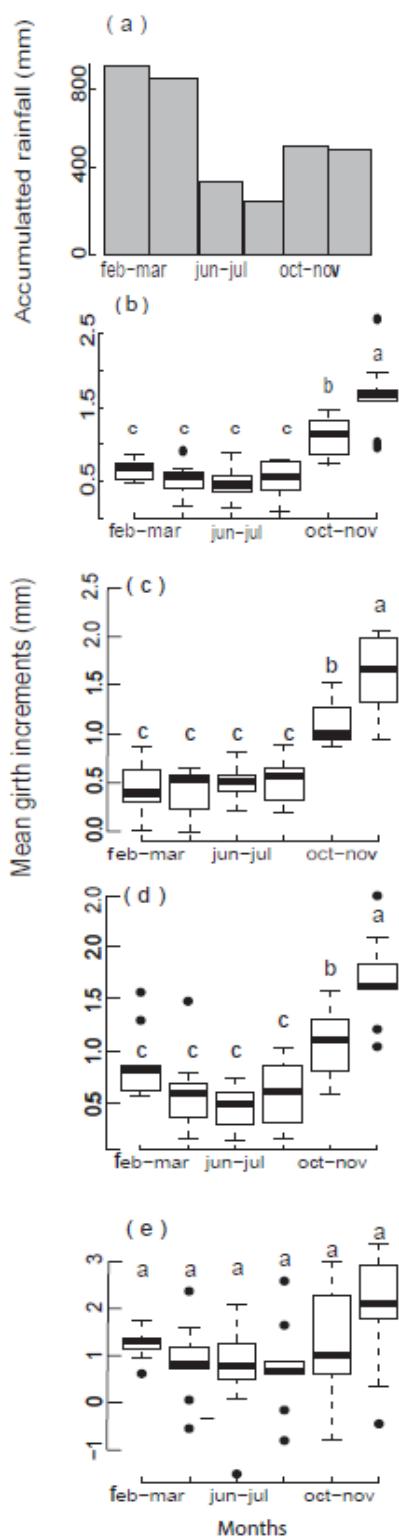


Figure 2. Accumulated 60 day rainfall for the six bimonthly study periods, Feb-Mar, 2013 to Dec-Jan, 2013/2014 (a); mean increments in circumference for each bimonthly period for all trees (b); for trees of high wood density (c); for trees of intermediate wood density (d); and for trees of low wood density (e).

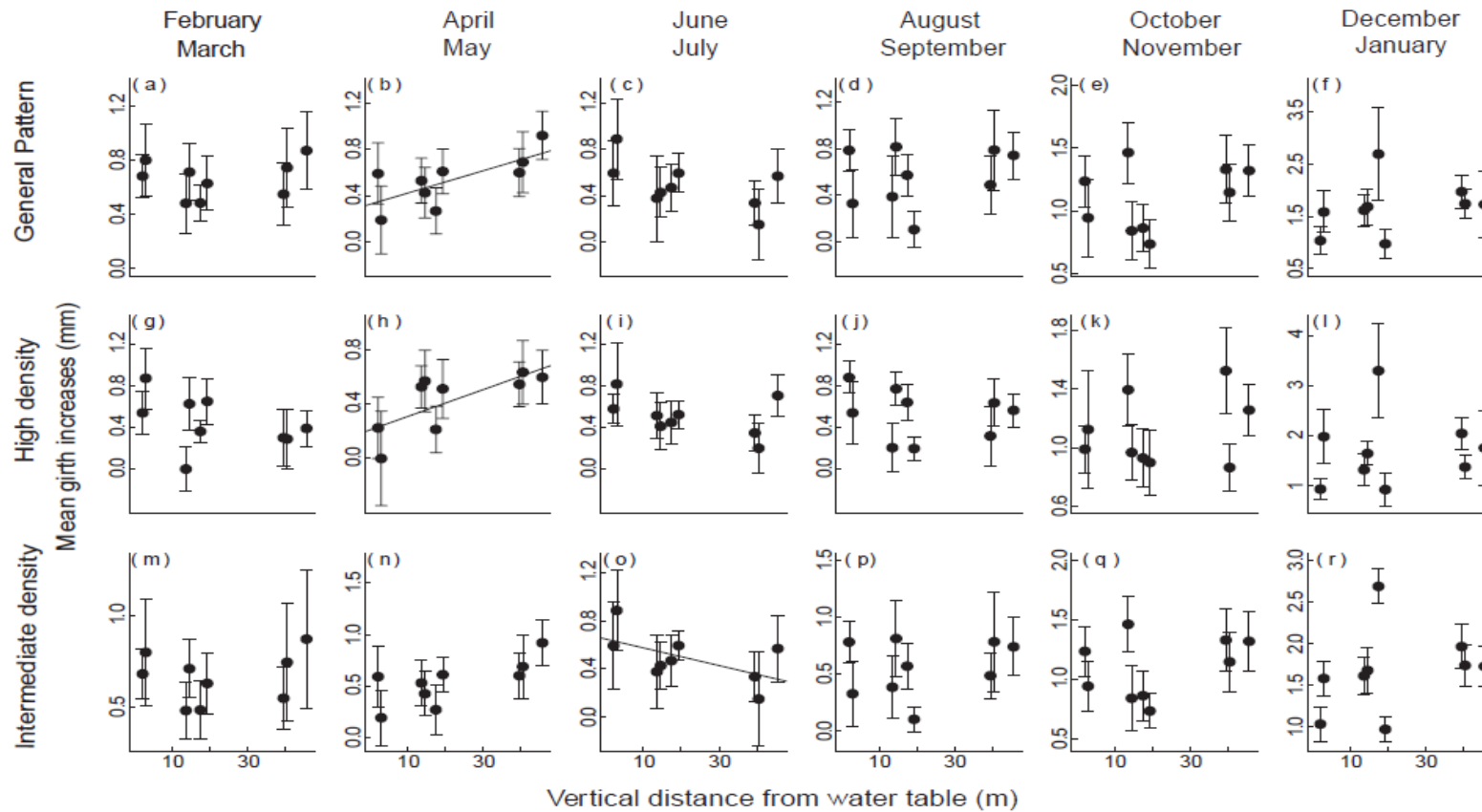


Figure 3. Relationship between Mean Increment in Circumference (MIC (mm)) in each period of monitoring and the terrain vertical distance from water-table (HAND(m)) in each plot, as a proxy to water-table depth. Each line refers to general pattern, high wood density trees pattern and intermediate wood density pattern of growth of trees. In most of year there is no trend in the relationships among the mean increment in circumference and the proxy to depth water-table. However, in the end of wet season (april-may) trees occurring in closest terrain from water-table, which tend to waterlogging, in average growing less than trees occurring in vertically areas more distant from drainage. At the beginning of dry-season (june-july), should be have an inversed pattern, with a trend the greater increment in vertically areas closest from drainage.

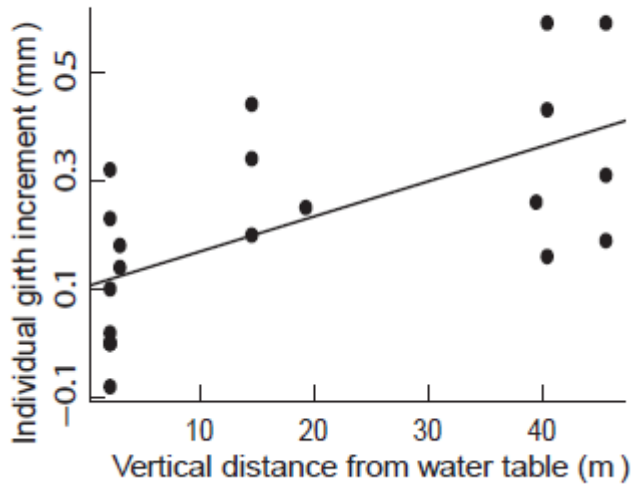


Figure 4. Individual increment in circumference (mm) of tree species *Ecclinusa guianensis* in the december-january period (wet season) and the vertical distance from water-table (m). The trees in the greater distance from water-table had the greater increment than other trees in other areas closest of water-table, as bottomlands.

SUPPORTING INFORMATION

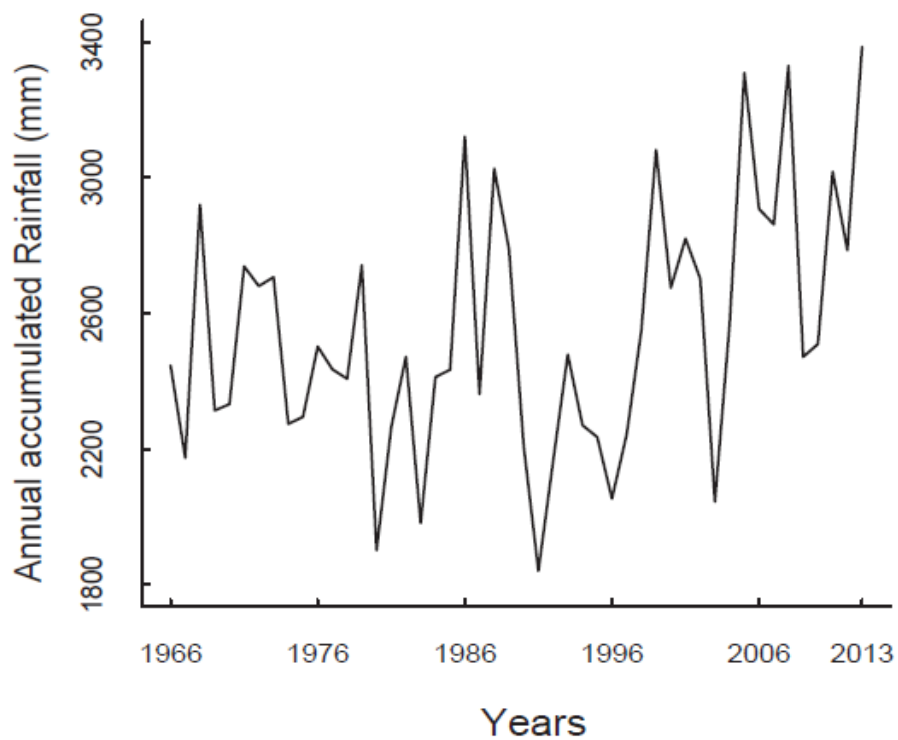


Figure S1. Temporal series (between years 1966-2013) of accumulated annual rainfall at Ducke Reserve, Amazonas (Brazil), which represents the increase of amount rainfall among years.

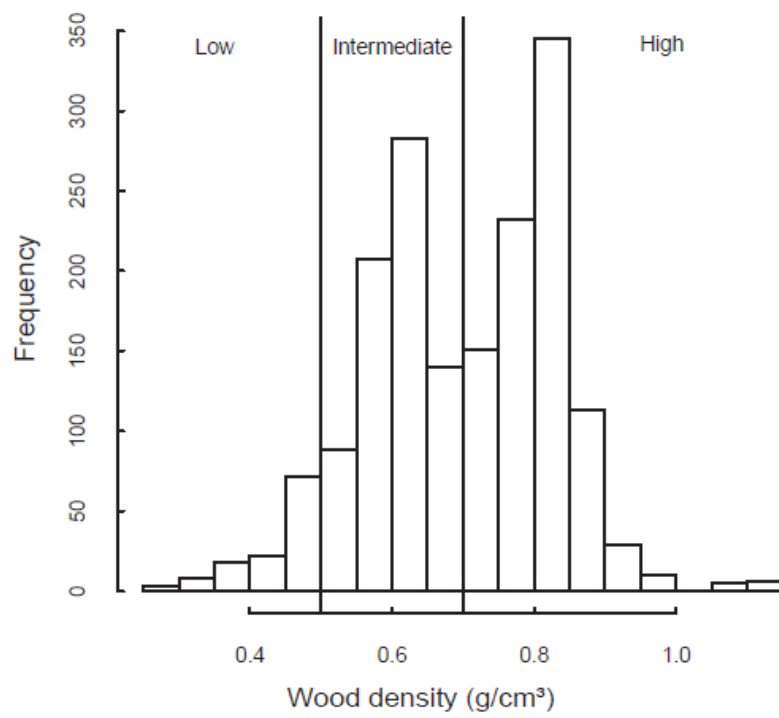


Figure S2. Frequency distribution of wood density (g/cm^3) from monitored trees with dendrometers at Ducke Reserve, Manaus, Amazonas.

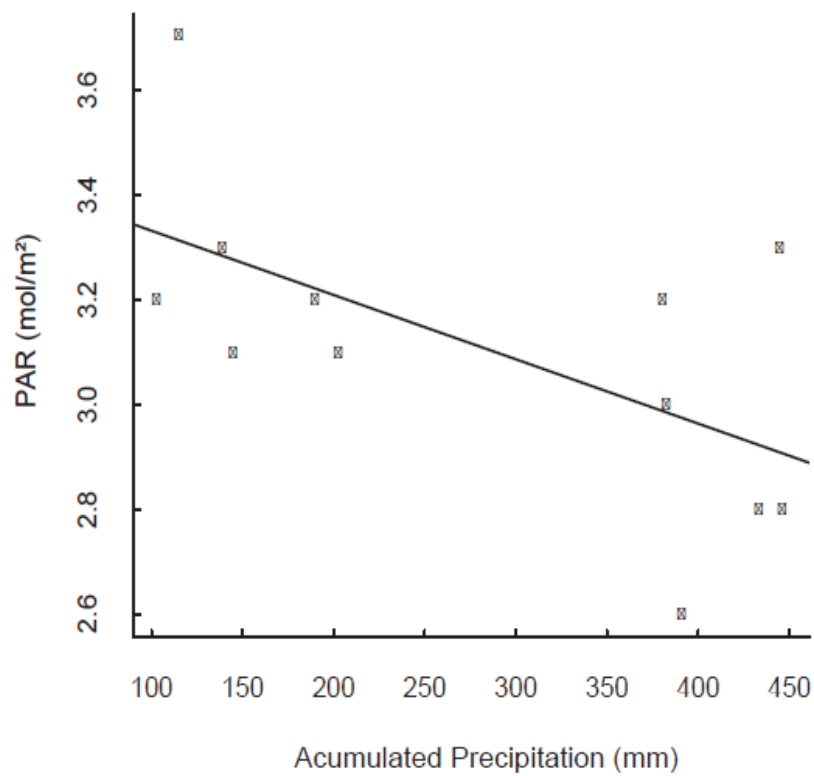


Figure S3. Correlation between accumulated monthly precipitation (mm) and photosynthetically active radiation (PAR, mol/m²) at Ducke Reserve, Manaus, Amazonas, in 2013 ($p=0.03$ e $r=0.3$).

Table S1. Number of individuals in plots with circumference at breast height greater than or equal to 10cm; percentage of number of individuals in plots relative to the total number of individuals in the plots (% individuals) and taxonomic entities monitored in each plot relative to their respective values of vertical distance from water-table (HAND).

Plot	HAND	Individuals	Monitored Individuals	% individuals	Number of Families	Number of Genus	Number of Species
LO62500	2.15	308	195	63.31	35	66	73
LO33500	3.02	269	210	78.06	34	63	83
LO31500	13.62	330	197	59.69	38	64	87
LO52500	14.56	321	187	58.25	32	68	90
LO6500	17.47	339	201	59.29	39	77	103
LO22000	19.31	379	198	52.24	40	73	93
LO43500	39.48	322	192	59.62	37	77	108
LO44500	40.44	345	212	61.44	41	73	105
LO42500	45.57	332	287	86.44	42	89	123
Total	-	2945	1879	63.80	57	189	452

Table S2. Values of b_{std} , p e r^2 from variance analyses of monitoring periods and mean increment in circumference (MIC), linear regressions between mean increment in circumference of life history type and the vertical distance from water-table (HAND).

Life history type	Predictor	Outcome Variable	b_{std}	P	r^2
	Periods	MIC		<0.01	
1) All trees		Feb-Mar	0.05	0.61	0.03
		Apr-May	0.29	0.03	0.50
		Jun-Jul	-0.22	0.10	0.33
	HAND	Aug-Sep	0.11	0.52	0.05
		Oct-Nov	0.16	0.37	0.11
		Dec-Jan	0.28	0.43	0.09
	Periods	MIC		<0.001	
High density wood		Feb-Mar	-0.49	0.23	0.19
		Apr-May	0.75	0.02	0.52
		Jun-Jul	-0.35	0.25	0.18
	HAND	Aug-Sep	-0.25	0.57	0.04
		Oct-Nov	0.28	0.47	0.07
		Dec-Jan	0.13	0.79	0.01
	Periods	MIC		<0.001	
Intermediate density wood		Feb-Mar	0.08	0.08	0.36
		Apr-May	0.09	0.07	0.38
		Jun-Jul	-0.06	0.0004	0.84
	HAND	Aug-Sep	0.06	0.11	0.32
		Oct-Nov	0.03	0.53	0.05
		Dec-Jan	0.03	0.36	0.11

	Periods	MIC	0.06		
Low density wood		Feb-Mar	-0.19	0.72	0.01
		Apr-May	0.11	0.93	0.001
		Jun-Jul	-0.37	0.67	0.02
	HAND	Aug-Sep	-0.37	0.67	0.02
		Oct-Nov	0.25	0.85	0.005
		Dec-Jan	-0.5	0.63	0.03
	Periods	MIC	0.2		
2) Palms		Feb-Mar	0.02	0.66	0.28
		Apr-May	-0.58	0.21	0.20
		Jun-Jul	0.25	0.62	0.03
	HAND	Aug-Sep	0.25	0.23	0.19
		Oct-Nov	-0.10	0.2	0.21
		Dec-Jan	0.40	0.19	0.22
	Periods	IIC	0.7		
3) <i>Brosimum rubescens</i>		Feb-Mar	0.20	0.10	0.13
		Apr-May	0.01	0.92	0.0004
		Jun-Jul	0.12	0.56	0.01
	HAND	Aug-Sep	0.07	0.59	0.01
		Oct-Nov	0.12	0.33	0.05
		Dec-Jan	-0.37	0.41	0.03
	Periods	IIC	0.10		
		Feb-Mar	0.18	0.22	0.07
		Apr-May	0.02	0.87	0.001

4) <i>Ecclinusa guianensis</i>		Jun-Jul	-0.04	0.63	0.01
	HAND	Aug-Sep	0.10	0.56	0.01
		Oct-Nov	0.22	0.36	0.04
		Dec-Jan	0.63	0.002	0.40
	Periods	IIC		0.002	
		Feb-Mar	0.13	0.2	0.03
		Apr-May	-0.08	0.47	0.01
4) <i>Eperua glabriflora</i>		Jun-Jul	0.14	0.20	0.03
	HAND	Aug-Sep	-0.04	0.64	0.004
		Oct-Nov	0.04	0.78	0.001
		Dec-Jan	0.23	0.25	0.02
	Periods	IIC		0.09	
		Feb-Mar	-0.11	0.42	0.04
		Apr-May	0.01	0.91	0.0009
5) <i>Iryanthera juruensis</i>		Jun-Jul	-0.24	0.40	0.05
	HAND	Aug-Sep	0.38	0.42	0.04
		Oct-Nov	0.31	0.52	0.03
		Dec-Jan	-0.04	0.73	0.008

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the author.

Conclusões

As previsões dos cenários das mudanças climáticas globais, como alterações nos padrões de chuvas e de disponibilidade de água no solo, podem ter efeitos diretos sobre o crescimento das plantas e, por isso, destacam a importância da compreensão do funcionamento do ciclo do carbono. Neste estudo, o aporte de chuvas no período de transição entre a estação seca e chuvosa e a interação desta com a distância do lençol freático e a textura do solo foi um direcionador do crescimento secundário das árvores.




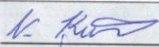
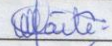
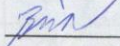
No final da estação chuvosa, as árvores das áreas de platôs, distantes do lençol freático e com solos argilosos, apresentaram os maiores valores de incremento em circunferência superiores às áreas de baixios, sugerindo que a retenção de água no solo, em função da baixa granulometria da argila, possibilitou que as plantas tivessem maior crescimento secundário. Já na estação seca, as árvores das áreas de baixios, com solos não encharcados ou inundados, como nos períodos anteriores, e com suas raízes próximas ao lençol freático, puderam ter um maior crescimento secundário do que as árvores das demais áreas, as quais possivelmente tinham seus solos ressecados ou as raízes sem acesso à água neste período.

Seguindo o mesmo padrão descrito a cima, as árvores de alta e intermediária densidade da madeira, tiveram crescimentos secundários com picos na transição do período seco para o chuvoso, o que pode ser explicado através da anatomia celular destas plantas: as árvores de alta densidade da madeira possuem uma baixa condutividade hidráulica em razão de vasos condutores finos, contudo esta característica confere maior segurança hidráulica à embolia. Além disso são árvores de crescimento mais lento e com menores taxas fotossintéticas, o que representa um comportamento mais conservativo às mudanças das condições ambientais. As árvores de baixa

densidade da madeira apresentam maior variabilidade de respostas entre os períodos e entre os ambientes topográficos, o que possivelmente pode ser atribuído as características anatômicas da madeira como o alto calibre de vasos condutores e altas taxas fotossintéticas, o que confere maior suscetibilidade a embolia e cavitação nos períodos de seca.

O presente estudo apresenta desdobramentos do crescimento secundário das árvores em relação à topografia e à densidade da madeira, podendo contribuir para uma melhor compreensão ecossistêmica do funcionamento das florestas tropicais e suas associações com as variáveis climáticas.

Anexos- Atas da Aula de Qualificação e Defesa Pública da Dissertação de mestrado

		
AULA DE QUALIFICAÇÃO		
PARECER		
Aluno(a): KARINA LIANA LISBOA MELGAÇO Curso: ECOLOGIA Nível: MESTRADO Orientador(a): FLÁVIA REGINA CAPELOTTO COSTA		
Título:		
"Respostas de Respiração e Crescimento de árvores às variações hídricas em uma escala temporal e espacial na Reserva Ducke, Manaus"		
BANCA JULGADORA:		
TITULARES: Norbert Kunert (Pos Doc INPA) Maria Teresa Fernández Piedade (INPA) Bruce Walker Nelson (INPA)	SUPLENTE: Jochen Schongart (INPA - Projeto Max Planck) José Francisco de Carvalho Gonçalves (INPA)	
PARECER		ASSINATURA
Norbert Kunert (Pos Doc INPA) Maria Teresa Fernández Piedade (INPA) Bruce Walker Nelson (INPA) Jochen Schongart (INPA - Projeto Max Planck) José Francisco de Carvalho Gonçalves (INPA)	<input checked="" type="checkbox"/> Aprovado () Reprovado <input checked="" type="checkbox"/> Aprovado () Reprovado <input checked="" type="checkbox"/> Aprovado () Reprovado <input type="checkbox"/> Aprovado () Reprovado <input type="checkbox"/> Aprovado () Reprovado	  
Manaus(AM), 13 de março de 2013		
OBS: (1) Repensar a inclusão de comportamentos ao longo do dia para uma mesma espécie, e variações entre espécies. (2) Incluir mais literatura relevante mencionada pela banca.		
INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA INPA PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA PPG-ECO Av. Efigênio Sales, 2239 - Bairro: Aleixo - Caixa Postal: 2223 - CEP: 69.060-020, Manaus/AM. Fone/Fax: (+ 55) 92 3643-1908/1909		
site: http://pg.inpa.gov.br		e-mail: pgecologia@gmail.com



ATA DA DEFESA PÚBLICA DA DISSERTAÇÃO DE MESTRADO DO PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA DO INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA.

Aos 16 dias do mês de maio do ano de 2014, às 09:00 horas, no Auditório do LBA, Campus II, INPA/Aleixo, reuniu-se a Comissão Examinadora de Defesa Pública, composta pelos seguintes membros: o(a) Prof(a). Dr(a). **Bruce Walker Nelson** do Instituto Nacional de Pesquisas da Amazônia - INPA, o(a) Prof(a). Dr(a). **Fabien Wagner** do Instituto Nacional de Pesquisas Espaciais - INPE e o(a) Prof(a). Dr(a). **José Luís Campana Camargo** do Instituto Nacional de Pesquisas da Amazônia - INPA, tendo como suplentes o(a) Prof(a). Dr(a). Carlos Alberto Nobre Quesada, do Instituto Nacional de Pesquisas da Amazônia - INPA, e o(a) Prof(a). Dr(a). Antônio Ocimar Manzi do Instituto Nacional de Pesquisas da Amazônia - INPA, sob a presidência do(a) primeiro(a), a fim de proceder a arguição pública do trabalho de **DISSERTAÇÃO DE MESTRADO** de **KARINA LIANA LISBOA MELGAÇO**, intitulado "Topografia e densidade da madeira modulam o crescimento sazonal na Amazônia Central" orientado pelo(a) Prof(a). Dr(a). Dra. Flávia Regina Capellotto Costa do Instituto Nacional de Pesquisas da Amazônia - INPA.

Após a exposição, o(a) discente foi arguido(a) oralmente pelos membros da Comissão Examinadora, tendo recebido o conceito final:

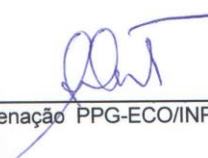
APROVADO(A) REPROVADO(A)
 POR UNANIMIDADE POR MAIORIA

Nada mais havendo, foi lavrada a presente ata, que, após lida e aprovada, foi assinada pelos membros da Comissão Examinadora.

Prof(a).Dr(a). **Bruce Walker Nelson**

Prof(a).Dr(a). **Fabien Wagner**

Prof(a).Dr(a). **José Luís Campana Camargo**


 Coordenação PPG-ECO/INPA