

INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA  
PROGRAMA DE PÓS-GRADUAÇÃO EM CIÊNCIAS DE FLORESTAS TROPICAIS

**INFLUÊNCIA DO *El Niño* 2015-2016 NO INCREMENTO DIAMÉTRICO DAS  
ÁRVORES DA AMAZÔNIA CENTRAL**

CAROLINA RAMÍREZ MÉNDEZ

MANAUS, AMAZONAS

ABRIL, 2018

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ÁRVORES DA AMAZÔNIA CENTRAL**

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Dissertação apresentada ao Instituto Nacional de Pesquisas da Amazônia como parte dos requisitos para obtenção do título de Mestre em Ciências de Florestas Tropicais.

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**DEFESA PÚBLICA DISSERTAÇÃO / PPG-CFT - INPA**

Ata da Defesa Pública da Dissertação de Mestrado de **CAROLINA RAMÍREZ MÉNDEZ** aluno (a) do Programa de Pós-Graduação *Stricto Sensu* em CIÊNCIAS DE FLORESTAS TROPICAIS, realizada no dia 04 de maio de 2018.

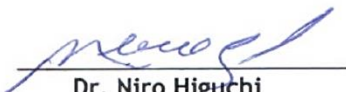
Aos quatro dias do mês de maio de 2018, às 08h30, no Auditório dos PPGs ATU/CFT/ECO, Campus III, INPA-V8, realizou-se a Defesa Pública da Dissertação de Mestrado intitulada: **“INFLUÊNCIA DO *El Niño* 2015-2016 NO INCREMENTO DIAMÉTRICO DAS ÁRVORES DA AMAZÔNIA CENTRAL”** em conformidade com o Artigo 68 do Regimento Interno do PPG-CFT e Artigo 52 do Regimento Geral da Pós-Graduação do Instituto Nacional de Pesquisas da Amazônia (MCTI-INPA) como parte final de seu trabalho para a obtenção do título de **MESTRE EM CIÊNCIAS DE FLORESTAS TROPICAIS**, área de concentração em *Manejo Florestal*. A Banca Examinadora foi constituída pelos seguintes professores doutores: **JULIANA SCHIETTI DE ALMEIDA (INPA)**, **FABIEN HUBERT WAGNER (INPE)** e **BRUCE WALKER NELSON (INPA)**. O (a) Presidente da Banca Examinadora, Dr (a) **Niro Higuchi (Orientador / INPA)**, deu início à sessão convidando os senhores membros e o (a) Mestrando (a) a tomarem seus lugares e informou sobre os procedimentos a serem observados para o prosseguimento do exame. A palavra foi, então, facultada ao (à) Mestrando (a) que apresentou uma síntese do seu estudo e respondeu às perguntas formuladas pelos membros da Banca Examinadora. Depois da apresentação e arguição, a referida Banca Examinadora se reuniu e decidiu por

A sessão foi encerrada às 10:50 e, para constar eu, Ana Serra Campos, Secretária do PPG-CFT lavrei a presente Ata, que depois de lida e aprovada foi assinada pelo Presidente e membros da Banca Examinadora. Banca Examinadora:

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### **Sinopse**

Foram monitoradas com dendrômetros 325 árvores um ano antes da seca ocasionada pelo *El Niño*, o ano da seca e um ano posterior da mesma, com medições mensais em uma floresta de terra-firme na Amazônia Central. Avaliou-se o incremento diamétrico anual e mensal de árvores durante os períodos de monitoramentos, com o fim de detectar as mudanças no incremento durante a seca e as diferenças deste entre os períodos. Identificou-se o tamanho em diâmetro das árvores, a densidade da madeira das árvores e a posição das mesmas no gradiente hidrotopográfico que mais se viram afetadas durante e após a seca. Durante o *El Niño* as árvores reduziram o incremento anual em mais da metade, sendo as árvores com diâmetros maiores e localizadas nos platôs as mais afetadas devido a uma maior sensibilidade ao déficit hídrico. Após um ano da seca, a floresta ainda não recupera o seu ritmo de crescimento.

**Palavras-chave:** seca, dendrômetro, topografia, diâmetro, densidade da madeira

## DEDICATÓRIA

*A todos os que lutam pela conservação da nossa floresta Amazônica,  
a todos os que se esforçam em cuidar da nossa mama Pacha,  
a todos os que tentam viver uma vida mais sustentável,  
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## RESUMO

A intensidade e frequência das secas severas na região amazônica estão aumentando. Diminuições na taxa de crescimento e aumento na mortalidade de árvores foram relatados em secas anteriores, conseqüentemente, diminuindo a produção primária líquida da floresta. Em 2015-2016, ocorreu a seca mais severa dos últimos anos causada pelo *El Niño*, assim o crescimento das árvores pode estar comprometido. Sendo assim, foi monitorado o incremento mensal e anual de 325 árvores com bandas dendrométricas um ano antes da seca, no ano do evento e um ano depois, em uma floresta de terra firme na Amazônia Central. O incremento anual e mensal do diâmetro das árvores durante os períodos monitorados foi calculado para detectar eventuais alterações nas taxas de incremento durante a seca e entre os períodos. Além disso, as árvores foram classificadas por diâmetro, densidade da madeira e posição topográfica para identificar quais características são mais vulneráveis durante a seca. Uma redução significativa no incremento em diâmetro anual e mensal foi encontrada em todas as árvores após a seca. Árvores maiores e árvores localizadas nos platôs foram as mais afetadas na taxa de incremento, o que pode estar associado à redução da fotossíntese e estresse hidráulico causado pelo déficit hídrico. As árvores do baixio sofreram menos com a seca apresentando pouca reação sazonal à variação de precipitação. Nenhuma variação de incremento do caule foi detectada em função da densidade da madeira. Além disso, este estudo demonstrou que um ano após a seca, a taxa de crescimento média da floresta ainda não tinha sido recuperada. Árvores de tamanho médio localizadas nos baixios foram as que apresentaram taxas de recuperação mais lentas. O presente estudo enfatiza o grande efeito da seca no crescimento das árvores e como este efeito é ainda observado no ano posterior à seca. Assim também, a caracterização de quais árvores são mais vulneráveis e resistentes à seca podendo contribuir em modelos de climáticos e de carbono.

Palavras-chave: seca, dendrômetro, diâmetro, topografia, densidade da madeira

## ABSTRACT

The intensity and frequency of severe droughts in the Amazon region is increasing. Decreases in growth rates and increases in tree mortality have been reported in previous droughts, consequently, forest net primary production declined. In 2015-2016, the most severe drought of this century caused by *El Niño* occurred, consequently tree growth might be committed. Most drought studies have monitored the forest after the event happens, which misses the intra-annual effect of the drought. In this study, the monthly and annual increment of 325 trees with dendrometer bands were monitored one year before the drought, the year of the event and one year after it in a *terra-firme* forest in the Central Amazon. The annual and monthly diameter increment during the monitored periods were calculated to detect differences in the increment rates during the drought and between the periods. Trees were classified by diameter, wood density and topographic position to identify which characteristics were more vulnerable during the drought. A significant reduction in the annual and monthly stem increment was found after the drought in all the tree categories. Larger trees and trees located on plateaus were most affected in growth rate, this might be associated with photosynthesis reduction, hydraulic stress due to water deficit and/or cells water loss. Trees on the valley had smaller month-by-month variation during the drought year presenting little seasonal reaction to precipitation variation. No stem increment variation was detected within wood density. Besides, this present study demonstrates that a year after the drought, the forest growth rate had not recovered yet. Medium sized trees and trees located in the bottomlands were the ones with slower rates of recovery. The present study emphasizes the great effect of drought on tree growth and demonstrates how this effect is still observed in the year after drought. Also, the characterization of which trees are more vulnerable and resistant to the drought can contribute in climate and carbon models.

**Keywords:** drought, dendrometer, stem diameter, topography, wood density



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## INTRODUÇÃO

Desde 1970, a temperatura está aumentando e o ciclo hidrológico está se intensificando, conseqüentemente, a intensidade, a frequência e a duração das secas estão aumentando na região amazônica (Trenberth *et al.*, 2007; Seneviratne *et al.*, 2012; Gloor *et al.*, 2015). Esse cenário pode se agravar, conforme sugerido pelos modelos climáticos (Marengo *et al.*, 2013; Gloor *et al.*, 2015). As secas na região amazônica estão associadas ao aquecimento da temperatura na superfície do mar do Oceano Pacífico Tropical, mais conhecido como *El Niño*, e/ou do Oceano Atlântico Norte Tropical (Marengo & Espinoza, 2016; Aragão *et al.*, 2018). Nas duas últimas décadas, três secas extremas (2005, 2010 e 2015-2016) atingiram a região amazônica, com cada seca sucessiva aumentando em intensidade. A última seca, originada pelo *El Niño*, foi a mais severa que a seca de 1997-1998, afetando 43% do bioma Amazônia brasileiro (Erfanian *et al.*, 2017; Aragão *et al.*, 2018).

Portanto, existe uma grande preocupação com os efeitos da seca na floresta tropical, uma vez que as taxas de aumento líquido da biomassa acima do solo (AGB) estão diminuindo e a mortalidade das árvores está aumentando durante esses eventos (Phillips *et al.*, 2009, 2010; Lewis *et al.*, 2011; Doughty *et al.*, 2015; Feldpausch *et al.*, 2016) transformando a floresta amazônica em uma fonte de carbono para a atmosfera (Tian *et al.*, 1998). Além disso, as altas temperaturas (Clark *et al.*, 2003, 2010) e o déficit hídrico durante a seca causam uma redução no incremento em diâmetro das árvores (Worbes, 1999; Brando *et al.*, 2008). Conseqüentemente, espera-se que a Produção Primária Líquida (PPL) da floresta diminua (Tian *et al.*, 1998; Clark *et al.*, 2003; Doughty & Goulden, 2008; Clark *et al.*, 2010) devido a grande contribuição da produção de madeira, crescimento primário e secundário da árvore, na PPL (Malhi *et al.*, 2011). Além disso, mudanças nas taxas de crescimento do caule podem causar alterações na dinâmica e estrutura da comunidade (Wagner *et al.*, 2014a), e nos ciclos atmosféricos e biogeoquímicos (McMahon *et al.*, 2010). Assim, é de grande importância entender a resposta do crescimento do caule das árvores em florestas tropicais, às secas extremas e às variações sazonais do clima para contribuir nos modelos ecossistêmicos e terrestres (Poorter *et al.*, 2010) e prever respostas futuras às mudanças climáticas.

Os padrões de crescimento das árvores variam de acordo com sua composição genética, interação com o ambiente e outros organismos, idade e condições climatológicas (Higuchi *et al.*, 2003; Banin *et al.*, 2015). O incremento mensal do caule varia ao longo do ano devido à sazonalidade climática (Wagner *et al.*, 2014b) sendo a precipitação e a radiação solar as variáveis que mais explicam o crescimento das árvores e sua alocação de carbono nas florestas tropicais (Wagner *et al.*, 2014b). Porém, durante eventos climáticos extremos, como secas e enchentes, o crescimento e a mortalidade das árvores podem ser alteradas. No entanto, é difícil detectar o impacto das secas na taxa de crescimento da floresta devido à escala temporal de monitoramento da maioria das parcelas permanentes.

O aumento da temperatura, mesmo em poucos graus (1° a 2°C ) aumentam a respiração das árvores, com conseqüentes diminuições no incremento em diâmetro, alterando a produtividade florestal (Clark *et al.*, 2003, 2010; Clark, 2004; Gliniars *et al.*, 2013). Também, Doughty & Goulden (2008) demonstraram que maiores temperaturas na folha provoca o fechamento dos estômatos devido à maior demanda evaporativa e conseqüente redução da fotossíntese e assimilação de carbono, o que pode levar a uma redução no incremento em diâmetro (Gliniars *et al.*, 2013). No entanto, a influência da temperatura no crescimento do caule não é tão significativa quanto a da precipitação (Rozendaal & Zuidema, 2011; Wagner *et al.*, 2014b).

Precipitação e radiação solar são as variáveis sazonais que mais influenciam o crescimento das árvores nas florestas tropicais (Wagner *et al.*, 2014b). A variação do incremento diamétrico ao longo do dia e do ano (Sheil, 2003) tem forte relação com a variação sazonal de precipitação e disponibilidade de água no solo (Worbes, 1999; Silva *et al.*, 2002; Higuchi *et al.*, 2011; Wagner *et al.*, 2012; Rowland *et al.*, 2014). O incremento é maior durante a estação chuvosa, devido à maior divisão celular no câmbio (Dünisch *et al.*, 2003). Durante o período seco, o incremento do caule pode ser negativo, devido à perda de água e ao encolhimento do caule (Worbes, 1999). Experimentos de exclusão de chuva em Caxiuanã e no Tapajós, onde ~50% da precipitação incidente foi excluída, mostraram que a produtividade de biomassa diminuiu com a redução contínua da precipitação, especialmente em árvores de grande e médio porte (Nepstad *et al.*, 2007; Brando *et al.*, 2008; da Costa *et al.*, 2010).

Variações sazonais na disponibilidade de água no solo das estão intimamente relacionadas com a variação sazonal da precipitação nas florestas tropicais (Stahl *et al.*, 2013). No entanto, a relação entre eles não é direta e pode variar dependendo do tipo de solo e da topografia. Assim, a baixa disponibilidade de água no solo é a principal causa da diminuição ou estancamento do incremento diamétrico da árvore, devido à necessidade de água nos processos biológicos, como o crescimento secundário (Wagner *et al.*, 2012). A topografia controla o teor de água e as propriedades físicas do solo (Daws *et al.*, 2002). Nos platôs da Amazônia Central, as árvores podem estar sob estresse hídrico durante o período de seca, devido à menor disponibilidade de água e à maior distância do lençol freático (Hodnett *et al.*, 1997). Durante a estação chuvosa, os platôs apresentam melhores condições de crescimento, considerando a maior disponibilidade de água associada à alta porosidade, boa drenagem e alta capacidade de retenção de água em solos argilosos. Por outro lado, as árvores dos baixios estão próximas do lençol freático e dos igarapés, sendo mais vulneráveis à anoxia provocada pela alta saturação de água no solo no período chuvoso (Hodnett *et al.*, 1997). As condições de solo saturado e inundação resultam na supressão do crescimento radial atribuído às condições de anoxia do solo (Schöngart *et al.*, 2002) que podem estar limitando o crescimento nos baixios.

Traços biológicos das árvores associados à taxa potencial de crescimento como a área foliar específica, densidade da madeira e tamanho da árvore, também afetam os padrões de incremento do caule. Sendo assim, existe uma relação inversa entre as taxas de crescimento do caule e a densidade da madeira (Chave *et al.*, 2009). Árvores com madeira mais densa produzem um volume menor de madeira por unidade de volume de caule o que levaria a um crescimento mais lento do caule (Enquist *et al.*, 1999). Essa variação na taxa de crescimento pode ser explicada pela arquitetura hidráulica dos vasos da madeira (Poorter *et al.*, 2010). Árvores com baixa densidade da madeira tendem a ser caracterizadas por vasos maiores (Poorter *et al.*, 2010; McCulloh *et al.*, 2011) que contribuem para uma maior condutividade hidráulica (Sperry *et al.*, 2008), enquanto que a alta densidade da madeira tem características opostas. No entanto, a alta densidade da madeira é menos sensível à variabilidade da água e mais resistente à embolia, devido à maior segurança hidráulica em casos de seca extrema. No entanto, espécies de baixa densidade de madeira tendem a ser mais sensíveis ao déficit hídrico durante secas extremas, com maior redução do incremento em diâmetro

e mais propensas à embolia (Hacke *et al.*, 2001; Nepstad *et al.*, 2007; Mendivelso *et al.*, 2014; Rowland *et al.*, 2014).

O incremento diamétrico depende do conteúdo de água das células do caule e do crescimento secundário do mesmo que é a divisão e engrossamento das células do meristema secundário localizadas entre a casa e o xilema (Zweifel *et al.*, 2016). Sendo assim, existe uma relação entre o incremento diamétrico das árvores e o tamanho do diâmetro do tronco (Clark & Clark, 1999). As árvores de 10-30 cm de DAP crescem em uma taxa menor e têm uma resposta menos sazonal em comparação com as árvores maiores ( $DBH \geq 50$  cm) que tiveram uma taxa de crescimento maior (Silva *et al.*, 2002; Vieira *et al.*, 2004). No entanto, nas condições de seca dos experimentos de exclusão de chuva, um declínio de até 45% na taxa de crescimento nas árvores grandes foi relatado, mas nenhum efeito foi encontrado nas árvores de menor porte (Brando *et al.*, 2008; da Costa *et al.*, 2010). Durante o primeiro ano de seca no Tapajós a produção de madeira diminuiu em 13% e após o término de 7 anos de experimento a produção de madeira se recuperou rapidamente aumentando de 42% da parcela de controle em 2003 para 77% em 2005 após o experimento (Brando *et al.*, 2008). Consequências semelhantes ocorrem nas secas naturais, árvores maiores sofreram maior redução da taxa de crescimento e aumentaram suas taxas de mortalidade (Phillips *et al.*, 2010; Bennett *et al.*, 2015).

Existem diversos estudos sobre os efeitos dos experimentos de redução de chuva na floresta tropical. No entanto, estes estão restritos a pequenas parcelas permanentes e não amostram a variação natural das características das árvores e da topografia típica das florestas. Consequentemente, pouco se sabe sobre quais características da árvore estão associadas com a diminuição na taxa de crescimento do caule induzida pela seca. Estudos de longo prazo sobre o crescimento e dinâmica da floresta, em geral utilizam parcelas permanentes que são monitoradas anualmente ou supra-anualmente, com uma média de recenso de 2 anos (Phillips *et al.*, 2009), sendo difícil observar o efeito da seca e a resposta das taxas de crescimento ao suprimento sazonal de água (Rowland *et al.*, 2014; Wagner *et al.*, 2014b). Além disso, pouco se sabe sobre quais características das árvores são mais afetadas durante a seca. A maioria dos estudos de seca são mais focados na redução da biomassa acima do solo causada pelo aumento da mortalidade das árvores (Phillips *et al.*, 2009, 2010; Brien *et al.*, 2015; Feldpausch *et al.*, 2016), no entanto, devido aos

longos intervalos entre os censos, estes estudos têm pouca precisão para estimar os efeitos das secas sobre a taxa de crescimento e a produção de madeira.

Assim, este trabalho tem como objetivo determinar: 1) diferenças entre o incremento anual do diâmetro durante o *El Niño* 2015-2016 e o incremento médio anual (2001-2015) da floresta; 2) se o incremento anual durante a seca difere do observado no ano anterior (2014-2015) e posterior à seca (2016-2017); 3) identificar quais são as características das árvores (densidade da madeira, tamanho da árvore) mais afetadas pela seca durante o *El Niño*; 4) quais as condições hidrológicas locais, definidas pela topografia, afetam mais as respostas do crescimento à seca; e 5) quais variáveis meteorológicas como precipitação, déficit hídrico climatológico (CWD), temperatura, déficit de pressão de vapor, radiação fotossinteticamente ativa e anomalia da temperatura da superfície do mar são as mais correlacionadas com o incremento mensal durante o *El Niño*.

Este estudo utiliza uma série histórica de 16 anos de medidas mensais de incremento do caule, um conjunto inestimável para entender a resposta do incremento diamétrico ao déficit hídrico mensal durante a seca extrema 2015-2016. Esperamos que o incremento anual do ano anterior à seca não seja diferente da média histórica de crescimento florestal, mas esperamos uma redução significativa no incremento mensal e anual durante o ano do *El Niño*, com recuperação da taxa de crescimento no ano seguinte. Além disso, espera-se forte correlação entre o incremento mensal e as variáveis climáticas precipitação, déficit hídrico climático e temperatura média, máxima e mínima. Espera-se que o incremento de caule terá uma redução maior em árvores maiores, como relatado nos experimentos de redução de chuva e que árvores de baixa densidade de madeira terão um decréscimo no incremento mensal de caules, porque são mais sensíveis à variabilidade de água. Também, espera-se que a redução de crescimento durante o el-niño seja maior nos platos, e que as árvores nos baixios possam ser beneficiadas pela seca, dada a redução na anoxia do solo.



## OBJETIVOS

O principal objetivo desta dissertação foi analisar as variações interanuais e intra-anuais do crescimento das árvores de uma floresta de terra firme na Amazônia Central sob a ocorrência da seca de 2015-2016 causada pelo fenômeno *El Niño* 2015-2016; comparando-as com o ano anterior e o ano posterior ao ano do evento. Sendo os objetivos específicos os seguintes:

1. Comparar o incremento anual durante o *El Niño* 2015-2016 e o incremento médio anual (2001-2015) da floresta.
2. Comparar o incremento anual durante o *El Niño* 2015-2016 e o do observado no ano anterior (2014-2015) e posterior à seca (2016-2017).
3. Identificar quais são as características das árvores (densidade da madeira, tamanho da árvore) mais afetadas pela seca ocasionada pelo *El Niño*.
4. Identificar quais são as condições hidrológicas locais, definidas pela topografia, que afetam mais as respostas do crescimento à seca.
5. Correlacionar o incremento mensal durante o ano da seca com as variáveis meteorológicas como precipitação, déficit de hídrico climatológico (CWD), temperatura, déficit de pressão de vapor, radiação fotossinteticamente ativa e anomalia da temperatura da superfície do mar.

## CAPITULO I

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**Tree stem increment response to *El Niño* 2015-2016 in the Central Amazon forest**

RAMIREZ MENDEZ, C.; COSTA, F.R.C., HIGUCHI, N. Manuscrito em preparação para *Global Change Biology*

## Tree stem increment response to *El Niño* 2015-2016 in the Central Amazon forest

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### Abstract

The intensity and frequency of severe droughts in the Amazon region is increasing. Decreases in growth rates and increases in tree mortality have been reported in previous droughts, consequently, forest net primary production declined. In 2015-2016, the most severe drought of this century caused by *El Niño* occurred, consequently tree growth might be committed. Most drought studies have monitored the forest after the event happens, which misses the intra-annual effect of the drought. In this study, the monthly and annual increment of 325 trees with dendrometer bands were monitored one year before the drought, the year of the event and one year after it in a *terra-firme* forest in the Central Amazon. The annual and monthly diameter increment during the monitored periods were calculated to detect differences in the increment rates during the drought and between the periods. Trees were classified by diameter, wood density and topographic position to identify which characteristics were more vulnerable during the drought. A significant reduction in the annual and monthly stem increment was found after the drought in all the tree categories. Larger trees and trees located on plateaus were most affected in growth rate, this might be associated with photosynthesis reduction, hydraulic stress due to water deficit and/or cells water loss. Trees on the valley had smaller month-by-month variation during the drought year presenting little seasonal reaction to precipitation variation. No stem increment variation was detected within wood density. Besides, this present study demonstrates that a year after the drought, the forest

growth rate had not recovered yet. Medium sized trees and trees located in the bottomlands were the ones with slower rates of recovery. The present study emphasizes the great effect of drought on tree growth and demonstrates how this effect is still observed in the year after drought. Also, the characterization of which trees are more vulnerable and resistant to the drought can contribute in climate and carbon models.

*Keywords:* drought, dendrometer, stem diameter, topography, wood density

## **Introduction**

Since the 1970's, global temperature has increased, and the hydrological cycle has intensified. Consequently, the intensity, the frequency and the length of droughts have been increasing in the Amazon region (Trenberth *et al.*, 2007; Seneviratne *et al.*, 2012; Marengo & Espinoza, 2016). Climate models suggest these trends will continue and aggravate (Marengo *et al.*, 2013; Gloor *et al.*, 2015). Droughts in the Amazon region are associated with warming of the sea surface in the Tropical Pacific Ocean, known as *El Niño*, and/or in the Tropical North Atlantic Ocean (Marengo & Espinoza, 2016; Aragão *et al.*, 2018). In the last two decades, three extreme droughts (2005, 2010 and 2015-2016) occurred in the Amazon region, with each successive drought increasing in severity. The last drought, which was caused by *El Niño*, was the most severe since the drought of 1997-1998, affecting 43% of the Brazilian Amazon Biome (Erfanian *et al.*, 2017; Aragão *et al.*, 2018).

There is much concern about drought effects in tropical forest since the net increase in rates of Above Ground Biomass (AGB) are decreasing and the mortality is increasing during these events (Phillips *et al.*, 2009, 2010; Lewis *et al.*, 2011; Doughty *et al.*, 2015; Feldpausch *et al.*, 2016) turning the Amazon Forest into a source of carbon to the atmosphere (Tian *et al.*, 1998). The main components of AGB are leaf, flower, fruit and wood production (Malhi *et al.*, 2004). The latter is directly related to stem growth rate and it is the main way of carbon entry in the forest biomass stock (Malhi *et al.*, 2011). Trees growth patterns vary according to their genetic composition, interaction with the environment and other organisms, age and climatological conditions (Higuchi *et al.*, 2003; Banin *et al.*, 2015). During dry season conditions, high

temperatures (Clark *et al.*, 2003, 2010) and water deficit cause a reduction of diameter increment (Worbes, 1999; Brando *et al.*, 2008). Consequently, the forest net primary production is expected to decrease (Tian *et al.*, 1998; Clark *et al.*, 2003; Doughty & Goulden, 2008; Clark *et al.*, 2010) due to the great contribution of wood production, primary and secondary growth, in PPL (Malhi *et al.*, 2011). Furthermore, changes in the stem growth rate may alter forest dynamics, forest community structure (Wagner *et al.*, 2014a), and atmospheric and biogeochemical cycles (McMahon *et al.*, 2010). Therefore, it is of great importance to understand the response of tropical tree stem growth to extreme droughts and to seasonal climate variations that contribute to ecosystem, carbon and climate models (Poorter *et al.*, 2010), which in turn are used to predict future responses of the forest to climate change.

Rising temperatures cause increases in tree respiration and decreases in stem increment rate, consequently altering forest productivity (Clark *et al.*, 2003; Clark, 2004; Gliniars *et al.*, 2013). Clark *et al.* (2010) found that a rise of 1°-2°C in nocturnal temperatures significantly reduced the annual diameter increment in six species in Costa Rica due to increased stem respiration. In addition, Doughty & Goulden (2008) showed that higher leaf temperature causes stomata closure due to higher evaporative demand, with consequent reduction of photosynthesis and carbon assimilation, which may lead to a reduction in stem increment (Gliniars *et al.*, 2013). So far, studies have concluded that the influence of temperature on stem growth is not as great as that of precipitation (Rozendaal & Zuidema, 2011; Wagner *et al.*, 2014b) and soil water availability (Wagner *et al.*, 2012).

Diurnal and annual stem increment changes have a strong correlation with the seasonal variation in precipitation and in soil water availability (Worbes, 1999; Silva *et al.*, 2002; Higuchi *et al.*, 2011; Wagner *et al.*, 2012; Rowland *et al.*, 2014). Higher stem increment rates occur during the rainy season because of the higher cellular division in the cambium (Dünisch *et al.*, 2003) and wood swelling. During the dry period stem increments may be negative due to water loss and stem shrinkage (Worbes, 1999). Throughfall exclusion experiments in Caxiuanã and Tapajós in Brazil, wherein approximately 50% of the incident rainfall was excluded, showed that the productivity of wood biomass decreased with the continuous reduction of precipitation, especially in large and medium sized trees (Nepstad *et al.*, 2007; Brando *et al.*, 2008; da Costa *et al.*, 2010).

Seasonal variations in soil surface water availability is closely related to precipitation in tropical forests (Stahl *et al.*, 2013). However, the relationship is not direct and could vary depending on soil type and topography. Topography controls soil water content and the physical properties of the soil (Daws *et al.*, 2002). On Central Amazon oxisol plateaus, trees could be under water stress during the dry period because of less soil water availability due to the great depth of the water table (Hodnett *et al.*, 1997). During the rainy season, the trees on these plateaus have better growth conditions, due to higher plant-available water associated with high water retention capacity of clay soils. On the other hand, trees in the valleys are closer to the water table and streams, being more susceptible to anoxia caused by soil water saturation in the rainy season (Hodnett *et al.*, 1997). Saturated soil conditions and flooding result in suppression of the radial growth which is attributed to soil anoxic conditions (Schöngart *et al.*, 2002) that might be limiting the growth in the valleys.

Biological tree traits associated with growth rate potential, such as specific leaf area, wood density, and tree size also affect the patterns of stem increment. An inverse relationship exists between stem growth rates and wood density (Chave *et al.*, 2009). Trees with denser wood produce a smaller volume of wood per unit volume of stem (Enquist *et al.*, 1999) which would lead to a slower stem growth. This growth rate variations can be explained by the hydraulic architecture of xylem vessels (Poorter *et al.*, 2010). Low wood density trees are mostly characterized by wider and fewer vessels (Poorter *et al.*, 2010; McCulloh *et al.*, 2011) which contribute to a higher hydraulic conductance (Sperry *et al.*, 2008), whereas high density wood has the opposite characteristics which could lead to a lower rate of transpiration, photosynthesis and biomass growth (Chave *et al.*, 2009). However, high density wood trees are mostly less sensitive to water variability and more resistant to embolism due to higher hydraulic safety margin during extreme drought. Species with low wood density are more sensitive to water deficit and more prone to embolism causing a greater reduction in stem increment rate (Hacke *et al.*, 2001; Nepstad *et al.*, 2007; Mendivelso *et al.*, 2014; Rowland *et al.*, 2014).

The diameter increase depends on the water content of the stem cells and on the secondary growth of the stem, which is the division and thickening of the cells of the secondary meristem located between the bark and the xylem (Zweifel *et al.*, 2016). Thus, there is a relation between the

diameter increment and the size of the stem diameter (Clark & Clark, 1999). Generally, larger trees have higher diametric increment rates and have been shown to have higher seasonal growth variation than smaller trees (Silva *et al.*, 2002; Vieira *et al.*, 2004). Under experimental drought conditions in Brazil, large trees showed high decline in growth rate (up to 45%) , while smaller trees were unaffected (Brando *et al.*, 2008; da Costa *et al.*, 2010). During the first year of drought in a rainfall exclusion experiment in the Tapajós National Forest in Brazil Central Amazon, the wood production rate averaged over all tree sizes classes fell by 13%. When rainfall exclusion stopped after 7 years of the experiment, mean wood production rate recovered rapidly, increasing from 42% of wood production of the control plot in 2003 to 77% in 2005 (Brando *et al.*, 2008). A similar higher vulnerability of larger trees has been recorded during natural droughts (Phillips *et al.*, 2010; Bennett *et al.*, 2015).

Several studies of experimental drought effects on tropical forests have been conducted. These, however, are restricted to small forest plots and do not sample the natural variation of tree traits and topography typical of forests. Consequently, little is known about which tree traits are associated with drought-induced decreases in stem growth rate. Most long-term studies of stem growth generally use forest plots that are inventoried at annual or multi-annual intervals, census interval average of 2 years (Phillips *et al.*, 2009), making it difficult to detect intra-annual drought effects and the response of stem growth rates to seasonal change in water supply (Rowland *et al.*, 2014; Wagner *et al.*, 2014b). Most drought studies have focused on the reduction of the above ground biomass caused by increases in tree mortality as well (Phillips *et al.*, 2009, 2010; Brien *et al.*, 2015; Feldpausch *et al.*, 2016). However, due to the long inventory repeat intervals, the precision of results for growth rate reductions, and therefore wood production, is questionable.

Thus, there is an information gap on the effects of natural extreme droughts on trees distributed across a wide variation of habitats and of tree traits typical of tropical forests, assessed at monthly time intervals. We here take advantage of a uniquely long-time series (16 years) of monthly stem increment measurements that include the strong 2015-2016 *El Niño* drought, to examine how growth has been affected according to tree traits and tree hydrological environment. We also examine which meteorological variables (precipitation, Climatological Water Deficit - CWD, temperature, vapor pressure deficit, photosynthetically active radiation and sea surface

temperature anomaly) are the most correlated with the monthly stem increment rate during the 2015-2016 *El Niño*. Monthly and yearly stem increment rate during and after the *El Niño* drought were compared to the forest's long-term historical increment rates, allowing a determination of the intensity of drought effects and of post-drought recovery.

We expected that the monthly and mean annual increments during the year before the drought would not differ from their respective historical averages; that a significant reduction in the monthly and the annual increment rates would be found for the year that encompassed the *El Niño* drought; and these rates would recover in the 12 months of post-drought. Positive correlation was expected between monthly increment rate and precipitation and CWD. Negative correlation was expected between monthly increment rate and the mean, maximum and minimum temperatures. Lastly, we expected that the tree response to drought is related to diameter, wood density and topographic position. Stronger reduction of stem increment was expected in taller trees, in trees with lower wood density, and in trees whose topographic positions make them more prone to soil moisture deficits.

## **Material and methods**

### *Study Area*

The study was conducted at the ZF-2 Forest Management Experiment Station maintained by Brazil's National Institute for Amazon Research (INPA), located ~90 km north of Manaus, Brazil (02° 35'S, 60° 12'W). The study consists of two transects (20 m x 2500 m each), one oriented East-West (E-W) and the other North-South (N-S). These were established in 1996 by the Jacaranda Project, a collaboration between INPA and the Japan International Cooperation Agency (JICA). The ZF-2 soil types vary with hillslope position: (i) the upland plateaus, have well drained Dystrophic Yellow Latosol with clay texture, (ii) slopes contain Dystrophic Red-Yellow Argisol with a mixed sand-clay texture and (iii) valley floors are seasonally waterlogged Hydromorphic Carbic Spodosol with sandy texture (Ferraz *et al.*, 1998).



The vegetation cover of the study site is dense *terra-firme* tropical moist forest (Higuchi *et al.*, 1997) with an average canopy height of about 35 m with emergent trees up to 40 m (Vieira *et al.*, 2005). The mean spatial density of trees, palms and vines above 10 cm DBH (Diameter at Breast Height, 1.5 m) is 670 individuals ha<sup>-1</sup>. The site has at least 245 species of this size in 48 families (Oliveira *et al.*, 2008). Lecythidaceae, Sapotaceae, Fabaceae, Euphorbiaceae, Chrysobalanaceae and Moraceae are the most abundant tree families. *Eschweilera micrantha* (O. Berg) Miers, *Pouteria gongrijpii* Eyma, *Chrysophyllum sanguinolentum* (Pierre) Baehni, *Protium apiculatum* Swart, *Eschweilera atropetiolata* S.A. Mori and *Swartzia reticulata* Ducke are the most common species (Oliveira *et al.*, 2008).

According to the Köppen classification the location has a tropical monsoon climate (Am) (Peel *et al.*, 2007). The mean annual precipitation for 2000 to 2014 was 2555 mm, based on the records of the micromet tower K34 (2° 36' 33" S, 60° 12' 34" W), near the crossing point of the two transects. The dry season has at least one month between August and November (Araújo *et al.*, 2002) with rainfall below 100 mm (Sombroek, 2001). However, the monthly means for 1971-2010 from the EMBRAPA Western Amazon Meteorological Station (2° 53' 25" S, 59° 58' 06" W) located ~40 km from K34 tower, does not register any months with precipitation below 100 mm (Antonio, 2017). Monthly mean relative humidity varies from 75% to 90%. The mean temperature is 26.5°C and the annual maximum and annual minimum mean annual temperatures vary from 31.4°C to 33.6°C, and 21.1°C to 22.8°C respectively.

#### *Data acquisition and analysis*

In 1999, 150 manually constructed dendrometers were installed at 1.5 m height on trees of the two 2.5 km long transects. Trees were selected to represent three diameter classes (10-30, 30-50 and ≥ 50 cm) and hillslope segments (plateau, slope and valley). In 2001 more dendrometers were installed, bringing the total to 463 trees. Trees that died by 2017 were excluded from analysis. Trees with six or more months of continuous missing measurements were also excluded, leaving a total of 325 trees (161 species). Sampled trees were topographically distributed as follows: 135 (42%) on plateau, 65 (20%) on slopes and 125 (38%) in valleys. The E-W and the N-S transects provided 135 and 190 trees respectively.

Since 1999, changes in stem circumference (spring displacement) have been measured monthly, between day 25 and 30 of each month, with digital calipers having a precision of  $\pm 0.01$  mm (Silva *et al.*, 2002; Higuchi *et al.*, 2003). Increment in circumference was transformed to diameter increment (Equation 1). Also, the first three monthly measurements of each newly fitted dendrometer band were discarded, to provide an adjustment period for stem expansion to take up any slack in the band (Keeland & Sharitz, 1993). The monthly stem increment (MI) was calculated by subtracting the diameter at the previous month (n-1) from the diameter at the current month (n) (Equation 2). The historical or long-term Mean Monthly Increment (MMI) of each tree was calculated for each of the twelve calendar months from May 2001 to April 2015 (Equation 3). Field and typing errors were checked and corrected. No adjustment was made for negative increments, nor were corrections made for bark and wood swelling and shrinking.

$$\text{Equation 1: } \text{Diameter} = \frac{\text{Circumference}}{\pi}$$

$$\text{Equation 2: } MI_{(n)} = \text{Diameter}_{(n)} - \text{Diameter}_{(n-1)}$$

$$\text{Equation 3: } MMI_{(2001-2015)} = \frac{MI_{2001-2002} + MI_{2001-2002} + \dots + MI_{2014-2015}}{\text{number of months } (n)}$$

The drought of 2015-2016 was caused by an *El Niño* event and between May 2015 and April 2016 the three-month running mean of the sea surface temperature anomaly (Oceanic Niño Index - ONI) in Niño region 3.4 (5°N - 5°S, 120°-170° W) exceeded +1°C (<http://www.cpc.ncep.noaa.gov/data/indices/oni.ascii.txt>). Besides, this period was selected to center the twelve months interval so that its midpoint is the month with the most negative CWD, September-October. The stem increment of the *El Niño* year (May 2015 to April 2016) were compared to the prior year (May 2014 to April 2015), to the following year (May 2016 to April 2017) and to the historical mean stem increments (May 2001 to April 2015).

Wood specific gravity (WD) was obtained from published studies near the study area (Supplementary Information S1 and S2). When data for WD were not available, the global wood-density data base was used (Chave *et al.*, 2009; Zanne *et al.*, 2009). Wood density data was available at the species level for 254 individuals (78%), at the genus level for 68 trees (21%) and family level for 3 individuals (1%). Three wood density categories were created based on breaks

is frequency distribution (Supplementary Information S3): low density ( $WD < 0.55 \text{ g cm}^{-3}$ ), medium density ( $0.55 \text{ g cm}^{-3} \leq WD < 0.75 \text{ g cm}^{-3}$ ) and high density ( $WD \geq 0.75 \text{ g cm}^{-3}$ ).

In May 2014 the monitored trees' breakdown by size class was 179 individuals (55%) with DBH 10-30 cm, 96 individuals (30%) with DBH 30-50 cm and 50 individuals (15%) with DBH  $\geq$  50 cm (Supplementary Information S3). These classes were chosen to allow the results of this study to be compared with other publications.

To obtain the hillslope position of each tree in order to place it into one of the three hillslope segments, we used the HAND (Height Above Nearest Drainage) algorithm developed by Rennó *et al.* (2008). This provides an estimate of the ground elevation relative to the nearest valley bottom that has perennially flowing surface water. HAND requires a digital elevation model (DEM). We used the DEM from the Shuttle Radar Topography Mission (SRTM) with 30 m horizontal resolution (<https://earthexplorer.usgs.gov/>). Deforestation in SRTM was corrected by filling as suggested by Rennó (2009). The ground elevations of the 325 trees ranged from 1 to 61 m (mean = 25 m) above the nearest drainage.

The meteorological data of precipitation, temperature, PAR and VPD from (2000-2017) was obtained from Tower K34 ( $2^{\circ} 36' 32.67'' \text{ S}$ ,  $60^{\circ} 12' 33.48'' \text{ W}$ ) that is administered by the Large-Scale Biosphere-Atmosphere Experiment in the Amazon (LBA). The missing values for precipitation were replaced with precipitation data from the Tropical Rainfall Measuring Mission (TRMM 3B43-v7, <https://giovanni.gsfc.nasa.gov/giovanni/>). The Oceanic Niño Index (ONI) and the Sea Surface Temperature (SST) anomaly records were taken from ERSST v5 (<http://www.cpc.ncep.noaa.gov>). The Climatological Water Deficit (CWD) was calculated as proposed by Aragão *et al.* (2007), the assumption of  $100 \text{ mm.month}^{-1}$  was made for the evapotranspiration values. The maximum value of CWD is zero ( $\text{Max CWD}_n = 0$ ). If  $\text{CWD}_{n-1} + P_n - E_n < 0$ , then  $\text{CWD}_n = \text{CWD}_{n-1} + P_n - E_n$ .

The meteorological data of precipitation, temperature, PAR and VPD from 2000 to 2017 was obtained from the K34 micromet tower ( $2^{\circ} 36' 33'' \text{ S}$ ,  $60^{\circ} 12' 34'' \text{ W}$ ), maintained by the Large-Scale Biosphere-Atmosphere Experiment in the Amazon (LBA). Missing monthly precipitation

values were filled with data from the Tropical Rainfall Measuring Mission (TRMM 3B43-v7, <https://giovanni.gsfc.nasa.gov/giovanni/>). The Oceanic Niño Index (ONI) and the Sea Surface Temperature (SST) anomaly were taken from ERSST v5 (<http://www.cpc.ncep.noaa.gov>). The Climatological Water Deficit (CWD) of each month was calculated as proposed by Aragão *et al.* (2007). CWD becomes progressively more negative for each successive month having  $P < 100 \text{ mm month}^{-1}$  and CWD goes to zero during any month that  $P > 100 \text{ mm month}^{-1}$ . Formally, if  $(P_n - E_n) < 0$ , then  $CWD_n = CWD_{n-1} + P_n - E_n$ , where  $P$  is monthly precipitation and  $E$  is monthly evapotranspiration demand. We assume  $E = 100 \text{ mm month}^{-1}$ . The maximum value of CWD is zero ( $\text{Max } CWD_n = 0$ ).

### *Statistical analysis*

To determine if there were significant difference between mean annual stem increment of the year before, during or after the drought against the historical mean annual increment (2001-2015), a paired t-test was used where each tree is paired with itself. We also compared the slopes of three regressions, each fitting the annual increment of each tree -- before, during or after the drought -- against the long-term mean annual increment of that same tree. Expected slope is 1.0 for the null hypothesis of no sample-wide difference in growth rate relative to the long-term growth rate. A repeated measures ANOVA was used to compare the mean annual stem increment between the *El Niño* year and the prior and posterior year across diameter, topography and density classes. Pearson's  $R$  was used to evaluate the correlations between the meteorological variables and the monthly stem increments from each of the three years: before, during and after the drought. Mixed-effect models (lmer, R package) were used to evaluate the effects of CWD and its potential interactions with topographic, diametric and wood density classes over the monthly anomalies in stem increment during the *El Niño* year ( $\text{Increment anomaly} = \text{El Niño monthly stem increment} - \text{Historical mean monthly stem increment for 2001-2015}$ ). The same predictor variables were also tested as continuous variables. We built a series of hierarchical models and used AIC to rank the best. Tree individuals were included in the models as the random effect. Statistical analyses were done in R (R 3.4.3, R Development Core Team 2017) and in SYSTAT 12.0.

## Results

### *Climate and stem increment*

Total annual rainfall during the year May 2015 to April 2016, that encompasses the full *El Niño* drought period, was 33% lower than the average over this same 12-month cycle for 2001-2015 (Table 1). There were six months with precipitation below 100 mm month<sup>-1</sup> (July 2015 - October 2015, December 2015 and January 2016), while in the historical series (2001-2015) this was very infrequent ( $2 \pm 0.6$  dry months per year, Table 1). The months that had a Climatological Water Deficit more negative than -100 mm were September 2015 (-167 mm) and October 2015 (-194 mm) (Figure 3). September 2015 was the month with the highest mean monthly temperature (29.8°C) since September 2009 (33.5°C). September (35.0°C) and October 2015 (34.5°C) were the months with highest maximum monthly temperatures; September 2015 (24.5°C) and January 2016 (25.0°C) were the months with highest minimum monthly temperatures.

The average monthly stem increment during the 12 months that include the drought decreased 64% compared to the 2001-2015 average (Table 1). The year before the drought had monthly increments (0.11 mm month<sup>-1</sup>) like the long-term average (0.11 mm month<sup>-1</sup>). During the 12-month period after the drought, April 2016 to May 2017, however, the average monthly increment (0.09 mm month<sup>-1</sup>) was still 18% lower than the historic average (Table 1, Figure 2). During the 2015-2016 drought, the month with lowest monthly stem increment was September 2015 (-0.16 mm month<sup>-1</sup>), which is also the month with highest mean, minimum and maximum temperatures and one of the two months with highest water deficits (Figure 3).

Monthly stem increment during the year that included the drought was positively correlated to monthly precipitation ( $r = 0.62$ ,  $p = 0.032$ ) and negatively correlated with water deficit ( $r = -0.67$ ,  $p = 0.017$ ), PAR ( $r = -0.52$ ,  $p = 0.084$ ) and VPD ( $r = -0.76$ ,  $p = 0.007$ ); negatively correlated to maximum ( $r = -0.6$ ,  $p = 0.039$ ), mean ( $r = -0.55$ ,  $p = 0.062$ ), and minimum temperature ( $r = -0.33$ ,  $p = 0.29$ ) and negatively but not significantly correlated with the Pacific sea surface temperature anomaly ( $r = -0.22$ ,  $p = 0.49$ ) and the Oceanic Niño Index ( $r = -0.27$ ,  $p = 0.4$ ) (Supplementary Information S4-S7).

The annual stem increment during the *El Niño* of 2015-2016 was  $0.51 \pm 0.10$  mm year<sup>-1</sup> (95% CI for the mean), 59% less than the historical mean annual increment over 2001-2015 ( $1.25 \pm 0.04$  mm year<sup>-1</sup>). The annual stem increment during the *El Niño* of 2015-2016 was  $0.51 \pm 0.10$  mm year<sup>-1</sup>, 59% less than the historical mean annual increment over 2001-2015 ( $1.25 \pm 0.04$  mm year<sup>-1</sup>) (Table 1). In a scatterplot where each tree's annual increment in the drought year was plotted against its long term annual increment, the fitted regression slope was only 0.37, significantly less than the expected slope of 1.0 under the null hypothesis of no difference from long-term historical data (Figure 4). Trees with historically high mean annual increments were the most strongly affected by drought (Figure 4).

There was no evidence of growth increment anomalies in the year before the *El Niño*. The increment was  $1.26 \pm 0.13$  mm year<sup>-1</sup>, not significantly different from historical mean annual increment ( $p = 0.9$ ). The year after the drought, the annual increment ( $1.03 \pm 0.13$  mm year<sup>-1</sup>) was almost double the stem increment rate in the year that included the *El Niño* drought but still was 18% lower than the annual historic long-term annual increment, a significant difference ( $p < 0.001$ ).

#### ***Stem increments within and between tree size classes***

Annual increment differed between the three tree sizes classes ( $p = 0.008$ , Table 2) across years ( $p = 0.012$ , Table 2). Trees with DBH of 10-30 cm had lower historical annual increment than trees with DBH 30-50 cm and more than 50 cm ( $p < 0.001$ , Table 3), the same being observed before ( $p = 0.035$ ) and after ( $p = 0.011$ ) the drought. During the year that included drought, the annual increment of smaller trees was 51% lower than their historic increment, medium trees were by 67% lower and larger were 66% than their respective historic rates. There were no significant differences in increment rates between the three tree DBH classes during the drought ( $p = 0.86$ ). One year after the drought, smaller and larger trees almost attained their respective historical mean annual increments, but were still 8% and 10% lower, respectively. Medium sized trees had the slowest recovery in increment rate, being 27% lower than their historical mean ( $p = 0.004$ ).

Mean monthly increments also decreased during and after the drought among the DBH size classes. The mean monthly increment during the drought decreased in the medium sized trees (30-50 cm) by 66%, in large size class ( $\geq 50$  cm) by 65% and in small size class (10-30 cm) by 51% relative to the historic monthly mean rates. The small tree diameter class decreased less (51%) during the drought and had less increment variations throughout the year (Figure 5).

#### ***Stem increment within and between wood density classes***

There was no significant difference in the annual increment rate between wood density classes ( $p = 0.6$ , Table 2) and between years ( $p = 0.192$ , Table 2). Relative to the mean historical annual increment, depressed increments were observed during the *El Niño* year in 69%, 58% and 56% of individuals for, respectively, the low, medium and high wood density classes (Table 4). The year after the drought, low and medium wood density trees did not fully recover to their historical annual increment rates. Trees with low wood density had an annual increment still 34% lower than their historic mean ( $p = 0.01$ ), while trees of medium wood density had a rate 27% below their historical mean ( $p < 0.001$ ). Individuals with high wood density, however, did recover by the year after the drought to an increment rate which was not significantly different from their long-term rate ( $1.27 \pm 0.22$  mm year<sup>-1</sup>). The monthly increments across the three wood density classes tracked one another closely in all the three year-long periods of observation (Figure 6). Nonetheless, during the year that included the drought, the monthly increments showed greater variation both within and between wood density classes.

#### ***Stem increment within and between topography position classes***

There were differences in annual increment between topographic classes ( $p = 0.011$ , Table 2) and the size of these differences were different between drought and non-drought years ( $p < 0.001$ , Table 2). Trees in valleys had slightly lower annual increments ( $1.17 \pm 0.06$  mm year<sup>-1</sup>) than the trees located on the plateaus ( $1.32 \pm 0.06$  mm year<sup>-1</sup>) and slopes ( $1.30 \pm 0.09$ ) ( $p = 0.046$ ) in the historical series. For the year before the drought this same pattern was seen but was only marginally significant ( $p = 0.112$ ). Relative to their historical long-term mean rate, stem increments declined in all tree DBH classes during the drought year but did so slightly less in the valley (55% lower

than the long-term mean) than in the slope (62%) and plateau habitats (61%). One year after the drought, trees in the slope and on the plateaus rapidly recovered to their respective long-term annual increment rates, but the trees in the valley did not, being 41% lower than their long-term mean annual increment (Table 5). Mean differences between the historical annual increment and the 2016-2017 (immediate post-drought) year was significantly different ( $p < 0.001$ ) only for trees in the valley. Tree increments in the valley did not vary much from month to month along the *El Niño* year while trees on slopes and plateaus showed marked shrinkage in the driest months, and a sharp recovery right after rains resumed (Figure 7).

### ***Climate, topography and plant traits interactions***

The model that best described the monthly increment anomaly (AIC=3741.7) included the interaction of DBH and topographic classes with CWD (Figure 8). Monthly increment anomaly increases with CWD in slopes and plateaus, and this effect increases with tree diameter. Models including wood density interactions with CWD (AIC=3830.5) or with other variables performed very poorly (Supporting Information S8 and S9). Also, in Figure 8 when the water deficit decreased by two standard deviations, the increment anomaly decreased by 0.20 on the plateau and by 0.22 on slope in standard deviations for the smaller trees, 0.41 on the slopes and 1.06 in the valleys in medium sized trees and, 0.90 on slope and 0.72 on the plateaus in large trees. In addition, when the water deficit is higher than 50 mm (more negative) the increment anomalies became higher, above this number the standard deviation of increment anomalies is generally positive.

## **Discussion**

### ***Stem increment reduction during drought***

This study has evaluated the effects of the strong El Niño induced drought of 2015-2106 on the growth of *terra-firme* forest trees in central Amazon. We detected a strong reduction of tree growth (59.2%) during the drought, with moderate average recover in the following year. Large trees in plateaus and slopes suffered the largest reductions in growth, while no effect of wood



density was observed. The valley habitat suffered less during the drought, but apparently is lagging in its recover after it, while plateaus and slopes recovered much faster.

The 2015-2016 was a very extreme drought in Central Amazon. There was 6 months with water deficit (July 2015- October 2015, December 2015 and January 2016), high VPD, high radiation and elevated temperatures. Central Amazon region experienced a Maximum Climatological Water Deficit (MCWD) less than -100 mm in 2005 and 2010 drought (Saatchi *et al.*, 2013). Thus, the 2015-2016 drought in ZF-2 experienced a greater water deficit of -194 mm. This extreme drought caused a reduction in more than a half of the annual increment, as compared to the 14 years historical series. Growth reductions may have been triggered by stomatal closure, decreased photosynthesis and by increased respiration or both. Rising leaf temperatures during droughts, from 30.5° to 37.5°C, were shown to lead to decreased photosynthesis, and above 37.5°C to stomatal closure (Doughty & Goulden 2008). The stomatal closure also increase with the high evaporative demand because of high solar radiation during extreme droughts (Bonal *et al.*, 2016) and soil water deficit leads to a reduction of stomatal conductance to reduce tree transpiration (Stahl *et al.*, 2013). During the *El Niño* of 1998 the net primary production declined due to reduced photosynthesis and increased autotrophic and soil respiration rates (Cavaleri *et al.*, 2017). Therefore, the reduction of photosynthesis, carbon uptake, the stomatal closure increase, and respiration increase may reduce the carbon allocation in the xylem causing a reduction of the monthly and annual increment during the 2015-2016 drought.

### ***Stem increment among tree diameter sizes***

Growth reduction during drought was higher for larger trees, above 30 cm DBH than the other size classes. In previous studies, large trees have also been shown to have more pronounced seasonal growth variations (Silva *et al.*, 2002; Vieira *et al.*, 2004). In addition, growth reduction in large trees recorded in 2015-2016 was 65.6% compared to the historical series. The results of larger growth reductions in larger trees would suggest that leaf exposure to higher temperatures and VPD during droughts may be more determinant for physiological responses that culminate in reduced growth (Clark *et al.*, 2013; Bennett *et al.*, 2015), than the limitation of soil moisture. However, the stronger growth reductions of large trees in plateaus and slopes indicate that, both, the depletion of

soil moisture and the increased stress in the leaf-atmosphere boundary are together responsible for the growth responses observed here. Taller trees have longer hydraulic pathways (Ryan & Yoder, 1997; Poorter *et al.*, 2010) that can lead to hydraulic stress under decreased soil moisture. Soil water deficit leads to a reduction of stomatal conductance that diminishes tree transpiration (Stahl *et al.*, 2013), consequently reducing the carbon allocation to the stem.

Emergent trees in ZF-2 have a height greater than 40 m (Vieira *et al.*, 2005) which creates a microclimate for the understorey trees (Bennett *et al.*, 2015), thus smaller trees have less light availability that may explain the lower growth rate (Vieira *et al.*, 2004). As well, competition with large trees for nutrients and water could be a factor of lower annual and monthly increments during the drought and in the historical series (Bennett *et al.*, 2015). The small understorey trees are expected to be more protected from drought by the canopy of larger trees, which are exposed to higher temperature, radiation and VPD (Bennett *et al.*, 2015; McDowell & Allen, 2015). However, smaller trees could be at higher drought stress due to smaller roots and low access to soil moisture (Condit *et al.*, 1995). At the same time, we must acknowledge that our small tree class (10-30 cm DBH) does not really represent small trees with small roots. Thus, better assessment of the hypothesis of root limitation needs to incorporate trees in the 1-10 cm DBH class.

One year after the drought small and large trees classes recovered their annual increment rate. However, the medium size class (30-50) trees did not recover their annual increment rate. The annual increment of those trees in non-drought conditions was above 2 mm year<sup>-1</sup> (Figure 4), and during the drought trees reduced their increment by more than a half. Fast-growing trees have hydraulic characteristics that are more sensitive to water deficit (Sperry *et al.*, 2008). However, no supporting information exists to confirm the last hypothesis because the correlation between these two variables is weak yet significant ( $r = 0.15$ ,  $p = 0.008$ ).

#### ***Stem increment among tree wood density***

There was no significant effect of wood density on growth reduction during the drought. Yet, low wood density trees (<0.55 g/cm<sup>3</sup>) had comparatively the highest reduction (68.8%) in annual increment. Low wood density trees are more sensitive to water deficit, which resulted in a

greater reduction of stem increment (Hacke *et al.*, 2001; Nepstad *et al.*, 2007; Mendivelso *et al.*, 2014; Rowland *et al.*, 2014). This sensitivity was also observed a year after the drought, low and medium density trees did not recover their stem growth rate. However, high wood density individuals reduced the annual increment by more than a half, but a year after the drought the annual increment was recovered. A community approach of wood density, which considered a wide range of species, lead to a weak correlation between wood density and growth rate ( $r=-0.08$ ,  $p=0.16$ ) (Chave *et al.*, 2009; Poorter *et al.*, 2010).

### ***Stem increment among topography***

During the months with greater water deficit (more negative CWD value) the monthly increment of trees located on plateaus and slopes had a significant decreased. These trees could be under water stress during the drought because of less soil water availability due to the far distance to the water table (Hodnett *et al.*, 1997; Cosme *et al.*, 2017). On the other hand, months with precipitation above 100 mm during the drought created a better growth conditions to trees in the plateaus and slopes, considering a higher water availability and high capacity of water retention in clay soils. These patterns suggested that plateaus individuals tended to have hydraulic traits associated with hydraulic safety (Cosme *et al.*, 2017) due to rapid growth rate recovered whenever a precipitation above 100 mm was observed. The trees in the valleys had lower annual increments compared to the trees on the slope and plateaus trees during the 2001-2015 period. During the drought year, valley trees reduced their monthly and annual increment as well, however, trees stem increment were more stable to precipitation variation suggesting a higher resistance to water deficit and higher efficiency of water uptake (Cosme *et al.*, 2017). However, even in the driest month (September 2015), trees in the valley did not increased their increment due to a more aerobic condition. Two possibilities may explain this behavior: (i) the 2015-2016 drought intensity may have caused water deficit in the valleys soils, which might have caused a water stress in the valleys trees due to their shallow roots (Fan *et al.*, 2017) or (ii) the soils of the valleys might have kept humidity without anoxic conditions, however, the high temperatures and high evaporative demand during the drought may have increased the stomatal closure and decreased the growth rate of trees in the valley. The first statement would have caused a greater decreased of the annual increment,

therefore, the second hypothesis suggested a moderate growth reduction as observed during this drought.

## **Conclusion**

The unprecedented drought of 2015-2016 caused by *El Niño* significantly reduced the monthly and annually stem diameter increments compared to the average forest increment. Stem increment had an immediate response to water deficit unlike tree mortality caused by hydraulic failure during the drought. Here we provide strong evidences that larger trees located on the plateaus suffered the most. A year after the drought, the forest growth rate did not attain the historical average growth rate. Specifically, the medium sized tree classes and trees located in the valleys may have difficulties in recovering their average growth rate. Droughts in the last decades were intensifying and the forest response to successive drought would endanger the forest carbon pool, the forest diversity and the forest resilience. For instance, this study emphasizes the negative response of the tree stem increment during and after a natural and unprecedented drought which may contribute to climate and carbon models. In addition, the importance of considering the decline in tree growth would not be observed, if the forest inventory have been occurred after the event. Therefore, monthly measuring of the stem increment contributes greatly to observation of the effect of extreme climate events. Future studies could be carried out to understand and identify which functional traits and mechanisms are better correlated to tree growth during extreme droughts such as dendrometric, physiological, hydraulic and xylem anatomical traits.

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## Tables

Table 1. Annual and monthly diameter growth increments in mm  $\pm$  95% CI of the mean of 325 trees in two transects.

	<b>2001-2015</b>	<b>2014-2015</b>	<b>2015-2016</b>	<b>2016-2017</b>
Annual increment (mm year <sup>-1</sup> )	1.25 $\pm$ 0.04	1.26 $\pm$ 0.13	0.51 $\pm$ 0.10	1.03 $\pm$ 0.13
Minimum individual annual increment (mm year <sup>-1</sup> )	-2.00 $\pm$ 0.86	-1.12	-3.50	-1.91
Maximum individual annual increment (mm year <sup>-1</sup> )	7.66 $\pm$ 0.83	6.96	4.29	6.79
Percentage of all individuals with negative annual growth rates	9.6% $\pm$ 1.7%	7.7%	25.8%	8.6%
Average monthly increment (mm month <sup>-1</sup> )	0.11 $\pm$ 0.01	0.11	0.04	0.09
Minimum monthly increment (mm month <sup>-1</sup> )	0.01 $\pm$ 0.02	-0.003	-0.16	-0.02
Maximum monthly increment (mm v)	0.22 $\pm$ 0.02	0.21	0.27	0.17
Annual total precipitation (mm)	2564.6 $\pm$ 164.3	2609.6	1715.6	2467.6
Number of dry season months (precipitation < 100 mm month <sup>-1</sup> )	2 $\pm$ 0.6	2	6	2
Total precipitation in the dry season (mm)	143.4 $\pm$ 47.5	133.3	317.9	146.8
Minimum monthly precipitation (mm)	51.3 $\pm$ 13.0	39.4	20.1	70.9
Maximum monthly precipitation (mm)	434.0 $\pm$ 38.4	399.3	342.9	371.6

Table 2. Repeated measures ANOVA for the 325 trees (subjects) in the four time periods analyzed: the historical long-term mean annual increment, the year 2014-2015, the drought year and the year 2016-2017 and the interaction between the diameter, wood density and topography classes.

Source of variation	SS	df	MS	F-ratio	P-value	G-G	H-F	
<i>Between Subjects</i>								
Diameter classes (DBH)	23.53	2	11.77	4.925	0.008			**
Wood density classes (WD)	2.55	2	1.28	0.534	0.587			
Topography classes (TC)	22.09	2	11.04	4.622	0.011			*
DBH x WD	42.87	4	10.72	4.486	0.002			**
DBH x TC	18.70	4	4.68	1.957	0.101			
WD x TC	33.38	4	8.34	3.492	0.008			**
DBH x WD x TC	74.97	8	9.37	3.922	<0.001			***
Error	709.66	297	2.39					
<i>Within Subjects</i>								
Time	65.37	3	21.79	38.694	<0.001	<0.001	<0.001	***
Time x DBH	9.30	6	1.55	2.753	0.012	0.015	0.012	*
Time x WD	4.90	6	0.82	1.451	0.192	0.199	0.192	
Time x TC	14.68	6	2.45	4.344	<0.001	<0.001	<0.001	***
Time x DBH x WD	24.37	12	2.03	3.606	<0.001	<0.001	<0.001	***
Time x DBH x CT	18.89	12	1.57	2.796	0.001	0.001	0.001	***
Time x WD x CT	15.07	12	1.26	2.230	0.009	0.012	0.009	**
Time x DBH x WD x CT	24.87	24	1.04	1.840	0.008	0.011	0.009	**
Error	501.78	891	0.56					

SS: Sum of squares; df: degrees of freedom; MS: Mean sum of squares G-G: Greenhouse-Geisser  $\epsilon = 0.906$ ; H-F: Huynh-Feldt  $\epsilon = 0.25$ .

Table 3. Annual stem increments in mm  $\pm$  95% CI of the mean of 325 trees categorized by diametric classes.

<b>Diametric class (cm)</b>	<b>~ N</b>	<b>2001-2015 (mm year<sup>-1</sup>)</b>	<b>2014-2015 (mm year<sup>-1</sup>)</b>	<b>2015-2016 (mm year<sup>-1</sup>)</b>	<b>2016-2017 (mm year<sup>-1</sup>)</b>
[10-30>	177	1.07 $\pm$ 0.05	1.10 $\pm$ 0.18	0.52 $\pm$ 0.11	0.93 $\pm$ 0.16
[30-50>	97	1.49 $\pm$ 0.08	1.33 $\pm$ 0.22	0.50 $\pm$ 0.20	1.08 $\pm$ 0.27
$\geq 50$	51	1.47 $\pm$ 0.11	1.65 $\pm$ 0.42	0.50 $\pm$ 0.34	1.32 $\pm$ 0.33

Table 4. Annual stem increments in mm  $\pm$  95% CI of the mean of 325 trees categorized by wood density.

<b>Wood density</b>	<b>N</b>	<b>2001-2015 (mm year<sup>-1</sup>)</b>	<b>2014-2015 (mm year<sup>-1</sup>)</b>	<b>2015-2016 (mm year<sup>-1</sup>)</b>	<b>2016-2017 (mm year<sup>-1</sup>)</b>
Low	43	1.37 $\pm$ 0.13	1.21 $\pm$ 0.49	0.43 $\pm$ 0.27	0.90 $\pm$ 0.37
Medium	169	1.25 $\pm$ 0.06	1.28 $\pm$ 0.18	0.53 $\pm$ 0.13	0.91 $\pm$ 0.18
High	113	1.21 $\pm$ 0.06	1.25 $\pm$ 0.22	0.53 $\pm$ 0.18	1.27 $\pm$ 0.22

Table 5. Annual stem increments in mm  $\pm$  95% CI of the mean of 325 trees categorized by topography.

<b>Topography</b>	<b>N</b>	<b>2001-2015 (mm year<sup>-1</sup>)</b>	<b>2014-2015 (mm year<sup>-1</sup>)</b>	<b>2015-2016 (mm year<sup>-1</sup>)</b>	<b>2016-2017 (mm year<sup>-1</sup>)</b>
Valley	125	1.17 $\pm$ 0.06	1.32 $\pm$ 0.21	0.52 $\pm$ 0.17	0.69 $\pm$ 0.15
Slope	65	1.30 $\pm$ 0.09	1.12 $\pm$ 0.33	0.49 $\pm$ 0.20	1.33 $\pm$ 0.36
Plateau	135	1.32 $\pm$ 0.06	1.27 $\pm$ 0.21	0.51 $\pm$ 0.15	1.22 $\pm$ 0.21

## Figures

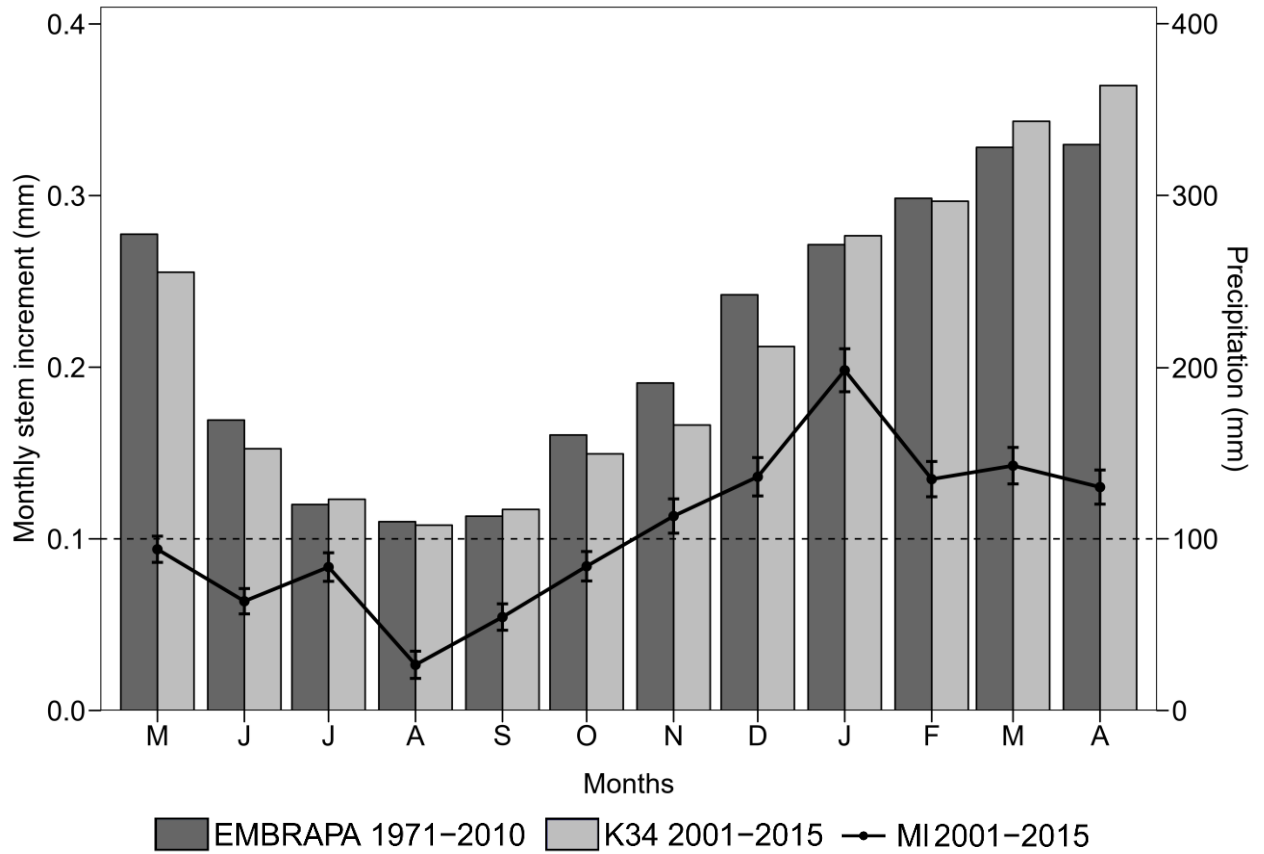


Figure 1. Mean monthly precipitation (mm) from the flux tower K34 (monthly mean of May 2001 to April 2015) and from EMBRAPA Western Amazon meteorological station (monthly mean of 1971-2010) in bars. Mean monthly increment (mm) from the 325 individuals of the transects since May 2001 to April 2015 in black solid line.

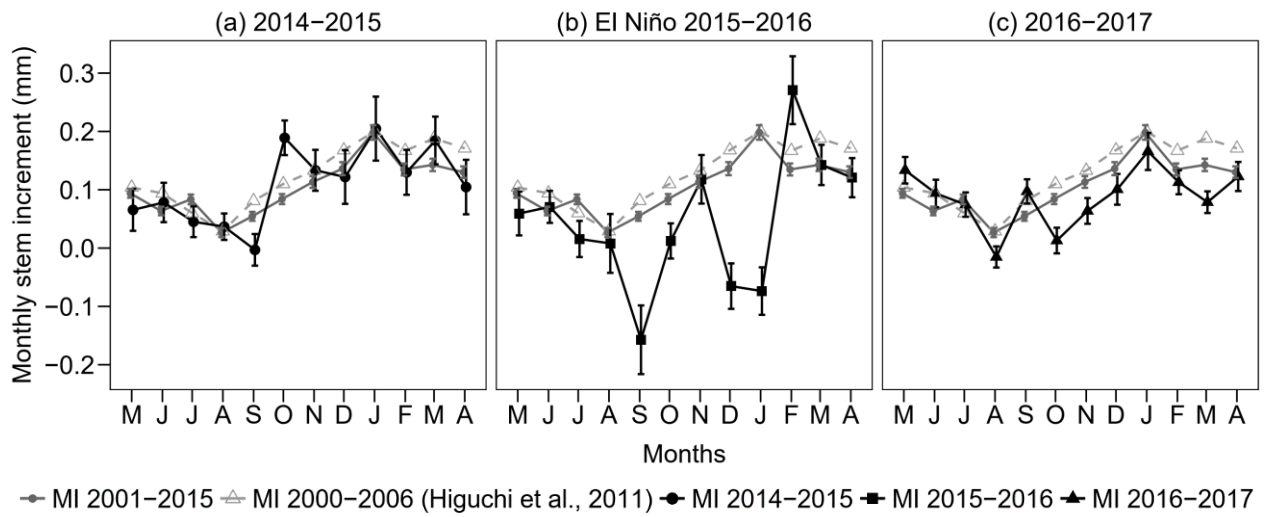


Figure 2. Historical Monthly Stem Increment (MI) of the 325 individuals (2001-2015) compared with the MI in (a) the pre-drought year of 2014-2015, (b) the *El Niño* drought year of 2015-2016 and (c) the post-drought year of 2016-2017.



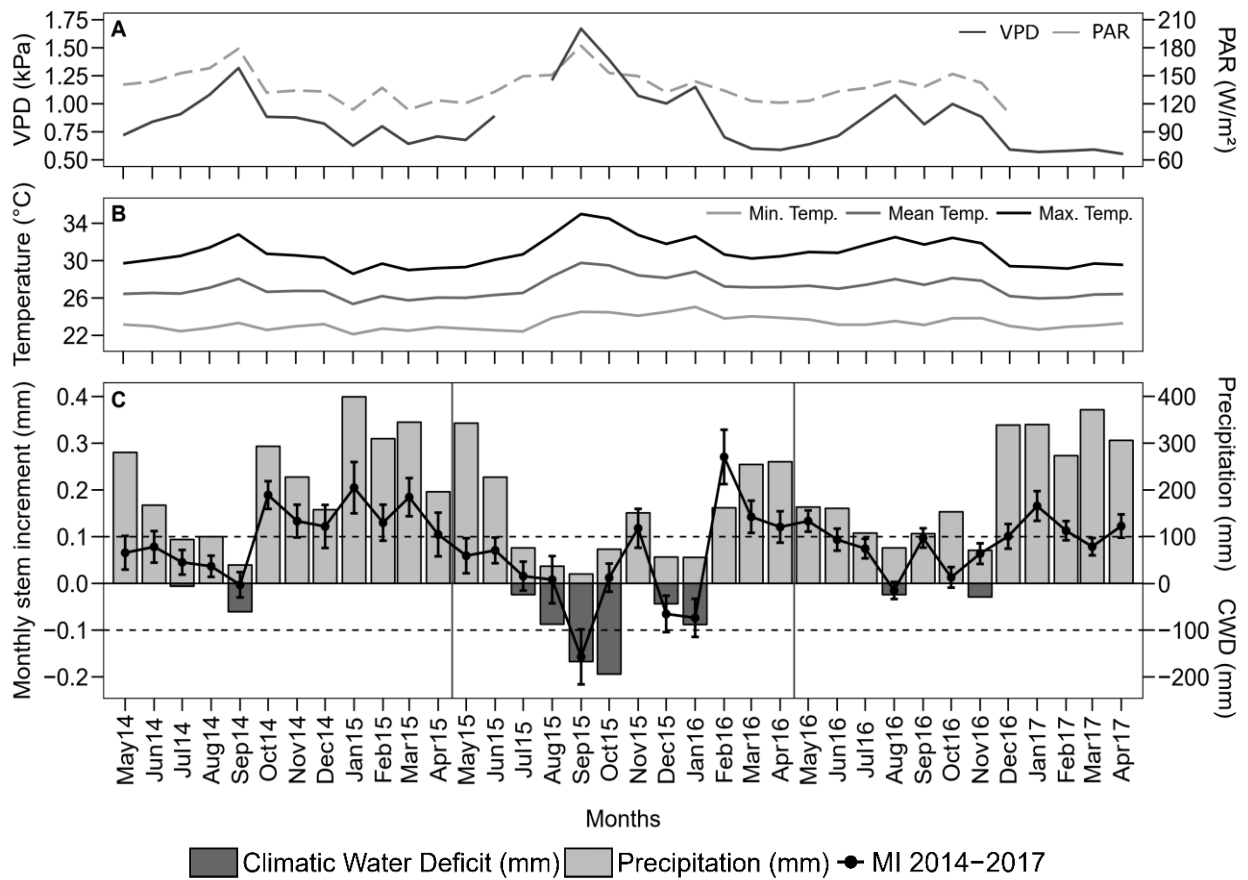


Figure 3. (A) Mean monthly Vapor Pressure Deficit (kPa) and mean monthly Photosynthetically Active Radiation ( $W/m^2$ ); (B) mean monthly minimum, mean and maximum temperatures; (C) monthly precipitation (mm), monthly Climatological Water Deficit (mm) and monthly stem increment with 95% CI (mm) from May 2014 until April 2017.

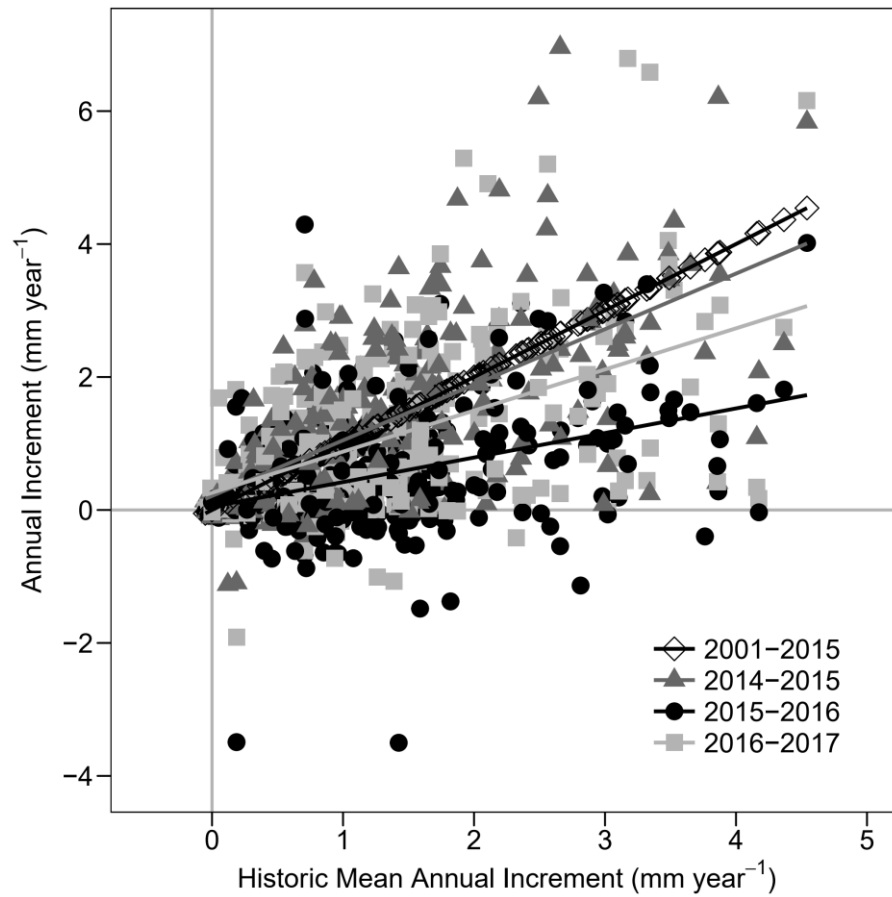


Figure 4. Scatterplots of the Annual Increment of each of the 325 individuals -- in the pre-drought year, the drought year and the post-drought year -- plotted against the same individual's historic mean annual increment (2001-2015). Slope values:  $\beta_1$  2001-2015 = 1.00,  $\beta_1$  2014-2015 = 0.84,  $\beta_1$  = 0.37 2015-2016,  $\beta_1$  2016-2017 = 0.62.

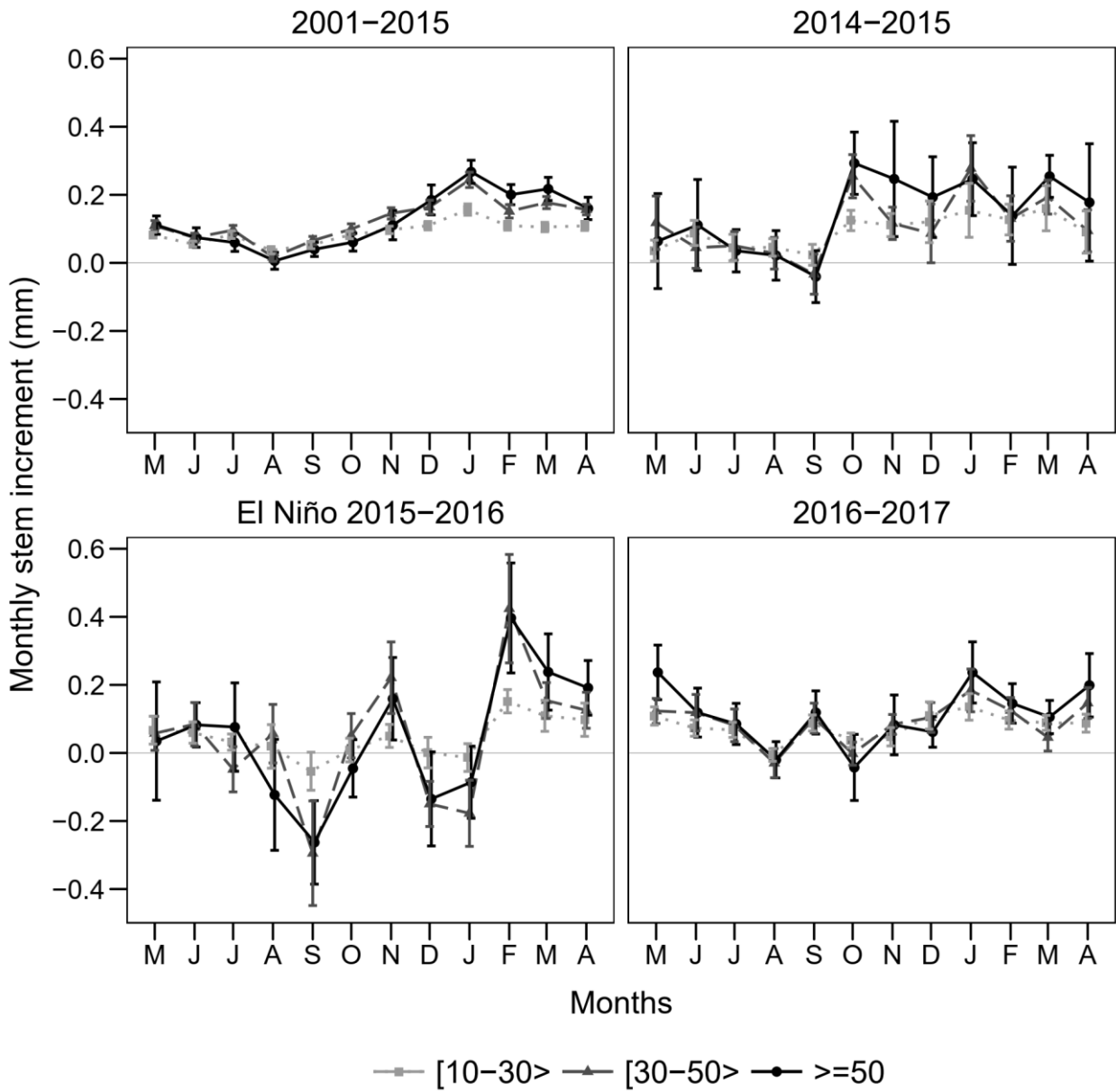


Figure 5. Monthly stem increment (mm) by Diameter Breast Height (DBH) classes.

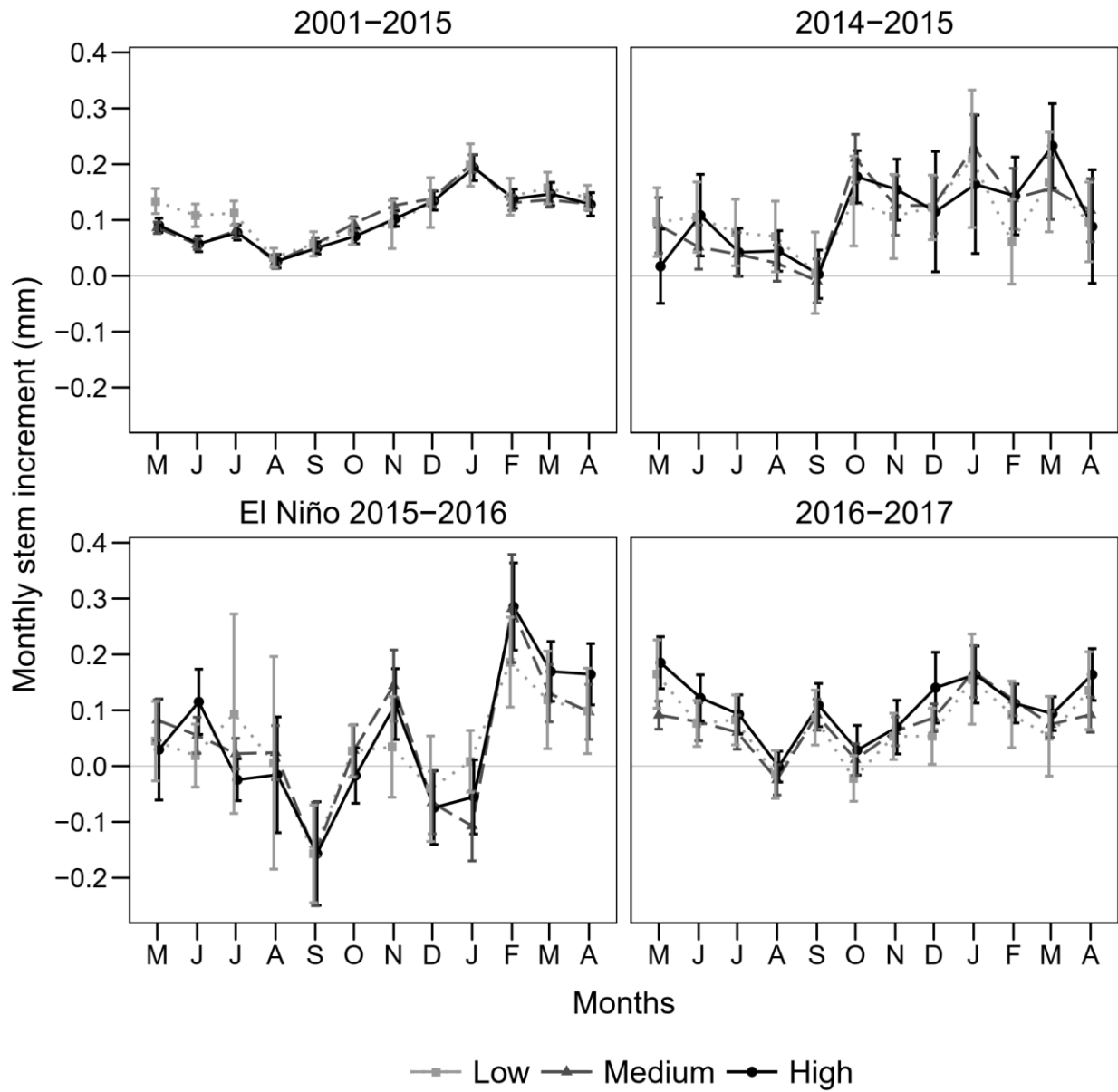


Figure 6. Monthly stem increment (mm) by wood density (WD) classes: low ( $WD < 0.55 \text{ g/cm}^3$ ), medium ( $0.55 \text{ g/cm}^3 \leq WD < 0.75 \text{ g/cm}^3$ ) and high density ( $WD \geq 0.75 \text{ g/cm}^3$ ).

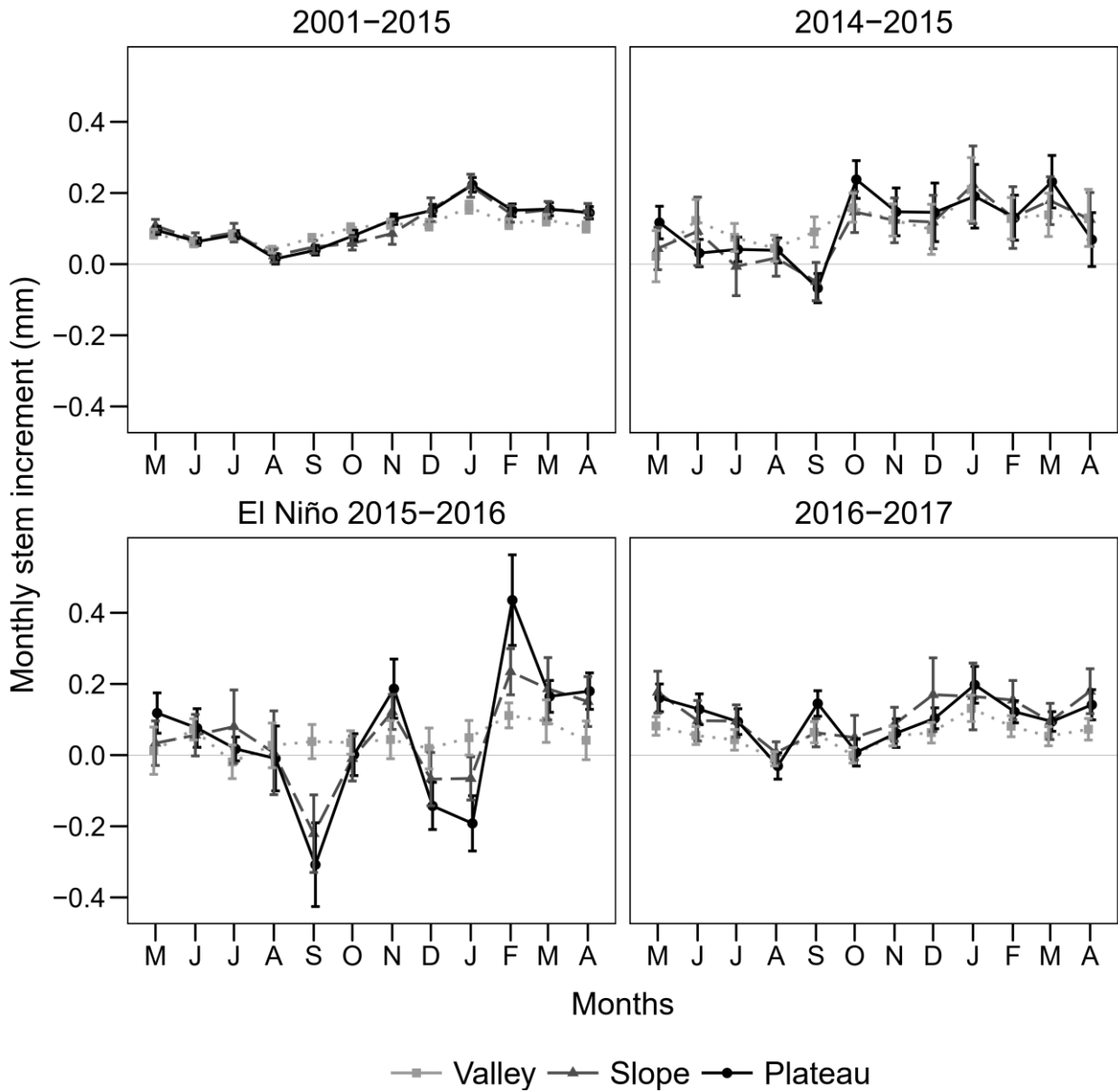


Figure 7. Monthly stem increment (mm) by topography: valley, slope and plateau.

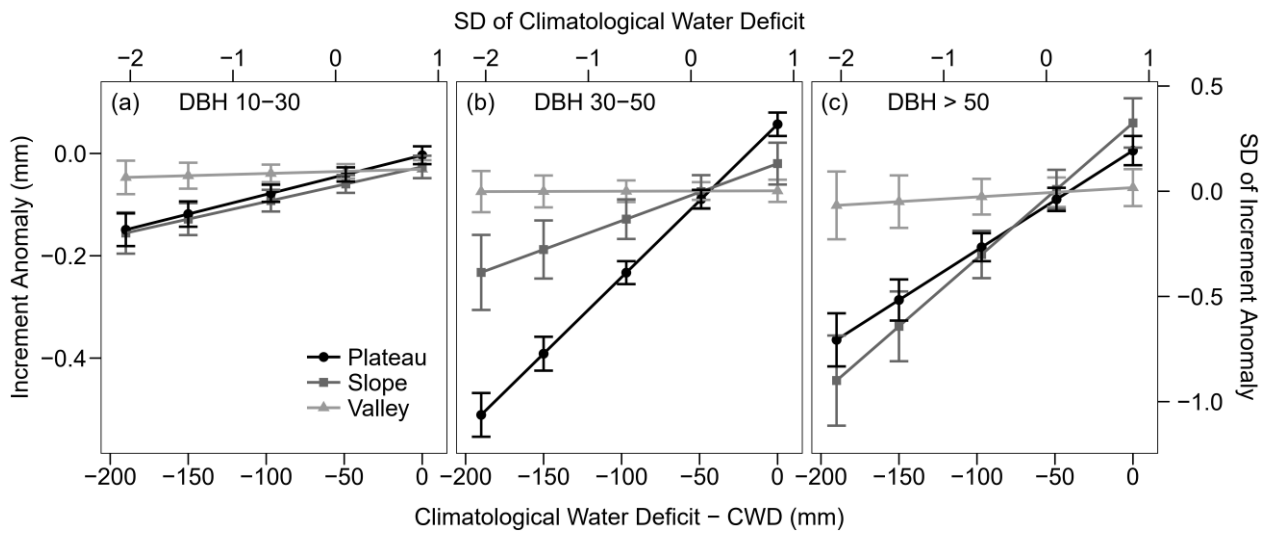


Figure 8. Effect of the interaction between Climatological Water Deficit (CWD), Diameter Breast Height (DBH) and topography classes: plateau (black line), slope (grey line) and valley (light grey line) to model increment anomaly.

## Supplementary information

S1. Wood density (WD – g cm<sup>-3</sup>) of the 161 species with dendrometer bands.

N	Family	Genus	Epithet	Subspecies	WD (g cm <sup>3</sup> )	Level	Ref.
1	Anacardiaceae	Astronium	lecointei		0.79	S	7
2	Annonaceae	Duguetia	pyncastera		0.729	G	20
3	Annonaceae	Guatteria	citriodora		0.516	S	15
4	Annonaceae	Guatteria	scytophylla		0.515	S	20
5	Annonaceae	Unonopsis	duckei		0.656	G	15
6	Apocynaceae	Aspidosperma	nitidum		0.764	S	20
7	Apocynaceae	Geissospermum	argenteum		0.85	S	18
8	Apocynaceae	Himatanthus	bracteatus		0.53	S	20
9	Apocynaceae	Parahancornia	fasciculata		0.473	S	20
10	Bignoniaceae	Jacaranda	copaia		0.35	S	11
11	Burseraceae	Dacryodes	nitens		0.49	S	20
12	Burseraceae	Protium			0.619	G	15,16,18
13	Burseraceae	Protium	apiculatum		0.63	S	18
14	Burseraceae	Tetragastris	panamensis		0.77	S	6
15	Burseraceae	Trattinnickia	burserifolia		0.5	S	9
16	Caryocaraceae	Caryocar	glabrum	glabrum	0.81	S	12
17	Chrysobalanaceae	Couepia	elata		0.769	S	20
18	Chrysobalanaceae	Licania	adolphoduckei		0.844	G	20
19	Chrysobalanaceae	Licania	caudata		0.844	G	20
20	Chrysobalanaceae	Licania	hypoleuca		0.844	G	20
21	Chrysobalanaceae	Licania	macrophylla		0.76	S	7
22	Chrysobalanaceae	Licania	micrantha		0.779	S	15
23	Chrysobalanaceae	Licania	oblongifolia		0.88	S	11
24	Chrysobalanaceae	Licania	reticulata		0.844	G	20
25	Chrysobalanaceae	Licania	sandwithii		0.882	S	20
26	Clusiaceae	Dystovomita	brasiliensis		0.654	F	20
27	Clusiaceae	Symphonia	globulifera		0.58	S	7
28	Combretaceae	Buchenavia	grandis		0.753	S	16
29	Combretaceae	Buchenavia	macrophylla		0.896	S	13
30	Combretaceae	Buchenavia	sericocarpa		0.711	G	20
31	Dichapetalaceae	Tapura	amazonica	manausensis	0.66	S	13
32	Dichapetalaceae	Tapura	guianensis		0.58	S	20
33	Elaeocarpaceae	Sloanea	nitida		1.1	S	17
34	Euphorbiaceae	Drypetes	variabilis		0.71	S	9
35	Euphorbiaceae	Hevea	guianensis		0.52	S	13
36	Euphorbiaceae	Micrandra	siphonioides		0.577	S	15
37	Euphorbiaceae	Pausandra	macropetala		0.59	G	20
38	Euphorbiaceae	Pera	bicolor		0.7	S	13

N	Family	Genus	Epithet	Subspecies	WD		Ref.
					(g cm <sup>3</sup> )	Level	
39	Fabaceae	Andira	unifoliolata		0.711	S	15
40	Fabaceae	Balizia	pedicellaris		0.497	S	20
41	Fabaceae	Dipteryx	odorata		0.97	S	12
42	Fabaceae	Eperua	duckeana		0.764	S	15
43	Fabaceae	Eperua	glabriflora		0.743	S	15
44	Fabaceae	Hymenolobium	excelsum		0.66	S	11
45	Fabaceae	Macrobium	limbatum		0.58	S	19
46	Fabaceae	Monopteryx	inpaie		0.73	G	19
47	Fabaceae	Peltogyne	excelsa		0.876	G	15
48	Fabaceae	Pterocarpus	officinalis		0.631	G	20
49	Fabaceae	Pterocarpus	rohrii		0.829	S	13
50	Fabaceae	Swartzia			0.871	G	20
51	Fabaceae	Swartzia	corrugata		0.808	S	15
52	Fabaceae	Swartzia	ingifolia		0.768	S	15
53	Fabaceae	Swartzia	lamellata		0.871	G	20
54	Fabaceae	Swartzia	panacoco		0.97	S	11
55	Fabaceae	Swartzia	recurva		0.9	S	19
56	Fabaceae	Swartzia	reticulata		0.871	G	20
57	Fabaceae	Tachigali	myrmecophila		0.56	S	8
58	Fabaceae	Tachigali	venusta		0.56	S	18
59	Fabaceae	Taralea	oppositifolia		1.1	S	13
60	Fabaceae	Zygia	racemosa		0.725	S	15
61	Goupiaceae	Goupia	glabra		0.69	S	11
62	Humiriaceae	Endopleura	uchi		0.74	S	7
63	Humiriaceae	Sacoglottis	ceratocarpa		0.77	G	7
64	Humiriaceae	Vantanea	guianensis		0.816	S	16
65	Lauraceae	Aniba	ferrea		0.597	G	20
66	Lauraceae	Aniba	hostmanniana		0.718	S	15
67	Lauraceae	Aniba	parviflora		0.67	S	11
68	Lauraceae	Licaria	cannella	angustata	0.82	S	13
69	Lauraceae	Licaria	cannella	cannella	0.82	S	13
70	Lauraceae	Licaria	cannella	tenuicarpa	0.82	S	13
71	Lauraceae	Licaria	martiniana		0.791	G	20
72	Lauraceae	Licaria	pachycarpa		0.791	G	20
73	Lauraceae	Licaria	rodriguesii		0.791	G	20
74	Lauraceae	Mezilaurus	itauba		0.7	S	11
75	Lauraceae	Ocotea	floribunda		0.408	S	20
76	Lauraceae	Ocotea	olivacea		0.545	G	20
77	Lauraceae	Ocotea	percurrens		0.525	S	15
78	Lauraceae	Ocotea	splendens		0.45	S	20
79	Lauraceae	Ocotea	subterminalis		0.545	G	20
80	Lauraceae	Rhodostemonodaphne	recurva		0.395	G	20



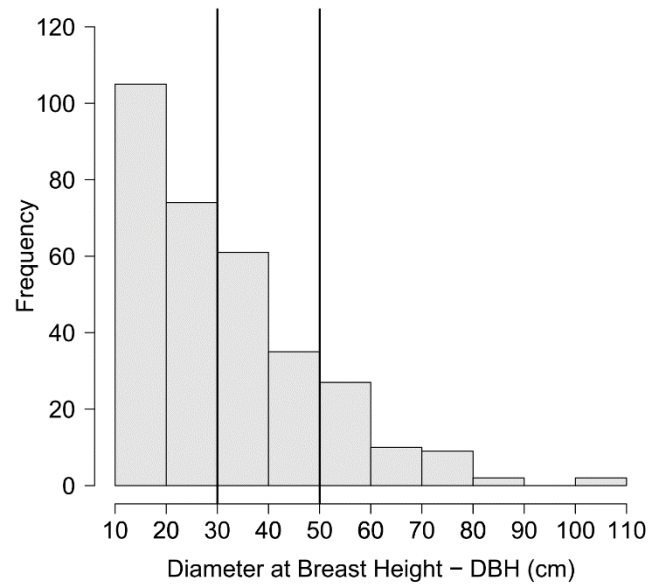
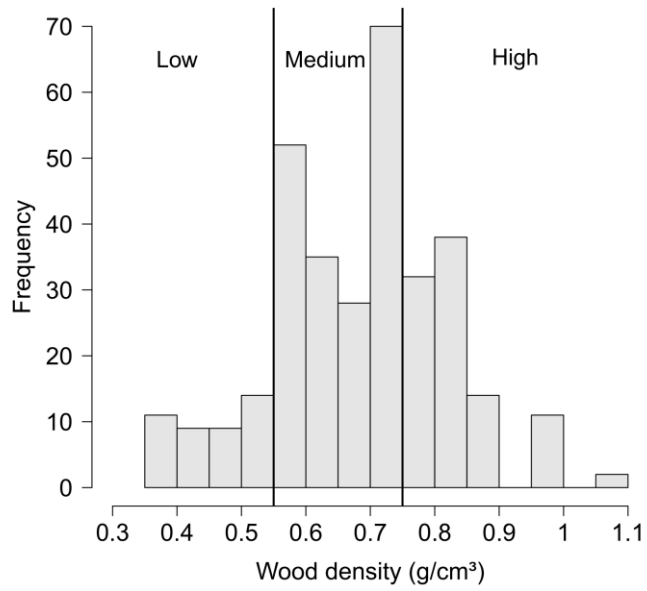
N	Family	Genus	Epithet	Subspecies	WD		Ref.
					(g cm <sup>3</sup> )	Level	
81	Lecythidaceae	Cariniana	integrifolia		0.49	S	11
82	Lecythidaceae	Cariniana	micrantha		0.71	S	13
83	Lecythidaceae	Eschweilera	bracteosa		0.83	S	18
84	Lecythidaceae	Eschweilera	coriacea		0.671	S	15
85	Lecythidaceae	Eschweilera	cyathiformis		0.75	G	15,18
86	Lecythidaceae	Eschweilera	laevicarpa		0.75	G	15,18
87	Lecythidaceae	Eschweilera	romeu-cardosoi		0.75	G	15,18
88	Lecythidaceae	Eschweilera	tessmannii		0.751	S	15
89	Lecythidaceae	Eschweilera	truncata		0.75	G	15,18
90	Lecythidaceae	Eschweilera	wachenheimii		0.75	S	15
91	Lecythidaceae	Gustavia	elliptica		0.648	S	15
92	Lecythidaceae	Gustavia	hexapetala		0.716	S	20
93	Lecythidaceae	Lecythis			0.817	G	20
94	Lecythidaceae	Lecythis	graciana		0.826	S	20
95	Lecythidaceae	Lecythis	pisonis		0.84	S	9
96	Lecythidaceae	Lecythis	prancei		0.833	S	15
97	Lecythidaceae	Lecythis	zabucajo		0.817	G	20
98	Malpighiaceae	Pterandra	arborea		0.652	F	20
99	Malvaceae	Bombacopsis	macrocalyx		0.56	S	19
100	Malvaceae	Rhodognaphalopsis	duckei		0.514	F	20
101	Malvaceae	Scleronema	micranthum		0.59	S	11
102	Malvaceae	Sterculia	excelsa		0.455	S	16
103	Moraceae	Brosimum	lactescens		0.78	S	13
104	Moraceae	Brosimum	parinarioides		0.57	S	8
105	Moraceae	Brosimum	parinarioides	parinarioides	0.57	S	8
106	Moraceae	Brosimum	rubescens		0.73	S	8
107	Moraceae	Brosimum	utile	ovatifolium	0.525	S	15
108	Moraceae	Helianthostylis	sprucei		0.591	S	15
109	Moraceae	Maquira	sclerophylla		0.57	S	8
110	Myristicaceae	Iryanthera	juvensis		0.614	S	15
111	Myristicaceae	Iryanthera	lancifolia		0.582	G	15,16
112	Myristicaceae	Iryanthera	macrophylla		0.582	G	15,16
113	Myristicaceae	Iryanthera	paradoxa		0.582	G	15,16
114	Myristicaceae	Iryanthera	sagotiana		0.551	S	16
115	Myristicaceae	Iryanthera	ulei		0.568	S	15
116	Myristicaceae	Osteophloeum	platyspermum		0.52	S	13
117	Myristicaceae	Virola	caducifolia		0.488	S	15
118	Myristicaceae	Virola	calophylla	calophylla	0.64	S	13
119	Myristicaceae	Virola	guggenheimii		0.565	G	8,13,15,19
120	Myristicaceae	Virola	mollissima		0.565	G	8,13,15,19
121	Myristicaceae	Virola	pavonis		0.45	S	19
122	Myristicaceae	Virola	sebifera		0.7	S	13

N	Family	Genus	Epithet	Subspecies	WD		Ref.
					(g cm <sup>3</sup> )	Level	
123	Myristicaceae	Virola	venosa		0.59	S	15
124	Myrtaceae	Marlierea	caudata		0.843	G	13
125	Myrtaceae	Myrcia	magnoliifolia		0.813	G	20
126	Nyctaginaceae	Neea	floribunda		0.62	S	20
127	Olacaceae	Aptandra	tubicina		0.605	S	16
128	Olacaceae	Minuartia	guianensis		0.766	S	15
129	Quiinaceae	Lacunaria	jenmanii		0.749	G	15
130	Rubiaceae	Chimarrhis	barbata		0.71	S	13
131	Rubiaceae	Duroia	longifolia		0.6	G	15
132	Rubiaceae	Henriquezia	verticillata		0.892	S	13
133	Sapindaceae	Toulicia	guianensis		0.671	S	16
134	Sapotaceae	Chromolucuma	rubriflora		0.977	S	13
135	Sapotaceae	Chrysophyllum	sanguinolentum	balata	0.763	S	13
136	Sapotaceae	Chrysophyllum	ucuquirana- branca		0.684	S	15
137	Sapotaceae	Ecclinusa	guianensis		0.613	S	16
138	Sapotaceae	Micropholis	casiquiarensis		0.648	G	20
139	Sapotaceae	Micropholis	guyanensis		0.67	S	17
140	Sapotaceae	Micropholis	guyanensis	duckeana	0.68	S	15
141	Sapotaceae	Micropholis	guyanensis	guyanensis	0.626	S	15
142	Sapotaceae	Micropholis	splendens		0.884	S	20
143	Sapotaceae	Pouteria			0.802	G	11,15,17,20
144	Sapotaceae	Pouteria	anomala		0.726	S	15
145	Sapotaceae	Pouteria	gongrijpii		0.72	S	17
146	Sapotaceae	Pouteria	guianensis		0.9	S	11
147	Sapotaceae	Pouteria	laevigata		0.802	G	11,15,17,20
148	Sapotaceae	Pouteria	opposita		0.802	G	11,15,17,20
149	Sapotaceae	Pouteria	venosa	amazonica	0.802	G	11,15,17,20
150	Sapotaceae	Pouteria	williamii		0.802	G	11,15,17,20
151	Sapotaceae	Pradosia	cochlearia		0.73	S	20
152	Simaroubaceae	Simarouba	amara		0.35	S	11
153	Sterculiaceae	Sterculia			0.446	G	20
154	Sterculiaceae	Sterculia	duckei		0.446	G	20
155	Urticaceae	Coussapoa	trinervia		0.466	G	20
156	Urticaceae	Pourouma	ovata		0.379	G	16
157	Verbenaceae	Vitex	sprucei		0.644	G	20
158	Violaceae	Amphirrhox	longifolia		0.71	S	19
159	Vochysiaceae	Erisma	bicolor		0.56	S	18
160	Vochysiaceae	Qualea	paraensis		0.66	S	11
161	Vochysiaceae	Ruizterania	cassiquiarensis		0.54	G	14

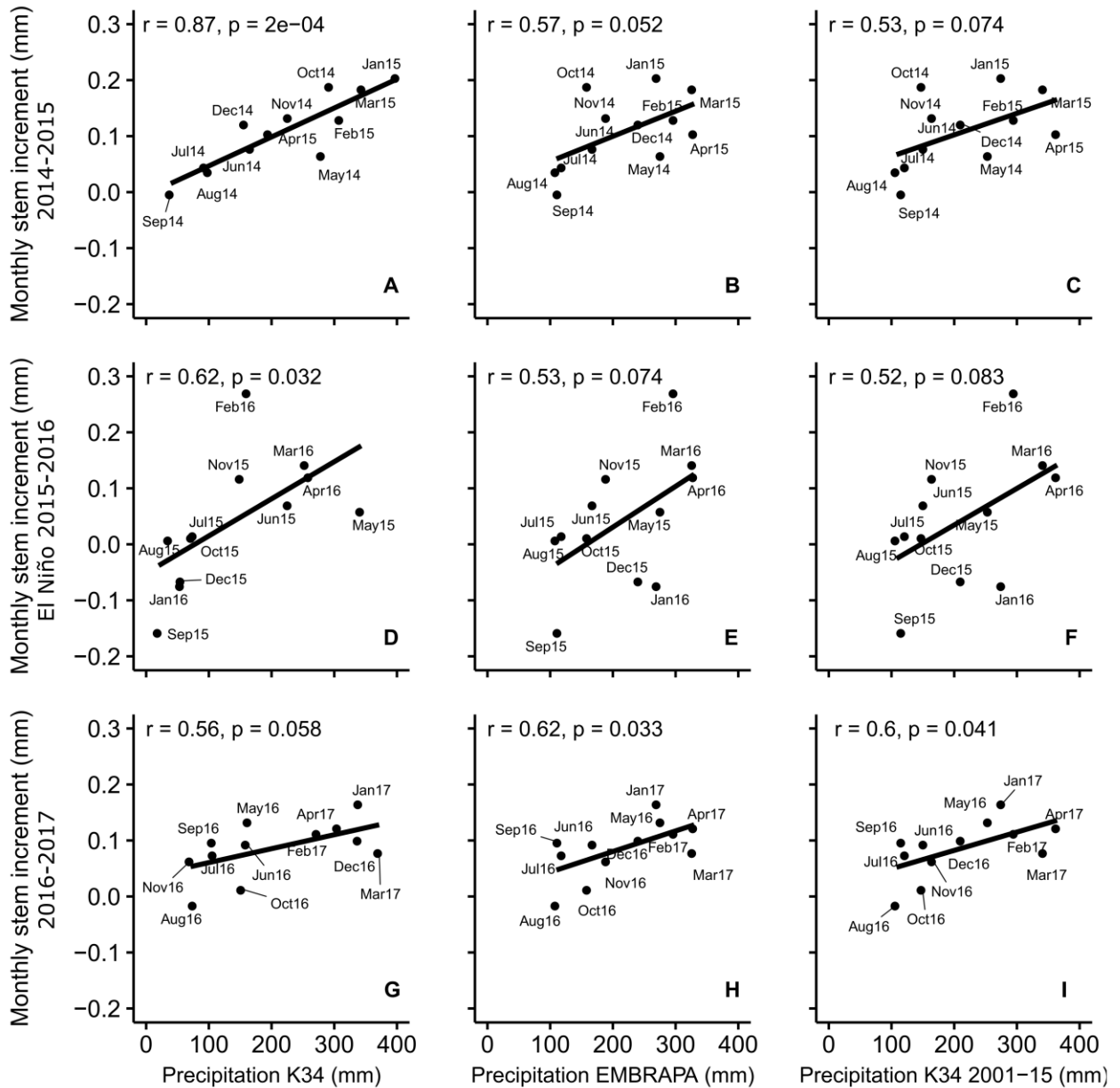
Wood density level: F= Family =S = Specie, G = Genus.

## S2. Wood density references.

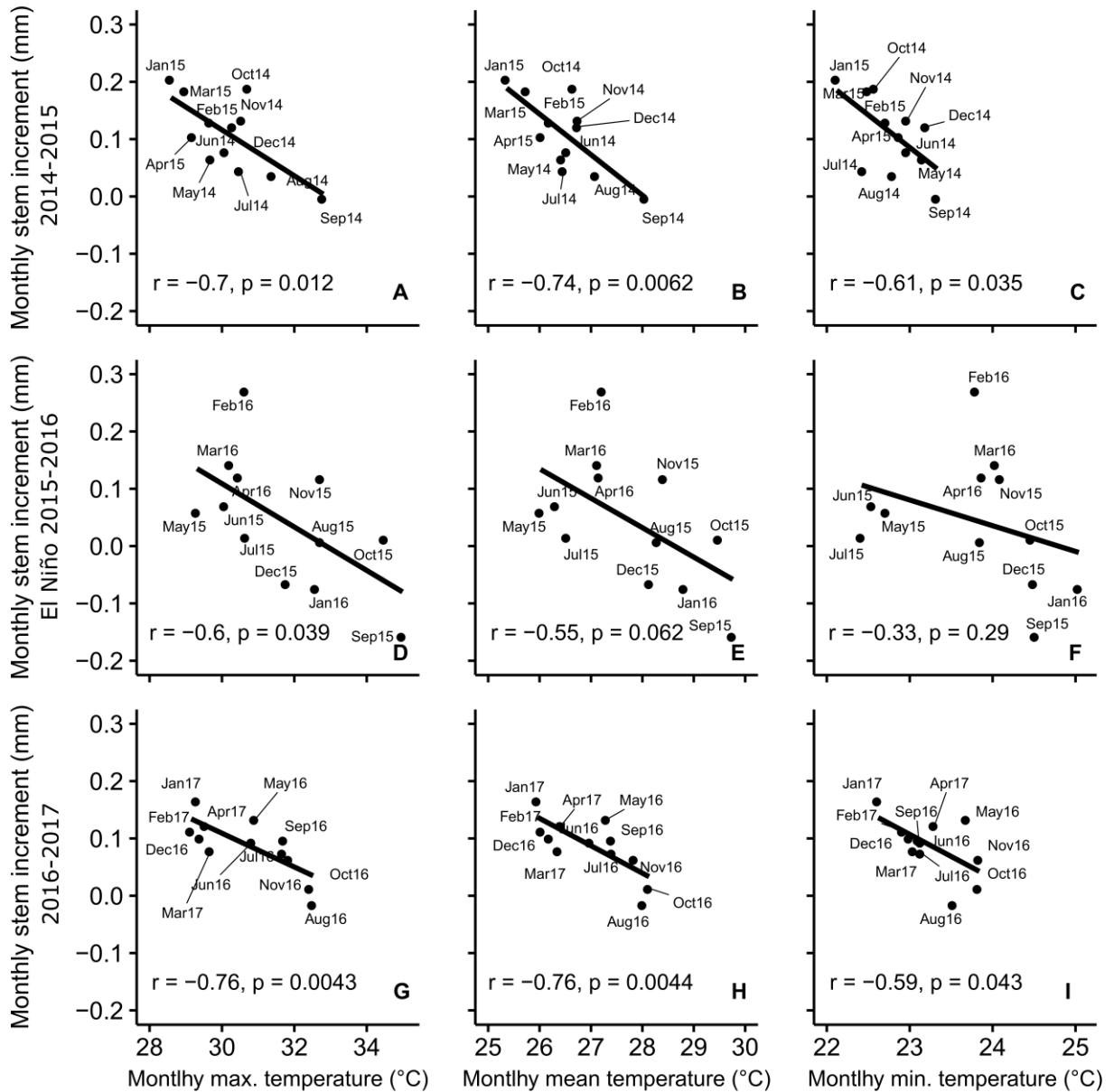
<b>Ref. Num.</b>	<b>Author</b>	<b>Title</b>
1	Loureiro & Silva (1968)	Catálogo das madeiras da Amazônia. Primeiro Volume
2	Loureiro & Silva (1968)	Catálogo das madeiras da Amazônia. Segundo Volume
3	Loureiro & Lisboa (1979)	Madeiras do Município de Aripuanã e suas utilidades (Mato Grosso).
4	Loureiro et al. (1979)	Essências madeireiras da Amazônia. Volume I
5	Loureiro et al. (1979)	Essências madeireiras da Amazônia. Volume II
6	Loureiro et al. (1997)	Essências madeireiras da Amazônia. Volume III
7	Loureiro et al. (2000)	Essências Madeireiras da Amazônia. Volume IV
8	Instituto Brasileiro de Desenvolvimento Florestal (1981)	Madeiras da Amazônia: Características e utilização; Floresta Nacional do Tapajós
9	Instituto Brasileiro de Desenvolvimento Florestal (1988)	Madeiras da Amazônia: Características e utilização; Estação Experimental de Curuá-Una
10	Mainieri & Chimelo (1989)	Fichas de características das madeiras brasileiras
11	Instituto Nacional de Pesquisas da Amazônia (1991)	Catálogo de madeiras da Amazônia: Características tecnológicas; Áreas de Hidrelétrica de Balbina
12	Vasconcellos et al. (2001)	Madeiras tropicais de uso industrial do Maranhão: Características tecnológicas
13	Paula & Costa (2011)	Densidade da madeira de 932 espécies nativas do Brasil
14	Instituto de Pesquisas Tecnológicas	Informações sobre madeiras < <a href="http://www.ipt.br/consultas_online/informacoes_sobre_madeira/busca">http://www.ipt.br/consultas_online/informacoes_sobre_madeira/busca</a> >
15	Nogueira et al. (2005)	Wood density in a dense forest in central Amazonia, Brazil
16	Nogueira et al. (2007)	Wood density in forests of Brazil's "arc of deforestation": Implications for biomass and flux of carbon from land-use change in Amazonia
17	Fearnside (1997)	Wood density for estimating forest biomass in Brazilian Amazonia
18	Dias & Marengo (2016)	Tree growth, wood and bark water content of 28 Amazonian tree species in response to variations in rainfall and wood density
19	Detienne & Jacquet (1983)	Atlas d'Identification des Bois de l'Amazonie et des Regions Voisines
20	Chave et al. (2009); Zanne et al. (2009)	Global Wood Density Database

S3. Frequency histogram for wood density ( $\text{g}/\text{cm}^3$ ) and Diameter Breast Height (cm).

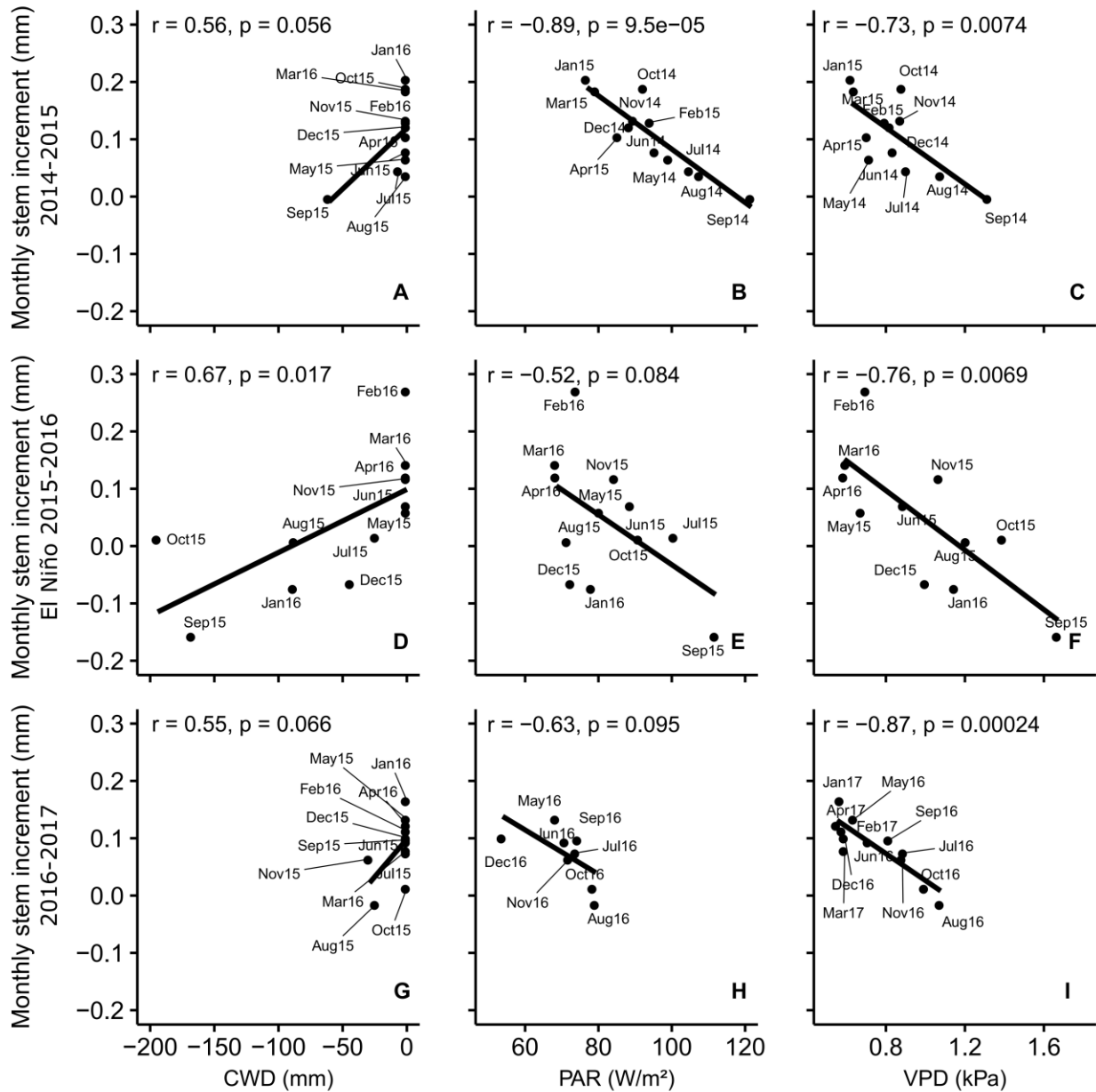
S4. Correlation between the monthly stem increment (mm) of 2014-2015, 2015-2016, 2016-2017 and the monthly precipitation (mm), monthly average precipitation (mm) from K34 tower (2001-2015) and the monthly historic precipitation (mm) from EMBRAPA Western Amazon meteorological station (1971-2010).



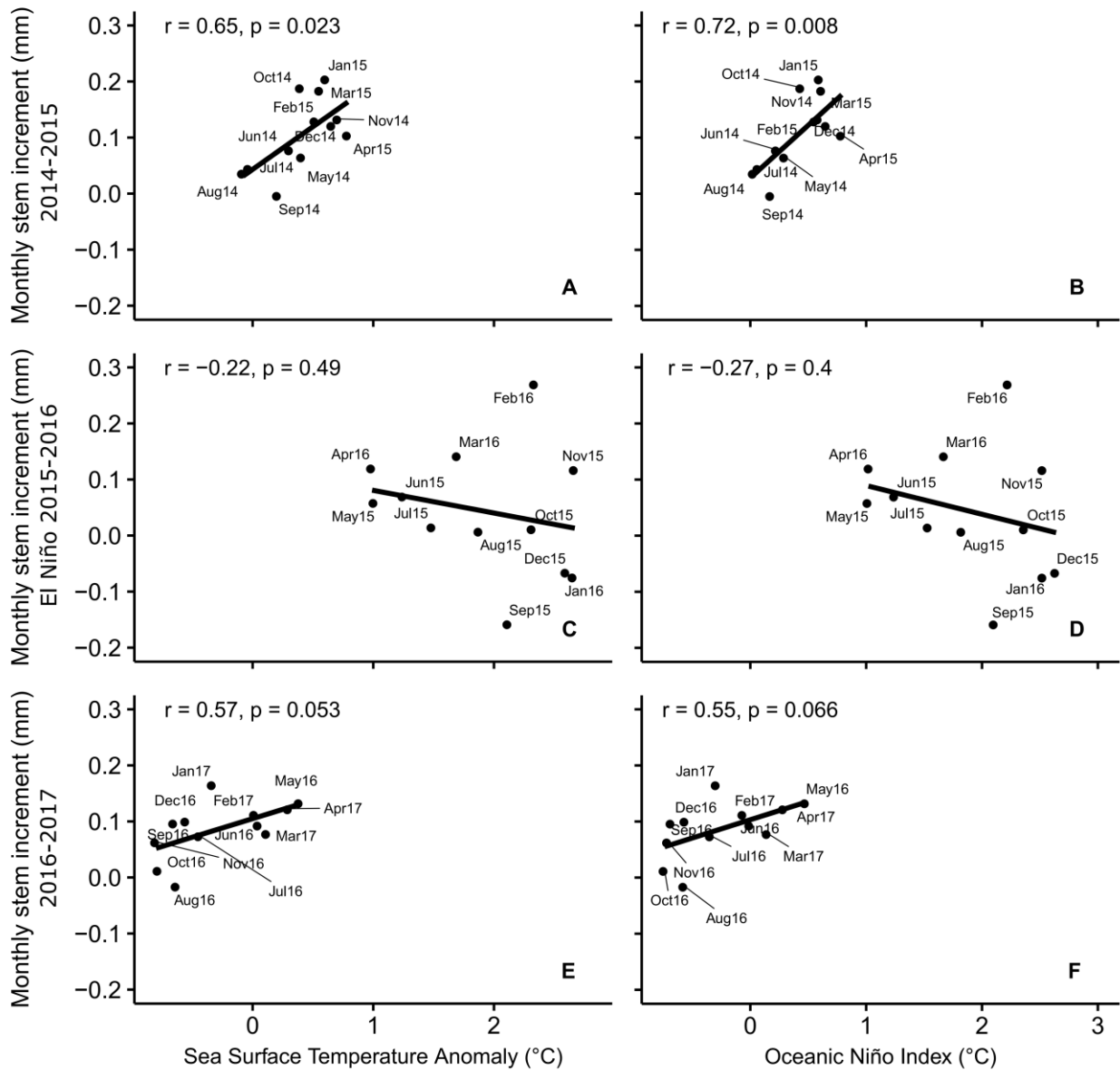
S5. Correlation between the monthly stem increment (mm) of 2014-2015, 2015-2016, 2016-2017 and monthly maximum, mean and minimum temperature (°C).



S6. Correlation between the monthly stem increment (mm) of 2014-2015, 2015-2016, 2016-2017 and Climatological Water Deficit (mm), Photosynthetically Active Radiation ( $W/m^2$ ) and Vapor Pressure Deficit (kPa).



S7. Correlation between the monthly stem increment (mm) of 2014-2015, 2015-2016, 2016-2017 and monthly sea surface temperature anomaly (°C) and the Oceanic Niño Index (°C).





S8. Linear Mix model parameters, standard errors, t values, AIC values and R<sup>2</sup> for categoric variables.

Parameter	Effect	Estimates	Std. Error	t value	Variance	St. Dev.	Pr(> t )	AIC	BIC	R <sup>2</sup> m	R <sup>2</sup> c
ANOM ~ CWD*CT + (1   ID)											
Tree individual	random				<0.001	<0.001		3780.6	3830.6	0.037	0.037
Residual	random				0.157	0.396					
(Intercept)	fixed	-0.050	0.013	-3.881			<0.001 ***				
CWD	fixed	<0.001	<0.001	0.459			0.646				
Slope	fixed	0.037	0.022	1.662			0.097 .				
Plateau	fixed	0.066	0.018	3.676			<0.001 ***				
CWD:Slope	fixed	0.001	<0.001	3.673			<0.001 ***				
CWD:Plateau	fixed	0.002	<0.001	7.302			<0.001 ***				
ANOM ~ CWD * WD + (1   ID)											
Tree individual	random				<0.001	<0.001		3830.5	3880.5	0.024	0.024
Residual	random				0.159	0.398					
(Intercept)	fixed	-0.055	0.022	-2.465			0.014 *				
CWD	fixed	<0.001	<0.001	1.835			0.067 .				
Medium WD	fixed	0.042	0.025	1.686			0.092 .				
High WD	fixed	0.050	0.026	1.918			0.055 .				
CWD:MediumWD	fixed	<0.001	<0.001	1.531			0.126				
CWD:HighWD	fixed	0.001	<0.001	1.781			0.075 .				
ANOM ~ CWD * DBH + (1   ID)											
Tree individual	random				<0.001	<0.001		3802.7	3852.7	0.031	0.031
Residual	random				0.158	0.397					
(Intercept)	fixed	-0.019	0.011	-1.763			0.078 .				
CWD	fixed	<0.001	<0.001	3.795			<0.001 ***				
[30-50> DBH	fixed	0.007	0.018	0.353			0.724				
>=50 DBH	fixed	0.011	0.023	0.495			0.621				
CWD:[30-50> DBH	fixed	0.001	<0.001	3.988			<0.001 ***				
CWD:>=50 DBH	fixed	0.001	<0.001	3.719			<0.001 ***				
ANOM ~ CWD * CT * WD + (1   ID)											
Tree individual	random				<0.001	<0.001		3793.6	3918.6	0.039	0.039

Parameter	Effect	Estimates	Std. Error	t value	Variance	St. Dev.	Pr(> t )	AIC	BIC	R <sup>2</sup> m	R <sup>2</sup> c
Residual	random				0.156	0.395					
(Intercept)	fixed	-0.082	0.037	-2.196			0.028 *				
CWD	fixed	<0.001	<0.001	-0.762			0.446				
Slope	fixed	0.042	0.056	0.759			0.448				
Plateau	fixed	0.042	0.052	0.812			0.417				
Medium WD	fixed	0.042	0.041	1.028			0.304				
High WD	fixed	0.024	0.045	0.523			0.601				
CWD:Slope	fixed	0.001	0.001	2.223			0.026 *				
CWD:Plateau	fixed	0.001	0.001	1.782			0.075 .				
CWD:MediumWD	fixed	0.001	<0.001	1.053			0.293				
CWD:HighWD	fixed	<0.001	0.001	0.666			0.506				
Slope:MediumWD	fixed	-0.050	0.067	-0.753			0.452				
Plateau:MediumWD	fixed	0.025	0.057	0.438			0.661				
Slope:HighWD	fixed	0.034	0.066	0.510			0.610				
Plateau:HighWD	fixed	0.036	0.061	0.580			0.562				
CWD:Slope:MediumWD	fixed	-0.001	0.001	-1.295			0.195				
CWD:Plateau:MediumWD	fixed	0.001	0.001	0.865			0.387				
CWD:Slope:HighWD	fixed	<0.001	0.001	-0.310			0.757				
CWD:Plateau:HighWD	fixed	<0.001	0.001	0.663			0.507				
ANOM ~ CWD * CT * DBH + (1   ID)											
Tree individual	random				<0.001	<0.001		3741.7	3866.7	0.052	0.052
Residual	random				0.154	0.393					
(Intercept)	fixed	-0.031	0.018	-1.747			0.081 .				
CWD	fixed	<0.001	<0.001	0.400			0.690				
Slope	fixed	0.004	0.028	0.160			0.873				
Plateau	fixed	0.027	0.025	1.103			0.270				
[30-50> DBH	fixed	-0.042	0.028	-1.513			0.131				
>=50 DBH	fixed	-0.036	0.040	-0.898			0.369				
CWD:Slope	fixed	0.001	<0.001	1.776			0.076 .				
CWD:Plateau	fixed	0.001	<0.001	2.308			0.021 *				

Parameter	Effect	Estimates	Std. Error	t value	Variance	St. Dev.	Pr(> t )	AIC	BIC	R <sup>2</sup> m	R <sup>2</sup> c
CWD:[30-50> DBH	fixed	<0.001	<0.001	-0.228			0.820				
CWD:>=50 DBH	fixed	<0.001	<0.001	0.206			0.837				
CTSlope:[30-50> DBH	fixed	0.049	0.054	0.901			0.368				
CTPlateau:[30-50> DBH	fixed	0.103	0.040	2.565			0.010	*			
CTSlope:>=50 DBH	fixed	0.122	0.066	1.839			0.066	.			
CTPlateau:>=50 DBH	fixed	0.045	0.052	0.864			0.387				
CWD:CTSlope:[30-50> DBH	fixed	0.001	0.001	0.807			0.420				
CWD:CTPlateau:[30-50> DBH	fixed	0.002	<0.001	4.788			<0.001	***			
CWD:CTSlope:>=50 DBH	fixed	0.002	0.001	2.374			0.018	*			
CWD:CTPlateau:>=50 DBH	fixed	0.001	0.001	1.746			0.081	.			

S9. Linear Mix model parameters, standard errors, t values, AIC values and R<sup>2</sup> for continuous variables.

Parameter	Effect	Estimates	Std. Error	t value	Variance	St. Dev.	Pr(> t )	AIC	BIC	R2m	R2c
ANOM ~ CWD*CT + (1   ID)											
Tree individual	random				<0.001	<0.001		10695.9	10733.4	0.043	0.043
Residual	random				0.956	0.978					
(Intercept)	fixed	0.001	0.016	0.063			0.950				
CWD	fixed	0.151	0.016	9.581			<0.001 ***				
HAND	fixed	-0.017	0.016	-1.100			0.271				
CWD:HAND	fixed	0.143	0.016	9.031			<0.001 ***				
ANOM ~ CWD * WD + (1   ID)											
Tree individual	random				<0.001	<0.001		10777.3	10814.8	0.023	0.023
Residual	random				0.977	0.988					
(Intercept)	fixed	0.001	0.016	0.055			0.956				
CWD	fixed	0.151	0.016	9.437			<0.001 ***				
WD	fixed	0.010	0.016	0.660			0.509				
CWD:WD	fixed	0.005	0.016	0.324			0.746				
ANOM ~ CWD * DAP + (1   ID)											
Tree individual	random				<0.001	<0.001		10735.5	10773	0.034	0.034
Residual	random				0.966	0.983					
(Intercept)	fixed	0.001	0.016	0.049			0.961				
CWD	fixed	0.151	0.016	9.500			<0.001 ***				
DBH	fixed	-0.051	0.016	-3.225			0.001 **				
CWD:DBH	fixed	0.090	0.016	5.652			<0.001 ***				
ANOM ~ CWD * CT * WD + (1   ID)											
Tree individual	random				<0.001	<0.001		10703.2	10765.7	0.044	0.044
Residual	random				0.956	0.978					
(Intercept)	fixed	0.001	0.016	0.056			0.955				
CWD	fixed	0.151	0.016	9.573			<0.001 ***				
HAND	fixed	-0.018	0.016	-1.120			0.263				
WD	fixed	0.012	0.016	0.743			0.457				

Parameter	Effect	Estimates	Std. Error	t value	Variance	St. Dev.	Pr(> t )	AIC	BIC	R2m	R2c
CWD:HAND	fixed	0.143	0.016	9.027			<0.001	***			
CWD:WD	fixed	0.001	0.016	0.081			0.936				
HAND:WD	fixed	0.005	0.016	0.322			0.747				
CWD:HAND:WD	fixed	0.003	0.016	0.199			0.842				
ANOM ~ CWD * CT * DAP + (1   ID)											
Tree individual	random				<0.001	<0.001		10647.3	10709.7	0.058	0.058
Residual	random				0.942	0.971					
(Intercept)	fixed	0.001	0.016	0.046			0.964				
CWD	fixed	0.143	0.016	9.094			<0.001	***			
HAND	fixed	-0.012	0.016	-0.782			0.434				
DBH	fixed	-0.050	0.016	-3.123			0.002	**			
CWD:HAND	fixed	0.132	0.016	8.356			<0.001	***			
CWD:DBH	fixed	0.063	0.016	3.931			<0.001	***			
HAND:DBH	fixed	0.002	0.016	0.104			0.917				
CWD:HAND:DBH	fixed	0.078	0.016	4.856			<0.001	***			
ANOM ~ CWD * CT * DAP * WDC + (1   ID)											
Tree individual	random				<0.001	<0.001		10652.1	10764.6	0.060	0.060
Residual	random				0.940	0.969					
(Intercept)	fixed	0.002	0.016	0.134			0.893				
CWD	fixed	0.149	0.016	9.353			<0.001	***			
HAND	fixed	-0.013	0.016	-0.816			0.415				
DBH	fixed	-0.051	0.016	-3.142			0.002	**			
WD	fixed	0.020	0.016	1.237			0.216				
CWD:HAND	fixed	0.134	0.016	8.392			<0.001	***			
CWD:DBH	fixed	0.071	0.016	4.372			<0.001	***			
HAND:DBH	fixed	-0.002	0.017	-0.125			0.901				
CWD:WD	fixed	-0.017	0.016	-1.041			0.298				
HAND:WD	fixed	0.008	0.016	0.516			0.606				
DBH:WD	fixed	-0.014	0.016	-0.886			0.376				
CWD:HAND:DBH	fixed	0.083	0.016	5.043			<0.001	***			

Parameter	Effect	Estimates	Std. Error	t value	Variance	St. Dev.	Pr(> t )	AIC	BIC	R2m	R2c
CWD:HAND:WD	fixed	-0.020	0.016	-1.211			0.226				
CWD:DBH:WD	fixed	-0.038	0.016	-2.469			0.014 *				
HAND:DBH:WD	fixed	0.009	0.016	0.563			0.573				
CWD:HAND:DBH:WD	fixed	-0.003	0.016	-0.170			0.865				

## CONCLUSÃO

A seca severa de 2015-2016 causada pelo *El Niño* reduziu significativamente o incremento diamétrico mensal e anual em comparação com a média. O incremento em diâmetro teve uma resposta imediata ao déficit hídrico, diferentemente da mortalidade das árvores por falhas hidráulicas durante a seca. Durante a seca, as árvores maiores localizadas nos platôs sofreram mais. No entanto, após o evento, a taxa de incremento anual da floresta não tinha sido recuperada, sendo as árvores de porte médio e as árvores localizadas nos baixios as que tiveram mais dificuldades para recuperar a taxa média de crescimento. As secas nas últimas décadas têm se intensificando e a resposta da floresta às secas sucessivas colocaria em risco o estoque de carbono da floresta, a e a resiliência da floresta. Sendo assim, este estudo enfatiza a resposta negativa do incremento de tronco de árvore durante e depois de uma seca severa e natural que pode contribuir na modelagem de modelos climáticos e de carbono. Além disso, a importância do declínio no crescimento das árvores não tivesse sido observada se o censo das parcelas permanentes fosse monitorado após o evento. Portanto, medidas mensais do incremento diamétrico contribuem grandemente para observar o efeito de eventos climáticos extremos, no entanto, muito recurso seria investido para fazer medições mensais em todas as parcelas permanentes da floresta tropical quando uma seca ameaça. Estudos adicionais devem ser realizados para entender e identificar quais características funcionais e mecanismos estão melhor relacionados com o crescimento das árvores durante secas extremas, como características anatômicas dendrométricas, fisiológicas, hidráulicas e do xilema.