

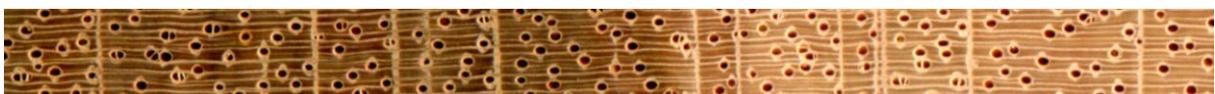
Giuliano Maselli Locosselli

Dendroecologia de *Hymenaea* spp. e *Podocarpus lambertii*, o papel do clima e do ambiente no crescimento destas espécies tropicais

“Dendroecology of *Hymenaea* spp. e *Podocarpus lambertii*, the role of climate and environment on the growth these tropical species”

São Paulo

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Dendroecology of *Hymenaea* spp. e *Podocarpus lambertii*, the role of climate and environment on the growth these tropical species

Tese apresentada ao Instituto de Biociências da Universidade de São Paulo, para a obtenção de Título de Doutor em Ciências Biológicas, na Área de Botânica.

Orientador(a): Gregório Ceccantini
Co-orientador; Jochen Schöngart

São Paulo

2015

Ficha Catalográfica

Locosselli, Giuliano Maselli

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158 páginas

Tese (Doutorado) - Instituto de Biociências da Universidade de São Paulo. Departamento de Botânica.

1. Anéis de crescimento, 2. Dendrocronologia
I. Universidade de São Paulo. Instituto de Biociências. Departamento de Botânica.

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Dedicatória

Dedico a todos!

Agradecimentos

Esta tese não é o fruto do trabalho de apenas uma pessoa. Muitos trabalharam diretamente e indiretamente para que ela se concretizasse. Acredito que eu fui muito afortunado de ter sempre pessoas brilhantes ao meu lado. Parte destas pessoas eu já conhecia na ocasião do início dos trabalhos desta tese, e outras eu tive a prazer de conhecer durante estes quatro anos. À vocês, eu dedico todo os frutos positivos deste trabalho.

Primeiramente agradeço à minha família. Basicamente por tudo! Mas em alguns detalhes recentes, pelo apoio durante estes quatro anos de doutorado. Por terem me encorajado em momentos de dificuldades. A compreensão de minha ausência nos últimos meses. Agradeço ao meu irmão e minha mãe que foram me visitar na Alemanha e ao meu pai que mesmo não tendo conseguido ir, sempre se fez presente! E lógico, pelo carinho e amor!

À Vivi Jono que me aturou e me atura dia após dia pacientemente!!! Que me deu conselhos valiosos e apoio para que este trabalho pudesse ser finalizado. Por ter me ajudado a tomar decisões certas. Por ter ido me visitar na Alemanha!!!! Por ser uma grande companheira! Também agradeço à Myuki Jono e ao Luiz Jono, pelo infindável carinho durante todos estes anos.

Ao Dr. Gregório Ceccantini, por mais de uma década de orientação! Obrigado por acreditar em mim no começo e ter me dado liberdade para crescer. Agradeço também à confiança durante o doutorado, na elaboração e execução de projetos. Agradeço também à amizade duradoura.

Agradeço à Dra. Verônica Angyalossy por ter me acompanhado durante todos estes anos na Anatomia. Também agradeço à Dra. Nanuza de Menezes por todo o carinho.

Agradeço ao Dr. Jochen Schöngart por ter me dado a oportunidade de conhecer e trabalhar no Pantanal, e por toda a ajuda com o presente trabalho. Também agradeço à Sejana Rosa por ter me recebido gentilmente em Cuiabá para realizar as coletas em Poconé. Agradeço à UFMT por ter disponibilizado alojamento para as coletas.

Ao meus amigos do laboratório por toda a amizade e ajuda. Ao Vitor Barão com quem tive muitas conversas produtivas sobre ciência. Por ter me acompanhado nas coletas no Pará, me ajudando gentilmente. À Luiza Teixeira pelas ajudas em campo e leitura de manuscritos. Ao Gustavo Burin, pela amizade e ajuda no começo do doutorado, incluindo a aprovação do nosso projeto de Dendro! Ao Ricardo Cardim, pela amizade e trabalho em conjunto com os podocarpos. À Nara Vogrado pelas conversas em ciência e amizade e também por ter conseguido o empréstimo dos valiosos data-loggers da Patrícia para nós! Também agradeço ao Fabio Coelho, Eric Becman, Erica Righetto Ifanger, Nathalia Alves Altobelli, pela enorme ajuda nos campos e na preparação do material. Sem vocês, este trabalho seria muito diferente. Também agradeço aos momentos agradáveis que tivemos no trabalho e fora dele. Agradeço ao Marcelo Pace, a quem eu considero um grande pesquisador. Posso dizer que você me inspirou a publicar os meus primeiros trabalhos. Agradeço à Ana Seghessi, uma das pessoas mais competentes com quem eu já trabalhei. Ela teve um papel central em todo este trabalho. A Gabriela Ambrosino por sempre estar disposta a ajudar, por ter me ajudado a preparar e a medir amostras.

A todos os mateiros que nos ajudaram nas atividades de campo: Adolfo Ferreira, Ramiro Hilario dos Santos, Nelson Donizetti Correa, Antônio Crema, Natanael Ozorio da Silva, Pedro Ozorio da Silva, Sergio Aparecido Esborini. Sem a sua experiência e conhecimento, este trabalho não existiria. Sem vocês, provavelmente eu estaria perdido na floresta sem nenhuma amostra!

Tenho um profundo sentimento de agradecimento ao Prof. Anhuf Dieter e ao Stefan Krottenthaler. Vocês abriram uma janela de oportunidades para mim que eu não vislumbrava. A oportunidade de trabalhar com um grupo internacional, com técnicas novas, participar da organização e da execução de campanhas de coletas, todas as ideias e discussões certamente me fizeram crescer. Ao Stefan, eu também agradeço ao companheirismo que tivemos tanto aqui no Brasil quanto na Alemanha. Eu admiro o seu jeito de resolver as coisas sem medo nem vergonha. Aprendi muito com isso. Espero que os frutos de nosso trabalho estejam à altura de tudo aquilo que eu recebi trabalhando com vocês.

I also thank Phillip Pitsch for the hard work in the field and in the lab. I thank you for all your help in reading the manuscripts and giving great contributions for the entire project. And, of course, I thank you for all the fun and the drinks here in Brazil and in Germany. And, I should not forget that you kindly hosted me in your house in Passau.

I also thank Dr. Gerd Helle for hosting me in his Lab in Potsdam. I must say that I had six wonderful months in Germany. Thank you for giving me support for everything that I needed during my stay. Thank you for the ideas and all talks that we had. I also thank you for borrowing me the blue bike with the basket. Really, it changed my life in Potsdam by giving me freedom to go everywhere.

I also thank Dr. Sonia Simard for always helping me since the first day in Potsdam. For all talks during lunchtime, for inviting me to fieldwork, for all the fun, for giving great tips about things to do in Potsdam and Berlin.

I also thank Heiko Baschek for supporting me in the laboratory work. And I also thank you for running all the analyses. I know that it is a huge work.

I also thank Regina Neun-Flux and her husband for being so kind with their tenant. Thank for inviting for the meeting in the University of Potsdam, for borrowing me a bike, for giving great tips about travelling in Germany. I really believe that all the assistance that you gave me in Potsdam makes you part of this work.

Agradeço ao Instituto Florestal do Estado de São Paulo, por ter fornecido as licenças de coletas nos Parques Estaduais: Morro do Diabo, Vassununga, Caetetus e Carlos Botelhos. Também agradeço os respectivos gestores

Agradeço ao Dr. Francisco William por nos ter convidado a trabalhar no PE de Terra Ronca. Agradeço também ao Dr. Jean-Sebastien Moquet por ter me acompanhado e ajudado no campo e por ter me apresentado as cavernas de Terra Ronca. Agradeço ao gestor Eric Rezende Kolailat por ter autorizado nossas coletas no PETER. Agradeço à SEMAHR de Goiás por ter expedido a licença para coletar no Parque Estadual de Terra Ronca

Agradeço ao Eduardo Reigruber, Gentil Chaves Clarice Andrade e a empresa AMATA por ter gentilmente cedido amostras de jatobá para este estudo. Também agradeço Carlos Aranha e as empresas Golf Indústria Comércio e Exportação de Madeiras Ltda, Ebata Produtos Florestais Ltda por ter nos hospedado no Pará e fornecido amostras para o presente estudo. Também

agradeço Anderson Serra e João Bosco Pereira e a empresa Cikel por ter nos hospedado no Pará e por nos ter fornecido amostras de jatobá.

Agradeço também ao Raphael Pigozzo, ao Takashi Yojo, ao Paulinho e ao Instituto de Pesquisas Tecnológicas do Estado de São Paulo por nos ter oferecido conhecimento e infraestrutura para realizar as medidas de gravidade específica.

Agradeço ao Dr. Marcos Buckeridge por ter emprestado equipamentos para realizar medições de gravidade específica no IB/USP. Também agradeço pela conversa que resultou na adição dos dados de taxa de assimilação do jatobá no quarto capítulo. Também agradeço à Eglee Igarashi e a Viviane Lopes pelo apoio à utilização dos equipamentos do laboratório.

E agradeço à Paula Jardim pela incrível ajuda nestes quatro anos. Isso inclui toda a paciência com as minhas bagunças!!!

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Apresentação Geral

Por serem organismos sésseis, as árvores possuem uma relação muito íntima com o ambiente a sua volta. Esta relação ocorre por meio da plasticidade funcional e estrutural (ex: Delagrange et al. 2004. Locosselli & Ceccantini 2012), necessárias para a sobrevivência às constantes mudanças regionais às quais elas estão sujeitas. O crescimento das árvores pode ser considerado uma medida integradora de grande parte das respostas funcionais e estruturais das plantas às mudanças ambientais. Quando este crescimento é sazonal e é registrado como anéis de crescimento, esta interação das árvores com o ambiente pode ser detectada por meio de métodos dendrocronológicos (Schweingruber 1988).

A relação entre o crescimento das árvores e o ambiente já havia sido apontada no século XVI por Leonardo da Vinci (Harley & Grissino-Meyer 2009). Mas foi apenas na primeira metade do século XX que o estudo dos anéis de crescimento emergiu como uma ciência. O astrônomo Andrew E. Douglass da Universidade do Arizona foi quem sistematizou o estudo dos anéis de crescimento e estabeleceu o princípio básico da dendrocronologia que é a datação cruzada (Stokes & Smiley 1996). Este procedimento consiste na identificação de padrões de crescimento que são compartilhados por diversas árvores de uma mesma população. Para isso, supõem-se que o crescimento de todas as árvores de uma população seja modulado por uma força maior, em geral o clima. Como existe uma variação inter-anual do clima, podemos associar a formação do anel de crescimento a um ano calendário (Schweingruber 1988). A simples contagem dos anéis de crescimento é

uma boa estimativa da idade de uma árvore, mas não necessariamente representa sua idade real.

A partir do início dos trabalhos de Andrew E. Douglas, a dendrocronologia cresceu muito no século XX nas áreas temperadas dos dois hemisférios. Durante todo este período, novas fronteiras da ciência foram sendo exploradas, e sub-áreas da dendrocronologia foram criadas. A dendroclimatologia é uma das áreas mais exploradas, provavelmente por remeter à própria origem da dendrocronologia. Ela tem como objetivo inicial avaliar como o clima modula o crescimento das árvores, e um objetivo maior que é a reconstrução climática (Fritts 1976; Hughes et al. 2011). Sob este aspecto, a dendrocronologia se destaca entre os registros naturais por fornecer uma datação precisa e uma resolução anual do paleo-clima (Hughes 2002). A dendroecologia também é uma área que se desenvolveu muito, e que estuda o crescimento, e mesmo as relações clima-crescimento, sob uma perspectiva ambiental. Outras áreas mais se desenvolveram como a dendrogeomorfologia, que estuda padrões geomorfológicos por meio de séries de anéis de crescimento, a dendroentomologia, que estuda ciclos de explosões populacionais de insetos, entre outras áreas (Schweingruber 1996).

As aplicações da dendrocronologia em regiões tropicais são mais recentes. A dúvida sobre anualidade dos anéis de crescimento em espécies tropicais foi por muito tempo um dos principais obstáculos ao desenvolvimento da dendrocronologia tropical. Apesar do crescimento anual de algumas espécies tropicais como *Tectona grandis* ter sido determinado no começo do Século XX (Worbes 2002), somente nas últimas décadas deste século que a dendrocronologia tropical começou a se desenvolver. Os primeiros estudos se concentraram no importante trabalho de avaliar a presença ou não de anéis de crescimento visíveis no lenho de diversas

espécies, assim como a determinação, ou não, da anualidade destes anéis (ex: Lucchi 1998, Westbrook 1996, Dünish *et al.* 2002, Lisi *et al.* 2008). Após estes passos iniciais, a dendrocronologia tropical tem sofrido um intenso florescimento nos últimos anos com diversas aplicações. Esta expansão não está restrita a algumas áreas, mas está presente nas Américas, na África e na Ásia (Worbes 2002). Novamente, destacam-se as áreas da dendroclimatologia e dendroecologia.

Na presente tese, a dendroecologia foi explorada nos três primeiros capítulos envolvendo duas espécies: *Podocarpus lambertii* e *Hymenaea courbaril*. O primeiro capítulo é um estudo dendroecológico de *P. lambertii* sob uma perspectiva biogeográfica. Ele teve como objetivo principal compreender o papel de afloramentos rochosos no crescimento desta espécie em um local de micro refúgio no Nordeste brasileiro. Este trabalho foi inspirado nos resultados iniciais obtidos durante o mestrado de Ricardo Cardim (Cardim 2012). Posteriormente, ele foi reiniciado e estendido durante os trabalhos da presente tese de doutorado. O segundo capítulo é um estudo das relações clima/crescimento de *H. courbaril* crescendo em uma área de mata seca sobre calcário na região central do Brasil. Neste capítulo, estas relações são avaliadas finamente por meio de análise de correlações, e interações entre as variáveis climáticas e seu efeito sobre o crescimento. O terceiro capítulo é um estudo do efeito da fragmentação de hábitat na idade das árvores e nos sinais climáticos presentes nos anéis de crescimento de *H. courbaril*.

As relações entre o clima e o crescimento avaliadas sob olhares diferentes nestes três capítulos são muito importantes dentro do contexto das mudanças climáticas globais. Estudos como estes possuem um papel muito importante na

previsão do que poderá acontecer com as árvores e as florestas no futuro (Zuidema *et al.* 2012).

No quarto capítulo, foi feito um estudo mais fino do crescimento de *Hymenaea parvifolia* e *Hymenaea courbaril*, focando em aspectos que vão além dos domínios da dendrocronologia. O crescimento neste capítulo é avaliado como sinônimo de adição de volume e biomassa nas árvores, em especial a alocação de carbono para formação do lenho. A formação do cerne no lenho destas espécies é ressaltada sobre dois pontos de vista, o das árvores e o das florestas. A escala espacial deste estudo é muito mais ampla do que a dos estudos anteriores. Ela abrange dez populações num gradiente latitudinal entre as linhas do Equador e do Trópico de Capricórnio, o que represente uma variação de aproximadamente 23° de latitude (cerca de 2600 km de distância).

Objetivos Gerais

A presente tese teve como objetivo compreender como o clima e o ambiente modulam o crescimento de duas espécies tropicais: *Podocarpus lambertii* e *Hymenaea courbaril*. Adicionalmente, buscou-se compreender como *Hymenaea* spp. aloca o carbono assimilado na formação do lenho, em especial o custo de formação do cerne.

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Capítulo 1

Rock outcrops reduce temperature-induced stress for tropical conifer by decoupling regional climate in the semi-arid environment

With: Ricardo Henrique Cardim and Gregório Ceccantini

Manuscript submitted to International Journal of Biometeorology (March 25th, 2015)

Abstract

We aimed to understand the effect of rock outcrops on the growth of *Podocarpus lambertii* within northernmost limits of its distribution. Our hypothesis holds that the growth and survival of this species depends on the regional climate decoupling provided by rock outcrops. To test this hypothesis, we characterized the microclimate of 1) surrounding vegetation, 2) hilltop rock outcrops, 3) rock outcrop corridors, and 4) adjacencies. We assessed population structure by collecting data of specimen stem diameter and height. We also assessed differences between vegetation associated or not with outcrops using satellite imaging. For dendrochronological analyses, we sampled 42 individuals. Tree rings of 31 individuals were dated and climate-growth relationships were tested. Rock outcrops produce a favorable microclimate by reducing temperature by 15% and increasing air humidity by 32%, supporting vegetation with higher LAI. Sampled specimens height was strongly constrained by the outcrop height. Temperature induced stress is the limiting growth factor for *P. lambertii*, while the precipitation in the beginning of the growth season stimulates a higher growth. The influence of temperature on this species growth is almost twofold higher than the precipitation. We conclude that this species growth and survival depends on the presence of rock outcrops. These topography elements decouple regional climate in a favorable way for this species growth. However, these benefits are restricted to the areas sheltered by rock outcrops. Although this microrefuge supported *P. lambertii* growth so far, it is unclear whether this protection would be sufficient to withstand the stress of future climate changes.

Keywords: microrefugia, distribution limit, tree-ring, microclimate, *Podocarpus lambertii*, Leaf Area Index, dendroecology, rock outcrops, climate change.

Introduction

Species distribution is determined by abiotic and biotic factors. Climate can be considered the main abiotic factor that regulates species distribution. Climate parameters vary across gradients of latitude, altitude and distances from shore and mountain ranges (Lomolino *et al.* 2010). However, some populations are able to grow outside the main distribution area in specific sites that provide more favorable conditions in a hostile regional climate. These populations are usually reminiscent of long histories in the contraction and expansion of species distribution (Rull *et al.* 2009; Hampe & Jump 2011). These singular sites provide insight into species dynamics and the ecological stresses that affect them, in particular due to climate changes (Hampe & Jump 2011).

For instance, conifers are distributed across all five continents with the exception of Antarctica. The two biggest conifer families in number of species are mainly found in opposite hemispheres (Florin 1960). Pinaceae is predominantly found at temperate and subtropical regions of the Northern Hemisphere, and Podocarpaceae is primarily found from temperate to tropical regions of the Southern Hemisphere. Apparently, this distribution has been strongly maintained since the end of the Cretaceous period. However, processes that resulted in this distribution pattern seem to be different for both families. Pinaceae species are more cold-resistant than Podocarpaceae species, which require mild temperatures and wetter environments (Leslie *et al.* 2012).

In Brazil, *Podocarpus lambertii* Klotzsch ex Endl. is usually associated with cool and wet climates from relatively higher southern latitudes (Ledru *et al.* 2001). This species used to have a broader distribution across the country during the end

of the Last Glacial Maximum (LGM) when northern areas had a cooler and wetter climate. Nowadays, it has a continuous distribution in southern and southeastern areas of Brazil and a discontinuous distribution in lower latitudes of northeastern Brazil (Ledru *et al.* 2007). In the northernmost area, this population is found in a semi-arid region and it grows within corridors and adjacencies of rock outcrops.

In previous research, we have shown that individuals of this population are able to jointly regulate stomatal distribution in leaves and dimension of stem tracheids in order to survive in this extreme habitat (Locosselli & Ceccantini 2012). However, we believe that anatomical plasticity is not enough to explain how this population is able to withstand the extremes of this habitat. Somehow, the presence of the rock outcrops seems to benefit the growth of these individuals. Elements of the topography, like mountains and deep valleys, as well as the rock outcrops, can reduce the effects of *in situ* climatic conditions, permitting the growth and survival of plants that would otherwise decline in the present regional climate (Austin & Niel 2011; Dobrowski 2011; Keppel *et al.* 2012). They are like outliers in the gradients of abiotic variables that influence species distribution.

These areas with favorable *in situ* conditions played an important role in species survival during glacial and interglacial climate changes and continue to influence plant life through the present day. Such areas are termed microrefugias, which allow small populations to survive away from their main distribution (Rull 2009). During glacial stages, microrefugias were related to warmer conditions that supported thermophilous species. In the course of interglacial periods, they provided cooler environments for cold-adapted species (Dobrowski 2011; Mee & Moore 2013), such as *P. lambertii*. Usually, populations inhabiting these microrefugias are

from a subset of species that retain traits allowing their survival within the confines of those singular sites (Mee & Moore 2013).

In order to understand the positive impact of microrefugias, one must identify the climate factors that limit species development within that singular site. The use of dendrochronological methods can provide precise information that help us to understand how climate variables modulate tree growth (Fritts 1976). Previous research successfully analyzed such limiting climatic factors on tree growth. Frequently, species distribution limits were studied on the basis of altitudinal (e.g., Morales *et al.* 2004; Dang *et al.* 2013; King *et al.* 2013) and latitudinal gradients (e.g., Carrer *et al.* 2010; Hart *et al.* 2010; Herrero *et al.* 2013).

The aim of this study is to understand the role of rock outcrops on the growth of *Podocarpus lambertii* within the semi-arid northernmost limits of its distribution. Our hypothesis holds that the growth and survival of this species depends on decoupling from the regional climate provided by rock outcrops as a microrefuge. We further investigated temperature as a factor limiting growth and the resilience of *P. lambertii* individuals inhabiting the corridors and adjacencies of rock outcrops.

Material and Methods

Species and sampling site

We sampled individuals of *Podocarpus lambertii* from a population at its northernmost distribution limit (11°12'24"S – 41°35'25"W, 1280m), as shown in Figure 1A. The area is located in Morro do Chapéu municipality (Bahia State). Plotted sites represent 467 herbaria and wood collection records from 35 institutions

obtained at speciesLink (CRIA) (Figure 1A). Climate of this area has a mean temperature of 20.1°C and annual precipitation of 653mm year⁻¹ (INMET). The growth season usually occurs between October and May in that site when monthly precipitation is higher than 60mm (Worbes 1999).

The sampling site was a hilltop with several rock outcrops. The height of these rock outcrops ranged from 0.6 to 15 meters, and their distribution formed continuous corridors along this area. In order to characterize that site, four categories of microenvironments were defined (Figure 1D): I) the transitional vegetation matrix between Caatinga and Cerrado formations, both types having xerophytic and heliophytic species (Rizzini 1997); II) rock outcrops, which are sandstone formations; and the areas inhabited by *P. lambertii* III) adjacencies having rock outcrops on one side only (Figure 1B) and IV) corridors formed by two or more rock outcrops (Figure 1C).

Population structure

In that hill top, we actively searched in about 40% of that area for all individuals of this species, from seedlings to mature trees, and obtained values of stem diameter, plant height and height of the closest rock outcrop. This resulted in a dataset of 135 specimens that was used to understand this small population structure and the influence of rock outcrops on the maximum dimensions of trees growing in this microrefuge. Population structure was analyzed by histogram graphics, and the relationship between tree size and rock outcrop height was tested by linear fit. For the former analyses, we used only the individuals with height equal to, or higher than, 90% of the height of the closest outcrop. By doing so, we could

test whether *P. lambertii* maximum height was constrained by the height of the closest rock outcrop. All previous analyses were performed using R (R Core Team 2013). The geographical positions of all individuals were recorded in the field.

It is important to highlight that the population structure fieldwork was performed after an unusually long dry season. During data acquisition, several dead individuals were found. Additionally, many living individuals had heavily damaged crowns with a high proportion of dry leaves in their crown. Based on our long experience in that site, we have never seen such a high number of damaged and dead *P. lambertii* trees. The geographical positions of those individuals were also recorded and plotted.

Site description

To understand the impact of rock outcrops on microclimate, we installed 15 data loggers for temperature and air relative humidity measurements during 96 hours at the beginning of January, 2013. This period represents the middle of the rainy season, and likely, the middle of the growth period for this species. Five data loggers were placed in the corridors, five were placed in the adjacencies, three were placed over the rock outcrops, and two were installed in the surrounding vegetation at 150 and 300 meters from the nearest rock outcrop at the western side of the hill. The 10-minute average values by site categories were calculated to represent a 24-hour period. The resulting values were plotted, and the temperature and relative humidity differences were tested during the three most physiologically demanding hours of the day: 11:00, 12:00 and 13:00. Differences were tested using the Kruskal-

Wallis test and a non-parametric multiple-comparison test from the “pgirmes” package (Giraudoux 2011).

Remote sensing techniques were used to collect data about *P. lambertii* growth area in the study site and differences in vegetation types. High-resolution panchromatic (0.5m of resolution) and multi-spectral (2m of resolution) images from the Pléides Satellite (Astrium-CNES, August 2012) were used in these analyses. Normalized Difference Vegetation Index (NDVI) was calculated using red and infrared images. Afterwards, the Leaf Area Index (LAI) was calculated based on the NDVI values (Zhu *et al.* 2013). LAI represents the one-sided green leaf area per ground surface area unit in broadleaf canopies. With the resulting image, classes of non-vegetated areas (lower values of LAI) and vegetation types (small, medium and higher values of LAI) were created. All specimens were plotted in the LAI classes image. Living and dead individuals were plotted using different colors. Analyses were performed using IDRISI Selva software (Clark Labs).

Dendrochronological sampling and analysis

We sampled stem discs and increment cores of 43 individuals of *P. lambertii* in: February of 2004, February of 2009 and January of 2013. Two to four cores were obtained for all individuals using an increment borer (5mm). All samples were left to dry and were polished using sandpaper. Tree rings were marked and counted under stereomicroscope and then measured using the Lintab 6 system (Rinntech, Heidelberg, Germany). The dating process was done using TSAP-Win software (Rinntech, Heidelberg, Germany), and it was verified using COFECHA software (Holmes 1983). We started dating cores from the same tree and later from different

trees. The final residual chronology was built using Arstan software (Cook & Kairiukstis 1990; Cook & Holmes 1996), in which linear regression and negative exponential functions were used to de-trend each dated radius. The Expressed Population Signal (EPS) was calculated in 30 years segments to verify if the growth signal was well represented by the number of samples in each segment (Wigley *et al.* 1984).

With the resulting residual chronology, the correlations between climate variables and growth residuals were performed. Climate data were provided by INMET (National Institute for Meteorology) from a climate station located in the same municipality as the sampling site. The following monthly variables were used: cloud cover, number of hours of sun, days of precipitation, precipitation and maximum temperature. Although the climate station was first installed in 1913, there are several gaps in the time series, and those gaps are different among all climatic variables. To address this problem, we decided to show the length of time series for each variable used in all correlations. In order to test if climatic variables had additive effects on tree growth or if they were collinear, we built three climate/growth linear models. For that purpose, we used temperature and precipitation, which are the variables with the longest time series. We built two models for each one of the variables and a third with the influence of both temperature and precipitation. All three models respect the assumptions of normality of response variable and residuals, and residual homoscedasticity. We chose the best linear model based on Akaike's Information Criterion (AIC). Two models are considered different if the AIC value is higher than two, and the best model is the one with the smallest AIC value (Faraway 2005). All analyses were performed using R software (R Core Team 2013).

Results

Site characteristics and population structure

The presence of rock outcrops decouples microclimate from regional climate in a favorable way for *P. lambertii*. The most relevant differences were found when the sun is at its highest position in the sky (Figure 2). Accordingly, from 11:00 to 13:00 hours, the recorded temperature was 15% lower inside the corridors and 11% lower in the adjacencies, while air relative humidity was 32% and 21% higher in the corridors and adjacencies, respectively. These differences found among protected and nonprotected areas are all statistically significant (Table 1).

Differences are also evident in the vegetation characteristics as imaged by satellite (Figure 3). The vegetation on hilltops, in areas protected by the outcrops, showed higher values of LAI. This means that this vegetation has higher values of leaf area per ground area, in contrast to the surrounding vegetation that is mainly formed by shrubs and small trees. Classes shown in Figure 3C were built using different ranges of LAI values. Individuals of *P. lambertii* are mainly found in Class 4 areas. Apparently, clusters of damaged and dead individuals are located in the least protected areas (Figure 4D). It is important to highlight that some shorter rock outcrops with a dense vegetation cover on top were not distinguishable in the LAI images and its classes, resulting in some distortions that could limit this method.

The results of the population structure analysis (Figure 4) show that few individuals reach heights of more than six meters and diameters wider than 15 centimeters. However, we found a high number of saplings in the field. It is important

to highlight that the height of *P. lambertii* trees is strongly limited by the height of the closest rock outcrop. The determination index (R^2) for the relationship between tree and rock outcrop height is 0.82. On the other hand, the diameter of the same individuals is not strongly related to the rock outcrop height ($R^2 = 0.11$).

Dendrochronology

Studied individuals showed frequent wedding rings that could merge up to five rings into one. Although wedding rings were relatively common, we were able to date 31 from 42 sampled specimens. The maximum length of the chronology is 138 years, though the EPS indicates that the chronology is well replicated until 1920 (Figure 5). This means that the chronology is robust within this period and that it could be used in the climate/growth analysis. Furthermore, the chronology has an inter-series correlation of 0.44 and a mean sensitivity of 0.67. Tree ring width is relatively small with an average value of 0.92 mm (Table 2).

Climate/growth correlations (Figure 6) show that climate during the beginning of the current growth season and the middle of the previous growth season played an important role in the growth of this species. Precipitation, days of precipitation and cloud cover in November have a positive effect on tree-ring width, while maximum temperature of November and December and hours of sun in September have a negative effect on radial growth. For the previous growth season, days of precipitation in January has a positive effect on radial growth, whereas maximum temperature in December and January has a negative effect on it. Overall, the correlations with current season climate variables are slightly higher than those from the previous season.

Out of the three tested models, the one with temperature and precipitation was the best model as tested by AIC (Table 3). This model shows that both variables have distinct effects on wood formation (Table 4). Temperature has a higher value of explained percentage (35.3%) than precipitation (18.2%). The small difference in the number of observations among the correlation analyses and the linear model is a result of the gaps found in the time series of each variable.

Discussion

Past research showed less than ideal wood features in *Podocarpus* spp. for dendrochronological studies, for instance: poorly defined tree-ring boundaries (Bauch *et al.* 2006; Buckley *et al.* 1995), high amount of wedding rings and the presence of lobate stem growth (Dunwiddie 1979; Buckley *et al.* 1995; Krepkowski *et al.* 2012; February & Stock 1998; Ferrero *et al.* 2014). Despite these typical problems, McDougall *et al.* (2012) successfully dated individuals of *Podocarpus lawrencei* in the Australian Alps. In this population, authors also described the negative impact of wedding rings and lobate growth on dating. In that study, they were able to date 52% of sampled trees. We also found wedding rings, but no lobate growth, in *Podocarpus lambertii* that resulted in 73% of dated trees. As highlighted by McDougall *et al.* (2012), stem discs were also essential for the precise dating of *P. lambertii* tree rings. An additional common feature between both studies is that the populations were from areas with clear limiting conditions, either relatively high altitude or low latitude.

At 11° of southern latitude, the individuals of *P. lambertii* analyzed in the current study belong to the northernmost limit of the present-day distribution for this species. There the presence of the rock outcrops seems decouple regional climate

in a favorable way for *P. lambertii*, and they can be regarded as key elements supporting this species growth. These rock outcrops can reduce the temperature up to 4.9°C and increase the air relative humidity up to 12%. Actually, their presence allows a different vegetation structure to inhabit the semi-arid. Leaf area index from the protected areas are closer to the values found in mixed forests and deciduous broadleaf forests. Meanwhile, the LAI values from the surrounding vegetation matrix are similar to the LAI from woody savanna areas (Zhu *et al.* 2013).

Rock outcrops can host species that have a disjunctive distribution and are far from their macroclimate optimum. By doing so, they can act as an interglacial microrefuge for species that retreated from their wide distribution to higher latitudes during the end of the Last Glacial Maximum (Rull 2009; Keppel *et al* 2012). For instance, these formations are microrefugia for species of the paleo-flora of Northern Patagonia (Speziale & Scurra 2012). Similar to the *P. lambertii* site in northeast Brazil, species found in areas protected by rock outcrops are different from those inhabiting the surrounding vegetation matrix. They are also components of colder vegetative areas in the south.

The importance of the rock outcrops to *P. lambertii* is evident, not only because specimens grow in their adjacencies and corridors, but also because the maximum tree heights are constrained by the rock outcrop height. Apparently, the favorable microclimate is restricted up to the rock outcrop edge, above which the regional climate prevails. However, to understand the real positive impact of the microclimate provided by this rock formation, we must know what limits the development of *P. lambertii* at that site. The climate/growth correlations and models showed that maximum temperatures during the beginning of the current and past growth seasons have a negative impact on the growth of this species. These results

indicate that 1) this species is strongly limited by high values of maximum temperature and 2) temperatures during midday regulate the growth of *P. lambertii*. That is precisely when temperature differences between areas protected by rock outcrops and unprotected areas are maximized.

Although the influence of precipitation on *P. lambertii* tree ring width is almost half of temperature influence, it is certainly a relevant variable for the growth of this species. Unfortunately, we cannot statistically separate the effects of precipitation, days of precipitation and cloud cover because they have different time series lengths. This fact does not allow testing collinearity among them using linear models. Nevertheless, they may be acting concurrently, and high amounts of well-distributed precipitation during the beginning of the growth season could be important for the growth of this species in well-drained sand soil. Regarding the cloud cover variable, it is usually related to the reduction of evapotranspiration, as well as drought stress (Fischer *et al.* 2009).

Other conifer species, like *Pinus sylvestris* and *P. nigra* in the Mediterranean basin, *Tsuga canadensis* in North America, and *Abies alba* in the Italian Alps, showed similar constraint at their low latitude distribution limit, also known as rear edge populations (Herrero *et al.* 2013; Hart *et al.* 2010; Carrer *et al.* 2010). All of them had a comparable history of expansion during a colder and wetter period and contraction during warmer and drier periods. Those populations seem to be systematically constrained by drought stress. Although precipitation also seems to be relevant, their distribution is mainly limited by temperature-induced stress. This pattern is not only limited to conifers, but it is also reported for eudicots like *Fagus* spp. (Fang & Lechowickz 2008; Tegel *et al.* 2014).

Even though rock outcrop corridors produce a more favorable microclimate for the growth of *P. lambertii*, we cannot say that it fully emulates the climate conditions from its main distribution area. First, individuals from this population must exert wood and leaf anatomical plasticity to survive in those conditions (Locosselli & Ceccantini 2012). Second, the average radial growth of these specimens is 0.9 mm, which is three times smaller than the growth reported for a population some 1980 km to the south with an average value of 2.7 mm (Mattos *et al.* 2007). In another site at 1750 km to the South of Morro do Chapéu, Canetti *et al.* (2014) report a radial increment of 4 mm per year in the same species. In fact, specific trait differences are expected between populations inhabiting microrefuge and the distribution core (Mee and Moore 2013). Despite these trait differences, we actually found no strong evidence of population decline. Surprisingly, several seedlings were found during fieldwork, as represented by population structure results. This probably means that these adaptations and the climate shelter by outcrops have thus far been effective.

It is well known that species ranges are highly dynamic and that they expand and contract according to changes in environmental conditions (Sexton *et al.* 2009). Usually, small populations at the distribution limit, such as this *P. lambertii* population, are more vulnerable to environmental changes. As a result of the isolation, one can expect losses in genetic diversity, higher probability of inbreeding and reduced individual fitness resulting in a lower capacity to adapt to fast environmental changes (Willi *et al.* 2006; Mee and Moore 2013). Therefore, the studied population could be in a threatened position in the context of fast climate changes from global warming (IPCC 2007), especially if the predicted changes are beyond the ability of this species to mount sufficient phenotypic plasticity to adapt

and/or beyond the capacity of rock outcrops to decouple local climate in a way that favors *P. lambertii*.

Acknowledgment

Authors thank Gisele Costa, Marcelo Pace, and Mariane Sallun for help during field work; Patrícia Morellato and Nara Vogrado for providing data loggers; Marisa Bittencourt for providing remote sensing facilities and expertise; and Vitor Barão for valuable input to the manuscript. Authors also thank FAPESP (12/50457-4) and CNPq (478503/2009-1; 142706/2011-6) for the funding.

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Figures

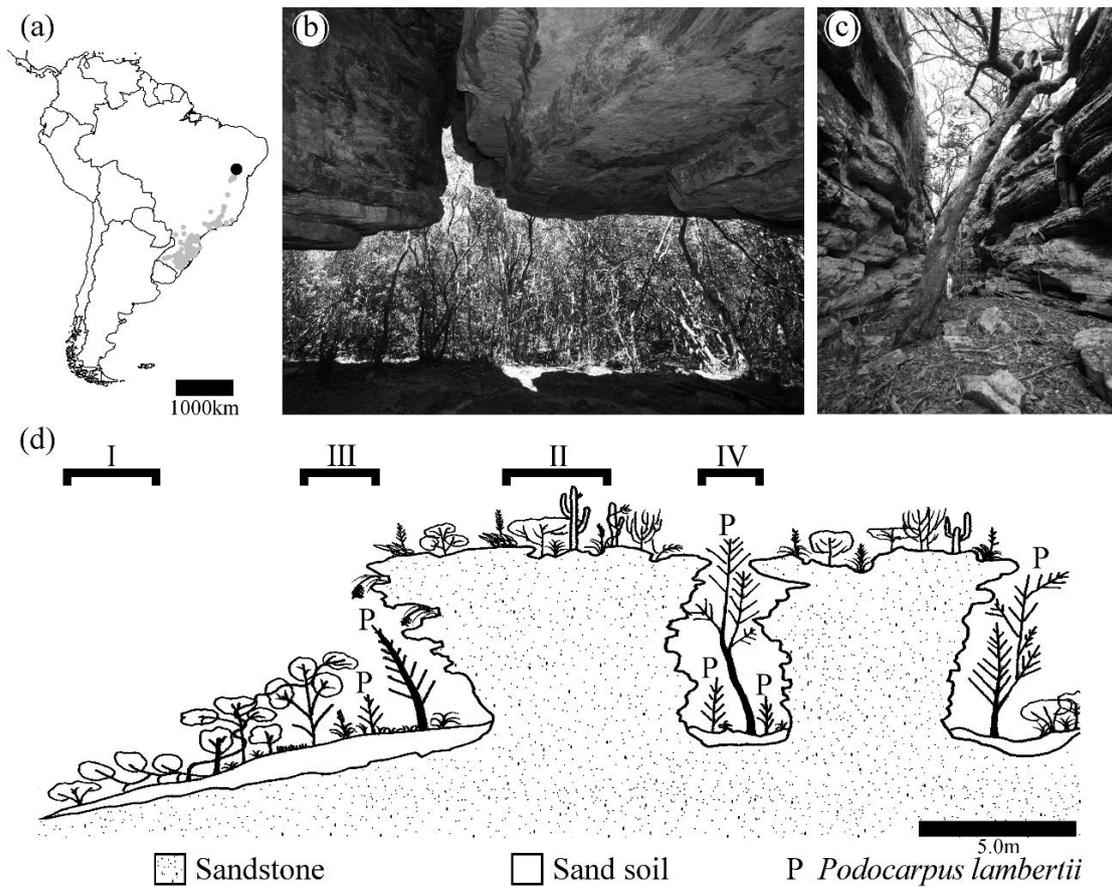


Figure 1: Sampling site. A) Distribution of *P. lambertii* based on herbaria records (grey) and the study area (black). B) Example of area in the adjacency category, with the rock outcrop shelter on one side (in the back). C) Photo of one of the biggest *P. lambertii* specimens. It was found growing in a rock outcrops corridor. D) Sketch of sampling site showing the four environmental categories: I) Surrounding vegetation, II) Rock outcrop top, III) Adjacency and IV) Corridors. *Podocarpus lambertii* specimens are indicated by the letter P.

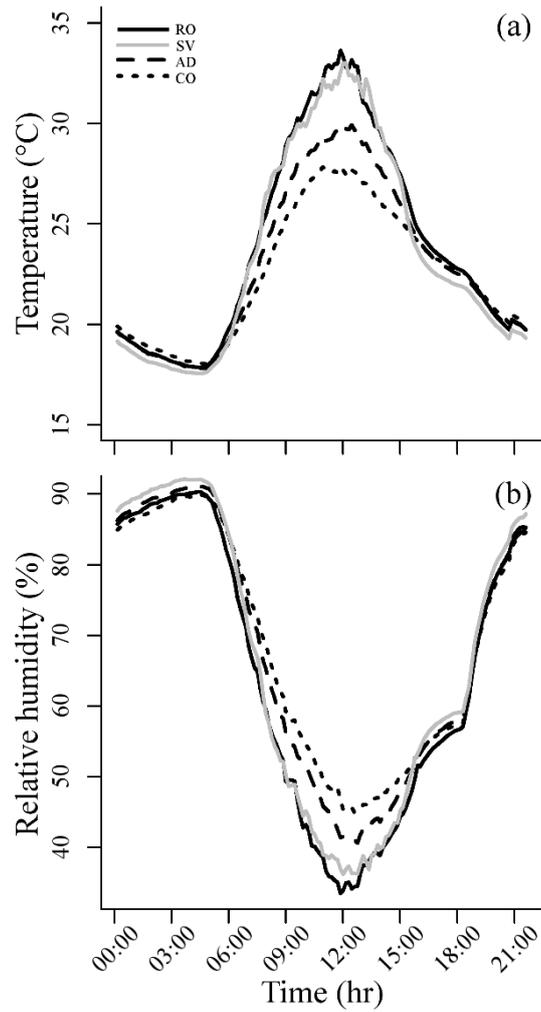


Figure 2: Daily variation of A) temperature and B) air relative humidity in the four environmental categories: surrounding vegetation (SV), rock outcrop top (RO), adjacencies (AD) and corridors (CO).

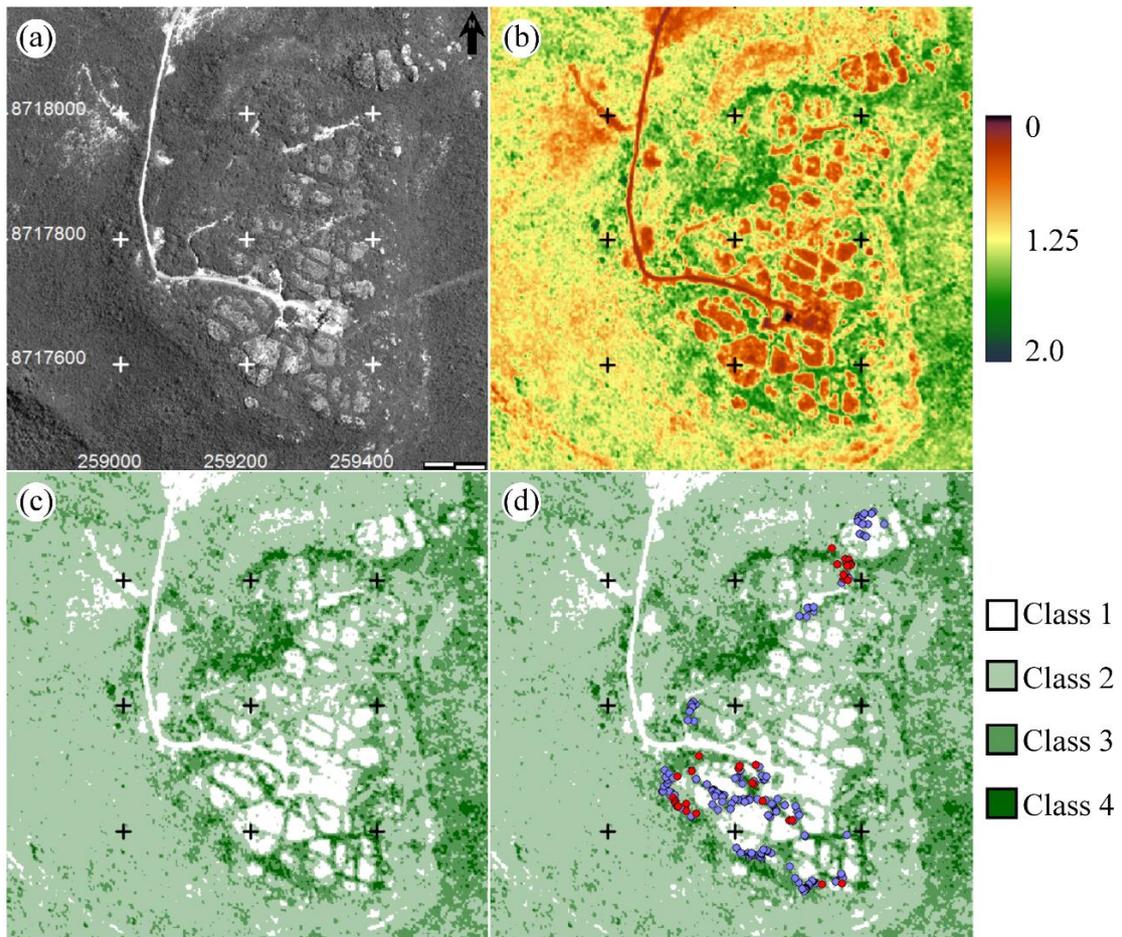


Figure 3: Results of the remote sensing analysis of the sampling site. A) Sampling site panchromatic image showing the rock outcrops (resolution: 0.5m and scale bar = 100m). B) Leaf area index (LAI) image. Lower values of LAI are indicated in red, and higher values of LAI are indicated in green (resolution = 2m). C) Reclassified image using the following range of LAI values: Class 1 shows areas with rock or naked soil. Class 2 shows areas with low LAI vegetation. Class 3 shows areas with medium LAI vegetation. Class 4 shows areas with high LAI vegetation.

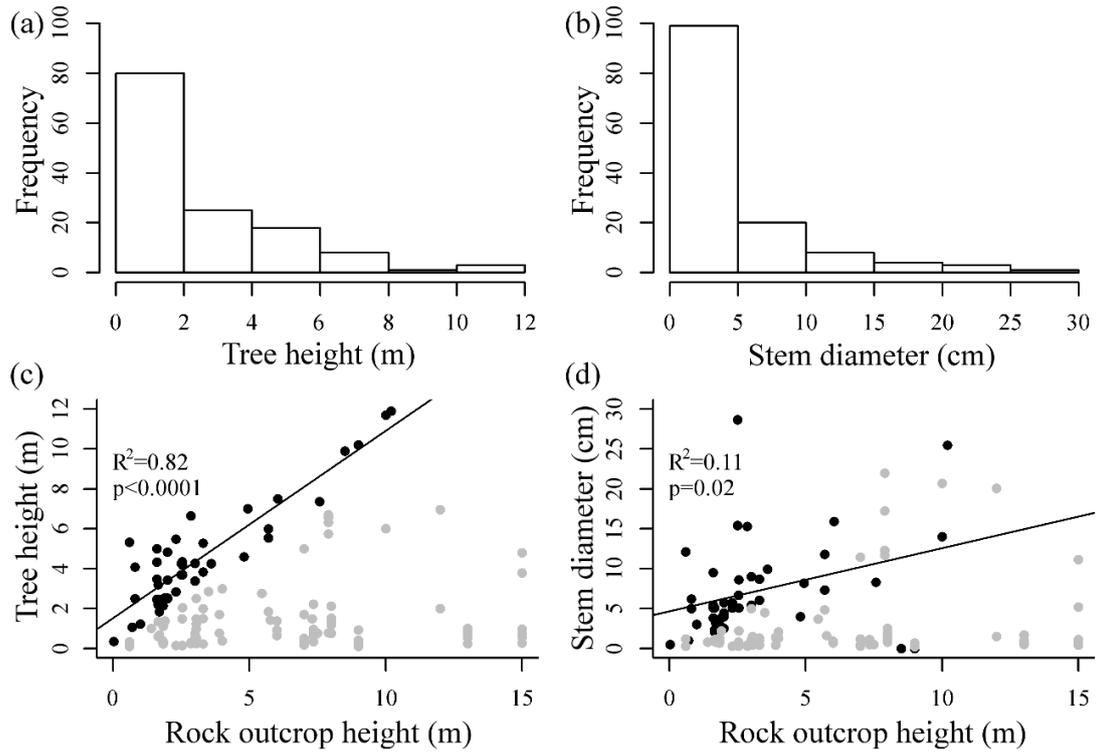


Figure 4: Population structure of *P. lambertii* and the influence of the nearest rock outcrop height on tree size. A) histogram of specimen height, B) histogram of specimen stem diameter, C) linear fit between trees with at least 90% of the rock outcrop height (black) plotted together with all other individuals (grey), D) linear fit between the stem diameter of the same individuals plotted in C and rock outcrop height.

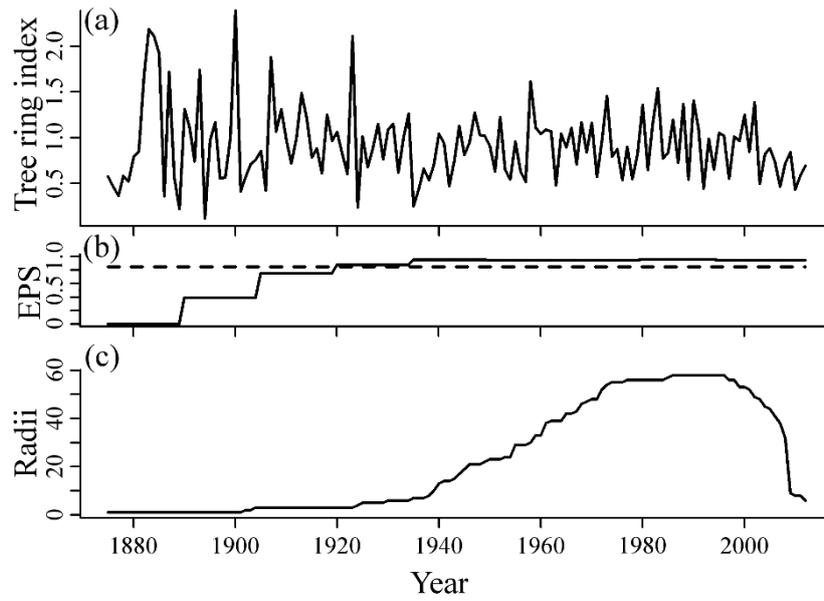


Figure 5: A) Residual chronology based on 31 specimens of *P. lambertii*. B) Calculated EPS for the dated tree rings. Dashed line indicates the EPS value of 0.85. C) Sample depth graphic showing the length in years of all dated radii.

Role of rock outcrops on *Podocarpus lambertii* growth

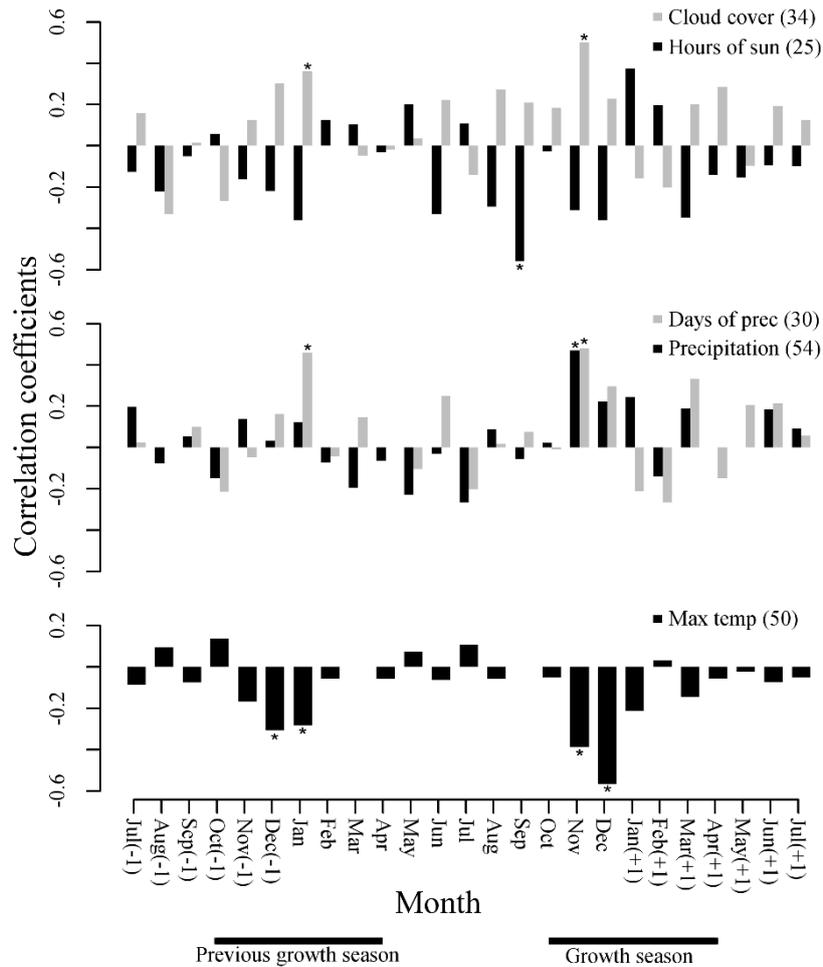


Figure 6: Monthly correlation among residual chronology and the following climate variables: hours of sun, cloud cover, days of precipitation, precipitation and maximum temperature. Correlations were calculated for the current and previous growth seasons. Negative labels for the months designate the previous calendar year, and positive values designate the next calendar year. Values shown in parentheses are the length of the available time series. (* statistically significant for $\alpha = 0.05$).

Tables

Table 1: Comparison of temperature and relative humidity among sites. Values of these two microclimatic variables represent the period between 11:00 and 13:00. The results of non-parametric multiple-comparison analysis are also shown. Different group letters indicate differences between sites.

Kruskal-Wallis	Temperature (°C)			Relative humidity (%)		
	Mean	STD	Groups	Mean	STD	Groups
	32.4	0.8	A	37.1	3.0	A
	31.7	0.9	A	39.3	2.7	A
	29.3	0.5	B	45.0	3.4	B
	27.5	0.3	B	49.0	3.0	B

Table 2: Chronology diagnostic showing the number of dated trees, maximum and mean series length (years), inter-correlation among series (IC), mean sensitivity (MS), mean and standard deviation of tree-ring width (Mean TRW and STD TRW, respectively; units in millimeters).

Trees	Max length	Mean length	IC	MS	Mean TRW	STD TRW
31	138	54.3	0.44	0.67	0.92	0.74

Table 3: Linear models comparison for climate / growth relationships in *P. lambertii*.

The smallest AIC indicates the best model (for differences higher than 2).

Linear Model	AIC
Res = MaxTemp (Dec) + Prec (Nov)	-27.3
Res = MaxTemp (Dec)	-13.1
Res = Prec (Nov)	-7.6

Table 4: Description of the best climate / growth model for *P. lambertii*, as indicated by the AIC. The number of observations (N), determination index (R^2), adjusted determination index for the number of variables (R^2_{adj}), p values, coefficients and explained percentage are given.

N = 49	$R^2 = 53.5$	$R^2_{adj} = 51.5$	P < 0.0001
Variables	Coefficient	Exp. Percentage (%)	
Intercept	3.503	-	
MaxTemp (Dec)	-1.049×10^{-1}	35.3	
Prec (Nov)	1.642×10^{-3}	18.2	
Residuals	-	46.4	

Capítulo 2

First rainfall events modulate *Hymenaea courbaril* (Leguminosae) growth in a tropical karst dry forest

With: Gregório Ceccantini

Manuscript submitted to *Trees, Structure and Function* (March 11th, 2015)

Abstract

Tropical dry forests have low annual precipitation and long dry seasons. Water availability, the main restrictive growth factor, becomes more pronounced in the shallow and highly porous soil of karst regions. Understanding how climate regulates tree growth in stressful environments is essential for predicting climate change impacts on trees. The aim of this study was to build a tree-ring chronology of *Hymenaea courbaril* growing in a karst dry forest and evaluate how climate modulates its growth. To accomplish this, increment cores of 19 individuals were sampled. After surface polishing, tree rings were identified, measured, dated, and a tree-ring chronology was built with 18 individuals. Climate/growth correlations were performed and significant climatic variables were analyzed with principal component analysis. Results show that both precipitation amount and distribution in the transition period between dry and wet seasons positively regulate this species growth. Considering karst topography, the first rainfall events are crucial for growth. On the other hand, growth is negatively correlated with temperature of the previous year's dry season. Temperature of the previous dry season seems to drive reserves allocation towards reproduction instead of growth since flowering starts at the end of the dry season and fruit ripening takes up to 8 months. As such, the first principal component represents a tradeoff between temperature and precipitation, and it is negatively correlated with growth. These relationships between climate and growth indicate that predicted increases in regional temperature and decreases in water availability may limit the growth of *H. courbaril* in karst dry forests.

Keywords: Tree ring; dendrochronology; limestone; reserves allocation; precipitation; temperature

Introduction

Tropical areas comprise an extensive range of environments that vary with topography, soil properties and climate. The combination of these variables results in the diverse vegetation types found in tropical regions (Gentry 1988). Plants inhabiting such environments may face different local conditions that will influence their development and growth. Some of those areas have conditions that are more physiologically demanding, in particular, tropical dry forests. Trees growing in this type of seasonal environment may be considered more vulnerable to future climate change in that current limiting growth conditions may become even more restrictive (Brienen *et al.* 2010).

By definition, dry forests inhabit seasonally dry regions with an annual precipitation lower than 1600mm. The dry season usually lasts for at least five months with a monthly precipitation smaller than 100mm (Gentry 1995; Grahan & Dilcher 1995). Vegetation in these areas is mostly represented by deciduous tree species with some brevi-deciduous and evergreen species (Mooney *et al.* 1995). In these forests, tree development is strongly restricted by seasonal ecological processes that lead to a reduced net primary production when compared to wetter environments, a natural consequence of the reduced growth period during a long dry season (Meier & Pennington 2006).

Some of those areas have characteristics that may increase the impact of climatic seasonality experienced by tree species. The largest South American areas of karst formations are found in central Brazil (Figure 1). In some of these karst regions, tropical dry forests grow over limestone bedrock (Rizzini 1997), resulting in even stronger effects of climatic seasonality, especially the lack of rainfall. Shallow

soil over limestone bedrock is typical of karst topology, as well as the highly porous underlying rocks, leading to a low capacity for water storage. These features may increase water deficit during the dry season (Querejeta *et al.* 2007; Fu *et al.* 2012). Consequently, drought stress is the main limiting growth condition in karst dry forests (Liu *et al.* 2011).

Dendrochronology is one of the most reliable tools for studying the association between climate and tree growth (Hughes 2002). In dendrochronology, it is generally assumed that a broad force, such as climate, will modulate population growth. The crossdating process depends on the presence of a common growth signal in a population of trees (Schweingruber 1998). This common growth signal is partially driven by interannual climatic fluctuations. However, this climatic signal can only be assessed in tree species that possess an annual tree-ring formation, which results from annual climatic seasonality causing cambial dormancy, which can induce distinct tree-ring boundaries (Fritts 1976). Temperature is the main seasonal variable affecting annual growth in temperate zones, while precipitation and flooding are the main seasonal variables in the tropics (Worbes 1995). Those climatic fluctuations are recorded in tree rings as differences in radial growth rate.

In the tropics, dendrochronological research has shown that several tree species produce annual rings and that interannual climatic variability is recorded therein (Callado *et al.* 2001; Worbes 2002; Rozendaal & Zuidema 2011). Dendrochronological research has also successfully assessed the effect of climate on tree growth in seasonally dry tropical forests. Several studies showed that precipitation is, indeed, the key limiting factor for tree growth in these dry conditions (e.g., Fichter *et al.* 2004; Trouet *et al.* 2006; Brien *et al.* 2010; Lopez & Vilalba 2011; Paredes-Vilanova 2013). However, those studies show that

precipitation/growth relationships are species- and site-dependent (Rozendaal & Zuidema 2011). Since the growth and development of these species are closely related to climate, their survivability may be impacted by precipitation regimes modified by climate change (Brienen *et al.* 2010). Tree-ring studies are fundamental to understanding climatic sensitivity in tropical tree species, especially in the context of climate change (Zuidema *et al.* 2012; Zuidema *et al.* 2013).

The present study aimed to build a tree-ring chronology of *Hymenaea courbaril* L. growing in a karst dry forest and evaluate the effect of climate on its growth. *Hymenaea courbaril* was chosen for this study because it has annual rings (Lucchi 1996, Westbrook *et al.* 2006, Lisi *et al.* 2008) and it has been successfully used in a dendrochronological study before (Locosselli *et al.* 2013). It also belongs to the Leguminosae family, which, in number, dominates the species growing in tropical dry forests (Pennington *et al.* 2006). The following hypotheses are tested: 1) tree rings of *H. courbaril* specimens have a common signal driven by climatic factors, 2) the growth of *H. courbaril* is mainly regulated by rainfall amount, as drought stress is the main limiting growth factor in tropical dry forests, and 3) mean annual temperature, although fairly high in central Brazil, does not influence radial growth based on its reduced seasonality.

Material and Methods

Study site

This study was performed in the Terra Ronca State Park (13°44'11"S and 46°21'40"W) located in Goiás State / Central Brazil (Figure 1). The site is characterized by dry forest ("mata-seca") that grows over limestone bedrock. The area has a typical tropical climate with a well-defined dry season (Figure 2), which lasts for five months from May to September. The total precipitation is 1424mm per year, and the average temperature is 24.7°C.

Species and sampling methodology

Individuals of *Hymenaea courbaril* L. (Leguminosae, Caesalpinioideae) were sampled at this site for the dendrochronological study. This species is considered brevi-deciduous based on its exchange of all leaves over a short period during the dry season (Lee and Langenheim 1975). Sampled trees were growing over the limestone formation in a dry forest, close to rock outcrops found in the karst formations. Trees were 9 to 12 meters tall with average diameters of 47 cm, and maximum and minimum DBH of 26 and 70 cm, respectively. We selected trees with no signals of injury and we tried to sample a wide range of tree sizes to avoid sampling bias (Bowman *et al.* 2012). This species is known for having annual rings characterized by marginal parenchyma (Figure 3) produced at the end of the growth season. For that reason, they are named as terminal marginal parenchyma (Luchi

1998). We sampled 19 trees using an increment borer coupled to a motor drill. The system produces increment cores 15 mm wide and up to 1 meter long. We sampled one to two cores per tree at breast height totalizing 32 increment cores. The remaining injuries were treated with a solution of sodium copper and calcium oxalate, and later closed with a natural cork.

Samples preparation and dating

All samples were fixed in wooden supports for air drying. Then, each sample was polished using sandpaper with different grits (50, 100, 200, 400, 600, 1000 and 2000). Tree rings were identified and marked under stereomicroscope. At this point, we performed visual crossdating within increment cores from the same tree to preidentify possible false rings and missing rings. Afterwards, we measured the width of all tree rings using the Lintab 6 System (Rinntech – Germany). A second crossdating process was performed with the tree-ring width data using TSAP-Win software (Rinntech – Germany). First, tree rings were crossdated within one tree and then to, latter, cross date samples from different trees. Quality of dating was checked using COFECHA software (Holmes 1983). During this process, an individual tree-ring series was considered unreliable if it had a low correlation value with all other series. Under such circumstances, that tree-ring series was rejected in order to improve the common signal (Brienen & Zuidema 2005).

Data analysis

After a proper tree-ring dating, the final chronology was built using the ARSTAN software (Cook & Kairiuksts 1990; Cook & Holmes 1996). A 32-year cubic spline function was used for tree-ring detrending. The Expressed Population Signal values (EPS) were calculated according to Wigley (1984) in 30-year segments. The final residual chronology was used to analyze climate/growth relationships. To accomplish this, precipitation, days of precipitation and temperature data from an INMET (National Institute of Meteorology – Brazil, Posse Municipality) climate station were used.

That station is at about 35km from the sampling site, at the same karst system that has a north to south axe. It is also in the east slope of that system similarly to the sampling site (Figure 1b). Although it does not have a long series, from 1977-2012, it is the data that better represents the sampling site specific conditions. Additionally, similar time spans were used before in relevant studies of tropical dendrochronology (eg. Brienen and Zuidema 2005) testing similar hypothesis to our study. These relationships were tested using Pearson's correlation of monthly climate data and the residual chronology. Climate data of current and previous growth years were used. Correlation results were represented in bar plot graphics, and all significant correlations ($p \leq 0.05$) were highlighted with different color bars.

Additionally, we performed a principal component analysis (PCA) with all statistically significant climate data from previous analyses to evaluate if these climate variables were highly correlated (collinear) or not. PCA was also used to

reduce the dimension of the climate data and, at the same time, gain new information about the effects of climatic variables on *H. courbaril* growth. Thus, with the three analytical approaches used in this study, we aimed to improve our understanding of how climate modulates the growth of *H. courbaril*. All analyses were performed using R software (R Core Team 2013); PCA used the Vegan package (Oksanen *et al.* 2014).

Results

Eighteen out of nineteen sampled individuals were dated using standard dendrochronological methods. Missing rings were not a common problem during this population dating since they represented only 2.2% of all dated rings, as revealed by the COFECHA software (Table 1). False rings were also present in the samples (Figure 3). Final tree-ring chronology has an inter-series correlation of 0.44 and a sensitivity value of 0.53. The tree-ring chronology has a total length of 183 years and an average length of 104 years (Table 1 and Figure 4). Although the chronology is almost two centuries long, EPS values are higher than 0.85 up to 1920. This result indicates that this period is well replicated in the population and could be used to inform our understanding of how climate influences the growth of this population (Figure 4).

Within the period between 1977 and 2012, correlations between climate variables and tree-ring residual chronology were performed. Results show that both precipitation and temperature modulate *Hymenaea courbaril* radial growth at the study site. Tree-ring residual chronology correlates with precipitation and days of precipitation of the current growth year. Precipitation during August and October

correlates positively with the tree-ring residual chronology. This means that higher precipitation at the end of the dry season and beginning of the wet season stimulates higher radial growth. Data for days of precipitation produced a similar result. More days of precipitation in September, during the transition period between dry and wet seasons, stimulate higher radial growth rate. On the other hand, the influence of temperature does not occur during the current year of growth, but rather in the previous one. Maximum July temperature has a negative influence on the radial growth of this species. This month corresponds to the middle of the dry season at the study site.

The principal component analyses shows that precipitation of August and October, days of precipitation of September and temperature of July (-1) are poorly correlated among themselves (Figure 7A and Table 1), which is a good indication that their effects on *H. courbaril* growth are not a result of collinearity. The first (PC1) and second (PC2) principal component explain 40% and 31% of data variability, respectively. The first component contains the variation of precipitation amount at the beginning of the current growth season and temperature in July from the previous growth year. Higher values of PC1 indicate conditions of growth with lower precipitation amount and higher July temperature (-1), while the second component includes the following variables: days of precipitation in September, precipitation of October, and July temperature (-1). Out of the two components, only the first correlates significantly with the residual growth chronology (Figure 7 B and C).

Discussion

The individuals of *Hymenaea courbaril* showed significant common growth related to local interannual climatic variability. The dating process was possible, despite the presence of some absent and false rings. Actually, the occurrence of false and missing rings is reported in many tropical tree species (e.g., Brienens & Zuidema 2005; Vlam *et al.* 2014).

As expected, precipitation has a marked effect on the growth of this species since it is the main limiting growth factor in tropical dry forests (Pennington 2006). Similar results have been reported in many other dendrochronological studies (e.g., Pumijumnong *et al.* 1995; Enquist & Leffer 2001; Fichtler *et al.* 2004; Brienens *et al.* 2010). However, precipitation does not always regulate the growth of tree species in similar ways. Radial growth can be driven by the precipitation amount in different periods, such as the entire growth year, the wet season, the dry season and the transition between dry and wet seasons (Rozendaal & Zuidema 2011). Therefore, species under such regimes may respond to annual climate variability in different ways. Our results showed that the growth of *H. courbaril* is mainly regulated by precipitation during the transition period. Actually, the first rainfall events seemed to play a key role in this *H. courbaril* growth in that specific condition.

Out of the 11 climate/growth relationships of species inhabiting actual dry forests, as summarized by Rozendaal and Zuidema (2011), only one species showed a similar result with exclusive effect of precipitation on growth during the transition period: *Pterocarpus angolensis* growing in the semiarid forests of Zambia. Precipitation in the transition period during the end of the dry season was found to

modulate the growth of this species (Fichtler *et al.* 2004). Most studies, as summarized by Rozendaal and Zuidema (2011), have shown that the chronologies of 27 tropical tree species depend on annual and/or wet season precipitation. Other studies, such as those of López and Villalba (2011) studying *Centrolobium microchaete* and Paredes-Villanueva *et al.* (2013) studying *Machaerium scleroxylon*, both from Bolivian dry forest, also showed growth/precipitation correlations during the wet season.

It is possible that the results found in the present study are a consequence of the soil characteristics of the study site. Since this *H. courbaril* population grows in a karst region, the soil is shallow, and the underlying bedrock is highly porous, creating an environment with high water deficit (Fu *et al.* 2012; Fan *et al.* 2011). It should be noted that these first precipitation events must be well distributed during the transition period. After those initial events, soil may retain a positive water balance during the rainy season (Brienen & Zuidema 2005). Apparently, these trees will have a longer growth season if these events begin earlier. A similar dependence on the length of the growth season was reported for *H. courbaril* growing in a semideciduous forest in southeastern Brazil (Locosselli *et al.* 2013).

Temperature is another climatic variable that influences the growth of this species. Negative correlations between growth and temperature in the tropics are typically related to temperature-induced stress. An increase in air temperature leads to a decrease in air water potential resulting in higher water stress from evapotranspiration (Rolland 1993). Another consequence of high temperature is higher photorespiration rate based on reduced affinity between RUBISCO and CO₂ molecules (Jackson & Volk 1970; Ogren 1984). Both have the potential to decrease tree radial growth. However, it was the temperature in July of the previous, not

current, growth season which correlated significantly with *H. courbaril* growth. Somehow, a stressful condition in one year will only influence tree growth of the following year. Similar results have been found in other studies, suggesting that a less than ideal growth condition in one year could lead to a smaller capacity in reserve formation used for the next year's growth (e.g., Dünish *et al.* 2003).

Both situations can explain the results found in *H. courbaril* growing over limestone. However, a third explanation is also possible. Reproduction is a process known to be highly demanding in terms of reserve consumption, implying a tradeoff between growth and reproduction (Obeso 2002). Besides flowering, fruit production in *H. courbaril* usually takes two months for development and another six months for ripening. Moreover, fruits of this species are woody and relatively large, demanding a high amount of carbon for their production. The flowering period of this species runs between the end of the dry season and the beginning of the rainy season (Lee & Langenhein 1975), right after the month of significant temperature correlation. Thus, in warmer years, it is possible that this species drives a high amount of carbon toward reproduction, leaving reduced reserves for the next year's growth. Similarly, Hacket-Pain *et al.* (2015) showed that the seed production of *Fagus sylvatica*, a masting species, influenced trees growth with a time lag of two years. That is the same that lag found for temperature influence on this species growth.

It is important to note that the PCA analysis revealed a tradeoff between precipitation and temperature data based on the climate of the study site and that this tradeoff seems to influence the growth of *H. courbaril*. The first component contains the variation of precipitation amount at the beginning of the current growth season and temperature in July from the previous growth year, demonstrating that years of high temperature in July (-1) and lower precipitation amount in the transition

period lead to a reduced growth rate. This represents a combined influence of higher drought stress and possible reduced reserve from the previous year. The opposite situation is also true. Years with lower drought stress and higher available reserves increases the radial growth rate. The second principal component is less intuitive in the context of climate growth relationships because it has vectors of precipitation and temperature in the same direction, possibly explaining why it has no significant correlations with the growth of this species.

This clear relationship between climate and growth of *H. courbaril* is highly relevant in the context of future climate changes. Understanding climate/growth relationships is important for all tree-inhabiting tropical dry forests (Brienen *et al.* 2010), particularly since temperature has been steadily increasing 0.26 ± 0.05 °C each decade since the mid-1970s in the tropics (Malhi & Wright 2004). Furthermore, future projections based on CO₂ emission scenarios indicate that temperature will increase in regions with dry tropical forests in a manner similar to, or even marginally higher than, the predicted planet temperature increase of 2°C to 4°C by 2100 (Christensen *et al.* 2007; Meier&Pennington 2011). A consistent reduction of soil water availability of 5 to 15 % is also expected in tropical Latin America by the end of the 21st century (Bates *et al.* 2008). All of these changes will likely have a negative impact on the growth of *H. courbaril*, especially in karst areas where sources of growth stress are highly pronounced.

Acknowledgments

Authors thank Paula Jardim and Viviane Jono for helping with the wood material processing, Jean-Sébastien Moquet and Ramiro Hilario dos Santos for helping with the field work, Francisco Willian for inviting our team to work at Terra Ronca State Park, and Eric Rezende Kolailat and the SEMAHR Goiás for providing the work license. Authors also thank FAPESP (Fundação de Amparo à Pesquisa do Estado de São Paulo; 12/50457-4) and CNPq (Conselho Nacional para Pesquisa e Desenvolvimento; 478503/2009-1, 142706/2011-6) for funding.

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Figures

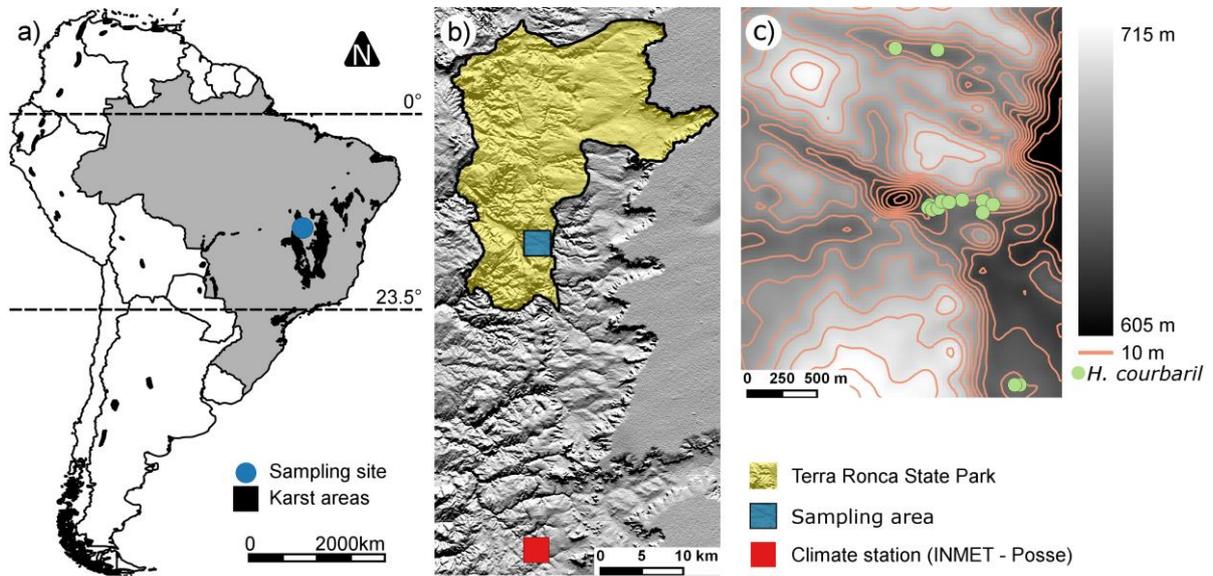


Figure 1: South American map with all known karst areas (in black), including the *Hymenaea courbaril* sampling site (dark grey circle) in the central region of Brazil (country in light gray). The karst areas are based on Williams and Fong (2010). Topographic data are from TOPODATA (MMA-Brazil).

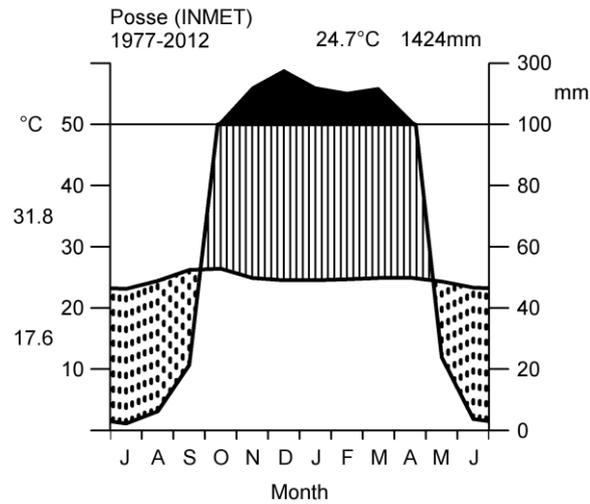


Figure 2: Walter and Lieth climate diagram showing temperature and precipitation curves from INMET data (National Institute for Meteorology – Posse). Average maximum and minimum temperatures are also given in temperature axes. It shows a typical tropical climate with a dry season lasting five months, from March to September.

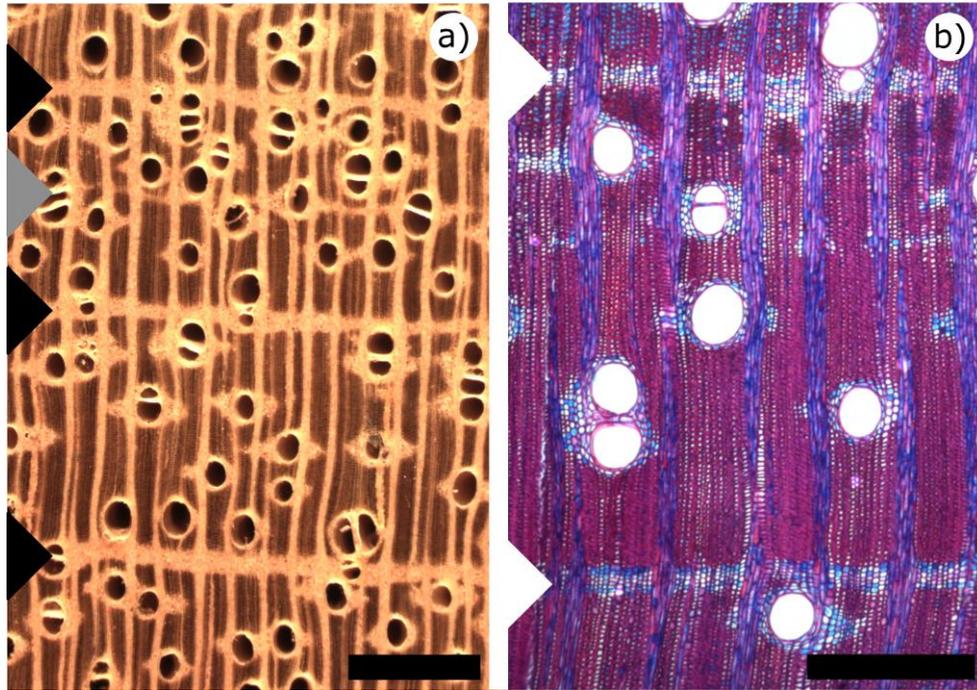


Figure 3: a) Macrograph of a *Hymenaea courbaril* sample showing real rings (black arrow) and a false ring (grey arrow), scale bar = 1mm. b) Micrograph of the transversal section of the wood showing details of the marginal parenchyma (white arrows), scale bar = 500 μm .

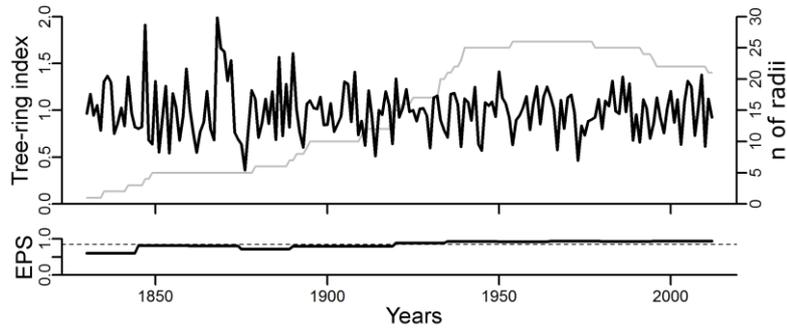


Figure 4: Residual chronology of *Hymenaea courbaril* growing in the limestone dry forest of central Brazil (black line). The grey line shows the sample depth, and the dashed line represents an EPS (Expressed Population Signal) value of 0.85. The chronology EPS values are higher than 0.85 up to 1920. That period is considered well replicated within all dated series.

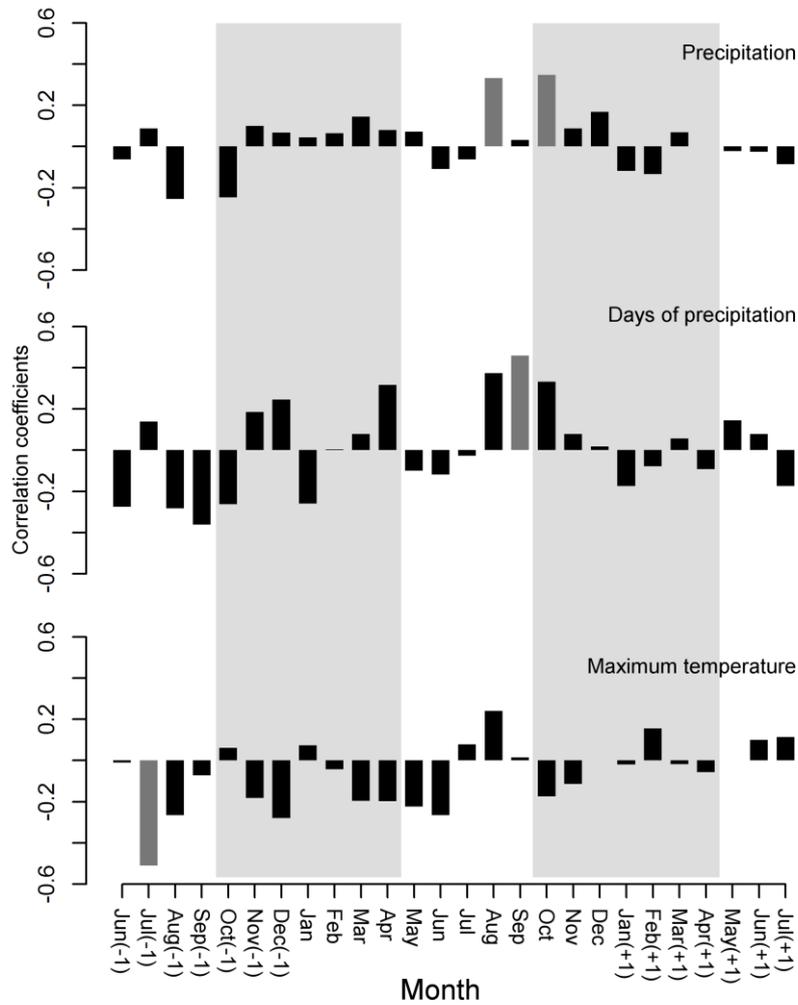


Figure 5: Correlation values between the residual chronology and monthly climate variables. Correlations were calculated for two wet seasons (areas in grey) that correspond to the current and previous growth years. Significant correlations ($\alpha=0.05$) are highlighted as grey bars.

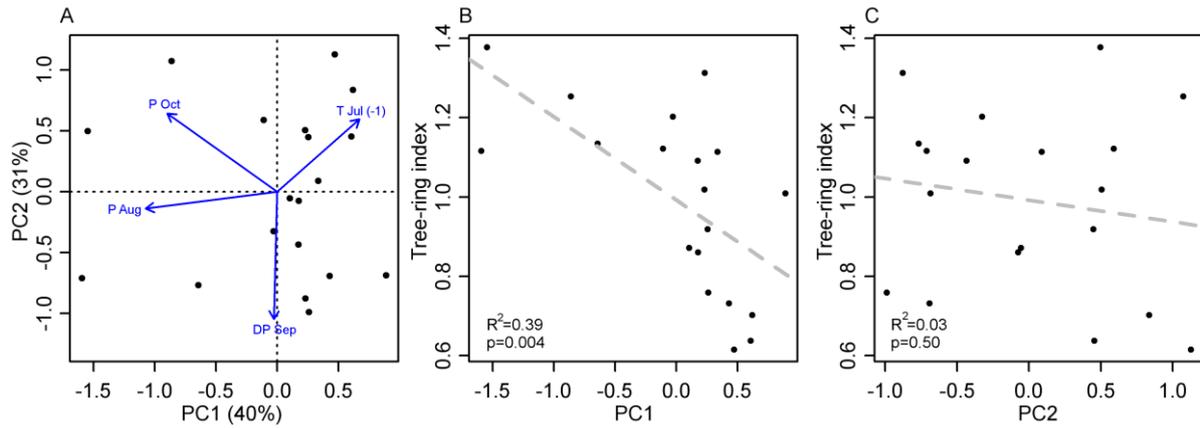


Figure 7: A) Principal component analysis of climate variables significantly correlated with *H. courbaril* growth, showing their noncollinearity. B) Linear regression between the first principal component and tree-ring residual chronology. C) Linear regression between the second principal component and tree-ring residual chronology. Determination index (R^2) significance values (p) are indicated in respective graphics.

Table 1: Descriptive statistics of *Hymenaea courbaril* residual chronology (Std = standard deviation and AC = autocorrelation).

	Residual Chronology
Number of trees (radii)	18 (26)
Average tree-ring width (Std)	1.7mm (0.6mm)
Total number of dated rings	2720
Percentage of missing rings	2.2%
Series correlation	0.44
Sensitivity	0.53
Total length (average length)	183 years (104 years)
First order AC	0.40

Table 2: Descriptive statistics of first and second principal components on sampling site climate data.

	Principal component 1	Principal component 2
Eigenvalue	1.59	1.24
Proportion of variance	0.40	0.31
Cumulative proportion	0.40	0.71
Eigenvectors		
Prec Aug	-0.69	-0.10
Prec Oct	-0.58	0.47
Days of Prec Sep	-0.02	-0.76
Temp Jul (-1)	0.43	0.43

Capítulo 3

Fragmentation of the Atlantic Rainforest affects climate sensitivity of tree growth

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Manuscript submitted to Biological Conservation (April 27th, 2015)

Abstract

Deforestation eradicated more than one third of the world's forest cover. In the tropics, the Atlantic Forest has been reduced to 11.7% of its original cover. This natural environment is now reduced to a few large and many small scattered patches. To further address this phenomenon, we used dendrochronological methods to study the effect of fragment size and disturbance on age and growth sensitivity to climate of *Hymenaea courbaril*. To accomplish this, 35 individuals were sampled in two conservation areas in southeast Brazil. One is the largest fragment of semi-deciduous forest in the region, and the other one is a smaller and highly disturbed patch, both within similar climatic regimes. Tree-ring chronologies were built and correlated with regional climate and sea surface temperatures (SST). We found old trees between 190 and 249 years of age, despite the historical selective logging. We found growth rate and temperature signals to be similar between populations. Annual and seasonal temperatures negatively influence tree growth. Equivalent SST signals were also found at both sites. On the other hand, temperature sensitivity was higher in the least disturbed population. Precipitation in the beginning and middle of the growth season positively influences tree growth of the less disturbed population, while precipitation of the previous growth season has a negative influence on the most disturbed population. Based on these results, it can be concluded that the climate/growth relationship is attenuated at the most disturbed site such that a higher disturbance may lead to lower climate sensitivity of *H. courbaril* growth.

Keywords: Dendrochronology, tree ring, edge effects, conservation, ENSO, Mata Atlântica.

Introduction

Forests of the world have experienced landscape transformation resulting in habitat fragmentation and degeneration. Deforestation activities in temperate and tropical zones have already led to a loss of more than one third of the global forest cover (Williams 2003). In tropical zones, increased land use has also accelerated during the last decade (Hansen *et al.* 2013), resulting in strong habitat fragmentation. Natural environments that were once continuous across the landscape are now fragmented in scattered patches of different sizes and shapes, making them vulnerable to anthropogenic disturbance and altered microclimatic conditions (Broadbent 2008). These effects are pronounced in smaller fragments (Haddad *et al.* 2015), and they may be exacerbated by the effects of climate change (Brodie *et al.* 2012).

Trees from smaller fragments compared to those in larger fragments are under higher environmental stress. Forest borders suffer the so-called edge effect, which includes a wide range of biotic and abiotic changes. For instance, edges are prone to the colonization of invasive species, changes in microclimate conditions, and the threat of fire (Murcia 1995). These effects are even stronger in small forest patches and those with irregular border shape because both features proportionately increase the forest area under the influence of the edge effect (Laurance and Yensen 1991). Other factors increase environmental stresses on these fragments, such as characteristics of the surrounding matrix, including proximity to roads. For example, open pasture land and the presence of crops can enhance abiotic changes at the forest edges (Driscoll *et al.* 2013). Roads constitute a threat by making remote

areas more accessible, dividing protected areas, increasing air pollution and the probability of fire (Freitas *et al.* 2010; Narayanaraj and Wimberly 2012; Newman *et al.* 2014).

The Atlantic Rain forest used to cover an extensive area with a latitudinal range of 27°, and almost half of that area was covered by semi-deciduous forests in the inlands (Câmara 2003). However, this area has been severely reduced from centuries of changes in land use (Dean 1996). In their extensive survey of the current state of the Atlantic Forest, Ribeiro *et al.* (2009) concluded that only 11.7% of the original 150 million hectares (ha) remain. Not only is its total area dramatically reduced, but 80% of existing fragments are smaller than 50 ha. Only 0.03% of them are larger than 10,000 ha.

As sessile and, sometimes, long-lived organisms, trees may suffer from the impact of fragmentation, especially in the smaller forest patches. Different levels of disturbance may affect tree metabolism, leading to different growth characteristics. Additionally, old-growth trees could not survive the changes induced by forest fragmentation (Andereg *et al.* 2012). In fact, the number of large, old trees is showing a declining trend, even though they play important ecological roles in the forest (Lyndenmayer *et al.* 2012). Additionally, evidence suggests that half of the large trees (DBH > 60 cm) are expected to die after three decades of fragmentation in the Brazilian rainforest (Laurance *et al.* 2000).

The impact of fragmentation on stand age and tree growth can be assessed through tree-ring analysis. Growth rate and age can be directly obtained through dendrochronological methods (Schweingruber 1988). Both data are important to understand if growth rates have been maintained or not during the fragmentation process and if these patches are still able to sustain old trees. Such analysis is also

useful to understand how climate modulates tree growth (Hughes 2002). Therefore, tree-ring analysis may shed light on how forest fragmentation affects the climate/growth relationship. To the best of our knowledge, only a few studies have generally addressed these aspects (e.g., McDonald and Urban 2004; Copenheaver *et al.* 2005), and no study has examined them in the Neotropics.

To accomplish this, we studied the tree rings of two populations of *Hymenaea courbaril* from fragments of semi-deciduous forest that belongs to the highly threatened Atlantic Forest Biome in southeastern Brazil. One population was sampled in one of the largest fragments of semi-deciduous forest in the region, and the other one was from a considerably smaller and highly disturbed fragmented patch, both within similar climatic regimes. This study is driven by two hypotheses: 1) that old-growth trees would not be found in the smaller forest patch based on a history of selective logging and, hence, possible decline in the number of old trees after fragmentation, and 2) that climate signal and sensitivity in the tree rings of these two fragment populations would differ by the more pronounced impact of edge effect on the smaller patch.

Material and Methods

Sampling took place in two state parks in the State of São Paulo, Brazil. Morro do Diabo State Park (22°34'43"S; 52°17'28"W, 340m a.s.l.), the largest semi-deciduous fragment in that state with 33,845 hectares, which is divided into two fragments. Vassununga State Park (21°43'16"S; 47°35'18"W; 650m a.s.l.) comprises a total area of 858 hectares spread over five fragments (Figure 1). Both conservation areas are located in the same latitudinal range, and the distance

between them is about 500km. The sampling sites show similar climatic characteristics with a short dry season from June to August. The average temperature is 21.7 °C and 21.1 °C, and annual precipitation is 1365 mm and 1553 mm in Morro do Diabo and Vassununga, respectively (Figure 1). These fragments are relicts of the semi-deciduous forest that once covered most of the plateau area of São Paulo State.

In Vassununga, most sampling took place at the borders of Capetinga Oeste and Capetinga Leste. Both patches are surrounded by sugarcane plantations and are bordered by 2 km of Highway SP-330 (Table 1). Up to 2010, sugarcane production in the region had been characterized by pre-harvest field burning and was the cause of several flashovers into the reserve (Mendes *et al.* 2009). In general, low species diversity, abundance of wild coffee trees, and remnants of coffee bean cleaning facilities, canopy openings, as well as the strong presence of lianas, are the key indicators of strong disturbance.

The Morro do Diabo site is less disturbed, mostly because the change in land use only started in the middle of the twentieth century, and, therefore, a vast area is still covered by forest. During that period, a railroad was built crossing the current area of the state park, and it was in service between 1951 and 1978. Selective logging took place at the site to provide sleepers for the railroad (Faria *et al.* 2006). Although we did not quantify the amount of liana and understory disturbance, our field observations suggest that the Morro do Diabo site is less disturbed (Table 1). Moreover, we found no evidence of fire in the trees in Morro do Diabo, but we did find fire scars in the sampled and surrounding trees in Vassununga, especially those sampled close to the road. (Table 1)

At both sites, we sampled individuals of *Hymenaea courbaril* L. (Leguminosae) for this study. We chose this species because it is relatively common in the semi-deciduous forest of southeastern Brazil, and it has proven annual rings delimited by terminal marginal parenchyma (Luchi 1998 and Westbrook et al. 2006), making it suitable for dendrochronological studies (Locosselli *et al.* 2013). Individuals can achieve DBH values up to 1.4 meters and height values over 25 meters, being regarded as an emergent species (Leite 2007). We recorded the geographical position of all trees in the field in order to later calculate the minimum distance between trees and the forest edge and the highway, using ArcGIS v.10.2 (ESRI 2010).

We used a nondestructive sampling method for the present study. A special increment borer coupled with a gas-powered drill was used to produce increment cores (Krottenthaler et al., in review). We sampled cores of 22 trees (41 cores) in Morro do Diabo site and 13 trees (25 cores) in the Vassununga site, respectively. The increment cores were later fixed in woody supports and air dried. Samples were polished using sandpaper with different grits (60-2000) to produce a clear surface. All tree rings were then identified under stereomicroscopy, and a visual cross-dating was performed, beginning with samples from the same tree. We measured tree-ring width using the Lintab 6 System (Rinntech-Germany), and the dating process was performed using TSAP software (Rinntech-Germany). We also used COFECHA software (Holmes 1983) to check crossdating quality. The final residual chronology was built using ARSTAN software (Cook & Kairiuksts 1990; Cook & Holmes 1996). For the detrending process, we applied linear regressions for all trees in both populations. Since the aim of the present study was to evaluate both climate signals and sensitivity in the tree-ring chronologies of two populations with different

disturbance levels, we decided to use only the last 50 years of the two residual chronologies. The expressed population signal (EPS) was also calculated (Wigley *et al.* 1984).

For climate correlations, we used climate data from the Climate Research Unit (Harris *et al.* 2014) at a resolution of 0.5° obtained through the KNMI Climate Explorer tool (Trouet and Van Oldenborgh 2013). We decided to use that data source because the closest climate station to Morro do Diabo with a reasonably long climate dataset was more than 100 km away. Although a climate station is located relatively close to Vassununga, we decided to standardize the climate data source and make the results comparable by obtaining all climate data from the Climate Research Unit. We correlated monthly, seasonal, and annual temperature and precipitation data with both tree-ring residual chronologies. Additionally, we performed correlations with monthly sea surface temperature anomalies (SST) from ENSO (El-Niño Southern Oscillation) regions 1-2, 3, 3-4 and 4. Data were obtained from the Hadley Centre Sea Ice and Sea Surface Temperature dataset (HadISST) (Rayner *et al.* 2003). We also performed a field correlation between tree-ring chronologies and SST using the KNMI Climate Explorer tool. Finally, we correlated the annual and seasonal temperature and precipitation of each site with the monthly SST data to understand how these anomalies modulate the regional climate (See Appendix 1).

Results

Most trees from Morro do Diabo were located in areas far from the forest edge and the highway. Most were between 2000 and 5000 meters away from the

forest border, with just a few samples closer to it, and none was close to the highway. The closest one to the road was located more than 600 meters from it. On the other hand, all trees sampled in the Vassununga site were positioned closer than 500 meters from the forest edge, and more than half the samples were found at less than 100 meters from the highway (Figure 2).

We were able to date most sampled trees for the last five decades at both sites, despite the presence of a few false rings. The final chronologies include 21 trees from Morro do Diabo and 13 trees from Vassununga. The maximum number of rings counted in an individual at Morro do Diabo is 190, while the maximum number of rings counted in Vassununga is 249, with an average of 117.6 and 108.8 rings, respectively. Both mean interseries correlation coefficients (r) and sensitivity value were higher in the Morro do Diabo population. However, the number of missing rings and the average tree-ring width are similar (Table 2). The EPS of both chronologies is higher than 0.85, meaning that the residual chronologies (Figure 3) of both sites are reliable for the last five decades.

Within this period, climate/growth correlations (Figure 4) show that precipitation has a positive correlation at the beginning and middle of the wet season at Morro do Diabo and a barely significant negative influence at the end of the wet season. In Vassununga, precipitation in the middle of the previous wet season has a negative correlation with tree-ring width. The annual and seasonal precipitation amounts do not correlate with tree-ring width at either site. Instead, significant correlations were found for monthly, annual and seasonal temperature. Overall, the correlation values are higher for temperature than for precipitation. Moreover, the annual and seasonal temperature correlations show the highest correlation values: -0.42 and -0.4 for Morro do Diabo and -0.48 and -0.49 for Vassununga, respectively.

The actual rate of that influence is about 33% and 44% higher in the trees of Morro do Diabo for annual and seasonal temperature, respectively, as revealed by the slope constant (ax) in the linear regression equations (Figure 5).

The growth of these two populations is also regulated by the influence of the SST in the ENSO regions of the Pacific Ocean. ENSO regions 1 and 2 have no influence on the growth of *H. courbaril* from Morro do Diabo, but they do have a small influence on Vassununga. The strongest correlations for both sites are with SST anomalies from regions 3, 3-4, and 4 (Figure 6). Overall, they have a negative influence on the growth of these populations. The maximum correlation values occur in the dry season and in the transition between the dry and wet season. Afterwards, the correlation values gradually decrease. The correlations with the SST are better visualized in the field correlation maps (Figure 7). The control of SST over the growth of these populations is mediated through regulation of regional temperature, not precipitation (see Appendix 1). The increase in SST results in higher annual temperatures at both sites.

Discussion

We were able to find old-growth trees in both Morro do Diabo (190 years) and Vassununga (249 years), despite the global trend of declining large old trees (Lyndenmayer *et al.* 2012). Actually, these trees are even older because we failed to hit the pith during the sampling work, and they can be considered relatively old by tropical standards (Worbes and Junk 1999). Our data highlight the importance of these two conservation units in the highly deforested and fragmented Atlantic Forest of southeastern Brazil. They also harbor other species with large and possibly old

trees like *Aspidosperma polyneuron* (or peroba-rosa) in Morro do Diabo and *Cariniana legalis* (or jequitibá-rosa) in Vassununga.

The average annual radial increment is quite similar between the two populations. From a climatic perspective, this is an expected result since both sites have similar temperature and precipitation regimes (Wagner *et al.* 2014). This similarity is also valid for some climate signals found in the tree rings of *H. courbaril* from both sites in which growth is strongly influenced by the average annual and seasonal temperature. The negative influence of temperature could be related to a decrease in the air water potential, leading to an enhanced water stress (Rolland 1993). An alternative, or complementary, explanation could be a higher photorespiration in warmer periods (Jackson & Volk 1970; Ogren 1984). Likewise, the influence of El-Niño anomalies mediated through regional temperature changes is similar for both sites. It is important to note that the El-Niño anomalies do not change the precipitation regime in either sampling sites (Coelho *et al.* 2002).

However, in the context of fragmentation, differences in the growth rates and climate signals could be expected. Higher stress is likely to be found in the most disturbed site. From our field observation, Vassununga showed evidence of fire in the sampled and adjacent trees. Human-caused fire is a possible consequence of roadway proximity and the nature of the surrounding matrices (Freitas *et al.* 2010; Narayanaraj and Wimberly 2012; Newman *et al.* 2014; Driscoll *et al.* 2013). In Vassununga, trees were closer to the road when compared to Morro do Diabo. Additionally, the surrounding matrix of the Morro do Diabo State Park is mainly pasture, while it is mainly sugarcane in the Vassununga State Park (Silva 2004). Fire was commonly used in the sugarcane crops to clear leaves before the harvest (Uriarte *et al.* 2009).

Another difference between the sites was the abundance of lianas. From our field observations, lianas were more abundant in Vassununga, with some trees completely infested by these woody vines. It is well known that forest fragmentation increases liana abundance and rates of tree infestation as a result of the highly disturbed and well-lighted environment (Schintzer and Bongers 2002; Schintzer and Bongers 2011). High abundance of lianas has a negative impact on tree communities, resulting in higher structural stress and competition for resources, especially light. In some cases, it can result in the death of the trees (Campbell *et al.* 2015). This higher abundance of lianas is actually expected in Vassununga since the fragments are smaller, and the forest border is highly irregular.

Although these forces did not influence the growth rate and the temperature signals in the tree rings of either site, they seem to influence the growth sensitivity to temperature of the sampled trees. Less sensitivity is seen in trees of Vassununga when compared to Morro do Diabo. Moreover, in Vassununga, the growth of *H. courbaril* trees is about 25% and 30% less dependent on average annual and seasonal temperature, respectively. A low sensitivity was also reported by Copenheaver *et al.* (2005) in *Juniperus virginiana* trees from the forest edge when compared to individuals from the forest interior. Similar results were found for *Quercus virginiana* in a highly disturbed urban environment (Bartens *et al.* 2012). In that study, authors suggest that conditions, both above and below ground, could affect the sensitivity of trees to climate. As also shown in the present study, the above-mentioned fragmentation forces seems to make the climate-growth relations weaker.

Another difference was found in the influence of precipitation on growth. The growth of trees from Morro do Diabo is positively correlated with precipitation at the

beginning and middle of the growth season. On the other hand, precipitation during the middle of the previous wet season has a negative influence on tree growth from Vassununga. Again, it is possible that differences found in the precipitation signal could be related to differences in the level of disturbance at both sites. If this is the case, the precipitation signal found in Morro do Diabo could be the standard signal for a less disturbed population under the tropical climate regime. In fact, the influence of precipitation from the beginning and, especially, the middle of the wet season is extensively reported for tropical environments (Rozendaal & Zuidema 2011).

The results of the present study showed that old trees are still found in both conservation units, despite their different sizes and disturbance levels. Our second hypothesis held that climate signal and sensitivity in the tree rings of these two fragment populations would differ by the more pronounced impact of edge effect on the smaller patch. Partially disproving this hypothesis, results also showed that only some climate signals are different between the sites. Climate sensitivity, on the other hand, was always found to be lower in the most disturbed smaller fragment. Overall, our study shows that the climate/growth relationship is attenuated at the most disturbed site such that the forces of disturbance lead, in part, to lower climate sensitivity of *H. courbaril* growth. Apparently, both populations might respond in different ways to future climate changes.

It should be noted that the results demonstrated in this study may only represent a fraction of all possible impacts of forest fragmentation on the growth of this species. It is well known that there is a lag of the effects of fragmentation on a forest community and that time span increases with species longevity (Metzger *et al.* 2009). Thus, the next step in understanding the impact of forest fragmentation on

the growth of these populations would be an evaluation of disturbance signals in longer chronologies in relation to known events, such as highway construction, changes in the land use around the state parks, and documented forest fires.

Acknowledgement

Authors thank Luiza Teixeira Costa, Julio Majcher, Jânio Fábio Oliveira, Nelson Correa and Antonio Crema for helping in the fieldwork; the Fundação Florestal do Estado de São Paulo for providing work permits; and Helder Faria and Heverton Ribeiro for providing accommodations during fieldwork. Authors also thank FAPESP (Fundação de Amparo à Pesquisa do Estado de São Paulo; 12/50457-4), DFG (AN 214/10-1) and CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico; 478503/2009-1, 142706/2011-6) for funding.

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Figures

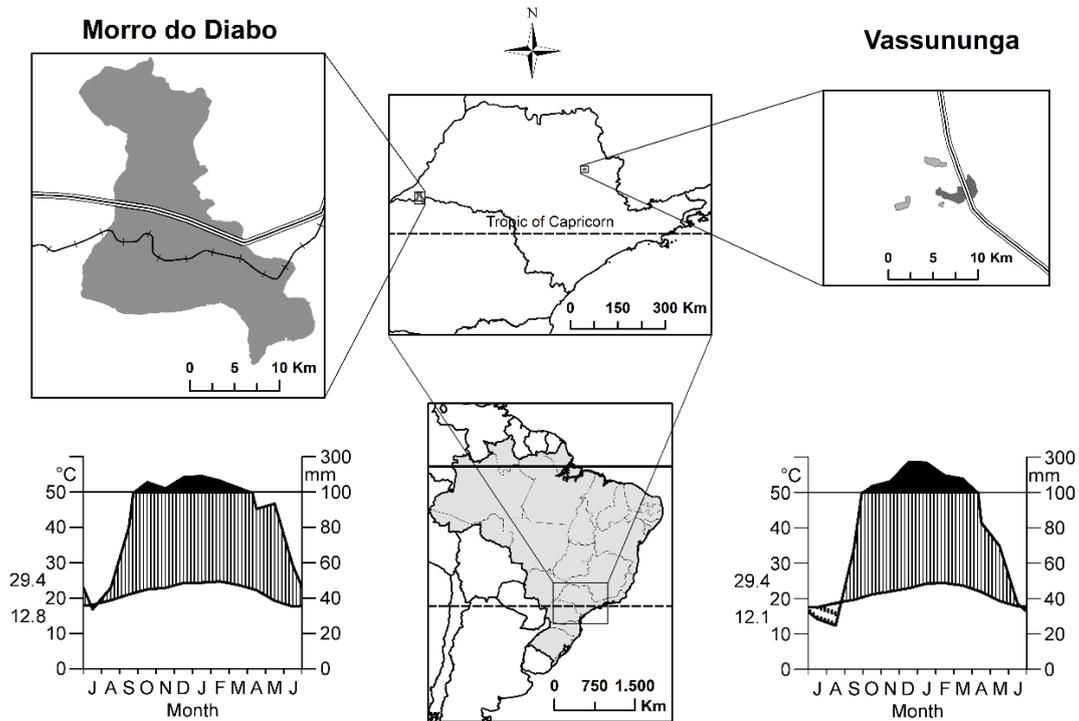


Figure 1: The two sampling sites in southeastern Brazil. They are located close to the Tropic of Capricorn (lower dashed line). The maps of the two conservation areas are shown in similar scale and *H. courbaril* trees were sampled in the forest patches highlighted in dark grey. Highways and railroad are indicate in the maps. The distance between them is 500 km. Climate diagrams show monthly precipitation and temperature for one year. Average maximum and minimum temperatures are also provided. Both sites show a rather typical tropical climate with a relatively short dry season.

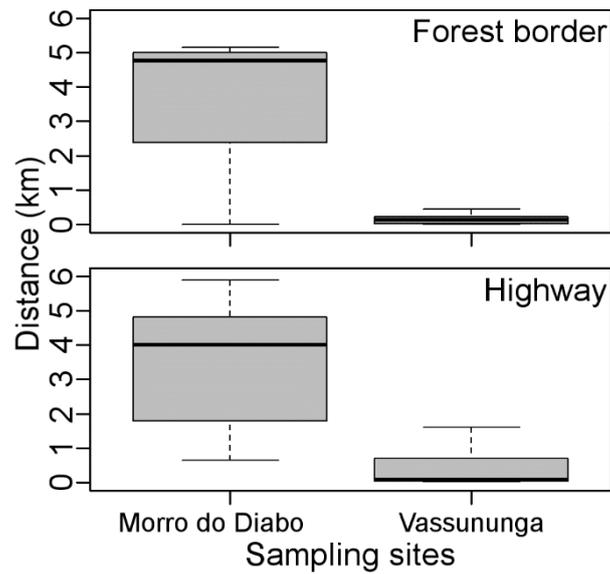


Figure 2: Boxplots of the minimum distance values from each sampled *Hymenaea courbaril* tree to the forest border and the highway at the Morro do Diabo and Vassununga sites.

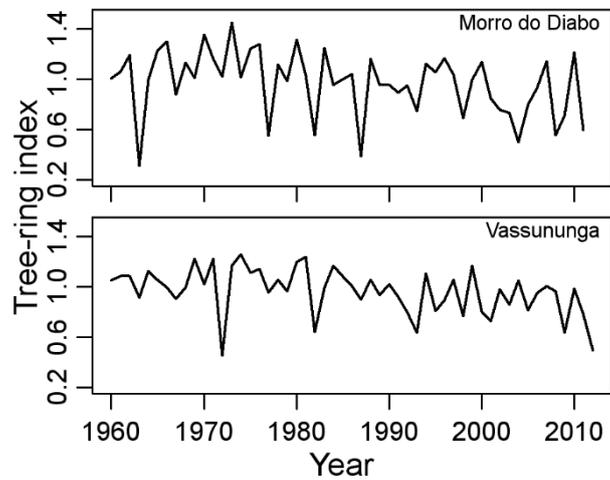


Figure 3: The final residual chronologies produced using tree-ring width data from Morro do Diabo and Vassununga sites. Both chronologies start in 1960.

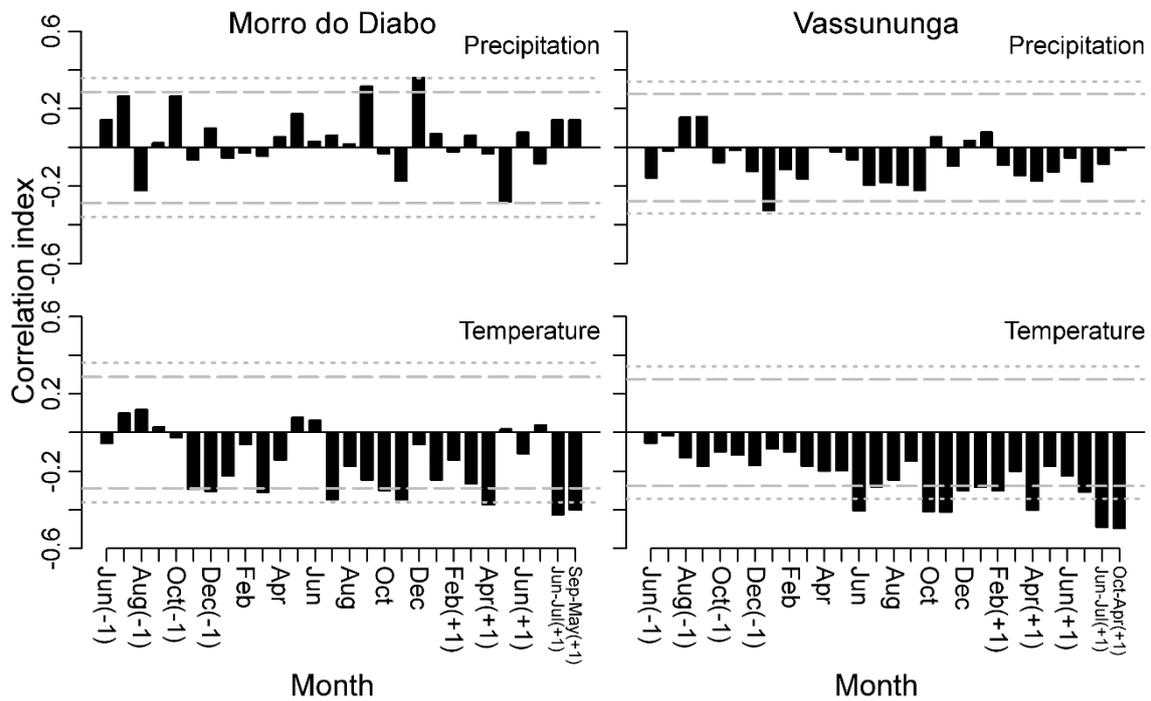


Figure 4: Climate growth correlations for Morro do Diabo and Vassununga sites. Correlations were performed using monthly, seasonal and annual precipitation and temperature data. Grey lines indicate the correlation indexes for $\alpha = 0.05$ (dashed lines) and $\alpha = 0.01$ (dotted lines).

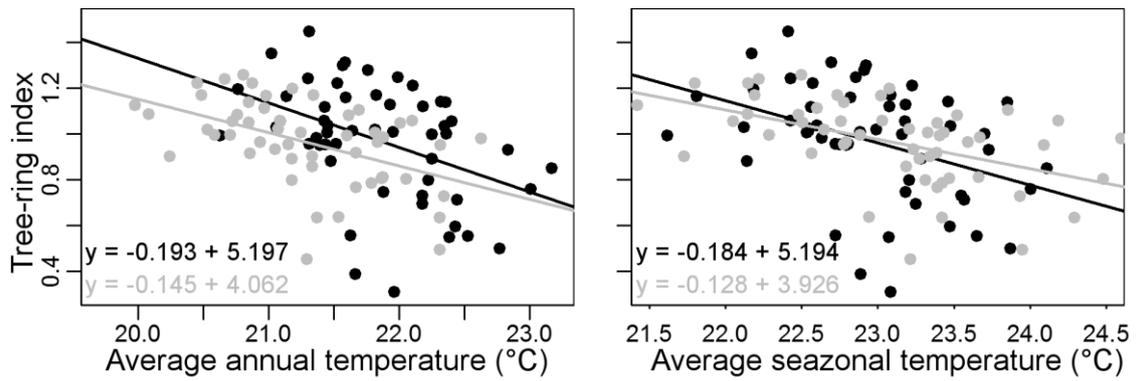


Figure 5: Linear regression between tree-ring index and average annual average seasonal temperatures for Morro do Diabo (black line and dots) and Vassununga (grey line and dots), with the respective linear fit equations. The slope coefficients are 33% and 44% higher in the Morro do Diabo population, respectively.

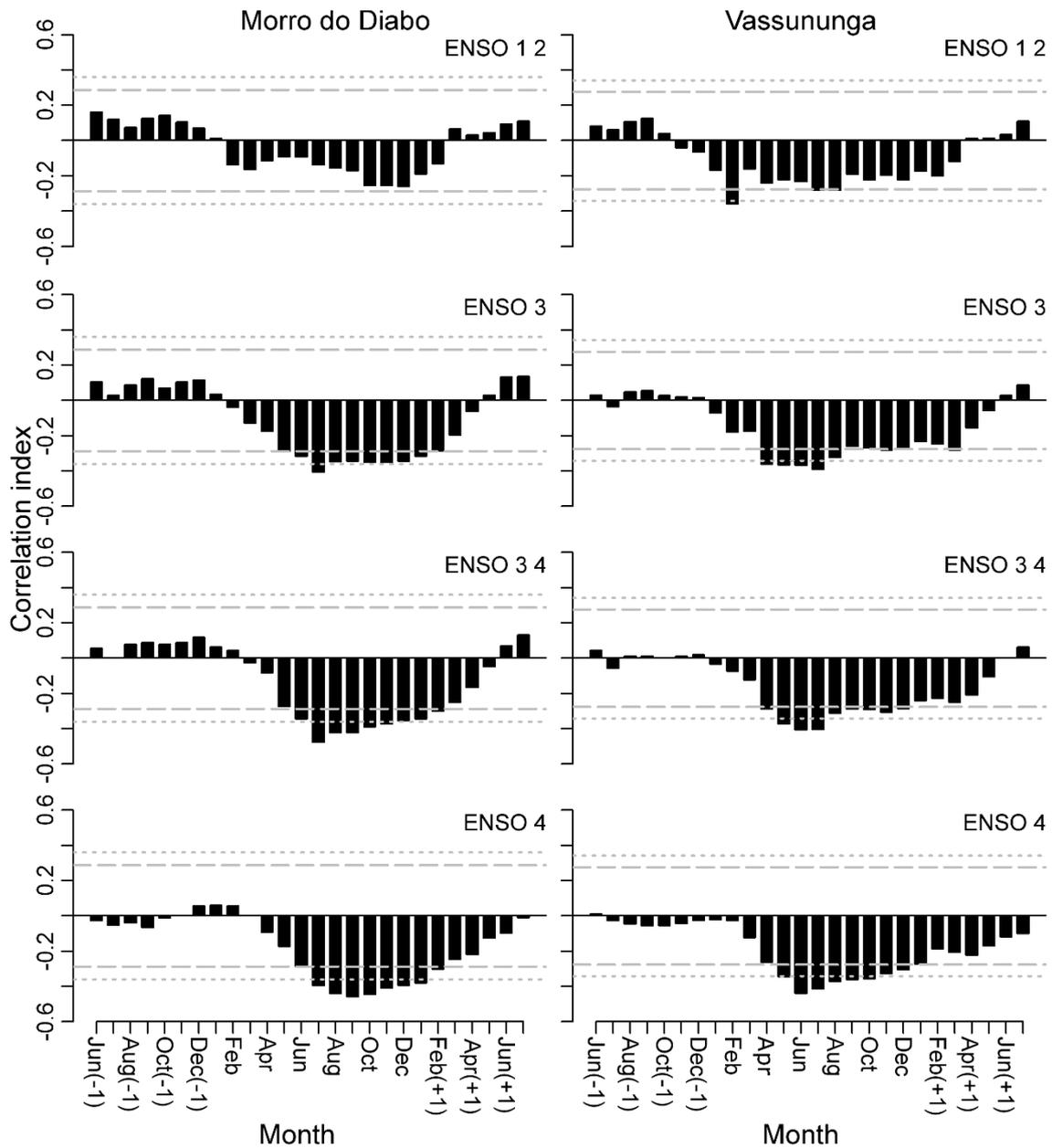


Figure 6: Correlations between monthly sea surface temperature anomalies from ENSO regions 1-2, 3, 3-4 and 4 and tree ring residual chronology from Morro do Diabo and Vassununga. Grey lines indicate the correlation indexes for $\alpha = 0.05$ (dashed lines) and $\alpha = 0.01$ (dotted lines).

Fragmentation effect on *H. courbaril* growth

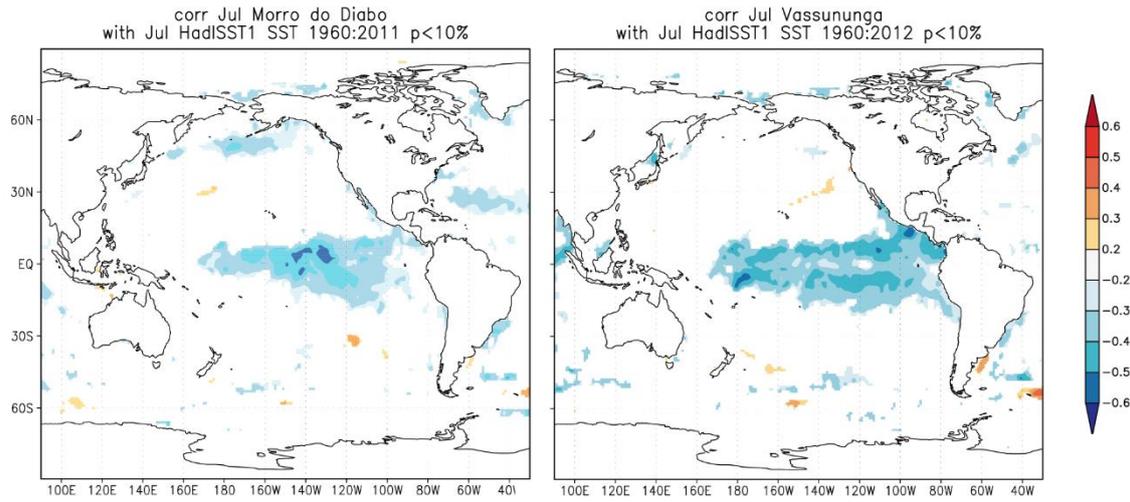


Figure 7: Example of spatial correlation of tree-ring residual chronology and sea surface temperature anomalies (HadISST1) over the Pacific Ocean in the month of July.

Table 1: Site descriptions, including official data and fieldwork observations.

Features	Morro do Diabo	Vassununga
Forest Type	Semi-deciduous	Semi-deciduous
Total area ^{1,2}	33,845 ha	858 ha
Number of Fragments ^{1,2}	2	5
Main past matrix ^{1,2}	pasture	coffee plantation
Main current matrix ^{1,2}	pasture	sugarcane
Crossed by highway	yes	yes
Cars per day ^{3,4}	2449	13000
Trucks and buses per day ^{3,4}	355	7000
Sampled trees close to the highway	none	6
Presence of lianas ⁵	moderate	high
Understory condition ⁵	moderately to not disturbed	heavily disturbed
Fire events ^{1,2}	yes	yes
Evidence of fire in the sampled trees ⁵	no	yes
Evidence of fire in adjacent trees ⁵	no	yes
Past selective logging ^{1,2}	yes	yes

¹ Faria *et al.* (2006)

² Mendes *et al.* (2009)

³ DER (2014)

⁴ AUTOVIAS, personal communication

⁵ Field observations

Table 2: Comparison between tree characteristics and chronological features from *Hymenaea courbaril* sampled in Morro do Diabo (largest and least disturbed forest fragment) and Vassununga (smaller and most disturbed forest fragment). DBH= diameter at breast height, EPS = Expressed Population Signal, TRW = tree-ring width and STD = standard deviation.

Site	Morro do Diabo	Vassununga
Trees (radii)	21(37)	13(24)
Average DBH (cm)	72.3	68.9
Max DBH (cm)	100.2	101.5
Average tree-ring number	117.6	108.8
Maximum tree-ring number	190	249
Series intercorrelation	0.44	0.35
EPS	0.94	0.87
Sensitivity	0.53	0.43
Missing rings (%)	1.03	1.11
Average TRW (mm)	2.61	2.78
STD TRW (mm)	0.68	0.88

Capítulo 4

The carbon cost of heartwood formation for *Hymenaea* spp. (Leguminosaea) trees
and its role as a carbon sink

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Manuscript will be submitted to Global Change Biology

Abstract

Forests retain one half of the terrestrial carbon, which is mainly fixed in the wood of trees. Accumulation of carbon biomass can be estimated by growth rate and sapwood specific gravity. However, during heartwood formation, later carbon deposition can occur. This process may represent a carbon cost to plants that is sometimes neglected. In this study, we hypothesized that heartwood formation represents a high carbon cost for trees, and it represents a carbon sink that is important for forests biomass and the carbon cycle. To test this hypothesis, we sampled 171 *Hymenaea* spp. trees from ten sites in the southern Neotropics. Within a latitudinal gradient, populations were labeled as North, Center and South. For each tree, we measured radial growth, sapwood and heartwood specific gravity, carbon amount, and heartwood transversal area. We also measured the assimilation rate by temperature under controlled conditions. Results show that radial growth and sapwood specific gravity are independent of climate. However, the specific gravity ratio between heartwood and sapwood does correlates with temperature in a way that is remarkably similar to the actual assimilation curve. Moreover, growth and sapwood specific gravity do not differ in North, Center and South, but the specific gravity ratio between heartwood and sapwood is smaller in the South. These results can be translated into carbon values since heartwood has, on average, 3.6% more carbon than sapwood. Therefore, heartwood has 21%, 19% and 14% more carbon per volume than sapwood in the North, Center and South, respectively. Results also show a clear tradeoff between carbon allocated for heartwood and sapwood formation. This tradeoff, together with a lower assimilation rate, leads to lower carbon availability for heartwood formation in the South population. These results

become more important for estimating biomass and carbon fluxes when they are scaled up to the forest level.

Keywords: Specific wood gravity, growth rate, carbon amount, Neotropics, sapwood, assimilation rate

Introduction

Forests are one of the largest carbon stocks in the biosphere, storing nearly half of the terrestrial carbon. Almost one fourth of that carbon is fixed in Tropical Forests (Bonan 2008), even though they cover less than 10% of the global terrestrial area (Lewis *et al.* 2006). Tropical forests store that carbon pool because they account for 34% of the terrestrial gross primary production (Beer *et al.* 2010). The assimilated CO₂ is used by plants to produce leaves, woody and reproductive tissues, volatile organic compounds, or it is stored as nonstructural carbohydrates (Chapin *et al.* 1990; Mahli 2011). Actually, 39% of that carbon is fixed in woody parts, including branches, stem and coarse roots (Mahli *et al.* 2011). Wood is not only an important component of carbon storage by volume, but it also represents an important carbon sink in the sense of residence time that can last for centuries or millennia, depending upon species longevity (Zhou and Luo 2008, Galbraith *et al.* 2013).

Xylem is produced by the activity of the cambium meristem. The first step of xylem production is cell division of the initial cambium cells (Plomion *et al.* 2001). The primary cell wall is formed at the beginning of cell differentiation. Derivative cells can undergo a few divisions until cells start to expand through the loosening of cellulose microfibrils mediated by expansins (Cosgrove 2000). Expansion is later constrained by the secondary wall deposition that is mainly formed by cellulose, hemicellulose and lignin (Barnett 1981). At this point, the basic wood structure is finished, and it leads to an increase in tissue volume and biomass. Seasonal cambial activity leads to the formation of tree rings that are typically used as a

reliable parameter to estimate tree growth and biomass increase over time (Babst *et al.* 2014).

However, the incorporation of carbon in basic xylem structure is not only a consequence of tree growth. Wood is a highly dynamic and complex tissue. On the cellular scale, it is formed by different cell types that have distinct life trajectories (Wolf *et al.* 2012). Each cell type has singular characteristics like cell wall size and composition. For instance, fibers and tracheids have thicker cell walls and higher proportion of lignin when compared to vessels and parenchyma cells (Donaldson 2001). The distribution of these cell types and cell wall features in the tissues leads to a wide range of biomass values per tissue volume (Swenson and Enquist 2007). These differences can be translated into wood specific gravity values that vary within a range of 0.08 to 1.39 among different species (Chave *et al.* 2009). Additionally, different organic molecules with distinct carbon amounts form xylem tissue. The combination of these molecules in the wood leads to wide variation in the carbon content of tree species. That wide range is found in all biomes, from 41.9% to 51.6% of carbon in the tropics, from 45.7 to 60.7% of carbon in subtropical and Mediterranean areas, and 43.4% to 55.6% of carbon in temperate and boreal areas (Thomas and Martin 2012).

On the tissue scale, other substances can be later deposited in the xylem, separating that tissue into sapwood and heartwood (Plomion *et al.* 2001). This addition of new substances to the “basic wood” structure can usually be distinguished by the color and, sometimes, the smell of the substances deposited there (Umezawa 2001). Heartwood formation is still not fully understood; however, it is known to be comprised of four main steps: cell death, deposition of extractives, xylem dehydration in the transition zone between heartwood and sapwood, and

changes in cell wall structures (Nakada and Fukatsu 2012). The senescence of parenchyma cells occurs at the boundary between sapwood and heartwood. During this process, these cells start to produce heartwood substances known as extractives. The relative amount of extractives in wood is usually small, reaching values up to 5% to 10% in temperate species. However, these values can be higher in some tropical species (Umezawa 2001). Parenchyma cell walls also change during heartwood formation with a later deposition of lignin leading to thicker cell walls (Nakada and Fukatsu 2012).

These biochemical changes in the wood during heartwood formation lead to differences in biomass per volume by the addition of components in the “basic” sapwood structure. Differences in heartwood and sapwood specific gravity have been described before. In a survey of 33 species from the Amazon Forest, 72% had a higher basic density in heartwood when compared to sapwood (Fearnside 1997). While the overall average value of heartwood and sapwood specific gravity ratio was 6%, some species, such as *Brosimum rubescens*, *Eschweilera* spp. and *Iryanthera tricornis*, presented values 41%, 28% and 25%, respectively, for this ratio. Even carbon concentration can change between sapwood and heartwood as a consequence of the later deposition of lignin and extractives. Reported values for carbon concentration in the wood can be from 1% to 15% higher in heartwood when compared to sapwood in some softwood and hardwood species (Peri *et al.* 2010; Aza *et al.* 2011; Bert and Danjon 2006; Lamloom and Savidge. 2003).

Therefore, to understand how trees sink carbon in the wood, it is necessary to consider growth rate, wood specific gravity and carbon content (Babst *et al.* 2014). These three factors show how trees increase wood volume seasonally, as measured by tree-ring analysis, how much mass per volume is added, based on specific gravity

data, and the proportion of actual carbon amount in that mass by carbon amount data. However, the presence of the heartwood adds some complexity to the way in which carbon is stored in wood. It is important to highlight two aspects of the carbon stored in the heartwood. That is, while its formation may represent a high carbon cost to the trees, it also may represent an important carbon pool in the forest biomass.

The aim of this study is to test the importance of heartwood formation from both points of view: at the tree level, as a matter of carbon cost, and at the forest stand and carbon cycle levels, as a matter of carbon sink. To accomplish this, we analyzed the growth rate, specific gravity and carbon amount of two forest *Hymenaea* species using a sampling design that comprises a latitudinal gradient of 23° (more than 2600 km) in the southern Neotropics.

Material and Methods

Species and sampling sites

The genus *Hymenaea* spp. belongs to the Leguminosae family. Trees are usually emergent with height values greater than 25 meters and stem diameter occasionally greater than 1 meter. The stem is usually cylindrical with rare presence of buttress. It is considered a brevi-deciduous species at sites with a well-defined dry season. It has an amphi-Atlantic distribution, with only one species present in Africa (*H. verrucosa*) and thirteen species found in the tropical New World. In the Neotropics, they inhabit almost all tropical environments from the Tropic of Cancer in the Northern Hemisphere to slightly south of the Tropic of Capricorn in the Southern

Hemisphere. *Hymenaea courbaril* L. has the widest distribution among all *Hymenaea* species and is present from northern Mexico to southeastern Brazil. Other species have a more restricted distribution, usually related to a single biome, like *H. parvifolia* Huber. It is found in the non-flooded areas (“terra firme”) of the Amazon Forest (Lee & Langenhein 1975).

For the present study, we sampled 171 trees at ten sapling sites. They were categorized according to their latitudinal position as North, Center and South (Figure 1). Trees sampled in the northern areas were from three sites located in the western, central and eastern Amazon Rainforest. Trees sampled in the central areas were from a huge wetland (Pantanal), a karst dry forest (PE Terra Roncas) and a semi-deciduous forest (Matozinhos municipality). In addition, trees from the southern regions belong to three semi-deciduous forests (PE Vassununga, PE Morro do Diabo and EE Caetetus) and one from the ombrophilous rainforest (PE Carlos Botelho) (Table 1). Out of ten sampled populations, nine belong to *Hymenaea courbaril*, while only one belongs to the *Hymenaea parvifolia* species in the western Amazon forest. The use of two species from the same genus should not be a problem for the present study because wood specific gravity is strongly conserved within Neotropical genera (Chave *et al.* 2006). Additionally, *Hymenaea* species have annual tree rings that are delimited by a marginal parenchyma (Luchi 1998; Locosselli *et al.* 2013).

Sampling methods and data acquisition

For nondestructive sampling in all populations from the Center and South groups, we used a special increment core coupled to a motor-powered drill

(Krottentaler *et al.* in review). One to four cores were obtained for each tree. In the northern sites, we obtained full stem discs at saw mills from legal logging companies. It should be noted that we tried our best to avoid sampling bias by collecting a wide variety of tree sizes within each population during fieldwork (Bowman *et al.* 2012). From these discs, two to four radii were cut to facilitate transportation and preparation. All samples were air-dried, and the woody surface was polished using sand paper with different grits (from 50 to 2000). With a fine surface, tree rings were identified using a stereomicroscope and measured using the Lintab 6 system (Rinntech-Germany). Whenever possible, false and wedging rings were identified, and tree-ring series were corrected with the help of the TSAP-Win software (Rinntech, Germany). With the tree-ring measurements, we produced the growth rate dataset. Additionally, we calculated the basal area increment for all samples. Nevertheless, this parameter was only used for the comparison of latitudinal groups because it is highly dependent on tree size (see Appendix S1).

The age derived from the tree-ring width measurements was underestimated for some trees because some of them were hollowed out, and we failed to hit the pith in others. To address this problem, we used the methodology proposed by Hietz (2011). First, we scanned all samples (EPSON V300). Then, we drew lines parallel to the wood rays and estimated the pith position at their intersection using the GIMP software (version 2.8.10), followed by measurement of the missing distance to the pith using ImageJ (Schneider *et al.* 2012). By using the average width of the innermost ten tree rings, we were able to calculate the number of missing rings and better estimate the age of each tree. We also calculated the sapwood and heartwood widths in all samples. After averaging these values among radii, we

calculated the proportional area of sapwood and heartwood of all samples in the stem transverse section.

For specific gravity analysis, we obtained one sample from the sapwood and one from the heartwood of each individual. Sapwood and heartwood were visually identified and could be easily separated by their distinct differences in color (Figure 2). The average number of rings in the sapwood and heartwood were 20 and 12, respectively. All sapwood samples were obtained close to the cambium, while heartwood samples were obtained closer to the sapwood-heartwood boundary. We also prepared one individual of each population to produce specific gravity profiles. For that purpose, we obtained consecutive samples from the pith to the cambium for each tree. By doing so, we were able to analyze the overall radial trend of the wood specific gravity (see Appendix S2 for these results). Each sample for wood specific gravity was first weighed after air-drying. Then, the volume of each sample was measured by water displacement. We placed a beaker with distilled water on a semi-analytical balance (Mettler Toledo PB303-L) and then measured the water displacement by immersing the sample fixed in a “volumeless” needle (Williamson and Wiemann 2010). Next, all samples were dried in a drying oven at 105°C for 48 hours before they were reweighed to calculate the initial water content.

We also calculated the proportion of carbon content in the heartwood and sapwood of 140 individuals representing all 10 sites. To do this, we produced wood powder from sapwood and heartwood by using a micro mill. Five milligrams of wood powder were weighed on an analytical balance (Mettler AX26) and encapsulated in tin caps for the analysis of carbon amounts, utilizing an Elemental Analyzer (Carlo Erba NA 1500, Milano, Italy).

In order to understand how temperature regulates assimilation rate in leaves of *Hymenaea courbaril*, we established an assimilation curve with saplings in controlled conditions. Seeds were obtained from the Forest Institute of São Paulo (Casa Branca Municipality in São Paulo State). Seedlings grew in natural photoperiod and atmospheric CO₂ concentration. Measurements were made in leaves of three seedlings for each temperature treatment. This was accomplished by building a chamber in order to have precise control of environmental temperature and relative humidity. Within that chamber, assimilation was measured using an I.R.G.A. (LI-6400XT) in different temperatures from 15°C to 40°C at 5°C steps.

Statistical analysis

After data acquisition, an extensive dataset was produced for the analysis (see appendix S3). The main variables analyzed in this study are average radial growth rate (GR), average radial growth rate of the last 60, 50, 40, 30, 20, 10 years (GR60, GR50, GR40, GR30, GR20, GR10), basal area increment (BAI) sapwood specific gravity (SWSG), heartwood specific gravity (HWSG), ratio between heartwood and sapwood specific gravity (HWSG/SWSG), proportional heartwood area (HWA/TA), tree age and diameter at breast height (DBH), sapwood carbon quantity (SWC), heartwood carbon quantity (HWC) and ratio between heartwood and sapwood carbon quantity (HWC/SWC).

With that data set, we tested the hypothesis that average GR, SW SG, HWSG and SWSG/HWSG are dependent on regional climate variables. Climate data of the last five decades were obtained from the Climate Research Unit (Harris et al. 2014) using 0.5° grids through the KNMI Climate Explorer tool (Trouet &

Oldenborgh 2013). The following variables were used: average annual temperature, months with precipitation higher than 50mm (Worbes 1999) and annual precipitation. We fitted linear curves for all wood and climate variables. Additionally, quadratic curves for the relationship between all wood variables and temperature were fitted. This final analysis was done only with temperature because the dependence of assimilation rate by temperature is represented by an optimum curve. We also fitted a quadratic curve to the real leaf assimilation rate and temperature data produced in controlled conditions.

The second group of analyses was performed using the three latitudinal groups: North, Center and South. We tested if trees presented differences in average GR, BAI SWSG, HWSG, SWSG/HWSG and HWA/TA among these regions. Because of the different number of individuals per group, we tested the differences using non-parametric Kruskal-Wallis analysis and the Dunn test. The former analysis was done using the 'dunn.test' package (Dinno 2014). Additionally, we built a correlation matrix among the following variables: GR, Age, CBH, SWSG, HWSG, HWSG/SWSG and HWA/TA. This correlation matrix was performed in order to understand the relationship among these variables and confirm if the studied variables are dependent or not on age and tree diameter.

To understand whether or not the results found for sapwood and heartwood specific gravity reflect differences in carbon amount, we first compared the carbon amount of the sapwood and heartwood using a Student's *t*-test. Thereafter, we multiplied the average heartwood and sapwood carbon amount by the heartwood and sapwood specific gravity of the specimens, respectively. The ratio between heartwood and sapwood carbon amounts (HWC/SWC) indicates the proportional extra carbon quantity deposited in the heartwood.

Finally, we tested the hypothesized potential tradeoff between “basic wood” formation, as determined by sapwood specific gravity and growth rate, and heartwood formation in the North, Center, and South populations. To accomplish this, we first tested the length of the average growth rate data (from 60 to 10 years) that had the best correlation with HWC/SWC. Since these two variables have a nonlinear relationship, we fitted asymptotic curves ($y=x^{-1}$) to choose the best growth rate average length. We then transformed the growth data using the resulting equation to produce a linear relationship between both variables. To test the tradeoff, we built mixed effect linear models for each latitudinal group and tested the effect of growth rate (1/GR and GR) and sapwood carbon quantity (SWC) on HWC/SWC variability (Faraway 2005). We compared all models using AICc values to choose the best models for each latitudinal group. In order to better understand how the predictive variables influenced the response variable, we built surface plots of the best models for each latitudinal group using the ‘rsm’ package (Lenth 2009). All analyses were performed using R (R Core Team 2013).

Results

The studied variables values vary among sampling sites. For instance, radial growth rate ranges from 1.40 to 3.05 mm, sapwood specific gravity ranges from 0.80 to 0.91, heartwood specific gravity ranges from 0.90 to 1.03, and the ratio between heartwood and sapwood specific gravities ranges from 1.07 to 1.19 (Table 2). However, we found that neither temperature nor months of precipitation with more than 50mm of rain, and annual precipitation significantly correlated with average growth rate (Figure 3). In fact, none of the tested wood features correlates with

variables related to precipitation. Nonetheless, temperature correlates with heartwood specific gravity ($R^2 = 0.48$) and the proportion of heartwood and sapwood specific gravity ($R^2 = 0.61$). An even better fit is achieved by adjusting a quadratic function ($R^2 = 0.88$) to HWSG/SWSG with an optimum between 25°C and 26°C. The assimilation rate data by leaf temperature also showed a typical optimum curve with a maximum measured value of assimilation rate at 25°C (Figure 4).

Differences in growth rate are also not statistically significant when compared among the three latitudinal groups, being equal in the North, Center and South (Figure 5). Basal area increment is also equal in the North and the South, but it is smaller in the Center. These relations in the BAI among the three groups are actually a result of the DBH of the sampled trees and the average growth. Since growth is similar among North, Center and South, and trees are smaller in the Center, a smaller BAI there is expected. Concerning sapwood specific gravity, no differences were found among the groups; nonetheless, heartwood specific gravity is higher in the North and Center groups. These findings result in a higher proportion between heartwood and sapwood specific gravity in the North and Center when compared to the South. The average specific gravity ratios are 1.17, 1.15 and 1.10 in the North, Center and South, respectively. Another difference was found for the proportional heartwood area. North and South groups have similar HWA/TA, while in the Center group, it is smaller.

We also found statistically significant differences in the relative carbon amount of sapwood and heartwood of the studied *Hymenaea* spp. individuals (Figure 7). The average carbon amount of sapwood is 46.9% with a mean error of 0.11, while the average carbon amount of heartwood is 48.5% with a mean error of 0.12. Hence, the values of specific gravity ratio (HWSG/SWSG) lead from 0.18,

0.15, and 0.10 to the values of carbon ratio (HWC/SWC) of 0.21, 0.19 and 0.14 in the North, Center, and South, respectively. Since all values of heartwood and sapwood specific gravity were multiplied by constant values of heartwood and sapwood carbon amounts, all results shown previously for HWSG/SWSG are equally valid for HWC/SWC.

Table 4 shows the results of the models selected to test the potential tradeoff between the production of “basic wood” and heartwood formation. From all four models tested for each site, those influenced by SWC and 1/GR had the lowest AICc. It is important to highlight that the models with asymptotic relationship, as indicated by the 1/GR (Figure 8 a,b,c), are actually better than those used with absolute growth rate values. Figure 8 also indicates three major differences in how this tradeoff works in a gradient from the North to the South. First, there is a gradient in the time span of the average growth rate that better correlates with HWC/SWC. It is the last 60, 50 and 10 years that better correlates in the North, Center and South populations, respectively. Second, a higher change in the predictors values is necessary to produce a similar change in the values of HWC/SWC in the South, when compared to the North and Center. And third, the importance of sapwood carbon quantity seems to increase from North towards the South. This last characteristic can be noted by the decreasing angle between the HWC/SWC lines and the X axes (1/GR axes).

Discussion

Carbon cost of heartwood formation

Tree growth measured through tree-ring data is a common feature used to estimate the increase of carbon and biomass stocks in trees and biomes (Babst *et al.* 2014). Despite the differences found in the average growth rate among sites, nor temperature nor precipitation could explain the variation found in the growth of *Hymenaea* spp. populations, even though these two climatic variables are generally regarded as key factors influencing growth variability (Wagner *et al.* 2014). Moreover, no differences were found in growth among the North, Center and South categories, indicating that biomass accumulation, as measured by tree radial growth, is equal among these three groups. Similar results were found with BAI, in which the North and South are not statistically different. Only the BAI from the Center is smaller, which is an expected result since trees are smaller and GR is equal.

However, radial growth is not the only way to measure tree biomass accumulation in the stem. The amount of organic matter fixed per unit of wood volume is also important (Fearnside 1997). Despite the fact that the average values of sapwood specific gravity vary among sites, neither temperature nor precipitation correlates with these values. Moreover, these differences are not significant when the data are evaluated through latitudinal group analysis. Thus, it can be concluded that sapwood specific gravity of *Hymenaea* spp., in the way that it is produced by the cambium, is quite similar in the North, Center and South. This result is quite unexpected because, according to Beer *et al.* (2010), a decreasing gradient of gross primary production exists from lower latitudes to higher latitudes. Hence, if trees are

assimilating more in lower latitudes, then such excess carbon must be allocated somewhere else in plants, such as the heartwood.

In that case, we would expect to find evidence of higher deposition of heartwood in areas with a higher assimilation rate. Actually, the ratio between heartwood and sapwood specific gravity seems to be a good estimator of the actual amount of heartwood substances deposited. Its dependence on temperature can be better described by an optimum curve that is quite similar to the real assimilation curve of *H. courbaril* measured under controlled conditions. Both curves show an optimum value around 25°C. Somehow, heartwood formation is strongly controlled by the assimilation rate. This finding is supported by the fact that the HWSG/SWSG is significantly smaller in the South group where the gross primary production is also smaller (Beer *et al.* 2010). Thus, with less carbon assimilated and a similar production of the sapwood, a reduced amount of carbon would be available for heartwood formation in the South population.

Although these results are interesting, they should be interpreted considering two important points: the specific gravity profiles and the actual sapwood and heartwood carbon amounts. First, these results are only reliable if specific gravity does not have a strong radial trend. Usually, three basic possibilities govern radial trends: increasing, stable and decreasing (Williamson and Wiemann 2010). Pioneer species show a general strong trend of increasing values of specific gravity, while later stages of succession species tend to have a weaker, or no, trend (e.g., Wiemann and Williamson 1988; Wiemann and Williamson 1989; Parolin 2002; Williamson *et al.* 2012; Plourde *et al.* 2015). *Hymenaea* spp. show a rather stable trend in the heartwood with an occasional increase in the first 20 to 30 years and the previously described drop in sapwood. The second point is that the carbon amount

in the heartwood is actually 3.6% higher than in the sapwood. This result indicates that the variability of the heartwood and sapwood specific gravity ratios can actually be translated into carbon quantity values. Moreover, that ratio was enhanced by the higher carbon amount values in the heartwood samples. Values of 21%, 19% and 14% more carbon in the heartwood of *Hymenaea* spp. from North, Center and South, respectively, reveals the high carbon cost of the heartwood formation to trees.

Moreover, the carbon cost of heartwood formation is also supported by the tradeoff found between the formation of sapwood and heartwood deposition in the trees of *Hymenaea* spp. If these trees were to invest more carbon in the production of the sapwood, then only a small amount of carbon would be available to produce the heartwood. With this in mind, it is interesting to note that trees change that tradeoff relation from the North to the South. The heartwood carbon deposition seems to be more prone to short-term oscillations in the growth rate in the South (best correlation with average growth rate of the last 10 years) when compared to the North group (best correlation with average growth rate of the last 60 years). Additionally, it seems that trees in the South group are probably operating at a minimum heartwood deposition and do not have much room to make changes on it. That could explain why larger changes in the growth rate and sapwood carbon are required in the South to make small change in the heartwood carbon deposition. Finally, the sapwood carbon content seems to play a major role in this trade-off. We could conclude that because it becomes more important towards the limiting conditions in the South.

These ideas allow us to formulate a new way of presenting the tradeoff of carbon allocation in wood formation that takes into account growth rate, sapwood

carbon content, and the heartwood carbon deposition. In contrast, studies in the literature that typically only present a tradeoff between growth rate and wood specific gravity (e.g., Chave *et al.* 2009), without out considering differences between heartwood and sapwood specific gravity and carbon content.

Heartwood as a carbon sink

It is important to highlight that *H. courbaril* and *H parvifolia* are not the only species in the tropics and temperate zones with a relevant deposition of heartwood substances. Additionally, the ratio between sapwood and heartwood specific gravity and carbon amount values found for *H. courbaril* and *H parvifolia* are not among the highest values described in the literature. For instance, the sapwood and heartwood specific gravity ratio in *Brosimum rubescens* is 41% (Fearnside 1997) and the heartwood and sapwood carbon amount ratio of *Pinus sylvestris* is 15% (Aza *et al.* 2011).

These differences between the sapwood and heartwood are highly relevant when they are scaled up to a tree or a forest ecosystem (Thomas and Martin 2012). In fact, wood specific gravity is responsible for 29.7% to 45.4% of the above ground biomass (AGB) variability in the stand level (Baker *et al.* 2004). If only sapwood or heartwood specific gravity and carbon amounts are used, it will clearly lead to bias in the above ground biomass estimation, particularly for species important to forest biomass. For example, in a western Amazon plot in Rondônia State, *Hymenaea* sp. trees are the second most important in terms of basal area, and they contributed to 12% of all plot basal area (Alves *et al.* 1997). At that site, the AGB is about 453 tons per hectare. In order to get an idea of heartwood importance, we will consider that

12% of the aforementioned AGB is represented by *Hymenaea* sp. trees (total of 54.36 tons per hectare). If we use the average North values of sapwood and heartwood proportional area and the ratio between the specific heartwood and sapwood, we can calculate an approximate value of 5.2 tons of heartwood substances in the population, considering a cylindrical stem. It is about 9.6% of all above biomass of this species per hectare in the North. In the South where the proportion of heartwood area is similar, but HWSG/SWSG is smaller, the contribution of the heartwood substances would still be important, but smaller. Overall, these statistics mean that heartwood substances are an important carbon pool which should not be neglected in that they play a key role as a carbon sink.

Conclusions

It is apparent that *Hymenaea* spp. trees from the North, Center and South areas produce similar annual sapwood characteristics that are not controlled by climate. On the other hand, heartwood deposition is controlled by temperature, as represented by an optimum curve that is surprisingly similar to the real assimilation curve. The similarity between curves indicates the close association between heartwood deposition and assimilation rate. Based on a tradeoff between sapwood production and heartwood deposition, trees from the South have similar sapwood characteristics and a smaller carbon budget, and they end up with less deposition of heartwood substances. This finding shows how expensive heartwood formation is for *Hymenaea* spp., and also suggests that an active allocation of carbon to sapwood formation is detrimental to heartwood deposition. Therefore, from the point of view of forest ecology, heartwood represents an important carbon sink that should

not be neglected in forest inventories. Moreover, the role of heartwood, as a carbon sink, changes along a latitudinal gradient for *Hymenaea* spp., being stronger in the North and comparatively weaker in the South, but nonetheless, always significant.

Acknowledgement

Authors thank Heiko Baschek, Fabio Coelho, Eric Becman, Erica Righetto Ifanger, Nathalia Alves Altobelli, Gabriela Ambrosino, Sejana Rosa, Adolfo Ferreira, Vitor Barão, Guilherme Freire, and Luiza Teixeira for field work and sample preparation; Paula Jardim and Viviane Jono for sample management in the Wood Collection (SPFw); the Forest Institute of São Paulo State (IF-SP) and SEMAHR Goiás for providing the fieldwork permits; the logging companies AMATA, Golf Indústria Comércio e Exportação de Madeiras Ltda, Ebata Produtos Florestais Ltda and Cikel for providing samples; and the Technological Research Institute of São Paulo (IPT), Raphael Pigozzo and Takashi Yojo for helping with the specific gravity measurements. Funding for this study was provided by the State of São Paulo Foundation to Support Research (FAPESP- 2012/50457-4), National Council for Scientific and Technological Research (CNPq 142706/2011-6, 309805/2011-2) and DFG (AN 214/10-1).

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Figures

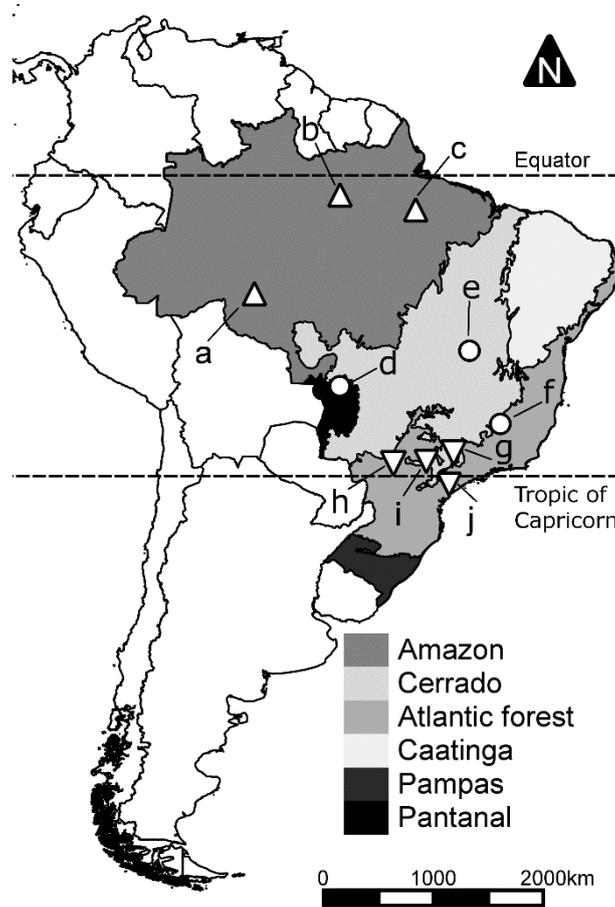


Figure 1: Map of South America showing the 10 sampling sites. *Hymenaea courbaril* populations were sampled from sites “b” to “j”, and the *Hymenaea parvifolia* population was sampled in site “a”. Sampled populations are found within the domain of four Brazilian biomes: Amazon Forest, Cerrado (woody savannah), Atlantic Forest and Pantanal (wetland). These populations are also distributed across a latitudinal gradient from Equator to slightly south of the Tropic of Cancer. Sites indicated as an upright triangle belong to the North group. Sites indicated as circles belong to the Center group, and sites indicated as an inverse triangle belong to the South group.

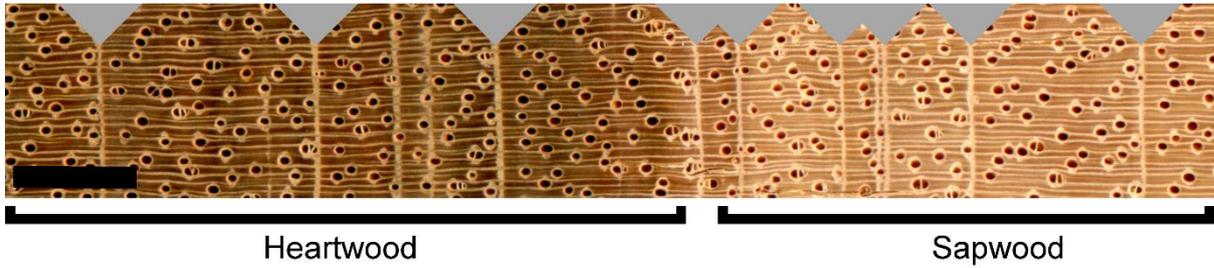


Figure 2: Sample of *Hymenaea courbaril* wood transversal surface showing the tree rings (grey arrows) and the visually distinct heartwood and sapwood (scale bar = 2mm).

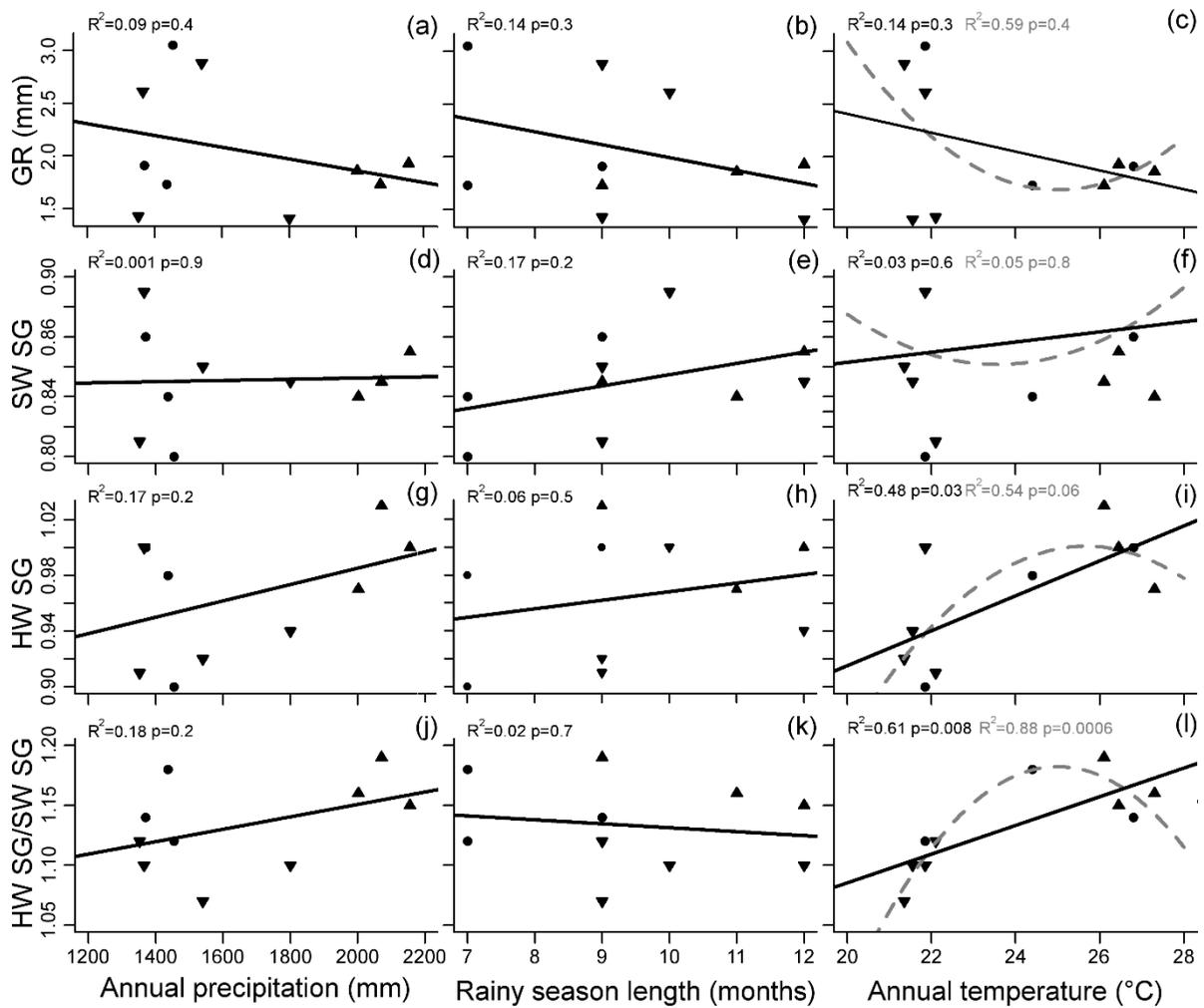


Figure 3: The influence of local climate on wood variables analyzed in the present work. Wood variables are growth rate (GR), sapwood specific gravity (SW SG), heartwood specific gravity (HW SG), ratio between heartwood specific gravity and sapwood specific gravity (HW SG/SW SG). Climate data are annual precipitation, rainy season length in months (precipitation higher than 50mm) and average annual temperature. Each point represents the average value for each site (upright triangle indicates North group, circle indicates Center group, and inverted triangle indicates South group). Linear regressions were fitted for all variables, and quadratic regressions were fitted just for temperature data.

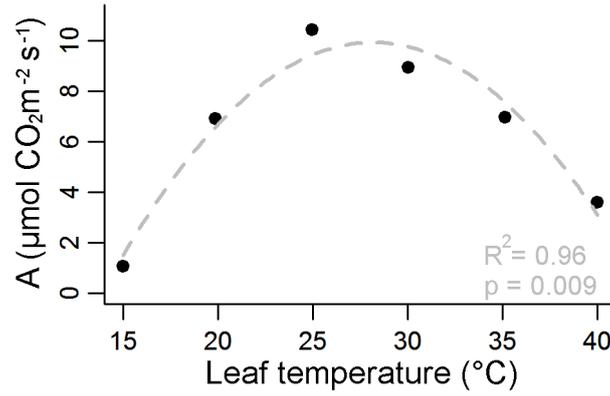


Figure 4: Assimilation rate (A) by leaf temperature curve produced in controlled conditions in the laboratory with *Hymenaea courbaril*. The maximum measured assimilation rate was at 25°C. Determination index (R^2) and p value are provided for the quadratic fit.

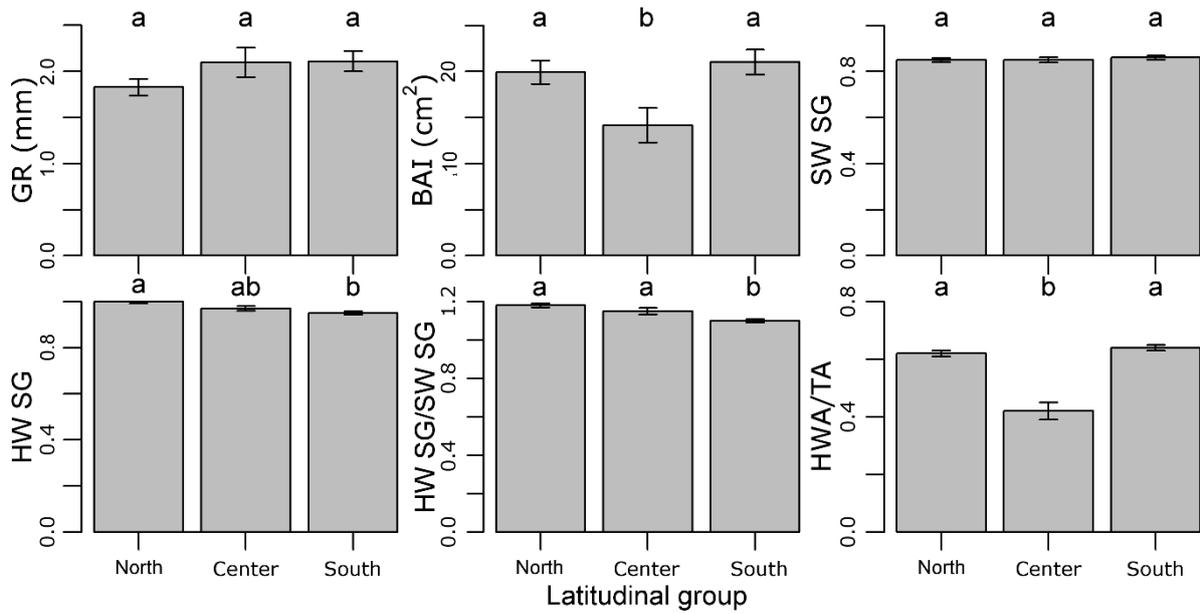


Figure 5: Bar plots of growth rate (GR), basal area increment (BAI), sapwood specific gravity (SW SG), heartwood specific gravity (HW SG), ratio between heartwood and sapwood specific gravity (HW SG/ SW SG), and heartwood relative area (HWA/TA) by latitudinal group. Letters indicate the result of the Kruskal-Wallis and Dunn tests. Different letters show statistically significant differences among groups.

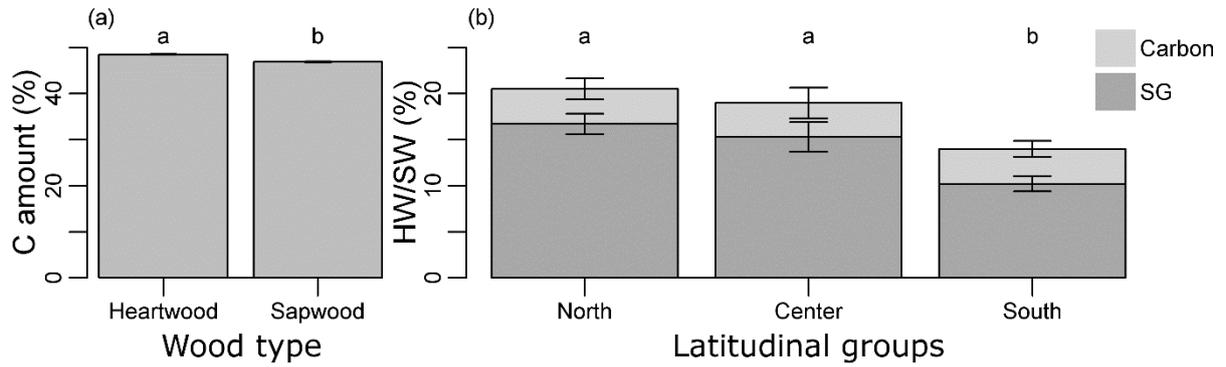


Figure 6: (a) barplot showing differences between heartwood and sapwood carbon amount (48.5% in the heartwood and 46.9% in the sapwood) and (b) barplot showing the differences in specific wood gravity among latitudinal groups (dark grey) and these differences translated as carbon amount (light grey). Letters indicate the result of the Student's *t*-test (a) and Kruskal-Wallis and Dunn tests (b). Different letters show statistically significant differences among groups.

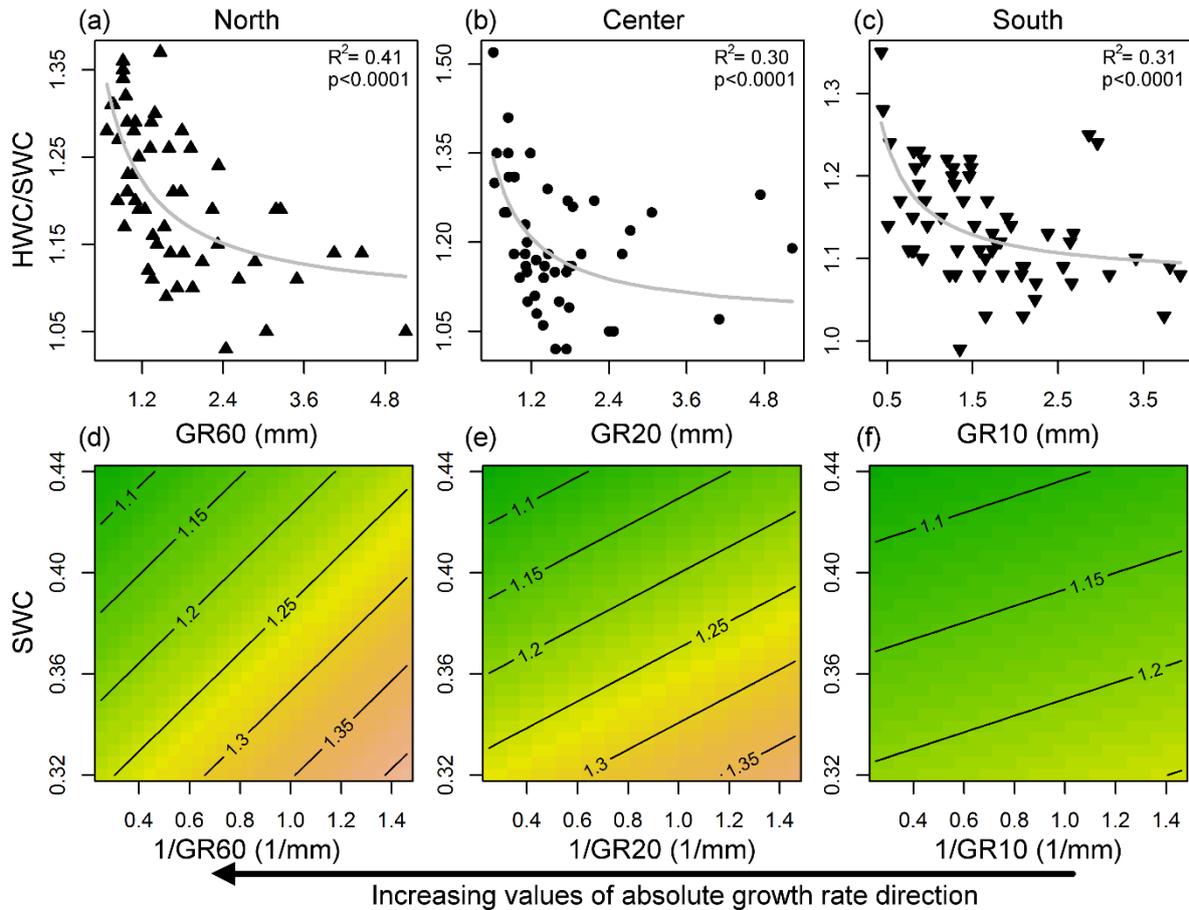


Figure 7: Asymptotic relationship ($1/X$) between heartwood and sapwood carbon ratio HWC/SWC and the growth rate for a) North, b) Center and c) South. Additionally, surface plots of the best mixed-effect models showing how sapwood carbon quantity and the inverse of average growth rate (of the last 60, 20 and 10 years for North, Center and South, respectively) modulate the carbon fixed during heartwood formation, as expressed by the ratio between heartwood and sapwood carbon amounts (HWC/SWC). The former variable is plotted as contour lines, and each line represents a 0.05 variation of HWC/SWC. The colored gradient shows the variation of HWC/SWC from higher values in brown to lower values in green. The arrow indicates the direction of increasing absolute growth rate values.

Tables

Table 1) Summary of sampling sites, including tree species, number of specimens (n), category of latitudinal grouping used in this study (Group), vegetation type, total annual precipitation (Prec, mm), number of months per year with precipitation higher than 50mm (Prec50, months) and average temperatures (Temp, °C).

Sites	Species	n	Group	Vegetation	Prec	Prec 50	Temp
a. West Amazon	<i>H. parvifolia</i>	19	North	Amazon Forest	2071	9	26.1
b. Center Amazon	<i>H. courbaril</i>	21	North	Amazon Forest	2002	11	27.3
c. East Amazon	<i>H. courbaril</i>	20	North	Amazon Forest	2155	12	26.4
d. Pantanal	<i>H. courbaril</i>	20	Center	Wetland	1370	9	26.8
e. Terra Ronca	<i>H. courbaril</i>	18	Center	Dry Forest	1436	7	24.4
f. Matozinhos	<i>H. courbaril</i>	10	Center	Semi-deciduous forest	1454	7	21.8
g. Vassununga	<i>H. courbaril</i>	12	South	Semi-deciduous forest	1540	9	21.3
h. Morro do Diabo	<i>H. courbaril</i>	22	South	Semi-deciduous forest	1365	10	21.8
i. Ceatetus	<i>H. courbaril</i>	20	South	Semi-deciduous forest	1352	9	22.1
j. Carlos Botelho	<i>H. courbaril</i>	9	South	Atlantic Rain- forest	1800	12	21.5

Table 2) Descriptive statistics of *Hymenaea* forest species sampled in ten sites across Brazil, and the three latitudinal groups. Mean and standard deviation are provided for age (years), diameter at breast height (DBH, cm), radial growth rate (GR, mm), basal area increment (BAI, cm²), sapwood specific gravity (SWSG), heartwood specific gravity (HWSG), ratio between heartwood and sapwood specific gravity (HWSG/SWSG), ratio between heartwood area and total area (HWA/TA) and Values are shown by latitudinal categories and for all 171 sampled specimens.

Location	Age		DBH		GR		BAI		SWSG		HWSG		HWSG/SWSG		HWA/TA	
West. Amazon	215.84	71.74	62.17	8.66	1.70	0.47	17.08	4.88	0.85	0.08	1.03	0.07	1.19	0.07	0.57	0.13
Cent. Amazon	204.05	38.84	69.01	11.85	1.86	0.53	22.88	9.61	0.84	0.07	0.97	0.04	1.16	0.08	0.68	0.58
East. Amazon	190.30	55.59	59.20	9.24	1.93	0.96	19.50	12.81	0.87	0.06	1.00	0.07	1.15	0.09	0.61	0.12
Pantanal	90.80	30.38	46.00	18.29	1.91	0.72	12.45	11.24	0.88	0.07	1.00	0.06	1.14	0.09	0.42	0.18
Terra Ronca	115.22	37.78	47.41	13.66	1.72	0.63	11.07	7.24	0.84	0.10	0.98	0.06	1.18	0.12	0.43	0.18
Matozinhos	88.50	26.32	37.89	12.38	3.05	1.72	23.20	20.06	0.80	0.06	0.90	0.10	1.12	0.10	0.39	0.17
Vassununga	123.25	75.34	68.91	16.87	2.88	0.78	29.46	9.34	0.86	0.04	0.92	0.03	1.07	0.04	0.63	0.07
Morro do Diabo	133.41	39.13	72.34	15.71	2.61	0.69	26.95	10.45	0.91	0.04	1.01	0.05	1.10	0.06	0.65	0.06
Caetetus	210.65	52.24	63.23	14.99	1.43	0.37	13.12	4.38	0.82	0.08	0.91	0.05	1.12	0.07	0.65	0.09
Carlos Botelho	220.00	45.83	64.01	18.48	1.40	0.27	14.22	5.75	0.85	0.07	0.94	0.04	1.10	0.09	0.63	0.12
North	203.20	56.44	63.64	10.76	1.83	0.69	19.92	9.86	0.85	0.07	1.00	0.07	1.17	0.08	0.63	0.11
Center	99.48	34.27	45.12	15.66	2.08	1.09	14.16	13.02	0.85	0.09	0.97	0.09	1.15	0.11	0.42	0.18
South	168.36	66.52	67.61	16.23	2.11	0.86	21.03	10.61	0.86	0.07	0.95	0.06	1.10	0.07	0.64	0.08

Table 3: Correlation matrix among all variables studied: age, radial growth rate (GR), basal area increment (BAI), sapwood specific gravity (SW SG), heartwood specific gravity (HW SG), ratio between heartwood and sapwood specific gravity (HW SG/SW SG), ratio between sapwood radial length and total radial length (SWL/TWL), ratio between sapwood area and total area (SWA/TA), ratio between heartwood area and total area (HWA/TA) and diameter at breast height (DBH). (highlighted numbers indicate statistical significance for * $\alpha < 0.05$, ** $\alpha < 0.0001$)

	GR	Age	DBH	BAI	SWSG	HWSG	HWSG/SWSG	HWA/TA
GR		-0.56**	0.18*	0.84**	0.14	-0.20*	-0.36**	-0.15*
Age	-0.56**		0.44**	-0.18*	-0.24*	0.06	0.33**	0.57**
DBH	0.18*	0.44**		0.55**	-0.11	-0.06	0.07	0.66**
BAI	-0.55**	0.39**	-0.04		-0.33**	0.06	0.45**	-0.04
SWSG	0.14	-0.24*	-0.11	0.05		0.56**	-0.62**	-0.16*
HWSG	-0.20*	0.06	-0.06	-0.20*	0.56**		0.29**	0.02
HWSG/SWSG	-0.36**	0.33**	0.07	-0.26**	-0.62**	0.29**		0.20*
HWA/TA	-0.15	0.57**	0.66**	0.14	-0.16*	0.02	0.20*	

Table 4: Best mixed effect model tested by the AICc value for each latitudinal group (Lat. group). The smallest value of AICc (corrected Akaike information criterion) indicates the best model. Two models are considered distinct when the Δ AICc is equal, or higher than, 2. The description of the best mixed effect model is also provided for each group. The R^2 and adjusted R^2 , coefficients (Coef) and explained percentage (Exp) are provided for the models. The response variable is the ratio between carbon quantity in heartwood and sapwood (HWC/SWC). The predictors are sapwood carbon quantity (SWC) and the inverse of growth rate (1/GR). (* significant for $\alpha=0.05$).

Lat. groups	North		Center		South	
Model	AICc	Δ AICc	AICc	Δ AICc	AICc	Δ AICc
HWC/SWC=SWC+1/GR	-164.9	0	-114.8	0	-196.8	0
HWC/SWC=SWC+GR	-157.1	7.8	-109.0	5.8	-193.9	2.9
HWC/SWC=SWC	-136.9	28.0	-108.7	6.1	-193.0	3.8
HWC/SWC= 1/GR	-136.2	28.7	-86.7	28.1	-174.3	22.5
Best model description						
	$R^2=0.66^*$ Adj $R^2=0.65^*$		$R^2=0.64^*$ Adj $R^2=0.62^*$		$R^2=0.54^*$ Adj $R^2=0.52^*$	
	Coef	Exp (%)	Coef	Exp (%)	Coef	Exp (%)
Intercept	1.68*	-	1.79*	-	1.57*	-
SWC	-1.43*	26	-1.69*	33.8	-1.15*	22.7
1/GR	0.14*	40.7	0.09*	30.4	0.04*	31.1
Residuals	-	33.3	-	35.8	-	46.2

Appendix S1

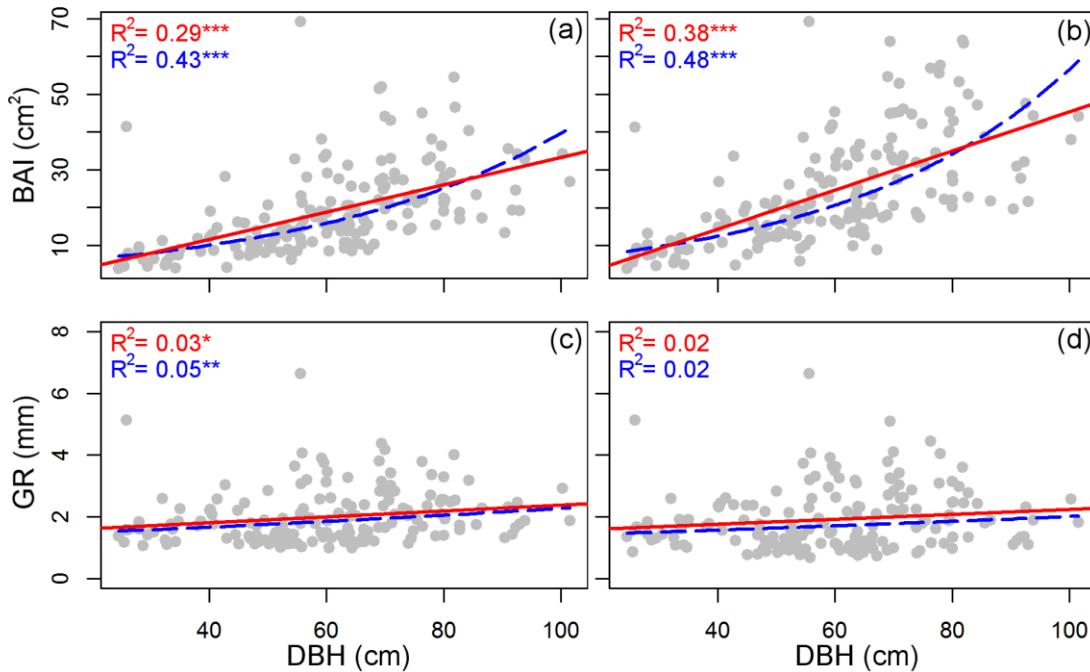


Figure S1: Linear (red) and exponential fit (blue) between average basal area increment (BAI) (a) and average BAI of the last 60 years (b) with circumference at breast height (CBH). Linear and exponential fit between average growth rate (GR) (c) and average GR of the last 60 years (d) with CBH. Fits are statistically significant at * $\alpha < 0.05$, ** $\alpha < 0.01$ and *** $\alpha < 0.0001$.

There is a clear dependence on basal area increment values and tree dimensions measured by CBH values (Figure S1 a and b). On the other hand, that relationship is definitely weaker for the average growth rate data, and it is absent in the average growth rate of the last 60 years (Figure S1 c and d). Radial growth rate independent of DBH makes it a better variable to use in the comparisons of the present study.

Appendix S2

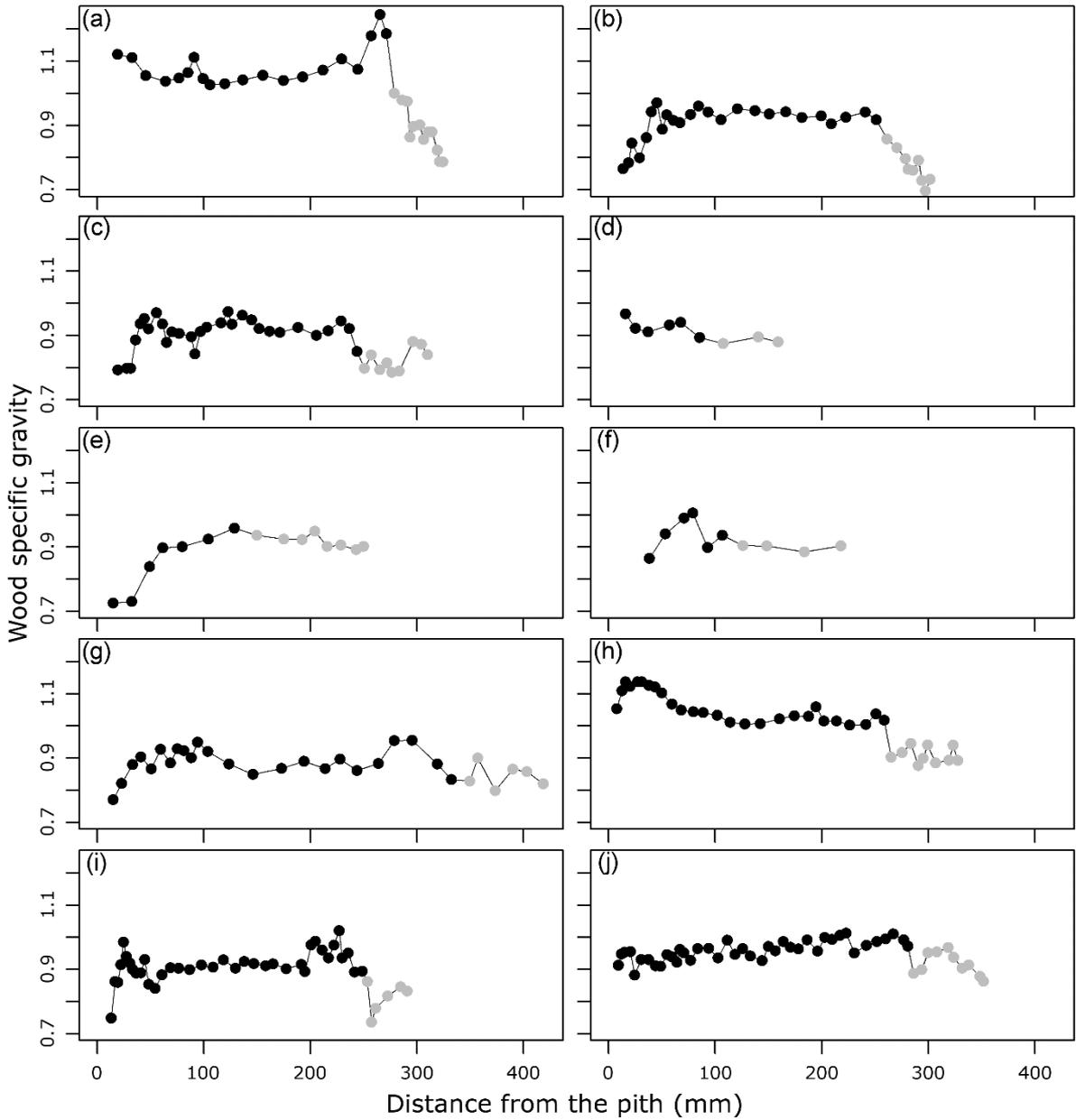


Figure S2: Specific gravity profiles of one sample per site: (a) Western Amazon Forest, (b) Central Amazon Forest, (c) Eastern Amazon Forest, (d) Pantanal, (e) Terra Ronca, (f) Matozinhos, (g) Vassununga, (h) Morro do Diabo, (i) Caetetus and (j) Carlos Botelho. Each graph starts on the pith and ends at the cambium zone (from left to right). Each point represents a five-year sample. Distances between each point pair correspond to the growth

rate of the rings within the sample. Heartwood samples are represented by black points, and sapwood samples are represented by grey points.

The specific gravity profiles were built to better understand previous results, particularly those concerning SWD/HWD values (Figure S2). These profiles show that wood specific gravity of the studied species of *Hymenaea* spp. increases in the region closer to the pith and then stabilizes in the heartwood. Wood specific gravity increases for about 20 to 35 years before it stabilizes. It is important to highlight the strong decline of wood specific gravity in sapwood. Apparently, the degree of decline is dependent on radial growth and age. That observation is supported by the results of the correlation matrix (Table 11). The ratio between heartwood specific gravity and sapwood specific gravity seems to increase with age and decrease with average growth rate, as well as recent growth rate (last 50 years). However, these correlations are not strong and can only explain a smaller drop in sapwood specific gravity in younger and faster- growing individuals.

Carbon cost of heartwood formation for *Hymenaea* spp. trees

Table S3: Data used in the manuscript with sampling site, tree number (ID), latitudinal group (Group), average growth rate: total (GR, mm), last 10 years (GR10, mm), last 20 years (GR20, mm), last 30 years (GR30, mm) last 40 years (GR40, mm), last 50 years (GR50, mm) and last 60 years (GR60, mm), age, circumference at breast height (CBH) heartwood specific gravity (HWSG), sapwood specific gravity (SWSG), ratio between heartwood and sapwood specific gravity (HWSG/SWSG), heartwood carbon quantity (HWC), sapwood carbon quantity (SWC), average basal area increment: total (BAI), last 10 years (BAI10), last 20 years (BAI20), last 30 years (BAI30) last 40 years (BAI40), last 50 years (BAI50) and last 60 years (BAI60), proportion of sapwood area per total area (SWA/TA) and proportion of heartwood area per total area (HWA/TA).

Site	ID	Group	GR	GR10	GR20	GR30	GR40	GR50	GR60	Age	CBH	HWSG	SWSG	HWSG/SWSG	HWC	SWC	HWC/SWC	BAI10	BAI20	BAI30	BAI40	BAI50	BAI60	BAI	SWA/TA	HWA/TA
Matozinhos	1 ^a	Center	5.13	6.75	6.58	6.22	5.40	5.13	5.13	50	25.90	0.64	0.73	0.88	0.30	0.33	0.91	92.92	77.42	64.35	50.41	41.32	41.32	41.32	0.83	0.17
Matozinhos	2	Center	6.63	3.88	5.23	5.81	6.44	6.63	6.63	50	55.52	0.93	0.80	1.16	0.44	0.37	1.19	71.70	90.28	89.16	82.21	69.20	69.20	69.20	0.73	0.27
Matozinhos	3	Center	1.86	1.05	1.10	1.08	1.06	1.02	1.02	92	34.70	0.97	0.85	1.14	0.46	0.39	1.18	6.79	7.46	8.44	8.97	8.71	8.85	7.33	0.42	0.58
Matozinhos	4	Center	1.61	0.92	0.93	0.90	1.05	1.36	1.43	117	27.97	0.86	0.75	1.14	0.41	0.34	1.18	10.59	10.53	9.89	11.08	13.16	13.14	9.48	0.55	0.45
Matozinhos	5	Center	1.18	0.73	0.82	0.84	0.82	0.80	0.86	100	25.46	1.03	0.85	1.21	0.49	0.39	1.25	5.57	4.83	5.04	5.48	5.39	5.53	4.35	0.45	0.55
Matozinhos	6	Center	2.25	1.58	1.62	1.65	1.69	1.81	1.91	56	35.01	0.93	0.88	1.06	0.44	0.40	1.10	11.63	11.03	11.96	11.42	9.92	8.95	8.95	0.73	0.27
Matozinhos	7	Center	3.04	1.41	1.38	2.02	2.10	2.18	2.39	97	42.70	0.90	0.88	1.02	0.43	0.41	1.06	25.93	24.40	32.16	33.04	32.65	33.67	28.17	0.76	0.24
Matozinhos	8	Center	4.06	3.70	4.74	4.35	4.06	4.06	4.06	101	55.90	0.97	0.78	1.24	0.46	0.36	1.28	33.12	35.74	27.62	21.72	21.21	21.21	21.21	0.40	0.60
Matozinhos	9	Center	1.93	1.63	1.46	1.41	1.35	1.29	1.46	108	*	0.95	0.83	1.14	0.45	0.38	1.18	21.45	17.46	16.73	15.41	14.27	14.43	12.60	*	*
Matozinhos	10	Center	2.87	3.63	2.73	2.72	2.60	2.53	2.47	114	*	0.84	0.70	1.19	0.40	0.32	1.22	75.23	50.94	48.24	45.59	41.68	39.03	29.45	*	*
Pantanal	11	Center	2.12	1.79	1.97	2.09	2.16	2.23	2.17	93	62.10	0.83	0.72	1.14	0.39	0.33	1.18	31.78	35.86	35.22	34.36	33.51	31.16	27.55	0.56	0.44
Pantanal	12	Center	2.55	1.51	2.17	2.29	2.27	2.41	2.47	102	80.00	0.97	0.79	1.23	0.46	0.36	1.27	18.01	26.39	30.34	28.20	28.28	28.49	22.46	0.43	0.57
Pantanal	13	Center	3.80	2.84	2.60	2.96	3.22	3.71	3.78	90	69.00	0.98	0.86	1.14	0.47	0.39	1.18	57.08	50.40	53.83	54.48	56.13	54.67	51.44	0.43	0.57
Pantanal	14	Center	3.30	2.96	3.06	3.18	3.21	3.19	3.14	131	80.00	1.04	0.86	1.21	0.49	0.40	1.25	31.20	28.37	25.55	23.68	21.95	20.29	19.02	0.40	0.60
Pantanal	15	Center	2.05	1.21	1.25	1.19	1.31	1.26	1.21	98	65.00	1.01	0.93	1.08	0.48	0.43	1.11	14.82	14.82	13.64	14.34	13.37	12.53	12.91	0.30	0.70
Pantanal	16	Center	2.45	1.27	1.45	1.58	1.81	1.99	2.37	67	46.00	1.04	0.84	1.25	0.49	0.38	1.29	13.61	14.85	15.31	16.08	15.98	15.86	15.83	0.41	0.59
Pantanal	17	Center	2.60	4.47	4.10	3.34	2.90	2.61	2.60	54	32.00	0.99	0.96	1.03	0.47	0.44	1.07	32.06	24.62	18.14	14.31	11.68	11.17	11.17	0.71	0.29
Pantanal	18	Center	1.54	1.34	1.57	1.56	1.54	1.54	1.54	40	*	*	0.90	*	*	0.41	*	4.30	4.13	3.34	2.78	2.78	2.78	2.78	*	*
Pantanal	19	Center	1.71	1.65	1.57	1.50	1.56	1.60	1.71	109	38.00	0.91	0.92	0.98	0.43	0.42	1.02	16.20	14.15	12.87	17.36	17.35	17.37	11.76	0.78	0.22
Pantanal	20	Center	1.80	1.17	1.28	1.35	1.60	1.73	1.77	89	47.08	0.96	0.92	1.05	0.46	0.42	1.08	10.80	11.18	11.25	12.17	11.91	11.11	8.69	0.49	0.51

Carbon cost of heartwood formation for *Hymenaea* spp. trees

Pantanal	21	Center	1.50	1.25	1.39	1.40	1.34	1.40	1.44	94	30.50	0.99	0.90	1.10	0.47	0.41	1.14	10.13	10.64	9.92	8.95	8.54	8.04	6.31	0.54	0.46
Pantanal	22	Center	1.75	1.46	1.56	1.78	1.67	1.75	1.75	74	28.00	1.04	0.94	1.11	0.49	0.43	1.15	10.91	10.79	11.01	9.59	10.18	10.18	9.20	0.82	0.18
Pantanal	23	Center	1.41	1.03	1.13	1.02	1.08	1.24	1.30	74	29.50	0.94	0.84	1.12	0.44	0.39	1.15	6.06	6.17	5.28	5.11	5.11	4.69	4.32	0.73	0.27
Pantanal	24	Center	1.38	1.36	1.14	1.14	1.34	1.31	1.37	63	24.50	1.00	0.93	1.07	0.47	0.43	1.10	6.75	5.33	5.00	5.01	4.40	3.87	3.75	0.79	0.21
Pantanal	25	Center	1.59	1.69	1.78	1.66	1.65	1.66	1.68	74	26.15	1.04	0.92	1.13	0.49	0.42	1.16	13.70	13.42	11.78	10.86	10.04	9.23	7.89	0.65	0.35
Pantanal	26	Center	1.84	1.69	1.82	1.65	1.80	1.84	1.84	57	28.00	1.00	0.89	1.12	0.47	0.41	1.16	10.69	10.40	8.74	8.27	7.50	7.50	7.42	0.78	0.22
Pantanal	27	Center	1.14	0.82	0.84	0.82	0.92	0.94	0.95	157	55.00	1.06	0.78	1.36	0.50	0.36	1.41	9.92	9.96	9.51	10.37	10.25	10.09	8.41	0.34	0.66
Pantanal	28	Center	1.35	1.09	0.84	0.76	0.77	0.73	0.77	115	54.00	0.98	0.75	1.31	0.46	0.34	1.35	9.56	7.19	6.37	6.22	5.83	5.86	6.20	0.36	0.64
Pantanal	29	Center	1.13	1.42	1.13	0.93	0.84	0.80	0.78	147	45.00	1.05	0.90	1.16	0.50	0.41	1.20	15.87	11.97	9.64	8.54	7.92	7.57	7.39	0.87	0.13
Pantanal	30	Center	1.19	0.77	1.27	1.31	1.20	1.15	1.08	88	34.20	1.13	1.00	1.13	0.54	0.46	1.17	4.86	7.34	7.01	6.08	5.48	4.89	3.91	0.61	0.39
Terra Ronca	31	Center	1.36	0.58	0.66	0.77	0.81	0.81	0.79	152	46.79	0.95	0.73	1.30	0.45	0.34	1.35	5.63	7.04	9.41	9.81	9.70	9.31	11.09	0.29	0.71
Terra Ronca	32	Center	1.38	0.64	0.78	1.08	1.25	1.37	1.42	121	46.79	1.02	0.84	1.21	0.48	0.39	1.25	13.16	13.62	12.65	12.28	12.07	11.12	7.18	0.49	0.51
Terra Ronca	33	Center	1.31	0.46	0.61	0.77	0.73	0.69	0.73	164	67.16	0.97	0.66	1.47	0.46	0.30	1.52	6.08	7.98	9.84	9.13	8.55	8.82	8.71	0.57	0.43
Terra Ronca	34	Center	1.39	0.81	0.85	1.05	1.11	1.14	1.23	148	48.06	1.02	0.80	1.27	0.48	0.37	1.31	9.72	10.00	11.81	12.04	11.88	12.02	9.83	0.42	0.58
Terra Ronca	35	Center	1.58	1.48	1.74	1.71	1.60	1.55	1.58	72	25.78	0.95	0.96	0.99	0.45	0.44	1.02	9.80	10.85	9.65	8.36	7.54	7.23	6.98	0.89	0.11
Terra Ronca	36	Center	1.36	1.04	0.94	0.92	0.98	0.97	1.03	195	63.03	0.96	0.76	1.27	0.46	0.35	1.31	8.62	9.05	8.35	8.23	9.35	9.88	9.11	0.40	0.60
Terra Ronca	37	Center	1.76	1.62	1.78	2.24	2.15	2.06	1.92	78	33.42	0.98	0.93	1.05	0.47	0.43	1.09	11.90	12.31	13.82	11.88	10.34	8.87	7.02	0.87	0.13
Terra Ronca	38	Center	1.10	0.92	1.02	1.10	1.04	1.08	1.08	122	32.79	1.04	0.95	1.10	0.49	0.43	1.14	7.55	7.87	7.99	7.15	6.95	6.62	5.67	0.74	0.26
Terra Ronca	39	Center	1.76	0.83	1.11	1.08	1.27	1.42	1.57	93	40.74	0.89	0.79	1.12	0.42	0.36	1.16	6.94	9.48	9.30	9.32	10.49	10.86	8.62	0.59	0.41
Terra Ronca	40	Center	1.26	1.13	1.18	1.20	1.38	1.36	1.32	88	32.47	0.89	0.68	1.31	0.42	0.31	1.35	6.55	6.71	6.40	6.63	6.03	5.46	4.70	0.77	0.23
Terra Ronca	41	Center	1.15	0.65	0.63	0.65	0.77	0.78	0.77	183	54.11	0.88	0.70	1.26	0.42	0.32	1.30	8.22	7.96	7.98	9.35	9.39	9.07	8.08	0.32	0.68
Terra Ronca	42	Center	1.85	1.02	1.10	1.29	1.41	1.59	1.79	77	38.52	1.03	0.87	1.19	0.49	0.40	1.23	8.90	8.46	9.58	9.33	9.29	9.34	8.27	0.68	0.32
Terra Ronca	43	Center	2.84	1.61	1.74	1.99	2.17	2.53	2.70	105	69.07	1.06	0.95	1.12	0.50	0.44	1.15	29.38	30.77	31.59	32.55	36.07	35.70	27.07	0.37	0.63
Terra Ronca	44	Center	3.07	2.15	2.47	2.57	2.77	3.07	3.23	93	69.71	0.93	0.91	1.01	0.44	0.42	1.05	37.18	40.53	39.99	40.12	40.30	38.36	27.61	0.43	0.57
Terra Ronca	45	Center	3.08	2.43	2.40	2.53	2.90	3.21	3.20	80	55.70	0.95	0.93	1.02	0.45	0.43	1.05	33.70	32.08	33.49	34.00	32.59	29.29	23.00	0.57	0.43
Terra Ronca	46	Center	1.30	1.87	1.76	1.42	1.43	1.37	1.24	97	42.97	1.02	0.83	1.23	0.48	0.38	1.27	10.47	8.95	6.91	6.30	5.55	4.79	4.03	0.50	0.50
Terra Ronca	47	Center	1.95	1.57	1.84	1.93	1.71	1.73	1.69	102	52.52	1.00	0.82	1.22	0.47	0.38	1.26	19.50	21.52	21.32	18.29	17.42	15.85	14.12	0.69	0.31

Carbon cost of heartwood formation for *Hymenaea* spp. trees

Terra Ronca	48	Center	1.60	0.59	1.40	1.69	1.71	1.70	1.62	104	33.76	1.09	0.97	1.12	0.52	0.44	1.16	6.05	13.43	14.39	13.95	13.03	11.92	8.23	0.68	0.32
Eastern Amazon	49	North	1.38	0.71	0.77	0.88	0.94	1.04	1.07	227	62.48	1.04	0.88	1.19	0.49	0.40	1.23	13.52	14.65	16.38	17.32	18.66	18.82	13.67	0.25	0.75
Eastern Amazon	50	North	1.04	0.66	0.65	0.66	0.65	0.65	0.68	316	55.79	1.02	0.82	1.24	0.48	0.38	1.28	11.75	11.32	11.49	11.08	11.04	11.32	10.30	0.37	0.63
Eastern Amazon	51	North	3.37	2.77	3.35	3.95	4.41	4.30	4.04	127	77.96	0.93	0.84	1.10	0.44	0.39	1.14	57.94	66.45	72.32	72.23	64.95	57.58	38.01	0.44	0.56
Eastern Amazon	52	North	1.49	0.76	0.81	0.93	0.98	1.03	1.15	217	60.02	1.03	0.85	1.21	0.49	0.39	1.25	12.46	13.10	14.53	14.95	15.23	16.59	13.13	0.28	0.72
Eastern Amazon	53	North	1.90	0.91	0.89	0.93	1.10	1.20	1.36	146	49.43	1.01	0.90	1.12	0.48	0.41	1.16	15.62	14.40	14.77	17.16	18.10	19.73	17.17	0.37	0.63
Eastern Amazon	54	North	2.07	2.13	2.09	2.59	2.61	2.57	2.63	233	71.68	1.02	0.95	1.08	0.48	0.44	1.11	46.47	44.30	51.76	49.91	47.25	46.02	27.33	0.41	0.59
Eastern Amazon	55	North	4.38	6.76	7.41	7.44	6.42	5.65	5.10	92	69.41	0.98	0.96	1.02	0.46	0.44	1.05	135.63	128.55	111.94	89.87	74.48	63.93	51.86	0.75	0.25
Eastern Amazon	56	North	1.72	1.17	1.14	1.23	1.35	1.50	1.56	151	52.44	0.95	0.89	1.06	0.45	0.41	1.09	18.54	17.76	18.52	19.69	20.81	20.69	14.37	0.38	0.62
Eastern Amazon	57	North	1.26	0.53	0.57	0.64	0.67	0.69	0.78	196	*	1.05	0.82	1.27	0.50	0.38	1.31	6.62	6.92	7.48	7.77	7.76	8.32	7.84	*	*
Eastern Amazon	58	North	1.20	0.97	0.90	0.96	0.98	1.08	1.10	223	48.49	1.05	0.84	1.25	0.50	0.39	1.29	15.40	13.98	14.50	14.49	15.49	15.25	11.38	0.36	0.64
Eastern Amazon	59	North	1.79	1.54	1.59	1.65	1.63	1.68	1.78	180	58.14	1.10	0.94	1.17	0.52	0.43	1.21	27.29	27.10	27.55	26.28	26.18	26.45	17.51	0.36	0.64
Eastern Amazon	60	North	1.49	0.99	1.01	1.11	1.15	1.19	1.29	200	51.40	0.94	0.86	1.09	0.44	0.40	1.12	14.74	14.72	15.87	16.00	16.02	16.75	12.84	0.33	0.67
Eastern Amazon	61	North	1.47	1.10	1.22	1.17	1.18	1.23	1.32	168	53.23	0.89	0.72	1.22	0.42	0.33	1.26	16.98	18.55	17.22	16.85	17.07	17.64	12.19	0.41	0.59
Eastern Amazon	62	North	1.17	0.71	0.73	0.84	0.89	0.96	0.99	228	50.55	1.15	0.98	1.17	0.54	0.45	1.21	10.89	10.80	12.13	12.80	13.43	13.58	9.24	0.30	0.70
Eastern Amazon	63	North	1.96	1.59	1.71	1.74	1.90	1.89	1.95	154	57.22	0.90	0.85	1.06	0.43	0.39	1.10	27.97	29.39	28.73	29.84	28.69	28.20	19.27	0.40	0.60
Eastern Amazon	64	North	3.12	3.49	3.45	3.96	3.79	3.53	3.49	149	59.95	0.89	0.82	1.08	0.42	0.38	1.11	67.05	61.20	63.94	56.86	49.89	45.30	34.04	0.39	0.61
Eastern Amazon	65	North	3.78	5.62	6.32	6.22	5.47	4.82	4.45	115	76.35	0.94	0.85	1.11	0.45	0.39	1.14	113.26	112.45	96.41	78.53	65.57	56.88	44.90	0.67	0.33
Eastern Amazon	66	North	1.01	0.78	0.89	0.99	1.00	0.97	0.92	288	52.13	1.06	0.81	1.31	0.50	0.37	1.35	12.10	13.51	14.91	15.00	13.99	13.03	8.10	0.41	0.59
Eastern Amazon	67	North	1.42	0.78	1.10	1.06	1.02	0.97	0.96	186	51.16	1.05	0.83	1.28	0.50	0.38	1.32	12.09	16.29	15.39	14.49	13.58	13.23	11.46	0.28	0.72
Eastern Amazon	68	North	1.53	1.09	1.16	1.56	1.69	1.67	2.09	210	67.02	1.03	0.94	1.10	0.49	0.43	1.13	21.67	22.43	29.14	30.54	29.25	33.93	15.38	0.28	0.72
Center Amazon	69	North	2.04	0.73	1.13	1.20	1.40	1.53	1.66	193	73.92	0.94	0.80	1.17	0.44	0.37	1.21	9.87	14.60	14.32	14.99	16.55	18.75	18.40	0.29	0.71
Center Amazon	70	North	2.32	1.11	1.07	1.14	1.16	1.15	1.24	210	91.08	1.01	0.88	1.15	0.48	0.40	1.19	29.89	28.22	29.61	29.49	29.00	30.84	35.48	0.19	0.81
Center Amazon	71	North	2.56	2.24	2.07	1.99	1.90	1.82	1.92	168	79.60	0.96	0.78	1.22	0.45	0.36	1.26	59.32	53.66	50.60	47.16	44.49	45.28	36.19	0.30	0.70
Center Amazon	72	North	1.33	0.84	1.03	1.04	1.12	1.14	1.15	203	51.88	0.93	0.81	1.15	0.44	0.37	1.19	14.04	16.59	16.20	17.33	16.90	16.69	12.89	0.37	0.63
Center Amazon	73	North	1.45	1.21	1.27	1.33	1.38	1.41	1.42	197	53.13	1.04	0.93	1.11	0.49	0.43	1.15	18.87	18.72	20.80	21.01	20.79	20.11	14.45	0.38	0.62
Center Amazon	74	North	1.33	0.38	0.54	0.59	0.60	0.82	0.92	252	60.86	0.98	0.75	1.30	0.46	0.35	1.34	6.73	9.79	10.32	10.53	14.18	15.60	15.08	0.25	0.75

Carbon cost of heartwood formation for *Hymenaea* spp. trees

Center Amazon	75	North	1.38	0.84	0.91	1.05	1.04	1.05	1.08	241	53.40	1.01	0.81	1.24	0.48	0.37	1.28	14.20	15.44	17.69	17.11	16.82	16.92	14.00	0.34	0.66
Center Amazon	76	North	2.36	0.79	1.21	1.47	1.56	1.60	1.62	171	77.23	0.89	0.80	1.10	0.42	0.37	1.14	18.19	27.33	33.12	34.28	34.62	34.47	32.48	0.30	0.70
Center Amazon	77	North	2.00	1.90	2.03	2.25	2.29	2.32	2.33	157	63.94	0.99	0.82	1.20	0.47	0.38	1.24	34.77	35.47	37.50	36.48	35.20	33.48	20.47	0.40	0.60
Center Amazon	78	North	1.12	0.80	0.80	0.81	0.85	0.91	0.94	227	53.43	1.00	0.88	1.13	0.47	0.41	1.17	12.07	11.57	11.59	11.91	12.36	12.49	8.90	0.37	0.63
Center Amazon	79	North	2.29	2.39	2.33	2.41	2.52	2.68	2.87	186	73.08	0.89	0.82	1.09	0.42	0.38	1.13	48.59	45.81	45.51	45.00	44.90	44.65	27.27	0.37	0.63
Center Amazon	80	North	1.40	0.61	0.76	0.86	0.92	0.90	0.98	231	62.29	0.96	0.82	1.17	0.45	0.38	1.21	10.71	14.35	15.66	16.26	16.12	17.14	15.37	0.25	0.75
Center Amazon	81	North	1.98	0.85	0.88	1.00	1.07	1.26	1.35	237	80.09	0.95	0.88	1.08	0.45	0.41	1.11	20.94	19.66	22.74	22.57	26.06	26.93	28.18	0.33	0.67
Center Amazon	82	North	1.44	1.18	1.16	1.16	1.24	1.37	1.39	192	54.37	0.99	0.79	1.26	0.47	0.36	1.30	19.58	18.29	17.49	18.14	19.27	19.07	13.49	0.35	0.65
Center Amazon	83	North	3.02	3.09	2.55	2.59	2.68	2.84	3.04	144	70.98	0.97	0.95	1.02	0.46	0.44	1.05	53.02	42.55	44.05	43.85	44.48	45.31	32.91	0.31	0.69
Center Amazon	84	North	1.48	0.91	1.09	1.01	1.01	1.02	1.10	236	63.74	1.07	0.92	1.16	0.51	0.42	1.20	18.85	22.31	20.40	20.17	20.06	21.14	17.27	0.37	0.63
Center Amazon	85	North	2.53	1.79	1.89	1.92	2.16	2.27	2.44	182	81.98	0.95	0.95	1.00	0.45	0.44	1.03	55.94	59.40	57.33	62.22	61.18	63.44	46.43	0.29	0.71
Center Amazon	86	North	2.35	1.82	1.92	1.87	2.05	2.11	2.24	126	69.65	0.94	0.82	1.15	0.45	0.38	1.19	33.74	34.37	32.38	33.86	33.38	33.40	24.77	0.29	0.71
Center Amazon	87	North	1.40	0.67	0.76	0.83	1.02	0.99	0.98	285	80.02	0.94	0.75	1.25	0.44	0.34	1.29	15.96	17.17	19.10	23.35	22.57	21.99	21.09	0.20	0.80
Center Amazon	88	North	1.74	2.02	1.83	1.81	1.72	1.75	1.81	237	85.60	1.03	0.93	1.11	0.49	0.43	1.14	50.08	43.17	41.39	38.94	38.54	38.71	23.38	0.32	0.68
Center Amazon	89	North	1.65	1.18	1.00	0.94	0.93	0.94	0.92	210	68.90	0.99	0.75	1.32	0.47	0.35	1.36	23.48	20.03	19.06	18.67	18.09	17.92	21.96	0.37	0.63
Western Amazon	90	North	2.43	2.61	2.81	3.09	3.28	3.32	3.18	119	63.43	1.02	0.89	1.15	0.48	0.41	1.19	42.57	42.99	43.74	42.38	39.34	35.12	20.43	0.70	0.30
Western Amazon	91	North	1.49	1.04	1.19	1.27	1.34	1.34	1.47	304	59.05	1.02	0.77	1.33	0.49	0.35	1.37	22.63	23.77	24.24	25.34	25.40	27.20	19.03	0.62	0.38
Western Amazon	92	North	2.25	2.11	1.91	2.02	2.01	2.21	2.32	134	40.13	1.02	**	**	0.48	**	**	32.46	28.19	27.72	26.57	27.26	26.83	18.93	0.44	0.56
Western Amazon	93	North	1.35	1.76	1.67	1.56	1.49	1.49	1.53	293	59.46	0.98	**	**	0.46	**	**	35.64	32.73	29.61	27.47	27.09	26.90	15.77	0.38	0.62
Western Amazon	94	North	1.14	0.96	0.93	0.85	0.81	0.80	0.83	371	73.99	1.00	**	**	0.47	**	**	23.01	21.25	19.72	18.45	18.10	18.16	13.98	0.31	0.69
Western Amazon	95	North	2.34	2.89	2.66	2.60	2.22	2.06	2.32	141	64.24	0.99	0.89	1.11	0.47	0.41	1.15	56.26	49.66	46.58	38.94	34.83	36.78	25.59	0.50	0.50
Western Amazon	96	North	1.12	0.34	0.66	0.61	0.68	0.77	0.85	262	64.86	1.01	0.82	1.23	0.48	0.38	1.27	6.24	11.95	11.01	11.97	13.26	14.38	10.21	0.28	0.72
Western Amazon	97	North	1.65	0.60	0.76	0.86	0.93	0.96	0.99	240	69.97	1.09	0.91	1.20	0.52	0.42	1.23	12.78	16.55	18.59	20.09	20.66	20.59	19.54	0.37	0.63
Western Amazon	98	North	1.25	0.70	0.73	0.91	1.02	1.10	1.15	185	49.57	1.11	**	**	0.52	**	**	8.60	9.29	11.20	12.03	12.50	12.43	8.02	0.53	0.47
Western Amazon	99	North	1.81	2.31	2.56	2.48	2.38	2.55	2.59	197	71.16	1.12	**	**	0.53	**	**	38.21	40.56	37.38	34.33	34.03	32.29	15.18	0.43	0.57
Western Amazon	100	North	1.79	0.85	0.88	1.00	1.24	1.47	1.60	151	55.60	0.85	0.69	1.22	0.40	0.32	1.26	12.93	12.94	14.59	17.68	20.07	20.86	14.58	0.40	0.60
Western Amazon	101	North	1.60	0.89	0.94	1.02	1.11	1.19	1.38	205	66.39	1.07	**	**	0.51	**	**	17.78	18.05	19.07	20.27	21.08	23.37	16.66	0.43	0.57

Carbon cost of heartwood formation for *Hymenaea* spp. trees

Western Amazon	102	North	2.39	1.27	1.64	1.53	1.52	1.61	1.72	143	66.47	1.02	0.96	1.06	0.49	0.44	1.10	25.17	31.22	28.64	27.74	28.46	29.19	25.30	0.33	0.67
Western Amazon	103	North	1.54	2.11	1.88	1.80	1.80	1.78	1.79	288	74.89	1.00	0.81	1.24	0.47	0.37	1.28	50.69	44.42	43.68	44.59	42.42	42.10	23.38	0.36	0.64
Western Amazon	104	North	1.41	1.32	1.41	1.51	1.65	1.56	1.53	248	63.82	0.95	0.84	1.13	0.45	0.39	1.17	25.01	26.04	27.10	28.55	26.41	25.24	15.36	0.29	0.71
Western Amazon	105	North	1.47	1.05	1.38	1.23	1.34	1.30	1.34	220	63.50	1.15	0.92	1.25	0.55	0.42	1.29	20.10	25.60	22.51	23.83	22.69	22.63	15.28	0.39	0.61
Western Amazon	106	North	1.47	0.69	0.69	0.71	0.69	0.70	0.75	196	63.91	1.02	0.80	1.27	0.48	0.37	1.31	13.29	12.36	12.27	11.77	12.10	13.31	15.40	0.29	0.71
Western Amazon	107	North	2.61	4.26	3.88	3.77	3.63	3.50	3.25	123	60.69	0.96	0.84	1.15	0.46	0.38	1.19	66.81	55.60	49.78	44.21	39.37	34.45	21.58	0.71	0.29
Western Amazon	108	North	1.13	1.10	1.05	0.96	0.94	0.88	0.84	281	50.22	1.09	0.94	1.17	0.52	0.43	1.20	15.34	14.31	14.42	14.04	13.15	12.31	10.38	0.40	0.60
Caetetus	109	South	1.00	1.26	0.97	0.81	0.88	0.93	0.99	265	64.30	0.83	0.71	1.16	0.39	0.33	1.20	20.82	15.79	13.04	13.79	14.10	14.68	8.49	0.43	0.57
Caetetus	110	South	1.17	0.87	0.77	0.77	0.82	0.97	1.02	202	64.94	0.95	0.82	1.15	0.45	0.38	1.19	17.32	15.13	14.78	15.69	17.99	18.45	19.27	0.29	0.71
Caetetus	111	South	2.20	2.64	2.44	2.37	2.14	2.25	2.38	110	44.88	0.98	0.90	1.08	0.46	0.41	1.12	32.42	28.20	25.67	22.19	21.45	20.42	16.04	0.54	0.46
Caetetus	112	South	1.77	0.83	1.01	0.99	0.98	0.99	1.11	195	92.95	0.90	0.77	1.18	0.43	0.35	1.21	17.57	21.19	20.32	19.94	19.64	21.63	19.05	0.37	0.63
Caetetus	113	South	1.69	0.43	0.59	0.78	0.89	1.07	1.16	206	76.39	0.88	0.67	1.31	0.42	0.31	1.35	9.65	13.09	17.23	19.26	22.60	23.87	22.11	0.29	0.71
Caetetus	114	South	1.21	1.73	1.70	1.37	1.37	1.29	1.29	231	63.66	0.93	0.87	1.07	0.44	0.40	1.11	29.31	27.96	22.16	21.67	19.98	19.36	10.55	0.32	0.68
Caetetus	115	South	1.88	1.77	1.94	2.06	2.21	2.43	2.63	159	60.16	0.91	0.84	1.09	0.43	0.38	1.12	30.26	31.78	32.18	32.65	33.35	33.06	18.58	0.41	0.59
Caetetus	116	South	1.59	1.58	1.90	2.38	2.42	2.65	2.77	242	82.76	0.85	0.81	1.05	0.40	0.37	1.08	35.95	41.95	50.11	49.04	50.65	50.00	18.67	0.23	0.77
Caetetus	117	South	1.17	0.81	1.00	1.10	1.14	1.24	1.20	243	63.66	0.93	0.86	1.07	0.44	0.40	1.11	13.38	16.21	17.39	17.44	18.35	17.44	10.10	0.36	0.64
Caetetus	118	South	1.21	1.65	1.40	1.31	1.29	1.25	1.20	236	68.12	0.89	0.83	1.07	0.42	0.38	1.10	26.84	22.29	20.39	19.61	18.54	17.43	10.22	0.35	0.65
Caetetus	119	South	1.73	1.52	1.82	1.84	1.87	2.01	2.17	184	48.06	0.96	0.87	1.10	0.46	0.40	1.14	20.12	23.01	22.22	21.46	21.44	21.07	13.79	0.46	0.54
Caetetus	120	South	1.33	0.80	0.91	1.06	1.08	1.08	1.10	241	90.40	0.92	0.82	1.12	0.43	0.38	1.15	15.71	17.54	20.09	20.05	19.71	19.68	13.26	0.25	0.75
Caetetus	121	South	1.41	0.79	0.97	1.27	1.57	1.88	1.89	153	44.42	0.97	0.90	1.07	0.46	0.41	1.11	10.51	12.51	15.72	18.11	19.89	18.84	9.52	0.47	0.53
Caetetus	122	South	1.19	0.93	1.03	1.03	1.00	1.11	1.23	244	65.89	0.89	0.75	1.18	0.42	0.35	1.22	15.77	16.91	16.62	15.92	17.08	18.23	10.19	0.29	0.71
Caetetus	123	South	1.00	0.87	0.86	0.86	0.92	1.04	1.09	287	60.48	0.95	0.80	1.19	0.45	0.37	1.23	14.38	14.11	13.88	14.43	15.87	16.19	8.42	0.29	0.71
Caetetus	124	South	1.19	0.45	0.55	0.56	0.61	0.78	0.87	235	63.03	0.87	0.70	1.24	0.41	0.32	1.28	7.61	9.27	9.27	10.00	12.32	13.48	10.61	0.24	0.76
Caetetus	125	South	1.28	0.91	0.83	0.91	0.97	0.95	0.89	241	48.24	0.90	0.84	1.07	0.42	0.38	1.10	13.54	14.75	14.32	14.19	13.23	12.33	9.00	0.34	0.66
Caetetus	126	South	1.31	0.81	0.84	0.86	0.89	0.91	0.91	248	74.48	0.83	0.70	1.19	0.39	0.32	1.23	13.62	15.89	17.28	16.94	17.34	17.35	14.46	0.16	0.84
Caetetus	127	South	1.13	0.51	0.63	0.66	0.75	0.86	0.97	214	47.75	0.95	0.86	1.11	0.45	0.39	1.14	7.97	8.98	9.31	10.09	10.97	12.08	8.01	0.41	0.59
Caetetus	128	South	2.21	2.09	2.34	2.73	2.56	2.60	2.36	77	40.11	0.99	0.99	1.00	0.47	0.45	1.03	21.04	21.70	22.29	19.24	17.29	14.83	12.02	0.44	0.56

Carbon cost of heartwood formation for *Hymenaea* spp. trees

Carlos Botelho	129	South	1.66	0.53	0.70	0.83	1.07	1.15	1.37	270	92.31	0.96	0.80	1.20	0.45	0.37	1.24	13.77	17.83	20.90	26.26	27.77	32.07	24.55	0.16	0.84
Carlos Botelho	130	South	1.20	0.97	0.83	0.79	0.93	0.98	0.96	230	66.53	0.95	0.87	1.10	0.45	0.40	1.14	20.82	17.24	14.94	16.18	17.91	18.68	13.89	0.31	0.69
Carlos Botelho	131	South	1.91	1.27	1.14	1.23	1.56	1.71	1.88	201	75.44	0.96	0.82	1.17	0.45	0.37	1.21	24.96	21.83	23.04	28.26	29.63	30.98	21.16	0.45	0.55
Carlos Botelho	132	South	1.32	1.35	1.19	1.21	1.16	1.16	1.18	273	66.16	0.98	1.02	0.96	0.46	0.47	0.99	25.10	21.92	22.03	20.90	20.29	20.13	13.78	0.30	0.70
Carlos Botelho	133	South	1.38	0.65	0.82	0.87	0.96	1.12	1.14	266	78.62	0.96	0.85	1.13	0.45	0.39	1.17	13.94	17.38	18.17	19.63	22.31	22.20	15.38	0.26	0.74
Carlos Botelho	134	South	1.63	1.47	1.35	1.62	1.93	2.12	2.07	174	63.66	0.93	0.79	1.18	0.44	0.36	1.22	22.25	19.49	22.24	24.63	25.32	23.57	13.64	0.41	0.59
Carlos Botelho	135	South	1.20	1.29	1.15	1.05	1.05	1.11	1.14	216	57.61	0.94	0.81	1.15	0.44	0.37	1.19	20.84	18.15	16.14	15.64	16.28	16.28	10.83	0.37	0.63
Carlos Botelho	136	South	1.29	1.65	1.56	1.32	1.38	1.51	1.52	212	47.11	0.85	0.86	0.99	0.40	0.39	1.03	19.06	17.31	14.20	14.27	14.56	13.90	8.62	0.53	0.47
Carlos Botelho	137	South	1.07	1.23	1.26	1.42	1.38	1.32	1.25	138	28.65	0.91	0.87	1.05	0.43	0.40	1.08	9.95	9.44	10.00	9.32	8.39	7.68	6.18	0.53	0.47
Morro do Diabo	138	South	2.92	2.07	2.63	2.84	2.74	2.63	2.57	144	100.27	0.93	0.89	1.05	0.44	0.41	1.08	39.80	53.93	50.87	42.78	39.57	38.01	34.14	0.26	0.74
Morro do Diabo	139	South	1.88	1.73	1.53	2.24	2.17	1.99	1.90	180	93.90	0.98	0.90	1.09	0.47	0.41	1.13	47.49	46.06	55.39	52.83	47.51	44.30	32.75	0.23	0.77
Morro do Diabo	140	South	3.76	1.95	2.21	2.43	2.99	3.46	3.65	79	59.60	0.98	0.88	1.11	0.46	0.41	1.14	39.25	37.79	45.34	46.83	45.19	41.88	33.25	0.29	0.71
Morro do Diabo	141	South	2.83	2.24	1.73	1.79	2.00	2.19	2.25	106	71.62	1.00	0.96	1.04	0.47	0.44	1.07	41.89	31.70	31.60	33.65	34.71	33.72	29.09	0.36	0.64
Morro do Diabo	142	South	4.01	2.86	2.94	4.07	4.14	3.49	3.61	99	81.81	0.97	0.80	1.21	0.46	0.37	1.25	68.97	67.94	86.06	78.88	66.13	64.22	54.52	0.31	0.69
Morro do Diabo	143	South	3.18	1.48	2.45	2.58	2.65	2.32	2.42	120	84.35	1.00	0.85	1.17	0.48	0.39	1.21	34.98	55.19	55.78	54.87	47.37	47.13	40.24	0.36	0.64
Morro do Diabo	144	South	2.58	2.56	2.71	3.75	3.53	3.04	2.96	88	58.89	1.03	0.97	1.06	0.49	0.45	1.09	32.01	31.48	35.92	30.98	25.76	22.83	18.25	0.45	0.55
Morro do Diabo	145	South	3.64	2.96	3.70	4.72	4.01	3.63	3.73	77	54.62	1.06	0.88	1.20	0.50	0.40	1.24	48.85	55.83	60.06	49.04	42.14	38.50	32.74	0.42	0.58
Morro do Diabo	146	South	1.93	1.67	2.36	2.50	2.53	2.41	2.48	179	80.21	1.05	0.92	1.14	0.50	0.42	1.17	36.42	48.49	48.84	47.56	43.96	42.91	21.96	0.31	0.69
Morro do Diabo	147	South	1.73	0.75	1.22	1.17	1.22	1.32	1.34	184	82.76	0.97	0.91	1.07	0.46	0.42	1.11	14.87	23.42	22.22	22.03	23.21	22.72	16.80	0.29	0.71
Morro do Diabo	148	South	2.28	1.70	1.33	1.47	1.52	1.71	1.89	106	86.58	1.09	*	*	0.52	*	*	24.84	18.18	19.72	19.77	21.08	21.75	17.15	*	*
Morro do Diabo	149	South	2.46	1.30	1.91	1.98	2.12	2.27	2.32	177	92.63	0.91	0.87	1.05	0.43	0.40	1.08	32.09	45.49	45.71	47.40	48.42	47.59	34.17	0.29	0.71
Morro do Diabo	150	South	3.14	1.90	2.28	2.03	2.61	3.15	3.25	102	69.39	1.01	0.91	1.11	0.48	0.42	1.15	36.67	42.25	36.56	43.56	47.22	44.94	32.31	0.32	0.68
Morro do Diabo	151	South	2.11	1.39	1.77	1.95	2.40	2.36	2.30	177	55.54	1.03	0.91	1.13	0.49	0.42	1.17	15.55	17.53	18.80	19.33	18.25	17.07	11.75	0.36	0.64
Morro do Diabo	152	South	2.71	1.58	1.86	2.36	2.43	2.72	3.09	153	77.76	0.98	0.91	1.08	0.46	0.42	1.11	36.84	42.00	50.76	50.32	53.08	55.45	33.25	0.44	0.56
Morro do Diabo	153	South	2.26	2.38	2.48	2.38	2.64	2.80	2.60	101	56.02	1.07	0.98	1.09	0.51	0.45	1.13	31.82	31.05	28.16	28.37	27.04	23.76	16.52	0.39	0.61
Morro do Diabo	154	South	1.59	1.85	2.22	2.11	2.16	2.16	2.13	174	52.20	0.95	0.91	1.05	0.45	0.42	1.08	28.68	32.82	30.06	29.36	27.68	26.04	13.22	0.45	0.55
Morro do Diabo	155	South	2.07	2.66	2.90	2.42	2.58	2.51	2.45	101	40.43	1.01	0.98	1.03	0.48	0.45	1.07	30.16	30.11	23.36	22.68	20.43	18.27	12.85	0.39	0.61

Carbon cost of heartwood formation for *Hymenaea* spp. trees

Morro do Diabo	156	South	2.10	2.10	2.32	2.01	2.14	2.20	2.06	187	79.58	0.97	0.92	1.06	0.46	0.42	1.09	47.96	51.22	43.53	44.63	44.10	40.19	26.27	0.38	0.62
Morro do Diabo	157	South	2.20	1.13	1.48	1.46	1.82	2.01	2.25	145	73.85	1.08	0.97	1.11	0.51	0.45	1.15	20.95	26.27	25.10	29.54	30.79	31.98	21.86	0.37	0.63
Morro do Diabo	158	South	3.46	2.23	2.66	3.04	3.56	3.74	3.62	95	60.16	0.97	0.96	1.02	0.46	0.44	1.05	31.45	34.94	36.40	36.88	33.42	30.93	29.08	0.37	0.63
Morro do Diabo	159	South	2.49	1.20	1.63	1.99	2.04	1.94	1.87	161	79.48	1.09	0.92	1.18	0.52	0.42	1.22	29.66	39.48	46.50	45.18	42.27	39.98	30.81	0.30	0.70
Vassununga	160	South	3.43	3.41	3.84	3.52	3.51	3.48	3.43	106	70.98	0.89	0.83	1.06	0.42	0.38	1.10	70.98	74.58	65.22	61.31	57.06	52.78	43.01	0.39	0.61
Vassununga	161	South	4.17	3.74	4.13	4.04	4.61	4.43	4.11	81	70.03	0.94	0.94	1.00	0.45	0.43	1.03	65.49	66.09	59.95	59.42	52.05	45.02	44.12	0.44	0.56
Vassununga	162	South	3.27	2.08	2.18	3.04	3.21	3.06	3.09	79	63.66	0.90	0.85	1.06	0.43	0.39	1.09	33.72	33.69	42.54	41.13	36.89	33.80	31.15	0.35	0.65
Vassununga	163	South	3.89	3.81	3.57	3.69	3.66	3.95	3.91	77	59.21	0.91	0.87	1.05	0.43	0.40	1.09	64.83	56.42	53.45	48.37	45.65	40.79	38.03	0.39	0.61
Vassununga	164	South	3.20	3.10	2.30	2.71	3.22	3.45	3.31	83	56.66	0.93	0.89	1.05	0.44	0.41	1.08	47.70	34.24	37.25	38.46	36.92	32.98	28.03	0.40	0.60
Vassununga	165	South	2.58	1.79	1.79	1.99	2.62	2.65	2.61	70	41.38	0.95	0.87	1.08	0.45	0.40	1.12	19.27	18.21	18.79	20.93	18.85	16.61	14.58	0.41	0.59
Vassununga	166	South	2.49	3.93	3.17	2.81	2.95	3.03	2.98	150	81.17	0.95	0.91	1.04	0.45	0.42	1.08	85.87	67.89	58.53	58.57	57.13	53.27	29.20	0.37	0.63
Vassununga	167	South	2.54	1.32	1.59	1.88	1.96	2.17	2.18	112	70.66	0.87	0.81	1.07	0.41	0.37	1.11	21.31	23.34	27.37	27.49	28.68	27.43	21.12	0.37	0.63
Vassununga	168	South	1.43	0.94	0.95	1.19	1.33	1.34	1.34	305	91.67	0.95	0.84	1.13	0.45	0.39	1.17	22.60	22.31	26.62	29.25	28.87	27.71	19.33	0.25	0.75
Vassununga	169	South	2.86	2.68	2.93	3.16	3.26	3.03	2.84	74	49.97	0.94	0.86	1.09	0.44	0.39	1.13	33.07	32.89	31.96	29.24	25.12	21.84	20.60	0.41	0.59
Vassununga	170	South	1.87	1.46	1.38	1.66	1.73	1.74	1.83	245	101.54	0.90	0.77	1.16	0.43	0.36	1.20	41.07	38.02	42.62	43.50	43.32	44.17	26.71	0.22	0.78
Vassununga	171	South	2.82	1.82	2.29	2.21	2.37	2.59	2.84	97	70.03	0.95	0.88	1.08	0.45	0.40	1.12	29.62	34.93	32.49	32.74	33.03	32.56	25.63	0.40	0.60

^a Individual not used in the models construction. It has a unusual heartwood shape and wood features values are outliers.

*Data not available.

** Sapwood damaged by fungi.

Conclusões Gerais

No presente estudo, ficou demonstrada a estreita relação entre o crescimento das espécies analisadas e o clima, mesmo havendo particularidades em cada população estudada. Aparentemente, esta relação também depende de outros fatores ambientais no qual as populações estão inseridas. Apesar da disponibilidade hídrica ser considerada um fator muito importante para a sazonalidade da atividade cambial nos trópicos, a temperatura é uma variável que se destacou em todas as cronologias. Todas as populações possuem uma relação negativa com a temperatura. Conforme discutido em alguns capítulos, esta relação com a temperatura pode ser resultado de aumento do estresse hídrico por diminuição do potencial hídrico da atmosfera e/ ou um aumento da fotorrespiração. Uma terceira possibilidade foi levantada no estudo da população de jatobá (*Hymenaea courbaril*) presente na região central do Brasil (Parque Estadual de Terra Ronca). Neste caso, a relação do crescimento com a temperatura pode ser fruto, além destes dois fatores apresentados, de um maior investimento em reprodução nos anos mais quentes.

Sob o contexto das mudanças climáticas globais, um aumento na temperatura dos locais de estudo poderia representar uma redução das taxas de incremento radial corrente. Mudanças nos padrões de precipitação também possuem o potencial de produzir resultados similares. A redução no volume da precipitação durante a estação de crescimento, e uma redução na amplitude da estação de crescimento também poderia resultar numa menor taxa de crescimento anual.

Os resultados dos capítulos apresentados também deixam clara a importância do ambiente sobre o crescimento das populações. No caso da população de *Podocarpus lambertii*, os afloramentos rochosos são essenciais para o crescimento destas árvores no semi-árido brasileiro. Eles reduzem a temperatura regional em até 15%, o que beneficia o crescimento desta população. Uma outra situação singular também foi encontrada na mata seca sobre calcário, onde o solo raso e drenado resulta numa alta sensibilidade das árvores de *H. courbaril* aos primeiros eventos de chuva. No Sudeste do Brasil, a fragmentação das floretas também criam condições ambientais diferenciadas que influenciam o crescimento de *H. courbaril*. As condições dos fragmentos de floresta semi-decídua influenciam especialmente a sensibilidade do crescimento de *H. courbaril* ao clima da região. Esta sensibilidade diminui em áreas mais perturbadas. A fragmentação possui um potencial de tornar as relações entre o clima e o crescimento das árvores ainda mais complexas, dificultando a elaboração de projeções futuras do crescimento.

Numa escala espacial mais ampla, a alocação do carbono para a formação da madeira de *Hymenaea* spp. também é dependente da temperatura. A formação do cerne parece ter uma relação direta com as taxas de assimilação nas folhas, sendo que em locais com maior assimilação, há um grande aporte de carbono para a formação do cerne, e em locais com menor assimilação há um menor aporte de carbono. Aparentemente, há um balanço entre o carbono alocado para a formação da madeira pelo câmbio e o carbono alocado para a deposição do cerne. Como há uma grande alocação de carbono para a formação do cerne, é possível dizer que sua formação

representa um alto custo para estas árvores. Adicionalmente, quando estes resultados são analisados na escala de uma floresta, o cerne representa um dreno de carbono importante que as vezes é negligenciado em levantamentos de biomassa.

De uma forma geral, um aumento na temperatura e uma diminuição na precipitação, ou uma concentração das chuvas em uma estação chuvosa mais curta, provavelmente terão um impacto negativo sobre o crescimento destas árvores. Entretanto, este efeito será dependente das condições ambientais nas quais as árvores estarão inseridas.

Resumo

As árvores, por serem organismos sésseis, lidam com as variações ambientais, ao longo da vida, por meio de plasticidade tanto estrutural quanto funcional. As respostas a estas variações resultam em regimes de crescimento diferentes que podem ser reconstruídos por meio do estudo dos anéis de crescimento. As alterações ambientais, principalmente as alterações climáticas, têm o potencial de modular o crescimento e assim ficarem registradas nos anéis de crescimento. O estudo da interação entre a árvore e o ambiente é muito importante principalmente em um momento de transformações rápidas tanto no clima como na paisagem. O objetivo do presente estudo foi compreender como o clima e o ambiente modulam o crescimento de algumas espécies arbóreas tropicais. Neste estudo o crescimento é sinônimo de formação do lenho, o qual foi avaliado sob dois pontos de vista, o dos anéis de crescimento e o da formação do lenho com enfoque na deposição do cerne. Para isso, foram coletadas espécies de ampla distribuição, *Hymenaea* spp. (Leguminosaeae) e *Podocarpus lambertii* (Podocarpaceae) que possuem anéis de crescimento visíveis. As populações de *Hymenaea* spp. foram coletadas em 10 localidades dentro de um gradiente latitudinal desde a linha do Equador até o Trópico de Capricórnio. A população de *Podocarpus lambertii* foi coletada num micro-refúgio no limite norte da distribuição desta espécie. Os resultados demonstram que tanto a precipitação quanto a temperatura influenciam o crescimento destas espécies. Estas relações entre o clima e o crescimento são dependentes do

ambiente em que as árvores estão inseridas. As altas temperaturas se destacaram como um fator limitante do crescimento para as espécies estudadas. A temperatura também se destaca como um forte controlador da deposição do cerne em *Hymenaea* spp. Vale ressaltar que a deposição do cerne representa um alto custo para estas árvores e há um balanço entre a alocação de carbono para a formação da madeira produzida pelo câmbio e a deposição do cerne. A precipitação também é um fator importante para o crescimento destas espécies. Porém, a forma como as árvores respondem à variabilidade da precipitação parece ser dependente do ambiente em que estão inseridas. Por exemplo, árvores em ambientes de maior disponibilidade hídrica respondem melhor à precipitação da estação chuvosa, enquanto árvores em ambientes mais drenados, e menor disponibilidade hídrica, respondem à precipitação logo no início da estação chuvosa. Vale ressaltar que esta relação entre o crescimento das árvores e o clima pode ser enfraquecida pela fragmentação das florestas, tão comum nos ambientes tropicais. Conhecer como as árvores responderam a mudanças ambientais no passado é muito importante para tentar entender como elas responderão às rápidas mudanças ambientais e climáticas previstas para o futuro. De uma forma geral, um aumento na temperatura e uma diminuição na precipitação, ou uma concentração das chuvas em uma estação chuvosa mais curta, provavelmente terão um impacto negativo sobre o crescimento destas árvores. Entretanto, este efeito será dependente das condições ambientais nas quais as árvores estarão inseridas.

Abstract

Trees are sessile organisms that relate with constant environmental change through both structural and functional plasticity. Changes in the plasticity result in different growth rates through the life of trees that can be accessed by the study of tree rings. Environmental changes, especially climate, have the potential to modulate tree growth and, consequently, be recorded in the tree rings. The study of the interaction between trees and the environment is relevant in a time of fast changes in the landscape and climate. The aim of this study was to better understand how climate and landscape features modulate the growth of tropical tree species. In the present study, growth is analyzed as a synonym of wood formation. Additionally, it was analyzed under two points of view, the first one is the tree-ring analyzes and second one is the carbon allocation in the process of wood formation. To accomplish that, tree species with wide distribution were sampled, including *Hymenaea* spp. (Leguminosae) and *Podocarpus lambertii* (Podocarpaceae) both with distinct tree rings. The populations of *Hymenaea* spp. were sampled in ten sites across a latitudinal gradient from the Equator line to the Tropic of Capricorn. The population of *P. lambertii* was sampled in a micro refuge in the northern limit of this species distribution. Results show that both temperature and precipitation influence these species growth and that relation depends on the environment in which trees grow. High temperatures seem to be a key limiting factor for the studied specie growth. Moreover, temperature is also an important factor that controls the heartwood deposition in *Hymenaea* spp. It is important to note that the heartwood

deposition represents a high carbon cost for these trees. Additionally, there is a trade-off between in the carbon allocation between the sapwood as produced by the cambium and the heartwood deposition. Precipitation is also a climate variable that influences these species growth. However, the precipitation influence seems to be more dependent on the environmental features of each population site. For instance, in sites higher water availability, trees' growth is more dependent on the precipitation during the wet season, while in sites with lower water availability, and well-drained soils, trees' growth is more dependent on the precipitation during the transition period between dry and wet seasons. It is important to highlight that forest fragmentation, commonly seen in tropical areas, has the potential to make this climate/growth relations weaker. Overall, an increase in air temperature and a decrease in the precipitation, or a concentration of it in a shorter wet season, will likely have a negative impact on trees growth. However, this effect will depend on the environmental characteristics of each population.