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O impacto das variações climáticas e hidrológicas no crescimento arbóreo de *Nectandra amazonum* (família Lauraceae) em uma floresta de várzea na Amazônia Central

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

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SINOPSE

Estudou-se os impactos das mudanças hidroclimáticas recentes no crescimento de árvores da espécie *Nectandra amazonum* em uma floresta de várzea localizada no Lago Catalão na Amazônia Central. Por meio da combinação das técnicas de dendrocronologia e densitometria de raio-X foram construídas cronologias da largura total dos anéis de crescimento, lenho inicial e lenho tardio e séries temporais datadas dos valores médios, mínimos e máximos da densidade da madeira. Observou-se a influência da temperatura mínima principalmente durante o período da fase aquática e da evapotranspiração principalmente durante o período de transição da estação seca para a estação chuvosa no crescimento radial. A separação da largura dos anéis de crescimento em lenho inicial e tardio e as análises dos parâmetros de densidade da madeira mostraram relações mais fortes com o clima.

Palavras-chave: variação climática, intensificação do ciclo hidrológico, floresta alagável, dendroclimatologia, densitometria de raio-X, lenho inicial, lenho tardio.

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SUMÁRIO

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RESUMO

Nas duas últimas décadas, a região da Amazônia Central tem sido impactada pelo aumento das temperaturas atmosféricas e pela intensificação do ciclo hidrológico caracterizado pelo aumento na magnitude e frequência de secas e cheias severas. As florestas alagáveis amazônicas são ambientes diretamente influenciados por tais alterações ambientais, principalmente por mudanças nos regimes hidrológicos. Entender como as espécies presentes em tais ambientes respondem a essas alterações é de grande relevância. *Nectandra amazonum* (Lauraceae), espécie arbórea perenifólia e bem adaptada às florestas alagáveis de várzea, foi selecionada para o presente estudo com o objetivo de entender os impactos das mudanças climáticas recentes no crescimento radial e nos parâmetros da densidade da madeira. Foram analisadas as relações intra e interanuais do clima com o crescimento por meio de técnicas convencionais de dendrocronologia, usando a largura do anel de crescimento como proxy, combinada à densitometria de raio-X que permitiu a determinação da largura do lenho inicial, largura do lenho tardio e seus respectivos valores de densidade. Nós utilizamos 32 árvores (52 raios) para a construção de uma cronologia robusta e sensível ao clima (sensibilidade média: 0,52; correlação entre séries: 0,37; EPS: 0,92), datando a série histórica entre 2001 e 2017. Não foram observadas correlações significativas entre os parâmetros do lenho de *N. amazonum* com variações do regime hidrológico ou forçantes climáticas de grande escala. As análises revelaram que evapotranspiração potencial e temperatura mínima desempenham um papel importante no crescimento arbóreo principalmente no período de transição entre estação seca e chuvosa e durante a inundação. Os resultados sugerem que processos fisiológicos, como fotossíntese e respiração, são fortemente associados ao clima influenciando o crescimento. A separação em lenho inicial e tardio assim como a análise dos parâmetros de densidade da madeira mostraram correlações mais fortes com o clima e também fornecem informações adicionais que podem elucidar questões a respeito do comportamento ecofisiológico da espécie.

Palavras-chave: Várzea, mudanças climáticas, ciclo hidrológico, evapotranspiração potencial, temperatura mínima, densitometria, dendrocronologia.

INTRODUÇÃO

A Amazônia abrange a maior extensão contínua de floresta tropical úmida no mundo ocupando aproximadamente 6,5 milhões de km^2 (Rocha et al. 2015). É considerada uma das áreas mais biodiversas do mundo formada por um mosaico de ecossistemas que abrigam cerca de 15.000 espécies de árvores fornecendo diversos serviços ecossistêmicos como o armazenamento de 60% da biomassa florestal global, nutrientes, carbono e regulação do ciclo hidrológico (Laurance et al. 2018, ter Steege et al. 2020). A floresta amazônica está inserida na maior hidrobacia do mundo contribuindo com aproximadamente 20% da descarga global de água doce nos oceanos (Richey et al. 1989). O Rio Amazonas sozinho é responsável por 6.300 km^3 da descarga média de água para o Oceano Atlântico anualmente, sendo a maior fonte de água doce no mundo (Dutra 2006). A hidrobacia desempenha um papel crítico na regulação climática em nível regional e global por ser um centro de convecção atmosférica profunda, responsável pelo processo de formação de precipitação em toda bacia, e, portanto, influencia a propulsão da circulação atmosférica global (Limberger e Silva 2016, Zhou e Lau 1998). Além das trocas de grandes quantidades de água, a floresta amazônica também influencia o clima global por meio das trocas de energia e carbono com a atmosfera (Gash e Nobre 1997, Silva-Dias et al. 2002).

Alterações no clima podem impactar o volume e a sazonalidade da precipitação (Marengo et al. 2008), a hidrologia dos rios (Malhi et al. 2008) e a dinâmica de carbono da floresta amazônica que é fortemente associada às variações do ciclo hidrológico regional (Gloor et al. 2015). Nas últimas duas décadas, tem sido observada uma elevação na temperatura atmosférica na Amazônia variando entre 0,6°-0,7°C (Marengo et al. 2018). Além disso, secas severas afetaram neste período a região amazônica como nos anos de 2005, 2010 e 2015/2016 com aumento progressivo em suas intensidades (Aragão et al. 2018, Espinoza et al. 2019). Já na região central, as cheias severas se tornaram recorrentes nas últimas duas décadas como nos anos de 2009, 2012-2015, 2017 e 2019 (Schöngart e Junk 2020). Esses eventos extremos de seca e cheia alteram o ciclo hidrológico da região devido ao aumento da frequência e magnitude de eventos hidroclimáticos extremos resultando numa intensificação do ciclo hidrológico (Gloor et al. 2013) causado principalmente por anomalias de temperatura da superfície do mar (TSM) do Pacífico Equatorial (El Niño e La Niña) e do Atlântico Tropical (Richey et al. 1989, Schöngart e Junk 2007, Marengo et al. 2008, 2011, Tomasella et al. 2013, Marengo e Espinoza 2016, Wang et al. 2018, Espinoza et al. 2019). Barichivich et al. (2018) mostraram que o aumento na frequência e magnitude das cheias é causado pela intensificação da circulação de Walker devido ao forte aquecimento da TSM do oceano Atlântico e ao simultaneamente resfriamento da TSM do Pacífico, resultando numa maior convecção de nuvens e aumento de chuvas, principalmente na região noroeste da Amazônia (Gloor et al. 2013, Wang et al. 2018). Apesar da TSM do Atlântico ser o principal elemento influenciador nessa alteração, também contribuem a Oscilação Multidecadal do Atlântico (Wang et al. 2018) e as correntes de águas quentes provenientes do oceano Índico via corrente das Agulhas (Barichivich et al. 2018).

Há uma crescente preocupação com possíveis efeitos causados pela variabilidade climática e o aumento na frequência e magnitude de eventos climáticos extremos na floresta tropical. Estudos têm demonstrado que altas temperaturas associadas ao déficit hídrico durante a seca resultam numa redução no incremento de diâmetro das árvores e aumento das taxas de mortalidade, podendo causar alterações na dinâmica e estrutura das comunidades arbóreas (Clark et al. 2003, 2010, Brando et al. 2008, Aleixo et al. 2019). Porém, os impactos da intensificação do ciclo hidrológico podem variar enormemente entre as diferentes fitofisionomias florestais. Um ecossistema diretamente afetado pelas mudanças no ciclo hidrológico são as florestas alagáveis que ocorrem ao longo dos grandes rios amazônicos.

As duas principais tipologias florestais alagáveis na Amazônia são as várzeas e os igapós (Prance 1979). Suas classificações são baseadas nos parâmetros físico-químicos e coloração das águas dos rios as quais estão associadas (Sioli 1984). As várzeas, foco deste estudo, são inundadas periodicamente por águas brancas provenientes dos Andes e encostas pré-Andinas apresentando alta quantidade de sedimentos ricos em sais minerais com pH próximo à neutralidade (Furch 1997). Devido à variação sazonal na precipitação da bacia Amazônica, as florestas alagáveis estão sujeitas ao pulso de inundação monomodal, previsível e de longa duração com uma fase aquática (águas altas) e uma fase terrestre (águas baixas) durante o ano. Esse fenômeno é a força motriz que determina a dinâmica dos processos ecológicos e biogeoquímicos das florestas alagáveis (Junk et al. 1989). Para tolerar as condições anóxicas da fase aquática, as espécies arbóreas contam com adaptações anatômicas, morfológicas, fisiológicas e bioquímicas específicas (Parolin et al. 2004, Parolin 2009). Destacam-se a formação de aerênquima, lenticelas hipertrofiadas e raízes adventícias no tronco, a incorporação de suberina na rizoderme e a mudança no metabolismo aeróbico para anaeróbico (Jackson 1990, Crawford e Braendle 1996, Jackson e Armstrong 1999, Armstrong e Drew 2002, De Simone et al. 2002, Parolin 2009, Piedade et al. 2010, Sauter 2013). Em consequência das condições anóxicas na rizosfera, muitas espécies arbóreas perdem ou trocam as folhas e reduzem ou cessam o crescimento radial em decorrência da dormência do câmbio secundário durante a fase aquática (Schöngart et al. 2002, Parolin et al. 2010), retomando a produção do lenho apenas ao final do alagamento (Worbes 1997). Esse processo resulta na formação do anel de crescimento que em muitas árvores são anuais e cuja largura reflete principalmente a duração da fase terrestre (Worbes 1989, Schöngart et al. 2004, 2005).

Os anéis de crescimento são amplamente utilizados para determinação da idade e das taxas de crescimento das árvores pela aplicação de métodos de dendrocronologia. A sequência cronológica dos anéis de crescimento armazena informações importantes que podem ser usadas para a reconstrução do clima (Schöngart et al. 2006, Mendivelso et al. 2013, Vlam et al. 2014, Xu et al. 2015, Baker et al. 2016, Granato-Souza et al. 2020) sendo também empregado para monitorar as respostas da floresta às variações climático-hidrológicas (Zuidema et al. 2012, van der Sleen et al. 2015, Brienen et al. 2016). Schöngart et al. (2004) observaram por meio de análises dendroclimáticas que o crescimento diamétrico de *Piranhea trifoliata* (Picrodendraceae) em florestas alagáveis de várzea tem periodicidade anual determinada pela variação do ciclo de inundação. Também detectaram a influência do fenômeno climático El Niño numa série temporal de 200 anos.

Tradicionalmente, estudos dendrocronológicos realizados nos trópicos relacionam a largura total do anel de crescimento com variáveis hidroclimáticas (Dünisch et al. 2003, Brienen e Zuidema 2005, Schöngart et al. 2004, 2005, 2015), porém, as correlações não são muito altas em comparação com estudos realizados em zonas climáticas temperadas ou boreais (Brienen et al. 2016). O anel de crescimento anual de espécies de árvores da família Lauraceae é dividido anatomicamente em duas camadas distintas: o lenho inicial caracterizado pela baixa densidade, células de cor clara, enquanto o lenho tardio é composto por células menores e escuras com paredes espessas e alta densidade (Reis-Avila and Oliveira 2017). O desenvolvimento diferenciado dessas duas camadas fornece informações adicionais sobre a variabilidade climática intra-anual quando comparado aos dados obtidos a partir da largura total do anel (Cleaveland 1986, Stahle et al. 1988). Considerando esse potencial, a contribuição inédita desse estudo é diferenciar estas relações para uma espécie arbórea tropical a partir da análise do lenho inicial (formado no início do período vegetativo) e lenho tardio (formado no final do período vegetativo) com a hipótese que essa diferenciação reflete melhor as variações interanuais do clima e da hidrologia resultando em correlações mais robustas. Também serão consideradas nas análises dendrocronológicas as variações de densidade ao longo da sequencia dos anéis de crescimento das árvores. Por meio da densitometria de raio-X serão produzidos perfis contínuos da densidade de madeira no sentido radial em intervalos micrométricos (Tomazello Filho et al. 2008) possibilitando a caracterização da variação inter e intra-anual dos anéis de crescimento.

HIPÓTESES

A partir da cronologia exatamente datada da espécie *Nectandra amazonum* (Lauraceae), uma árvore abundante em florestas alagáveis de várzea da Amazônia Central, serão produzidas séries temporais de vários parâmetros do lenho que abrangem a largura do anel de crescimento e as larguras do lenho inicial e tardio com seus respectivos valores da densidade da madeira para testar as seguintes hipóteses:

- *Nectandra amazonum* é uma espécie arbórea sensível às variações do regime hidrológico.
- A intensificação do ciclo hidrológico observada nas últimas décadas está registrada nas séries temporais dos anéis de crescimento.
- As cronologias do lenho inicial e tardio apresentam correlações mais fortemente associadas ao clima e hidrologia comparada à cronologia da largura total do anel de crescimento.
- Parâmetros da densidade de madeira revelam informações adicionais sobre relações entre o crescimento e clima.

OBJETIVOS

Objetivo geral

Entender o efeito das variações climáticas e hidrológicas no crescimento de árvores da espécie *Nectandra amazonum* (Lauraceae) em uma floresta de várzea na Amazônia Central.

Objetivos específicos

I. Desenvolver uma cronologia baseada nos anéis de crescimento da espécie *Nectandra amazonum.*

II. Desenvolver séries temporais datadas baseadas do lenho inicial e tardio e dos valores de densidade da madeira correspondentes da espécie *Nectandra amazonum.*

III. Identificar os fatores climáticos (regionais, globais) e hidrológicos que influenciam o crescimento da espécie arbórea diferenciado em lenho inicial e tardio.

IV. Identificar a influência dos fatores hidroclimáticos nos parâmetros de densidade da madeira dos anéis de crescimento da espécie *Nectandra amazonum.*

Capítulo 1

Minimum temperature and evapotranspiration in Central Amazonian floodplains limit tree growth of *Nectandra amazonum* (Lauraceae)

Goncalves, J.Q, Durgante, F.M., Piedade, M.T.F., Wittmann, F., Ortega, D.R.R., Tomazello-Filho, M., & Schöngart, J. Impacts of recent extreme hydro-climatic intensification on growth of *Nectandra amazonum* in a Central Amazonian floodplain forest.

(submitted to *Trees*)

ABSTRACT

During the last two decades the Central Amazon region has been impacted by increasing atmospheric temperatures and an intensified hydrological cycle characterized by enhancing magnitudes and frequency of severe floods and droughts. Little is known about the effects of these climate trends on tree growth in floodplain forests. In this study we analysed *Nectandra amazonum* Nees (Lauraceae), an evergreen and flood-adapted tree species, dominant in the nutrient-rich Amazonian floodplains (*várzea*) but also occurring in other environments outside the Amazon basin. For the period from 2001 to 2017 intra and interannual climate-growth relationships of *N. amazonum* were analysed, applying a combination of conventional dendrochonological (cross-dating) and densiometric techniques to construct a robust tree-ring chronology. Six wood parameters were derived from the chronology (ring width, width of earlywood and latewood and corresponding wood density values) and correlated with local climate and hydrologic data. The analysed 32 trees did not show correlation between wood parameters and variation of the hydrological regime. Climate-growth relationships indicated that potential evapotranspiration and minimum temperature play an important role on tree growth mainly during the period of transition between the dry and the wet season, and during the aquatic phase affecting physiological processes such as photosynthesis and respiration, respectively. The results suggest that this species probably colonized the Amazonian floodplains originating from environments of higher altitudes or latitudes in the Southern Hemisphere conserving its growth responses to temperature seasonality and water deficit, which turns the species resilient against flood-pulse disturbances.

Keywords: Várzea, climate change, hydrological cycle, potential evapotranspiration, minimum temperature, densitometry, dendrochronology.

INTRODUCTION

Over the last four decades warming reached 0.6°–0.7°C in the Amazon region and extreme climatic events that affected the region (Marengo et al. 2018). Extreme droughts were recorded in the southern region of the basin in the years 2005 and 2010 and (Aragão et al. 2018; Espinoza et al. 2019) and in 2015/2016, a severe El Niño drought affected approximately 43% of the area of the Brazilian Amazon, especially in the central, eastern and northern regions (Erfanian et al. 2017). On the other hand, an increase in precipitation in the north-western region mainly during the rainy season (Gloor et al. 2013; Wang et al. 2018) resulted in a significant increase and magnitude of severe flood events in the Central Amazon region over the past 30 years (Barichivich et al. 2018; Schöngart and Junk 2020). The intensification of the hydrological cycle is primarily caused by a strong warming of the sea surface temperature (SST) of the Tropical Atlantic Ocean and simultaneously cooling of the SST of the Equatorial Pacific forcing the Walker Circulation (Barichivich et al. 2018) but also has underlying feedback mechanisms (Gouveia et al. 2019).

The manifestation of climate change in the Amazon basin is of rising concern as it affects physiology, growth and mortality of trees, which may cause changes in the dynamics and structure of tree communities and consequently affect important ecosystem services provided by the Amazon rainforest (Aleixo et al. 2019; Brando et al. 2008; Clark et al. 2003, 2010). However, climate impacts on trees can vary enormously among different species and forest types. Severe droughts in the Amazon, which have negative impacts on tree growth in the non-flooded upland forests (*terra-firme*) (Foley et al. 2002; Granato-Souza et al. 2020) may result in reduced flood heights and durations in floodplain forests, potentially providing favourable growth conditions (Schöngart et al. 2004). However, depending on their leaf phenology, floodplain tree species show different responses to hydroclimatic variation (Schöngart et al. 2002).

Amazonian floodplains cover about 14% of the basin and occur along the large rivers providing essential ecosystem services and natural resources for indigenous and traditional populations (Junk et al. 2011). Due to seasonal variation of precipitation in the vast catchments, large Amazonian rivers present regular and predictable flood pulses with high amplitudes inducing a distinct seasonality in the floodplains, characterized by an annual aquatic (high water period) and a terrestrial phase (low water period) (Junk et al. 1989). Among these floodplains, the *várzea* covers about 450,000 km² and occur along the mainstem of the Amazon river and its large white-water affluents draining the Andean region (Wittmann and Junk 2016). *Várzea* floodplains developed after the onset of the Amazon transcontinental river around 9.4–9.0 million years ago, bringing a new and fertile landscape element into the mainly oligotrophic Amazonian lowlands (Hoorn et al. 2017). This allowed the colonization, diversification, and speciation of the existing tree flora in the *várzea*, comprising more than 1000 species many tree species, among them 10% endemic species (Wittmann et al. 2006, 2013). Long-term relative stability of climatic conditions favoured the development of these adaptations over millions of years (Wittmann et al. 2010a; Wittmann 2012). To endure seasonal anoxic soil conditions imposed by flooding, tree species rely on specific anatomical, morphological, physiological and biochemical adaptations (De Simone et al. 2002; Parolin et al. 2004, Parolin 2009; Piedade et al. 2010). Anoxic conditions as caused by flooding result in leaf shedding or exchange of many tree species and reduce or cease radial wood growth due to the secondary cambium dormancy during the aquatic phase (Schöngart et al. 2002; Parolin et al. 2010) causing the formation of annual tree rings (Worbes 1989). Earlier studies indicate that ring width reflects mainly the duration of the terrestrial phase (Schöngart et al. 2004, 2005; Batista and Schöngart 2018). Considering that climate and hydrology are important factors that influence tree growth in Amazonian floodplains, tree-ring analysis can be employed to detect the recent intensification of the hydrological cycle (Cook and Kairiukstis 1990; Speer 2010).

Traditionally, dendrochronological studies carried out in the tropics relate the total ring width to interannual hydroclimatic variables (Brienen and Zuidema 2005; Dünisch et al. 2003; Schöngart et al. 2004, 2005, 2015; Granato-Souza et al. 2020). Yet, the correlations are not very high compared to studies in temperate, boreal or semi-arid climate zones (Brienen et al. 2016). Furthermore, most dendroclimatic studies tended to ignore temperature in the analysis due to the lack of a distinct seasonality in the tropics (Worbes 2002). In this study we developed a tree-ring chronology for the evergreen Central

Amazonian tree species *Nectandra amazonum* Nees (Lauraceae) using conservative dendrochronological techniques (cross-dating) and X-ray densitometry, which creates intra-annual wood density profiles allowing an accurate characterization of the tree ring and the definition of earlywood (lower wood density) and latewood (higher wood density) formation (Dodd and Nancy 1988). From the exactly dated ring width, earlywood and latewood chronologies and corresponding time series of their respective wood density values were generated to test the following hypotheses: (1) *N. amazonum* is a well-adapted tree species to flooding and responds sensitively to the variation of the flood-pulse; (2) the intensification of the hydrological cycle during the last decades is archived in tree-ring series; (3) intra-annual variation in wood density allows an accurate definition of the annual ring boundaries avoiding dating errors induced by false or missing rings and the development of well-replicated tree-ring chronologies; (4) earlywood and latewood chronologies show stronger relationships to climate and hydrology than the ring-width chronology; and (5) wood density variations of *N. amazonum* reveal additional information about the relationships between tree growth and climate.

MATERIAL AND METHODS

Study region

This study was conducted in the nutrient-rich and geomorphological dynamic white-water floodplains (*várzea*) of Catalão Lake located close to the confluence of the Negro and Solimões rivers near to the city of Manaus, in the State of Amazonas, Brazil (3°10’ S, 59°55’ W) Lake (Fig. 1). The studied floodplain forest is subject to an annual and regular flood pulse with high amplitude of more than 10 m (Junk et al. 1989; Schöngart and Junk 2007). This induces a distinct seasonality characterized by an alternation between one terrestrial and one aquatic phase during the annual cycle. Maximum annual water levels normally occur during June, followed by the receding water period, which attains the minimum water levels regularly between mid-October and mid-November, which is the period of the onset of the rainy season (Schöngart et al. 2002). The annual hydrological cycle shows a temporal shift of about three months compared to the seasonal precipitation regime, which traces back to the huge area of the Solimões and Negro rivers catchment with approximately 3 million km² (Irion et al. 1997; Schöngart and Junk 2007) (Fig. 2).

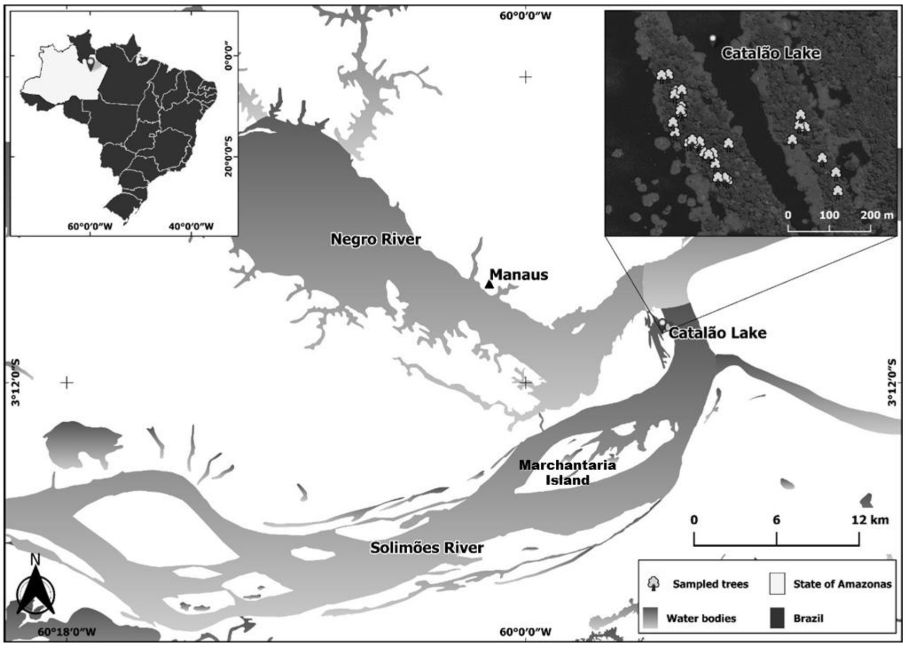

Fig. 1 Location of the Catalão Lake (State of Amazonas) close to the city of Manaus and the confluence of the Negro and Solimões rivers. Map on the top right corner displaying the geographic location of sampled *Nectandra amazonum* trees.

The climate in the study region is characterized by an annual precipitation (*P*) of 2111 mm (SD± 339) (July 2000 to June 2017), with a distinct seasonality (Fig. 2). The rainy season comprises the period from November to May with highest rainfall during March (mean 321 SD ± 109 mm), while the dry season occurs from July to September with monthly precipitation below 100 mm reaching its minimum in August with 57 mm (SD ± 47). Mean annual temperature (T_{mean}) is 28.4°C (SD ± 1.0) with minimum monthly temperatures (T_{min}) of 24.3°C (SD ± 0.3) and maximum monthly temperatures (T_{max}) of 32.6°C (SD ± 1.2) (Fig. 2) with only small variations throughout the year. Potential evapotranspiration (ET_{pot}) in the study region is 130.9 mm (SD ± 9.3) with higher values during the dry season and transition periods between dry and rainy season, potentially leading to water deficits during this period (ET_{pot} exceeding monthly *P*) (Fig. 2).

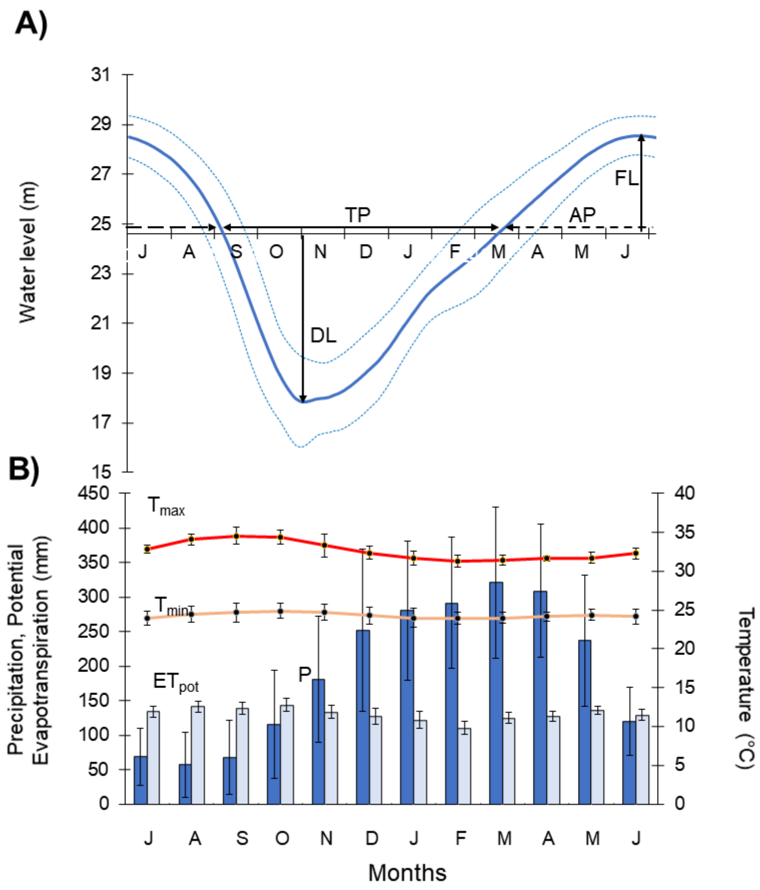

Fig. 2 Average hydrological conditions and climate for the study region and period (2000-2017) shown from July to June. A) Mean (blue line) and standard deviation (dotted line) of daily water levels obtained from the Port of Manaus (data: Agência Nacional de Águas – ANA; above) in relation to the mean topography of the studied population of *Nectandra amazonum* (mean 24.6 SD ± 0.44 m). Based on the daily water level record the annual duration of the aquatic phase (AP), terrestrial phase (TP), flood level (FL) and drought level (DL) have been calculated for each year. B) Mean and standard deviation of monthly precipitation (*P*; blue bars), potential evapotranspiration (ET_{pot}; bars in light blue), minimum (T_{min}; yellow line) and maximum (T_{max}; red line) monthly temperature (data for *P*, T_{max} and T_{min}: Instituto Nacional de Meteorologia – INMET; data for ET_{pot}: Empresa Brasileira de Pesquisa Agropecuária – EMBRAPA).

As a consequence of the flood pulse, *várzea* forest soils are enriched through the deposition of alluvial sediments originating from the Andes. Those sediments have higher concentration of macronutrients (P, K, Na, Ca and Mg) which increases cation-exchange capacity, resulting in higher soil fertility compared to other Amazonian forest types (Sombroek 1984; Furch 1997; Furch and Klinge 1989). *Várzea* soils presents low or no profile development, comprising groups of Neosols, Gleysols, Organosols, and Vertisols that are classified as eutrophic or dystrophic according to the topographic location and the quality of water and sediments (Victoria et al. 1989).

Approximately 75% of the Central Amazonian *várzea* is covered by highly diverse floodplain forests (Wittmann et al. 2006). Tree species are partially endemic to the highly inundated low *várzea*, defined as flooded by more than 3 m in height (Wittmann et al. 2013). Tree species are generally well-zoned along the flood-level gradient and according to successional series (Ayres 1993; Junk 1989; Wittmann et al. 2002; Worbes et al. 1992). The *várzea* forests in the study region are a mosaic of natural successional stages and secondary forests, which established after abandonment of areas used for agriculture and jute (*Chorchorus* spp.), especially in the period from the 1960s to the late 1980s (WinklerPrins 2006).

The tree species *Nectandra amazonum*

Nectandra amazonum (Lauraceae family) is a widespread tree species that occurs mainly in Amazonia up to elevations of 300 m above average sea level (Fig. S1). In *várzea* forests, where it is commonly known as louro canela, *N. amazonum* it is one of the most frequent tree species (Wittmann 2012), preferentially occurring in late-secondary stages, where flood levels range 4–5 m (Wittmann et al. 2010b). Trees usually reach heights of up to 20 m, are relatively short-lived (mean 28 SD ± 4 years), and present high average radial growth (mean 4.84 SD ± 1.21 mm yr^{-1}) and moderate wood density (ρ) of 0.47 g cm^{-3} (Worbes et al. 1992). The species belongs to the evergreen ecotype that exchanges and replaces leaves continuously, with new leaves being flushed around the flood peak during the aquatic phase, occasionally showing a second leaf exchange during the dry season (Schöngart et al. 2002; Waldhoff and Parolin 2010). Flowering starts during the period of leaf flush in the aquatic phase while fruits reach maturity at the beginning of subsequent aquatic phase (Parolin 2000). Tree-ring formation occurs during the aquatic phase when trees face unfavourable environmental conditions induced by oxygen depletion in flooded soils (Schöngart et al. 2002). Monthly diameter increment, monitored during a 26-month period (1998–2000) by Schöngart et al. (2002), shows for *N. amazonum* a significant correlation to monthly precipitation, but no correlation with monthly water level variations. Many studies on the ecophysiology of *N. amazonum* are available comparing specific leaf mass, leaf area, leaf water and nitrogen content (Parolin 2002; Parolin et al. 2002), mean and maximum CO_2-assimilation, stomatal conductance (Parolin 1997; Parolin et al. 2001; Piedade et al. 2000), photochemical efficiency (*Fv*/*Fm*) (Parolin 1997), sap flow and stem respiration rates (Horna et al. 2010) during both, the aquatic and terrestrial phases (more information on the ecophysiology of *N. amazonum* is available as Supplementary Material Fig. S2). Overall, *N. amazonum* shows sophisticated physiological adaptations which allows the species to maintain a carbon metabolism at low, but almost constant levels along the year, despite of the anoxic conditions during the aquatic phase which lead to a reduction of the cambial activity and annual tree-ring formation.

The wood anatomical structure of Lauraceae family is divided in two distinct zones due to differences in wood density which result from the variation of lumen size and wall thickness of fiber cells (Worbes 1986; Worbes and Fichtler 2010). Earlywood, formed at the beginning of the growing season, comprises a brighter zone with lower wood density due to the larger lumen and thin walls of fiber cells, while the latewood has a higher wood density due to increasing thickness of cell walls and decreasing size of lumen appearing as a dark zone (Worbes 2002). In *N. amazonum,* tree rings are usually clearly visible by naked eye. However, intra-annual wood density variations, lacking an abrupt transition of the cell sizes, are frequent, indicating the occurrence of false tree rings. Vessels are visible by naked eye, predominantly solitary without specific arrangements (diffuse-porous) (Fig. 3).

Fieldwork

Wood samples from 38 living trees were collected in September 2018 and November 2019 at *várzea* secondary forests around Lake Catalão (Fig. 1). Trees were selected avoiding differences in the occurrence of their topographic elevations and assuring the inclusion of a range of diameter and age classes.

Two wood cores of 12 mm in diameter of perpendicular position were extracted from 34 trees at breast height using a power-driven increment borer. Additionally, stem discs from four trees were obtained at 1.3 m stem height in November 2019 to improve the characterization of false rings and tree-ring dating (authorization nº124/2019 – DEMUC/SEMA). The height of the maximum flood level printed on the trunk was measured to estimate the topographical elevation using daily water level records from the nearby Port of Manaus (12.3 km in direct distance) provided by the Hydroweb platform operated by the Brazilian Water Agency (Agência Nacional de Águas – ANA). Therefore, the observed flood height in the field was subtracted from the previously recorded maximum water level allowing to estimate the topographic elevation of the studied trees (mean 24.6 SD ± 0.44 m).

Tree-ring analyses

The wood samples were air dried and mechanically polished with sandpaper (80–600 grains). Tree rings were identified by the intra-annual wood density variations (earlywood/latewood pattern), marked and measured to the nearest 0.01 mm under a LEICA-MS5 microscope, coupled to a digital measuring device (LINTAB, Rinntech, Germany) supported by the software TSAP-Win (Time Series Analyses and Presentation, Rinntech, Germany) to produce individual ring-width time series. These were processed using dplR package in R software (Bunn 2008) for cross-dating. Frequently occurring false tree rings in *N. amazonum* resulted consequently in dating errors and it was not possible to construct a reliable tree-ring chronology with robust statistics based on the macroscopically analysed wood anatomical features.

X-ray densitometry

To improve the examination of growth boundaries avoiding dating errors induced by frequently occurring false rings as observed in *N. amazonum*, we applied X-ray fluorescence analysis of the collected wood samples at the Department of Forest Science (ESALQ/USP) at Piracicaba, São Paulo State. To prepare the cores for densitometry analyses, a thin wood sample from each polished core was transversely cut (2.0 mm thickness) with a parallel double circular saw and conditioned in a climatic chamber at 20°C and 60% relative humidity until reaching a stable moisture content of 12% (Tomazello Filho et al. 2008). The samples were then scanned with a calibration scale of cellulose acetate using an X-ray densitometry chamber (Faxitron MX20-DC12, Faxitron X-Ray, Illinois, USA). The images were analysed by WinDendro® software (Regent Instruments Inc.) creating tree ring microdensity profiles (interval of 1.7 µm).

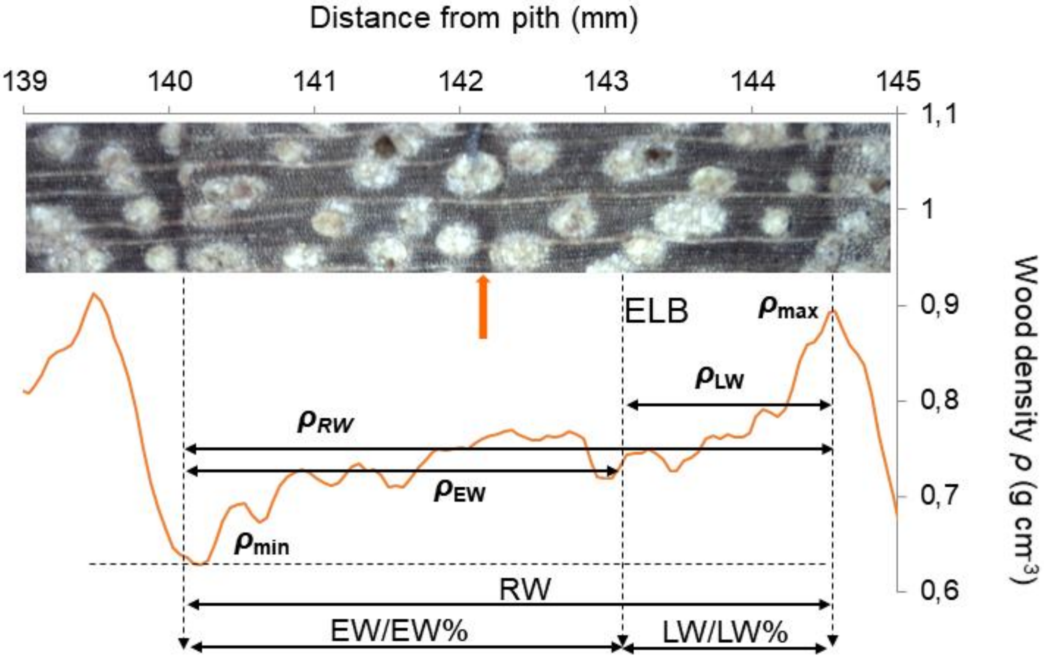

Fig. 3 Schematic figure of obtained wood parameters from tree rings: Ring width (RW), earlywood width (EW), latewood width (LW), mean wood density of ring width (ρ_{RW}), earlywood density (ρ_{EW}) and latewood density (ρ_{LW}). Earlywood-latewood boundary (ELB) was determined by the absolute minimum (ρ_{min}) and maximum (ρ_{max}) wood density as a floating threshold for each tree ring (Eq. 1). The percentage of earlywood (EW%) and latewood (LW%) was calculated to determine the period of EW and LW formation based on monthly diameter increments (Fig. S2). In the upper panel an image of macroscopic wood anatomy of *N. amazonum* shows a tree ring with intra-annual density fluctuation, and a false tree ring indicated by the arrow, which results in a gradual variation of wood density.

Tree rings were defined by the sharp contrast between maximum (ρ_{max}) and minimum wood density (ρ_{min}). Based on the definition of ring boundaries, ring width (RW), earlywood width (EW), latewood width (LW), mean wood density of the ring width (ρ_{RW}), earlywood (ρ_{EW}) and latewood (ρ_{LW}) were obtained (Fig. 3). The earlywood-latewood boundary (ELB) within a tree ring was calculated by 50% of the difference between maximum (ρ_{max}) and minimum wood density (ρ_{min}). The so-called relative method uses only ring-specific minimum and maximum profile values to find the position of ELB as a floating threshold. Equation 1 indicates how the boundary between early and latewood (ELB) is calculated (Windendro®software, Regent Instruments Inc.):

$$\mathrm{ELB} = \rho_{max} + (X/100)*(\rho_{min}–\rho_{max}), \qquad (1)$$

where X is the percentage of ρ_{min} related to ρ_{max}. From the resulting measurements, we developed a ring-width chronology using the same method of statistical validation for cross-dating accuracy as for the time series based on macroscopic analysis (dplR package in R software; Bunn 2008). Based on the exactly dated RW chronology also time series were derived for the corresponding wood density parameters (ρ_{RW}, ρ_{EW} and ρ_{LW}). We opted for using raw wood density values and not detrended series, as the annual wood density values are composed of trees with different ages (Table S1).

Climate data

We compiled a set of hydrological and climatic data, for the period between 2000 and 2017, from different sources. Monthly precipitation (P), monthly minimum (T_{min}) and maximum (T_{max}) temperature were obtained from INMET (Instituto Nacional de Meteorologia; station code 82331, latitude: 3°06’ S, longitude: 60°01’ W, located in Manaus). Monthly mean potential evapotranspiration (ET_{pot}), calculated by the method proposed by Thornthwaite and Matter (1955), was obtained from EMBRAPA (Empresa Brasileira de Pesquisa Agropecuária, latitude 2°53’ S, longitude: 59°58’ W). The Cumulative Water Deficit (CWD) defined as the sum of negative differences ($P–ET_{pot}$)

during consecutive months was calculated for each year (Aragão et al. 2007). From the daily water level records we calculated for each year (2000–2017) the duration (in days) of the aquatic (AP) and terrestrial (TP) phase for the mean topographic elevation of each tree for which the tree-ring chronology was analysed (Fig. 2). Additionally, the annual flood level (FL) and drought level (DL) (in cm), defined as the difference between the mean topography and the annual minimum water level) were derived. To examine the influence of large-scale oceanic forcing of the hydrological cycle (Barichivich et al. 2018), we obtained from the NOAA website (National Oceanic Atmospheric Administration; https://psl.noaa.gov/data/climateindices/list/) monthly sea surface temperature (SST) anomalies from the Equatorial Pacific in form of three-month averages (Oceanic Niño Index – ONI) and from the tropical north (TNA) and south Atlantic (TSA) as well as for the Atlantic Meridional Mode (AMM) in form of monthly SST anomalies.

Statistical analyses

To determine the periods of earlywood and latewood formation, we used monthly diameter increment data of *N. amazonum* (Fig. S2) observed for a period of 26 months (June 1998 – August 2000) at a nearby *várzea* site (Marchantaria Island) with similar environmental conditions and tree sizes (Schöngart et al. 2002). Based on these data monthly mean diameter increments were cumulated to annual increments and transformed in relative values. Based on the determined mean EW% (67.8%) and LW% (32.2%) by densitometry analysis of those individuals used for the tree-ring chronology, the periods of EW and LW formations were estimated, indicating the occurrence of ELB in February.

In order to relate tree growth to climate, the individual tree-ring series were detrended by the ’mean-value function’, fitting a horizontal line using the mean of the series to transform raw values into ring-width indices (RWI) (Cook and Kairiukstis 1990). Residual chronologies from the standardized RWI, EWI and LWI were built through a robust bi-weighted mean function. Cores that could not be reliably cross-dated were discarded. To evaluate the growth synchronism among detrended ring-width series, the intercorrelation series (*r*), RBAR and the expressed population signal (EPS) were calculated (Wigley et al. 1984). The mean sensitivity indicating environmental response of tree growth over the time was calculated according to Speer (2010).

RESULTS

Chronologies of tree-ring parameters

A ring-width (RW) chronology based on the microdensity profiles was developed chronologies from 32 out of 38 sampled trees (84%) comprising a total of measured 52 radii. The descriptive statistics of the RW chronology and the derived earlywood (EW) and latewood (LW) time series are presented in Table 1 and the chronologies in Figure 4. The RW, EW and LW chronologies are negatively correlated with the wood density parameters (Table S2). The developed RW chronology (Fig. 4) had a total length of 26 years and individual time series presented an average length of 16.8 yrs (SD ± 5). From 2001 to 2017, the interseries correlation of 0.37 and RBAR of 0.28 were significant, suggesting a common growth variation among trees reflected by the EPS of 0.92 which exceeded the suggested threshold of 0.85 (Wigley et al. 1984). The sensitivity of 0.52 showed that tree rings of *N. amazonum* were sensitive to environmental changes (Fritts 2001). The statistical parameters indicated that the chronology was successfully cross-dated, which allowed to derive the chronologies for EW and LW. Computing the dendrochronological statistics for the EW chronology showed a slight decrease in the statistical robustness compared to the RW chronology with RBAR of 0.21, however, the EPS of 0.88 (Table 1) still attained the required minimum value (Wigley et al. 1984). The LW chronology presented lower mean interseries correlation, RBAR and EPS values, below the required threshold. On the other hand, sensitivity of the LW chronology was higher compared to the RW and EW chronologies, indicating that there was low synchronicity between latewood width which became excessively sensitive (Table 1).

Table 1. Descriptive statistics of *Nectandra amazonum* chronologies.

	Chronologies		
Parameter	Ring width (RW)	Earlywood (EW)	Latewood (LW)
Mean interseries correlation	0.37	0.33	0.16
Rbar	0.28	0.21	0.07
Expressed Population Signal (EPS)	0.92	0.88	0.68
Mean Sensitivity	0.52	0.64	0.77

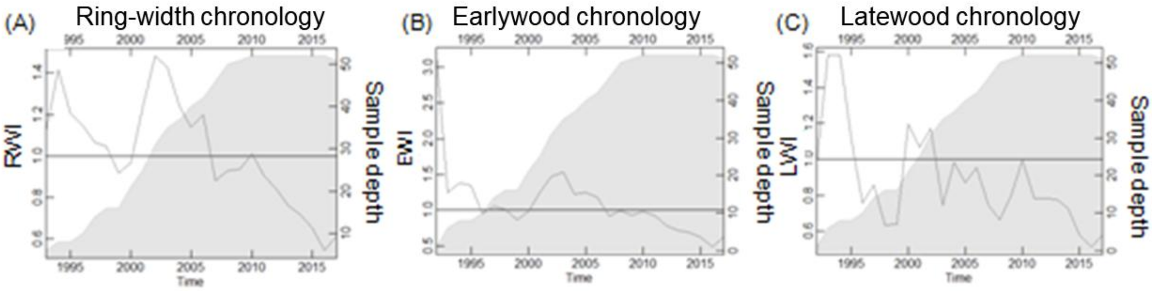

Fig. 4 Indices for the A) ring-width, B) earlywood and C) latewood chronologies of the tree species *Nectandra amazonum* from Central Amazonian *várzea* floodplains. The grey area represents the sample depth of individual time series.

Climate-growth relationships of *Nectandra amazonum*

From the analysed six wood parameters, EW contained the strongest climate signal (2001–2017), however, the most significant correlations were obtained for ρ_{RW}. In general, LW chronology and ρ_{LW} showed lower correlations with climate variables. None of the six wood parameters showed any significant correlation with the calculated hydrological variables (AP, TP, FL and DL). Negative correlations ($p<0.05$) of RW and EW were observed with monthly precipitation of November, corresponding to the minimum water level at the beginning of the rainy season. Concerning to wood density parameters, only ρ_{LW} indicated positive correlations with monthly precipitation of August and September (Fig. 5A).

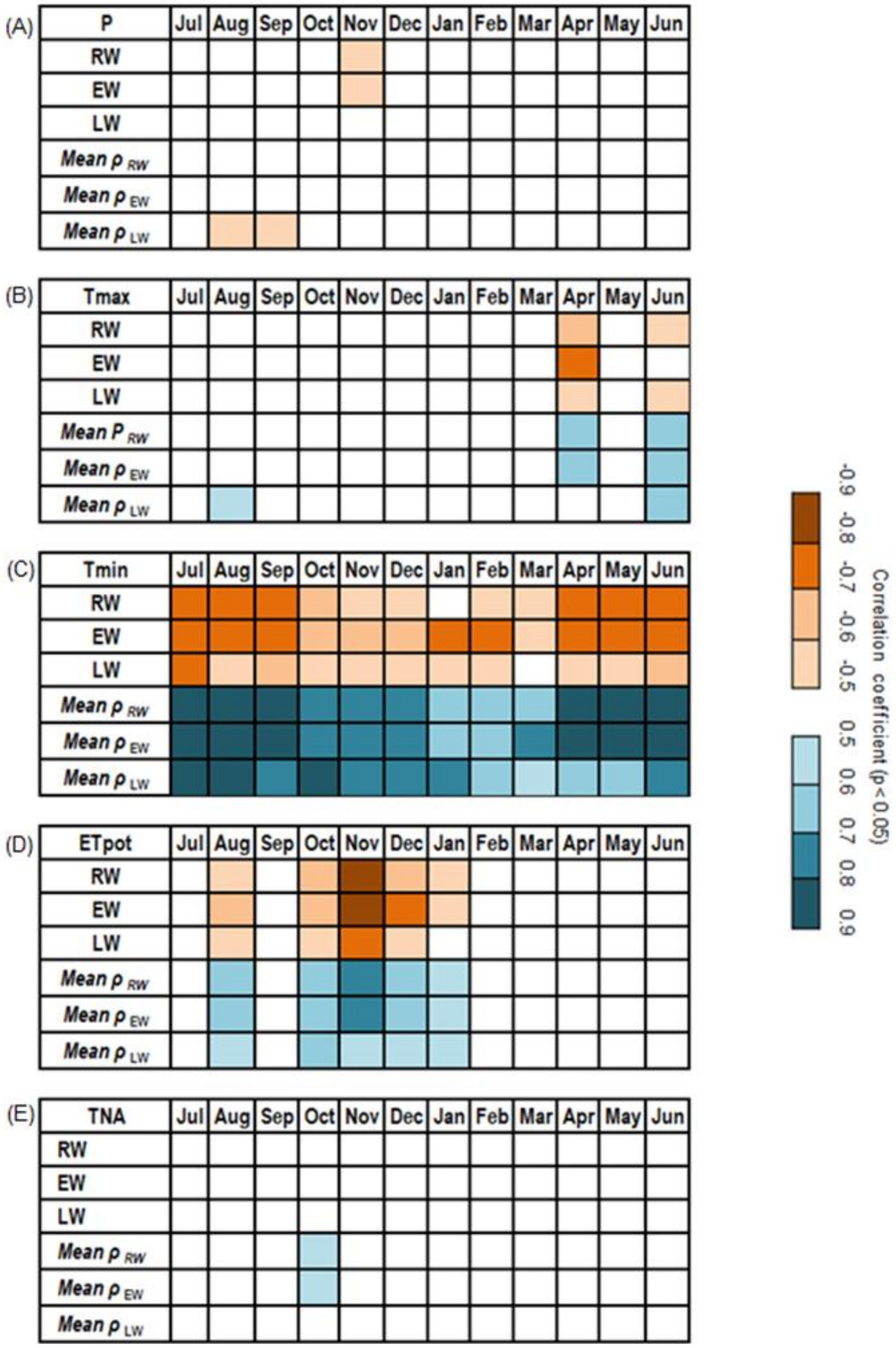

Fig. 5 Correlation (Pearson coefficient) values between ring width (RW), earlywood (EW), latewood (LW) chronologies, mean ring width wood density (ρ_{RW}), earlywood (ρ_{EW}) and latewood (ρ_{LW}) density with monthly climate data: A) precipitation (P), B) maximum temperature (T_{max}), C) minimum temperature (T_{min}), D) potential evapotranspiration (ET_{pot}), and E) tropical North Atlantic SST anomalies (TNA), during the period ranging from July 2000 to June 2017.

The RW, EW and LW chronologies were negatively correlated with maximum temperature (T_{max}) during April, already at the beginning of the aquatic phase and showed a weak correlation in June around the maximum water level, when tree ring formation already finished (Schöngart et al. 2002). The wood density parameters presented for the same month positive correlation with T_{max} (except for ρ_{LW} showing significant correlation with T_{max} of August and not April) (Fig. 5B). The strongest correlations were found with T_{min} (Fig. 5C) which seems to have strong influence on tree growth of *N. amazonum*. Significant correlations were observed for all months, with exception of January (RW) and March (LW). The correlations were stronger during the months of the aquatic phase (April to September) reaching negative correlation of up to –0.8 (p<0.01) for RW, EW, LW and positive correlations of even up to 0.9 (p<0.01) for ρ_{RW}, ρ_{EW} and ρ_{LW}. The EW chronology also showed high correlations with T_{min} of January and February.

All wood parameters correlated with potential evapotranspiration (ET_{pot}) (Fig. 5D), again, negative for the tree ring parameters and positive for wood density parameters. Correlations (p<0.05) comprised the months from August to January with a gap in September at the beginning of the terrestrial phase and showed the highest correlation in November during the occurrence of the minimum water level. The period of October, November, and December (onset of the rainy season during terrestrial phase) revealed the strongest correlations between ET_{pot} and tree-ring parameters (RW, EW) and the corresponding wood density parameters (ρ_{RW}, ρ_{EW}). No correlation was observed between the six wood parameters and *CWD*. The correlations among wood parameters and large-scale climate drivers from the surrounding tropical ocean sectors (ONI, TNA, TSA and AMM), showed only weak positive relationships (p<0.05) between TNA-SST anomalies of October and ρ_{RW} and ρ_{EW} (Fig. 5E).

Spatial correlation of 0.5° gridded T_{min} (CRU TS 4.04) with RW and ρ_{RW} for three-month averages spanning the dry season (July-September), transition period (October-December) and rainy season (January-March) showed congruent patterns for both wood parameters, however, with opposite signals (negative for RW and positive for ρ_{RW}) (Fig. 6). For the dry season both wood parameters indicated large-scale correlations (p<0.05) covering most of the

Amazon but also NW-South America and NE and SE-Brazil. For the transition period between dry and rainy season correlations were almost absent and appeared again for the rainy season covering mainly the central and eastern part of the Amazon basin.

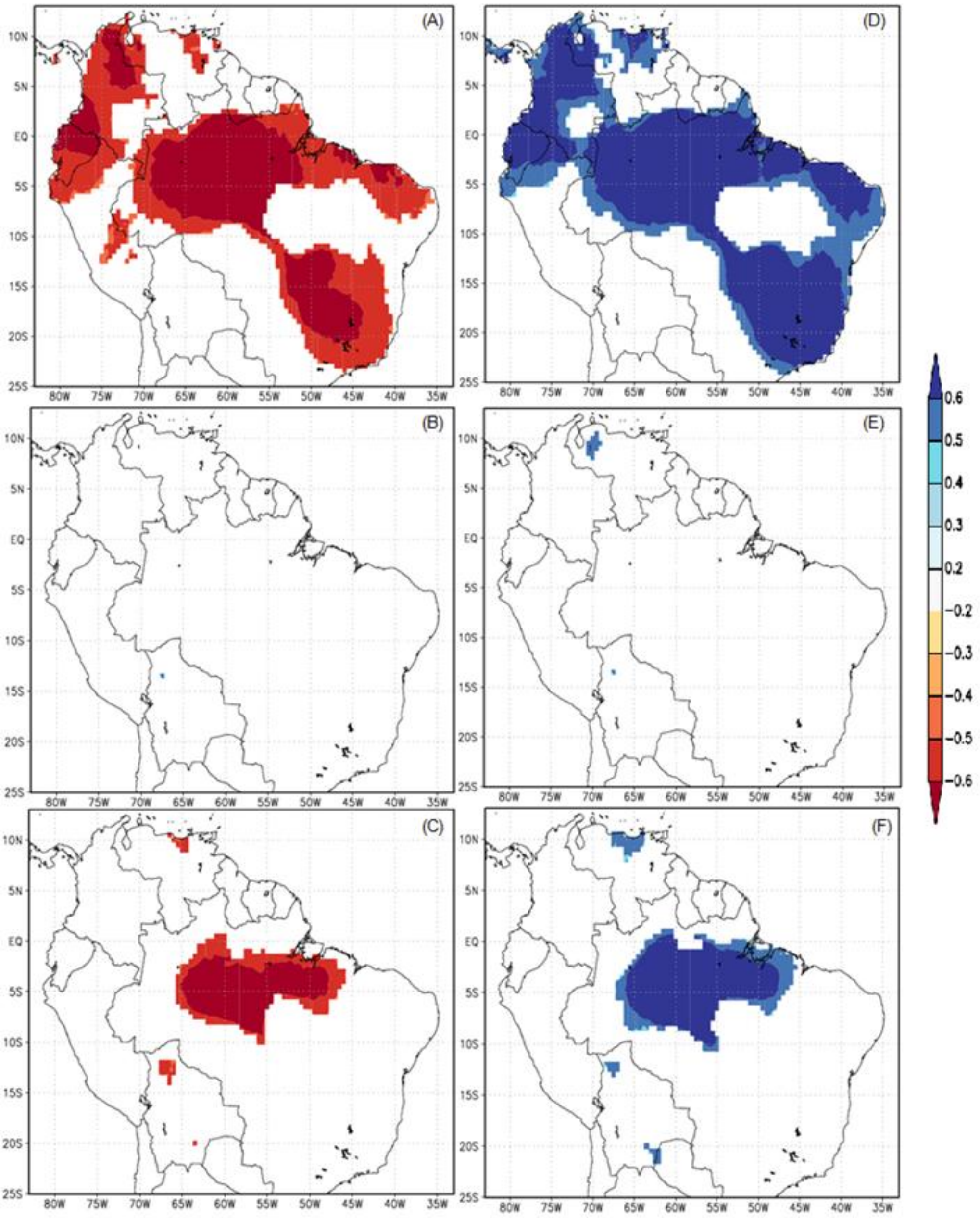

Fig. 6 Spatial correlation pattern (*p*<0.05) computed by the KNMI-Climate Explorer between the ring-width chronology (panels A-C) and mean ring wood density (panels D-F) with CRU TS 4.04 0.5° gridded minimum temperature (T_{min}) for the dry season (July-September, panels A and D), the transition period from the dry to the rainy season (October-December, panels B and E) and the rainy season (January-March, panels C and F) from 2001 to 2017.

DISCUSSION

Nectandra amazonum forms distinct annual growth rings (Schöngart et al. 2002; Worbes 1986), as many other Lauraceae tree species occurring in tropical (Schöngart et al. 2017) and tropical-subtropical regions of the Coastal Atlantic rainforests (Mata Atlântica) in Brazil (Alves and Angyolossy-Alfonso 2000; Barros et al. 2006; Granato-Souza et al. 2017; Spathelf et al. 2010). However, in this study it was not possible to develop a reliable tree-ring chronology for *N. amazonum* based on macroscopic analyses of the earlywood/latewood patterns, due to the high frequency of false tree rings occurrence, visible as intra-annual wood density variation, typical for tropical trees (Brienen et al. 2016; Worbes 2002). An improved examination of growth rings in the wood, especially when these structures are hard to distinguish, like in tropical trees, is autofluorescence (Godoy-Veiga et al. 2019), intra-annual stable isotope patterns (e.g., Evans and Schrag 2004; Ohashi et al. 2009; Pons and Helle 2011; Verheyden et al. 2004,), intra-annual variation in wood density highlighted by X-ray (e.g., Nepveu 1976; Vetter 1995) or high-frequency (HF) densitometry (e.g., Schnackenburg et al. 2008). Tree species from the Lauraceae family have generally tree rings defined by intra-annual wood density variations (earlywood and latewood pattern) (Fontana et al. 2019; Reis-Avila and Oliveira 2017; Worbes 1986) with high potential for densitometry analysis. Hansen (2004) demonstrated for some Lauraceae tree species (*N. megapotamica* and *Ocotea pulchella*) from the subtropical southern Brazilian region promising results applying HF-densitometry, reflecting well the intra-annual wood density variations. The application of densitometry was essential in this study to define the ring boundaries by the sharp contrast between ρ_{max} of the latewood and ρ_{min} of the earlywood of the subsequent tree ring (Fig. 4). The majority of intra-annual wood density variation was eliminated by the wood density profile, as false tree-rings are reflected by gradual changes in the intra-annual wood density spectrum (e.g., Pagotto et al. 2017). This technique improved the individual series dating and allowed the construction of a tree ring chronology with a robust sample size including more than 80% of the sampled trees, meeting the statistical requirements for climate-growth analyses (Wigley et al. 1984).

Although considered a valuable technique widely applied in studies of temperate and boreal climates (e.g., Helama et al. 2012; Klusek et al. 2015; Schweingruber et al. 1978; Wang et al. 2001), densitometry has found so far limited application in the tropics. Most studies in tropical regions applied densitometry with the aim to detect indistinct ring boundaries by the intra-annual wood density profiles (e.g., Lisi et al. 2008; Pagotto et al. 2017). X-ray densitometry has been successfully applied for the African tree species *Terminalia ivorensis* (Combretaceae) demonstrating a good congruence between tree rings and wood density patterns (Nepveu 1976). However, it was not possible to match interannual wood density variations with visible tree rings from the African species *Aucoumea klaineana* (Burseraceae) (Mariaux 1967) or *Scleronema micranthum* (Malvaceae) in Central Amazonian *terra-firme* (Lisi et al. 2008). Over time methods of densitometry improved, developing more sophisticated X-ray densitometry techniques (Tomazello Filho et al. 2008) and high-frequency densitometry (Schinker et al. 2003) improving the application of this method for tropical tree species.

However, only a few studies in the tropics have achieved successful results in relating wood density profiles to climate variation. Worbes et al. (1995) have built chronologies of maximum wood densities from *Macrolobium acaciifolium* and *Swartzia polyphylla* (both Fabaceae) from the Central Amazonian floodplains and reported on a positive relation between the duration of the terrestrial phase on wood density variations. Another study performed with *Rhizophora mangle* (Rhizophoraceae) in mangroves of northeast Colombia, revealed a negative correlation between minimum wood densities and rainfall (Ramírez Correa et al. 2010). One reason for the limited application of densitometry in tropical tree species is related to the wood anatomical patterns that define the annual ring. Tree species with tree rings delimited by fine marginal parenchyma bands or alternating fibre and parenchyma tissues appear less promising for densitometry analysis (Eshete and Ståhl 1999; Lisi et al. 2008; Vetter 1995). On the other hand, tree species that present tree rings with intra-annual density variations, like conifer species (*Araucaria angustifolia*, *Prumnopitys montana*), Lauraceae (*N. amazonum*, *N. megapotamica*, *Ocotea pulchella*) and others (Worbes 2002) possibly have more potential for densitometry (Hansen 2004; Lisi et al. 2008; Schnackenburg et al. 2008). In this sense, our study confirms the potential of applying densitometry analysis to assist the construction of chronologies in tropical trees. Densitometry additionally provides a variety of wood density parameters (ρ_{RW}, ρ_{EW}, ρ_{LW}, ρ_{min}, ρ_{max}) (Fig. 3), which can be used to build chronologies of specific wood features and proxies (e.g., Ferreira and Tomazello Filho 2009; Klusek et al. 2015). This opens new insights into several functional traits, which are important to understand the functional ecology of tropical tree species and dynamical processes of ecosystems, both natural and anthropogenically driven (e.g., Seidl et al. 2017). Although the majority of tree-ring data sets are based upon ring width, the measurements of wood density at annual or even higher resolution (i.e., microdensitometry) can provide additional knowledge on climate-growth relationships, paleoclimatology, tree physiology and ecophysiological processes, especially those related to the hydrological cycle and carbon dynamics (Sullivan et al. 2020).

Despite the construction of only a short RW chronology, it was robust enough to provide an exactly dated timeseries for EW and LW and the corresponding wood density parameters (ρ_{RW}, ρ_{EW} and ρ_{LW}). This is, to the best of our knowledge, the first time that EW and LW parameters have been provided for a tropical angiosperm species. However, since *N. amazonum* hardly achieves ages above 30 yrs (Schöngart 2003; Worbes et al. 1992) the produced chronologies were short, which limits to some degree the extrapolation of the obtained results. Only the EW chronology presented robust statistical parameters, while the LW chronology did not achieved the statistic requirements presenting a high sensitivity (Table 1) which might be the reason for weak correlations with the tested climate and hydrological data (Fig. 5). The wood density parameters achieved higher correlations with T_{min} as the corresponding ring-width parameters (Fig. 5C). Ring-width parameters showed a strong negative correlation with its wood density counterparts (Table S2). Across species, wood density is positively associated with survival and lifespan, but mostly negatively associated with diameter growth rates (Poorter et al. 2010; Schöngart et al. 2010; Siefert et al. 2015), explaining the opposite trend of ring width (RW, EW, LW) and wood density parameters (ρ_{RW}, ρ_{EW}, ρ_{LW}). The strong negative correlation between ring-width and wood density parameters might also be caused by strong ontogenetic effects, as *N. amazonum* presents short lifespans and high diameter increment rates that rapidly decline with increasing tree age (Schöngart et al. 2010).

Annual tree-ring formation in *N. amazonum* is triggered by the anoxic conditions induced by the annual flood pulse (Worbes 1997) and the species grows mainly during the terrestrial phase (Schöngart et al. 2002). For this reason, we expected strong relationships of ring width and wood density parameters (Schöngart et al. 2004, 2005; Worbes et al. 1995) with hydrological variables (AP, TP, FL, DL), especially considering the differences between EW and LW and the wood density counterparts. However, no correlation was found, which also has been observed by Schöngart et al. (2002), who related monthly diameter increment rates of *N. amazonum* to monthly water levels for a period of 26 months, indicating no significant correlation between tree growth and inundation. However, the authors observed weak, but still significant correlations between monthly diameter increment and precipitation. On the interannual scale weak correlations with monthly precipitation were observed only for some months during dry season.

Our postulated hypothesis that the intensification of the hydrological cycle affects tree growth of *N. amazonum* was not corroborated. To test this hypothesis, there is probably no better site in the Amazon region than the Central Amazonian floodplains, where daily water-level records are available for more than 100 years, evidencing significant changes in the hydrological regime resulting in an increase of the flood amplitude by 1.5 m during the last 30 years compared to the period 1903–1990 (Schöngart and Junk 2020).The intensification of the hydrological cycle is mainly driven by large-scale climate anomalies originating from a warming tropical Atlantic and simultaneously cooling equatorial Pacific during the last 2–3 decades (Barichivich et al. 2018). Large-scale SST anomalies from these oceanographic regions influence rainfall regimes and hydrological cycles across the Amazon basin with a high spatiotemporal variability (Aragão et al. 2018; Gloor et al. 2015; Marengo and Espinoza 2016; Marengo et al. 2012; Yoon and Zeng 2010), and were detected in the tree growth of many tree species (e.g., Brienen et al. 2012, Granato-

Souza et al. 2020; Schöngart et al. 2004, 2005). However, as the analysed six wood parameters of *N. amazonum* are not sensitive to the precipitation regime and hydrological cycle, it is not surprising that no relations with SST anomalies are observed (ONI, AMM, TNA, TSA) (except of a weak correlation between SST of the TNA of October with ρ_{RW} and ρ_{EW}).

Especially the period from October to December (Fig. 5D) corresponding to the low-water period and the transition from the dry to the rainy season (Fig. 2) seems to be critical for tree growth of *N. amazonum* with ring width responding sensitively and negatively (positively with ρ) to ET_{pot}. This time of the year corresponds to the low-water period and the transition from the dry to the rainy season (Fig. 2) and is critical for the tree growth of *N. amazonum*. In years of a shortened aquatic phase after El Niño occurrence (Schöngart and Junk 2007) and a delayed onset of rainfall leading to enhanced maximum temperatures, ET_{pot} might impact growth performance of *N. amazonum*. Photosynthetic rates in these months are low, even in comparison to those measured during the aquatic phase (Parolin 1997; Piedade et al. 2000). Trees of *N. amazonum* often present a small, second leaf exchange during this period (Schöngart et al. 2002). In consequence monthly diameter increments are often reduced in this period (Fig. S2) and possibly lead to the frequently observed formation of false tree rings in form of intra-annual wood density variation. The variation of ρ during EW formation, turns EW more sensitive against ET_{pot} compared to RW (Fig. 5D). Horna et al. (2010) observe a linear increase in xylem sap flux (Js) with increasing vapour pressure deficit (VPD) suggesting no stomata control. Periods of water deficit result in reduced CO_2 assimilation, a second leaf exchange, reduced diameter growth and frequent formation of false tree rings, which impeded the development of a tree-ring chronology based on macroscopic wood anatomy.

Our results show further a strong influence of T_{min} throughout the year, especially during the aquatic phase. Although several studies carried out in tropical forests have shown similar results (Anderegg et al. 2015; Ballantyne et al. 2017; Clark et al. 2003; Fontana et al. 2019; Sullivan et al. 2020), this was no expected for a tree growing in the Amazon *várzea* floodplain. Minimum temperature is associated with night-time temperatures. Clark et al. (2010)

found that an increase of 1–2°C in night-time temperatures severely reduced radial growth in six species in Costa Rica, due to a rise in stem respiration. Rahman et al. (2018) also showed that strong negative correlation between RW and minimum temperature indicated respiration-related growth reduction during the growing season. The minimum temperature of our study region is 24.3°C (SD ± 0.3) during the period 2000–2017 showing almost no seasonal variation (Fig. 2). However, these data refer to non-flooded sites which have stable night-time temperatures throughout the year (Góes Ribeiro 1976). In floodplains, however, minimum temperatures at night can be up to 4°C higher during the aquatic phase compared to the terrestrial phase as the warm water acts as a buffer (Irmler 1986). It is likely, that the higher night-time temperature during the aquatic phase increases stem respiration leading to reduced diameter growth of *N. amazonum* (Anderegg et al. 2015; Ballantyne et al. 2017; Clark et al. 2003) and increased wood density particularly at the beginning and the ending of the growing season. Further, it is notable that minimum annual temperature in the Manaus region increased by more than 0.3°C since 1980 with reference to the long-term period (1910–1979) (Schöngart and Junk 2020), especially during the last decade. The increased frequency and magnitude of floods during this period (2009, 2012–2015) (Barichivich et al. 2018) might have increased night-time temperatures even more during the prolonged aquatic phase and extensive flooded areas.

Overall, our results indicate that tree growth and variation of the analysed wood parameters of *N. amazonum* are mainly triggered by T_{min}, especially during the aquatic phase and ET_{pot}, mainly during the low-water period (transition from dry to rainy season). This has strong influence on respiration (T_{min}) and photosynthesis (ET_{pot}) affecting tree growth. The species is well adapted to the regular occurring anoxic conditions through long-term flooding. It maintains throughout the year a photochemical efficient canopy formed by leaves with comparatively small leaf area, but high specific leaf mass (Parolin 1997, 2002) with almost constant stomatal conductance (Parolin 1997) and no control of xylem sap flux (Horna et al. 2010). This allows the species to maintain photosynthesis active throughout the year, even under unfavourable conditions (Parolin et al. 2001; Piedade et al. 2000). The anoxic conditions during flooding, however, lead to a reduction of cambial activity which coincides with leaf flush and flowering (Schöngart et al. 2002). Compared to other floodplain tree species in previous studies (Schöngart et al. 2002, 2004, 2005; Worbes et al. 1995), *N. amazonum* presents different climate-growth relationships which are not related to the hydrological regime and associated oceanic forcing. The species seems to be resilient to flood-pulse induced disturbances which have been recently observed in the Uatumã River of the Central Amazon region. The implementation of the hydroelectric power plant Balbina in the Uatumã River (1983–1987) caused in the floodplains downstream of the Balbina dam massive hydrological disturbances (Assahira et al. 2017) which seem to have favoured the establishment of this species in the affected areas during the construction and operation of the Balbina dam (Neves et al. 2019; Targhetta et al. 2015). Future climate scenarios of increased temperatures and severe dry seasons as already observed in the southern Amazon basin (Marengo et al. 2018) might impact the tree species if this is coupled to changes in the hydrological regime towards drier conditions.

CONCLUSIONS

Our findings indicate that tree growth of *N. amazonum* responds sensitively to variations in potential evapotranspiration and minimum temperature but not to the flood pulse. This is contrary to earlier studies which have showed that the flood pulse is the main trigger of tree growth of many species in Central Amazonian floodplains. Congruent to our findings, many Lauraceae tree species in the Neotropics present seasonal growth pattern related to seasonal air temperature at high elevation sites decreasing growth rates with enhanced temperature and water deficit (Reis-Avila and Oliveira 2017). Wittmann (2012) postulated the hypothesis that the high competitveness of flood-tolerant species is linked to functional characteristics which not necessarily had to be developed in the flooded environment. Therefore species with rare occurrence in non-flooded environments, such as *N. amazonum*, often reach high abundances and dominaces in the floodplains. Especially *várzea* floodplains, representing a new and dynamic landscape element cutting the oligotrohic Amazon craton by the development of the water drainage system to the east starting 9.4 million years ago, offered for many tree species new habitats for tree species colonization (Hoorn et al. 2017). The most competitive tree species in the dynamic *várzea* are pioneers with short lifespans, high growth rates and other functional characteristics which favour their fitness (Wittmann 2012). This suggests that *N. amazonum* probably colonized the *várzea* floodplains originating from other environments with a stronger seasonality of temperature such as the Andean region or higher latitudes in the Southern Hemisphere (Fig. S1). This is supported by the maps of spatial correlations of RW and ρ_{RW} with T_{min} for the period July-September (Fig. 6) with a wide geographic coverage including regions of higher latitudes and altitudes, such as the Andes and the Coastal Atlantic rainforests (*Mata Atlântica*). Conserving the growth responses to potential evapotranspiration and minimum temperature, turns *N. amazonum* also more resilient to disturbances of the hydrological cycle compared to those tree species showing an intrinsic relationship with the flood pulse. These are important findings in the background of ongoing climate and land-use changes in the Amazon floodplains such as the intensification of the hydrological cycle or disturbances of the flood pulse by the implementation of several dozen hydropower dams (Assahira et al. 2017; Resende et al. 2020).

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SÍNTESE

Neste estudo foi possível construir uma cronologia exatamente datada por meio da densitometria de raio-X que permitiu a diferenciação da largura do anel de crescimento em lenho inicial e tardio, assim como obter os valores respectivos de densidade da madeira. Estes parâmetros do lenho foram correlacionados com variáveis climáticas (regionais e de larga escala) e hidrológicas no período de 2000-2017. Contrário às hipóteses formuladas, não foi observada uma relação entre os parâmetros do lenho e a variação do regime hidrológico. Foram observadas relações entre a evapotranspiração potencial e a temperaturas mínimas mensais que influenciaram o crescimento da espécie arbórea *Nectandra amazonum* durante o período de transição da estação seca para a estação chuvosa que corresponde ao período de águas baixas (evapotranspiração potencial) e também durante a fase aquática (temperaturas mínimas). Os resultados encontrados sugerem que processos fisiológicos, como fotossíntese e respiração, são fortemente associados aos fatores climáticos influenciando o crescimento do lenho da espécie estudada. *Nectandra amazonum* é uma espécie perenifólia que apresenta adaptações sofisticadas ao regime de inundação permitindo a manutenção dos processos fisiológicos essenciais durante todo o ano, como evidenciado por vários estudos ecofisiológicos. O estudo indica que a separação em lenho inicial e tardio, assim como a análise dos parâmetros de densidade da madeira além de apresentarem correlações mais fortes com o clima podem fornecer informações adicionais, permitindo um melhor entedimento sobre o comportamento da espécie.

Nectandra amazonum tem uma vida média de 44 anos, porém devido ao curto período analisado de 18 anos (2000-2017), as interpretações são limitadas. Considerando a forte influência do crescimento da espécie por processos ecofisiológicos, sugerimos estudos futuros com aplicação de análises de isótopos ($\delta^{18}O$ e $\delta^{13}O$) (Cintra et al. 2019) que têm o potencial de apresentar relações ainda mais fortes entre o crescimento e a variação do clima (Brienen et al. 2012). Um desafio promissor seria combinar vários parâmetros do lenho, como diferentes variáveis da largura do anel de crescimento (total, inicial e tardio), densidade da madeira (média, mínima e máxima) e elementos da anatomia (fibras, vasos, parênquima) criando um multiproxy para extrair o máximo de informação climática armazenada nos anéis de crescimento. Esse tipo de abordagem é de grande relevância para estudos de ecofisiologia e paleoclima na Amazônia que podem elucidar os impactos de eventos hidroclimáticos severos na região e os impactos das mudanças climáticas globais.

REFERENCES

Aleixo I, Norris D, Hemerik L, Barbosa A, Prata E, Costa F, Poorter L (2019) Amazonian rainforest tree mortality driven by climate and functional traits. Nat Clim Chang 9:384–388. https://doi.org/10.1038/s41558-019-0458-0

Alves ES, Angyolossy-Alfonso V (2000) Ecological trends in the wood anatomy of some Brazilian species, I: Growth rings and vessels. IAWA J 21:3–30. https://doi.org/10.1163/22941932-90000233

Anderegg WRL, Schwalm C, Biondi F, Camarero JJ, Koch G, Litvak M, Ogle K, Shaw JD, Shevliakova E, Williams AP, Wolf A, Ziaco E, Pacala S (2015) Pervasive drought legacies in forest ecosystems and their implications for carbon cycle models. Science 349:528–532. https://doi.org/10.1126/science.aab1833

Aragão LEOC, Malhi Y, Roman-Cuesta RM, Saatchi S, Anderson LO, Shimabukuro YE (2007) Spatial patterns and fire response of recent Amazonian droughts. Geophys Res Lett 34:L07701. https://doi.org/10.1029/2006GL028946

Aragão LEOC, Anderson LO, Fonseca MG, Rosan TM, Vedovato LB, Wagner FH, Silva CVJ, Silva Junior CHL, Arai E, Aguiar AP, Barlow J, Berenguer E, Deeter MN, Domingues LG, Gatti L, Gloor M, Malhi Y, Marengo JA, Miller JB, Philips OL, Saatchi S (2018) 21st Century drought-related fires counteract the decline of Amazon deforestation carbon emissions. Nat Commun 9:536. https://doi.org/10.1038/s41467-017-02771-y

Armstrong W, Drew MC (2002) Root growth and metabolism under oxygen deficiency. Plant roots: the hidden half, 3: 729-761.

Assahira C, Piedade MTF, Trumbore SE, Wittmann F, Cintra BBL, Batista ES, Resende AF, Schöngart J (2017) Tree mortality of a flood-adapted species in response of hydrographic changes caused by an Amazonian river dam. Forest Ecol Manag 396:113–123. https://doi.org/10.1016/j.foreco.2017.04.016

Ayres JMC (1993) As matas de várzea do Mamirauá: Médio Rio Solimões. Estudos Mamiraua, CNPq, Sociedade Civil de Mamirauá, Brasília.

Baker JCA, Gloor M, Spracklen DV, Arnold SR, Tindall JC, Clerici SJ, Leng MJ, Brienen, RJW (2016) What drives interannual variation in tree ring oxygen isotopes in the Amazon? Geophys Res Lett 43:11831–11840.

Ballantyne A, Smith W, Anderegg W, Kauppi P, Sarmiento J, Tans P, Shevliakova E, Pan Y, Poulter B, Anav A, Friedlingstein P, Houghton R, Running S (2017) Accelerating net terrestrial carbon uptake during the warming hiatus due to reduced respiration. Nat Clim Change 7:148–152. https://doi.org/10.1038/nclimate3204

Barichivich J, Gloor E, Peylin P, Brienen R, Schöngart J, Espinoza JC, Pattnayak KC (2018) Recent intensification of Amazon flooding extremes driven by strengthened Walker circulation. Sci Adv 4:2375–2548. https://doi.org/10.1126/sciadv.aat8785

Barros CF, Ferreira-Marcon ML, Callado CH, Lima HRP, Cunha M, Marquete O, Costa CG (2006) Tendências ecológicas na anatomia da madeira de espécie da comunidade arbórea da Reserva Biológica de Poço das Antas, Rio de Janeiro, Brasil. Rodriguésia 57(3):443–460. https://doi.org/10.2307/23498739

Batista ES, Schöngart J (2018) Dendroecology of *Macrolobium acaciifolium* (Fabaceae) in Central Amazonian floodplain forests. Acta Amazon 48:311–320. https://doi.org/10.1590/1809-4392201800302

Brando PM, Nepstad DC, Davidson EA, Trumbore SE, Ray D, Camargo P (2008) Drought effects on litterfall, wood production and belowground carbon cycling in an Amazon forest: results of a throughfall reduction experiment. Philos T R Soc B 363:1839–1848. https://doi.org/10.1098/rstb.2007.0019

Brienen RJW, Zuidema PA (2005) Relating tree growth rainfall in Bolivian rain forest: a test for six species using tree-ring analysis. Oecologia 146:1–12. https://doi.org/10.1007/s00442-005-0160-y

Brienen RJW, Helle G, Pons TL, Guyot J-L, Gloor E (2012) Oxygen isotopes in tree rings are a good proxy for Amazon precipitation and El Niño-Southern Oscillation variability. PNAS 109(42):16957–16962. https://doi.org/10.1073/pnas.1205977109

Brienen RJW, Schöngart J, Zuidema PA (2016) Tree rings in the tropics: insights into the ecology and climate sensitivity of tropical trees. In: Goldstein G, Santiago LS (eds) Tropical tree physiology: adaptations and responses in a changing environment. Springer International Publishing, pp 439–461.

Bunn A (2008) A dendrochronology program library in R (dplR). Dendrochronologia 26:115–124. https://doi.org/10.1016/j.dendro.2008.01.002

Cintra BBL, Gloor M, Boom A, Schöngart J, Locosselli GM, Brienen R (2019) Contrasting controls on tree ring isotope variation for Amazon floodplain and terra firme trees. Tree Physiol 39(5):845–860. https://doi.org/10.1093/treephys/tpz009

Clark DA, Piper SC, Keeling CD, Clark DB (2003) Tropical rain forest tree growth and atmospheric carbon dynamics linked to interannual temperature variation during 1984-2000. PNAS 100:5852–5857. https://doi.org/10.1073/pnas.0935903100

Clark DB, Clark DA, Oberbauer SF (2010) Annual wood production in a tropical rain forest in NE Costa Rica linked to climatic variation but not to increasing CO_2. Global Change Bio 16:747–759. https://doi.org/10.1111/j.1365-2486.2009.02004.x

Clevealand MK (1986) Climatic response of densitometric properties in semiarid site tree rings. Tree-Ring Bull 46:13-19.

Cook ER, Kairiukstis LA (1990) Methods of Dendrochronology: Applications in the Environmental Sciences. Springer Netherlands.

Crawford RMM, Braendle, R (1996) Oxygen deprivation stress in a changing environment. J Exp Bot 47(2):145-159.

De Simone O, Haase K, Müller E, Junk WJ, Gonsior GA, Schmidt W (2002) Impact of root morphology on metabolism and oxygen distribution in roots and rhizosphere from two Central Amazon floodplain tree species. Funct Plant Biol 29:1025–1035. https://doi.org/10.1071/PP01239

Dodd SR, Nancy KW (1988) Cyclophytic effects on wood structure in Pinus radiata D. Don. I. Densitometry and grain angle. Can J For Res 18:406–412. https://doi.org/10.1139/x88-060

Dünisch O, Montóia VR, Bauch J (2003) Dendroecological investigations on *Swietenia macrophylla* King and *Cedrela odorata* L. (Meliaceae) in the central Amazon. Trees 17:244–250. https://doi.org/10.1007/s00468-002-0230-2

Dutra R, Paulista C, Paulo S, Marengo JA (2006) On the Hydrological Cycle of the Amazon Basin: A historical review and current State-of-the-art. Centro de Previsão de Tempo e Estudos Climáticos do Instituto Nacional de Pesquisas Espaciais (CPTEC / INPE).

Erfanian A, Wang G, Fomenko L (2017) Unprecedented drought over tropical South America in 2016: Significantly under-predicted by tropical SST. Sci Rep 7:5811. https://doi.org/10.1038/s41598-017-05373-2

Eshete G, Stahl G (1999) Tree rings as indicator of growth periodicity of acacias in the Rift Valley of Ethiopia. Forest Ecol Manag 116:107–117. https://doi.org/10.1016/S0378-1127(98)00442-3

Espinoza JC, Ronchail J, Marengo JA, Segura H (2019) Contrasting North–South changes in Amazon wet-day and dry-day frequency and related atmospheric features (1981–2017) Clim Dyn 52:5413–5430. https://doi.org/10.1007/s00382-018-4462-2x

Evans MN, Schrag DP (2004) A stable isotope-based approach to tropical dendroclimatology. Geochim Cosmochim Acta 68:3295–3305. https://doi.org/10.1016/j.gca.2004.01.006

Ferreira ATB, Tomazello Filho M (2009) Caracterização dos anéis de crescimento de árvores de *Pinus caribaea* var. *hondurensis* Barr. et Golf. por densitometria de raios X. Sci For 37(83):287–298.

Foley JA, Botta A, Coe MT, Costa MH (2002) El Niño-Southern Oscillation and the climate, ecosystems and rivers of Amazonia. Global Biogeochem Cy 16:1132. https://doi.org/10.1029/2002GB001872

Fontana C, Santini-Junior L, Olmedo GM, Botosso PC, Tomazello-Filho M, Oliveira JM (2019) Assessment of the dendrochronological potential of Licaria bahiana Kurz, an endemic laurel of lowland Atlantic forests in Brazil. Acta Bot Bras 33:454–464. https://doi.org/10.1590/0102-33062019abb0028.

Furch K (1997) Chemistry of várzea and igapó soils and nutrient inventory of their floodplain forests. In: Junk WJ (ed) The Central Amazon Floodplain: Ecology of a Pulsing System. Ecological Studies, 126, Springer Verlag, Berlin, pp 47–68.

Furch K, Klinge H (1989) Chemical relationship between vegetation, soil and water in contrasting inundation areas of Amazonia. In: Proctor J (ed) Mineral nutrients in tropical forest and savanna ecosystems. Blackwell, Oxford, pp 189–204.

Gash JHC, Nobre CA (1997) Climatic effects of Amazonian deforestation: some results from ABRAÇOS. B Am Meteorol Soc 78(5):823-830.

Gloor M, Brienen RJW, Galbraith D, Feldpausch TR, Schöngart J, Guyot J-L, Espinoza JC, Lloyd J, Phillips OL (2013) Intensification of the Amazon hydrological cycle over the last two decades. Geophys Res Lett 40:1729–1733. https://doi.org/10.1002/grl.50377

Gloor M, Barichivich J, Ziv G, Brienen R, Schöngart J, Peylin P, Cintra BBL, Feldpausch T, Phillips O, Baker J (2015) Recent Amazon climate as background for possible ongoing and future changes of Amazon humid forests. Global Biogeochem Cy 29:1384–1399. https://doi.org/10.1002/2014GB005080

Godoy-Veiga M, Slotta F, Alecio PC, Ceccantini G, Buckeridge MS, Locosselli GM (2019) Improved tree-ring visualization using autofluorescence. Dendrochronologia 55:33–42. https://doi.org/10.1016/j.dendro.2019.03.003

Goes Ribeiro MN (1976) Aspectos climatológicos de Manaus. Acta Amazon 6(2):229–233.

Gouveia NA, Gherardi DFM, Aragão LEOC (2019) The role of the Amazon river plume on the intensification of the hydrological cycle. Geophys Res Lett 46:12221–12229. https://doi.org/10.1029/2019GL084302

Granato-Souza D, Adenesky-Filho E, Esemann-Quadros K (2017) Dendrochronology and climatic signals in the wood of *Nectandra oppositifolia* from a dense rain forest in southern Brazil. J For Res 30:545–553. https://doi.org/10.1007/s11676-018-0687-5

Granato-Souza D, Stahle DW, Torbenson MCA, Howard IM, Barbosa AMC, Feng S, Fernandes K, Schöngart J (2020) Multidecadal Changes in Wet Season Precipitation Totals Over the Eastern Amazon. Geophys Res Lett 47(8):e2020GL087478. https://doi.org/10.1029/2020GL087478

Hansen N (2004) Zur retrospektiven Lokalisation von Zuwachszonen in subtropischen Laubhölzern mittels der Methode der Hochfrequenz-Densitometrie. Freiburger forstliche Forschung, Schriftenreihe 27.

Helama S, Bégin Y, Vartiainen M, Peltola H, Kolström T, Meriläinen J (2012) Quantifications of dendrochronological information from contrasting microdensitometric measuring circumstances of experimental wood samples. Appl Radiat Isot 70(6):1014–1023. https://doi.org/10.1016/j.apradiso.2012.03.025

Hoorn C, Bogotá GR, Romero-Baez M, Lammertsma EI, Flantua SGA, Dantas EL, Dino R, Carmo DA, Chemale Jr F (2017) The Amazon at sea: Onset and stages of the Amazon River froma marine record, with special reference to Neogene plant turnover in the drainage basin. Glob Planet Change 153:51–65. https://doi.org/10.1016/j.gloplacha.2017.02.005

Horna V (2001) Carbon release from woody parts of trees of a seasonally flooded Amazon forest near Manaus, Brazil. Unpublished Ph.D. thesis, Department of Plant Ecology, University of Bayreuth.

Horna V, Zimmermann R, Müller E, Parolin P (2010) Sap Flow and Stem Respiration. In: Junk WJ, Piedade MTF, Wittmann F, Schöngart J, Parolin P (eds) Central

Amazonian Floodplain Forests: Ecophysiology, Biodiversity and Sustainable Management. Ecological Studies, vol 210, Springer Verlag, Dordrecht-Heidelberg-London-New York, pp 223–242.

Irion G, Junk W, Mello J N (1997) The large Central Amazonian River floodplains near Manaus: geological, climatological, hydrological and geomorphological aspects. In: The Central Amazon Floodplain, Springer, Berlin, pp 23–46.

Irmler U (1986) Temperature dependent generation cycle for the cicindelid beetle *Pentacomia egregia* Chaud. (Coleoptera, Carabidae, Cicindelidae) of the Amazon valley. Amazoniana 9(3):431–439.

Jackson MB (1990) Hormones and developmental change in plants subjected to submergence or soil waterlogging. Aquat Bot 38(1): 49-72.

Jackson MB, Armstrong W (1999) Formation of aerenchyma and the processes of plant ventilation in relation to soil flooding and submergence. Plant Biol 1(3): 274-287.

Junk WJ (1989) Flood tolerance and tree distribution in Central Amazonian floodplains. In: Nielsen L, Nielsen IC and Baisley H (eds). Tropical forests: botanical dynamics, speciation and diversity, Academic Press, London, pp 47–64.

Junk WJ, Bayley PB, Sparks RE (1989) The Flood pulse concept in river-floodplain systems. In. Dodge D.P. (ed) Proceedings of the International Large River Symposium. Can Spec Publ of Fish and Aquat Sci 106, pp 110–127.

Junk WJ, Piedade MTF, Schöngart J, Cohn-Haft M, Adeney JM, Wittmann F (2011) A classification of major naturally-occurring Amazonian lowland wetlands. Wetlands 31:623–640. https://doi.org/10.1007/s13157-011-0190-7

Klusek M, Melvin TM, Grabner M (2015) Multi-century long density chronologyof living and sub-fossil trees from Lake Schwarzensee, Austria. Dendrochronologia 33:42–53. https://doi.org/10.1016/j.dendro.2014.11.004

Laurance WF, Camargo JLC, Fearnside PM, Lovejoy TE, Williamson GB, Mesquita RCG, Meyer CFJ, Bobrowiec PED, Laurance SGW (2018) An Amazonian rainforest and its fragments as a laboratory of global change. Biol Rev 93, 223–247.

Limberger L, Silva MES (2016) Precipitação na bacia amazônica e sua associação à variabilidade da temperatura da superfície dos oceanos Pacífico e Atlântico: uma revisão. Geousp Espaço e Tempo 20(3): 657-675. ISSN 2179-0892.

Lisi CS, Tomazello Filho M, Botosso PC, Roig FA, Maria VRB, Ferreira-Fedele L, Voigt ARA (2008) Tree-ring formation, radial increment periodicity, and phenology of tree species from a seasonal semi-deciduous forest in southeast Brazil. IAWA J 29:189–207. https://doi.org/10.1163/22941932-90000179.

Malhi Y, Roberts JT, Betts RA, Killeen TJ, Li W, Nobre CA (2008) Climate change, Deforestation, and fate of the Amazon. Science 319:169–172.

Marengo JA, Espinoza JC (2016) Extreme seasonal droughts and floods in Amazonia: causes, trends and impacts. Intern J Climatol 36:1033–1050. https://doi.org/10.1002/joc.4420

Marengo JA, Nobre CA, Tomasella J, Cardoso MF, Oyama MD(2008) Hydro-climatic and ecological behaviour of the drought of Amazonia in 2005. Philos T R Soc B 363: 1773-1778.

Marengo JA, Tomasella J, Soares WR, Alves LM, Nobre CA (2012): Extreme climatic events in the Amazon basin – climatological and hydrological context of recent floods. Theor Appl Climatol 107:73–85. https://doi.org/10.1007/s00704-011-0465-1

Marengo JA, Souza Jr CA, Thonicke K, Burton C, Halladay K, Betts RA, Alves LM, Soares WR (2018) Changes in climate and land use over the Amazon Region: current and future variability and trends. Front Earth Sci 6:228. https://doi.org/10.3389/feart.2018.00228

Mariaux A (1967) Les cernes dans les bois tropicaux africains, nature et périodicité. Bois For Trops 113:3–14.

Mendivelso HA, Camarero JJ, Obregón OR, Gutiérrez E, Toledo M (2013) Differential growth responses to water balance of coexisting deciduous tree species are linked to wood density in a Bolivian tropical dry forest. PLoS One 8:e73855.

Nepveu G (1976) Croissance et qualité du bois de Framiré. Evolution de la largeur de cerne et composantes densitométriques en function de l’âge. Bois For Trops 165:39–58.

Neves JRD, Piedade MTF, Resende AF, Feitosa YO, Schöngart J (2019) Impact of climatic and hydrological disturbances on black-water floodplain forests in Central Amazonia. Biotropica 51:484–489. https://doi.org/10.1111/btp.12667

Ohashi S, Okada N, Nobuchi T, Siripatanadilok S, Veenin T (2009) Detecting invisible growth rings of trees in seasonally dry forests in Thailand: isotopic and wood anatomical approaches. Trees 23:813–822. https://doi.org/10.1007/s00468-009-0322-3

Pagotto MA, DeSoto L, Carvalho A, Nabais C, Tomazello Filho M, Ribeiro A, Lisi CS (2017) Evaluation of X-ray densitometry to identify tree-ring boundaries oftwo deciduous species from semi-arid forests in Brazil. Dendrochronologia 42:94–103. http://dx.doi.org/10.1016/j.dendro.2017.01.007

Parolin P (1997) Auswirkungen periodischer Vernässung und Überflutung auf Phänologie, Photosynthese und Blattphysiologie von Baumarten unterschiedlicher Wachstumsstrategie in zentralamazonischen Überschwemmungsgebieten. Ph.D. thesis, University of Hamburg.

Parolin P (2002) Seasonal changes of specific leaf mass and leaf size in trees of Amazonian floodplains. Phyton 42:169–185.

Parolin P (2009) Submerged in darkness: adaptations to prolonged submergence by woody species of the Amazonian floodplains. Annal Bot 103:359–376. https://doi.org/10.1093/aob/mcn216

Parolin P, Junk WJ, Piedade MTF (2001) Gas exchange of six tree species from Central Amazonian floodplains. Trop Ecol 42(1):15–24.

Parolin P, Armbrüster N, Junk WJ (2002) Seasonal changes of leaf nitrogen content in trees of Amazonian floodplains. Acta Amazon 32(2):231–240.

Parolin P, De Simone O, Haase K, Waldhoff D, Rottenberger S, Kuhn U, Kesselmeier J, Schmidt W, Piedade MTF, Junk W (2004) Central Amazon floodplain forests: tree survival in a pulsing system. Bot Rev 70:357–380.

Parolin P, Wittmann F, Schöngart J (2010) Tree phenology in Amazonian floodplain forests. In: Junk WJ, Piedade MTF, Wittmann F, Schöngart J, Parolin P (eds) Central Amazonian Floodplain Forests: Ecophysiology, Biodiversity and Sustainable Management. Ecological Studies, vol 210, Springer Verlag, Dordrecht-Heidelberg-London-New York, pp 105–126.

Piedade MTF, Junk WJ, Parolin P (2000) The flood pulse and photosynthetic response of trees in white water floodplain (várzea) of the Central Amazon, Brazil. Verh Internt Verein Limnol 27(4):1734–1739.

Piedade MTF, Ferreira CS, Oliveira Wittmann A, Buckeride M, Parolin P (2010) Biochemistry of Amazonian floodplain trees. In: Junk WJ, Piedade MTF, Wittmann F, Schöngart J, Parolin P (eds) Central Amazonian Floodplain Forests: Ecophysiology, Biodiversity and Sustainable Management. Ecological Studies, vol 210, Springer Verlag, Dordrecht-Heidelberg-London-New York, pp 127–140.

Pons TL, Helle G (2011) Identification of anatomically non-distinct annual rings in tropical trees using stable isotopes. Trees 25:83–93. https://doi.org/10.1007/s00468-010-0527-5

Poorter L, McDonald I, Alarcón A, Fichtler E, Licona J-C, Peña-Claros M, Sterck F, Villegas Z, Saas-Klaasen U (2010) The importance of wood traits and hydraulic conductance for the performance and life history strategies of 42 rain forest tree species. New Phytologist 185:481–492. https://doi.org/10.1111/j.1469-8137.2009.03092.x

Prance GT (1979) Notes on the vegetation of Amazonia. III. Terminology of Amazonian forest types subjected to inundation. Brittonia 31:26–38.

Rahman M, Islam M, Bräuning A (2018) Tree radial growth is projected to decline in South Asian moist forest trees under climate change. Global Planet Change 170:106–119. https://doi.org/10.1016/j.gloplacha.2018.08.008

Ramírez Correa JA, Grajales ECM, Escobar MB (2010) Anillos Anuales y Clima en *Rhizophora mangle* L. de la Bahía de Cispatá, Colombia. Rev Fac Nac Agron Medellín 63(2):5639–5650.

Reis-Avila G, Oliveira JM (2017) Lauraceae: A promising family for the advance of neotropical dendrochronology. Dendrochronologia 44:103–116. http://dx.doi.org/10.1016/j.dendro.2017.04.002

Resende AF, Piedade MTF, Feitosa YO, Andrade VHF, Trumbore SE, Durgante FM, Macedo MO, Schöngart J (2020) Flood-pulse disturbances as a threat for long-living Amazonian trees. New Phytolt 227. https://doi.org/10.1111/nph.16665

Richey JE, Mertes LA, Dunne T, Victoria RL, Forsberg BR, Tancredi AC, Oliveira E (1989) Sources and Routing of the Amazon river Flood wave. Global Biochem Cy 3(3): 191-204.

Sauter M (2013) Root responses to flooding.Curr Opin Plant Biol 16(3): 282-286.

Schinker M, Hansen N, Spiecker H (2003) High-frequency densitometry - a new method for the rapid evaluation of wood density variations. IAWA J 24(3):231–239. https://doi.org/10.1163/22941932-90001592

Schnackenburg P, Bräuning A, Helle G (2008) Detecting annual growth rhythms from high-frequency densitometry and carbon isotopes in tropical mountain rain forest trees in southern Ecuador. In: Elferts D, Brumelis G, Gärtner H, Helle G, Schleser G (eds) TRACE - Tree Rings in Archaeology, Climatology and Ecology, Vol 6: Proceedings of the Dendrosymposium 2007, Riga, Latvia. GFZ Potsdam, Scientific Technical Report STR 08/05, Potsdam, pp 96–99.

Schöngart J (2003) Dendrochronologische Untersuchungen in Überschwemmungs-wäldern der Várzea Zentralamazoniens. Göttinger Beiträge zur Land- und Forstwirtschaft in den Tropen und Subtropen 149, Erich Goltze Verlag, Göttingen.

Schöngart J, Junk WJ (2007) Forecasting the flood-pulse in Central Amazonia by ENSO-indices. J Hydrol 335: 124–132. https://doi.org/10.1016/j.jhydrol.2006.11.005

Schöngart J, Junk WJ (2020) Clima e hidrologia nas várzeas da Amazônia Central. In: Junk WJ, Piedade MTF, Wittmann F, Schöngart J (eds) Várzeas Amazônicas: Desafios para um Manejo Sustentável, Editora INPA, Manaus, pp 44-65.

Schöngart J, Piedade MTF, Ludwigshausen S, Horna V, Worbes M (2002) Phenology and stem-growth periodicity of tree species in Amazonian floodplain forests. J Trop Ecol 18:581–597. https://doi.org/10.1017/S0266467402002389

Schöngart J, Junk WJ, Piedade MTF, Ayres JM, Hüttermann A, Worbes M (2004) Teleconnection between tree growth in the Amazonian floodplains and the El Niño-Southern Oscillation effect. Glob Change Biol, 10:683–692. https://doi.org/10.1111/j.1529-8817.2003.00754.x

Schöngart J, Piedade MTF, Wittmann F, Junk WJ, Worbes M (2005) Wood growth patterns of *Macrolobium acaciifolium* (Benth.) Benth. (Fabaceae) in Amazonian black-water and white-water floodplain forests. Oecologia 145:454–461. https://doi.org/10.1007/s00442-005-0147-8

Schöngart J, Orthmann B, Hennenberg KJ, Porembski S, Worbes M (2006) Climate-growth relationships of tropical tree species in West Africa and their potential for climate reconstruction. Glob Change Biol 12:1139-1150.

Schöngart J, Wittmann F, Worbes M (2010) Biomass and NPP of Central Amazonian floodplain forests. In: Junk WJ, Piedade MTF, Wittmann F, Schöngart J, Parolin P (eds) Central Amazonian Floodplain Forests: Ecophysiology, Biodiversity and Sustainable Management. Ecological Studies, vol 210, Springer Verlag, Dordrecht-Heidelberg-London-New York, pp 347–388.

Schöngart, J, Gribel R, Ferreira da Fonseca-Junior S, Haugaasen T (2015) Age and growth patterns of Brazil Nut Trees (Bertholletia excelsa Bonpl.) in Amazonia, Brazil. Biotropica 47:550–558. https://doi.org/10.1111/btp.12243.

Schöngart J, Bräuning A, Barbosa ACMC, Lisi SG, Oliveira JM (2017) Dendroecological studies in the Neotropics: History, status and future challenges. In: Amoroso MM, Daniels LD, Baker PJ, Camarero JJ (eds) Dendroecology. Ecological Studies (Analysis and Synthesis), Vol. 231, Springer, Cham, pp 35–73.

Schweingruber FH, Bräker OU, Schär E (1978) X-ray densitometric results for subalpine conifers and their relationship to climate. In: Fletcher J (ed) Dendrochronology in Europe. Brit Archaeol Rep In 51:89–100.

Seidl R, Thom D, Kautz M, Martin-Benito D, Peltoniemi M, Vacchiano G, Wild J, Ascoli D, Petr M, Honkaniemi J, Lexer MJ, Trotsiuk V, Mairota P, Svoboda M, Fabrika M, Nagel TA, Reyer CPO (2017) Forest disturbances under climate change. Nature Clim Change 7:395–402. https://doi.org/10.1038/nclimate3303

Siefert A, Violle C, Chalmandrier L, Albert CH,Taudiere A, Fajardo A, Aarssen LW, Baraloto C, Carlucci MB, Cianciaruso MV, Dantas VL, Bello F, Duarte LDS, Fonseca CR, Freschet GT, Gaucherand S, Gross N, Hikosaka K, Jackson B, Jung V, Kamiyama C, Katabuchi M, Kembel SW, Kichenin E, Kraft NJB, Lagerström A, Le Bagousse-Pinguet Y, Li Y, Mason N, Messier J, Nakashizuka T, Overton JM, Peltzer DA, Pérez-Ramos IM, Pillar VD, Prentice HC, Richardson

S, Sasaki T, Schamp BS, Schöb C, Shipley B, Sundqvist M, Sykes MT, Vandewalle M, Wardle DA (2015) A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. Ecol Lett 18:1406–1419.

Silva Dias MAF, Rutledge S, Kabat P, Silva Dias PL, Nobre C, Fisch G, Dolman AJ , Zipser E , Garstang M, Manzi AO, Fuentes JD, Rocha HR, Marengo J, Plana-Fattori A, Sá ALDA, Alvalá RCS, Andreae MO, Artaxo P, Gielow R, Gatti L (2002) Cloud and rain processes in a biosphere-atmosphere interaction context in the Amazon region. J Geophys Res 107(D20): 8072.

Sioli H (1984) The Amazon. Limnology and landscape ecology of mighty tropical river and its basin. Dordrecht Pub. Junk. 800 p.

Sombroek WG (1984) Soils of the Amazon Region. In: Sioli H (ed) The Amazon, limnology and landscape ecology of a mighty tropical river and its basin. Dr. W. Junk Publishers, Dordrecht/Boston/ Lancaster, pp 521–536.

Spathelf P, Tomazello Filho M, Tonini H (2010) Dendroecological analysis of *Ocotea pulchella* and *Nectandra maegapotamica* on two sites near Santa Maria, Rio Grande do Sul (Brazil). Floresta 40(4):777–788.

Speer, J (2010) Fundamentals of Tree Ring Research. The University of Arisona Press, Tucson.

Stahle DW, Cleaveland MK, Hehr JG (1988) North Carolina climate changes reconstructed from tree rings: A.D. 372 to 1985. Science 240: 1517–1519.

Sullivan MJP, Lewis SL, Affum-Baffoe K, Castilho C, Costa F, Sanchez AC, Ewango CEN, Hubau W, Marimon B, Monteagudo-Mendoza A, Qie L, Sonké B, Martinez RV, Baker TR, Brienen RJW, Feldpausch TR, Galbraith D, Gloor M, Malhi Y, Aiba SI, Alexiades MN, Almeida EC, de Oliveira EA, Dávila EA, Loayza PA, Andrade A, Vieira SA, Aragão LEOC, Araujo-Murakami A, Arets EJMM, Arroyo L, Ashton P, Aymard CG, Baccaro FB, Banin LF, Baraloto C, Camargo PB, Barlow J, Barroso J, Bastin JF, Batterman SA, Beeckman H, Begne SK, Bennett AC, Berenguer E, Berry N, Blanc L, Boeckx P, Bogaert J, Bonal D, Bongers F, Bradford M, Brearley FQ, Brncic T, Brown F, Burban B, Camargo JL, Castro W, Céron C, Ribeiro SC, Moscoso VC, Chave J, Chezeaux E, Clark CJ, de Souza FC, Collins M, Comiskey JA, Valverde FC, Medina MC, da Costa L, Dancák M, Dargie GC, Davies S, Cardozo ND, de Haulleville T, de Medeiros MB, del Aguila Pasquel J, Derroire G, Di Fiore A, Doucet JL, Dourdain A, Droissant V, Duque LF, Ekoungoulou R, Elias F, Erwin T, Esquivel-Muelbert A, Fauset S, Ferreira J, Llampazo GF, Foli E, Ford A, Gilpin M, Hall JS, Hamer KC, Hamilton AC, Harris Dj, Hart TB, Hédl R, Herault B, Herrera R, Higuchi N, Hladik A, Coronado EH, Huamantupa-Chuquimaco

I, Huasco WH, Jeffery KJ, Jimenez-Rojas E, Kalamandeen M, Djuikouo MNK, Kearsley E, Umetsu RK, Kho LK, Killeen T, Kitayama K, Klitgaard B, Koch A, Labrière N, Laurance W, Laurance S, Leal ME, Levesley A, Lima AJN, Lisingo J, Lopes AP, Lopez-Gonzalez G, Lovejoy T, Lovett JC, Lowe R, Magnusson WE, Malumbres-Olarte J, Manzatto ÂG, Marimon BH, Marshall AR, Marthews T, de Almeida Reis SM, Maycock C, Melgaço K, Mendoza C, Metali F, Mihindou V, Milliken W, Mitchard ETA, Morandi PS, Mossman HL, Nagy L, Nascimento H, Neill D, Nilus R, Vargas PN, Palacios W, Camacho NP, Peacock J, Pendry C, Peñuela Mora MC, Pickavance GC, Pipoly J, Pitman N, Playfair M, Poorter L, Poulsen JR, Poulsen AD, Preziosi R, Prieto A, Primack RB, Ramírez-Angulo H, Reitsma J, Réjou-Méchain M, Correa ZR, de Sousa TR, Bayona LR, Roopsind A, Rudas A, Rutishauser E, Abu Salim K, Salomão RP, Schietti J, Sheil D, Silva RC, Espejo JS, Valeria CS, Silveira M, Simo-Droissart M, Simon MF, Singh J, Soto Shareva YC, Stahl C, Stropp J, Sukri R, Sunderland TCH, Svátek M, Swaine MD, Swamy V, Taedoumg H, Talbot J, Taplin J, Taylor D, Ter Steege H, Terborgh J, Thomas R, Thomas SC, Torres-Lezama A, Umunay P, Gamarra LV, Van Der Heijden G, van der Hout P, Van der Meer P, van Nieuwstadt M, Verbeeck H, Vernimmen R, Vicentini A, Vieira ICG, Torre EV, Vleminckx J, Vos V, Wang O, White LJT, Willcock S, Woods JT, Wortel V, Young K, Zagt R, Zemagho L, Zuidema PA, Zwerts JA, Phillips OL (2020) Long-term thermal sensitivity of Earth’s tropical forests. Science 368:869–874. https://doi.org/10.1126/science.aaw7578

Targhetta N, Kesselmeier J, Wittmann F (2015) Effects of the hydroedaphic gradient on tree species composition and aboveground wood biomass of oligotrophic forest ecosystems in the central Amazon basin. Folia Geobot 50:185–205. https://doi.org/10.1007/s12224-015-9225-9

Thornthwaite CW, Mather JR (1955) The water balance. Johns Hopkins Univ, Laboratory in Climatology, Publ in Climat 8(1).

Tomasella J, Pinho PF, Borma LS, Marengo JA, Nobre CA, Bittencourt ORFO (2013) The droughts of 1997 and 2005 in Amazonia: Floodplain hydrology and its potential ecological and human impacts. Climatic Change 116: 723–746.

Tomazello Filho M, Brazolin S, Chagas MP, Oliveira JTS, Ballarin AW, Benjamin CA (2008) Application of X-ray technique in nondestructive evaluation of Eucalypt wood. Maderas: Ciência y Tecnologia 10:139–145. http://dx.doi.org/10.4067/S0718-221X2008000200006 van der Sleen P, Groenendijk P, Vlam M, Anten NP, Boom A, Bongers F, Pons TL, Terburg G, Zuidema PA (2015) No growth stimulation of tropical trees by 150 years of CO2 fertilization but water-use efficiency increased. Nat Geosci 8:24–28.

Verheyden A, Helle G, Schleser GH, Dehairs F, Beeckman H, Koedam N (2004) Annual cyclicity in high-resolution stable carbon and oxygen isotope ratios in the wood of the mangrove tree *Rhizophora mucronata*. Plant Cell Environ 27:1525–1536. https://doi.org/10.1111/j.1365-3040.2004.01258.x

Vetter RE (1995) Untersuchungen über Zuwachsrhythmen an tropischen Bäumen in Amazonien. PhD Thesis, University of Freiburg.

Victoria RL, Martinelli LA, Richey JE, Forsberg BR (1989) Spatial and temporal variations in soil chemistry on the Amazon Floodplain. Geojournal 19:45–52. https://doi.org/10.1007/BF00620548

Vlam M, Baker PJ, Bunyavejchewin S, Zuidema PA (2014) Temperature and rainfall strongly drive temporal growth variation in Asian tropical forest trees. Oecologia 174:1449–1461.

Waldhoff D (2003) Leaf structure in trees of Central Amazonian floodplain forests (Brazil). Amazoniana 17:451–469.

Waldhoff D, Furch B (2002) Leaf morphology and anatomy in eleven tree species from Central Amazonian floodplains (Brazil). Amazoniana 17:79–94

Waldhoff D, Parolin P (2010) Morphology and anatomy of leafs. In: Junk WJ, Piedade MTF, Wittmann F, Schöngart J, Parolin P (eds) Central Amazonian Floodplain Forests: Ecophysiology, Biodiversity and Sustainable Management. Ecological Studies, vol 210, Springer Verlag, Dordrecht-Heidelberg-London-New York, pp 179–202.

Wang L, Payetete S, Bégin Y (2001) 1300-year tree-ring width and density series based on living, dead and subfossil black spruce at tree-line in Subartic Québec, Canada. Holocene 11(3):333–341. https://doi.org/10.1191/095968301674769686

Wang X, Li X, Zhu J, Tanajuta CAS (2018) The strengthening of Amazonian precipitation during the wet season driven by tropical sea surface temperature forcing. Environ Res Lett 13:094015. https://doi.org/10.1088/1748-9326/aadbb9

Wigley TML, Briffa KR, Jones PD (1984) On the average value of correlated time series with applications in dendroclimatology and hydrometeorology. J Climate Appl Meteorol 23:201–21. https://doi.org/10.1175/1520-0450(1984)023<0201:OTAVOC>2.0.CO;2

WinklerPrins, AMGA (2006) Jute cultivation in the lower Amazon, 1940–1990: an ethnographic account from Santarém, Pará, Brazil. J Hist Geogr 32:818–838. https://doi.org/10.1016/j.jhg.2005.09.028

Wittmann F (2012) Tree species composition and diversity in Brazilian freshwater floodplains. In: Pagano M, (ed) Mycorrhiza: Occurrence and role in aquatic and riparian environments. Nova Science, New York, pp 223-263.

Wittmann F, Junk, WJ (2016) The Amazon River basin. In: Finlayson CM, Milton GR, Prentice RC, Davidson NC (eds) The Wetland book II: Distribution, description and conservation, Springer Verlag, Heidelberg, Berlin, New York, pp 1-20.

Wittmann F, Anhuf D, Junk WJ (2002) Tree species distribution and community structure of Central Amazonian várrzea forests by remote sensing techniques. J Trop Ecol 18:805–820. https://doi.org/10.1017/S0266467402002523

Wittmann F, Schöngart J, Montero JC, Motzer T, Junk WJ, Piedade MTF, Queiroz HL, Worbes M (2006) Tree species composition and diversity gradients in white-water forests across the Amazon Basin. J Biogeogr 33:1334–1347. https://doi.org/10.1111/j.1365-2699.2006.01495.x

Wittmann F, Schöngart J, Junk WJ (2010a) Phytogeography, species diversity, community structure and dynamics of central Amazonian floodplain forests. In: Junk WJ, Piedade MTF, Wittmann F, Schöngart J, Parolin P (eds) Central Amazonian Floodplain Forests: Ecophysiology, Biodiversity and Sustainable Management. Ecological Studies, vol 210, Springer Verlag, Dordrecht-Heidelberg-London-New York, pp 61–102.

Wittmann F, Schöngart J, Brito JM, Oliveira Wittmann A, Piedade MTF, Parolin P, Junk WJ, Guillaumet JL (2010b) Manual of Trees from Central Amazonian Várzea Floodplains: Taxonomy, Ecology, and Use – Manual de Árvores de Várzea da Amazônia Central. Taxonomia, Ecologia e Uso. Editora INPA, Manaus, Brazil.

Wittmann F, Householder E, Piedade MTF, Assis RLJ, Schöngart J, Parolin P, Junk WJ (2013) Habitat specifity, endemism and the neotropical distribution of Amazon white-water floodplain trees Ecography 36:690–707. https://doi.org/10.1111/j.1600-0587.2012.07723.x

Worbes M (1986) Lebensbedingungen und Holzwachstum in zentralamazonischen Überschwemmungswäldern. Erich Goltze, Göttingen. Scripta Geobotanica 17:1–112.

Worbes M (1989) Growth Rings, Increment and Age of Trees in Inundation Forests, Savannas and a Mountain Forest in the Neotropics. IAWA J 10:109–122. https://doi.org/10.1163/22941932-90000479

Worbes M (1997) The forest ecosystem of the floodplains. In: Junk WJ (ed) The Central Amazon Floodplain: Ecology of a Pulsating System. Ecological Studies, vol 126, Springer Verlag, Berlin-Heidelberg-New York, pp 223–265.

Worbes M (2002) One hundred years of tree-ring research in the tropics – a brief history and an outlook to future challenges. Dendrochronologia 20:217–231. https://doi.org/10.1078/1125-7865-00018

Worbes M, Fichtler E (2010) Wood anatomy and tree-ring structure and their importance for tropical dendrochronology. In: Junk WJ, Piedade MTF, Wittmann F, Schöngart J, Parolin P (eds) Central Amazonian Floodplain Forests: Ecophysiology, Biodiversity and Sustainable Management. Ecological Studies, vol 210, Springer Verlag, Dordrecht-Heidelberg-London-New York, 329–346.

Worbes M, Klinge H, Revilla JD, Martius C (1992) On the dynamics, floristic subdivision and geographical distríbutíon of várzea forests in Central Amazônia. J Veg Sci 3:553–564. https://doi.org/10.2307/3235812

Worbes M, Klosa D, Lewark S (1995) Rohdichtestruktur von Jahresringen tropischer Hölzer aus zentralamazonischen Überschwemmungswäldern. Holz als Roh- und Werkstoff 53:63–67.

Xu C, Pumijumnong N, Nakatsuka T, Sano M, Li Z (2015) A tree-ring cellulose δ^{18}O-based July–October precipitation reconstruction since AD 1828, northwest Thailand. J Hydrol 529:433–441.

Yoon JH, Zeng N (2010) An Atlantic influence on Amazon rainfall. Clim Dyn 34:249–264. https://doi.org/10.1007/s00382-009-0551-6

Zhou J, Lau KM (1998) Does a monsoon climate exist over South America? J Climate 11:020-1040.

SUPPLEMENTARY MATERIAL

Ecophysiological background of *Nectandra amazonum* Nees (Lauraceae)

Nectandra amazonum shows a prolonged leaf life span of about two years (Walfhoff and Parolin 2010) and a high density of up to 1,188 sunken stomata mm^{-2} compared to other floodplains tree species (Waldhoff 2003; Waldhoff and Furch 2002). Leaf area of *N. amazonum* is low compared to other *várzea* tree species and about 25% higher during the aquatic phase (mean 52.3 SD ± 18 cm^2) than in the terrestrial phase (mean 42.0 SD ± 12 cm^2). On the other hand specific leaf mass is high compared to other *várzea* tree species, also presenting higher values during the aquatic phase (mean 140.1 SD ± 17.0 g m^{-2}) compared to the terrestrial phase (mean 118.9 SD ± 14.0 g m^{-2}) (Parolin 2002). Leaf water content is low in relation to other studied *várzea* tree species (mean 49 SD ± 4 g m^{-2}) showing no difference between the aquatic and terrestrial phases, while leaf nitrogen content is 32% higher during the aquatic phase (mean 1.7 SD ± 0.4%) than in the terrestrial phase (mean 1.3 SD ± 0.2%), but low in comparison to other studied *várzea* tree species (Parolin 2002). Leaf nutrient content is high during the period of leaf flush in the second half of the aquatic phase but gradually decreases as leaves are getting older (Fig. S2).

Photochemical efficiency (*Fv/Fm* ratio), which measures stress conditions, remains above 0.7 for terrestrial and aquatic phases (Parolin 1997) indicating an undamaged photochemical apparatus during almost six-month period of flooding. Mean stomatal conductance is slightly higher during the aquatic phase (mean 225 SD ± 114 mmol m^{-2} s^{-1}) compared to the terrestrial phase (mean 210 SD ± 105 mmol m^{-2} s^{-1}) (Parolin 1997). These adaptations assure photosynthetic activities during the whole year, however with a reduction of about 18.7% in mean CO_2 assimilation during the aquatic phase (mean 7.6 SD ± 3.1 µmol CO_2 m^{-2} s^{-1}) compared to the terrestrial phase (mean 9.3 SD ± 2.4 µmol CO_2 m^{-2} s^{-1}) (Parolin et al. 2001). Absolute maxima of CO_2 assimilation (A_{max}), however, can be higher during the aquatic phase (20 µmol CO_2 m^{-2} s^{-1}) compared to the terrestrial phase (10 µmol CO_2 m^{-2} s^{-1}) (Parolin et al. 2010; Piedade et al. 2000). CO_2 assimilation increases during the first months after leaf flush still during the aquatic phase. With the begin of the terrestrial phase, yet in the dry season, CO_2 assimilation shows a remarkable drop increasing again along the terrestrial phase until flooding reaches again the trees leading to a sharp decrease in photosynthesis (Parolin 1997) (Figure S2). *Nectandra amazonum* shows a linear increase in sap flux (*Js*) with increasing vapour pressure deficit up to 1.5 kPa suggesting no signs of stomata control, and sapwood area increases linearly with increasing stem diameter (Horna et al. 2010). Diurnal patterns of *Js* and lag periods between crown and stem sap flow measured during the terrestrial phase (October) and aquatic phase (March) by Horna et al. (2010) indicate no difference, suggesting that this species does not develop strategies of water storage. Stem respiration measurements indicate high stem carbon releases during the aquatic phase in the magnitude of 8-10 mmol CO_2 m^{-2} s^{-1} which is low compared to other deciduous and evergreen *várzea* tree species (Horna 2001).

Table S1 Annual wood density of ring with (ρ_{RW}), earlywood (ρ_{EW}) and latewood (ρ_{LW}) of *Nectandra amazonum* (Lauraceae) from Central Amazonian floodplain forests.

Year	ρ_{RW} (g cm^{-3})	ρ_{EW} (g cm^{-3})	ρ_{LW} (g cm^{-3})
1992	0.524	0.513	0.584
1993	0.463	0.433	0.518
1994	0.509	0.473	0.430
1995	0.505	0.479	0.580
1996	0.531	0.494	0.599
1997	0.522	0.496	0.592
1998	0.554	0.522	0.638
1999	0.568	0.541	0.631
2000	0.533	0.504	0.597
2001	0.538	0.518	0.561
2002	0.550	0.524	0.643
2003	0.566	0.539	0.652
2004	0.590	0.562	0.645
2005	0.587	0.560	0.607
2006	0.587	0.558	0.650
2007	0.602	0.571	0.653
2008	0.604	0.576	0.670
2009	0.613	0.585	0.641
2010	0.632	0.603	0.691
2011	0.632	0.601	0.687
2012	0.653	0.617	0.713
2013	0.654	0.620	0.711
2014	0.658	0.623	0.690
2015	0.670	0.640	0.672
2016	0.676	0.645	0.711
2017	0.672	0.646	0.710
mean	**0.583**	**0.554**	**0.629**
SD	**0.060**	**0.058**	**0.066**
maximum	**0.676**	**0.646**	**0.713**
minimum	**0.463**	**0.433**	**0.430**

Table S2 Correlation coefficients and corresponding *p*-values (shaded) of the relationships between ring width (RW), earlywood (EW), latewood (LW) chronologies and wood density of ring width (ρ_{RW}), earlywood (ρ_{EW}) and latewood (ρ_{LW}) of *Nectandra amazonum* from Central Amazoian floodplain forests.

	RW	**EW**	**LW**	ρ_{RW}	ρ_{EW}	ρ_{LW}
RW		<0.001	<0.001	<0.001	<0.001	0.003
EW	0.989		0.001	<0.001	<0.001	0.002
LW	0.803	0.740		<0.001	<0.001	0.013
ρ_{RW}	–0.927	–0.937	–0.753		<0.001	<0.001
ρ_{EW}	–0.933	–0.940	–-0.759	0.998		<0.001
ρ_{LW}	–0.672	–0.698	–0.587	0.846	0.828	

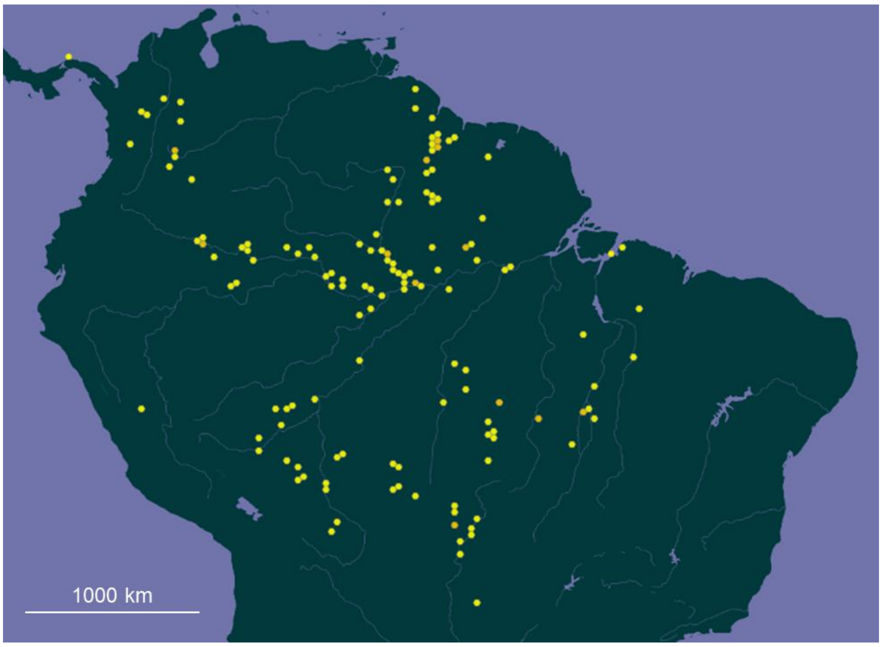

Fig. S1 Distribution map of *Nectandra amazonum* (Lauraceae) in the Neotropics. The yellow dots represent locations where taxonomic samples of the species have been collected (Brazil, Guyana, Bolivia, Colombia and Peru). Data were obtained from the Global Biodiversity Information Facility (https://gbif.org/species/nectandraamazonum).

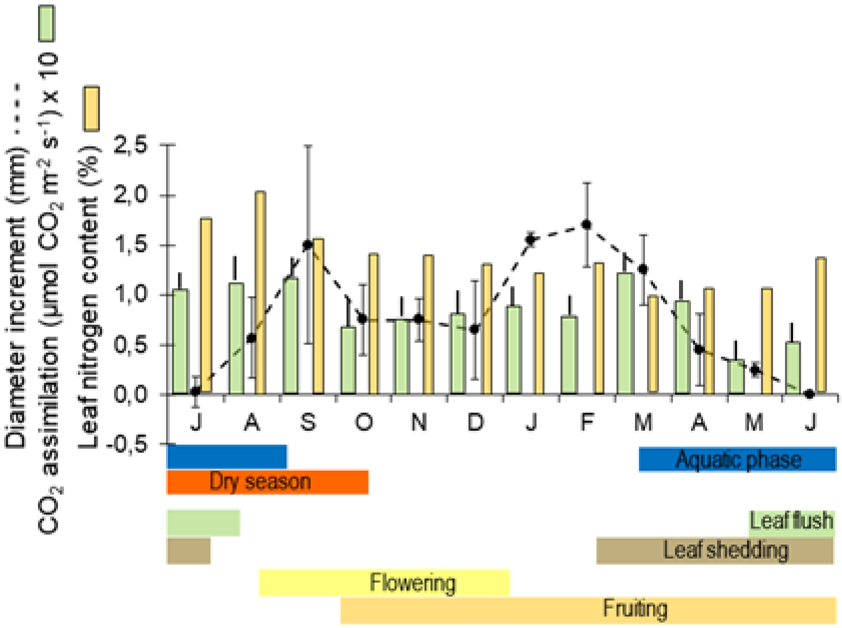

Fig. S2 Monthly diameter increment (black dots, averages and standard deviation from 1998–2000), mean CO_2 assimilation (green bars) and leaf nitrogen content (yellow bars) (period 1994/1995) during the annual cycle (July-June) in relation to the occurrence of flooding (blue horizontal bar) and the dry season (red horizontal bar). Colored horizontal bars in the lower panel indicate periods of leaf shedding and flushing, flowering, and fruiting (data: Parolin 1997; Parolin et al. 2002; Schöngart et al. 2002).