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ORIGINAL ARTICLE

Dendroecology of *Macrolobium acaciifolium* (Fabaceae) in Central Amazonian floodplain forests

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ABSTRACT

The forest dynamics in the Amazonian floodplains is strongly triggered by the flood pulse. Trees respond to unfavorable growth conditions during the flood period by cambial dormancy, which results in the formation of annual growth rings. We determined tree age and compared the mean annual rates of increase in the diameter of *Macrolobium acaciifolium* with hydrological and climatic factors in three regions of central Amazonian floodplain forest. A wood sample was obtained from each tree using an increment borer. Ring growth was assessed by marginal parenchyma bands to determine tree age and the mean diameter increment. Ring widths were indexed to construct cross-dating chronologies and correlated with climatic and hydrological variables. The analyses demonstrate that the mean annual diameter increment did not differ between the three study sites. The chronologies correlated significantly with the terrestrial phase. There was no significant difference in the ring-width index between El Niño years and other years, and between La Niña and other years. These results show that the hydrological variables can be considered crucial to the rates of tree growth and diameter increment in floodplains, and El Niño signals were not detected in the tree-ring chronologies.

KEYWORDS: tropical forests, El Niño, tree rings, dendroclimatology, sea surface temperature (SST)

Dendroecologia de *Macrolobium acaciifolium* (Fabaceae) em florestas alagáveis da Amazônia central

RESUMO

A dinâmica das florestas alagáveis da Amazônia é fortemente influenciada pelo pulso anual de inundação. As árvores respondem às condições de crescimento desfavoráveis durante o período de inundação através da dormência cambial, resultando na formação de anéis de crescimento anuais. Neste estudo, determinamos a idade das árvores e comparamos as taxas anuais médias de incremento em diâmetro de *Macrolobium acaciifolium* com fatores hidrológicos e climáticos em três regiões de florestas alagáveis na Amazônia central. Para cada árvore, uma amostra de madeira foi obtida usando uma broca dendrocronológica. O crescimento do anel foi avaliado por bandas de parênquima marginal, para determinar a idade da árvore e o incremento médio em diâmetro. As séries de anéis foram indexadas, para construir cronologias, e correlacionadas com variáveis climáticas e hidrológicas. Nossas análises demonstraram que o incremento anual médio em diâmetro não diferiu entre os três locais de estudo. As cronologias correlacionaram-se significativamente com a fase terrestre. Não houve diferença significativa no índice de largura dos anéis entre os anos de El Niño e outros anos, e entre os anos de La Niña e outros anos. Estes resultados mostraram que as variáveis hidrológicas podem ser consideradas cruciais para as taxas de crescimento e de incremento em diâmetro das árvores em florestas alagáveis, e que não foram detectados sinais de El Niño nas cronologias das árvores analisadas.

PALAVRAS-CHAVE: florestas tropicais, El Niño, anéis de árvores, dendroclimatologia, temperatura da surpefície do mar

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INTRODUCTION

Different types of forested wetlands cover about 30% of the humid tropics of the Amazon lowlands (Junk *et al.* 2014). The most representative types in the Brazilian Amazon vegetation are periodically flooded by white-water rivers locally known as várzea (approximately 400,000 km^2), black-water or clear-water rivers (igapó) (200,000 km^2) (Prance 1979; Melack and Hess 2010), and paleo-várzeas (125,000 km^2). One of the most obvious characteristics of tree species in response to flooding forests is the annual growth rhythm of the secondary cambium (Worbes 1985).

During the aquatic phase, anaerobic conditions in the soil lead to reduced root respiration and uptake of water and nutrients (Worbes 1985). As a result, many species lose their leaves (Schöngart *et al.* 2002; Parolin *et al.* 2010). Additionally, the cambium enters dormancy, resulting in the formation of annual rings (Worbes 1985; Schöngart *et al.* 2002). Dendrochronology in tropical forests and its applications to dendroecology have been used to determine age, growth rates, criteria for forest management (Schöngart *et al.* 2007; Schöngart 2010; Rosa *et al.* 2016), carbon sequestration in woody biomass (Schöngart *et al.* 2011; Cintra *et al.* 2013; Batista 2015), tree mortality in response to hydrographic changes caused by a river dam (Assahira *et al.* 2017), and dendroclimatology (Schweingruber 1996).

El Niño–Southern Oscillation (ENSO) is the dominant component of tropical interannual variability and affects the weather and climate on a global scale. The phenomenon results from an ocean–atmosphere interaction in the equatorial Pacific (Li *et al.* 2015). El Niño, La Niña, and the meridian gradient of sea surface temperature (SST) anomalies in the Tropical Atlantic jointly modulate a large part of the variability of precipitation and hence the hydrological cycle in South America (Marengo 2006). In large parts of the Amazon basin, El Niño anomalies are associated with a decrease in rainfall in the wet season (Foley *et al.* 2002; Ronchail *et al.* 2002). Marengo *et al.* (2011) suggest that changes in the dry season and hydrology of the Amazon Basin are related to warming of the tropical North Atlantic SST, and the observed changes in the duration and intensity of the dry season are associated with very low levels of rivers and water discharge at the end the dry season. Weaker floods in El Niño years result in an extension of the vegetation phase (the terrestrial phase) in floodplain forests (Schöngart and Junk 2007) and significantly wider growth rings than in other years (Schöngart *et al.* 2004, 2005).

Macrolobium acaciifolium (Benth.) Benth. (Fabaceae) is a dominant, semi-deciduous tree species that occurs at low elevations of areas flooded by nutrient-poor black-water or clear-water rivers (igapó) and nutrient-rich white-water rivers (floodplains) (Schöngart *et al.* 2005). It has distinct rings and a wide geographical distribution with high abundance in floodplain forests (Wittmann *et al.* 2006). The growth of this species and many others is determined by the flood pulse, which results in a cambial dormancy in the early submerged phase and induces the formation of annual rings in the wood (Schöngart *et al.* 2002, 2005). It is a medium-sized tree that grows up to 25 m tall and has a diameter greater than 1 m. During the aquatic phase, anaerobic conditions in the soil lead to reduced respiration of the roots and uptake of water and nutrients (Worbes 1985). Trees with estimated age over 500 years have been found in igapó forests, while in várzea, the maximum recorded age is 157 years (Schöngart *et al.* 2005).

In this study, we compared the relationship between ring-width indices of *M. acaciifolium* with hydrological and climatic factors in three regions of Central Amazonian floodplain forests. We addressed the following hypotheses: (a) *Macrolobium acaciifolium* trees register the interannual variation of climate and hydrology and record this information in the time series of ring growth; (b) SST anomalies can be detected in the time series of ring growth; and (c) signals of SST anomalies vary between regions and chronologies.

MATERIAL AND METHODS

Study areas

This study was conducted in three floodplain areas (one paleo-várzea area and two igapó areas) in Central Amazonia (Figure 1). Igapó forests are considered unproductive because of low nutrient stocks in the soil with low potential fertility (Furch 1997), while in paleo-várzeas, the surface substrates are more fertile, although less fertile than várzea soil (Irion *et al.* 2010; Junk *et al.* 2011; Assis *et al.* 2015). The RDSA (Amanã Sustainable Development Reserve) is located in the western part of the state of Amazonas on the left bank of the lower Japurá River, which is a tributary of the Solimões River. The region covers an area of 2,350,000 ha of interfluves and is located between the Japurá River and Solimões River. The collection area was near Amanã Lake, one of the largest lakes in the Amazon (1°30'-3°00"S, 63°00'-65°00'W). The region has terra firme forests and paleo-várzea forests. The climate of the area is characterized by a mean temperature of 26.9 ˚C, annual mean rainfall of 2,393 mm, and a distinct dry season during from July to October (Schöngart *et al.* 2005).

Anavilhanas National Park (PNA) is located on the lower Negro River (02°43'54.5"S, 60º45'47.5"W) and contains the second largest river archipelago in the world, which consists of about 430 islands with a total area of 350,018 ha. The region has a predominance of igapó and terra firme forests. The climate is characterized by an annual mean temperature of 25 °C (ICMBIO 2018), a mean annual rainfall of 2,235 mm, and a dry season from July to September. The Uatumã Sustainable Development Reserve (RDSU) is located in Northeastern Amazonas along the Uatumã River, a tributary of the Amazon River (02˚13'-02˚15'S, 59º25'-60º25'W). The region covers an area of 424,430 ha and has terra firme forests, igapó forests, campina, and campinarana. The climate is characterized by an annual mean temperature of 28 °C throughout the year (IDESAM 2018), a mean annual rainfall around 2,026 mm, and a dry season between June and October.

Field sampling

Samples were collected in RDSA in November 2009, PNA in March 2010, and RDSU in November 2010. At each site, 20 individuals of emergent *M. acaciifolium* with a diameter at breast height (DBH) > 60 cm were sampled. For each tree, we measured DBH (130 cm above ground) and the flood height, which is visible as a distinct mark on the trunk from the last flood of 2009. After the measurements, one wood core sample per tree was taken with an increment corer (5 mm in diameter) with a length of 60 cm for a total number of 60 trees. After the extractions, the holes in the trunks were covered with wax.

Sample preparation, ring-width measurements, and data treatment

The wood samples were analyzed in the Dendroecology Laboratory at the National Institute for Amazonian Research (INPA) within the framework of a collaboration project with the Max Planck Institute for Chemistry (Germany). For the dendrochronological analysis, wood samples were fixed with white glue on wooden supports and progressively sanded using sand paper with decreasing grain sizes from 80 to 600. The structure of annual growth rings was viewed with a microscope (Leica MZ 8) to identify the growth rings bordered by marginal parenchyma bands (Worbes 1985) (Figure 2). We used a digital measuring device (Schöngart *et al*. 2004) with an accuracy of 0.01 mm (LINTAB) supported by software for tree ring measurement, TSAP-Win (Time Series Analysis and Presentation, version 4.64, Rinntech, Heidelberg, Germany). The results were used for the analysis of temporal sequences, which provides individual curves of radial increment for each individual. TSAP-Win also allows for cross-dating, calculating the percentage of coincidence between two curves (GLK; Gleichläufigkeit in German) (Eckstein and Bauch 1969), and a Student's t-test (Baillie and Pilcher 1973).

Growth curves were compared visually and statistically to obtain ring-width series in a synchronous position (Pilcher 1990; Worbes 1995; Schöngart *et al*. 2004). To obtain reliable results, the series should have a minimum overlap of 40 years,

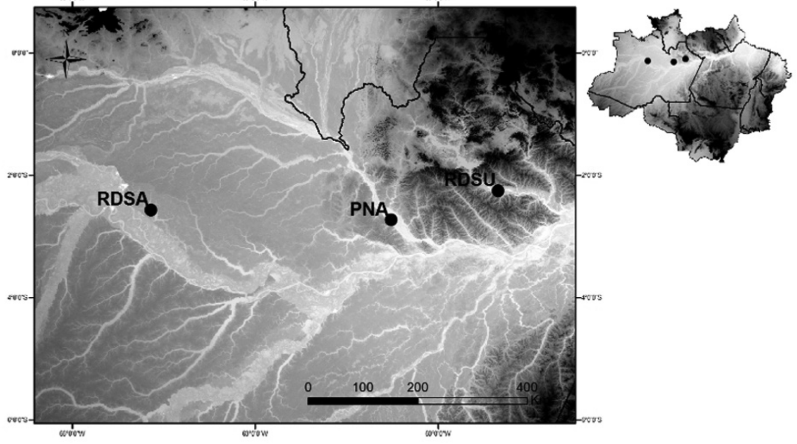

Figure 1. Location of the study areas for *Macrolobium acaciifolium* dendroecology in Central Amazonia. (RDSA – Amanã Sustainable Development Reserve, PNA – Anavilhanas National Park, RDSU – Uatumã Sustainable Development Reserve).

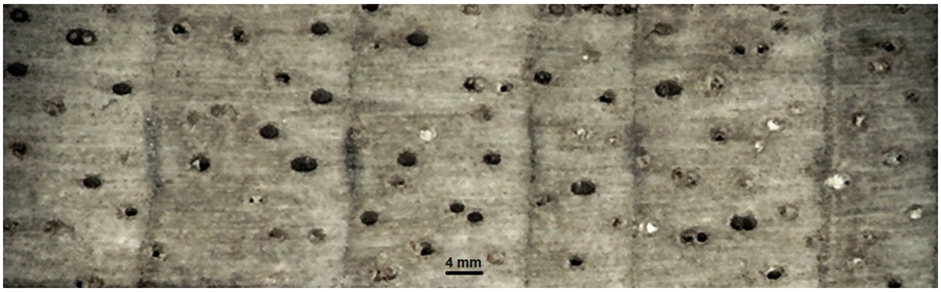

Figure 2. Wood anatomical structure of *Macrolobium acaciifolium* from a floodplain forest of central Amazonia. Ring width is characterized by parenchyma bands. This figure is in color in the electronic version.

and the degree of the relationship of the time series was expressed by a two-sample Student's t-test (Schöngart *et al.* 2005). GLK was used to indicate the year-to-year agreement in the oscillations of two curves within the overlapping interval (Schweingruber 1988). To relate ring growth with climate, the raw ring curves were transformed into index curves of all trees analyzed by applying a 5-year moving average to eliminate possible undesirable long-term trends (Schweingruber 1983) arising from competition between the trees or by the tendency of the trees to senesce. The indexing results in a normal distribution of data that is a basic condition for correlating the data with chronological climatic data (Cook and Briffa 1990).

Tree age was estimated using the ratio of DBH to the mean diameter increment (MDI) determined for the wood samples (Worbes *et al.* 2003; Schöngart *et al.* 2005). A simple analysis of variance (ANOVA) was carried out to compare the tree MDIs and ages from the three study areas. At each study area, DBH was correlated with age, which was in turn correlated with the MDI. The sensitivity of the growth response to possible environmental and climatic factors was calculated using the following sensitivities (Schweingruber 1983):

$$S_{i+1} = \frac{(x_{i+1}) \times 2}{(x_{i+1} + x_i)}$$

$$\overline{S} = \frac{\sum_{i=2}^{n} |S_i|}{n-1}$$

$$SI = \frac{S_{i+1}}{\overline{S}}$$

where S_{i+1} is the annual sensitivity, $\overline{S}$ is the average sensitivity, *SI* is the index of sensitivity, x_i is the observation value at time *i*, x_{i+1} is the observation value at time *i*+1, and *n* is the number of trees.

Climate and hydrological data

The climate data used to analyze the correlation with growth rings included: (a) annual precipitation data obtained from the GPCC (Global Precipitation Climatology Centre), (b) water levels provided by the ANA/SNPH (Brazilian National Water Agency/State Agency for Navigation, Ports and Waterways), and (c) SST anomalies in the Pacific Ocean for the NINO 3.4 region (5°N - 5°S, 170°- 120°W), the North Atlantic region (NATL; 5°- 20°N, 60°- 30°W), and the South Atlantic Ocean (SATL; 0°- 20°S, 30°W - 10°E) for 1950 to 2009 (National Oceanic and Atmospheric Administration -NOAA 2017). Precipitation data recorded from 1901 to 2007 were obtained from the GPCC for the three study areas and used to calculate the mean and standard deviation of annual precipitation.

To examine the correlation with hydrological data, we used the water levels of rivers recorded at stations near the study areas: Fonte Boa (RDSA - Japurá River) from 1977 to 2008, Moura (PNA - Negro River) from 1979 to 2006, and Cachoeira da Morena (RDSU - Uatumã River) from 1973 to 2006. The daily fluctuation of water levels at each study area was used to calculate the duration of the terrestrial phase using the heights of the watermarks on the tree trunks (corresponding to the peak of the 2009 flood), as well as the minimum and maximum flooding levels determined for the topography. The water levels below the topography of the study area were counted as days of the terrestrial phase.

To correlate the chronologies, annual precipitation, maximum and minimum water levels, and the duration of the terrestrial phase with the SST anomalies, we used a period of 24 months including the previous year (indicated by -1) and the current year with a data series from 1950 to 2009. A t-test was used to analyze the ring-width indices with respect to El Niño, La Niña, and other years. We used simple ANOVA to check for statistically significant differences between the total precipitations for the three study areas. The statistical analyses were performed using the programs STATISTICA 9.0 and Bioestat 5.0.

RESULTS

The populations of *M. acaciifolium* in the three study areas remained flooded for an average of 240 days per year in RDSA, 231 days in PNA, and 222 days in RDSU. The average DBH and MDI were higher in RDSU, but the estimated age was similar in the three study areas (Table 1). There were no significant differences in MDI ($F = 2.94$, $p > 0.05$) and estimated tree age ($F = 0.67$, $p = 0.51$) among the study areas. The mean tree age was higher in PNA than in RDSU and RDSA. The maximum estimated ages were 341 years (DBH = 81 cm) in RDSA, 418 years (DBH = 105 cm) in PNA, and 443 years (DBH = 137 cm) in RDSU.

Age was significantly and positively correlated with DBH in all study areas [(RDSA ($R^2 = 0.12$, $p < 0.05$), PNA ($R^2 = 0.26$, $p < 0.01$), RDSU ($R^2 = 0.45$, $p < 0.001$)]. Age was significantly and negatively correlated with MDI in all study areas [RDSA ($R^2 = 0.50$, $p < 0.01$), PNA ($R^2 = 0.79$, $p < 0.01$), RDSU ($R^2 = 0.61$, $p < 0.01$)]. There was no correlation between DBH and MDI. Chronologies were determined using eight individuals in RDSA for the period of 1747 - 2005 (258 years), 10 individuals in PNA covering the period of 1752 - 2006 (254 years), and 10 individuals in RDSU for 1758 - 2004 (246 years) (Figure 3). A sensitivity analysis showed that the growth of M. acaciifolium was sensitive to climatic factors (Table 1).

Table 1. Diameter, mean diameter increment rates, age, and sensitivity of the growth response of *Macrolobium acaciifolium* trees sampled in three floodplain areas in Central Amazonia (RDSA, PNA and RDSU).

Parameter	RDSA	PNA	RDSU
Mean flood amplitude (m)	8	8	2.5
Sample size	20	20	20
Mean dbh (min-max) cm	88 (66.8-121.7)	86 (72.5-105.6)	97 (74-137)
MDI (mm)	3.2 (± 0.37)	3.1 (± 0.35)	3.8 (± 0.41)
Tree age (years)	263 (± 63)	275 (± 88)	268 (± 88)
Mean sensitivity	0.9	1.00	1.05

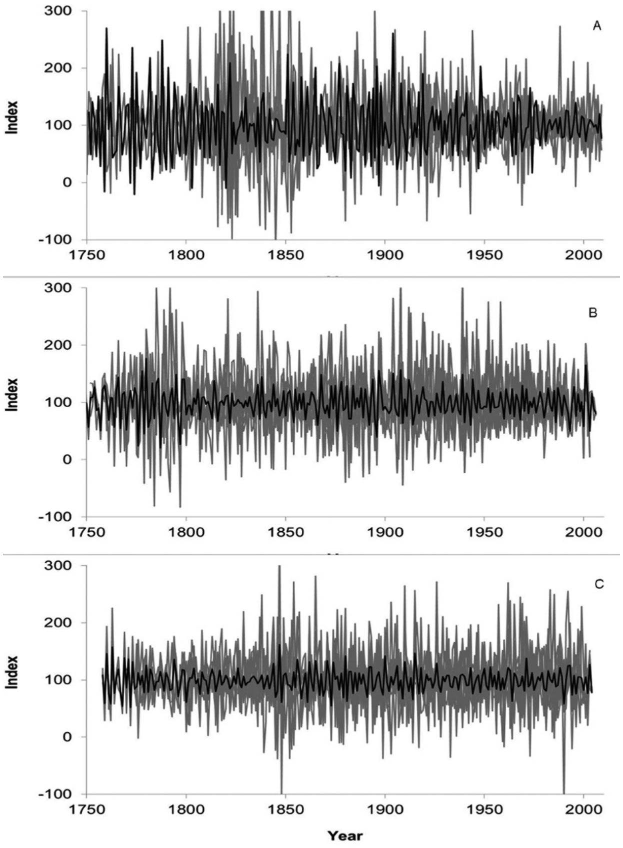

Figure 3. Indexed tree-ring chronologies of *Macrolobium acaciifolium* in (a) RDSA (paleo-várzea forest), (b) PNA and (c) RDSU (igapó forests) in central Amazonia. Gray lines indicate the individual indexed curves; the black line indicates the chronology.

Rainfall and SSTs

The total precipitation in the period of 1901 - 2007 differed significantly among the study areas (F = 23.87, $p < 0.0001$). The mean annual rainfall was 2393 ± 441 mm in RDSA, 2235 ± 358 mm in PNA, and 2026 ± 366 mm in RDSU. However, during the wet season (December - May), the rainfall totals were similar among the areas [RDSA (1531 ± 308 mm), PNA (1571 ± 291 mm), RDSU (1485 ± 280 mm)].

Correlations between annual precipitation and SST anomalies in the equatorial Pacific and tropical Atlantic indicated different climate signals (Supplementary Material, Figure S1). The NATL SST anomalies influenced the annual rainfall for five months at RDSA and in all months at RDSU during the current year. No influence of the NATL SST anomalies on annual precipitation was detected at PNA. The SATL SST anomalies influenced the annual precipitation at PNA and RDSU from May to August or September of the current year but did not show effects at RDSA. The SST anomalies in the NINO 3.4 region correlated significantly with annual precipitation during the second part of the previous year for more than 12 consecutive months at RDSA and RDSU. Annual precipitation at PNA correlated significantly with the months of the first part of the current year. Evidence of SST anomaly signals in the time series of annual precipitation decreased in the order RDSU, RDSA, and PNA.

Hydrological cycle and SSTs

The study areas were subjected to a monomodal flood pulse. The mean amplitude of the water level was around 8 m in RDSA and PNA and 2.5 m in RDSU, where it was calculated for only the period of 1973 to 1987, prior to the construction of a dam at Cachoeira da Morena. After the dam was put into operation (1989), the hydrological cycle was regulated through the control of discharge. Flooding at RDSA and RDSU occurred in May and June. The terrestrial phase showed little difference between the study areas with durations of 125 (RDSA), 134 (PNA), and 143 days (RDSU). The terrestrial phase correlated significantly with NINO 3.4 anomalies during the second half of the current year in RSAD, with the NATL and SATL anomalies during a few months of the current year in PNA, and only with SATL anomalies during some months of the previous and current years in RDSU (Supplementary Material, Figure S2).

Relationship of chronologies with climatic and hydrological variables

The indexed ring-width chronologies did not correlate with precipitation and flood levels in RDSA and RDSU, while there was a significant correlation with the minimum flooding level in PNA (Table 2). The chronology correlated significantly with the duration of the terrestrial phase in all study areas (Table 2, Figure 4). The correlation between indexed ring-width chronologies and SST anomalies showed variable responses of trees among areas. At RDSA (Figure 5), correlations indicated significant negative signals for NATL early in the previous year, as well as significant positive signals early in the current year. There was no significant correlation for SATL. For the NINO 3.4 region, the signals were significant from negative to positive throughout the previous year and were positive early in the current year.

Table 2. Correlation of the ring-width index of *Macrolobium acaciifolium* trees in three floodplain forest areas in Central Amazonia, with annual precipitation, duration of the terrestrial phase, and minimum and maximum flooding levels (R^2 = coefficient of determination, p = significance level).

Study area	Precipitation	Terrestrial phase	Mínimum	Maximum
RDSA	0.0202 (0.4796)	0.26 (0.0080)	0.0003 (0.9376)	0.0007 (0.8927)
PNA	0.002 (0.6215)	0.37 ($p < 0.001$)	0.18 ($p < 0.05$)	0.01 (0.5794)
RDSU	0.01 (0.3027)	0.56 ($p < 0.001$)	0.05 (0.2516)	0.07 (0.1668)

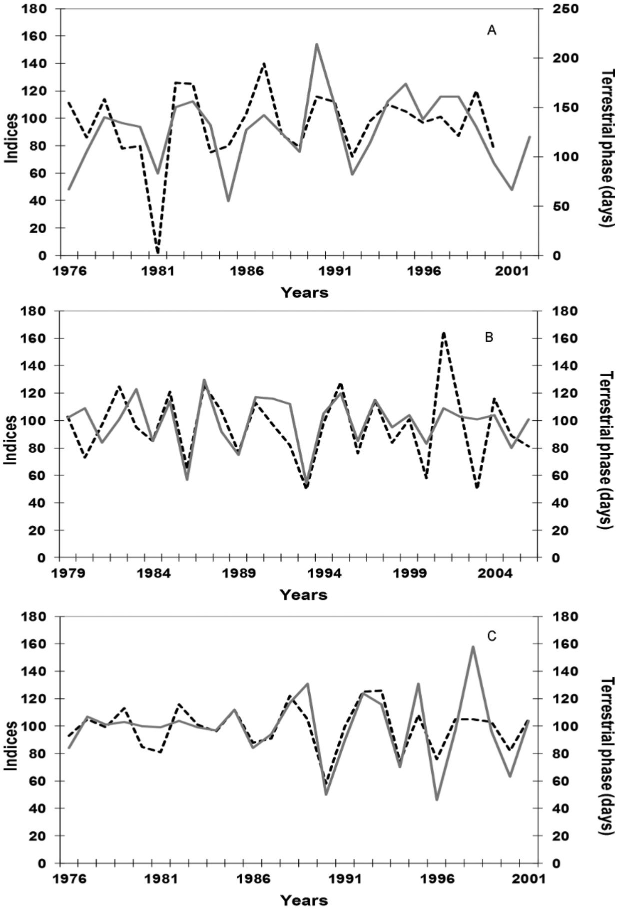

Figure 4. Relationship between the indexed ring-width chronology of *Macrolobium acaciifolium* (dotted black line) and the length of the terrestrial phase (gray line) in (a) RDSA, (b) PNA, (c) RDSU.

At PNA (Figure 6), there was no correlation with SST anomalies overall except for weak positive signals for SATL and NINO 3.4 in January of the previous year. At RDSU (Figure 7), correlations were significant and positive in the first half of the previous year for NATL and especially for NINO 3.4, while no signal was detected for SATL. Ring-width indices did not differ significantly between El Niño years and other years and between La Niña years and other years (Table 3).

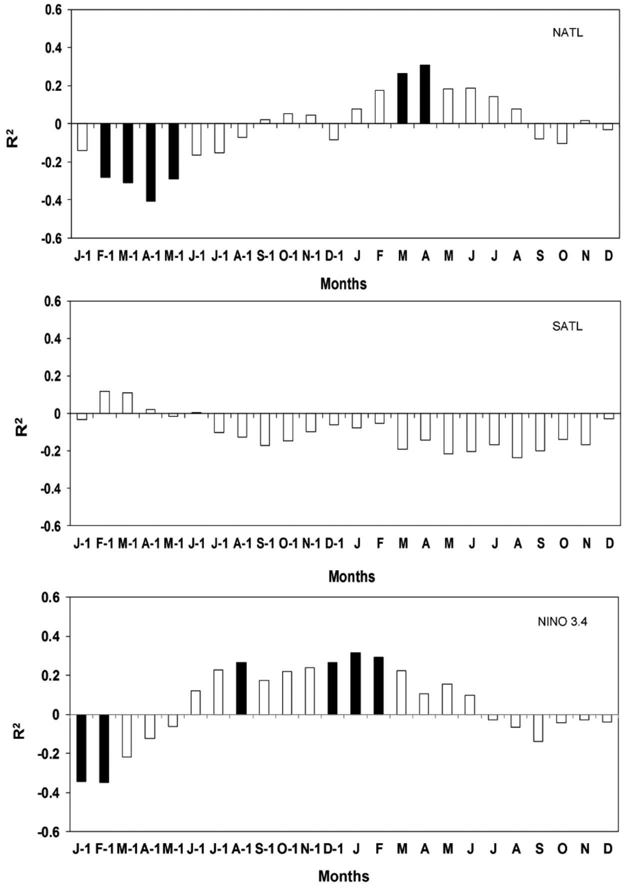

Figure 5. Correlation of the ring-width index for RDSA with the SST anomalies of the tropical Atlantic (ATLN and ATLS) and equatorial Pacific (Nino 3.4) oceans considering 12 months of the current year and 12 months of the previous year (indicated by -1). Black columns indicate the months with significant correlations ($p < 0.05$).

DISCUSSION

The occurrence of annual ring growth has been demonstrated for *M. acaciifolium* by a combination of independent dendrochronological methods and has shown potential for dendrochronological studies. We were able to clearly correlate the indexed ring-width chronologies with the duration of the terrestrial phase in two areas, PNA and RDSU, which are separated by approximately 500 km along the Negro/Amazonas rivers, and one paleo-várzea area, RDSA. Our correlations between the ring-width index and the duration of the terrestrial phase were higher than those obtained previously for RDSA and for the várzea area of the Mamirauá Sustainable Development Reserve (Schöngart *et al.* 2005). This probably occurred because Schöngart *et al.* (2005) calculated the duration of the terrestrial phase based on river level data from the port of Manaus, which is more than 550 km away from Amanã and Mamirauá. In contrast, the present study used data from the hydrological stations nearest to the study areas.

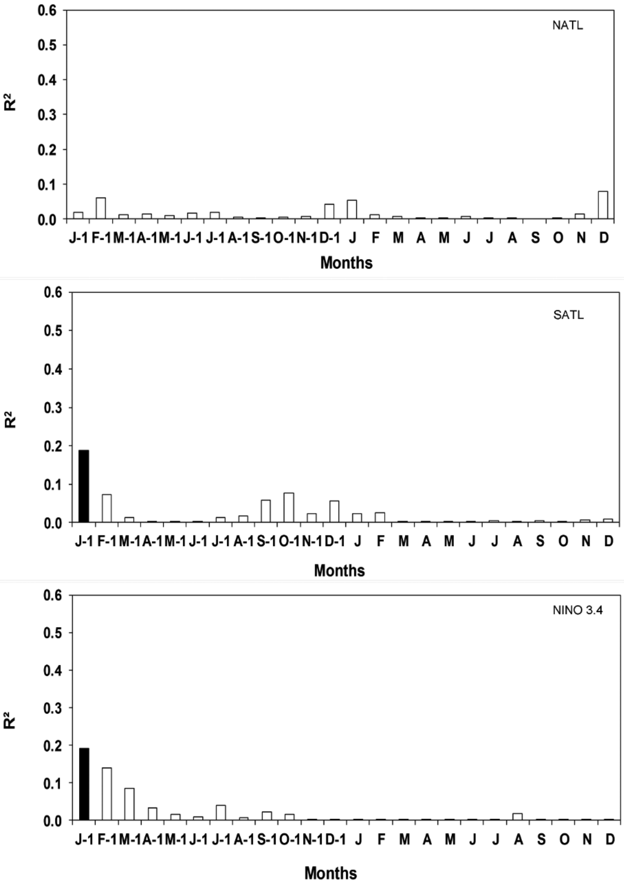

Figure 6. Correlations of the ring-width index for PNA with the tropical Atlantic SST anomalies (ATLN and ATLS) and equatorial Pacific (Nino 3.4) considering 12 months of the current year and 12 months of the previous year (indicated by -1). Black columns indicate months with significant correlations ($p < 0.05$).

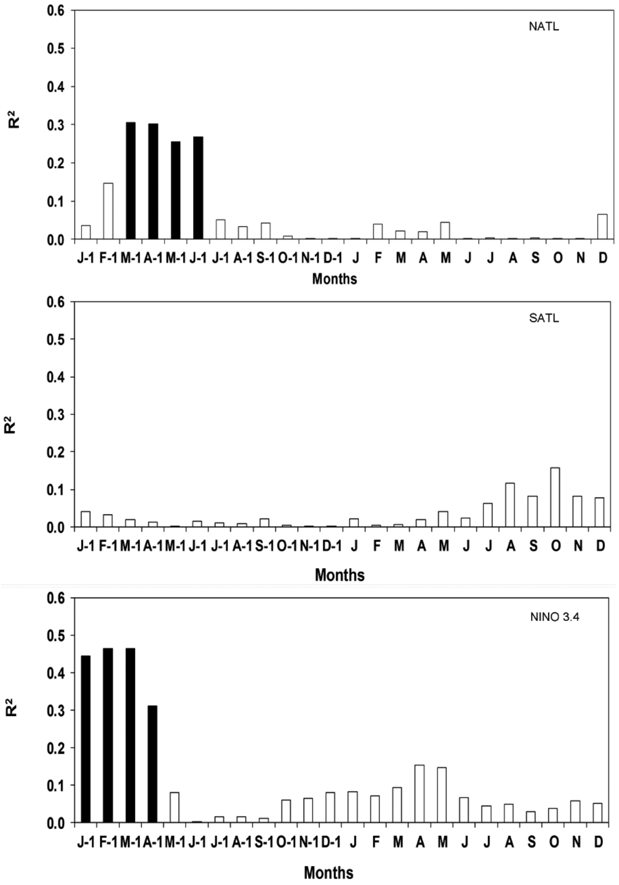

Figure 7. Correlations of the ring-width index for RDSU with the tropical Atlantic SST anomalies (ATLN and ATLS) and equatorial Pacific (Nino 3.4) considering 12 months of the current year and 12 months of the previous year (indicated by -1). Black columns indicate months with significant correlations ($p < 0.05$).

Table 3. Differences in the ring-width indices from the tree-ring chronologies of *Macrolobium acaciifolium* trees in three floodplain areas in Central Amazonia between El Niño, La Niña, and other years (two-sample t-tests indicate significant differences between the mean index; NS = not significant). * Part of the chronologies used to indicate the years of occurrence of the El Niño and La Niña.

Teste T	Mean index (years)*	El Niño events	Other years	T value	La Niña events	Other years	T value
RDSA	1877-2006	96.76	107.26	-1.09 (NS)	91.83	107.28	-1.50 (NS)
PNA	1877-2006	97.33	99.52	-0.53 (NS)	100.45	97.86	-0.59 (NS)
RDSU	1877-2004	100.44	98.65	0.59 (NS)	99.16	99.48	0.09 (NS)

The positive correlation between age and DBH in all study areas confirmed that older trees have higher DBH (Schöngart 2010). The negative correlation between age and MDI indicated that the tree growth rates decrease with age, which has also been determined for *Tabebuia barbata* and *Vatairea guianensis* in the igapó in RDSA (Fonseca *et al.* 2009). MDIs showed little variation between the three sites studied, indicating that environmental factors such as climate, hydrology, and soil conditions did not vary greatly between the study sites. This suggests that the growth rates are intrinsic and independent of environmental variability.

Ronchail *et al.* (2002) showed that precipitation anomalies are related to ENSO in the northeast region of the Amazon Basin. Negative anomalies of precipitation in the central, northern, and eastern Amazon Basin are generally associated with ENSO events and SST anomalies in the tropical Atlantic (Ronchail *et al.* 2002; Marengo 2004). These studies explain the influence of these events in the precipitation in the regions of PNA and RDSU, which helps to understand the variation in the precipitation of these sites, which was lower than in RDSA. The tree growth in RDSA, which is the furthest west among the study areas, was clearly influenced by SST anomalies. As expected, it also experienced the highest precipitation rates.

Ronchail *et al*. (2002) showed this difference in precipitation between the Amazon basin regions, indicating that the Western Amazon is on the boundary between Southeastern South America and the Northeastern Amazon basin, two regions where the ENSO signals are strong and inverse. Consequently, the rainfall anomalies oscillate between excess rain associated with intense frontal activity during the colder period of the year. This study helped to understand the variation in rainfall related to ENSO in RDSA, even with obvious signals of anomalies with higher rainfall than in PNA and RDSU due to other climatic factors associated with El Niño events.

There were no differences in the ring-width indices in El Niño years compared with other years. This contrasts with the results of Schöngart *et al*. (2005), who found significant differences between ring growth in El Niño years and other years in the same region. The growth rings are significantly wider in El Nino years than in other years (Schöngart *et al*. 2004, 2005) because of an extension of the terrestrial phase in floodplain forests (Schöngart and Junk 2007). In RDSA, there was a significant influence of NINO 3.4 SST anomalies on the duration of the terrestrial phase, while in PNA and RDSU, these signals were absent.

The absence of El Niño signals in our ring-growth chronologies could also have resulted from the low elevation of the floodplain forests in the study areas, since El Niño and La Niña signals are less pronounced at low elevations than middle elevations (Schöngart and Junk 2007). The impact of El Niño on flood pulses appears during a time of the year when there is already flooding in floodplain forests at low elevation, where *M. acaciifolium* naturally occurs (Wittmann *et al*. 2002). Thus, tree growth does not respond to the climatic anomalies caused by ENSO (Schöngart *et al*. 2005), and climate anomalies are no longer recorded by species that have low cambial activity at the beginning of the aquatic phase (Schöngart *et al*. 2002).

A comparison of the MDI of *M. acaciifolium* from different studies in igapó and várzea (Table 4) indicated significantly lower values in igapó, which are due to the lower macro and micronutrient stocks in igapó soil (Furch 1997). Scabin *et al*. (2012) found higher MDIs in PNA than in this study, which resulted from the inclusion of young trees in their samples, and because *M. acaciifolium* has higher growth rates, probably due to being a pioneer species.

The results of this study suggest that *M. acaciifolium* should be managed in only várzea forests. The management of the timber of this species in igapó forests should be prohibited because of the low MDIs that result in cutting cycles of 10 years (Schöngart 2010). The annual radial increment of tree species in várzea forests is twice as high as in igapó forests (Worbes 1997), and due to the low rates of radial increment, trees in igapó tend to be older (Schöngart *et al*. 2005). To establish management criteria in wetlands, the specificity of the growth of each species and its areas of occurrence should be considered (Schöngart 2008). Further dendroclimatological studies should concentrate on areas where the signals of SST anomalies are stronger in the Amazon basin to understand the growth behavior of other tree species in future climate scenarios.

Table 4. Comparison of MDI (mean diameter increment) and mean age of *Macrolobium acaciifolium* trees from different central Amazonian floodplain forests and different studies. (RDSA - Reserva de Desenvolvimento Sustentável Amanã; PNA - Parque Nacional de Anavilhanas; RDSU - Reserva de Desenvolvimento Sustentável Uatumã).

Study area	Floodplain type	Mean age (years)	MDI (mm/year)	Source
Mamirauá	Várzea	135	5.3	Schöngart *et al.* (2005)
RDSA	Paleo-várzea	268	3.0	Schöngart *et al.* (2005)
PNA	Igapó	66	6.46	Scabin *et al.* (2012)
RDSA	Paleo-várzea	274	3.2	This study
PNA	Igapó	288	3.1	This study
RDSU	Igapó	268	3.8	This study

CONCLUSIONS

The annual MDI of *Macrolobium acaciifolium* varied significantly among the three study areas, and RDSA and PNA had lower rates compared to RDSU. Overall, MDI values were within the normal range for igapó forests reported in other studies. Indexed ring-growth chronologies were positively correlated with the terrestrial phase, indicating that the hydrological cycle has an important role in determining the growth rhythm and MDI. Signals of SST anomalies in the tropical Atlantic and equatorial Pacific oceans varied among the study areas and were more evident in the most eastern area of RDSU.

Macrolobium acaciifolium is widely distributed at low elevations in the Amazon basin in both várzea and igapó floodplains. It reaches ages of up to 500 years in igapó forests, which makes it suitable for studying the variation in ring-growth chronology. The creation of a basin-wide network of *M. acaciifolium* chronologies would advance our knowledge about dendroecology and aid in understanding the dynamics of floodplain forests. Such efforts are important for the development of sustainable management plans of timber species to ensure the conservation of these ecosystems.

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SUPPLEMENTARY MATERIAL (only avaliable in the electronic version)

BATISTA & SCHÖNGART. Dendroecology of *Macrolobium acaciifolium* (Fabaceae) in Central Amazonian floodplain forests

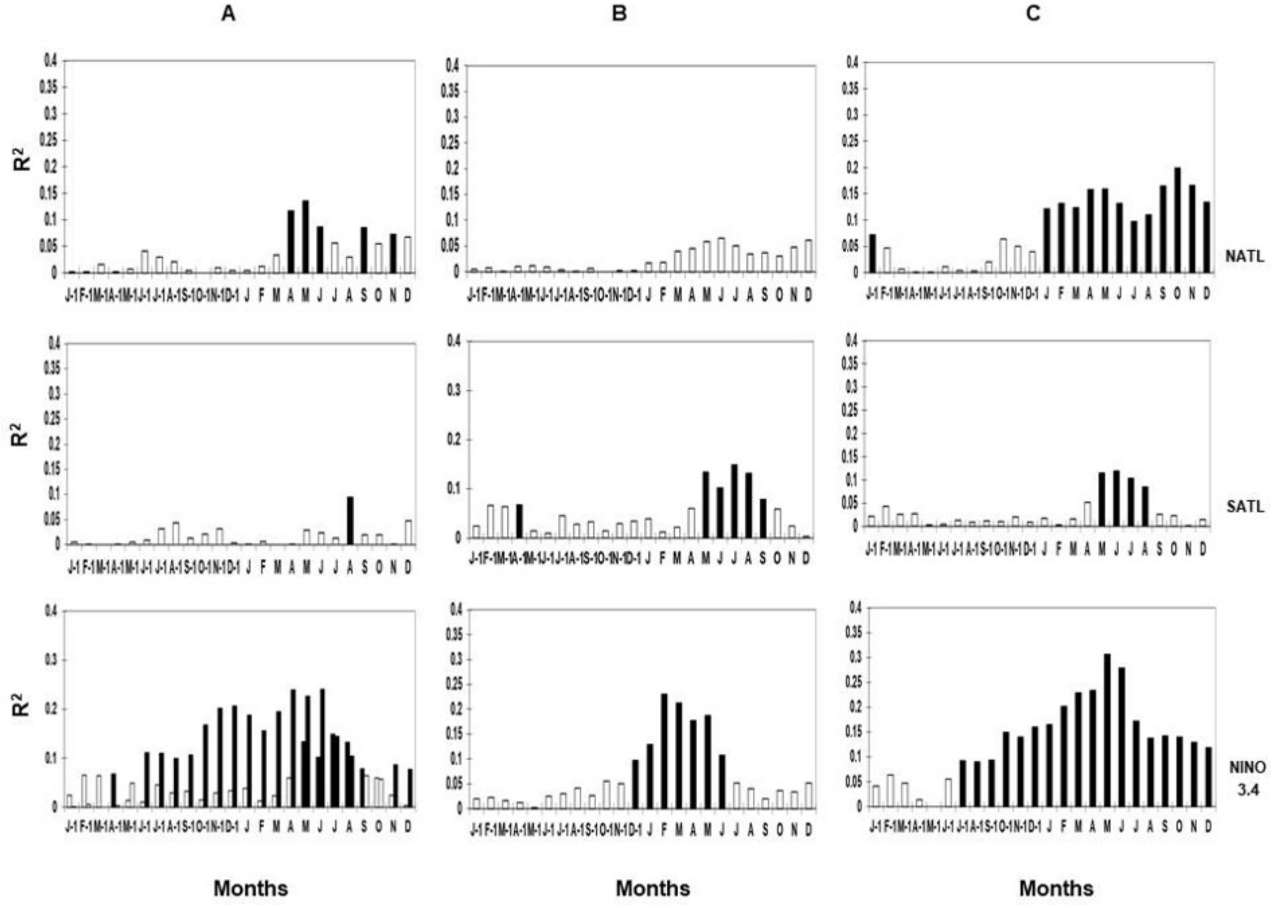

Figure S1. Correlations between annual precipitation in three floodplain areas in Central Amazonia [(a) RDSA, (b) PNA, (c) RDSU] with the SST anomalies in the tropical Atlantic (ATLN and ATLS) and equatorial Pacific (Nino 3.4) oceans considering 12 months of the current year and 12 months of the previous year (indicated by -1). Black columns indicate the months with significant correlations ($p < 0.05$).

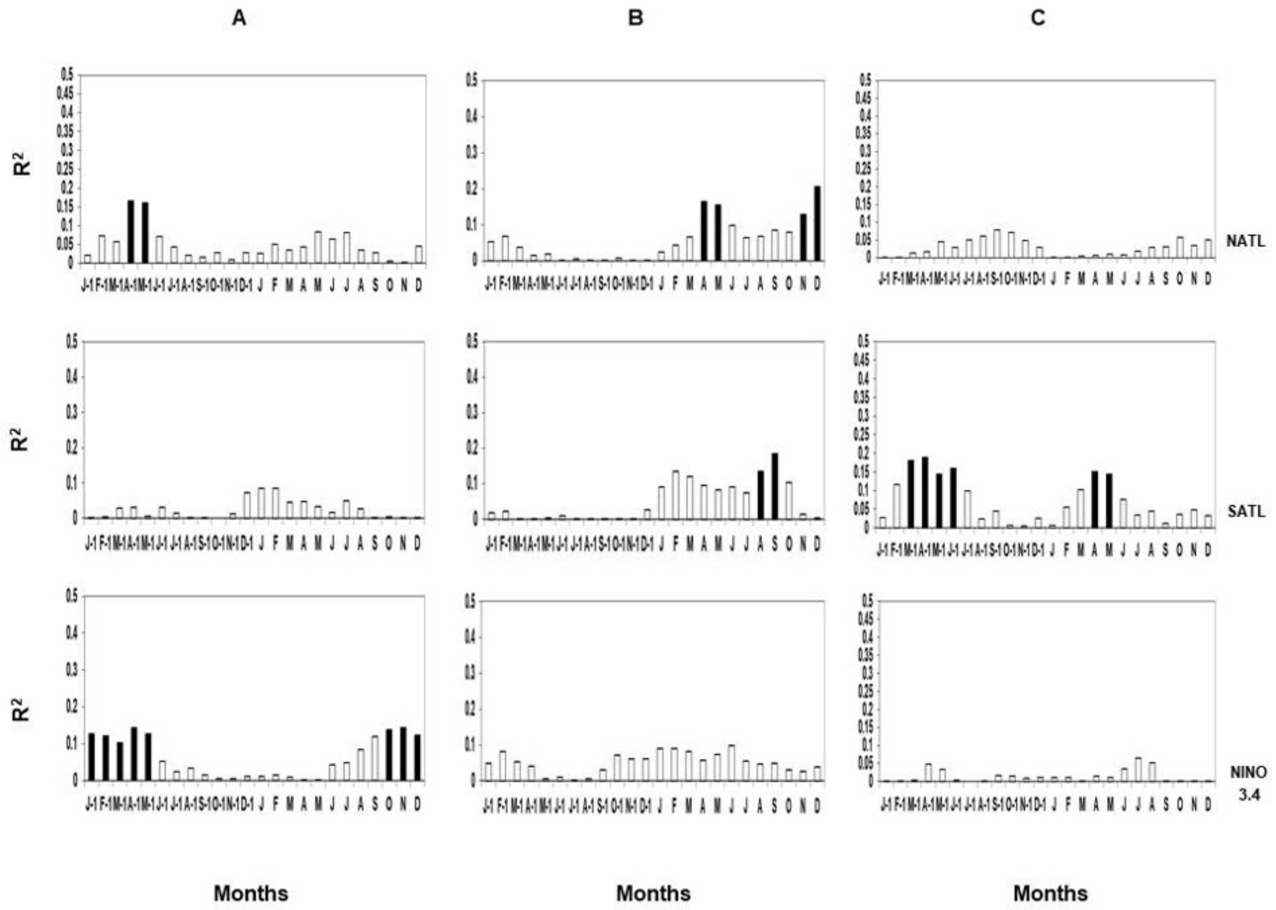

Figure S2. Correlations between the length of the terrestrial phase in three floodplain areas in the central Amazon [(a) RDSA, (b) PNA, (c) RDSU] with the SST anomalies in the tropical Atlantic (ATLN and ATLS) and equatorial Pacific (Nino 3.4) oceans considering 12 months of the current year and 12 months of the previous year (indicated by -1). Black columns are the months with significant correlations ($p < 0.05$).