



Invited review paper

Influence of regional rainfall and Atlantic sea surface temperature on tree-ring growth of *Poincianella pyramidalis*, semiarid forest from Brazil



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ABSTRACT

A tree-ring width chronology was developed from samples of thirteen *Poincianella pyramidalis* trees from the Caatinga semiarid region of northeastern Brazil, where the climate is characterized by marked seasonality in precipitation levels. Although a thin continuous marginal parenchyma band represents the limit of seasonal xylem production, and in spite of the presence of false rings, cross-dating is possible. In this sense, an interseries correlation of 0.572 was found indicating a considerable degree of consistency in the variability found among trees. Precipitation between January and July has a direct influence on growth, while a five month dry season interrupts the active division of cambial cells. A significant positive correlation was also found between sea surface temperatures (SSTs) in the tropical Atlantic and tree growth, but with a lag of six months. As the rainfall regime of northeastern Brazil presents a great deal of inter-annual variability due to fluctuations in global factors such as the SSTs of the tropical Atlantic and the intertropical convergence zone, the close relationship observed between *P. pyramidalis* tree growth and regional climate fluctuations appears as a logical plant-environment interaction that can be used as a reliable parameter for dendroecological inferences on tree growth dynamics and the reconstructions of past droughts in the Caatinga region.

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Contents

1. Introduction	14
2. Material and methods	16
2.1. Study area	16
3. Sample collection, tree-ring data treatment and climate data	16
4. Results	18
5. Discussion and conclusion	20
Acknowledgments	22
References	22

1. Introduction

In the tropics, seasonal dry forests occur in semiarid regions, and are generally subject to severe or absolute periods of drought (Mooney et al., 1995). As a consequence, many tree species are highly sensitive to unfavorable hydrological conditions, and interrupt their cambial activity during drought periods, leading to the

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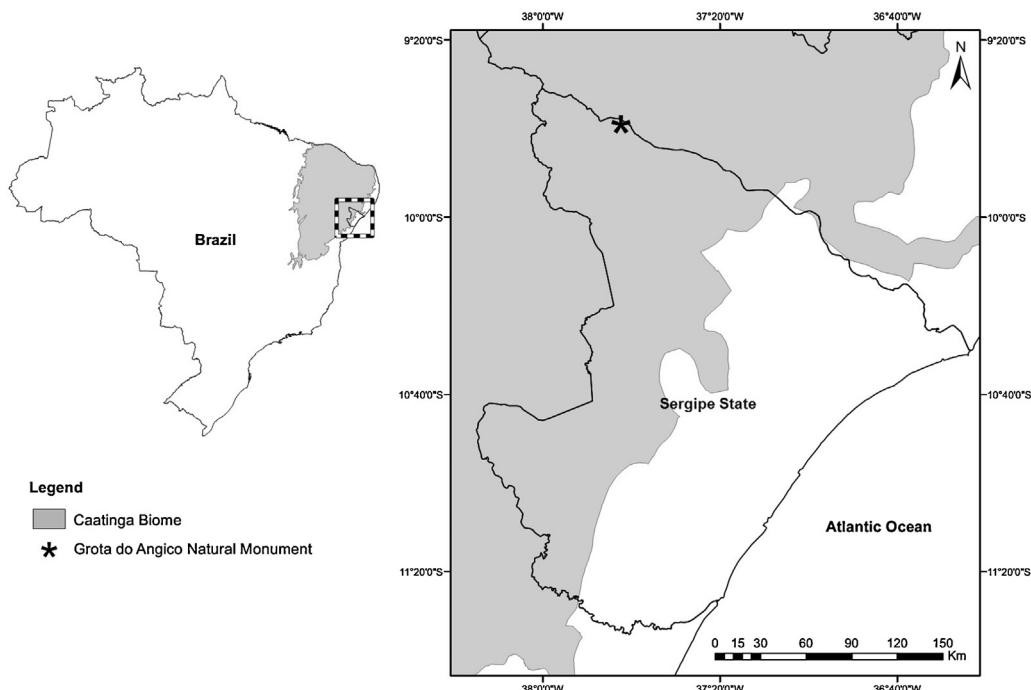


Fig. 1. Location of the semiarid zone in Brazil and detailed map of the study site Grota do Angico Natural Monument in the state of Sergipe.

formation of anatomically discernible growth rings (Worbes, 1995; Fichtler et al., 2004).

A number of studies have confirmed the presence of growth rings in tree species found typically in semiarid environments, although they have also emphasized the problems associated with the identification of rings, which may be narrow or irregular, often with poorly-defined limits (Cherubini et al., 2003; Schöngart et al., 2006). However, other studies have found well-defined and synchronizable growth rings in tree species native to semiarid environments, enabling the extraction of dendrochronological data on

tree age, growth rates, and their relationship with environmental factors (Fichtler et al., 2004; Sass-Klaassen et al., 2008).

In Brazil, the largest semiarid forest system is known as the Caatinga, which is characterized as a spiny deciduous savanna (Tsuchiya, 1995). The Caatinga is located in northeastern Brazil, covering a total area of approximately 850,000 km². Temperatures are relatively constant, at around 25 °C throughout the year, while evapotranspiration rates are high (1500–2000 mm year⁻¹), and the soils are shallow, with a reduced capacity for water absorption. The mean annual precipitation ranges between 300 mm and 1000 mm, depending on the region, with the rainy season being restricted to a

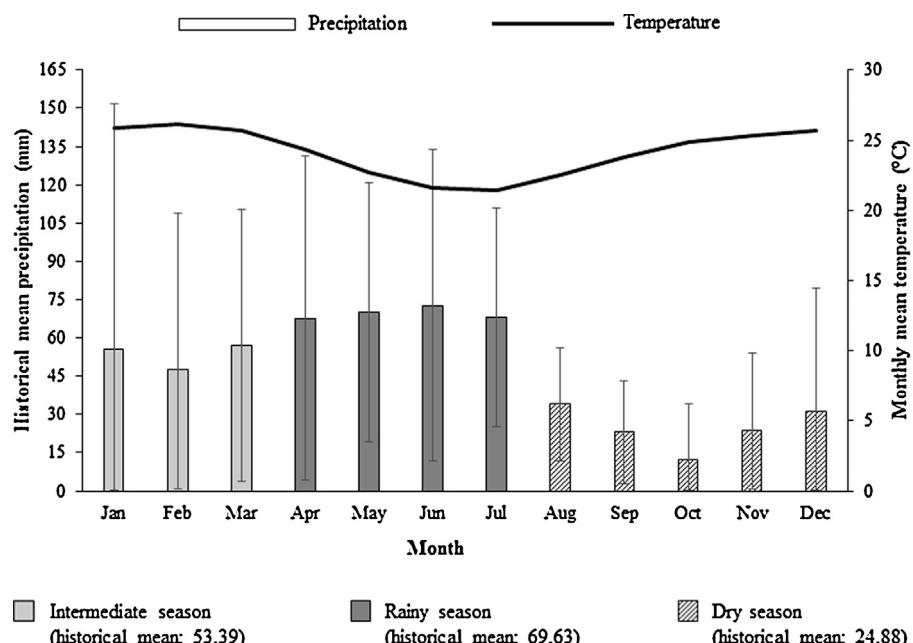


Fig. 2. Mean monthly precipitation (with standard deviation) between 1963 and 2010, and air temperatures between 1977 and 1983, recorded in Poço Redondo, Sergipe, Brazil (Source: SEMARH, 2013).

3–4 month period, followed by a prolonged dry season of between 8 and 9 months (Sampaio, 2010). As the rains are concentrated in a relatively short period, the hydrological deficit of the dry season tends to be high (Tsuchiya, 1995).

The climate of the semiarid zone of northeastern Brazil is determined by influences of atmospheric and oceanic processes that determine the spatial and temporal distribution of precipitation patterns. The primary factors are the inter-tropical convergence zone (ITCZ), the southeast trade winds, and atmospheric disturbances originating in the Atlantic Ocean. These disturbances are modulated by the sea surface temperatures (SSTs), both in the tropical Atlantic and the equatorial Pacific, global-scale factors that determine wetter and drier years in the Brazilian Northeast region (Magalhães, 2012).

The Caatinga is characterized by considerable variations between years in total precipitation, reflecting the effects of these large-scale atmospheric systems on the region's climate (Andreoli and Kayano, 2007). This annual variation in rainfall includes prolonged droughts in some years, and an extended rainy season in others, which may often be characterized by major local downpours (of over 100 mm) concentrated irregularly into a few days or even hours (Nobre, 2012).

The deciduous vegetation of the Caatinga is well-adapted to these climatic conditions, and is known to include more than 5300 species, of which at least 318 are endemic (Giulietti et al., 2006). The most prominent plant family in the Caatinga is the Fabaceae, which is represented by 278 species (Giulietti et al., 2006), including *Poincianella pyramidalis* Tul. L.P. Queiroz, from sub-family Caesalpinoideae, known locally as the catingueira. This tree species is endemic but widespread to the Caatinga (Maia, 2012), and is frequently used by rural communities for firewood and charcoal production (Dias Leme and Gasson, 2012). Large tracts of catingueira still exist because it reacts with vigorous growth following coppicing or pollarding, even during the dry season, producing trees of up to 4–6 m in height, although larger individuals may reach 12 m (Maia, 2012).

Recent studies have shown that *P. pyramidalis* produces distinct growth rings, which boundary is anatomically defined by a fine border of the marginal parenchyma, with one or two cells in width (Paula and Alves, 1980; Gasson et al., 2009; Silva et al., 2009; Dias Leme and Gasson, 2012). As the analysis of tree rings can provide important insights into the influence of environmental factors on the seasonal formation of the xylem and variation in growth rates in the semiarid Caatinga (Tsuchiya, 1990), the present study investigated how growth in *P. pyramidalis* is affected by regional and global weather phenomena.

Specifically, this study tested the hypothesis that tree-ring chronologies of *P. pyramidalis* responds systematically to the variation in local hydrological variables, as well as to global climatic conditions, such as the SSTs of the Atlantic Ocean. The results provide important insights into the dynamics of the Caatinga forest, the ecology of catingueira, and the potential reconstruction of past climate changes in this semiarid region.

2. Material and methods

2.1. Study area

This study was conducted in the Grotão do Angico Natural Monument ($9^{\circ}40'00''S$; $37^{\circ}40'30''W$), a conservation unit located on the right margin of the São Francisco River in Poço Redondo, Sergipe, Brazil (Fig. 1). The climate is semiarid (Bsh in Köppen, 1948), and characterized by two distinct precipitation conditions: a rainy season between April and July, and a dry season in the second half of the year, August–December (Fig. 2). The first three months of the year

(January–March) are relatively dry (Magalhães, 2012), although major fluctuations are observed among years – as shown by the standard deviations of the historic means during this period (Fig. 2) – and heavy downpours may occur at any time during this period, and in any place (Nobre, 2012).

In the study area, mean annual precipitation is approximately 600 mm and air temperatures are relatively constant, with a mean of $25.6^{\circ}C$ (Fig. 2). December is the hottest month and August, the coolest. Leptosols and luvisols, usually associated with rocky outcrops, are the principal types of soil found in the study area (Embrapa, 2006). In addition to the reduced water storage capacity of these soils, they present a physical barrier to root growth, due to their reduced depth, high levels of erosion, and major variation in fertility (Silva and Silva, 1997).

The vegetation at the site of the present study is of the hyper-xerophytic deciduous open forest type (Ribeiro and Mello, 2007; Fig. 3). Due to its history of exploitation, the vegetation of the study area is a mosaic of habitats at different stages of regeneration (Ribeiro and Mello, 2007). In the Caatinga, forests exploited for their timber resources or livestock grazing are rarely managed for sustainable use (Maia, 2012). As a result, most habitats in the Caatinga are fragmented, with a loss of plant diversity, and few patches of pristine vegetation (Pagano et al., 2011).

3. Sample collection, tree-ring data treatment and climate data

A total of 13 *P. pyramidalis* trees was sampled. From these samples, eight were obtained by a non-destructive method (one sample per tree), using a motorized Stihl BT45 wood-boring drill, with a single radial core being collected from each tree. The other five trees were sampled destructively, with a disk being obtained at a height of 1.30 m above the ground in each case. Two radial cores were obtained from two of these disks, with a total of 15 cores being collected for the construction of the chronology. The stem diameter at breast height (DBH) was over 15 cm for all trees, and the trunks from which the samples were taken were absolutely straight and free of imperfection in order to guarantee the reliability of the ring width measurements.

To facilitate the anatomical identification of the boundary ring, the transversal surfaces of the wood samples were polished carefully with sandpaper of different grits (ISO86: P80–P600), following Orvis and Grissino-Mayer (2002). The growth rings were then marked and dated under a microscope at magnifications between $10\times$ and $40\times$, and then digitalized with a scanner (HP Deskjet F4100) at a resolution of 1200 dpi. The TIFF-format digitized images were transferred to the Image-Pro Plus program (version 4.5.0.29) for the measurement of the growth rings from pith to bark, with an accuracy of 0.01 mm. Subsequently, the ring-width measurements were cross-correlated using visual and statistical techniques, such as the COFECHA computer software (Holmes, 1983). The cross-dating comparison helped us to identify missing rings and other potential errors during measurement.

The final tree-ring width index chronology was computed using the ARSTAN (ARS41d_xp version) software package (Cook, 1985). This program computes chronologies from tree-ring data that have been de-trended by curve-fitting. This procedure removes portions of the variance related to factors other than climate. The individual ring-width series analyzed here were de-trended using a linear regression and a cubic smoothing spline function with a 50% cutoff filter (Cook and Peters, 1981). The indices for the series were computed as the ratios between the original measurements and the values selected by the curve-fitting procedure. Mean function values were then calculated to produce a robust function to enhance

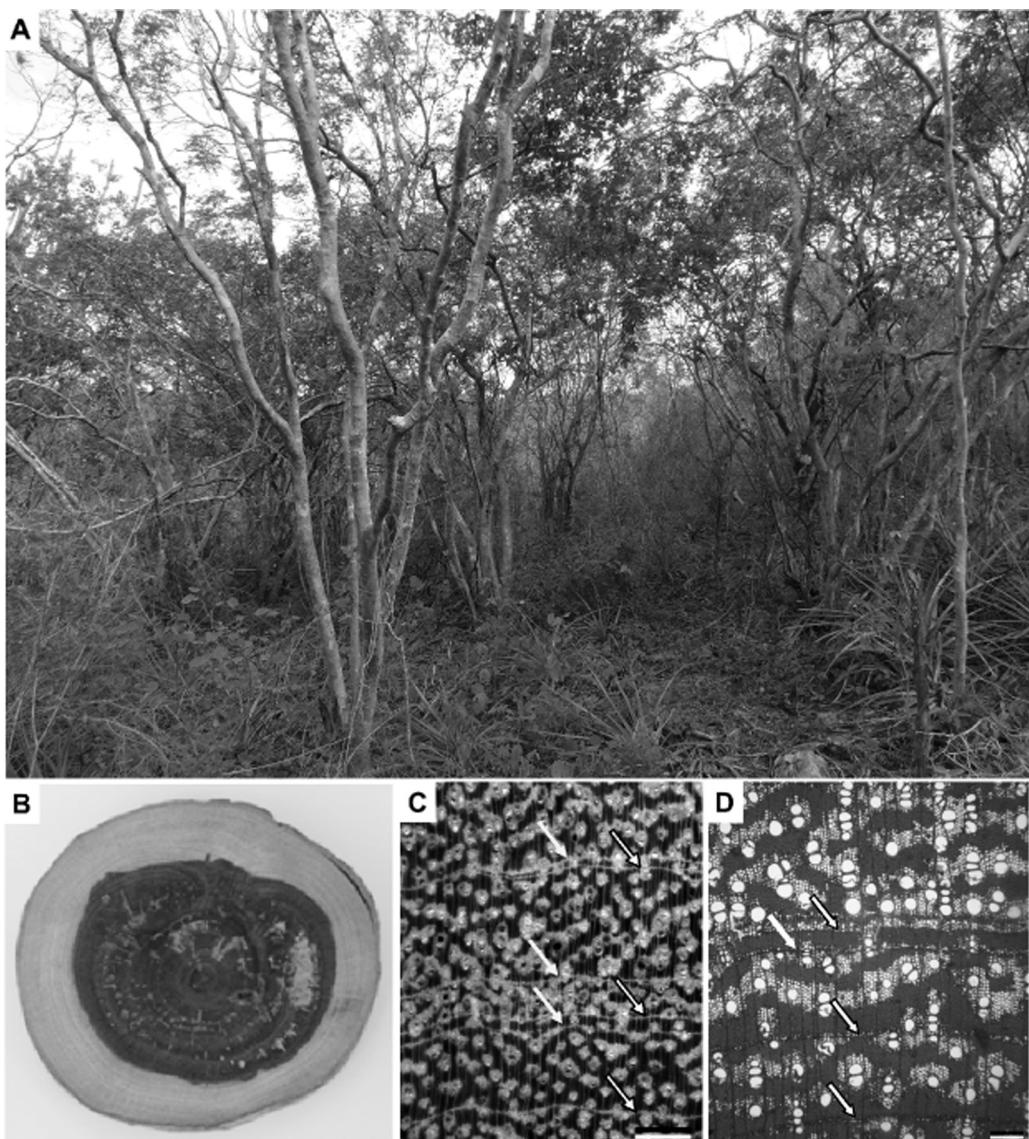


Fig. 3. (A) Photograph of the study site illustrating the vegetation physiognomy of *Poincianella pyramidalis* forests. Below, from left to right, images of the wood of *P. pyramidalis*: (B) A polished disc from the basal stem position; (C) polished macroscopic image (scale bars = 1 mm); (D) sliding microtome section image (scale bars = 30 μm). Arrows outlined in black indicate true boundary rings while the white arrows indicate the false growth rings.

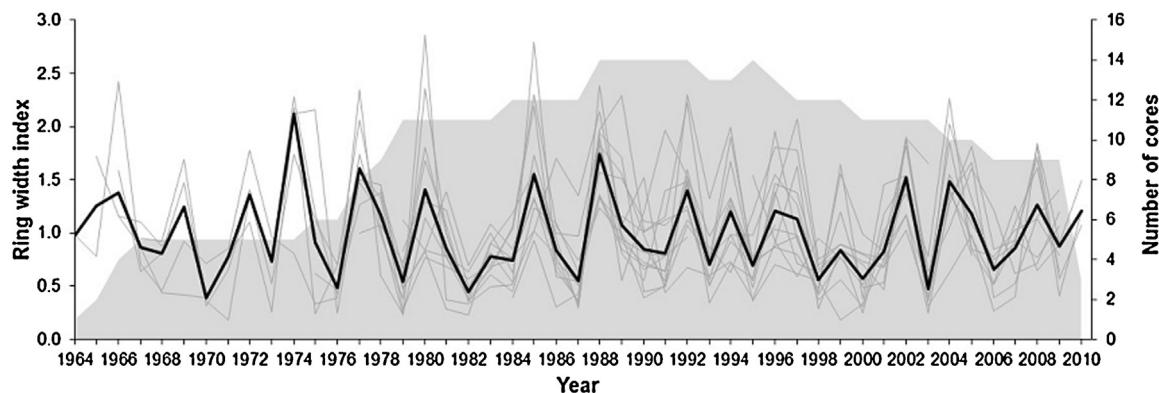


Fig. 4. Standard tree-ring chronology of *Poincianella pyramidalis* from Grotto do Angico, Sergipe, Brazil after ARSTAN (solid line). Individual index series (light lines) are included for comparison. The background polygon represents the number of wood samples analyzed at each year.

the common signal. The standard chronology version was used for further comparisons between tree growth and climate.

The influence of climatic factors on tree-ring width was analyzed using a Pearson correlation coefficient (r) with a 99% significance

Table 1

Pearson correlations, considering the period from January of the previous year ($y-1$) and December of the current year, between: annual rainfall at Poço Redondo and the surface temperature of the Atlantic Ocean (STA) between Equator-20S and 10E-30W (STA/precipitation); tree-ring chronology and STA (STA/chronology); tree-ring chronology and annual precipitation at Poço Redondo (Precipitation/chronology); tree-ring chronology and the regional air temperature in 10S-37.5W (Air temperature/chronology). Analyzed period between 1964 and 2010.

Month	STA/Precipitation	STA/Chronology	Precipitation/chronology	Air temperature/chronology
January $y-1$	0.23	0.19	-0.15	-0.20
February $y-1$	0.28	0.20	-0.24	0.05
March $y-1$	0.28	0.20	-0.44	0.13
April $y-1$	0.31 ^a	0.27	0.00	0.04
May $y-1$	0.38 ^a	0.32 ^a	-0.17	0.06
June $y-1$	0.32 ^a	0.30 ^a	-0.19	-0.15
July $y-1$	0.27	0.22	-0.26	-0.08
August $y-1$	0.27	0.21	0.06	-0.01
September $y-1$	0.36 ^a	0.35 ^a	0.21	0.07
October $y-1$	0.22	0.18	0.20	0.05
November $y-1$	0.20	0.15	-0.06	0.16
December $y-1$	0.13	0.01	-0.22	0.20
January	0.17	0.08	0.39 ^a	0.19
February	0.01	0.01	0.49 ^a	-0.24
March	-0.07	-0.01	0.39 ^a	-0.11
April	-0.09	0.04	0.37 ^a	-0.08
May	-0.08	0.08	0.35 ^a	-0.07
June	-0.07	0.04	0.33 ^a	0.03
July	0.00	0.09	0.37 ^a	0.05
August	0.01	0.07	0.16	-0.12
September	-0.07	-0.07	-0.26	-0.11
October	0.02	0.01	-0.21	0.01
November	0.06	-0.01	0.05	-0.14
December	0.25	0.11	0.43 ^a	0.05

^a Critical correlation ($r=0.29$) considering a significance level of 1%.

level (Fritts, 1976; Blasing et al., 1984). We used monthly rainfall data from the Poço Redondo meteorological station, approximately 15 km from the study site for the period between 1964 and 2010, and the monthly tropical South Atlantic index (TSA) defined as the anomaly of the average of the monthly sea surface temperature (SST) from the spatial coordinates between Equator-20S and 10E-30W (<http://www.esrl.noaa.gov/psd/data/correlation/tsa.data>). For comparison with land air temperature we got this variable in 10S-37.5W (<http://www.esrl.noaa.gov/psd/cgi-bin/data/timeseries/timeseries1.pl>). The degree of correlation between this tree-ring chronology and each of these series of monthly variables was then verified, with the series being matched to either the current or the preceding year for comparisons of the possible influence of previous climatic conditions on current growth. Thus, the correlation matrix comprised the period between January of the year $n-1$ (previous year) and December of year n (current year), and the analyzed period spanned between 1964 and 2010. These comparisons supported the documentation of the seasonality and strength of the tree-growth response to climate variability. The resulting correlations permitted the identification of the specific months in which climatic variables were highly correlated with radial growth in *P. pyramidalis*. Once these periods had been identified and delimited, a multiple linear regression was run to define the relative importance of each period in the chronology analyzed. In this case, the multiple linear regression was especially important for the estimation of the value of one variable (period) based on a set of other variables. This permitted the identification of the period of the year that has the greatest influence on the radial growth of *P. pyramidalis*.

A strong positive correlation was found between the chronology and the historical series of local annual rainfall (Spearman's $\rho=0.70$; Fig. 5)

In addition to identifying the climate characteristics from those months that influenced the formation of tree growth rings, the data were also analyzed for the presence of an association between years that were more (or less) rainy than average and the highest (or lowest) growth rates. This analysis was based on Spearman correlation coefficients for comparison between the standard chronology and

Table 2

Multiple regression analysis between the chronology (dependent variable) and the historical mean precipitation of January to July (Jan-Jul) and December (Dec).

Variables	b	Standard error	β
Intercept	0.4807	0.0773	–
Jan-Jul	0.0072	0.0011	0.6584 ^a
Dec	0.0015	0.0007	0.2045

^a $p < 0.001$; $F=28.85$; $R^2=0.56$; standard error of estimate = 0.24; $n=47$. R^2 = coefficient of determination; b = regression coefficient; β = standardized coefficient.

Table 3

Multiple regression analysis between the chronology (dependent variable) and the historical mean precipitation of January to March (Jan–Marc), April to July (Apr–Jul) and December (Dec).

Variables	b	Standard error	β
Intercept	0.5051	0.0801	–
Jan–Marc	0.0037	0.0007	0.5159 ^a
Apr–Jul	0.0032	0.0010	0.3439 ^a
Dec	0.0017	0.0008	0.2356

^a $p < 0.001$; $F=19.77$; $R^2=0.58$; standard error of estimate = 0.24; $n=47$. R^2 = coefficient of determination; b = regression coefficient; β = standardized coefficient.

both total annual precipitation and total seasonal precipitation of the wettest period of the year (January–July).

One further set of analyses was done to assess spatial relationships between the chronology and gridded precipitation, air temperature, and SSTs. To show these relationships three correlation maps were generated by means of the facilities offered at the national oceanic and atmospheric administration (NOAA) website (<http://www.esrl.noaa.gov/psd/data/correlation>). A common period between 1964 and 2010 were used for all datasets.

4. Results

The growth rings of *P. pyramidalis* are visible under hand lens (Fig. 3B) and obviously under microscope (Fig. 3C,D). These growth

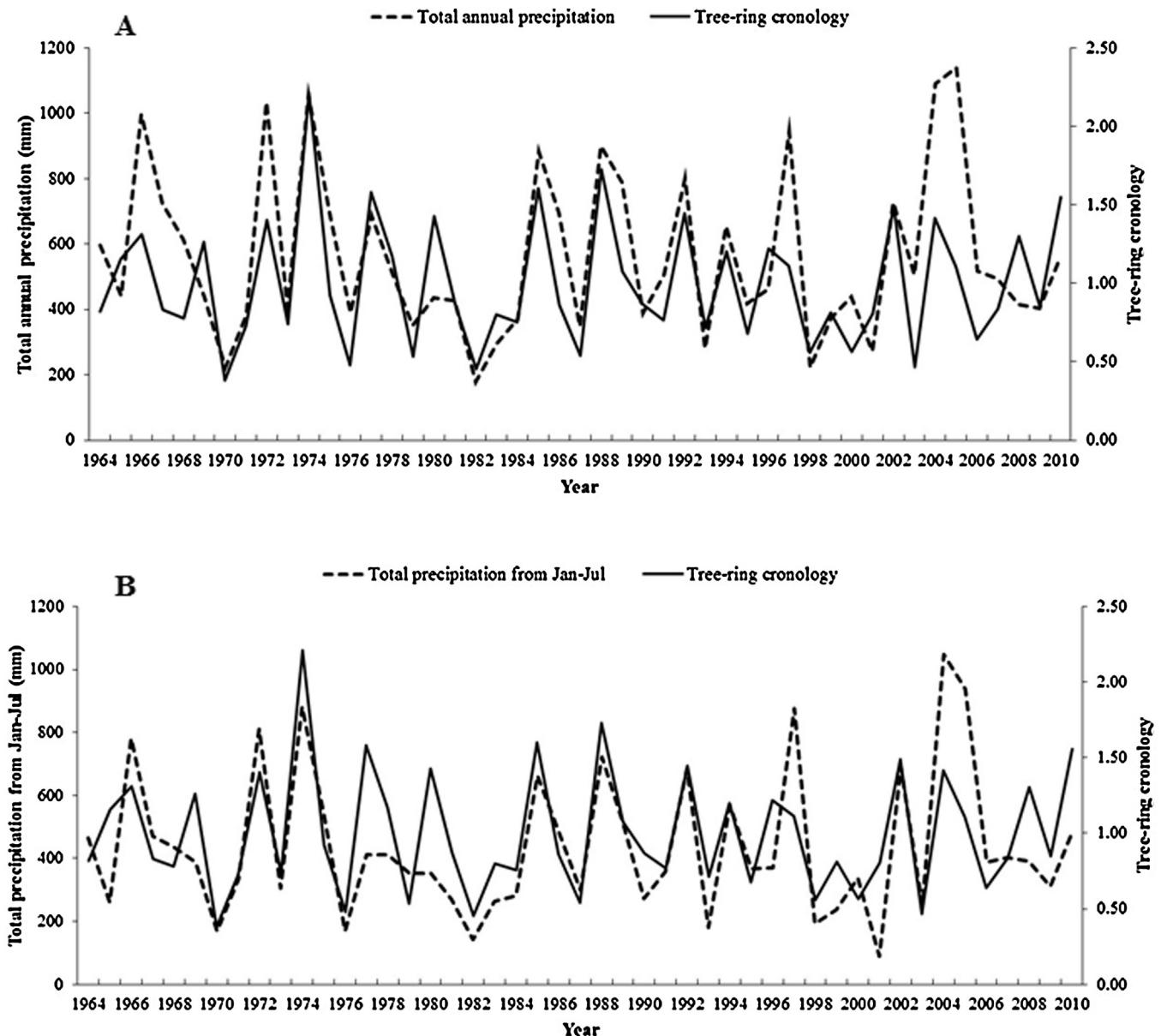


Fig. 5. Relationship between the standard chronology of *Poincianella pyramidalis* and (A) total annual precipitation, and (B) total seasonal precipitation between January and July. Rainfall data is from Poço Redondo meteorological station (Sergipe, Brazil), spanning between 1964 and 2010.

rings are revealed by concentric changes in their wood anatomy particularly associated to a narrow band of marginal parenchyma (Fig. 3). However, false growth rings were also observed in all trees, which initially hampered the analytical dating procedures. It was possible to identify these false rings through the cross-dating process. In general, these false growth rings are characterized by boundaries of fibers with thicker walls, often associated with vasicentric parenchyma forming semi-continuous lines (Fig. 3C,D). Because of the rainy season in the study region occurs between April and July (Fig. 2), we assumed that the tree rings are formed in this period.

Similarities among trees in the annual growth pattern were evident during the cross-dating process, which indicated mean inter-correlation values of 0.572 (ranging from 0.4 to 0.7) among the radial samples of all the trees, with a mean sensitivity of 0.607. The number of growth rings varied from 15 to 46, with a mean of 29.4 (standard deviation = 8.73). Rotting heartwood was found in five trees, impeding the observation of some of the rings in this area.

All the other rings were included in their respective time series. The chronology resulted from a total of 15 radial series (Fig. 4).

The correlation between the chronology and climatic variables is shown in Table 1. A significant positive relationship was found between local precipitation and the TSA in April–June, and September during the preceding year. With the exception of April, these same months of the preceding years were also correlated positively with the tree-ring chronology. In relation to rainfall, the most significant months for the *P. pyramidalis* radial growth were January through July and December of the current year. Comparison between the chronology and land air temperature, however, did not show any significant correlation, although negative values were obtained for the whole growth period between February and May.

The multiple linear regression between the chronology and the historical mean precipitation recorded in the months with the highest precipitation (January–July and December) indicated significant differences between periods. Only the historical mean

precipitation of January–July period played a relevant role in the growth of the plants (Table 2). The historical mean precipitations of January–March (intermediate season), April–July (rainy season), and December were also compared in relation to the chronology through multiple linear regression analysis and confirmed the prior results, that only December was not significant (Table 3A), and between the chronology and total precipitation corresponding to the wettest season of the year between January and July (Spearman's $\rho=0.70$; Fig. 5B). The correlation coefficient does not necessarily indicate a relationship of cause-and-effect, but it shows the degree of association between variables. Thereby, these variables are associated with one another and they can be considered to be indicators of uniformity, that is, the increase in annual precipitation (x values) corresponds to an increase in the growth values recorded in the chronology (y values).

Nevertheless, in six of the total years analyzed between 1964 and 2010, values were not conform to the predominant pattern as shown in Fig. 5A, corresponding to years 1964, 1965, 1969, 1997, 2000 and 2008. Other cases showed that wet extremes in the precipitation were not matched by extremes in growth, most notably in 1966, 1980, 2004, and 2005.

On a sub-hemispheric scale, spatial correlations were found between the chronology, precipitation and air temperatures, as well as with the SSTs of the tropical Atlantic Ocean between 20°N–60°S and 90°E–10°W for the period between 1964 and 2010 (Fig. 6). As found in the direct association between the growth of *P. pyramidalis* and local precipitation levels, the correlations on a spatial scale indicate a positive relationship with the land precipitation occurring between January and July (Fig. 6B). This correlation is strongest in the region of the present study, but may be extrapolated to the whole northeastern Brazil. A negative correlation was observed between tree growth and the land surface air temperatures recorded during the same period (Fig. 6A). The *P. pyramidalis* trees also presented a positive correlation with the SSTs of the Atlantic comprised between latitudes 10°N and 30°S, with a nucleus of higher correlations near the west coast of Africa (Fig. 6C).

5. Discussion and conclusion

The results of the anatomical observations indicate that *P. pyramidalis* forms distinct annual growth rings, as confirmed in previous studies of this species growing on different sites in the Brazilian Caatinga (Paula and Alves, 1980; Tsuchiya, 1990; Silva et al., 2009; Nogueira, 2011).

One problem for the analysis of the specimens was the presence of areas with rotten heartwood near the medulla. This feature impeded the identification of the complete age of the analyzed trees. While it has not been reported in previous studies, observations in the field indicated that this rotting may be the result of termite activity. Despite this problem, the formation of the growth rings and their dating control by cross-dating procedures proved their effectiveness in using this species for constructing a precise calendar chronology, particularly during the process to identify true and false rings.

The chronology obtained in this study was associated with the rainiest months of the year that is, between April and July. Precipitation is considered to be the most important determinant of the secondary growth of tropical tree species (Worbes, 1989). In the present study, however, the months between January, February, and March, that is, the transitional rainy season, were also correlated with the chronology, even though they are not strictly considered to be part of the rainy season in the study area (Magalhães, 2012; Nobre, 2012). This may be accounted for by the historical variation in rainfall levels recorded during this period.

In other words, while mean precipitation during this period is between 47 mm and 55 mm, variation between years is considerable, and rainfall may be more than 100 mm in some years, in the form of sporadic downpours. After a long period of drought, *P. pyramidalis* promptly responds with biomass production to this sudden peak in humidity, evidencing that cambial activity of this drought deciduous species starts soon after the rains commence.

Brazil's semiarid Caatinga scrublands are considered to have an anomalous rainfall pattern in comparison with other regions located at the same latitude (Alves and Repelli, 1992). The seasons are not well defined by simple fluctuations in rainfall levels, given that the distribution of the rains may vary considerably among years in both time and space (Magalhães, 2012). Even when total annual precipitation is close to mean levels, prolonged periods of drought may occur, being interrupted by much shorter periods of intense and localized rainfall (Nobre and Melo, 2001). In addition to the annual dry-rainy cycle, total precipitation varies considerably (Embrapa, 2006), and may begin and end in different months, with considerable variation in the duration of the rainy season among years (Sampaio, 2010).

In December, rainfall correlated significantly with the defined chronology (Pearson coefficient). However, a multiple regression analysis indicated the opposite result. This is probably due the lack of rain in December in most years of the historical series. According to the historical precipitation data (Fig. 2), sporadic torrential downpours occur between January and March, and also in December. In December, however, these downpours do not occur every year, as in a typical cycle, so the month should not have a systematic influence on the growth of *P. pyramidalis*. When there is abnormally high precipitation in December, false growth rings will probably form. On the other hand, the intermediate season (January–March) is as important to plant growth as the rainy season (April–July), and a prolonged rainy period (January–July) will have a far more pronounced effect on growth than a single torrential downpour. A strong intra-annual variability in primary production in relation to water availability is consequence that cambial activity triggers the formation of intra-annual secondary cell wall thickenings resembling latewood-like cells, changes in vessel diameter or density or any other particular arrangements in the anatomical pattern outside the expected structure of wood. This phenomenon happens irregularly in space and in time, making difficult to assign a date to the formation of rings (Cherubini et al., 2003).

In the August–December period, then, the lack of rainfall (typically <50 mm) will disrupt the formation of vascular cambial cells. This is consistent with the findings of Worbes (1995) who concludes that regions with a dry season during which three or more months have precipitation of less than 60 mm may normally induce a period of dormancy.

According to Ferrero et al. (2014) rainfall seasonality reinforces the weak seasonality in temperature that results in an interval of cambial dormancy and the consequent formation of annual bands in more temperate regions. The results of this study not only indicate a close relationship with local and regional rainfall patterns, but also considerable variation within seasons. In the comparative analysis of the chronology and historical annual precipitation patterns (Fig. 5A), it is possible to observe that occur years (i) drier than average, but with increased plant growth and (ii) rainier than average, with reduced or intermediate plant growth. The first of these scenarios may be accounted for by local downpours, which sometimes exceed 100 mm in a day, but occur within a small physical area (Sampaio, 2010). The other correspond to years of normal or above normal rainfall, when precipitation was concentrated within a small number of months, resulting in a prolonged period of drought, which restricted plant growth. Furthermore, it is possible to observe that the higher the amount of rainfall during the January–July period, the greater the plant growth (Fig. 5B), in

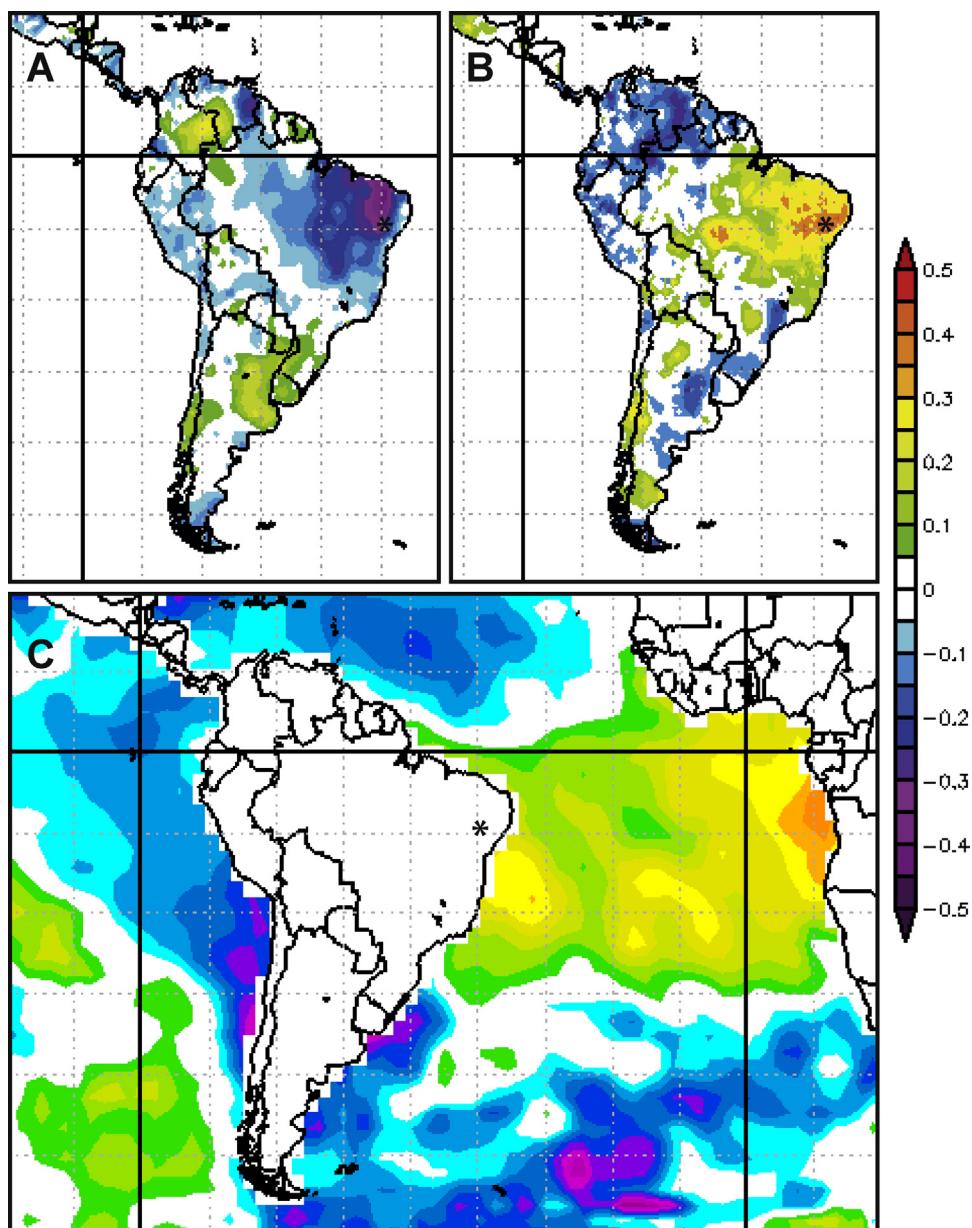


Fig. 6. Spatial correlation patterns between the standard chronology of *Poincianella pyramidalis* and: (A) land air temperatures, (B) land precipitation (both during the months of January to July), and (C) SSTs of the Atlantic Ocean (during months between April and September of the preceding year). Correlation coefficients are shown at the right. Maps A and B show the area between 20°N–60°S and 80°E–30°E, and map C between 20°N–60°S and 90°E–10°W. All climate data were obtained from NOAA website (<http://www.esrl.noaa.gov/psd/data/correlation/>).

agreement with what is observed in comparisons with the annual rainfall. Clearly, then, understanding the distribution of rainfall over the course of the year is at least as important as the total precipitation for the analysis of dendrochronological patterns in the Caatinga.

These features of the rainfall patterns in the Caatinga also affect the phenology of *P. pyramidalis*, and the definition of these phenological patterns is essential for the understanding of the formation of growth rings in this species. The phenology of *P. pyramidalis* appears to be closely synchronized with rainfall patterns (Maia, 2012), given that the trees begin to lose their leaves between August and October (early dry season), becoming leafless from November onwards. The trees will generally become fully leaved again by approximately 30 days after the onset of the rains (Braga et al., 2003). The activity of the cambium and the formation of the growth rings appear to follow the same sequence. In this case, the prin-

pal factor limiting the growth of *P. pyramidalis* is the annual dry season, when the trees are totally leafless, inhibiting the activity of the cambium, and defining the limits of the growth rings and their radial width.

A similar situation has been recorded in tree species in the semi-deciduous forests of southeastern Brazil (Lisi et al., 2008), where the stress caused by the start of the dry season was the key determinant of the onset of leaf-fall and the formation of growth rings. A number of other studies have recorded a similar pattern in tree species in semiarid tropical regions (Détienne, 1989; Gourlay, 1995; Eshete and Stahl, 1999; Gebrekirstos et al., 2008).

The false growth rings may also be a result of the rapid phenological response of the trees to changes in precipitation levels. During years when the dry season is interrupted by sporadic downpours, leaf flush may appear suddenly, leading to the reactivation of the cambium, and the formation of false growth rings. In tropical dry

forests in Mexico, Bullock and Solís-Magallanes (1990) observed that leaf flush and reproduction in most species occurred not only during the rainy season, but also in association with the rains occurring sporadically during the dry season.

The relationship between climate and tree growth is consistent with the phenology of the species, but few studies of tropical or subtropical species have demonstrated a clear relationship between phenological phases and cambial activity, and the formation of growth rings (Roig, 2000). Given this, additional data will be necessary to better determine whether the false growth rings observed in *P. pyramidalis* are related systematically to isolated downpours occurring during the dry season, and whether a similar pattern can be observed in other woody plants in the Caatinga.

Pearson correlation between the chronology and land air temperature indices did not show any significant correlation, indicating that this variable, at least from the available data, is not a critical factor influencing growth in our species. The negative trend observed between February and May (Table 1) and also detected from the spatial correlations corresponding to the period January–July (Fig. 6A) suggests, however, that air temperature, despite being a relatively constant element throughout the year in the Caatinga region, reflects a negative incidence relative to plant growth at the rainiest months. In dry environments, although the first rains cause a decrease in air temperature, it tends to remain high enough to cause extensive evaporation. This is a result that can be observed in dry areas of southern South America, in which the high temperatures in spring increase evapotranspiration, reduces water availability to plants and results in an inverse growth response (Giantomaso et al., 2008; Roig and Villalba, 2008). For this reason, it is possible that periods with high temperatures and low precipitation will restrict the secondary growth of *P. pyramidalis*.

Comparing the tree-ring chronology of *P. pyramidalis* with the TSA, growth is clearly favored by above-average temperatures during the previous growing season, consistent with the cross-correlation between rainfall and Atlantic SSTs (Table 1 and Fig. 6C). This indicates that the occurrence of large-scale climatic phenomena affects the climate at the Caatinga region and hence, the tree growth of *P. pyramidalis*. In the specific case of northeastern Brazil, the SSTs of the tropical Atlantic and the equatorial Pacific oceans and the intertropical convergence zone (ITCZ) over the Atlantic Ocean are global factors that control atmospheric circulation and determine rainfall patterns in the region (Uvo et al., 1998; Nobre, 2012). The ITCZ can be defined as a band of clouds encircling the Earth near the equator, formed mainly by the confluence of the trade winds from the Northern Hemisphere with those of the Southern Hemisphere. The collision of these systems causes warm moist air to rise, forming rainclouds. The ITCZ is the most important factor determining rainfall levels in northeastern Brazil. It migrates seasonally from the north, in August–October, to a more southerly position, between February and April. This displacement is related to the patterns of SSTs in the tropical Atlantic Ocean (Uvo et al., 1998; Ferreira and Mello, 2005). The ITCZ is most pronounced over the oceans and, consequently, the SST is a factor that most influence its position and intensity. In years that are drier than normal, the ITCZ remains in its southern phase from February to March, whereas, in rainier years, it remains there until May (Ferreira and Mello, 2005).

A number of other aspects of the region's large-scale circulation patterns may also influence the volume of precipitation in northeastern Brazil. In particular, a direct link can be observed between droughts and a combination of abnormally low temperatures in the South Atlantic and abnormally high ones in the North Atlantic. During rainy years, this configuration of SSTs is inverted (Moura and Kagano, 1986). This may result in considerable variation in total rainfall levels between years, often resulting in alternating wet and dry years (Nobre, 2012).

The between-year variation in SSTs and winds over the Atlantic Ocean have a profound influence on climatic fluctuations in South America in general, and in northeastern Brazil in particular (Hastenrath, 1990; Rao et al., 1993; Nobre and Shukla, 1996; Alves et al., 1997). The results of the present study indicate that rainfall patterns in the semiarid zone of Sergipe area are dependent on the warming of the Atlantic Ocean near the coast during the preceding year (in April–June and September). In other words, the SSTs of the Atlantic in a given year has a significantly positive influence on the precipitation between January and July of the following year in this region.

The SSTs of the Atlantic during the same period (May, June, and September) of the previous year also had a significantly positive influence on the formation of growth rings in the trees studied here. Furthermore, the period in which tree growth was identified (January–July) coincides with that of the highest precipitation levels. This supports the conclusion that the local tree population of *P. pyramidalis* responds to regional and global climatic conditions, indicating its potential for inclusion in climate reconstruction. The results also support the idea that tree-ring data can provide one of the best sources of proxy information on these phenomena, extending the potential for the understanding of the effects of climatic variability on an annual timescale, due to their precise dating and comparability with meteorological data (Briffa et al., 2001; Büntgen et al., 2011; Zhang et al., 2014).

Overall, then, the present study confirmed that *P. pyramidalis*, a species endemic to the semiarid Brazilian Northeast, forms annual growth rings, which permitted the construction of tree-ring chronologies, which annual variation is well correlated with rainfall levels and SSTs at the Atlantic Ocean. Future dendrochronological studies in the Caatinga should incorporate a longer series of growth rings. It is possible to find larger individuals of *P. pyramidalis* in preserved areas but it is also feasible to expand the number of available chronologies, and climatic reconstructions, through the analysis of *P. pyramidalis* timbers that have been used in the construction of houses or fences on local rural properties. These considerations have potentially important transcendence for applications in dendroecology, wildlife conservation, climate reconstruction, and the assessment of anthropogenic impacts in the semiarid Caatinga of northeastern Brazil.

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