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High-fidelity representation of climate variations by *Amburana cearensis* tree-ring chronologies across a tropical forest transition in South America

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A B S T R A C T

Numerous ring-width chronologies from different species have recently been developed in diverse tropical forests across South America. However, the temporal and spatial climate signals in these tropical chronologies is less well known. In this work, annual growth rings of *Amburana cearensis*, a widely distributed tropical tree species, were employed to estimate temporal and spatial patterns of climate variability in the transition from the dry Chiquitano (16–17°S) to the humid Guarayos-southern Amazon (14–15°S) forests. Four well-replicated chronologies (16–21 trees, 22–28 radii) of *A. cearensis* were compared with temperature and precipitation records available in the region. The interannual variations in all four *A. cearensis* tree-ring chronologies are positively correlated with precipitation and negatively with temperature during the late dry-early wet season, the classic moisture response seen widely in trees from dry tropical and temperate forests worldwide. However, the chronologies from the dry Chiquitano forests of southern Bolivia reflect the regional reduction in precipitation during recent decades, while the chronologies from the tropical lowland moist forests in the north capture the recent increase in precipitation in the southern Amazon basin. These results indicate that *A. cearensis* tree growth is not only sensitive to the moisture balance of the growing season, it can also record subtle differences in regional precipitation trends across the dry to humid forest transition. Comparisons with previously developed *Centrolobium microchaete* chronologies in the region reveal a substantial common signal between chronologies in similar environments, suggesting that regional differences in climate are a major drivers of tree growth along the precipitation gradient. The difficulty of finding *A. cearensis* trees over 150-years old is the main limitation involved in the paleoclimate application of this species. The expansion of monocultures and intensive cattle ranching in the South American tropics are contributing to the loss of these old growth *A. cearensis* trees and the valuable records of climate variability and climate change that they contain.

1. Introduction

Given the close interactions with the global cycles of water, energy and carbon, the tropics regulate climate on a planetary scale. Tropical forests in South America represent the largest area of rainforest on the planet and harbor thousands of tree species (Slik et al., 2015). Numerous studies show the importance of these neotropical forests in the global climate system by modulating moisture recycling, contributing to atmospheric circulation, and regulating large-scale biogeochemical cycles (Nobre et al., 2016; Zemp et al., 2017). Nevertheless, accelerated rates of deforestation and agricultural expansion in the Neotropics are causing unprecedented environmental impacts in this region and surrounding areas (Davidson et al., 2012; Marengo et al., 2018). Global climate change and local anthropogenic processes are intensifying the environmental impacts on these tropical forest ecosystems (Zemp et al., 2017). Therefore, documenting climate variations at different time scales, identifying the forcing responsible for these variations, and establishing their interactions with climate at higher latitudes, are priority research topics for the international scientific community. However, climate records in tropical regions rarely exceed 50–70 years in length, seriously limiting the accurate characterization of climate variability and climate dynamics. Therefore, the development of high-resolution paleoclimatic records, as a valid tool for the temporal extension of instrumental climate records, has become a central objective for climate research in the tropics (Stahle et al., 2020).

Within the set of high-resolution paleoenvironmental records, tree

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rings offer some comparative advantages. Trees are widely distributed allowing the development of chronologies over vast sectors of the temperate and tropical landmasses (Brienen et al., 2016; Sthale, 1996; Villalba et al., 2011). With hundreds to thousands of years in length, the dendrochronological records have annual or even seasonal resolution, facilitating the characterization of climatic variability on a wide range of time scales (interannual to secular), and the identification of the climatic forcing associated with different modes of variability. Dating of dendrochronological records is absolute (Büntgen et al., 2019; Sthale, 1996), allowing characterization of the response of regional and/or global climate to punctuated events in climatic dynamics such as volcanic eruptions (Sigl et al., 2015). Finally, sampling is simple and the development of chronologies from ring widths comparatively inexpensive.

Dendrochronological studies have been widely conducted in the middle and high latitudes of both hemispheres where the annual seasonality in temperature (winter and summer) facilitates the formation of growth rings (Fritts, 1976). In contrast, tropical forests are dominated by broadleaved species with more complex woody structure and generally poor definition of the growth ring boundaries (Brienen et al., 2016; López and Villalba, 2016; Schöngart et al., 2017). The lack of a marked thermal seasonality in the tropics reduces the possibility of finding species with well-demarcated rings. Nevertheless, these limitations have been overcome for a growing number of tropical species and the development of annual tree-ring chronologies is increasing in the tropics of South America (Brienen et al., 2016; Stahle et al., 1999).

Brienen et al. (2016) and Schöngart et al. (2017) provide comprehensive reviews of the development of dendrochronological records in tropical regions of South America. Wood anatomical studies suggest that more than 220 tree species, belonging to 46 botanical families, exhibit annual growth rings (Brienen et al., 2016). The maximum ages in tropical trees rarely exceed 200 years, even though in some regions with extreme growing conditions, they may reach 400–600 years in age (Schöngart et al., 2017).

Tree rings in tropical South America have mostly been used to obtain information on tree species ecology and forest dynamics. In contrast, the analysis of tree growth response to climate has been rare for tree species from the Neotropics (Granato-Souza et al., 2018; López et al., 2017; Stahle et al., 2020). Most studies based on tropical records report climate-growth relationships at the local level (Brienen and Zuidema, 2005; Locosselli et al., 2013; López and Villalba, 2011). Networks with numerous tree-ring chronologies are not yet available from most tropical regions, as it is the case in temperate and cold forests in South America (Morales et al., 2020). It has therefore not been widely possible to evaluate climate-growth relationships for tropical tree species along the strong environments gradients that exist in many tropical forests (López et al., 2019).

Given its wide distribution in the Neotropics, the dendrochronological characteristics of *Amburana cearensis* have been explored in different biomes of South America. Brienen and Zuidema (2005) were the first to evaluate the dendrochronological properties of *A. cearensis* in the tropical lowland moist forests in northern Bolivia. These authors determined the annual nature of the *A. cearensis* growth rings and noted that it can exceed 200 years in age. They also noted that *A. cearensis* radial growth is modulated by variations in precipitation at the beginning of the rainy season (October-December). Paredes-Villanueva et al. (2015) developed an *A. cearensis* chronology based on 8 individuals from the tropical dry forests in Bolivia. At the dry Chiquitano forest, tree growth was directly related to precipitation and inversely to temperature during the growing season (November-March). More recently, Godoy-Veiga et al. (2021) examined variations in *A. cearensis* growth rings at contrasting sites (dry vs. wet) in the tropical dry forests of the Brazilian Cerrado. *A. cearensis* tree growth at the wetter sites is not associated with rainfall during the wet growing season and showed only a moderate association with temperature. However, growth was affected in both environments during years with extreme precipitation and temperature conditions. In years with severe drought, the growth of all trees, regardless of their microenvironmental conditions, was severely affected by water deficit (Godoy-Veiga et al., 2021).

A pronounced precipitation gradient is recorded along the transition between dry and humid tropical lowland moist forest in eastern Bolivia. Rainfall in the dry Chiquitano forests is approximately 1000 mm/year, but it nearly doubles only 100–150 km further north in the humid forests of the southern Amazon basin. It is also interesting to note that precipitation records in the low plains of Bolivia show opposite trends since the mid-20th century. Rainfall has decreased in the Chiquitano dry forests since the 1970 s, while it increased in the Beni plains at the transition to the more humid forest of the southwestern Amazon basin, particularly in the last 20–30 years. A regional analysis recently conducted by Espinoza et al. (2019) at the Upper Madeira Basin in eastern lowland Bolivia showed that in the southern sector of the basin (south of 14°S), rainfall have diminished and the frequency of dry days increased over the period 1981–2017. In contrast, the frequency of wet days (> 10 mm) increase north of 14°S (Espinoza et al., 2019).

The main objective of this study was to investigate the potential of *Amburana cearensis* to record the opposing precipitation trends in the dry and moist biogeographical districts of eastern Bolivia. To this end, we first developed four chronologies of *A. cearensis* strategically located along this environmental transition (Fig. 1) and evaluated their quality using statistical analyses often employed in dendrochronology. Subsequently, radial climate-growth relationships were determined for each study site, as well as the ability of these records to reproduce temporal and spatial variations in precipitation along the precipitation gradient. Finally, the new *A. cearensis* records were compared with the *Centrolobium microchaete* chronologies previously developed in the region (López et al., 2019) to assess the similarities in ring width growth for both species along the Chiquitano-Amazonian moisture gradient.

2. Materials and methods

2.1. Species under study

Amburana cearensis is a Neotropical tree of the Fabaceae family, widely distributed in dry tropical biomes and in the transitions to the Amazonian and Yungas humid biomes (Fig. 2a). Specimens of this species are present in southeastern Peru, throughout central Brazil, mainly in the Caatinga, Cerrado, Mata Atlantica and Pantanal biomes (Godoy-Veiga et al., 2021; Seleme et al., 2015). In Bolivia, *A. cearensis* is distributed in the eastern sector of the country, mainly in the Cerrado and Chaco biomes, although the presence of *A. cearensis* trees has also been recorded in the Cerrado-Amazon transitional forests (Jardim et al., 2003; Killeen et al., 1993). Its southern distribution is in Argentina at the subtropical Chaco Serrano and the southern Yungas forests, while in Paraguay, *A. cearensis* is present in the Cerrado and Chaco biomes, as well as in their transition areas (Morales et al., 2019).

The trees of *A. cearensis* reach a large size with diameters exceeding 70 cm, its bark is smooth, orange-brown, with thin papyrus plates that fall off naturally (Killeen et al., 1993). *A. cearensis* is an obligate deciduous species and appear leafless for periods of several weeks to months during the year. in Bolivia, *A. cearensis* lose their leaves in July and produce new leaves in October-November (Brienen and Zuidema, 2005).

The wood of *A. cearensis* is light yellowish-gray in the sapwood and yellowish-brown in the heartwood. The wood is diffuse porous with large vessels of relatively uniform size (Godoy-Veiga et al., 2021). Growth rings are visible to the naked eye and best defined during the juvenile phase or periods of increased radial growth (López and Villalba, 2016). The boundaries of the rings are marked by denser and darker fibrous tissue at the end of the growth period (Fig. 2b). In most rings, the abundant fibers at the end of the annual ring contrasts with the lighter color of the earlywood mostly composed by vessels surrounded with vasicentric, confluent paratracheal and aliform parenchyma. No false

Fig. 1. The dry forests of the Chiquitano district (left) and the moist forests of the Guarayos district (right) illustrate the south to north vegetation transition into southern Amazonian biome (both photographs taken during the dry season). During the annual dry period, most of the tree species of the Chiquitano forest lose their leaves in contrast to the evergreen or brevi-deciduous species dominant in the humid forest. The characteristics of the vegetation in both forests respond mainly to differences in the total amount of precipitation received and the duration of the dry season.

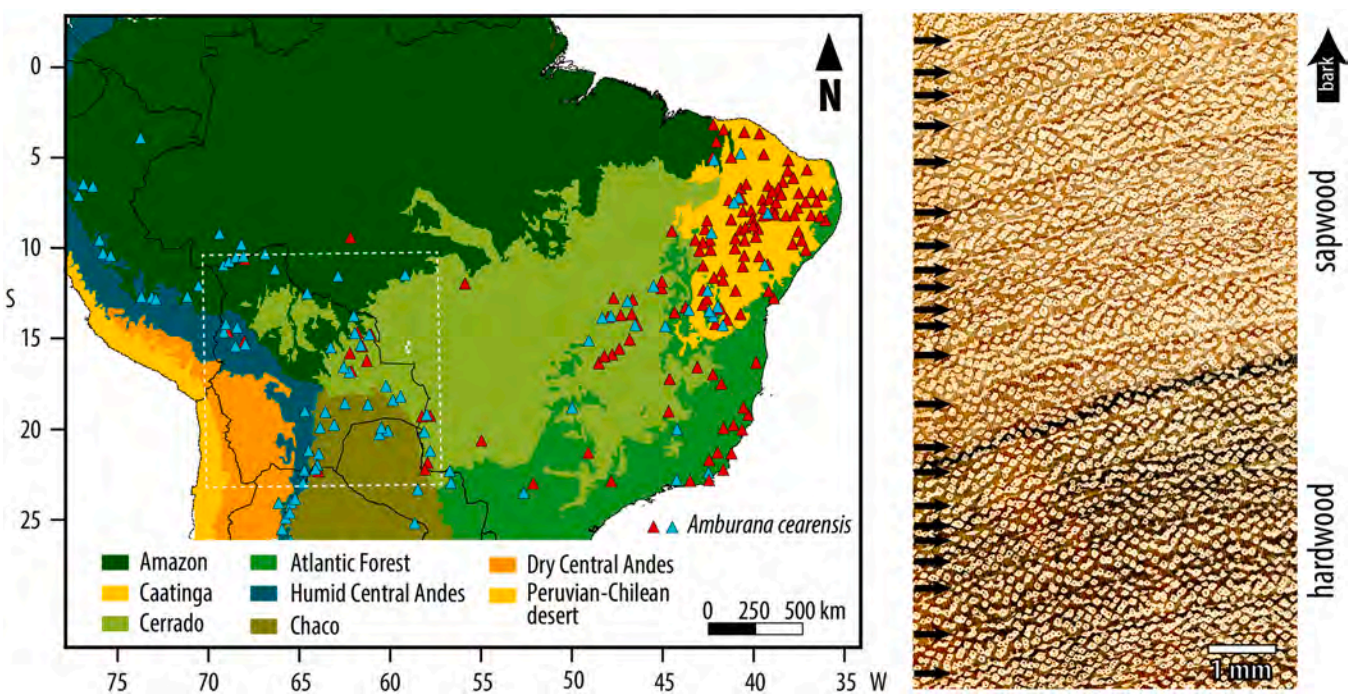

Fig. 2. (left) Distribution of *Amburana cearensis* in tropical South America based on (Morales et al., 2019) (light blue triangles) and (Godoy-Veiga et al., 2021) (red triangles). (right) Cross-sectional view of *A. cearensis* wood for heartwood and sapwood, arrows indicate the boundaries between growth rings. The dotted white square illustrates the area included in Fig. 3.

rings or growth lenses were observed. However, in large diameter trees (> 80 cm), very narrow rings or micro-rings are common, particularly in the sapwood. In these narrow rings the parenchyma is more abundant and dark fibers defining the boundary between contiguous rings is greatly reduced or absent (Fig. 2b).

2.2. Study area

The study sites are located in the Cerrado dry forest and its transition to the Amazon moist forest in eastern lowland Bolivia (Navarro, 2011). Together with Amazonia, the Cerrado phytogeographic region is one of the most extensive tropical vegetation domains in South America, extending from north-central Brazil to eastern Bolivia and northeastern

Paraguay (Josse et al., 2003).

The Bolivian Cerrado biogeographic province is divided into vegetation districts based on botanical composition largely associated with total annual precipitation. The Guarayos and Chiquitos are the most important districts in the Cerrado since they contain the largest area of forest in Bolivia (Navarro, 2011). The Bajo Paraguá site (BPA) is located in the Guarayos district where there are moderately deep to very deep soils with a large capacity for moisture retention, favored in turn by abundant rainfalls (Fig. 3). The Bella Vista (BTA), San Pablo del Sur (SPS) and Santa Rosita (STA) sites are in the Chiquitos district with shallow and stony soils in a landscape dominated by small hills and plateaus (Table 1). Based on records from meteorological stations located near the most populated centers of the Bolivian low plains, the mean annual temperature is close to 24.4 °C. Total annual precipitation has a marked concentration in summer months (monsoonal regime) and varies from 1100 mm in San Ignacio de Velasco in the south Chiquitano district to just over 1800 mm in Trinidad located to the northwestern moist forests (period 1943–2019 for both records).

Given the lower precipitation in San Ignacio de Velasco, the winter dry season has a mean duration of 6 months (April-September), one month longer than in Guarayos (May-September) and two months longer than in Trinidad (June-September; Fig. 3). Due to these differences in total precipitation and the duration of the dry season, the Guarayos biogeographic district has more plants characteristic of moist evergreen forests in Amazonia, than the dry Chiquitano woodlands (Fig. 1).

2.3. Sample collection

The *Amburana cearensis* cross sections were collected in logging areas at the time of tree felling. The samples are from native forests without previous silvicultural interventions and, therefore, with not alterations in the growth patterns due to the effect of previous logging. Most collected sections came from dominant trees with good trunk morphology. Cross-sections were taken at stem heights ranging from 1.5 to 2 m, depending on the extent of buttresses on the stem, felling practices and trunk healing. The number of samples per site depended on the intensity of harvesting and the abundance of *A. cearensis* trees (Table 1). Given the difficulties in delimiting the tree-ring boundaries, the use of cross sections instead of narrow increment cores is recommended. Cross sections or wedges from trees allow better evaluation of woody structure, which in turn facilitates delimitation of the annual rings, visual dating, and precise measurement of ring width.

Table 1
The geographical location of study sites is listed along with elevation and vegetation type. For each site the code is indicated in parentheses. CD = Chiquitano vegetation district, GD = Guarayos vegetation district according to (Navarro, 2011).

Site (code)	Latitude (S)	Longitude (W)	Elevation (m. a.s.l)	District and vegetation type
Bajo Paraguá (BPA)	14°31'55"	61°44'57"	247	GD. tropical humid forest
Bella Vista (BTA)	15°40' 38"	60°59'21"	290	CD. tropical dry forest
San Pablo del Sur (SPS)	16°29' 44"	61°26'06"	463	CD. tropical dry forest
Santa Rosita (STA)	17°18' 56"	60°58'17"	420	CD. tropical dry forest

2.4. Sample processing and chronology development

Cross sections were polished with progressively finer sandpaper (from 80 to 1200) to allow clear microscopic examination of the minute wood anatomy (Fig. 2). Tree rings were dated visually under a binocular microscope using a high-quality cold-type light. Samples were illuminated from different angles to achieve the best contrast. Following the Southern Hemisphere convention, annual rings were assigned to the year in which their formation began (Schulman, 1956). Two or more

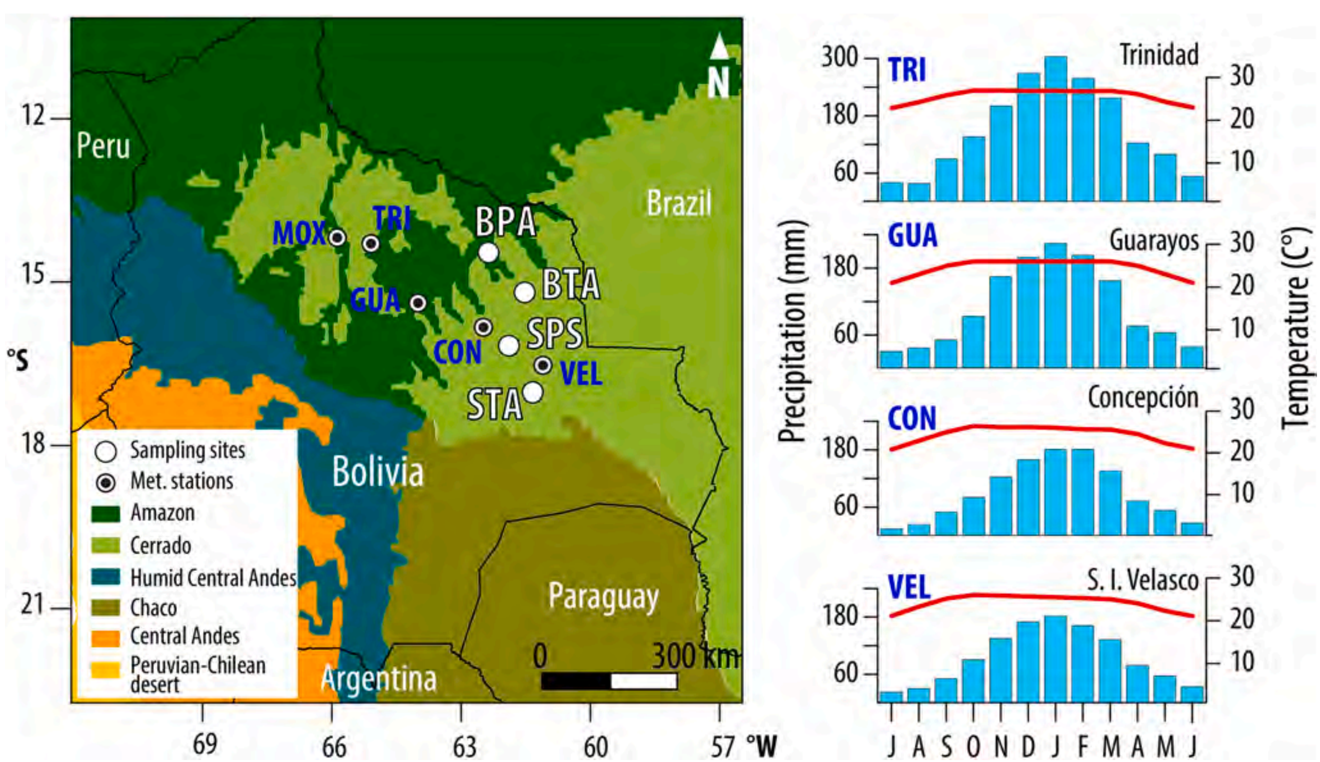

Fig. 3. The *Amburana cearensis* collection sites in Bolivia and the weather stations used in this analysis are mapped. Phytogeographic districts are shown with color shading. Climate diagrams for the instrumental meteorological stations of Trinidad, Ascención de Guarayos, Concepción, and San Ignacio de Velasco, located along the northwest-southeast precipitation gradient.

radii were dated on each cross section. Following the visual cross-dating of the different radii on each cross section, the ring widths were measured with a precision of 0.001 mm using a Velmex Uni Slide Tablet connected to a digital counter (Metronics Quick-Chek QC – 10V). The quality of the visual dating and measurement was checked with the computer program COFECHA (Holmes, 1983). This program calculates correlation coefficients between individual ring-width series and the master chronology by averaging all other dated samples at a particular site. This procedure provides a statistical basis to help identify absent or false rings on the measured radii. Following sample cross-dating, all correctly dated series were standardized by fitting age-dependent spline curves to the raw ring width measurement timeseries using the program ARSTAN 0.48 (Cook et al., 2007; Cook and Holmes, 1999) Starting from an initial spline value set by the user, in our case 20, the stiffness of the spline increases with tree age. The age-dependent smoothing spline ensures that the low frequency variability in the derived chronology will be based primarily on the longest ring width time series from the oldest trees (Melvin et al., 2007). The objective of ring-width standardization is to remove long-term growth trends due to the increasing size and age of the tree. Standardization also eliminates differences in the absolute growth rates of trees so that the rates are centered on a mean index of 1. In consequence, standardization seeks to maximize common variance among the individual ring width series included in the chronology (Fritts, 1976).

Several statistics were calculated to estimate the quality of the derived chronology, including the standard deviation, first-order autocorrelation, and mean sensitivity, a measure of the relative change in ring width from one year to the next, often associated with variations in climate (Fritts, 1976). Other statistics used in dendrochronological studies, such as the RBAR and EPS, were also calculated. The RBAR is a measure of the common signal in a sample of tree-ring series, calculated as the average correlation coefficient between all possible pairs of segments of a given length included in the chronology (Briffa, 1995). The EPS (or expressed population signal) is a measure of the total signal present in the chronology (e.g., 50 years) in comparison to a fully replicated chronology. EPS values > 0.85 indicate that the number of radii included in a particular segment of the chronology is large enough to capture an adequate percentage of the theoretical signal present in the fully replicated chronology (Wigley et al., 1984). EPS values < 0.85 often indicate that replication and shared variance in that segment of the chronology are low and that the number of specimens should be increased to strengthen the common signal (Briffa, 1995).

3. Climate-Amburana cearensis growth relationships

3.1. Temporal relationships

Relationships between climate and *Amburana cearensis* radial growth were quantified using correlation functions (Blasing et al., 1984). Monthly variations in precipitation were compared with interannual variations in radial growth (i.e., ring-width index) during the time period in common between the records. Since growth in a given year can be influenced by climatic conditions during the previous year, comparisons were extended from January in the previous growing season to April during the current growing season (16 months). Precipitation records from Concepción (1943–2019) and San Ignacio de Velasco (1943–2009) were compared with the *A. cearensis* chronologies located in the dry Chiquitano district, whereas the Ascención de Guarayos (1955–2019) in the humid Guarayos district, and Trinidad (1943–2019) and San Ignacio de Moxos (1946–2019) in the hyper-humid transition to the Amazon forest (Navarro and Maldonado, 2004) were used for comparison with the northernmost-located tree-ring chronology.

In a second step, the spectral properties of the *A. cearensis* chronologies and the seasonal precipitation variable most strongly associated with radial growth were computed using a combination of Blackman-Tukey (Jenkins and Watts, 1968) and singular spectrum (SSA; (Vautard and Ghil, 1989) analyses. The power spectra quantify the distribution of variance of each series as a function of frequency, while the coherence spectra provide a measure of the relative agreement between precipitation and *A. cearensis* radial growth at various frequencies. Consequently, coherence can be interpreted as a series of Pearson squared correlation coefficients between the compared series across the frequency domain. SSA is related to *Empirical Orthogonal Function (EOF)* analysis and is used to determine oscillatory modes in time series. Quasi-periodic signals appear as pairs of degenerate eigenmodes in SSA and their corresponding eigenfunctions in the time domain are in quadrature with each other (Vautard and Ghil, 1989).

3.2. Spatial relationships

The spatial response of the tree-ring indices to precipitation was documented by correlating each chronology with the gridded monthly precipitation data from ERA5 reanalysis using the analytical tools of the Climate Explorer (https://climexp.knmi.nl/start.cgi). The spatial pattern of correlation of seasonal precipitation (Oct-Jan) of Concepción with the ERA5 reanalysis was compared with the corresponding pattern from the mean of the STA and SPS chronologies, both located in the dry Chiquitano forests, with the ERA 5 reanalysis during the interval 1979–2017. The spatial correlation fields resulting from correlating the composite precipitation record of Ascención de Guarayos-Trinidad-Moxos (transition to Amazonian rainforests) and the BPA chronology with ERA5 reanalysis precipitation data were also compared over the common period 1979–2017. Differences between spatial correlation fields were estimated using the analytical facilities provided by Climate Explorer.

3.3. Comparison with C. microchaete growth patterns

During the last decade, more than 10 chronologies of *Centrolobium microchaete* have been developed in the dry tropical Chiquitano forests and the transition to the moist Amazonian forests (López et al., 2019, 2011). In order to determine whether *A. cearensis* and *C. microchaete* chronologies record comparable growth patterns in similar environments, the BPA and SPS chronologies, representative of wet and dry environments along the precipitation gradient, were correlated with seven well-replicated *C. microchaete* chronologies in the region. In this analysis, environmental similarities between sites and distances between BPA, SPS and *C. microchaete* chronologies were considered.

4. Results

4.1. Precipitation trends

The instrumental precipitation records at representative stations in the study area are plotted in Fig. 4. While climatic events common to all records are observed, such as the period of low precipitation in the 1960s and early 1970s, there is a marked contrast in precipitation trends between the dry and wet sectors over the last 50 years. The increasing trends in precipitation since the 1970 s are evident in the northernmost weather stations such as San Ignacio de Moxos and Trinidad. No trend is apparent at Ascención de Guarayos, but a negative precipitation trend has been measured at Concepción and San Ignacio de Velasco in the dry forests to the south (Fig. 4).

4.2. Characteristics of the chronologies

The number of individuals comprising the *Amburana cearensis* chronologies varies between 16 and 21 for the San Rosita (STA) and San Pablo del Sur (SPS) sites, respectively. All chronologies span over 100 years, beginning between 1889 (STA) and 1854 (Bella Vista, BTA). Replication is greater than 10 trees from 1925 (92 years) in STA and 1895 (116 years) in BTA (Fig. 5). Finally, mean ring width varies from

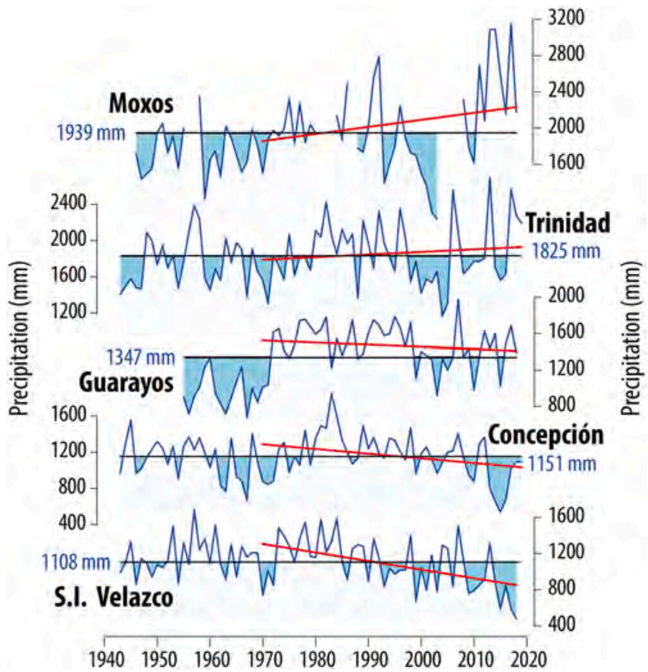

Fig. 4. Interannual variations in precipitation at five stations located along the humidity gradient from the Chiquitano dry forest to the Guarayos moist forest in the transition to Amazonia. Total annual precipitation is indicated for each station and varies from approximately 1100 mm at Concepción and San Ignacio in the Chiquitania to more than 1900 mm at San Ignacio de Moxos in the southern sector of the Amazon basin. Rainfall trends since 1970 are illustrated (red).

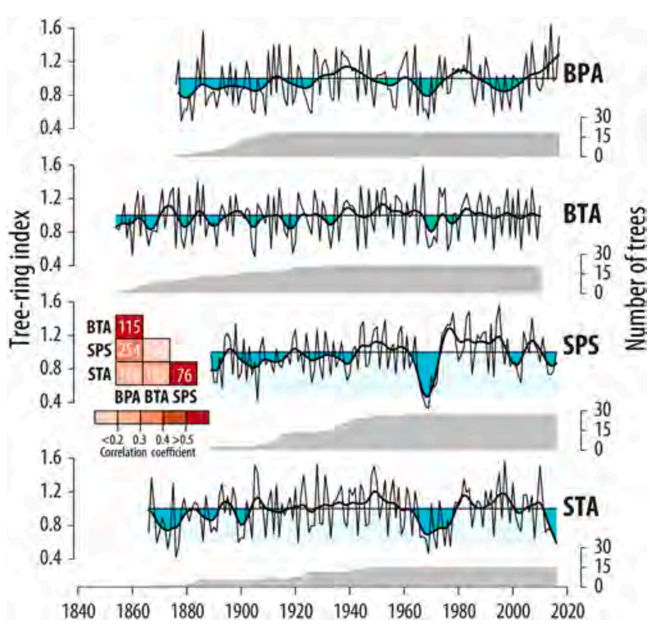

Fig. 5. The *Amburana cearensis* standard chronologies from four sites in the Bolivian lowlands are plotted. To emphasize long-term variations, the chronologies are also shown with a cubic spline curve highlighting low-frequency variations centered on 20-year period (Cook and Peters, 1981). The variation in sample size over time is indicated below for each chronology (gray). Pearson correlations computed for all chronologies for the common period of 1920–2015 are also shown. The distances between sites (in km) are indicated in the respective box.

2.31 mm/year at BTA to 2.80 mm/year for both BPA and SPS (Table 2).

The statistics most commonly used to assess the quality of tree ring chronologies indicate that *A. cearensis* trees from the same site share a strong common signal in tree growth. RBAR ranges from 0.35 to 0.46 from STA and BAP, respectively, while EPS values are always higher than the critical value of 0.85 (Wigley et al., 1984); Table 2). Mean sensitivity, a measure of interannual variability in ring width varies between 0.37 and 0.43 for the wettest BPA and driest STA site along the gradient, respectively. These values are consistent with standard deviations of 0.36 and 0.38 at the same locations. Given the high interannual viability in *A. cearensis* growth, the first order autocorrelation is extremely low, varying between 0.010 and 0.124 for BTA and SPS, respectively.

Since the beginning of the 20th century, the chronologies from STA and SPS have been strongly correlated with each other reflecting common growth patterns under a similar precipitation regime in the Chiquitano district (Fig. 4). SPS and STA are only weakly correlated with BPA and BTA. In contrast, the BTA record is significantly correlated with BPA, particularly in the high-frequency variations, with some differences in the long-term cycles (Fig. 5).

4.3. Relationships between climate and tree growth

At the four sampling sites, *Amburana cearensis* radial growth is favored by abundant rainfall particularly during the growing season (Fig. 6). At the BPA site, radial growth is significantly related to rainfall in February, March and May during the previous growing season and in November, January and February during the current growth period. At this site, radial growth is weakly related to temperature, being significant negative only during January in the current growing season. At the BTA site, radial growth is positively associated with precipitation from October to April of the current growing season, but inversely with temperature, showing significant negative relationships in September, January and February during the current growing period. At both SPS and STA, radial growth is positively correlated with precipitation from November to February during the current growing season, whereas temperature is inversely related to growth most of the year, particularly in January, February and March during the current growth period (Fig. 6).

The variations in seasonal precipitation and *A. cearensis* radial growth at different environments along the humidity gradient from the Chiquitano dry forests to the Guarayos-Southern Amazonian moist forests are illustrated in Fig. 7. Consistent with the correlation functions, tree growth at the site BPA in the moist forest is strongly associated with late spring to summer (Oct-Mar) precipitation at Trinidad, Moxos, and Guarayos. Since the early 1960s, both records share not only common interannual variations but also a long-term oscillation with low precipitation-reduced growth centered in the 1970s and 1990s. Wide growth rings in response to abundant Oct-Mar precipitation totals were recorded in the 1980s and particularly from 2006 onward. In contrast, STA and SPS chronologies in the dry Chiquitano forests share with precipitation the dry period between the late 1960s-early 1970s and a clear declining trend since the 1980s, consistent with the October to January precipitation at Concepción that measured very severe droughts in the late spring-early summer seasons in 2014 and 2017. Contrasting with the steady trends of decreasing precipitation and tree growth in the Chiquitos district over the last decades, precipitation and *A. cearensis* radial growth in the Guarayos-Amazon Forest transition increased (Fig. 7). The relationship between climate and growth is not consistent at the BTA site, even though the BPA and BTA records are highly correlated (Fig. 4).

Spectral analyses indicate that instrumental precipitation records and *A. cearensis* ring-width chronologies share similar oscillations (Fig. 8). During the common period 1943–2016, the SPS and STA chronologies show common cycles with seasonal precipitation at Concepción centered at 3, 5, and > 30 years. Coherence analysis indicates

Table 2
Statistics for the four *Amburana cearensis* standard chronologies from sites along the precipitation gradient from the dry Chiquitano to the moist Gaurayos-southern Amazonia forests. The chronology RBAR and EPS statistics were estimated over the 1900–2010 interval using a 50-year window shifted 25 years between segments. For each chronology, the first year with EPS > 0.85 is indicated in parenthesis.

Site	No. of samples	Radial growth (mm)	Period	Standard deviation	Auto- correlation	Mean sensitivity	RBAR	EPS (> 0.85)
(BPA)	11 (18)	2.85	1876–2017	0.36	0.050	0.37	0.46	0.93 (1897)
(BTA)	17 (21)	2.33	1854–2010	0.34	0.020	0.39	0.43	0.95 (1873)
(SPS)	22 (27)	2.90	1889–2016	0.36	0.124	0.39	0.43	0.94 (1919)
(STA)	11 (15)	2.55	1866–2016	0.38	0.010	0.43	0.35	0.88 (1930)

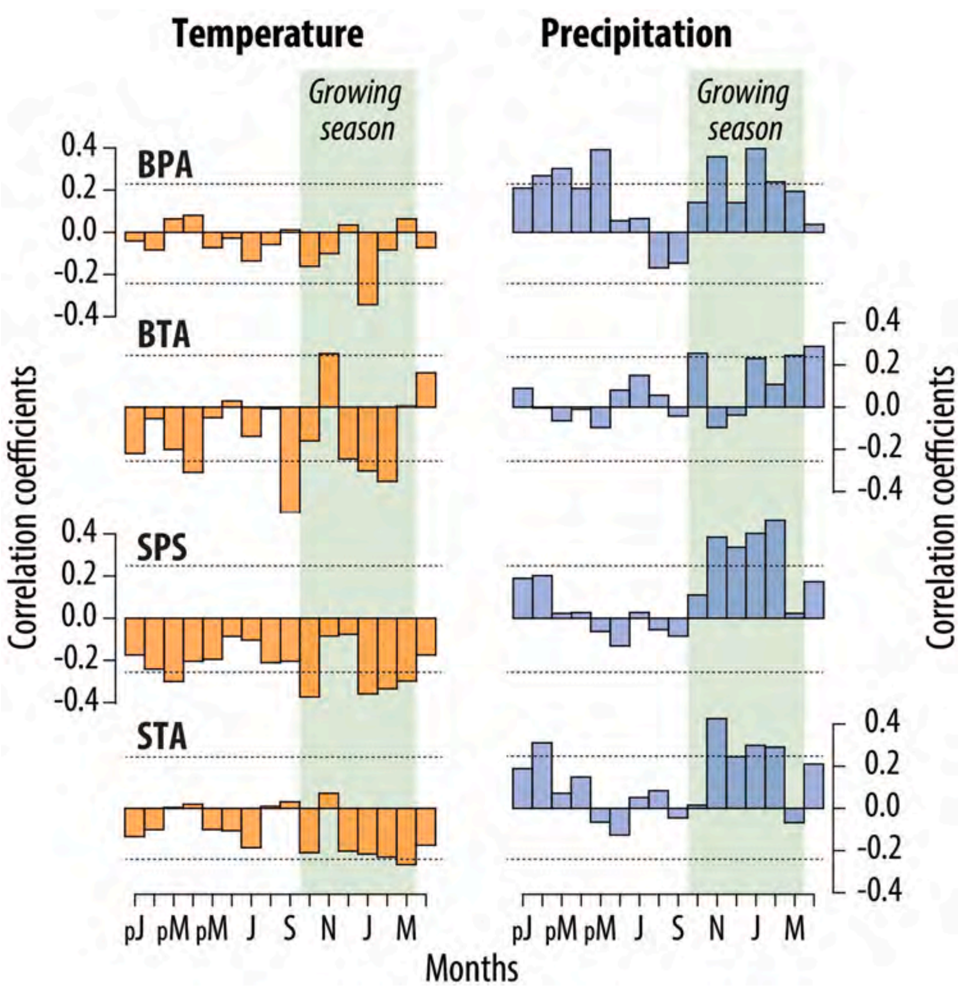

Fig. 6. Correlation functions for the four *Amburana cearensis* standard chronologies based on the comparison with monthly precipitation and temperature records starting in January in the previous growing season and ending through April of the current growing season. Correlation coefficients > r = 0.267 (gray dotted line) are statistically significant ($p < 0.05$; 1943–2005 common period). The vertical light green bars indicate the growing season (October–April), which corresponds to the wet season at all sample location (e.g., Fig. 3).

that these cycles are highly consistent in both series, particularly at 2.8–3 years. Similarly, the BPA chronology and the composite Trinidad-Moxos-Guarayos precipitation record show over the common period 1960–2017 coherent common cycles at periodicities of 3, 7 and > 50 years, the latter associated with the change from the dry periods in the 1970s and 1990s to the wet periods centered at 1980 and 2015 (Fig. 7).

4.4. Spatial correlation patterns

The instrumental precipitation records from Concepción and the composite from Trinidad-Moxos-Guarayos were used to represent the regional differences in precipitation from the Chiquitano to the Guarayos-Southern Amazonian vegetation districts. The spatial pattern resulting from correlating October-January seasonal precipitation from Concepción with ERA5 gridded data is centered (higher correlation coefficients) over southeastern Bolivia, coincident with the geographical locations for Concepción and the SPS and STA chronologies (Fig. 9a). Even with somewhat weaker relationships, the correlation pattern between the mean SPS-STA tree-ring record and ERA5 is very similar spatially to the Concepción precipitation record (Fig. 9c). The differences between both spatial patterns are minimal over the area with significant relationships between Concepcion and ERA5 precipitation (Fig. 9e), suggesting that the SPS-STA chronologies are good proxies for precipitation in the Chiquitano dry forest (Fig. 9). The spatial relationships between the regional precipitation record for Trinidad, Moxos and Guarayos and ERA5 is somewhat weaker than that observed for Concepción, but it is clearly shifted to the northeast and is not centered over the Chiquitano forest (Fig. 9b). A similar pattern is observed when the BPA chronology is used as a surrogate for precipitation. The spatial pattern is weaker and shifted farther north over the Guarayos vegetation district. Again, the differences in the spatial patterns based on the instrumental precipitation data and the tree-ring chronologies are minimal over the area most strongly related with ERA5 (Fig. 9f), suggesting that the BPA dendrochronological record is a good proxy for

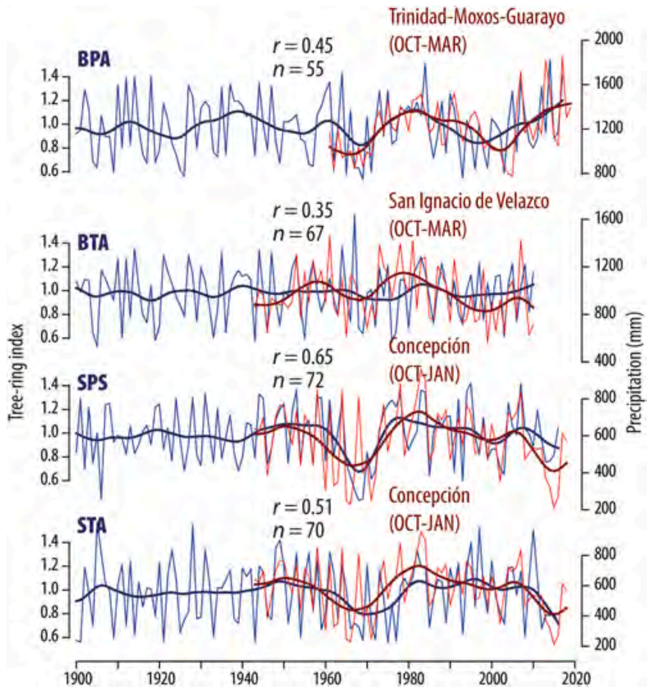

Fig. 7. Interannual variations in *Amburana cearensis* growth and seasonal variations in precipitation are plotted. The chronologies, arranged from the wettest (BPA) to the driest (STA) sites, are compared with precipitation records along the humidity gradient from the Guarayos-Amazon moist forest (Trinidad-Moxos-Guarayos) to the dry Chiquitano (Concepción) forest. Correlation coefficients (r) and the number of years (n) used in the comparison are indicated for each chronology.

seasonal precipitation (October-March) over the transition between the Guarayos and the southern Amazonian forests.

4.5. *Amburana cearensis and Centrolobium microchaete tree-ring chronologies*

Finally, the *Amburana cearensis* chronologies representative of the wet (BPA) and dry (SPS) environments in the Bolivian lowlands were compared with 7 dendrochronological records of *Centrolobium microchaete* successfully employed to reconstruct precipitation variations in the region (López et al., 2017). Over the last 100 years when the chronologies from both species are well replicated, they are also significantly correlated (Fig. 10). More importantly, these relationships are stronger between chronologies of *A. cearensis* and *C. microchaete* from the same vegetation district. The BPA chronology in the transition to the Amazonian Forest is strongly related to the *C. microchaete* record BPC located at 91 km distance in the same district ($r = 0.55$, $n = 94$, $p < 0.001$). These relationship between *A. cearensis* and *C. microchaete* weaken at the sites located at greater distance and in different vegetation districts (e.g., at INP near Concepción in the Chiquitano forest, $r = 0.28$, $n = 85$, $p = 0.01$, 200 km from BPA). In contrast, the SPS chronology is most strongly related to the *C. microchaete* records from the Chiquitano district. Therefore, the relationships between SPS and *C. microchaete* chronologies are strong with INP ($r = 0.50$, $n = 85$, $p < 0.001$) SPO ($r = 0.48$, $n = 95$, $p < 0.001$) and PUR ($r = 0.45$, $n = 85$, $p < 0.001$), tree-ring records at 37, 70 and 72 km distance, respectively (Fig. 10).

5. Discussion

Important dendrochronological advances have recently been achieved in tropical regions, however, the number of tree-ring records in the Neotropics still remains low compared with the temperate latitudes of both hemispheres (Brienen et al., 2016; Schöngart et al., 2017). The recently developed Drought Atlas in South America (Morales et al., 2020) extends from the southern tip of the continent to 20° S, a geographical limit imposed by the limited number of well-replicated dendrochronological records with a consistent climatic signal. This relatively low number of tropical records contrasts with the enormous diversity of tree species in the Neotropics. For instance, 283 species have been recorded in the tropical lowland moist forests from Bolivia, with an average of 75 species per hectare (Superintendencia Forestal, 1999), suggesting that the dendrochronological characteristics of new species need to be evaluated and the climatic information present in their growth rings precisely identified (Brienen et al., 2016; Schöngart et al., 2017).

With the aim of increasing our knowledge on the dendrochronological properties of Neotropical species, in this paper we present four new chronologies of *Amburana cearensis* located along the precipitation gradient from the dry forests in the Chiquitania to moist forests in Guarayos in transition to the Amazonian rainforest in the Bolivian lowlands. Although the first dendrochronological record of *A. cearensis* was presented by Brienen and Zuidema in 2005, only two subsequent publications refer to the use of this species in dendrochronology. Brienen and Zuidema (2005) used 16 of totals of 27 collected individuals and provided little information on length of the chronology, replication over time, or common signal in tree growth. More recently, (Paredes-Villanueva et al., 2015) showed that some samples cover up to 200 years, but the chronology was well replicated only from 1943 onwards. Finally, Godoy-Veiga et al. (2021) developed a chronology composed of 51 trees covering the period 1947–2018 (78 years) to study the effects of landscape heterogeneity on trees' sensitivity to climate. Comparatively, the chronologies presented here cover the period 1854–2017 with EPS values larger than 0.85, a measure of well-replicated records, starting in 1897, 1873, 1919 and 1930 for BTA, BPA, SPS and STA, respectively.

The comparison of the *A. cearensis* tree-ring chronologies with monthly temperature and precipitation instrumental records from the region indicate that these chronologies are positively correlated with precipitation and negatively with temperature during the wet season (Fig. 6), the classic moisture response seen widely in trees from dry tropical and temperate forests worldwide. The moisture response is strongest in the relatively dry Chiquitano forests. But these results demonstrate that useful reconstructions of precipitation or available soil moisture should be possible with *A. cearensis* tree-ring chronologies across eastern Bolivia.

Differences in rainfall amounts along the precipitation gradient, from aprox. 1000–1100 mm/yr in the dry Chiquitano forests to 1800–2000 mm/yr in the transition to the forests of the Southern Amazon, induced a spatial grouping among the *A. cearensis* chronologies (Fig. 5). Common interannual variations in ring width are recorded at the SPS and STA sites ($r = 0.55$, $n = 96$ years) both located in the dry forest of the Chiquitano district, and between BPA and BTA sites ($r = 0.56$, $n = 90$) in the humid forests of the Guarayos district. In contrast, these two groups are weaker related (range between $r = 0.23$ and $r = 0.35$, $n = 90$ years), suggesting different conditions for tree growth between the Chiquitano and Guarayos forests. The evidence suggests that these spatial differences in *A. cearensis* tree-growth reflect different site conditions and different precipitation regimes between the two districts.

Although precipitation variations in the Chiquitano and Guarayos-Amazonian transition districts share similar precipitation seasonality and even some dry and wet years, the long-term trends in rainfall appear to diverge between the two regions, particularly during the last 50-years. While the Trinidad and Moxos precipitation records show a positive trend in precipitation since the 1990s, rainfalls in Concepción and San Ignacio show a decreasing trend since the mid-1980s (Fig. 4). The recorded trends in rainfall are consistent with a recent study by Espinoza et al. (2019) on the evolution of wet-day (WDF) and dry-day (DDF) frequencies over the upper Madeira Basin over the interval 1981–2017.

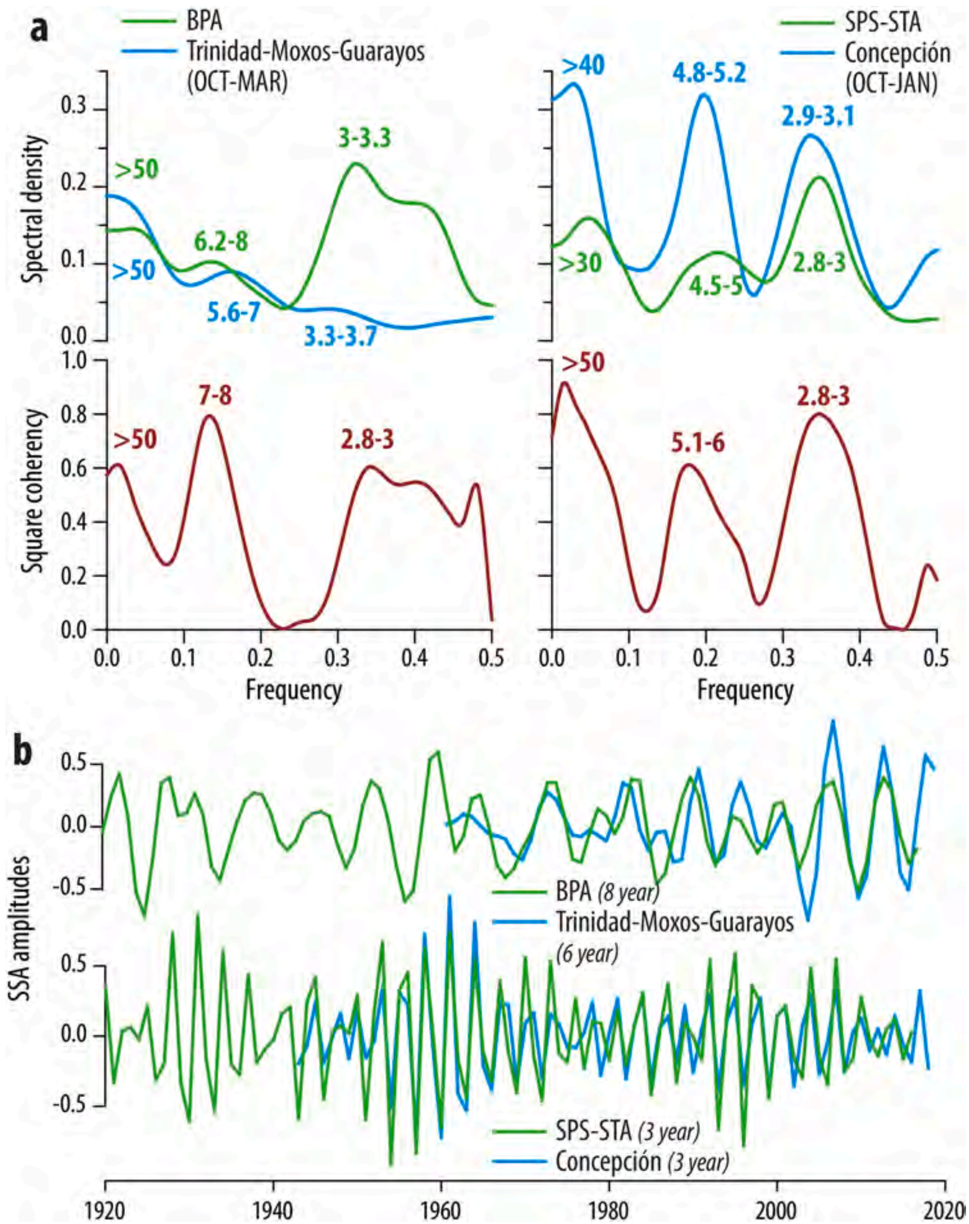

Fig. 8. (a) Blackman-Tuckey spectral analyses for the mean precipitation record of Trinidad-Moxos-Guarayos and the BPA chronology (left) and for precipitation at Concepción and the SPS-STA mean chronology (right), respectively. Frequencies, expressed in years, corresponding to the most important spectral peaks are indicated for instrumental and dendrochronological records. The coherence between these records is shown below. (b) Decomposition using Singular Spectral Analysis of the precipitation (light blue line) and *A. cearensis* growth (green line) illustrate the coherent oscillations in both records. The Trinidad-Moxos-Guarayos precipitation amplitudes centered on a cycle around 6 yr are fully in phase with the BPA growth amplitudes centered on a cycle around 8 yr ($r = 0.64$, $n = 57$ yr), while the Concepción precipitation amplitudes and the SPS-STA composite chronology, both centered on a 3 yr cycle, show high consistency in magnitude and phase ($r = 0.81$, $n = 74$ yr).

A significant reduction of WDF and an increase of DDF were observed south of 14°S, suggesting increasing drier conditions over the Chiquitano forests in the southern Madeira basin. In contrast, the WDF significantly increase over the Guarayos-Amanzon forests in the northern part of the Madeira basin, particularly to the north of 14°S (Espinoza et al., 2019). These results, showing similar precipitation trends to those observed in the meteorological records selected in our study, support the contrasted evolution of rainfall intensity across lowland northeastern Bolivia. Consistent with these differences in precipitation trends, the chronologies in Guarayos (particularly BPA, as BTA ends in 2009) exhibit the highest growth rates from 2010 onwards, whereas SPS and STA records show a decreasing trend since the mid-1980s, accentuated in the last decade (Fig. 7). Differences in tree growth patterns between districts contrast with the marked similarities within each region, suggesting a high sensitivity of *A. cearensis* growth to regional variations in precipitation. This high climatic sensitivity observed in *A. cearensis*, capable of recording minor differences in precipitation patterns between contiguous regions, has not been reported for tropical species in South America (Schöngart et al., 2017).

Compared to dendrochronological records at mid- and high latitudes in South America, the low persistence in *A. cearensis* tree growth, as reflected by the extremely low values of autocorrelation in the chronologies, appears to reflect the low persistence present in the instrumental precipitation data (Fig. 8). The first-order autocorrelation in the *A. cearensis* chronologies ranges from 0.010 to 0.124, while the first-order autocorrelation for the nearby instrumental precipitation between 0.11 and 0.23. Fig. 8 also illustrates the high consistency between the cycles centered on 3 years recorded in both the Concepción precipitation and the SPS-STA composite chronology ($r = 0.82$, $n = 74$). Similarly, the composite Trinidad-Moxos-Guarayos precipitation record and the BPA chronology ($r = 0.64$, $n = 57$) in the humid sector, share a common cycle centered between 6 and 8 years. The SSA shows that high-frequency oscillations of less than 8 years in length in the chronologies account for more than 80% of the total variability in *A. cearensis* tree growth over the past century in both the dry and moist forest regions. The spatial correlation patterns between the *A. cearensis* chronologies and the ERA5 gridded precipitation reanalysis are similar to those obtained using the most representative precipitation records from both

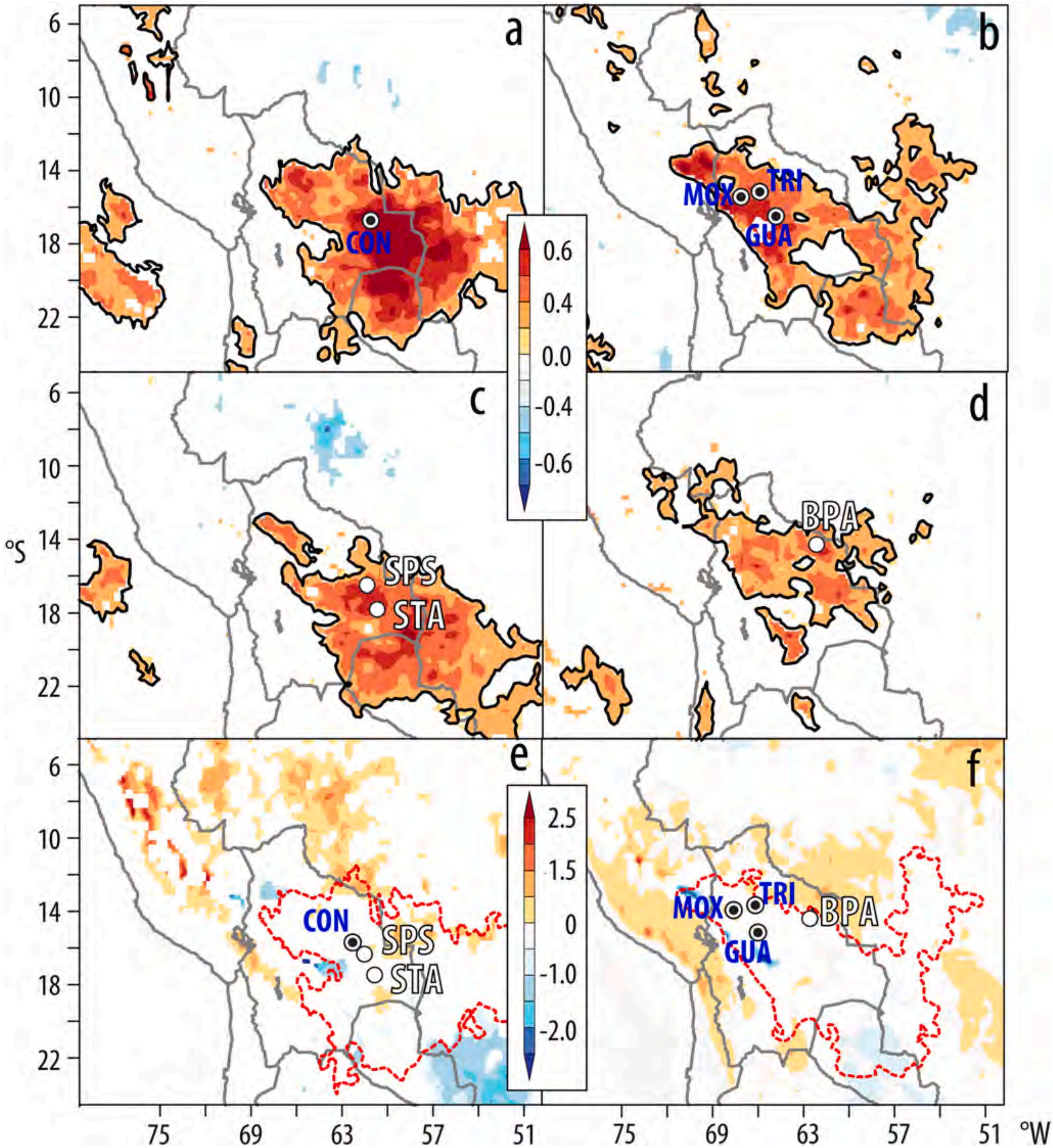

Fig. 9. Spatial correlation patterns between gridded precipitation from ERA5 reanalysis, instrumental rainfall records from the Chiquitano and Guarayos-Amazonico Sur forests, and the *A. cearensis* chronologies in both vegetation districts. The Concepción (a) and Trinidad-Moxos-Gaurayos precipitation records (b) were used as representative of regional rainfall records in the Chiquitano and Guarayos-Amazonico Sur forest districts, respectively. The STA-SPS (c) and BPA (d) chronologies were used to represent the *A. cearensis* growth variations from the dry and moist forests along the transect, respectively. Differences between spatial correlation patterns (meteorological minus dendrochronological patterns) are shown for the Chiquitano (e) and Guarayos-Amazonico Sur (f) vegetation districts. The red dotted line in (e) and (f) corresponds to the sectors where precipitation in Concepción (a) and in Moxos-Trinidad-Guarayos (b) are significantly related to the ERA5 reanalysis precipitation data, respectively. In those sectors, differences between instrumental and spatial patterns are minimal.

vegetation districts (Fig. 9). These results document the potential for *A. cearensis* dendrochronological records to register precipitation variations in the South American tropics.

Finally, the comparison between the *A. cearensis* chronologies with those previously developed for *C. microchaete* in the region reveal similarities among the records, particularly for chronologies from similar environments along the humidity gradient (Fig. 10). The relationships are stronger between the closely located chronologies for each species and with relationship tends to decrease with distance. These results would indicate that environmental conditions, determined by differences in total precipitation and duration of the dry period (Fig. 3), have a larger influence on tree growth than those related to differences between

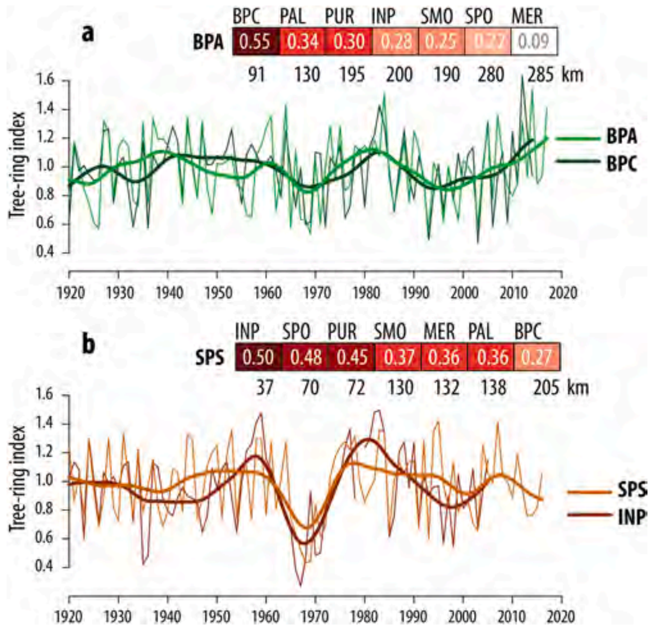

Fig. 10. The interannual variations in *A. cearensis* and *Centrolobium* radial growth are compared in the tropical forests of Bolivia. (a) Comparison between *A. cearensis* (BPA) and *C. microchaete* (BPC) chronologies in the Bajo Paraguá area corresponding to the tropical lowland moist forests at the Guarayos district in transition to the Amazon. (b) Comparison between *A. cearensis* (SPS) and *C. microchaete* (INP) chronologies from the dry forests of the Chiquitano district. The *A. cearensis* record from SPS is significantly related to the *C. microchaete* records from the dry forest, but the strength of the relationship decreases as we move towards the humid forest. The relationships, measured through the correlation coefficient (r), between the *A. cearensis* BPA and SPS chronologies and the seven *C. microchaete* chronologies are shown in (a) and (b) as well as the distances in kilometers between sites.

species.

(López et al., 2019) postulated, based on a network of *C. microchaete* chronologies in the Cerrado region, the existence of a convergence in tree growth responses to climate determined by regional precipitation regimes. The growth patterns of *C. microchaete* trees on the drier sites of the Bolivian Cerrado are more similar among trees than on sites with higher water availability and a shorter dry season. Our results with *A. cearensis* support these conclusions based only on *C. microchaete*. For the SPS and STA sites in the dry Chiquitano forest, the relationships with regional precipitation at the onset of the rainy summer months (October to January) are stronger than those observed in humid environments (Figs. 6 and 7). These observations are also consistent with the Godoy-Viega (2021) study on *A. cearensis* growth patterns in tropical dry forests of Brazil which found that the most sensitive trees were those individuals located in sites with higher seasonality in response to shallower and drier soils.

Despite the sensitivity of *A. cearensis* to precipitation variations on different time scales, the relatively short chronologies and the difficulty of finding old trees is a major limitation in the use of *A. cearensis* tree-ring records to reconstruct past climatic variations in Bolivia. While at the four sampling sites the chronologies exceed 120 years, only the BTA record reaches 160 years. Brienen and Zuidema (2005) reported ages for *A. cearensis* up to 240 years in northern Bolivia. Paredes-Villanueva et al. (2015) reported specimens over 200-years old near San Ignacio de Velasco. Nevertheless, the search for long-lived individuals is currently hampered by the intense logging in most tropical regions and the low density of *A. cearensis* trees in many forests [e.g., only 0.5–2.5 individuals with diameters > 20 cm per hectare were recorded by Jardim et al. (2003)]. Unfortunately, tree-ring records of many tropical species such as *A. cearensis* are disappearing very rapidly, reducing our capacity to document the natural climatic variability and climate change in the tropics. This information is relevant to the development of socio-environmental policies to guide conservation and sustainable resource management in these threatened tropical forests (Marengo et al., 2018).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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