Rainfall and temperature variability in Bolivia derived from the tree-ring width of *Amburana cearensis* (Fr. Allem.) A.C. Smith

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A R T I C L E   I N F O

A B S T R A C T

Amburana cearensis is an important timber species in tropical lowland dry forests in Bolivia. We used dendrochronological methods to evaluate its climatic sensitivity and to identify its potential for the reconstruction of climate. For that, we collected eleven wood discs from randomly-selected mature trees. Despite the eccentricity of the discs and existence of false and wedging rings, all samples were successfully cross-dated. The average radial growth was $0.58 \, \text{cm yr}^{-1}$. Significant correlation was found between the *A. cearensis* samples (0.34). Tree-ring width was positively correlated with monthly rainfall and negatively correlated with maximum temperatures during the 6-month rainy season (November–April). *A. cearensis* exhibits a potential for reconstructing climate in the Bolivian Chiquitania region.

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1. Introduction

The tropical dry forest in Bolivia, also locally known as Chiquitania forest, occupies an area of approximately 20 million hectares and contains one of the most diverse arrays of tree species in the world (Parker et al., 1993). Chiquitania forests are reported to have a very low radial growth rates, ranging from 0.143 to 0.211 cm yr^{-1} (Dauber et al., 2003; López, 2011; López et al., 2012). As a consequence, these forests regenerate slowly after disturbances (Uslar et al., 2004), particularly during drought.

Little is known about the growth rates of Chiquitania tree species and their sensitivity to climate. To date, growth data of tree species in Chiquitania forests have been provided by forest inventories on permanent plots. However, these measurements represent only a short period of a tree's life span and age-related growth-rate variations must be estimated (Brienen, 2005; Brienen and Zuidema, 2005b). Therefore, there is a need to improve the knowledge of

tree growth within Chiquitania forests as well as to identify the sensitivity of forest growth to environmental variability.

Knowledge of forest growth response to climate variability is particularly important in supporting decision-making processes that determine sustainable forest harvesting cycles (López et al., 2012; Brienen and Zuidema, 2005a,b). Tree-ring data offer the opportunity to study growth as well as the impact of variability in the physical environment throughout a tree's entire lifespan. As a source of proxy climate data, trees possess an unmatched temporal resolution due to forming annual rings (Harle et al., 2005). Additionally, since tree rings are records of past growth, dendrochronological studies offer insights into species-level sensitivity to a large number of environmental factors. Such information is not only useful for commercially valuable species, but it is also critical for species threatened by their intrinsic rarity, human disturbance or climate change.

Despite the potential that tree-ring data hold as an aid for forest management and conservation, few dendrochronological analyses have been conducted on Bolivia's endemic species. About 40 years ago Eckstein et al. (1981) reported that many woody species in tropical and intra-tropical forests, such as Bolivia's, do not form distinct growth rings. The basis of this argument is the belief that cambial activity does not vary throughout the year (Dave and Rao, 1982; Borchert, 1999). Conventionally, low winter temperatures induce

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periods of inactivity in the cambium, while warm and humid conditions stimulate its activation (Ajmal and Iqbal, 1987; Lim and Soh, 1997). Consequently, demarcated and well-defined growth rings are prominent features of most trees and shrubs that grow in the high latitudes (Villalba et al., 1998). However, the annuality of tree rings in many forest species in the tropics have been unexplored (Paredes-Villanueva et al., 2013). This combined with the irregular diametric growth associated with wedging rings and lenses in some species (Villalba, 1997; López, 2003) have limited the development of dendrochronology in Bolivia.

Despite the apparent limitations, it is now clear that local climatic variability in tropical regions is in fact sufficient to permit the formation of annual rings in many endemic species (Worbes, 2002; Brienen and Zuidema, 2005a; Ferreira et al., 2009). For example, the annual periodicity of tree rings in seven species from a tropical moist forest in Bolivia was determined using fire scars as time marker points to verify the annuality of tree rings. In most cases, boundaries between rings were marked by a marginal band of axial parenchyma and/or thick-walled fibers formed at the end of the growing season (López et al., 2012). Recently, tree-ring data for Bolivian tree species has proven to be useful for evaluating forest management practices (Brienen and Zuidema, 2006b; Rozendaal, 2010; López et al., 2013; Paredes-Villanueva et al., 2013), estimating future timber yield by providing direct age information (Brienen and Zuidema, 2006a; Rozendaal, 2010) and growth of the harvestable trees (Soliz-Gamboa et al., 2011) as well as providing climate-related growth information (Brienen and Zuidema, 2005a; Ferrero and Villalba, 2009; López and Villalba, 2011). Thus, the analysis of tree rings in Bolivian forests is currently contributing to an improved ecological understanding of tropical rainforest trees and forest-level population dynamics.

Amburana cearensis (Fabaceae) – a species endemic to Bolivia, Perú, Ecuador, south-eastern Brazil and northern Argentina – is among a suite of Bolivian tree species that exhibit clear potential for dendrochronology. The species is commercially significant as its moderately heavy wood is valued in manufacturing fine furniture and interior finishing. However, overutilization of the species means that populations of *A. cearensis* have declined considerably in recent years (Superintendencia Forestal, 1999). In a review of the dendrochronological potential of six Bolivian rain forest trees in the Amazon region, Brienen and Zuidema (2005a) reported that the annual tree rings of *A. cearensis* can be dated precisely and a strong and positive correlation exists between ring width and rainfall. This potential of tree rings as a source of information may not only offer the possibility to evaluate the yield of the species for its forest management, but also greater ecological understanding for the development of conservation strategies, through further data analysis on the sensitivity of *A. cearensis* tree-rings to climate and environmental variability.

As Brienen and Zuidema (2005a) have restricted their analysis on seasonal rainfall, we examine the sensitivity of *A. cearensis* to variation in monthly, seasonal and annual temperature as well as rainfall with the aim of identifying the broader potential of the species for climatological reconstruction in a tropical dry forest. In addition, we aim to construct a master tree-ring width chronology for *A. cearensis* to support dendrochronological studies of other Bolivian tree species.

2. Materials and methods

2.1. Study area and sample collection

Sample material was collected from a logging concession area (16°9′S, 60°47′W; 366–390 m a.s.l.) 31 km from the town of San Ignacio in the Central Chiquitania sector in the Western Cer-

rado Biogeographic Province of the Brazilian-Paranense Region (Navarro, 2011). Forests within the region are semi-deciduous with several canopy layers and are rich in lianas. The canopy height in this type of forest generally ranges from 16 to 22 m, with representative species of the Chiquitania forest such as *A. cearensis*, *Machaerium scleroxylon*, *Anadenanthera colubrina*, *Schinopsis brasiliensis*, *Acosmium cardenasii* and *Astronium urundeuva*.

A. cearensis (Fr. Allem.) A.C. Smith is a deciduous and partly light-demanding species that is common in semi-deciduous broadleaf forests, the Amazon forest and transition zones to moist montane forests in Bolivia. The species is generally restricted to shallow well-drained soils near rocky outcrops. *A. cearensis* flowers from March to May and fruit ripens between July and September. Seeds are dispersed by wind (Mostacedo et al., 2003).

Discs, representing the entire circumference of the bole at breast height (1.3 m above ground level), were collected from 11 *A. cearensis* trees. The use of cross-sections provides a larger field of observation than increment cores (López, 2003) and overcomes difficulties presented by stem eccentricity, high wood density, indistinct tree rings and presence of growth lenses and wedging rings.

2.2. Sample preparation and analysis

Samples were prepared using sandpaper with grit sizes from 26.8 to 425 μm (Orvis and Grissino-Mayer, 2002). Tree-ring identification was conducted along three radii of each sample disc. Tree-ring boundaries were identified based upon variations in the vessel frequency and distribution and axial parenchyma bands, as described by Brienen and Zuidema (2005a) and López (2011), and marked with a pencil. *A. cearensis* exhibited clearly visible rings during the juvenile stage of the trees where annual bands were bounded by a larger proportion of fibrous tissue with small lumens and thick cell walls at the end of each growing season. There was a contrast between latewood and earlywood. Earlywood appeared lighter with a higher percentage of vessels and aliform/confluent paratracheal axial parenchyma (Fig. 2a). However, as tree diameter increased, tree rings became more difficult to identify. In all instances, rings towards the periphery were narrower than in the centre of the sample. In many cases, tree-ring boundaries followed each other very closely. As reported by López (2011), we observed annual growth rings that were defined by narrow bands of terminal parenchyma (Fig. 2c). These features were particularly useful in identifying narrow rings in the periphery of our samples.

Cross-dating involves cross-matching samples from different specimens based upon the pattern of wide and narrow rings (Speer, 2010). By allowing each ring to be assigned to a calendar year, cross-dating overcomes problems arising from false or missing rings (Fritts, 1976). Visual cross-matching within each sample was achieved by comparing and reconciling tree-ring identification between radii using a binocular microscope (Leica MZ 125) coupled to a cold light source.

Once tree rings within each sample were correctly compared and matched, visual cross-dating was carried out within samples to avoid an eccentricity-related bias. Quantitative cross-dating was then conducted between samples by comparing and measuring tree-ring width series within a TSAP/LINTAB (Frank Rinn, Heidelberg, Germany) software/hardware combination to a resolution of 0.01 mm. Where necessary, corrections to previously measured series were made using WinDendro[TM] (Regents Instruments Inc., Canada) with a 0.001 mm resolution. Missing and false rings, suggested by cross-dated samples, were also evaluated using high-magnification digital microscopy.

The quality of inter-sample cross-dating was verified using COFECHA (Holmes, 1983). As our samples were obtained from closed-canopy stands, tree-ring widths were likely to be signifi-

cantly affected by stand-level factors. To overcome this problem, we applied a cubic smoothing spline (Cook and Holmes, 1986) with a 50% frequency cut-off over 32 years to our measurement series in COFECHA for the verification of cross-dating.

2.3. Chronology development

Standardization typically aims to remove non-climatic environmental- and age-related noise from tree-ring width series allowing high-frequency variability, usually climatic, to be analysed (Grissino-Mayer, 2001). We used ARSTAN 40c (Cook and Krusic, 2006) to develop a tree-ring chronology. However, standardization may also remove important low-frequency trends that are induced by climate. To minimize the loss of low-frequency climate information, we used a negative exponential function to account for the progressive decrease in ring width associated with increasing longevity and diametric size (López et al., 2012). Autoregressive modeling was performed to remove autocorrelation from the tree-ring series and a biweight robust mean was calculated to produce detrended chronologies of tree-ring width.

The ARSTAN program produced three versions of chronologies – STD, RES and ARS. The STD chronology comprises the mean of the detrended series, RES the mean of residual indices once all autocorrelation is removed and ARS the mean of autoregressed indices with the autocorrelation common to all series retained (Cook and Holmes, 1986). We made a preliminary analysis of the correlation between each resulting index and climate data to determine the chronology version with the greatest climate sensitivity. As the ARS chronology contained the strongest climatic signal and highest autocorrelation common to all trees, we used it for the following analyses.

In addition to generating the final chronology, ARSTAN also calculates (a) the mean inter-series inter-correlation, quantifying the similarity average among trees (R_{bar}), (b) first-order autocorrelation as a measure of the dependence of the tree-ring widths from their preceding tree-ring width (AC1), (c) mean sensitivity as a measure of year-to-year variability in width of consecutive rings (MS) and (d) the expressed population signal (EPS), reflecting the degree to which a chronology approximates the theoretical population chronology based on an infinite number of trees (Briffa and Jones, 1990; Grissino-Mayer, 2001). We restricted the chronology span to the period for which the EPS approximated or exceeded the threshold of 0.85 (Wigley et al., 1984). In addition, the annual growth trends of the chronology were analyzed.

2.4. Climatological analysis

We correlated the ARS chronology with climate data from the San Ignacio meteorological station (16°23′S, 60°58′W; 413 m a.s.l.), 32 km from the sample site (SENAMHI reporting agency). Mean annual rainfall is 1192 mm with a distinct rainy season from November to April. Mean annual temperature is 24.7 °C with a maximum of 31.5 °C during October and a minimum of 14.4 °C in June (Fig. 1). The annual average of the relative air humidity is 70%.

The meteorological data were available for the period 1950–2010. Instrumental climate (temperature and rainfall) data accessibility presents many limitations in Bolivia. The frequency of measurements, accuracy and existence of meteorological stations are some of the limiting factors for dendroclimatological analyses. For these reasons, we restricted our analysis to the 61-year window based on the measured and available climate data.

We analysed rainfall data for 24 months covering the previous and current growing periods (September$_{t-1}$ to May$_{t+1}$ in the southern hemisphere). We also correlated the ARS chronology with annual precipitation totals and mean annual temperatures.

Table 1
Statistics of the ring-width chronology of *Amburana cearensis*.

Chronology span	1788–2010 (223 years)
N. samples	8
N. radii	22
Mean sensitivity	0.41
Mean correlation	0.34

3. Results

3.1. Tree-ring chronology

The annual growth rings were defined by a band of marginal axial parenchyma and fibers (Fig. 2a). False rings were generally discontinuous around the circumference of the sample discs despite being well-defined locally.

Of the 33 radii collected and measured, cross-dating was verified for 22 radii on 8 sample discs. The ring-width data span the period from 1788 to 2010 (223 years) (Fig. 4). The mean tree-ring width ± standard deviation of *A. cearensis* during this period was 0.575 ± 0.22 cm yr^{-1}. Although the statistics used to evaluate the chronology were low, the mean inter-series correlation (R_{bar}) was significant ($\alpha < 0.01$) at 0.34 and the mean sensitivity (MS) was 0.41 indicating a high inter-annual variability in radial growth (Table 1). Difficulties in dating due to radial eccentricity, wedging rings and anomalies resulted in low replication in the earliest period covered by our data and limited the chronology to an EPS threshold fluctuating around 0.85 (Fig. 3). The resulting verified chronology was restricted to the 68-year period between 1943 and 2010 with a minimum sample depth of 17 for the following climate/growth analysis (Fig. 4).

Growth increased significantly during 1982–1992 and presented a general decreasing trend during recent years. Growth was fastest during 1983 and the lowest during 1882 (Fig. 4).

3.2. Climate-growth relationship

The tree-ring width indices of *A. cearensis* were positively and significantly ($\alpha < 0.05$) correlated with rainfall during October, November and May of the current growth year as well as April of the previous growth year. Significant negative correlations were evident between the chronology and maximum temperature during March, April and September of the current growth year and June of the previous growth year (Fig. 5).

Annual precipitation totals and mean annual temperature were also significantly ($\alpha < 0.05$) correlated with the ARS chronology (Fig. 6). For the common period analyzed, we observed some remarkable favorable periods. For example, the growth during the time between 1972 and 1981 was above average and clearly showed high rainfall values. Then, there was a decay of growth associated with low rainfall to around the year 2000. This behavior was also observed in the annual mean temperature data, with a decreasing trend from 1993 to 2003 and high growth during 1983 and 2005 (Fig. 6).

4. Discussion and conclusion

4.1. Tree-ring chronology

Our study is a new contribution to the understanding of the dendrochronological/climatological potential of *A. cearensis* in Bolivia. The average radial growth, reported here, of 0.575 cm yr^{-1} is consistent with that reported by López et al. (2013) for the Chiquitania region (0.58 cm yr^{-1}), but exceeds the measurements from permanent plots (0.309 cm yr^{-1}) reported by Dauber et al. (2003), who
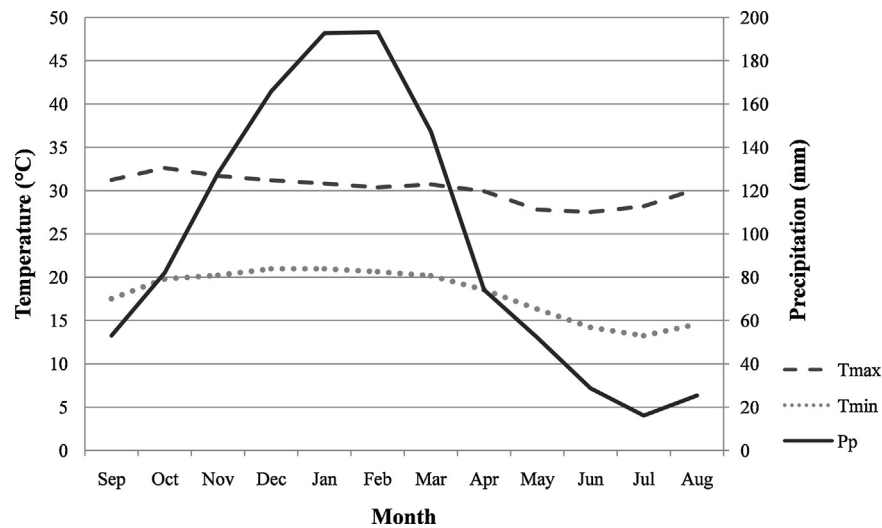
Fig. 1. Climate diagram for the San Ignacio region for the period 1950–2010 according to the SENAMHI database.

found that differences in annual increments depend on the tree crown position and on the degree of infestation by lianas. Growth appears to increase when trees received more light and were less infested by lianas (Mostacedo et al., 2009).

In this study, we observed low inter-radial correlation both between and within trees. This condition reflects the incidence radial-growth eccentricities that are common to tropical forest species (Sousa et al., 2012; Paredes-Villanueva et al., 2013). Specifically, our analysis revealed that irregular diametric growth associated with wedging rings and lenses – isolated sectors of growth associated with localized cambial activity during the

annual cycle (Villalba, 1997; López, 2003) – significantly affected cross-dating. Nevertheless, we report similar mean inter-series correlation (0.34) to that reported by Brienen and Zuidema (2005a) for *A. cearensis* (0.35).

We observed that the growth rates of *A. cearensis* decrease after specimens reach approximately 30 cm diameter. However, it is also important to note the shade tolerance and eventual canopy emergence expressed on the sensitivity and variation of growth along the first years of growth of the species. This may explain the low correlation of small diameter trees and suggests that these trees may not be useful for dendroclimatology assessment (Fig. 4).
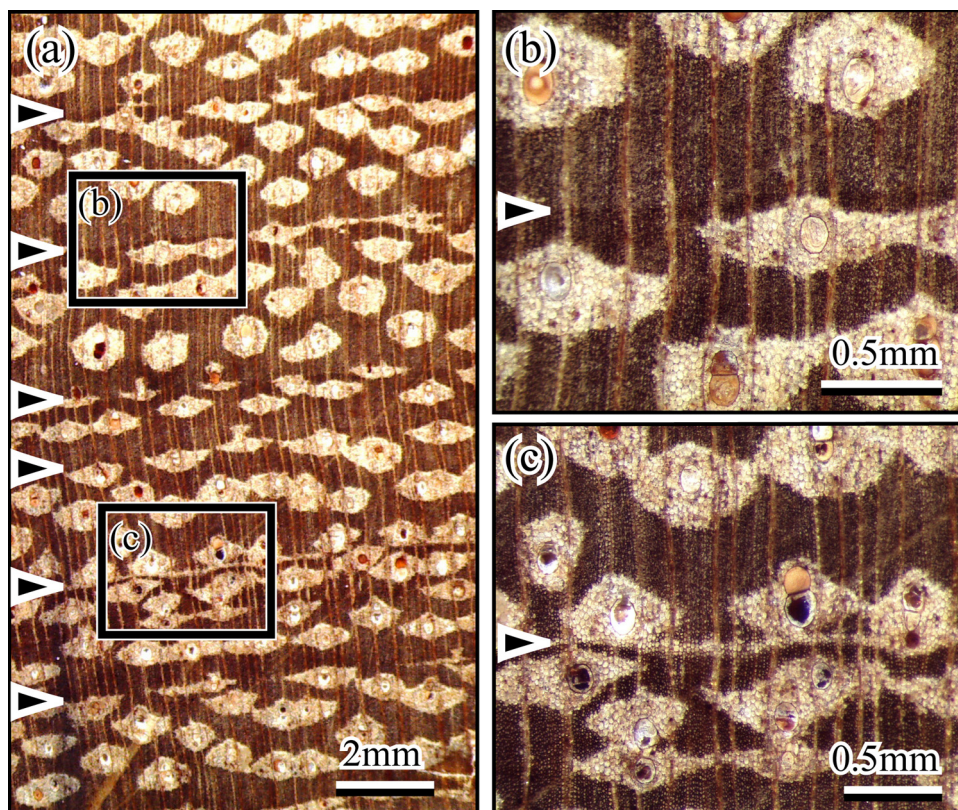

Fig. 2. Tree-ring boundaries in *Amburana cearensis* (a) varied considerably in structure. While many rings were characterized by a (b) distinct earlywood-latewood boundary, rings were also delimited by (c) terminal parenchyma. Ring boundaries are indicated by an arrow in each instance.
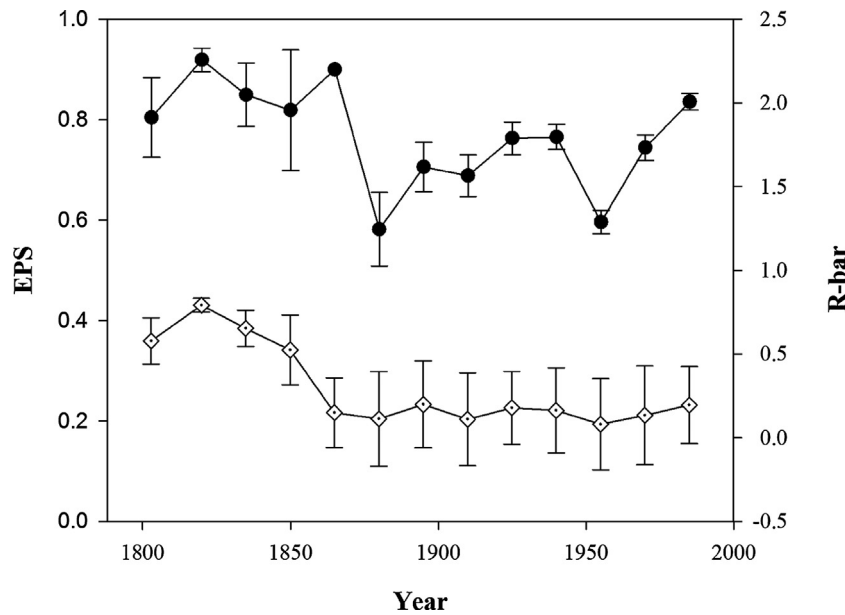
Fig. 3. Mean correlation coefficient (R_{bar}; open diamonds) and Expressed Population Signal (EPS; filled circles) for the *A. cearensis* chronology in San Ignacio.

4.2. Climate-growth relationship

High-frequency ring-width variability in *A. cearensis* partially reflects inter-annual climate variability (Brienen and Zuidema, 2005a). All seasonal processes, including shoot growth, flowering, cambial activity and leaf shedding are strongly inhibited by water stress (Borchert, 1994a). In this study we found a significant relationship between tree growth and precipitation (Brienen and Zuidema, 2005a; Rozendaal, 2010; López and Villalba, 2011; Soliz-Gamboa et al., 2011), although the relationship weakens from the middle of the rainy season onwards. This may reflect an increase in the variability of water stored in the soil (Markesteijn et al., 2010). In tropical climates with a severe dry season, rainfall constitutes a climatic determinant of tree phenology though many other environmental variables can determine it as well. Access to water stored in the soil or in stem tissues buffers the impact of drought. Addi-

tionally, flushing is suggested as a consequence of changes in tree water status caused by leaf shedding (Borchert, 1999).

Monthly correlation analysis also revealed an apparent effect of the maximum temperature and rainfall on tree growth. This result may partially reflect the inverse relationship between maximum temperature and rainfall during rainy season. This further suggests that inter-annual variation in tree growth is related to water supply (i.e., the balance between precipitation and evapotranspiration), which in turn is largely regulated by temperature (López and Villalba, 2011).

Correlation with precipitation totals are positive throughout the growing season, but fluctuate between positive and negative correlations after the dry season starts. The significant positive correlation during October and November suggests that growth of *A. cearensis* predominantly occurs at the start of the rainy season. Since this species is from the tropical dry forest, this early reac-
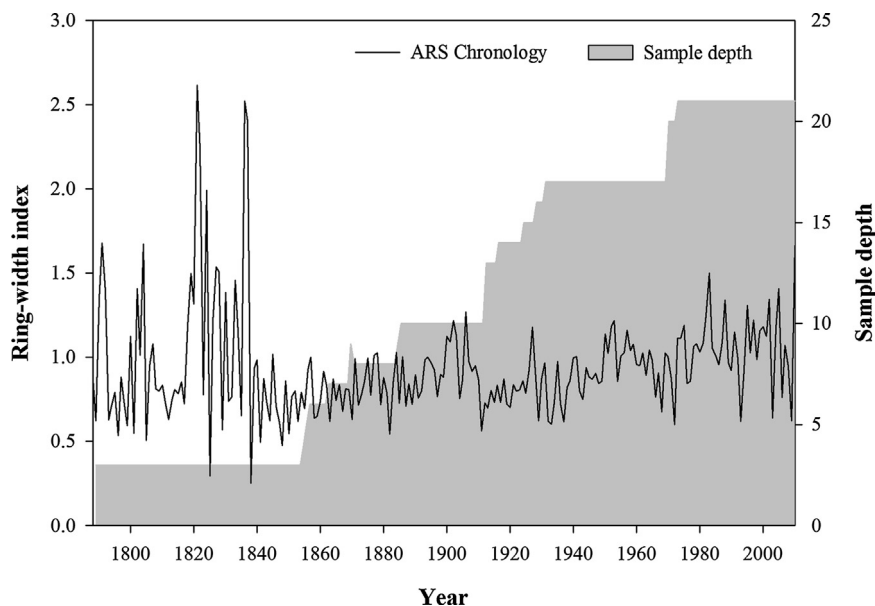

Fig. 4. ARS chronology and sample depth for *A. cearensis* from San Ignacio.
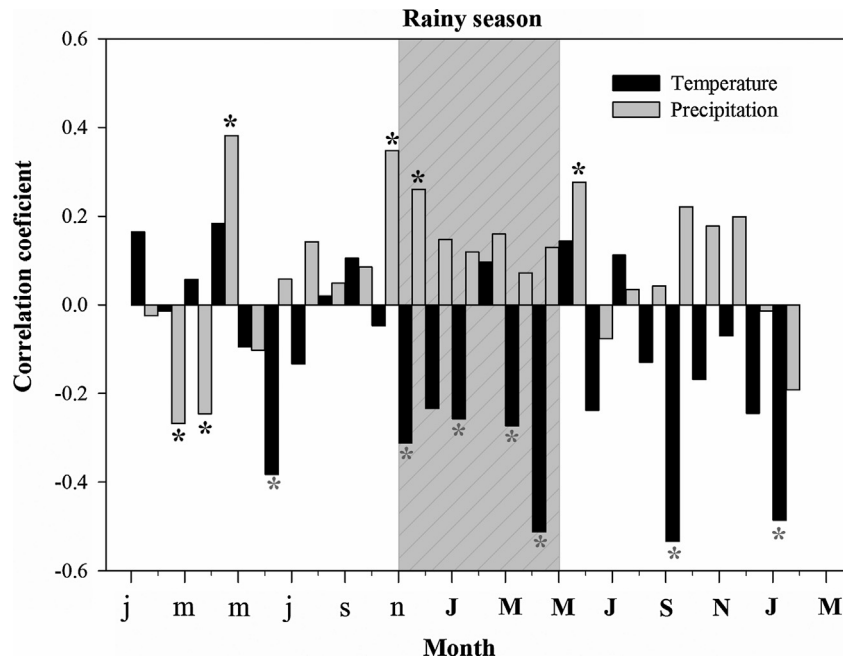
Fig. 5. Climatological sensitivity of the *A. cearensis* chronology to monthly maximum temperatures and monthly rainfall; *denotes significance at 0.05. The annual rainy season is shaded.
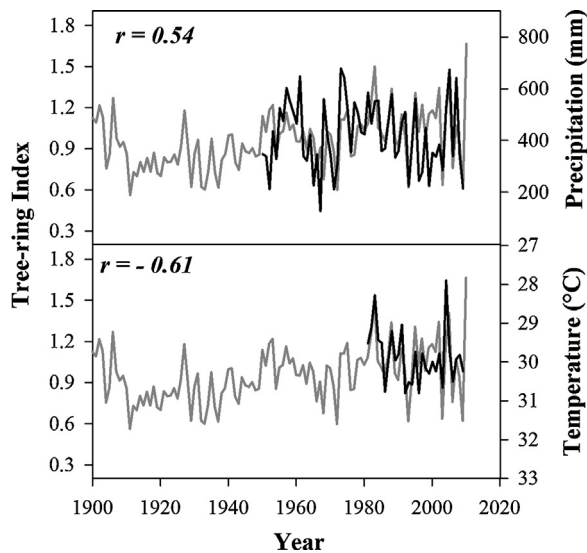

Fig. 6. Correlation between ring-width indices (solid gray line) and rainy season temperature/precipitation (solid black line).

tion may explain the high sensitivity of the species to the change of water availability as soon as the rainy season commences. It may also reflect a decreasing sensitivity in growth to precipitation later in the rainy season as water stored in the soil gradually increases and critical levels needed to initiate growth are exceeded (Brienen and Zuidema, 2005a).

In addition to the apparent effect of current conditions, variation in ring width appears to be related to conditions during the previous growing season. This is consistent with the analysis of *A. cearensis* from the Bolivian Amazon done by Brienen and Zuidema (2005a) which attributed the variation to the storage on water table depth or tree stem (Borchert, 1994b) during the previous growth year (Dünisch et al., 2003). They also explained that low correlation between growth and late rainy season conditions might be related to the decreasing photosynthetic capacities of older leaves

(Mooney et al., 1981; Ackerly and Bazzas, 1995; Kitajima et al., 1997), soil water reserves surpassing critical levels needed to support growth or the break of bud dormancy concurrent with rainy season (Brienen and Zuidema, 2005a). However, in contrast to our samples from tropical lowland dry forest, bud dormancy break partially explained correlation of growth with rainfall during early (October–November) rainy season that continues until May.

From the analysis of the tree ring and climate data, we conclude that dendrochronological data extracted from *A. cearensis* holds potential for climate reconstruction. Variability in the correlation between the ring-width chronology and climatic data indicates that that potential is limited to monthly rainfall and maximum temperature data during the rainy season. On the other hand, low correlation between ring-width indices and minimum temperature suggests that this variable is not suitable for climate reconstruction.

Despite the eccentricity presented in some samples, significant correlation was found among the *A. cearensis* samples, with an average growth of 0.575 cm yr^{-1}. Correlations between growth indices and rainfall were significant particularly during the rainy season. Significant correlations between maximum temperature and growth indices may explain the species' high dependency on the water availability. Consistent with these results, *A. cearensis* exhibits a potential for reconstructing monthly rainfall and maximum temperature during rainy season in the Chiquitania region. Since many zones in Bolivia lack continuous, publicly-available meteorological data, the results of this study offer an alternative source for climatological data to support ecological and forest management studies in the Chiquitania region. Through revealing trends in ring width and the sensitivity of ring width to climate data, our results also offer potential insights into the ecology of *A. cearensis*.

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