Dendrochronological growth characterization of timber species from moist to dry tropical forests in Bolivia

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Contenido

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presented by:
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Resumen

En la búsqueda de mayor información y entendimiento de las especies *Machaerium scleroxylon*, *Amburana cearensis*, *Cedrela fissilis* y *Cedrela angustifolia*, muy valiosas y comerciales en nuestro país pero cuyas poblaciones han disminuido considerablemente, hemos aplicado la dendrocronología como factor común en cada uno de los análisis realizado en la presente tesis, además de la relación del crecimiento y el clima. Las aplicaciones y casos variaron según la novedad del estudio, avances y vacíos de conocimiento.

Capítulo II: Empezamos con el análisis del potencial dendrocronológico de una especies nueva y poco conocida, *Machaerium scleroxylon*. Las características de la madera y fenología de esta especie presentan variaciones lo que ha dificultado el avance en las investigaciones, mayor conocimiento de la especie y consecuentemente ha causado deficiente manejo forestal. Las características anatómicas de la madera (anillos falsos, lentes de crecimiento y anillos sobrepuestos) requirieron mucho tiempo y paciencia para el reconocimiento e identificación de los anillos de crecimiento pero, una vez sobrellevado este contratiempo, se pudo estimar el Diámetro Mínimo de Corta (DMC), ciclo de corta y crecimiento medio anual. Además de analizar este último en relación al clima local (bosque tropical seco) y a los patrones de circulación atmosférica (El Niño-Oscilación del Sur).

Capítulo III: Para el caso del roble (*Amburana cearensis*), ya se contaba con información previa de estudios que determinaron la anualidad de la especie. El objetivo de la investigación fue el de ir un paso más allá para conocer a la especie demostrando así otra aplicación de la dendrocronología en especies locales, reconstrucciones climáticas, además de su utilidad en proporcionarnos mayor información sobre el crecimiento y comportamiento de la especie en el bosque tropical seco.

Capítulo IV: Finalmente y debido a la urgencia de conocer más sobre el crecimiento de *Cedrela* por su importancia en el CITES y normativas locales para regular el mercado internacional, se analizaron las diferencias de crecimiento de *Cedrela fissilis* y *Cedrela angustifolia* en 3 diferentes

tipos de bosque: Bosque Seco Chiquitano, Chiquitano Transicional Amazónico y montano Tucumano.

Posteriormente se presenta una síntesis de la aplicación de la metodología propuesta, resultados obtenidos e implicaciones para el manejo forestal en Bolivia y cambio climático. Finalmente, se proponen temas para investigaciones futuras en relación a los datos e información analizada.

Summary

In search of more information and understanding of the species *Machaerium scleroxylon*, *Amburana cearensis*, *Cedrela fissilis* and *Cedrela angustifolia*, valuable in our country but whose populations have significantly decreased, we applied dendrochronology as a common factor in each of the analyzes done in this thesis, in addition to the relationship of growth and climate. Applications and new cases varied by study, advances and knowledge gaps.

Chapter II: We start with the analysis of dendrochronological potential of a new and little known species, *Macherium scleroxylon*. The characteristics of the wood and phenology of this species exhibit variations which have hindered progress in research, greater understanding of the species and consequently caused poor forest management. The anatomical characteristics of wood (false rings, lenses and wedging rings) required much time and patience for the recognition and identification of tree rings, but once overcome this setback, we could estimate the Minimum Logging Diameter (MLD), cutting cycle and mean annual growth. The later was also analyzed relative to the local climate (tropical dry forest) and atmospheric circulation patterns (El Niño-Southern Oscillation).

Chapter III: In the case of roble (*Amburana cearensis*), we already had prior information of researches that confirmed the annuity of the species. The aim of our research was to go a step further to know more about this species therewith demonstrating another application of dendrochronology to local species, climate reconstructions, in addition to its usefulness in providing us more information on the growth and behavior of the species in the tropical dry forest.

Chapter IV: Finally, because of the urgency to know more about the growth of *Cedrela* species and its importance in the CITES and local regulations governing international market, growth differences in *Cedrela fissilis* and *Cedrela angustifolia* were analyzed in 3 different types of forest: dry Chiquitano forest, Chiquitano transitional Amazonian and Tucuman montane forests.

Then a summary of the application of the proposed methodology, results and implications for forest management and climate change in Bolivia are presented. Finally, future research topics are proposed in relation to the data and information analyzed.

Chapter 1

General Introduction

Forest degradation through agricultural expansion, conversion to pasture, the development of infrastructure, illegal logging and fires account for almost 20% of global green house gas emissions - more than the entire global transport sector and second only to the energy sector (Averchenkova 2010). Added to these factors, selective harvesting of valuable timber species as morado (*Machaerium scleroxylon*), roble (*Amburana cearensis*) and cedro (*Cedrela fissilis*), has negative impacted causing population reduction and degradation of species in natural forests (Gullison *et al.*, 1996; Killeen *et al*., 1993).

International negotiations (REDD-plus) have been considering approaches and incentives relating to reducing emissions from deforestation and forest degradation and the role of conservation, sustainable forest management and enhancement of carbon stock of forests in developing countries. This prompted us to test more systematically forest management in Bolivia. As the behavior of timber species and impact of climate change on forest may be different depending on forest type and environmental conditions, dendrochronology can be used to characterize timber species and regions of origin supporting monitoring systems. Through the use of tree rings analysis as an alternative for the determination of past and present growth rates in different regions will allow getting ecological and forest dynamics information of Bolivian tropical forests.

During the last decade Bolivia has implemented a comprehensive reform of its forest sector. However, unsustainable practices still lead to loss of natural resources. Historical management in tropical forests has shown a general trend towards the adoption of polycyclic selective logging systems where harvesting is the first and most important silvicultural treatment applied. For this reason, special attention has been given on how to improve harvesting operations for commercial species (García-Fernández, *et al*., 2007). Unfortunately, forest regulations adopted in Bolivian Forestry Law are based on arbitrary assumptions of growth rather than profound ecological knowledge. Therefore, understanding the ecological dynamics of the target species is essential to establish truly sustainable management policies in tropical forests.

Forest dynamics can be understood from the study of growth rings, allowing fill information gaps about the behavior of forest species, reconstruct historical patterns of growth and the impact of the variability in the physical environment during the entire tree life (Brienen, 2005; Jagels *et al*., 1994; Pumijumnong and Park, 1999). The knowledge of these species-level sensitivy to environmental factors 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.

Initially, it was argued that the pattern of cambial activity in the development of tropical and intertropical species, as those in Bolivia, differed significantly to that of temperate species bearing no distinctive rings, because the vascular cambium remained active all year round or great part of it (Dave and Rao, 1982; Borchert, 1999). However, in the last decade it has been found that many tropical trees form annual rings (Worbes, 1999; Fichtler *et al*., 2003; Fichtler *et al*., 2004; Brienen and Zuidema, 2005a, Brienen and Zuidema, 2006a; Ferreira *et al*., 2009) with variants to the temperate zones. 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 some endemic species (Worbes, 1999; Wimmer, 2002; Brienen and Zuidema, 2005a; Ferreira *et al*., 2009). The dendrochronological potential studies of some species in Bolivia such as *Schinopsis lorentzii* (Ferrero and Villalba, 2009), *Bertholletia excelsa*, *Cedrelinga catenaeformis*, *Tachigali vaquezii* and *Peltogine* cf. *heterophylla* (Brienen and Zuidema, 2005a; Brienen and Zuidema, 2006a, 2006b; Rozendaal, 2010; Soliz-Gamboa *et al*., 2011), *Amburana cearensis, Anadenanthera colubrina, Platimiscium ulei, Ficus boliviana, Hymenaea courbaril, Cedrela fissilis* (López *et al*., 2012; López *et al*., 2013), *Clarisia racemosa* (Rozendaal, 2010; Soliz-Gamboa *et al*., 2011), *Cedrela odorata* (Brienen *et al*., 2012b) and *Centrolobium microchaete* (López and Villalba, 2011; López *et al*., 2013) specify that these species develop annual visible rings.

However, it is important to study other useful species such as morado (*Machaerium scleroxylon*), whose populations have declined considerably in recent years, and provide deeper information of those already explored as roble (*Amburana cearensis*) and cedro

(*Cedrela spp.*). Estimates of growth rates, Minimum Logging Diameter and growth patterns in relation to climate variability give us information not only from the studied species but also study from the environment in which they grown thus allowing us further explore the potential for climate reconstructions.

This thesis was conducted in order to analyze the dendrochronological potential of *Machaerium scleroxylon* and *Cedrela angustifolia*, the climate reconstruction potential of *Amburana cearensis* and the differences of growth and behavior of *Cedrela* species (*Cedrela fissilis* and *Cedrela angustifolia*) in different environmental conditions to contribute to an improved ecological understanding of these threatened tropical trees leading to best decisions, harvesting and conservation practices in a context of global climate change.

Forest management in Bolivia

To date, logging activities on public, private and community lands in Bolivia have been governed by the Forest Act 1700 (Ley 1700, 1996).They are done with prior inventory and census of trees, analyzing the population structures and ecosystems conditions to intervene. With the information of trees diameter distribution of each species it is possible to set the harvesting intensity through Minimum Logging Diameter (MLD) by species (BOLFOR/FMT, 2003a) so that each one is seized with equal intensity and impact to be distributed evenly between the species (Hutchinson, 1993). In addition, a cutting cycle is established (BOLFOR/FMT, 2003b), which should be a minimum of 20 years before returning to the same harvesting area (annual harvesting area), allocating 20% of the current abundance for seed trees and 10% of total area for reserves and conservation easements (Normas Técnicas 248, 1998). This forest management acquired in Bolivia is characterized by being based in a polycyclic system where it is possible to make two or more selective harvesting during the rotation age estimated for the forest (cutting cycles) according to market demands and abundance of commercially valuable species (Lamprecht, 1990).

Cuadro 1: Minimum Logging Diameter for some species and their corresponding Life Zones (Normas Técnicas 136, 1997).

	Forest type (Life Zones)		
Species	Tropical and subtropical moist	Transition and dry Chiquitano	Montane and lower montane
Swietenia macrophylla (mara)	70	NA[1]	NA
Cedrela spp. (cedro)	60	60	60
Hura crepitans (ochoó)	70	NA	NA
Ficus spp. (bibosi)	70	NA	NA
Ceiba pentandra (mapajo)	70	NA	NA
Amburana cearensis (roble)	50	45	NA
Juglans spp. (nogal)	NA	NA	60
Podocarpus spp. (pino)	NA	NA	60
Nectandra spp. (laurel)	NA	NA	60
Ocotea spp. (laurel)	NA	NA	60
Other species	50	40	50

The proposed rules and parameters for operation in a given area are followed according to a Management Plan which is the instrument for forest management resulted from a process of rational planning based on the evaluation of forest characteristics and potential of the area to be used. The plan is prepared in accordance with the rules and regulations for the forest protection and sustainability and it is duly approved by the competent authority responsible for defining the uses of the forest, the activities and practices applicable to the sustainable yield, the replacement or qualitative/quantitative improvement of resources and the preservation of the balance of ecosystems (Ley 1700, 1996).

However, the application of the Minimum Logging Diameter is only efficient when the species have a diameter distribution type of inverted "J", as is the case with many shade tolerant, and not in the bell-shaped trend of light species, heliophytes (Oliver and Larson, 1900; Orozco, 2002). For the MLD be set for each species, it is necessary to know its diameter distribution and

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[1] _NA = not aplicable

ecology through quantitative analysis which will contribute to the adoption of sustainable practices and prevent species extinction or genetic erosion of species selected for harvesting.

Harvesting alone is not sufficient to cause positive and uniform reactions in young trees or natural regeneration of desired species after cutting and should apply an appropriate and planned ahead silvicultural treatment (Hutchinson, 1993). Today Bolivian forest rules do not require obtaining information on natural regeneration before use and only recommends a precautionary principle (Article 9, Ley 1700, 1996) and the inclusion of a monitoring system over forests in the Management Plan to assess their growth, yield and response to silvicultural treatments. Although the establishment of permanent sample plots (PPM), temporary plots and sampling diagnostics have been suggested, to determine growth rates (forest yield), regeneration density of commercial species and natural regeneration potential and future harvesting trees, there is freedom to choose other sampling techniques to generate the information necessary to adjust management practices (Directriz Técnica 003, 2006). For this purpose, in recent years most of the used data have come from the permanent sample plots (PPM); however, they provide short historical data unlike data provided by the analysis of tree rings through dendrochronology.

Theory and application of dendrocronology

From the Greek "chronology" = time and "dendro" = trees, is the scientific method of age estimation based on the analysis of patterns of tree rings (Liutsko, 2008). This technique was developed during the first half of the twentieth century by the astronomer A.E. Douglas, who founded the Tree-Ring Research Laboratory at the University of Arizona, United States. Douglas, trying to better understand the cycles of solar activity, reasoned that changes in solar activity can affect weather patterns in land and would later be recorded in tree rings. Like most trees have annual growth increment, information related to formation (and the factors that influence it) can be represented by the specific characteristics of each ring: width, density and other visual or analytical parameters that may differ one ring from the others (Fritts, 1976; Schweingruber, 1988). The dendrochronological techniques allow, by dating and study of annual tree rings of woody species, to reconstruct the life of the tree and forest dynamics in terms of the major disturbances as climate or other environmental factors (Fritts, 1976). Therefore, the dendrochronological techniques are essential to study the production of wood in the forests and to estimate the optimal cutting cycle of timber species in addition to growth based modeling of these processes to obtain forecasts on production of the species (Fritts, 1976).

Dendrochronology is divided into many sub-fields, many of which have applications to problems of the environment and climate. Dendroclimatology refers to the application of analysis of tree rings for understanding the past and present climate, while being able to identify periods of extreme weather conditions. However, a number of environmental factors can affect the growth of plants, which can be classified into external and internal. Water and temperature are some of the most important external factors. In addition, complex interactions can occur, not only between the internal and external factors, but also between physiological and growth (Fritts, 1976) processes.

El Niño-Oscilación del Sur (ENSO)

The El Niño phenomenon is the pattern of abnormal warming of surface water of the Pacific Ocean in the equatorial region and coasts of Ecuador, Peru and Chile, which is a manifestation of the changes occurring in the upper layers of the ocean linked to processes produced in the equatorial Pacific Ocean. For its study and monitoring, the international scientific community divided the ENSO in the Pacific Ocean into four regions: Niño 1.2 including both 1 and 2 defined by 0° -5° S, 90° W-80° W and 5° S -10° S, 90° W-80° W, respectively; Niño 3 bounded by 5° N-5° S, 150° W-90° W; Niño 3.4 bounded by 5° N-5° S, 170° W-120° W and Niño 4 bounded by 5° N-5° S, 160° E-150° W (Figure 1). The Southern Oscillation Index (SOI) is the difference in surface atmospheric pressure between Tahiti (French Polynesia) and Darwin (Australia), when this value is negative it indicates a reversal of pressure systems in the Pacific Ocean and the presence of El Niño. There is a relationship between the behavior of SOI and El Niño (ENSO). The warm phase of ENSO coincides with El Niño (ocean warming) and negative SOI; the cold phase of ENSO, matches La Niña (ocean cooling) and a positive SOI (SENAMHI, 2002). ENSO records are available at the National Oceanic and Atmospheric Administration (NOAA web page).

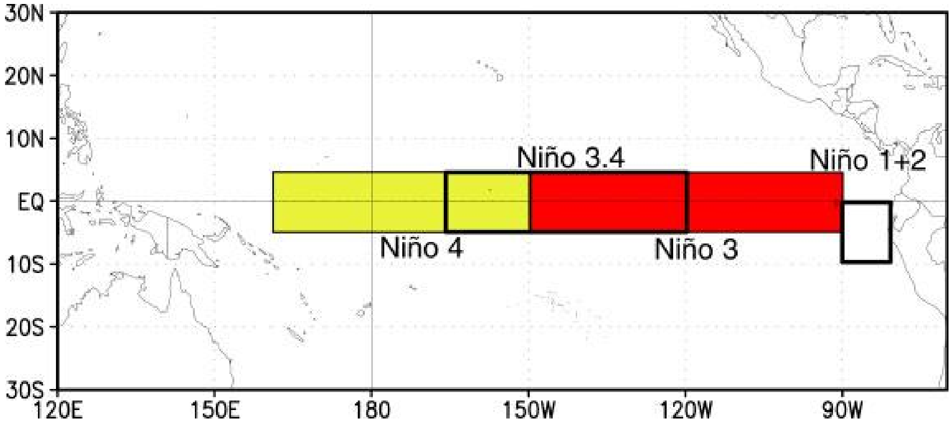


Figure 1. Graphic representation of El Niño regions. Source: NOAA/ National Weather Service (2005)

Methodology application and aim of this thesis

We selected the stands and regions for the studies and also prioritized areas according to the species distribution. Trees of each population were sampled from the areas identified and dendrochronological analysis was done using standard procedures (Brienen and Zuidema, 2006a, 2006b; López, 2003; López and Villalba, 2011). The ring widths were then compared to the local temperature and precipitation based on meteorological stations data for all the cases.

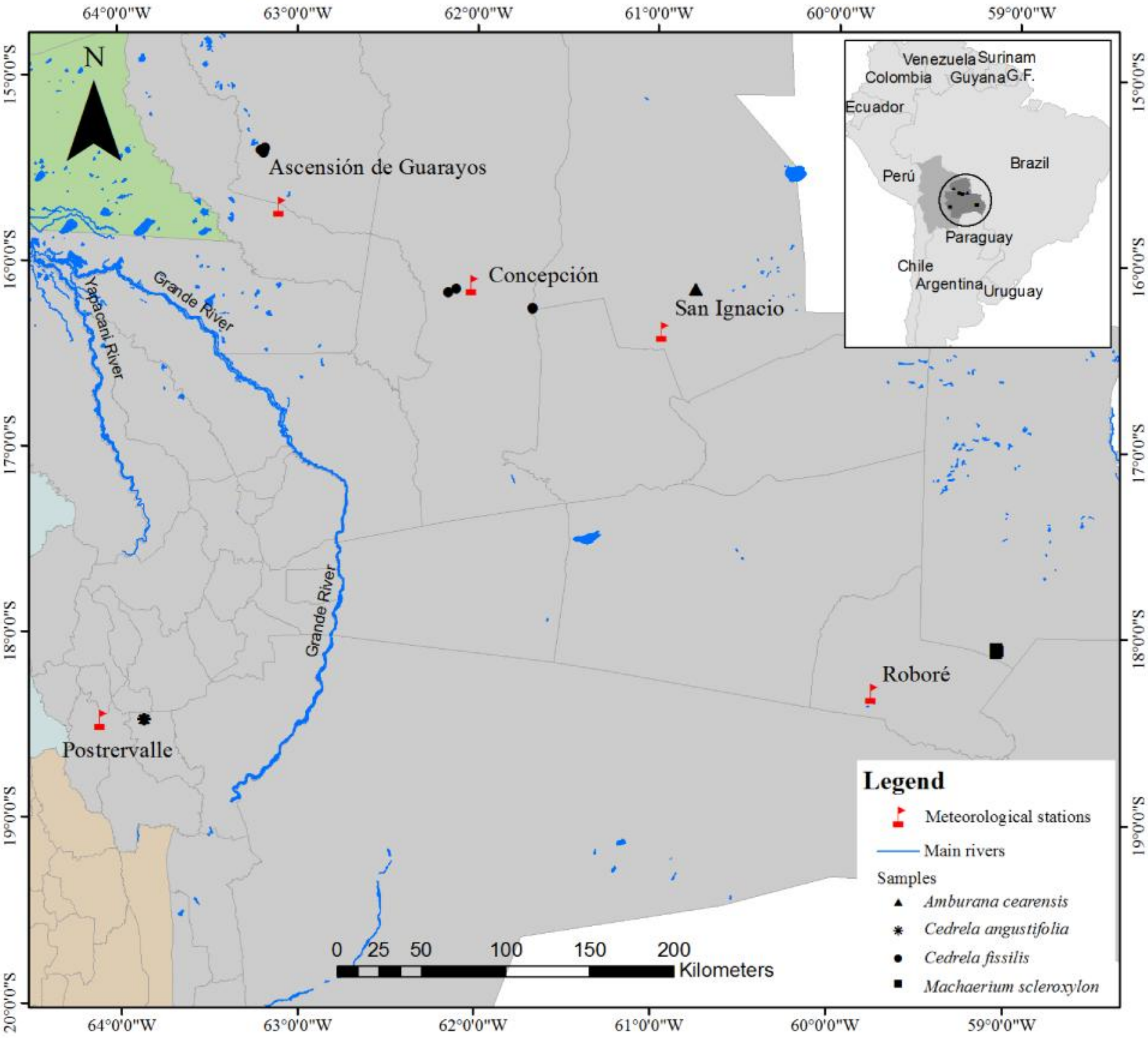


Figure 2. Sample sites and meteorological stations of the four study species

Objectives

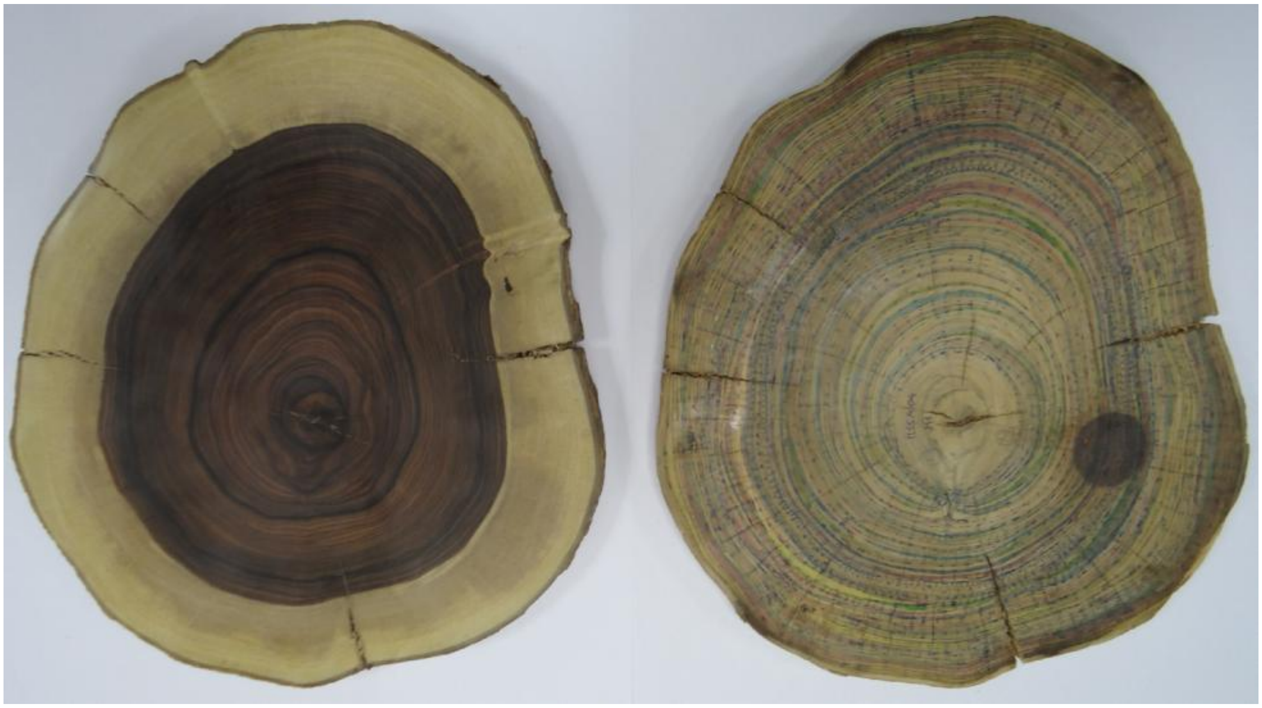
(i) to develop the chronologies of *Machaerium scleroxylon*, *Amburana cearensis*, *Cedrela fissilis* and *Cedrela angustifolia*, some of the most valuable and fragile timber species from the dry and moist forests in Santa Cruz de la Sierra, Bolivia,

(ii) to quantify the changes in recent radial growth in response to climatic variables such as rainfall, temperature and atmospheric circulation patterns (El Niño-Southern Oscillation) and

(iii) to estimate growth differences based on local environmental conditions and ring-width data as input for decision-making to improve forestry and sustainable use of the species.

Chapter 2

Growth rate and climatic response of *Machaerium scleroxylon* in a dry tropical forest in Southeastern Santa Cruz, Bolivia



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Growth rate and climatic response of *Machaerium scleroxylon* in a dry tropical forest in Southeastern Santa Cruz, Bolivia

Abstract

Machaerium scleroxylon (morado) is an important timber species from the lowland tropical dry forests in Bolivia. We followed a dendrochronological approach to (i) evaluate the responses of radial growth to climatic variables and atmospheric circulation patterns; and (ii) to quantify the growth rate in order to estimate the Minimum Logging Diameter, age and optimal cutting rotation. We measured tree-ring width in wood discs taken from ten randomly selected mature individuals. We used previous histological analyses to distinguish and visually crossdate tree rings. Despite the existence of false rings, lenses and wedging rings, the species showed defined annual ring boundaries thus enabling a tree-ring chronology analysis. Correlations between residual ring-width indices and monthly climatic variables (temperature and rainfall) and atmospheric circulation patterns (El Niño-Southern Oscillation) index were calculated. Growth showed a significant positive correlation with monthly rainfall and a negative correlation with mean temperature during the late rainy season (i.e., from December up to March). A positive correlation found between the ring width and ENSO indices indicates that the growth of *M. scleroxylon* was significantly affected by atmospheric circulation patterns. Growth rate is slow in morado, suggesting a MLD of 50 cm and an optimal cutting cycle longer than 40 years depending on each site.

Keywords: Tree rings, *Machaerium scleroxylon*, tropical dendrochronology, El Niño-Southern Oscillation, Minimum Logging Diameter.

Introduction

Historical management in tropical forests has shown a general trend towards the adoption of polycyclic selective logging systems. In such systems, harvesting operations are the first and most important silvicultural treatment applied. For this reason, special attention has been given on how to improve harvesting operations for commercial species, mainly based on the Minimum Logging Diameter (MLD; García-Fernández *et al*., 2007). Unfortunately, MLD values adopted in Bolivian Forestry Law are based on arbitrary assumptions of growth rather than profound ecological knowledge. However, understanding the ecological dynamics of the target species is essential to establish truly sustainable management policies in tropical forests.

Tropical dry forests in the lowlands of Bolivia, also known as Chiquitano forest, are among the most diverse in the world (Parker *et al.*, 1993) and occupy an area of approximately 20 million hectares. Forests in Chiquitanía have very low diameter growth rates, with an overall average of 0.173 cm year^{-1}, ranging from 0.143 cm year^{-1} to 0.211 cm year^{-1} (Dauber *et al*., 2003). These forests are fragile due to slow regeneration capacity under drought conditions, the continuing threat of deforestation and human-made fires that eliminate forest cover for agriculture and livestock (Uslar *et al.*, 2003). The high vulnerability of tropical dry forest to weather and climate hazards, associated with the history of forestry, make this one of the regions where potential changes in the hydrological cycle due to global warming could lead to extreme impacts on ecosystems (Toledo *et al.,* 2011b).

The behavior of Bolivian forests under climate change conditions can be understood from the study of tree rings. This type of study allows closing information gaps about the behavior of forest species and reconstructing historical growth patterns during the entire life of trees (Brienen, 2005; Ferrero and Villalba, 2009). Similarly, tree-ring characteristics (width and density) reveal details of the natural history of an individual and its ecosystem (Jagels *et al.*, 1994; Pumijumnong and Park 1999). For example, diseases attacks, pests, prolonged drought stress and damage by fire can be detailed in ring characteristics (Shortle *et al.*, 1995; Weber, 1997).

Previous tree-ring studies have analyzed the growth dynamics in tropical forests (Worbes, 1992; Pumijumnong and Park, 1999; Tomazello and da Silva Cardoso, 1999), the construction of tree rings chronologies in young individuals (Soliz-Gamboa *et al.*, 2011), growth patterns related to variation in age (Brienen and Zuidema, 2006a; Rozendaal, 2010), to support the determination of MLD (Brienen and Zuidema, 2006b; Rozendaal, 2010; López *et al.*, 2013) and the climate-related growth of several species (Wimmer, 2002; Brienen and Zuidema, 2005; Ferrero and Villalba, 2009; López and Villalba, 2011).

Dendrochronology can aid in modeling growth to make predictions on the availability and potential of each species in a future climate scenario and secondary effects on forest management. The phases of growth and relative inactivity in many plants are closely related to environmental factors e.g., water availability effect on the seasonal cambial activity (Borchert, 1994). Thus, knowledge of the relationship between environmental variables and tree growth is important in predicting future growth responses to climatic variation (Pumijumnong, 1999) and to long-term phenomena as El Niño Southern Oscillation (ENSO) (Cook, 1992). Such knowledge will be useful to understand the behavior of fragile Bolivian ecosystems in a context of global climate change, to provide guidelines to a suitable forest management (Stahle *et al.* 1999; Brienen and Zuidema 2005).

Previous studies in species such as *Bertholletia excelsa*, *Cedrelinga catenaeformis*, *Centrolobium microchaete*, Tachigali *vaquezii* and *Peltogine* cf. *heterophylla* (Brienen and Zuidema, 2006a, 2006b; López and Villalba, 2011) have shown the dendroclimatic potential of several tree species in Bolivia, illustrating that these species develop visible annual rings (Brienen and Zuidema, 2005). It is important to study other useful unexplored species such as *Machaerium scleroxylon* (hereafter abbreviated as morado), whose population has declined considerably in recent years. In Bolivia, species considered valuable in the main trade group, including morado (Justiniano and Fredericksen, 1998), are scarce, with values of basal area and volumes that remain low and often absent in diameter classes above the MLD, established by the Bolivian Forestry Law 1700.

The present study had the following objectives: (i) to develop the first chronology from *M. scleroxylon*, one of the most valuable and fragile timber species from the Chiquitano forest in Santa Cruz de la Sierra, Bolivia, (ii) to quantify the changes in recent radial growth in response to climatic variables such as rainfall, temperature and atmospheric circulation patterns (El Niño-Southern Oscillation) and (iii) estimate growth rate, MLD and optimal cutting rotation based on age and cumulative ring-width data as input for decision-making to improve forestry and sustainable use of the species. Dendrochronological methods were used to evaluate the response of morado growth to climate and its management implications.

Materials and Methods

Study site and climate data

The study site is located in the southeastern part of Santa Cruz, Bolivia. This area belongs to the Brazilian-Paranense region of Western Cerrado Biogeographic Province and is covered by semideciduous Chiquitano forest, usually rich in lianas. The canopy is 16 to 22 m high on average, with *Amburana cearensis*, *Machaerium scleroxylon*, *Anadenanthera colubrina*, *Schinopsis brasiliensis*, *Acosmium cardenasii* and *Astronium urundeuva* as representative species of the Chiquitano forest (Navarro, 2011).

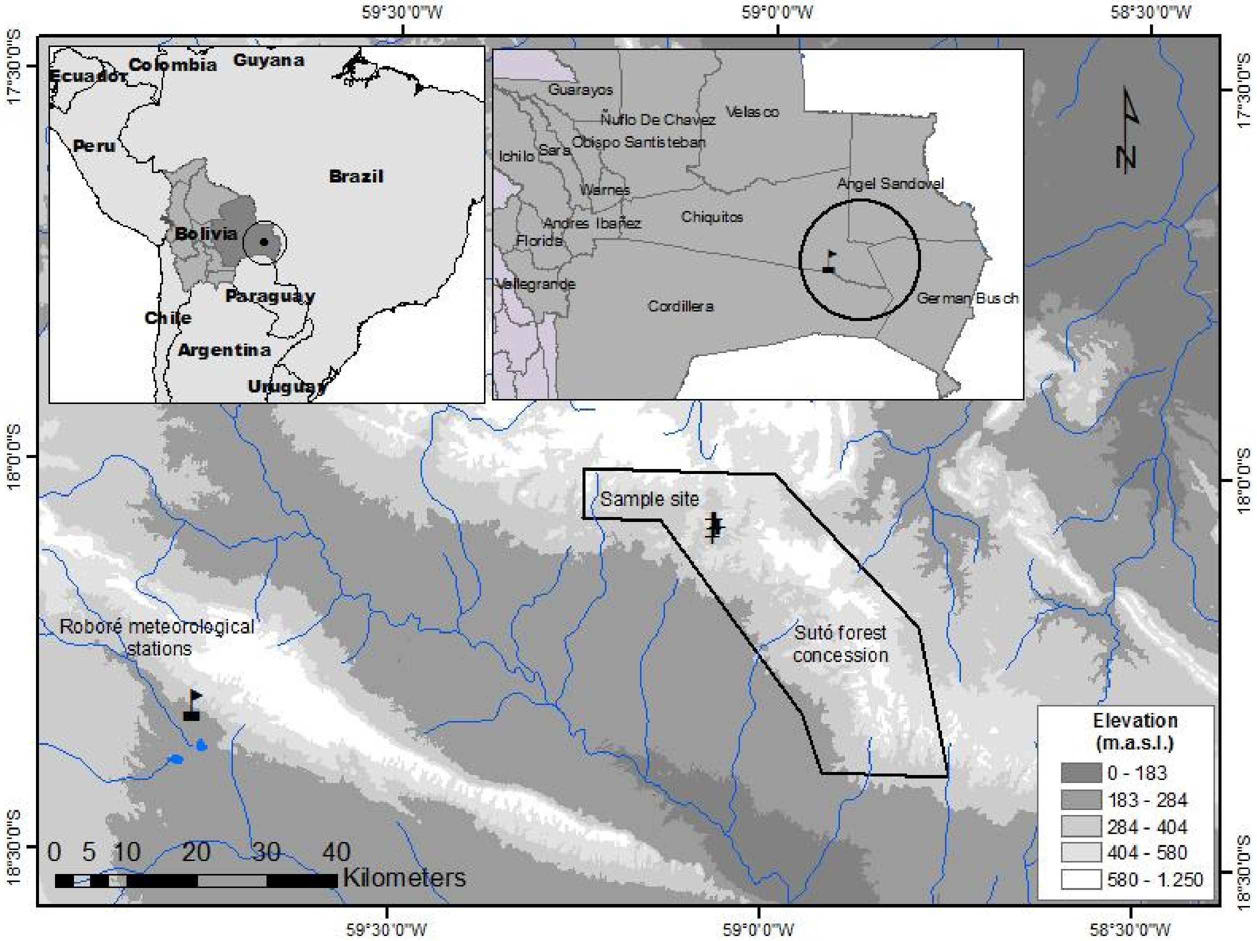

Figure 1. Sampling site in Sutó forest concession, Chiquitos province (Santa Cruz, Bolivia).

The climate in this area is warm (infratropical) to hot tropical (thermo). Annual rainfall ranges from 651 to 2029 mm and it is mainly concentrated from November to April and with low rainfall from May to October. Annual averaged temperatures range from 12.8ºC to 39.5°C (Navarro, 2011). The nearest weather station is located in Roboré (18°19'S, 59°46'W, altitude 277 m) (Figure 1). It is approximately 75 km from the study site and belongs to the Bolivian National Service of Meteorology and Hydrology (SENAMHI). We used climate data for two purposes: to quantify changes in climatic trends in the study area during the available time span and to assess climate-growth relationships. The climate data set used for the study contained rainfall records from 1942 to 2010 and temperature from 1978 to 2010. We calculated annual rainfall and temperature starting from October of the previous year (i.e., the beginning of the rainy season and flowering of morado) until September of the current year.

In addition, the study also explored correlations of the response of growth ring widths to the ENSO signal, defined by the Southern Oscillation Index (SOI; Ropelewski and Jones, 1987) and the Sea Surface Temperature Index for the Niño 1.2 (0°-10°S, 90°-80°W) and 3.4 regions (5°N-5°S, 170°-120°W) (Trenberth and Stepaniak 2001). The time-series of these indices were obtained from the NOAA Climate Prediction Centre (http://www.cpc.ncep.noaa.gov/data/indices/index.html).

Tree species

Machaerium scleroxylon (Fabaceae) is considered the most important logging species in the Chiquitano forest (Killeen *et al*., 1993). Dauber *et al*. (2003) found that this species has an overall average diameter increment of 0.237 cm year^{-1}. It is a semi-deciduous and partially shade tolerant species common in the dry forest of the Great Chiquitanía. It flowers from November to December and its seeds are wind-dispersed, between June and August (Justiniano and Fredericksen, 2000; Mostacedo *et al*., 2003). Morado is light demanding during its early years, but is more shade tolerant than pioneer species such as *Centrolobium microchaete*, *Anadenanthera macrocarpa* and others. Morado thrives in various soil conditions such as stony ground and slopes with rapid drainage (Lorenzi, 1992). The sapwood is yellowish white distinct to the black purple color of the heartwood. Its timber is considered of high density with ranges from 0.85 to 0.95 g cm^{-3} (Nisgoski, 1999; Gutiérrez and Silva, 2002; Roque *et al*., 2007).

Field sampling and histological analysis

Several factors make it difficult to obtain samples for tree-ring analysis using traditional dendrochronological techniques in the dry tropics of South America (López, 2003). Cross-sections of trees provide a larger field of observation, as it is much easier to delimit the annual growth increments in such samples than in cores. Based on these considerations, we collected ten wood discs (DBH range 13.5 - 53.4 cm) from the area of the logging company Sutó Ltd. (18°45'S, 59°40'W) between the towns of Roboré and Santa Ana de Chiquitos (Figure 1). It was not feasible to sample a large number of trees, as it is commonly examined in dendrochronological studies (Fritts 1976), due to the limitations to the activities of the logging company. The samples were taken at breast height (1.30 m) from randomly distributed trees of different diameters with dominant and/or co-dominant height on the forest canopy during harvesting activities.

There is little available information about the yearly phenology of morado. Therefore, according to the literature on others species (Wimmer, 2002; Brienen and Zuidema, 2005; Ferrero and Villalba, 2009; López and Villalba, 2011; López *et al.*, 2013); previously to tree-ring identification, histological analyses of the samples were done to identify the boundaries of the rings, and in order to facilitate identification with the naked eye (Figure 3A). The reagents used for staining tissues of anatomical slices for the analyses of tree rings were ethyl alcohol, sodium hypochlorite, astrablue and safranin. Further, for the identification of tree rings in the heartwood and due to wood’s grain characteristics, after grinding the samples discs they were immersed in sodium hypochlorite from 12 hours (Figure 3B) to improve the transversal visibility of tree rings located in the heartwood.

Dendrochronological data analysis

Cross-sections were air dried and carefully polished with progressively finer sandpapers until tree rings were clearly visible. After this, we selected 3 radii on each discs using a stereomicroscope. This was the approach taken due to the difficulty of identifying wedging rings with the naked eye. Similarly, areas with reduced visibility of tree rings were moistened with water. Once tree rings were identified and dated, wedging and false rings were identified and analyzed by checking their length and characteristics in the entire contour of the discs (Figure 3C). For crossdating purposes, each annual tree ring was assigned to the year in which the growth season started (from October of the current year to September of the following year; Schulman 1956).

After the identification process, the last 68 rings of each radius were crossdated. Due to the difficulty of ring identification and pith rot, dating complete sections of discs from bark to pith was not possible. Then, ring widths were measured using LINTAB-TSAP^{TM} measuring device (Rinntech, Heidelberg, Germany) with a 0.01 mm resolution. Also, dating and measurements were revised with WinDendro^{TM} (Regents Instruments, Canada) with a 0.001 mm resolution.

The software COFECHA (Holmes 1983) was used to statistically check errors in visual crossdating and to obtain a synchronized master chronology. For each tree, the series of raw data were detrended and standardized using ARSTAN software (Cook and Holmes, 1986). This was done in order to remove biological and geometrical trends (age and size related growth trends). A cubic smoothing spline was used with a 50 % frequency response cutoff of 25 years to maintain the high-to-medium frequency response to climatic variability (Cook and Peters, 1981). Autoregressive modeling was performed on each detrended ring-width series to remove most of the first-order autocorrelation, and the prewhitened series were finally averaged using a biweight robust mean to obtain residual chronology. Residual chronology for assessing growth–climate relationships was used (Monserud, 1986). In order to assess the quality of tree-ring width series dendrochronological statistics were calculated considering the common 1942-2009 interval (Fritts, 1976). For each chronology, we computed: the first-order autocorrelation of raw tree-ring width data, a measure of the year-to-year growth similarity (AR1), the mean sensitivity of residual chronologies which measures the year-to-year variability in width of consecutive rings (MS), the mean between-trees correlation which quantifies the similarity in residual width indices among trees (*rbt*) and the percentage of variance explained by the first principal component which is an estimate of the common variability in growth indices among all trees (PC1). The chronology segment with Expressed Population Signal (EPS) values higher than 0.85 was regarded as reliable and used in further climate-growth analyses, where EPS is a measure of the statistical quality of the mean site chronology as compared with a perfect infinitely replicated chronology (Wigley *et al.*, 1984).

Minimum Logging Diameter (MLD) Estimation

In order to assess the cumulative growth in the basal area and to remove the trend of decreasing ring width with increasing tree size, we converted radial increment into Basal Area Increment (BAI), considering all the trees and using the following formula:

$$\mathrm{BAI} = \pi\,(R^2_{\mathrm{t}} - R^2_{\mathrm{t-1}}) \qquad [1]$$

where R is the radius of the tree and t is the year of tree-ring formation. In wood discs without pith, we estimated the missing rings using a geometrical method and taking into account the mean growth rate of the innermost rings dated in samples with pith. Based on the radial increments and BAI results, we estimated the MLD presented by tree cumulative DBH curves and the physiological age for each sampled tree (López *et al.*, 2013). The purpose of this analysis was not to date each growth ring accurately but to cumulate ring-width data, beginning with the pith ring and ending with last complete ring formed before bark. The relationship between age and cumulative diameter for sampled trees was calculated from the three measured radii per tree, which were first doubled to estimate diameter, such diameter increments were then cumulated from the pith to the bark ring (Stahle *et al.*, 1999; Schöngart *et al.*, 2007). In cases where the available cross-section did not extend to the pith, the true position of the pith ring and the width of the first growth rings had to be estimated from the curvature and growth rate of the innermost rings dated in samples with pith. The relation between cumulative diameter and age was adapted to sigmoidal regression model.

Radial growth – climate relationship

To determine the influence of local and regional climatic variables (atmospheric circulation patterns and climatic variables –rainfall and temperature–) in morado radial growth, we related tree-ring width residual indexed chronology to monthly climate data. The relationships between interannual variations in morado growth index and climate were established using Pearson correlation coefficients and response functions (Fritts, 1976; Holmes, 1999). Response function coefficients were based on bootstrapped stepwise multiple regressions computed on the principal components of climatic variables (Fritts, 1976) using the DendroClim 2002© software (Biondi and Waikul, 2004). The significance of correlations was evaluated using 95% confidence limits and establishing comparisons with bootstrapped regression coefficients. This method correlates variations in the tree-ring chronology with sequential monthly temperature and rainfall records. Considering that tree growth might be influenced by climate conditions during both current and previous years, this analysis includes climate variables for the current and previous year of tree-ring formation (Vaganov *et al.*, 2006). In our study, growth index was compared with monthly climate series of temperatures and rainfall for the common period 1978-2009 in climatic data - from January of the previous growing season to December of the year of tree-ring formation - based on previous dendrochronological studies (Ferrero and Villalba, 2009).

We used monthly values for ENSO and SOI indices to determine their associations with tree-ring width indices and the influences on cumulative growth. We analyzed the correlation patterns between the growth index and monthly El Niño-Southern Oscillation (ENSO) indices, using two different regions in the Pacific Ocean: El Niño 1.2 and El Niño 3.4, and monthly values of the Southern Oscillation Index (SOI) for the 1978-2009 periods.

Results

Climate trends

The climatic characteristics of the study area are presented in ombrothermic diagrams prepared from Roboré weather station with SENAMHI data for periods 1980-1995 and 1996-2009. It should be noted that the decrease in precipitation amount during the growing season was more intense in the latter period (F= 3.85, $P < 0.05$) (Figure 2). Over the last 14 years (1996-2009), the dry season has increased significantly in length (from June-August to June-September) whereas the rainy season has become shorter (from October-March to November-March) and rainfall in June has decreased. Moreover, there are slight fluctuations in temperature in Roboré and the period of high temperatures coincides with the November to March rainy season.

There was a high variability of rainfall during the period 1942-2009. There were also extreme years, with the highest rainfall recorded in 1978 and the driest period recorded in 2009. Rainfall showed a slight overall decline in the last decade, whereas the temperature increased between 1°C to 2°C from the mean in the period 1978-2009. Furthermore, we found a negative relationship between annual rainfall and mean annual temperature (Figure 2). Spring and summer rainfall values greatly influence the annual mean estimations. Although there was greater data stability in annual average temperatures during summer, maximum and minimum temperatures values showed major fluctuations during spring and autumn.

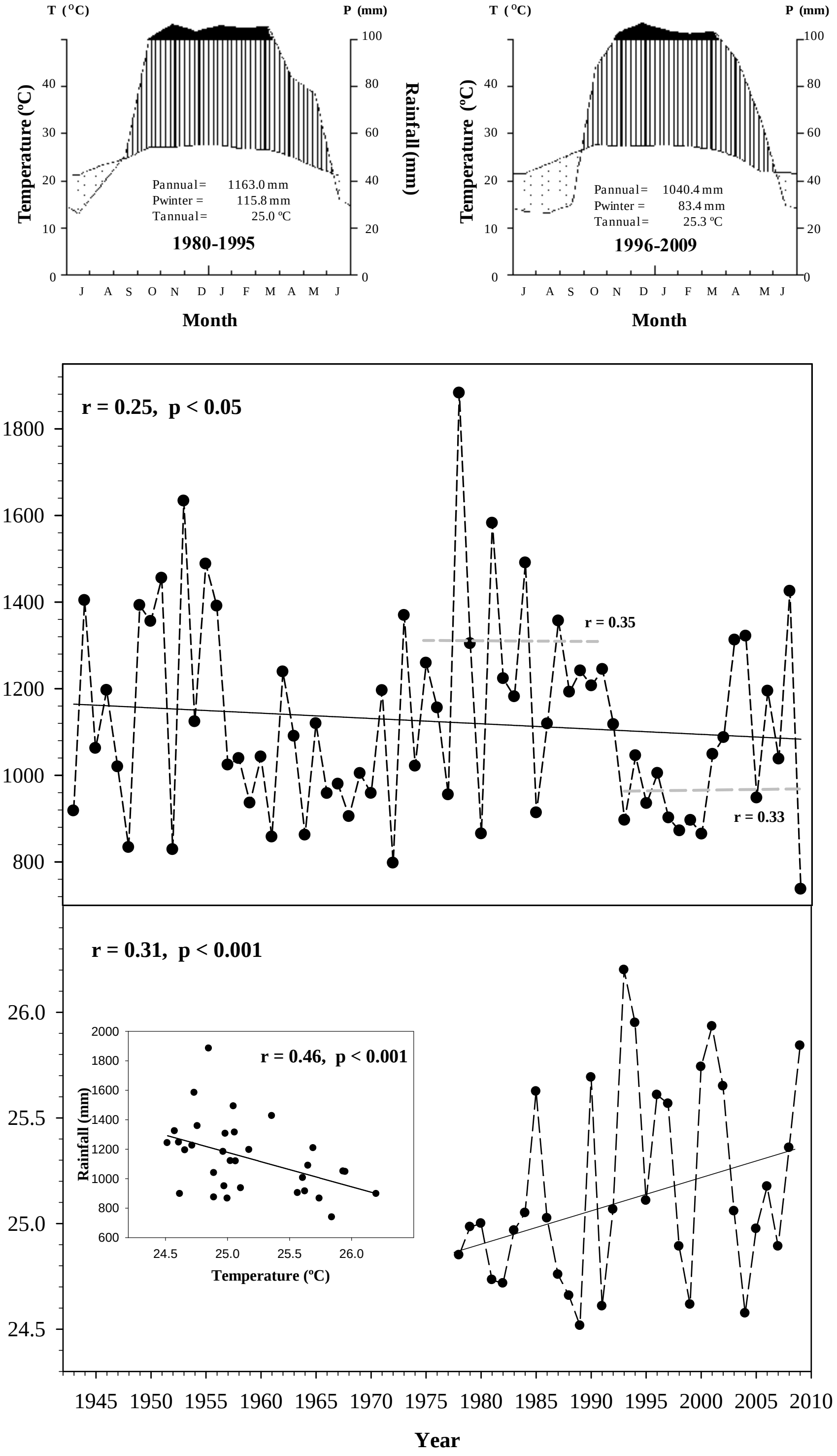

Figure 2. Ombrothermic diagrams from Roboré region for the periods 1980-1995 and 1996-2009 according to SENAMHI database and climatic trends in mean annual rainfall for the period 1942-2009 (top) and mean annual temperature for the years 1978-2009 (bottom) as well as the relationship of temperature and rainfall in Roboré.

Chronology

Based on anatomical analysis and local climatic conditions (most species have growth and leaf fall when wet and dry periods, respectively, are present during each year), the wood structure of *M. scleroxylon* was characterized by tree rings defined by marginal parenchyma fine lines and diffuse pores (Figure 3A and C). Furthermore, lenses, false and wedging rings were identified, generally located where deformation occurred or where the discs did not have a circular shape.

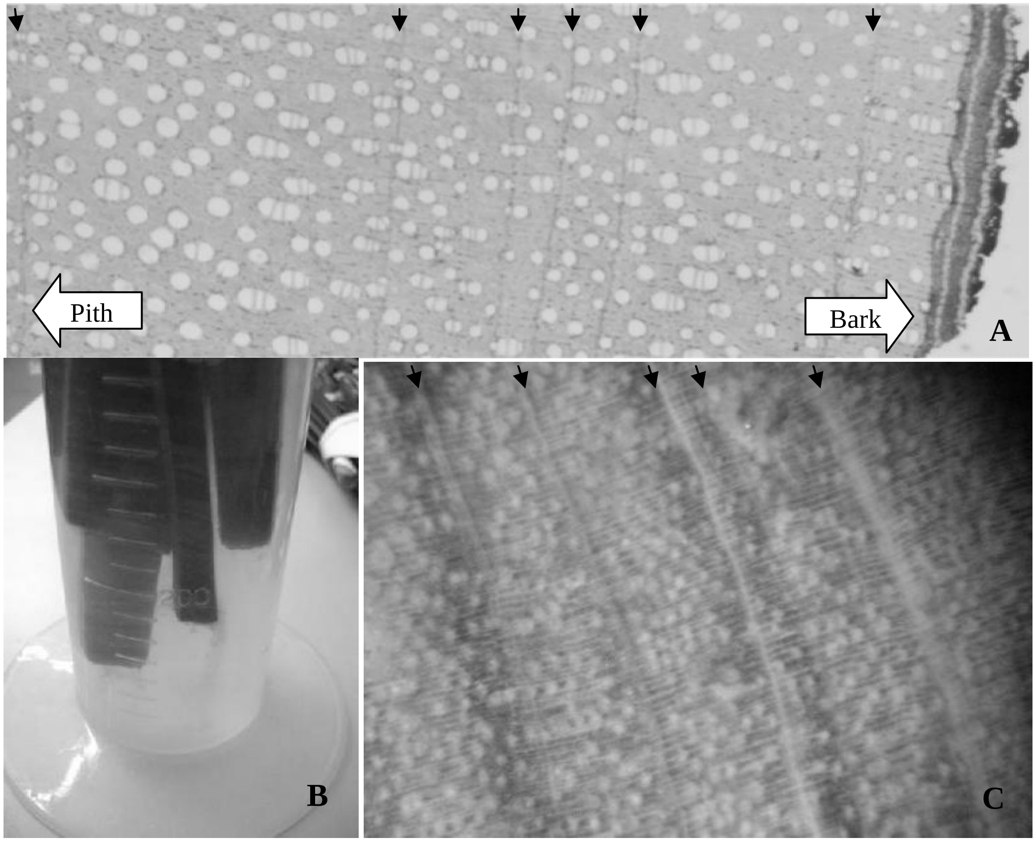

Figure 3. Visibility of tree rings after immersion in sodium hypochlorite. (A) Anatomical analysis and identification of tree rings, (B) Testing the effect of sodium hypochlorite in the samples, (C) Identification of rings in the heartwood after immersion.

We analyzed a total of 30 radii, corresponding to 10 cross-sections of *M. scleroxylon* composed of 3 radii each. These radii covered the period 1913-2009. Although for the present dendroclimatic study we worked from 1942 due to the availability of climate data and the difficulty in dating the rings before that year. Thus, we analyzed a total of 68 years of data.

The mean tree-ring width for the common period 1942-2009 was 1.43 mm year^{-1}. The first-order autocorrelation (AR1) of the tree-ring width series was 0.25, suggesting a low year-to-year persistence in growth, whereas the mean sensitivity (MS) was 0.67 indicating a higher inter-annual variability of radial growth (Table 1). The mean correlation between trees (*rbt*) was 0.47 and the Expressed Population Signal (EPS) were higher than 0.85 in the period 1942-2009. The higher growth consistency among trees, the number of samples collected and the measured radii showed an adequate representation of the tree growth variability in the study area (Table 1).

We found a variation in growth which suggested the existence of three significant stages or periods: 1942-1966, 1967-1982 and 1983-2009 (Figure 4A and B). During the period 1966-1988, growth increased and decreased by more than 1 mm. The difference was more distinct for the period 1978-1982. The greatest growth took place during 1978.

Table 1. Site description and characteristics of *M. scleroxylon* chronology in eastern Bolivia. The statistical values were calculated for the common period 1942-2009. All dendrochronological statistics were calculated for residual series excepting AR1 which was obtained for raw tree-ring width data. Values are expressed as means (± 1 standard deviation).

Location	**Dbh (cm)***	**Tree-ring width (mm)**	**Estimated Age (years)**	**AR1**	***rbt***	**MS**	**PC1 (%)**	**EPS**
Santa Ana-Roboré	39.0 ± 14.6	1.43 ± 0.53	120 ± 35	0.25 ± 0.15	0.47 ± 0.11	0.67 ± 0.06	45.73	0.930

* Diameter at breast height measured at 1.3 m; AR1, first-order autocorrelation; *rbt*, mean between-tree correlation; MS, mean sensitivity; PC1, variance accounted for by the first principal component; EPS, Expressed Population Signal.

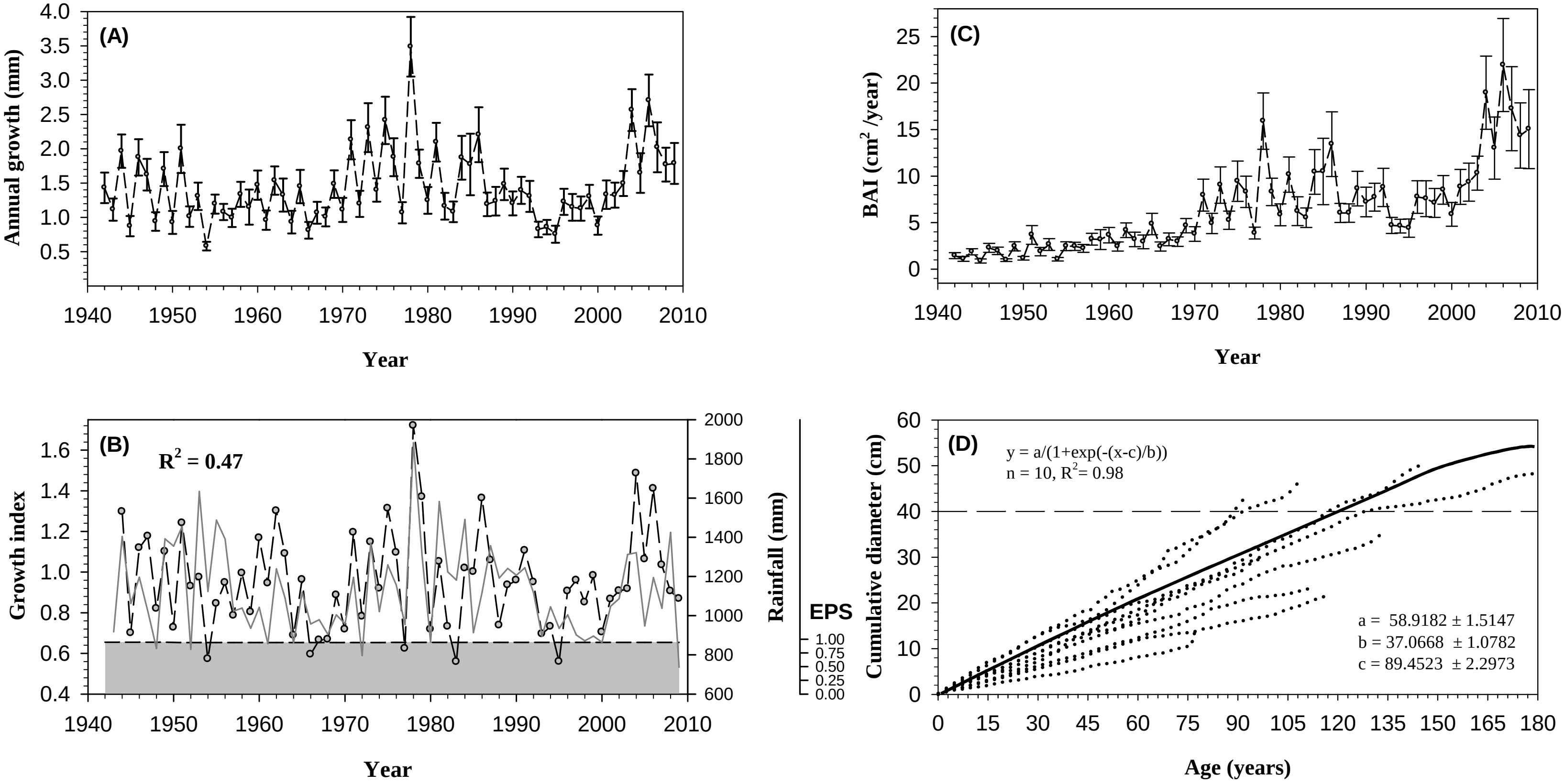

Figure 4. Radial growth changes in morado through the 1942-2009 period. Recent trend in (A) Master chronology of ring width, (B) relationship of morado radial growth rate (black dotted line) and October-September local rainfall (gray solid line) during the growth period of the species and EPS statistics for morado chronology; the total interannual variation (R^2) in the growth of morado explained by rainfall is indicated, (C) average basal area increment and (D) relationship between physiological age and cumulative diameter for sampled trees, fitted with a sigmoidal regression model.

We observed a direct relationship between water availability and growth in morado (Figure 4B); with good synchrony between growth reductions and documented drought events in the study sites in 1954, 1977, 1983, 1995, 2000 and 2007. Similarly, positive growth levels were consequent with observed wet years in 1951, 1963, 1978, 2004 and 2006 (Figure 4B). These positive growth levels mainly coincided with rainfall in December, January and February.

Minimum Logging Diameter (MLD) Estimation

The accumulated growth and Basal Area Increment showed an almost constant slope during the period 1940-1970, followed by relatively high growth and finally a slight decrease starting from 1996 (Figure 4C). The Basal Area Increment showed a trend toward higher growth, which may indicate that the species has not reached its optimum production shift and requires a cutting cycle over 40 years, since the trend based on the adjusted sigmoidal regression equation remains positive after 140 years.

The average DBH of the morado population was 39 cm, with 6 individuals exceeding the MLD of 40 cm established by the 1700 Bolivian Forestry Law (Table 1). The greatest contribution to total basal area was found at a DBH around 50 cm. Tree estimated age of morado varied between 77 and 193 years (Figure 4D). The relationship between tree age and DBH of morado is statistically significant ($R^2 = 0.98$, $P < 0.001$) allowing the modeling of cumulative diameter growth curves described by a sigmoidal regression model where y is the cumulative diameter (cm) and x the tree age in years (Figure 4D). After 140 years, an average tree reaches approximately 50 cm of DBH. From the mean diameter growth curve we derived the current and mean diameter increment. Trees reach their maximum current diameter increments at an age of 70–86 years, with a rate averaging 0.83 cm year^{-1}, while the highest increment rate observed exceeded 1.49 cm year^{-1}.

Climate-growth relationship

We found a significant correlation between growth and rainfall during previous January (r = 0.32), and non significant but high correlation with previous September (r = 0.24) and the current

January (r = 0.29) for the period 1978-2009. This was consistent with the rainy season, which provided support for a strong relationship between morado growth and late spring–summer rainfall in the semi-arid region of Chiquitanía. We found negative correlations with both mean and minimum temperatures in current February (r = -0.30, r = -0.31) and March (r = -0.26, r = -0.33). Maximum temperatures showed a significant positive correlation with previous February (r = 0.27) and the current June (r = 0.26); and significant negative correlation with the current October (r = -0.27) for the common period 1978-2009 (Figure 5). Above-average temperatures in spring and summer seem to have increased water deficit, reducing tree growth.

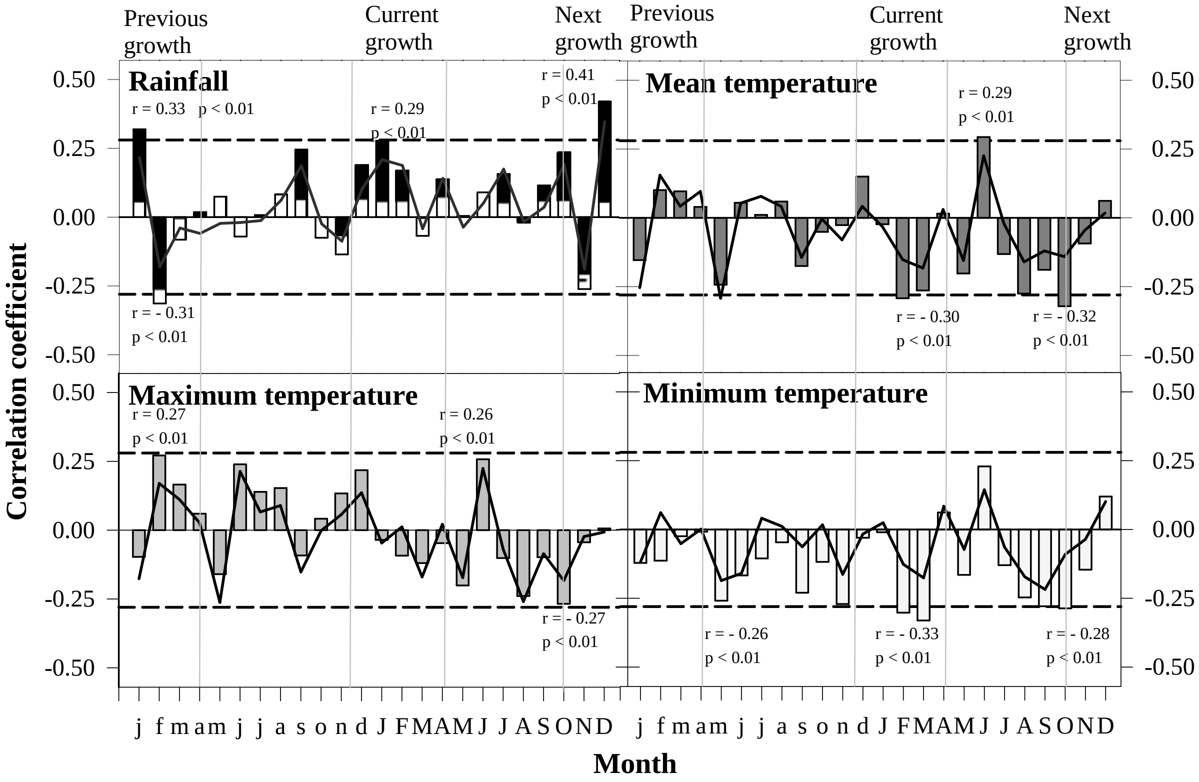

Figure 5. Correlation (bars) and bootstrapped response coefficients (lines) between monthly climate variables and radial growth of morado (residual indices of ring width) during the common period 1978-2009 for rainfall and mean, maximum and minimum temperatures. Growth was correlated with climatic variables of previous year (months abbreviated in lowercase) and current or ring formation year (months abbreviated in capital letters). The horizontal dashed lines

indicate the level of significance ($p < 0.05$) and describes the r and p values for those with $r > 0.25$.

The chronology of *M. scleroxylon* showed a positive correlation with El Niño-Southern Oscillation (ENSO) (Figure 6). Specifically, the chronology response to SOI indices was generally positive throughout the growing season, showing the highest correlation in previous July ($r = 0.43$) (Figure 6A). In contrast, the response to El Niño 3.4 and El Niño 1.2 regions for the ENSO in the Pacific Ocean was negative overall. El Niño 3.4 showed a significant negative correlation at the end of growing season during the previous July ($r = -0.27$) and a significant positive correlation during current September ($r = 0.33$). El Niño 1.2 showed extreme negative values during October ($r = -0.31$) and April ($r = -0.27$) of the growing season (Figure 6B and C). Additionally, if we compare the behavior of SOI with the rainfall and growth shown in Figure 2 and Figure 4, respectively, it can be observed the effect of El Niño in the growth of the species in 1951-1952, 1963-1964, 1977 -1978, 1986-1988, 2004-2005 and 2006-2007 where the thickness of the rings were greater than in other years. Similarly, growth in the years 1954-1956, 1964-1965, 1989-1990, 1999-2000 and 2007-2008 remarkably represented La Niña (Figure 4). This behavior could be also explained for the relation between SOI and winter rainfall (dry season).

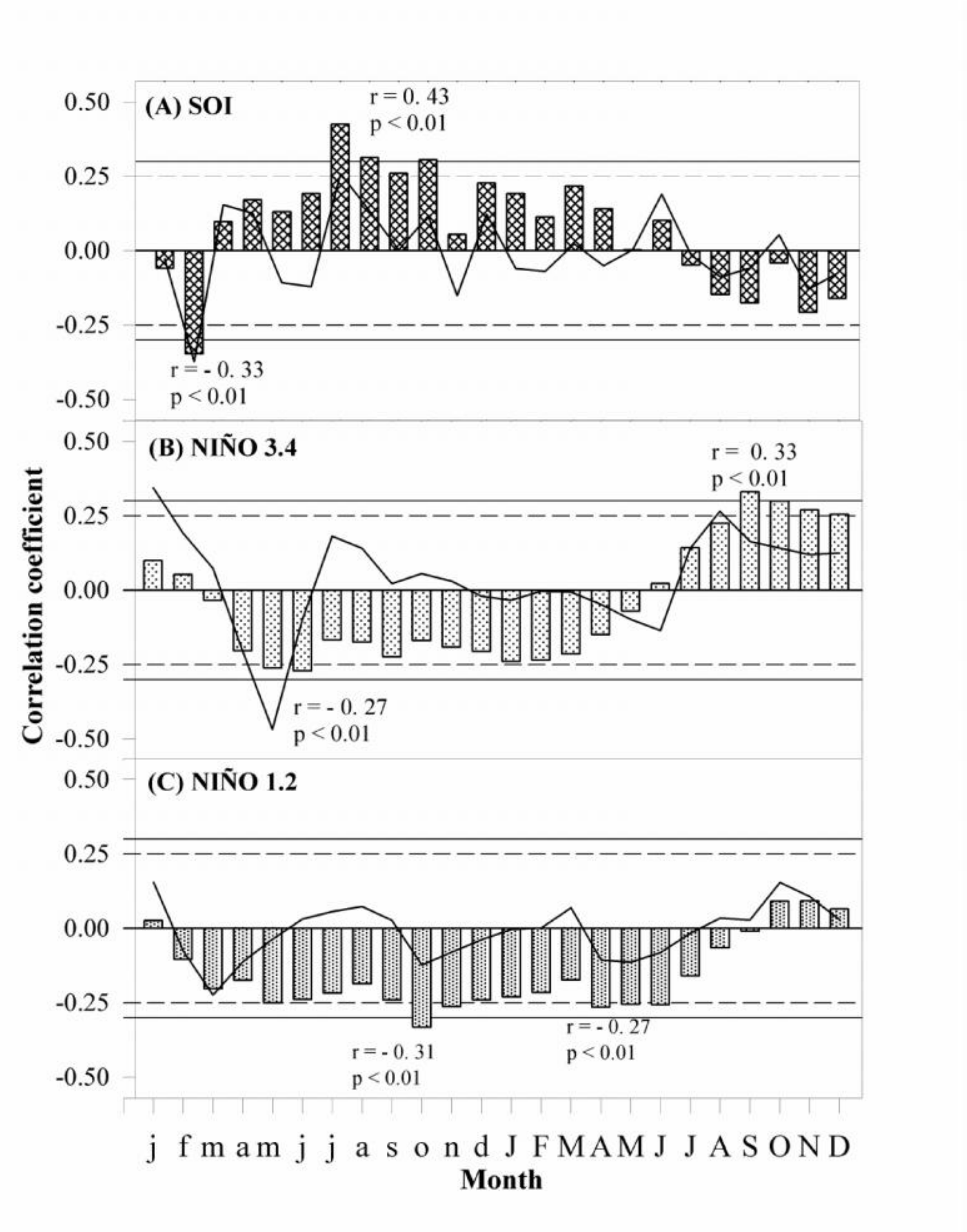

Figure 6. Correlations functions (bars) and bootstrapped response coefficients (lines) between (A) SOI, (B) El Niño 1.2 and (C) El Niño 3.4 global climate variables and morado radial growth (growth residual indices) during the common period 1978-2009. Growth was correlated with climatic variables of previous year (months abbreviated in lowercase) and current or ring formation year (months abbreviated in capital letters). The horizontal lines indicate the level of significance (dashed for bars, $p < 0.05$; solid for lines, $p < 0.01$) and describes the r and p values for those with $r > 0.25$.

Discussion

Tree rings of *M. scleroxylon* (morado) have fine marginal parenchyma lines, which facilitated the identification of their boundaries although this species forms hardly distinguishable tree rings (Roig, 2000). During the analysis of morado tree rings, we found lenses and false rings. Lenses are known as growth in certain sectors of the circumference of a tree due to stimulus in cambial activity and/or vascular growth during the annual cycle (Villalba, 1997; López, 2003). We also found a high occurrence of wedging rings, which hampered the identification and measurement of tree rings (López, 2003). The wedding rings were found in places of buttresses formation on the trunk. Still, there was a significant correlation among the radii of a single tree but not between different trees; therefore we used three radii to reflect the geometry in each of them. Morado is considered of semideciduous habit, and since the existence of annual rings is more common in deciduous species than those in semideciduous or evergreen species (Borchert, 1999; Worbes, 1999), the intermediate characteristic that morado presented, both in dominance in the forest and abscission of leaves, may have affected the formation and growth of tree rings and consequently the correlation between them and climate during some periods.

We developed the first tree-ring chronology of morado, an important timber species from the lowland tropical dry forests in Bolivia. According to our results, morado tree rings are annual in nature. Statistics commonly used in tree-ring studies show a strong common signal between the individual series of the chronology. Additionally, analyzes revealed the approximate age of *M. scleroxylon* trees, which mostly comprised 30%-70% of the dated radii from bark to pith. It is thus seen that this species may have a long lifespan, with approximately 140 years at 50 cm of DBH, which suggests the possibility of constructing larger series and chronologies.

Our results agree with previous dendroecological research on Bolivian forests (López and Villalba, 2011; López *et al.*, 2013). We found a close relationship between interannual variations in tree growth and local-regional climate. The water availability effect on the seasonal development of apical growth/leaf, flowering and cambial activity (Borchert, 1994), occurred together in alternating periods of dry and rainy seasons in deciduous tree species, is an important factor for the formation of marginal parenchyma bands that delimit the growth rings in this species. Unfavorable climate conditions result in partial cambial activity and growth (Kozlowski, 1971) and even complete cambial dormancy, especially when there are dry periods of at least two months with rainfall below 50 mm (Worbes, 1999). The seasonality in rainfall delimits the rings growth (Eckstein *et al*., 1981; Jacoby, 1989).

In the studied area, temperature rose and precipitation decreased, particularly in the growing seasons, during the second half of the 20th century, showing a trend towards aridification since the 1970s as observed in other forested sites in Bolivia (Brienen and Zuidema, 2006a; López and Villalba, 2011). Over the last decade, it has been widely observed that tree rings are formed annually in tropical forest with rainfall seasonality (Stahle *et al*., 1999; Worbes, 1999, 2002; Dünisch *et al*., 2002a; Fichtler *et al*., 2003; Brienen and Zuidema, 2005; Ferrero and Villalba, 2009). We propose that morado has annual ring formation based in the tree-ring structure described, considering marginal parenchyma as the main trait to define ring boundaries. The high correlation values obtained between growth and annual climatic parameters strongly supports our hypothesis (see Figure 4B and 5). The negative correlation of growth-temperature when growth is positively correlated to rainfall appears to be related to the seasonal rainfall distribution and to morado phenology. We also found that the dry season has apparently become longer and more intense over the last 14 years in Roboré (Figure 2) and it is related to changes in El Niño-Southern Oscillation (Figure 3).

We found a high correlation between morado radial growth and rainfall during December, January and February, corresponding to the rainy season. Soriano (2005) also found a high positive correlation between rainfall and reproductive period in *M. scleroxylon*, confirming the relationship between diameter growth and rainfall during the current and previous year of tree-ring formation found in this study (Figure 5). Oppositely, we found a negative correlation between growth and temperature during the growing season, thus demonstrating the connection to the radial growth. Interannual variation in tree growth is directly related to water supply (i.e., the balance between rainfall and evapotranspiration, which in turn is largely regulated by temperature) (López and Villalba, 2011).

High summer temperatures inhibit tree growth due to water deficit (Ferrero and Villalba, 2009), as water resources act as a limiting factor of growth (Borchert 1994, 1999; Toledo *et al*. 2011b). Our results are consistent with those found in *Centrolobium microchaete* (López and Villalba, 2011) where growth appears to be favored by abundant rainfall in combination with lower-than-average temperatures during late spring and early summer. Also, *Swietenia macrophylla*, in the Amazon has shown a strong correlation between changes in rainfall and growth from November to January (Dünisch *et al*., 2003).

The results of this study, through tree rings analysis and climatic fluctuations, show the effect of ENSO on the local climate, which in turn influences the annual growth variability of the species expressed in their diametric development. Therefore, we obtained a high correlation between SOI events and *M. scleroxylon* chronology, SOI fluctuations appear to have great influence in the growing season of this species and the dry periods of our study area, showing a negative correlation with El Niño 3.4 and El Niño 1.2 (negative phase of SOI) at the end of the growing season. In a broader context, we observe the effect of El Niño on regional rainfall behavior (with high rainfall events including flooding in the study area) and in the morado growth during specific years: 1951-1952, 1963-1964, 1977-1978, 1986-1988, 2004-2005 and 2006-2007 and the effect of La Niña during the very dry years: 1954-1956, 1964-1965, 1989-1990, 1999-2000 and 2007-2008. These results confirm that the effects of atmospheric circulation patterns on morado growth in the study area are probably an indirect expression of their effects on local precipitation conditions and drought regimes.

Additionally, there are many conditions affecting not only the formation (growth activation) of rings but also their width. The ring-width series also reflect a complex set of variations in tree growth affected by a wide range of non climatic factors (Brookhouse, 2006). For example, light availability is one of the most important factors for growth and establishment of many tree species in the dry forest of Chiquitanía, where most species are codominant in relation to the position of the tree canopy (Killeen *et al*., 1998). Therefore, the codominant nature of morado in the Chiquitano forest may explain certain periods of negative correlation between ring width and climate. Other factor related to morado-tree-growth is the presence of lianas (Putz, 1991). It was found that tropical dry forests in Bolivia have about 75% and 77% infestation of lianas (Carse *et al*., 2000; Uslar *et al*., 2003) which was confirmed in a further regional comparative analysis, with results of 50%-80% of liana infestation in dry forests and percentages below 50% in tropical rainforests in northern Bolivia (Toledo *et al*., 2008b). In addition to this, recent studies in South America have found that the presence of lianas has increased due to climate change (Phillips *et al*., 2002, van der Heijden and Phillips, 2009). Despite the possible effect of lighting, lianas and competition on growth, rainfall has been found to be a very important factor in most cases. Toledo *et al*. (2011b) concluded that climate and water availability are strong factors that determine variations in growth rates in different types of forests in Bolivia. According to Markesteijn *et al*. (2010), the surface of the dry forest soil is drier than deeper layers during the dry season, being opposite in the wet season. In addition, climatic and edaphic factors are correlated and species can coexist in areas with topographical differences, drawing water from different soil layers and/or doing so in different seasons.

Regarding the estimation of MLD, several authors have found that the diameter is a poor indicator of tree age (Harper, 1977; Sarukhan *et al*., 1984; Stahle *et al*., 1999). Some studies have used radial-growth averages to eliminate bias caused by age-related long-term size and variations of short-term growth caused by climate (Nowacki and Abrams, 1997), but for growth-rate analysis purposes, the use of the mean or median tends to overestimate the age of trees (Brienen and Zuidema, 2006a). It has been estimated that *M. scleroxylon* has a general average diameter increment of 2.37 mm year^{-1} (Dauber *et al*., 2003), and according to the results obtained, the species had an annual increase of 1.43 mm year^{-1} with high variations in growth during the period 1913–2009, which are probably caused mostly by variations in climate (rainfall and temperature). A similar result, using tree-ring analysis, was found in *C. microchaete* (López and Villalba, 2011) for the Chiquitanía region (Concepción), with an average annual increase of 1.80 mm year^{-1}. That raises concern about the general overestimation of species growth rates in the dry forest in the Bolivian Forestry Law and its consequence for management.

Our results provide interesting insight into the radial growth of morado in the Chiquitania region with important implications for timber management (Figure 4D). The growth rate was quite slow in trees studied, which makes us question the MLD recommended for this species. The minimum harvestable size of morado in Chiquitano forests is 40 cm diameter at breast height (DBH) with a minimum cutting cycle (20 years) recommended by the Technical Standards of the Forestry Act 1700 in Bolivia (MDSP, 1998). The power functions to the cumulative diameters indicate that on average it will take an estimated 122 years beyond the suffrutex stage to achieve this harvestable size for the ten sampled morado trees. These results suggest that the arbitrary 40 cm DBH minimum size requires a long rotation period but bears little relation to the age structure or stand dynamics of forests in Santa Cruz Region (Brienen and Zuidema, 2006b; López *et al.*, 2013). There is also an appreciable variability in the growth rate of sampled trees, but based in our results the optimal period to harvest the trees is at the peak of the current volume increment, when morado trees have a biological rotation age greater than 140 years (Schöngart *et al.*, 2007; López *et al.*, 2013). Tree diameter at the maximum current volume increment seems to indicate the preferred time for logging. In this species, based on the diameter growth model (Figure 4D), this corresponds to a DBH of 50 cm, which seems to be an appropriate MLD (Stahle *et al.*, 1999; Brienen and Zuidema, 2006b). The cutting cycle, calculated from the mean passage of time through 10 cm DBH classes until the tree reaches the MLD of 50 cm (Figure 4D), is approximately 40 years depending on each individual tree (Brienen and Zuidema, 2006a,b; López *et al.*, 2012, 2013).

Furthermore, it should be considered that the productivity of seeds in *M. scleroxylon* remains high in trees of 100 cm DBH (Soriano, 2005). Both, seed productivity and positive growth in diameters greater than 40 cm, indicate that a greater MLD should be considered in forest management plans for this species. Similar results have been found in *Amburana cearensis*, *Anadenanthera colubrina*, *Platimiscium ulei*, *Ficus boliviana*, *Hymenaea courbaril* and *Cedrela fissilis* in the Chiquitano and Guarayos regions respectively (López *et al.*, 2012, 2013). However, silvicultural treatment applied and pith rot in trees should also be reviewed before determining the MLD. Our results suggest that careful studies of tree age, size, and environmental conditions could produce useful volume and yield tables for species ecological settings, and may lead to improved management of this important species. It should be noted that the results of this study are based on the mean diameters of the samples of different sizes, without dating central, pith rot area that *M. scleroxylon* species often presented in this study (60% of samples), but can be useful to provide an idea of morado growth and behavior.

Conclusion

In southeastern of Chiquitano forests, annual temperature has increased and the rainfall in the rainy season has decreased during the twentieth century, leading to a long-term reduction in water availability, which is expressed in the tree-rings width and related to radial growth. Due to the seasonality of the study area, in which leaf senescence and growth significantly correlated with rainfall, it is considered that the rings of *M. scleroxylon* are formed annually. Rainfall was the most influential climatic variable on radial growth, confirming that water availability is a limiting factor for this growth. We found a significant positive correlation between rainfall and growth during January of previous year and December, January and February of the year of ring formation that is the rainy season. Moreover, the temperature had a negative correlation for those months, which seems consistent with the growth inhibition associated with drought stress and atmospheric pressure indexes as SOI. El Niño-Southern Oscillation (ENSO) also showed a positive correlation with the chronology constructed, which was also positively correlated with SOI indices but negative correlated with El Niño 3.4 and El Niño 1.2 throughout the growing season. However, despite the significant correlation of these variables, there are still not matching periods seemingly affected by other factors such as light availability, competition and lianas, which requires a deep analysis on the effect of ENSO on *M. scleroxylon* growth.

In addition, wedging rings, false rings and lenses in morado seem to be the result of climatic and non-climatic variables which were a challenge for the identification and measurement of morado tree rings; to resolve these problems alternative techniques were used, such as immersion of the discs in sodium hypochlorite. Based on the available data, the number of samples taken and the variety of selected sizes, we suggest that growth and diameter increment of morado remain positive in trees older than 140 years and MLD around 50 cm, but with low growth rates in small-diameter trees. Therefore, despite the limited number of samples analyzed, our findings indicate an optimal cutting cycle higher than 40 years. To improve this knowledge, future studies should include phenological analysis and repeated sampling of cambial activity and xylem formation in morado.

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Chapter 3

Tree rings of *Amburana cearensis* (Fr. Allem.) A.C. Smith as indicators of rainfall and temperature variability and potential for climate reconstruction

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Submitted

Tree rings of *Amburana cearensis* (Fr. Allem.) A.C. Smith as indicators of rainfall and temperature variability and potential for climate reconstruction

Abstract

Amburana cearensis (roble) is an important timber species from the tropical lowland dry forests in Bolivia. We used dendrochronological methods to evaluate the climatic sensitivity of *A. cearensis* in the tropical dry forest region and identify its potential for climatological reconstruction. We collected eleven wood discs from mature individuals randomly selected. Despite the eccentricity of discs and existence of false and wedging rings, the samples were successfully dated and exhibited a common signal from the same tree and between trees of the sampled species. Significant correlation was found among the *A. cearensis* samples (0.337) and an average growth of 0.575 cm/year. Correlations between the growth indices and monthly climatic variables (maximum temperatures and rainfall) were calculated. Tree-ring width was positively correlated with monthly rainfall and negatively correlated with maximum temperatures during the rainy season. *A. cearensis* exhibits a potential for reconstructing climate data in the Bolivian Chiquitania region.

Keywords: tropical dry forests, dendrochronology, Chiquitania forest, parenchyma bands

Introduction

The tropical dry forest in Bolivia, also known locally as Chiquitania forest, occupies an area of approximately 20 million hectares and is among the most diverse in the world (Parker *et al*., 1993). Chiquitania forests have a very low radial growth rate, ranging from 0.143 to 0.211 cm/year (Dauber *et al*., 2003; López, 2011; López *et al*., 2012). As a consequence, Chiquitania forests are slow to regenerate after disturbance (Uslar *et al*., 2004), particularly during drought.

Little is known about growth rates of Chiquitania forests species and their sensitivity to climate. To date, growth data for Chiquitania forest species have been provided by growth forest inventories and permanent plots. However, these measurements represent only a short period of the 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, 2005b). Tree-ring data offers the opportunity to study growth as well as the impact of the variability in the physical environment throughout a tree's entire lifespan. As a source of proxy climate data, trees are unmatched in their distribution and provide a high resolution related to 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 host 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 holds as an aid for forest management and conservation few dendrochronological analyses have been conducted on Bolivia's endemic species. It has long been argued that many woody species of tropical and intra-tropical forests, such as Bolivia’s, do not form distinct growth rings (Eckstein *et al.*, 1981). 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 periods of inactivity in the cambial meristem, 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, nearer to the equator, seasonality in temperature is far less prominent (Worbes, 1999). As a consequence, cambial activity may vary little in, and tree rings may be absent from, many near-equatorial species. This combined with the short life-span of many tropical species (Worbes, 1999) and rapid decomposition of timber in tropical forests (Bultman and Southwell, 1976) has 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 some endemic species (Worbes, 1999; 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 marker points to verify the annual nature of tree rings. In most cases, boundaries between rings were marked by the presence of marginal parenchyma and wall-thicked fibers formed at the end of the growing season (López *et al*., 2012). Recently tree-ring data for Bolivian forest 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 harvestable trees (Soliz-Gamboa *et al*., 2011) as well as providing climate-related growth information (Wimmer, 2002; Brienen and Zuidema, 2005a; Ferrero and Villalba, 2009; López and Villalba, 2011). Thus, in addition to quantifying differences between age and growth rates, the analysis of tree rings in Bolivian forests also is currently contributing to an improved ecological understanding of tropical rainforest trees and forest-level population dynamics.

Amburana cearensis (family Fabaceae) – a species endemic to Bolivia, Perú, Ecuador, south-eastern Brazil and northern Argentina – is among a suite of Bolivian forests species that exhibit clear potential for dendrochronology. The species is significant commercially 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 in *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 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.

In this study, we examine the climatic sensitivity of *A. cearensis* growth in the tropical dry forest region. Although Brienen and Zuidema (2005a) have previously reported on the climatic sensitivity of the species, their study was restricted to analysis of seasonal rainfall in Bolivian rain forests. In this study 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 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 species.

Materials and Methods

Study area and sample collection

Sample materials for this study were collected from a logging concession area (16°9'S, 60°47'W) between 366-390 m.a.s.l. approximately 31 km from the town of San Ignacio

(Fig. 1) in the Chiquitania region of Santa Cruz, Bolivia. The samples were collected in the Central Chiquitania sector in the Western Cerrado 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. Canopy height in this type of forest generally range from 16 to 22 m high, with representative species of the Chiquitania forest as *Amburana cearensis* (Roble), *Machaerium scleroxylon* (Morado) *Anadenanthera colubrina* (Curupaú) *Schinopsis brasiliensis* (Soto Chiquitano) *Acosmium cardenasii* (Tasaá) and *Astronium urundeuva* (Cuchi).

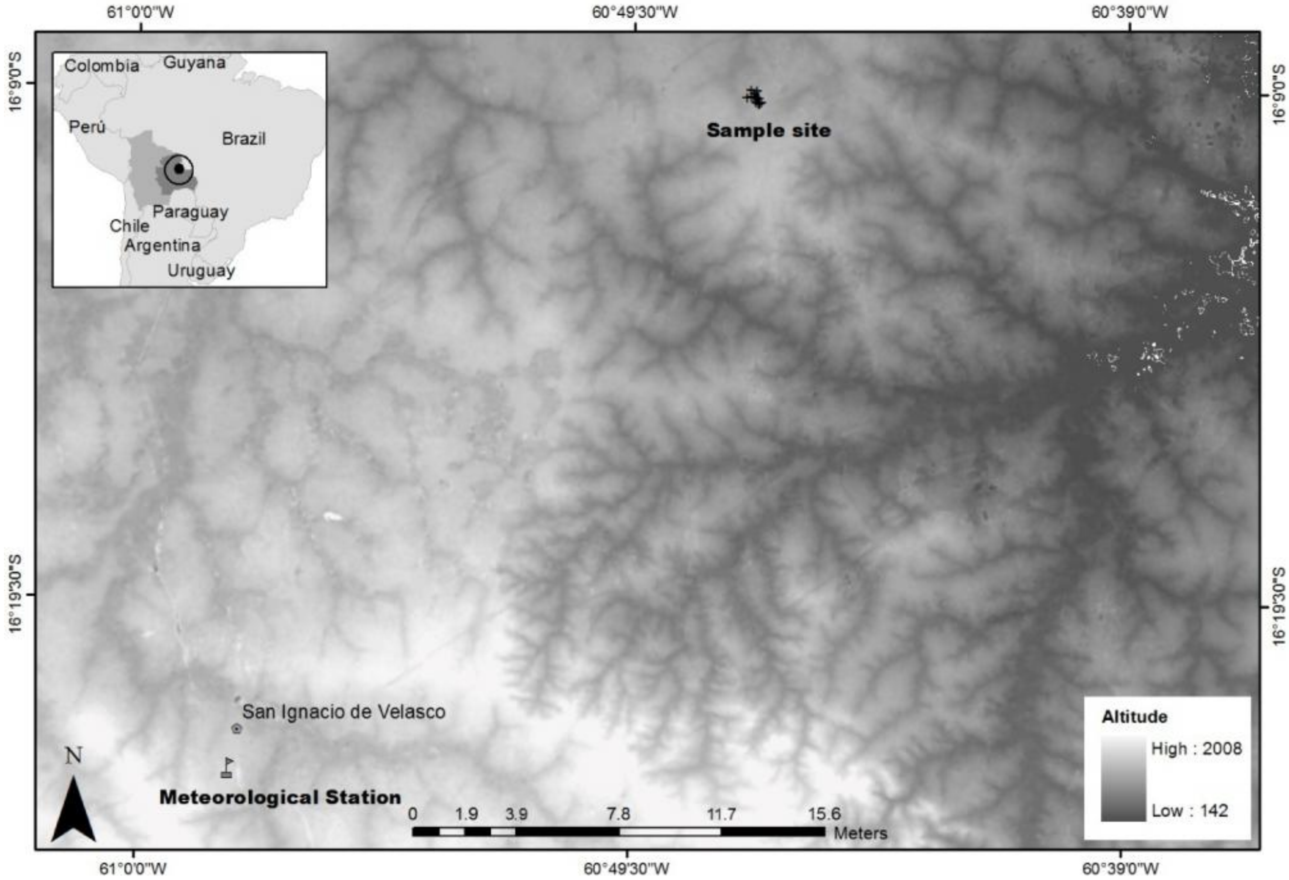

Figure 1: Location of *Amburana cearensis* samples and meteorological station at Chiquitania region (Bolivia).

Samples were collected from 11 felled *Amburana cearensis* specimens. *A. cearensis* is a deciduous and partly-light demanding species that is common in semi-deciduous broadleaf forest, the Amazon forest and transition zones to moist montane forest 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).

A sample disc, representing the entire circumference of the bole at breast height (1.3 m above ground level), was removed from each specimen tree. The use of cross-sections provides a larger field of observation than increment cores (López, 2003), allowing the difficulties presented by stem eccentricity, high wood density, indistinct tree rings and presence of growth lenses and wedging rings to be overcome.

Sample preparation and analysis

Samples were prepared using sandpaper using grit sizes ranging from 26.8 to 425 µm (Orvis and Grissino-Mayer, 2002). Tree-ring identification was conducted on three radii across the diametric area of each sample. Tree-ring boundaries were identified based upon variations in vessel distribution and parenchyma bands as described by Brienen and Zuidema (2005a) and López (2011) and marked with lead pencil. *A. cearensis* exhibited clearly visible rings during the juvenile stage of the tree samples used in this study. During this period, 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. A contrast was present between the latewood and earlywood. Earlywood appeared lighter with higher percentage of vessels and aliform/confluent paratracheal parenchyma (Fig. 3a). However, as tree diameter increased, tree rings became more difficult identify. In all instances, the outermost rings were narrower than those in the centre of the sample and in many cases one tree boundary was next to the other. As observed by López (2011), parenchyma was present throughout narrow rings and delimiting fiber bands partially disappeared (Fig. 3b).

Cross-dating involves cross-matching samples from different specimens based upon characteristic sequences of radial growth (Yamaguchi, 1991). By allowing each ring to be assigned to a calendar year, cross-dating overcomes problems arising from of 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 at radii-level to avoid bias caused by eccentricity. Quantitative cross-dating was then conducted between samples by measuring tree-ring widths with 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 significantly affected by stand-level factors. To overcome this problem, we applied a cubic smoothing spline (Cook and Holmes, 1999) with a 50% frequency cut-off over 32 years to our measurement series in COFECHA for verification of cross-dating.

Chronology development

Standardization aims to remove non-climatic environmental- and age-related noise from tree-ring width series allowing low-frequency variability, usually climatic, to be analysed (Grissino-Mayer, 2001). We used ARSTAN 40c (Cook and Krusic, 2006) to develop a tree-ring chronology from our verified data. We used a negative exponential function as initial growth was higher and tree rings became narrower with increasing longevity and diametric size (López *et al*., 2012). Autoregressive modeling was performed to remove autocorrelation from the tree-ring series and biweight robust mean was estimated to produce detrended chronologies of tree-ring width.

The ARSTAN analysis produced three 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 conducted a preliminary analysis of the correlation between each resulting index and climate data to determine the chronology 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, which quantifies the similarity in residual width indices among trees (R_{bar}), (b) first-order autocorrelation, a measure of the year-to-year growth similarity (AC1), (c) mean sensitivity, which measures the year-to-year variability in width of consecutive rings (MS) and (d) the expressed population signal (EPS) statistic, which reflects 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 also analyzed.

Climatological analysis

We assessed correlation between the ARS chronology and climate data from San Ignacio meteorological station (16°23'S, 60°58'W; 413 m.a.s.l.), approximately 32 km from the sample site (Fig. 1, SENAMHI reporting agency). Mean annual rainfall in this location is 1192 mm with a distinct rainy season from November to April. Mean annual temperature is 24.7ºC with a maximum of 31.5ºC during October and a minimum of 14.4ºC in June (Fig. 2). The annual average of the relative humidity is 70%.

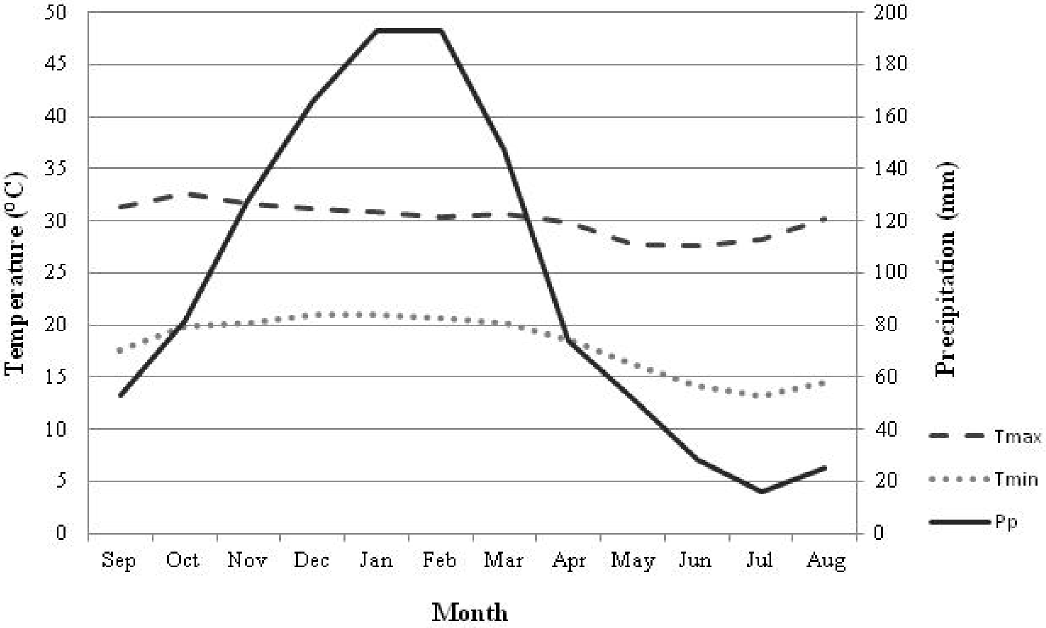

Figure 2: Ombrothermic diagram from the San Ignacio region for the periods 1950–2010 according to the SENAMHI database.

Meteorological data were available from San Ignacio for the period 1950-2010. Instrumental climate (temperature and rainfall) data accessibility presents many limitations in Bolivia. Frequency of measurement, accuracy and existence of meteorological stations are some of the limiting factors for the dendroclimatological analysis. 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 the 24 months spanning the previous and current growing periods (September$_{t-1}$ to May$_{t+1}$ in the southern hemisphere). We also tested correlation between the ARS chronology and annual precipitation totals and mean annual temperatures.

Results

Tree-ring chronology

Tree-ring boundaries and annual tree rings were identifiable on the sample discs. Annual rings were defined by a band of marginal parenchyma and fibres (Fig. 3a). False rings were generally discontinuous around the circumference of the sample discs despite locally well defined anatomic structure (Fig. 3b).

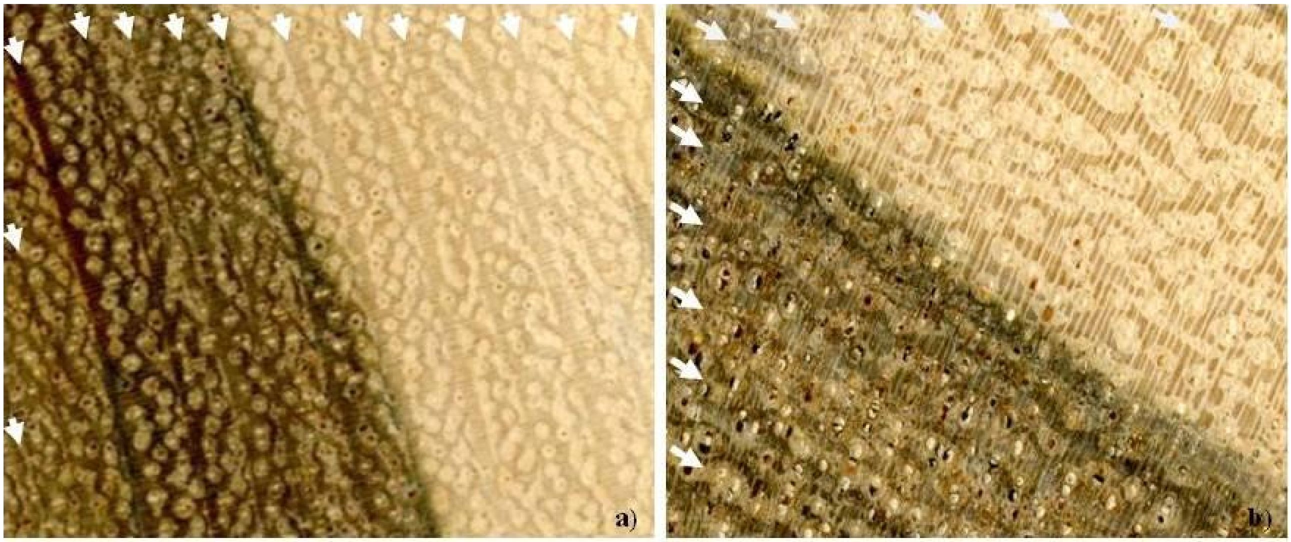

Figure 3: Contrast between the latewood and earlywood and visibility of tree rings. a) Bands of fibers defining tree-rings. b) Expanded parenchyma over the rings' transversal surface and delimiting fibre bands partially disappearing.

Of the 33 radii collected and measured, cross-dating was verified for 22 radii in 8 samples. The ring-width dataset spans 1788-2010 (223 years) (Fig. 5). Mean tree-ring width (standard deviation) of *A. cearensis* during this period was 0.575 cm yr^{-1} (±0.22 SD). Although the statistics used to evaluate the chronology presented low values, mean inter-series correlation (R_{bar}) was significant ($\alpha<0.01$) at 0.337 and mean sensitivity (MS) was 0.406 indicating relatively high inter-annual variability in radial growth data (Table 1). Difficulties in dating associated with radial eccentricity and radii exhibiting 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. 4).

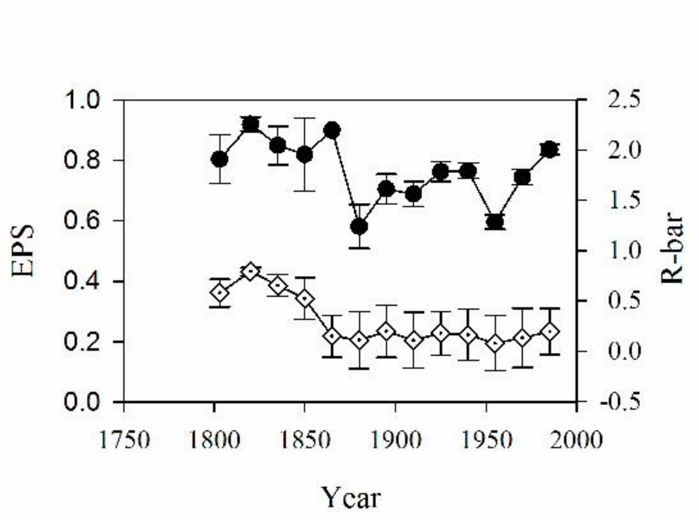

Figure 4: Mean correlation coefficient (R_{bar}; open diamonds) and Expressed Population Signal (EPS; filled circles) statistics for *A. cearensis* chronology in San Ignacio.

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 climatic analysis (Fig. 5).

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

Chronology span	1788-2010 (223 years)
N. samples	8
N. radii	22
Mean Sensitivity	0.406
Correlation	0.337

We found a variation in growth during the period of measured ring widths. Growth increased significantly during 1982-1992 and presented a general decreasing trend during recent years. The greatest growth took place during 1983 and the lowest during 1882 (Fig. 5).

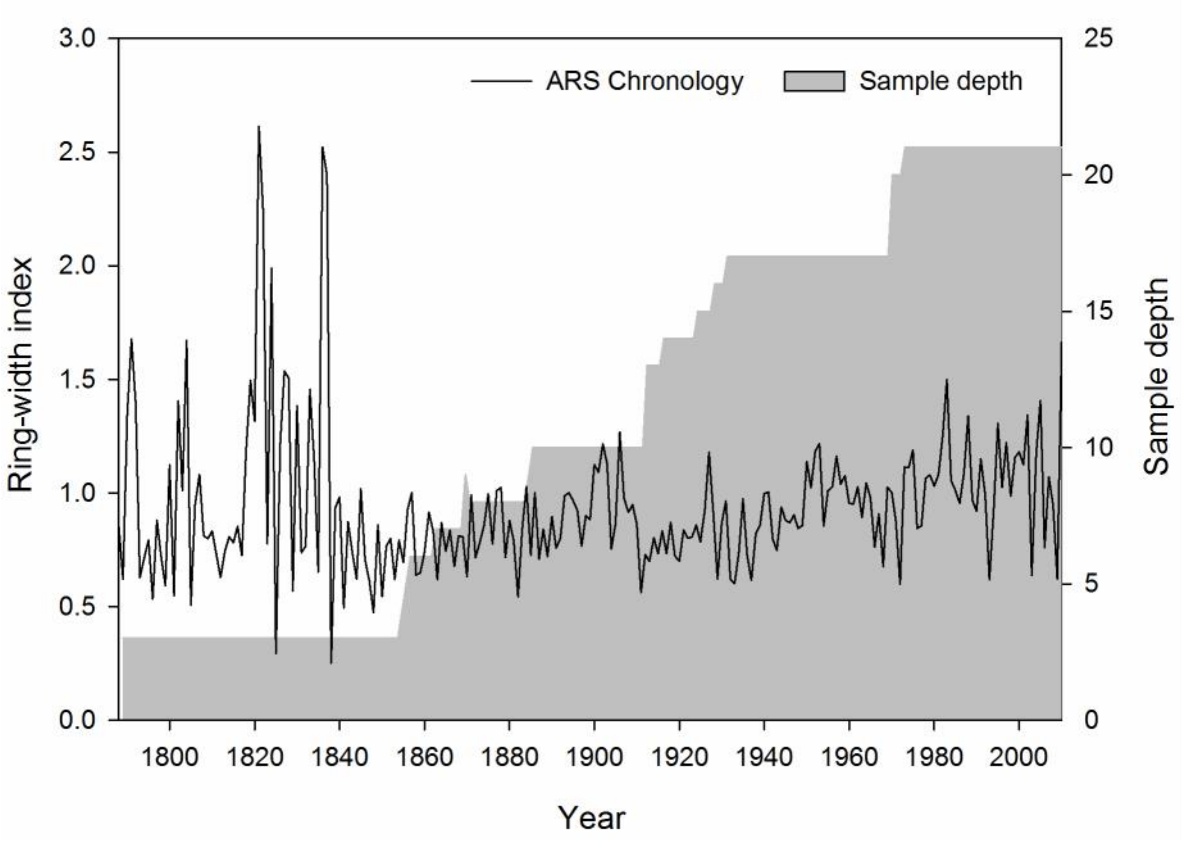

Figure 5: ARSTAN chronology and sample depth for *A. cearensis* from San Ignacio site.

Climate-growth relationship

Standardized ring widths in *A. cearensis* were positively and significantly correlated ($\alpha<0.05$) 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. 6).

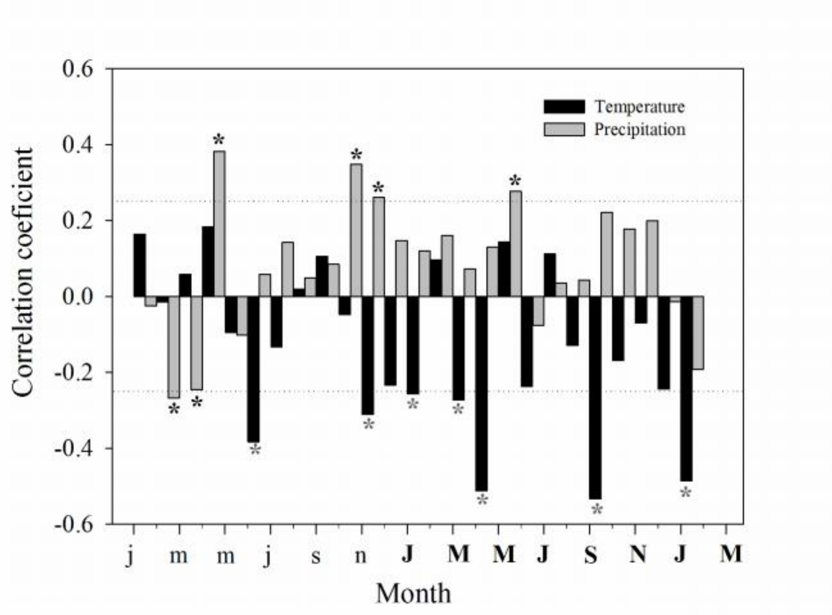

Figure 6: Climatological sensitivity of *A. cearensis* chronology to monthly maximum temperatures and monthly rainfall.

Annual precipitation totals and mean annual temperature were also significantly ($\alpha<0.05$) correlated with the ARS chronology (Fig. 7). 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 caused by the low level of rainfall up to 2000 approximately. This behavior was likewise observed in the annual mean temperature data, with a decreasing trend from 1993 to 2003 and high growth during 1983 and 2005 (Fig. 7).

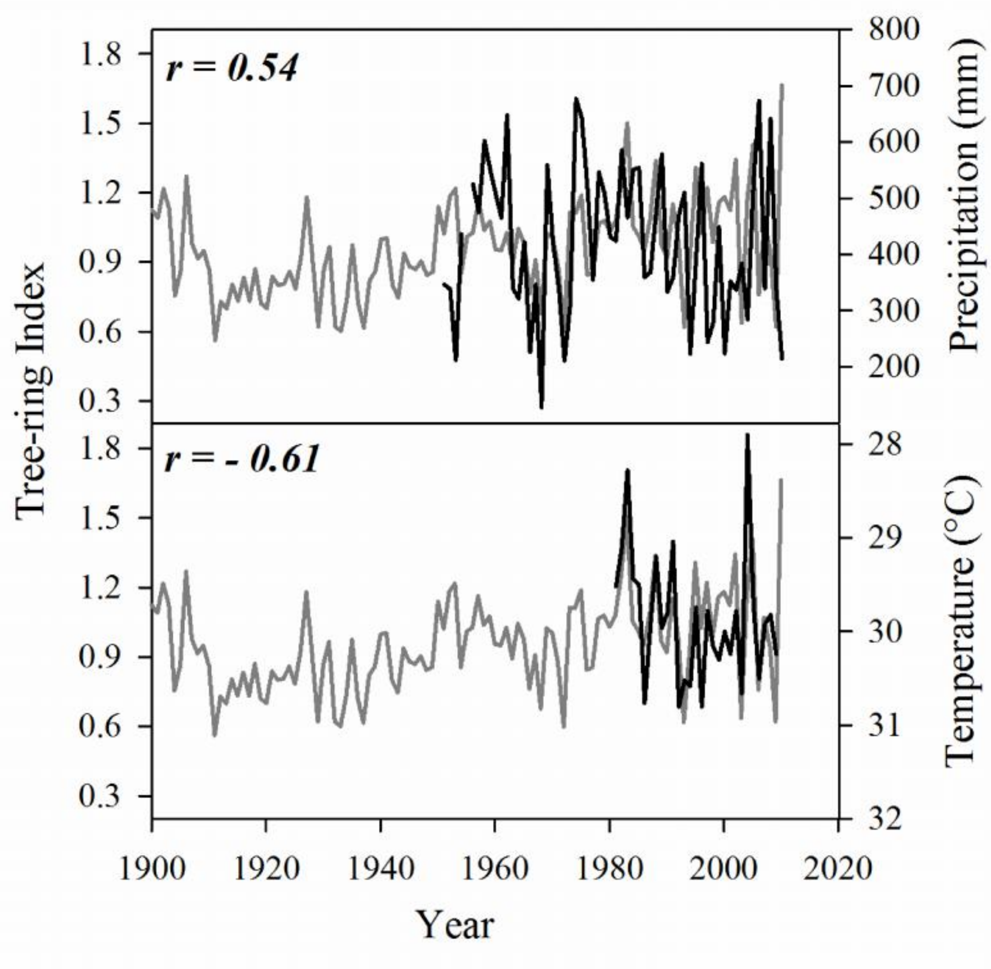

Figure 7: Correlation between ring-width indices (solid gray line) and rainy season temperature/precipitation (solid black line).

Discussion

Tree-ring chronology

Our study is a new contribution to the potential of *A. cearensis* for dendrochronological and climatological reconstruction among other Bolivian tropical species. Average radial growth in the *A. cearensis* samples examined in this study was 0.575 cm yr^{-1}. This result is consistent with that reported by Lopéz *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). The latter also found that differences in annual increments are explained by the tree crown position and degree of lianas infestation. Growth appeared to increase when trees received more light and presented fewer lianas infestation (Mostacedo *et al*., 2009). Although the major differences found among these reports and the present study were due to the number of measurements analyzed through permanent plots (4 years) and tree rings (223 years) data which clearly affects the averages.

In this study, we observed low inter-radial correlation between and within trees as a consequence of growth eccentricities. This fact is not only common in tropical forest species (Sousa *et al*., 2012; Paredes-Villanueva *et al*., 2013) but is also evident in some temperate genera (Brookhouse and Brack, 2008). The majority of the discarded series came from short radii constituting 33% of the measured samples. Our tree-ring analysis revealed that irregular diametric growth with wedging rings and lenses significantly affected crossdating. Lenses are known as growth in certain sectors of the circumference of a tree due to the stimulus in cambial activity and/or vascular growth during the annual cycle (Villalba, 1997; López, 2003). However, despite the low number of series in the chronology, it remained with consistent results for the climate reconstructions.

Brienen and Zuidema (2005a) reported that mean inter-series correlation in *A. cearensis* was 0.350. We report a similar value of 0.337. The difference might be due to the number of samples as well as the sample site conditions (16 trees/23 series from the Bolivian Amazon). Their analyses of diameter and tree growth relationships are also comparable to our results. The growth rates of *A. cearensis* start decreasing after it reaches 30 cm of diameter approximately. 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 on trees of small diameters and may not be useful for dendroclimatology assess (Fig. 5).

Climate-growth relationship

Variation 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, 1994b). In this study we found that there is a significant relationship between tree growth and precipitation, although it starts decreasing from the middle of the rainy season onwards. It would probably be due to 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. Additionally, it is suggested flushing as a consequence of changes in tree water status caused by leaf shedding (Borchert, 1999).

Monthly correlation analysis reveals an apparent effect of the maximum temperature and rainfall on tree growth. These results may partially reflect the inverse relationship between maximum temperature and rainfall during rainy season. This 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 reaction 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 in *A. cearensis* from Bolivian Amazon done by Brienen and Zuidema (2005a) which attributed it to the storage of water reserves during previous growth year (Dünisch *et al*., 2003) on long-term water-table depth or stem water storage (Borchert, 1994c). They also explained the low correlation of growth and late rainy season related to the decreasing photosynthetic capacities of older leaves (Mooney *et al*., 1981; Ackerly and Bazzas, 1995; Kitajima *et al*., 1997), soil with water reserves surpassing critical levels and break of bud dormancy concurrent with rainy season. However, as opposed 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 *Amburana 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.

Conclusion

Despite the eccentricity presented in some samples, significant correlation was found among the *A. cearensis* samples and 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 to 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 offers 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 variables data our results also offered potential insights into the ecology of *A. cearensis*.

Acknowledgements

This project was funded by World Wildlife Fund (WWF) and the Spanish Agency for International Development Cooperation through the project “Advanced Forest Tech Center (CTAF) – Universidad Autónoma Gabriel René Moreno/University of Córdoba”. We would like to thank the Fenner School of Environment and Society at the Australian National University (ANU) for the time spent there and permitting us to use the tree-ring measurement equipment. We also thank Roberto Quevedo at UAGRM and Angel Chavez at Consultora Forestal Bosques e Industria for providing us the sample material we used for this research. We also acknowledge the SENAMHI in Bolivia for providing us meteorological data required. We thank Quirine Hakkaart, Annemarijn Nijmeijer and Peter van der Sleen who kindly supported the measurement of the samples.

Chapter 4

Regional chronologies of *Cedrela fissilis* and *Cedrela angustifolia* in three forest types and their relation to climate

Kathelyn Paredes-Villanueva, Lidio López, Rafael María Navarro Cerrillo

Regional chronologies of *Cedrela fissilis* and *Cedrela angustifolia* in three forest types and their relation to climate

Abstract

Cedrela species are high valued because its timber quality. Those species grow from a wide range of environmental gradients to different types of forest in Bolivia. This study used dendrochronological methods to analyse grow-rainfall relationship of two different *Cedrela* species coming from three different zones and environmental conditions: dry Chiquitano, Chiquitano transitional Amazonian and Bolivian-Tucuman montane forests. 12 *Cedrela fissilis* specimens were sampled from dry Chiquitano, 11 *Cedrela fissilis* from Chiquitano transitional Amazonian and 30 *Cedrela angustifolia* specimens from Bolivian-Tucuman montane forests. Despite tree rings from the transitional forest were narrower and presented blurred bands of parenchyma in the boundaries, the samples were crossdated and exhibited a common signal between trees of 3 different sample sites. Significant correlation was found among the *C. fissilis* species series from dry Chiquitano and Chiquitano transitional Amazonian forests with r=0.261 and r=0.284 respectively and for *Cedrela angustifolia* from Bolivian-Tucuman montane forests with a series inter-correlations of r=0.374. Mean annual growth were 2.07 mm/year, 1.92 mm/year and 2.82 mm/year respectively. Concepción and Postrervalle *Cedrela* species were sensitive to precipitation from October to April (wettest season) and low temperatures during the driest months (from May to July); and Guarayos samples seemed to be more sensitive to precipitation during late rainy season (March, April and May of the current year) and high temperatures corresponding to the rainy months (November to December). These growth differences between sites and species and their response to climate variations should be considered and handled with different guidelines of forest management.

Keywords: *Cedrela*, tropical dry forests, Chiquitania forest, Chiquitano transitional Amazonian forests, Bolivian-Tucuman forests, dendrochronology.

Introduction

Cedrela species are one of the most economically valuable timber species that have been affected by deforestation due to its high quality wood. The genus belongs to the group of softwood and valuable timber species in Bolivia. In general, they are deciduous species and partially light demanding. They rapidly grow in forest clearings in variable soils and topography but requiring good drainage (Mostacedo *et al.*, 2003). These species were included in the list of priority species for conservation in 1981, during the Fifth Meeting of the Panel of Experts on Forest Genetic Resources (FAO, 1984). Due to their vulnerable nature, population dynamics and habitat preferences, in addition to reduce overexploitation, the international conservation community called for further protection of *Cedrela odorata* (CITES, 2007). This species has been listed in Appendix III of the Convention on International Trade in Endangered Species of Wild Fauna and Flora in five Range States: Peru and Colombia (2001), Guatemala (2008), Bolivia (2010), and Brazil (2011) (UNEP-WCMC, 2011). For the countries implementing the convention plans, a better understanding of the species ecology may be necessary to implement better measures of conservation and forest management.

Bolivia is one of the most important range states of *Cedrela* species in terms of habitat and harvesting. During the period 2001-2005, Bolivia was the largest exporter of *C. odorata*, trading 96,909 m^3 (CITES, 2007). However, *Cedrela*'s populations in Santa Cruz, northern La Paz and Pando regions were expected to be exhausted within a decade due to the long unsustainable management (Toledo *et al.*, 2008a). National laws established that all of these species should be exploited when present diameters higher than 60 cm in tropical and subtropical in Bolivia.

In addition to *C. odorata* timber, other species as *C. fissilis, C. montana, C.angustifolia* and *C. balansae* cannot easily be visually distinct among each other. In Bolivia, those species are found along different climatic and environmental gradients and from moist to dry tropical forests and between a wide range of altitudinal storey (Mostacedo *et al.*, 2003; Aguirre *et al.*, 2011; Navarro, 2011; Navarro-Cerrillo, 2013; Cavers *et al.*, 2013). This wide range of distribution represents a great opportunity to assess the tree growth and the effect of different environmental conditions on the lifetime growth patterns of these species.

The growth rings of some species of the genus *Cedrela* were successfully applied in several studies. Previous studies have identified their tree rings and proved their annual ring formation showing their dendrochronological potential (Worbes, 1999; Dünisch *et al.*, 2002a; Brienen and Zuidema, 2005a; Bräuning *et al.*, 2009). In general, these species in tropical regions have growth rings in visible to the naked eye, sometimes before polishing the cross section (Lopez, 2011). The wood of these species exhibit semicircular to circular porosity, with more numerous and larger vessels in the early wood, arranged as solitary or multiple. A conspicuous parenchyma band demarks growth rings boundaries at the beginning of each growth period (López, 2011).

Understanding the behaviour of each different *Cedrela* species and their ecology could be a major boost to ensuring that forest harvesting and management do not endanger the survival of natural populations. This studies aims to analyse growth-climate relationship of two different *Cedrela* species coming from three different zones and environmental conditions as a contribution to better understanding, management and conservation of these species. For these purposes, we calculated (a) the year-to-year variability in width of consecutive tree rings, (b) the annual growth trends of the chronology and (c) a site index to express the level of site conditions' influence on tree growth.

Materials and methods

Study site and climate data

Sample materials for this study were collected from 3 regions in Santa Cruz with different environmental conditions: dry Chiquitano (Concepción), Chiquitano transitional Amazonian (Guarayos) and Bolivian-Tucuman montane forests (Postrervalle; Figure 1). According to the Bolivian Biogeographic Map (Navarro, 2011) the samples collected in Postrervalle belongs to the Bolivian-Tucuman Province in the Piray – Grande River Sector (Tropical Andean Region). This site is located in the Mountainous, Sub-Andean and xeric Inter-Andean valleys of the high Piray and Grande rivers basin, with mostly pluviseasonal subhumid and humid bioclimate. The discontinuities observed in the flora and vegetation of this biogeographic province differed mostly in sectors following topographic boundaries between the basins of major Inter-Andean rivers whose dividing regional waters played an orographic barrier role between the deep valleys. Mixed forest with canopy of 10-15 m tall on average is usually dominated by pine forest, as *Podocarpus parlatorrei* which occurs in mosaic with forests of Myrtaceae locally interspersed in humid areas such as streams, headwaters and slopes or canyons frequently exposed to mists. The discontinuous subcanopy of 5-8 m height is dominated by small trees and large shrubs. The understory of shrubs and bushes is relatively scarce in the best preserved forest and herbaceous understory, which often is made up of several species of ferns (Navarro, 2011).

The Guarayos sample site belongs to the Central-Southern Amazon Province (Madeira and Tapajós), Guaporé Sector (Amazon Region). It occupies much of the middle and lower basin of the Iténez river. The bioclimate is sub-mesophytic pluviseasonal with superior sub-humid ombroclima and with infratropical thermo type in the west and thermotropical in the east of the district. Forests within the sample site are Chiquitano transitional Amazonian on well-drained soils poor in nutrients (oligotrophics) of the oldest and highly corrugated surfaces of the weathered lateritic dissected peneplain in the northern part of

Bolivia. Forests are 30-35 m tall, with a seasonal evergreen canopy and emergent to 40 m. The understory is made up of several layers, including understory tree, shrub and herbaceous levels, with moderate to medium abundance of woody lianas and epiphytic (Navarro, 2011).

Finally, Concepción sample site belongs to the Western Cerradense Province in the Central Chiquitano Sector (Brazilian-Paranean Region). This area is dominated by sub-humid deciduous Chiquitano forests on well drained soils. This group of pluviseasonal deciduous forests represents the climatophilous zonal potential of well to moderately well drained deep soils in the Chiquitano vegetation. The contents of mineral nutrients in these soils are variable. In general, poor soils predominate developed on old crystalline rocks of the Precambrian Shield. However, the soils of the mountains formed on Mesozoic Paleozoic metamorphic or sedimentary rocks are richer in minerals nutrients, especially calcium. The canopy of this forest also presents semi-deciduous to almost deciduous in very dry years, 16-22 m high on average ranging up to 25 m in mesotrophic soils of hills and low metamorphic mountains in northern Chiquitanía. The understory is differentiated in a layer of subcanopy trees of medium to low coverage; an usually dense to semi-dense shrub or thickets layer; and an herbaceous layer, usually dominated by colonies of terrestrial bromeliads or subfructicosas herbs. Lianas and woody climbers or frequent subfructicosas are always abundant (Navarro, 2011).

Climate data from the meteorological stations in Concepción (16º 8' 18'' S, 62º 1' 39'' W; 497 m.a.s.l.) approximately 10-38 km from the sample site, Vallegrande (18º 28' 55''S, 64º 6' 29''W; 2030m.a.s.l.) approximately 28 km from the sample site and Ascensión de Guarayos (15º 43' 0''S, 63º 6' 0''W; 247 m.a.s.l.) approximately 38 km from the sample site, were used for this study.

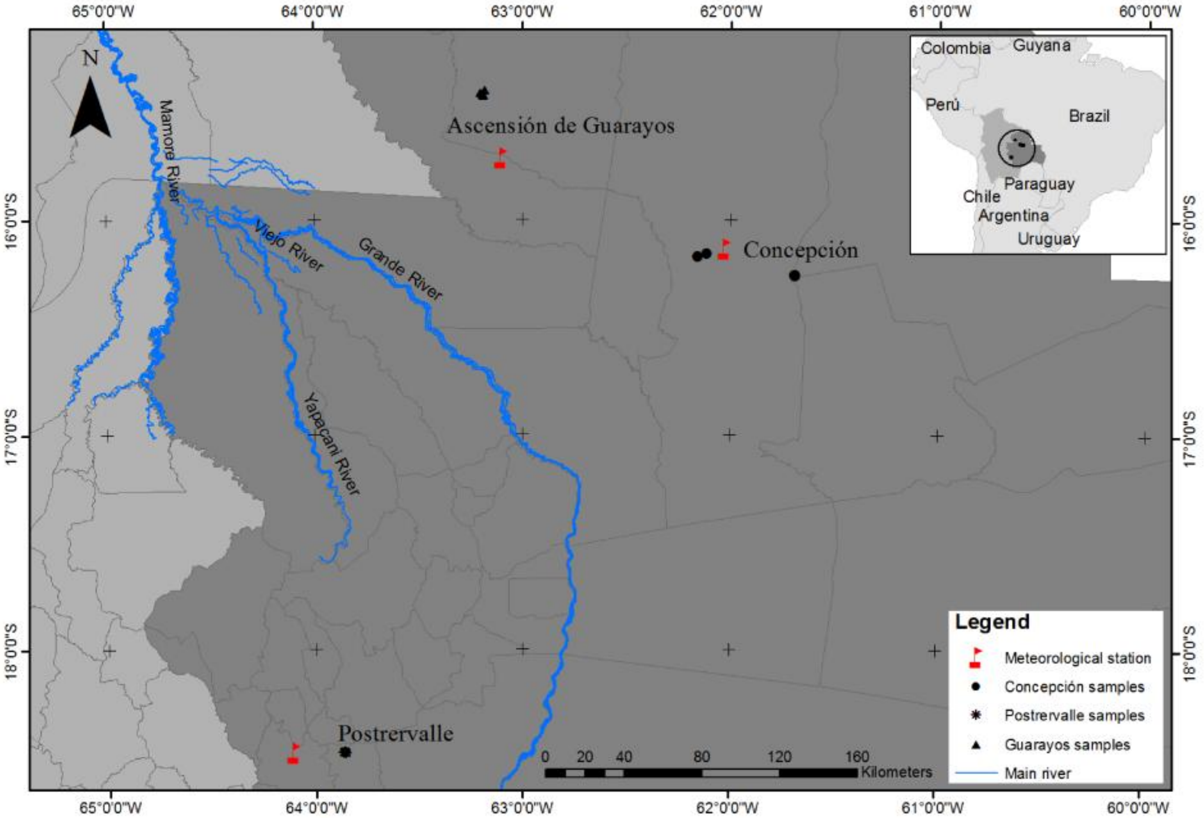

Figure 1: Meteorological stations and sample sites in Santa Cruz (Bolivia).

Mean annual rainfall in Concepción is 1171.3 mm (1943-2013 period of measured data) and mean annual temperature is 23.8 ºC (1949-2013). For Postrervalle sample site, Vallegrande meteorological station reported a mean annual rainfall of 624.8 mm (1960-2013) and mean annual temperature of 16.6 °C (1990-2013). Guarayos sample site reported a mean annual rainfall of 1297.3 mm (1946-2013) and mean annual temperature 25 °C (1981-2013). All the sample sites presented a distinct rainy season from November to April (Figure 2, reporting agency of Servicio Nacional de Meteorología e Hidrología - SENAMHI).

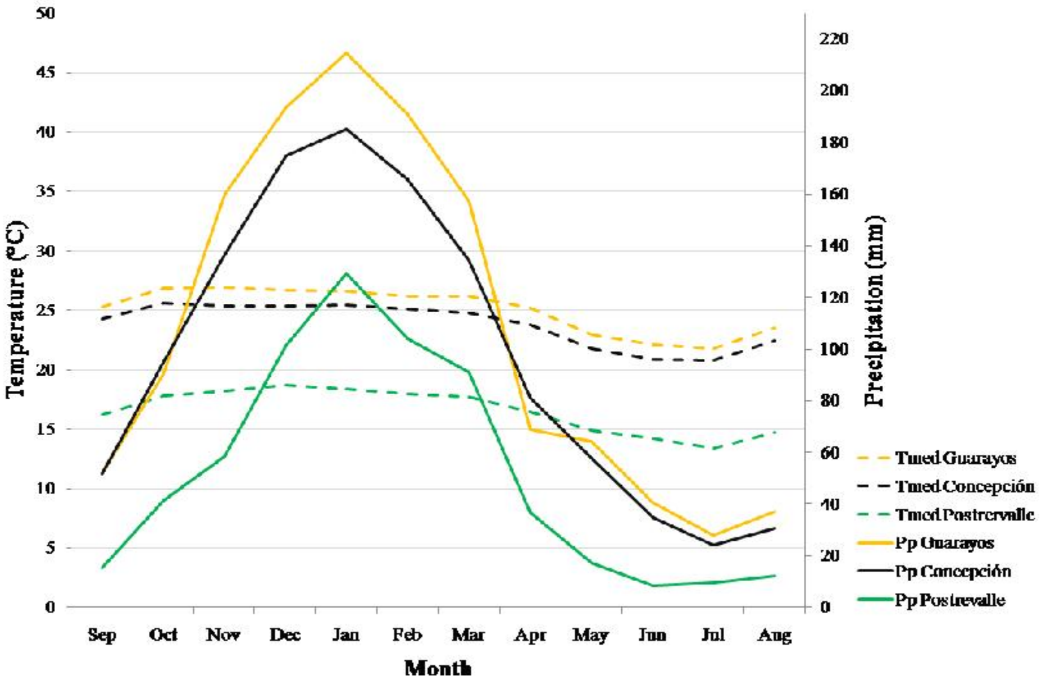

Figure 2: Ombrothermic diagrams from Concepción, Postrervalle and Ascensión de Guarayos sampling sites according to the SENAMHI database.

Tree species

The genus belongs to the group of softwood and valuable timber species in Bolivia. In general, they are deciduous species and partially light demanding. They rapidly grow in forest clearings in variable soils and topography but requiring good drainage (Mostacedo *et al.*, 2003). It can be found from moist to dry tropical forests and between a wide range of altitudinal storey (Mostacedo *et al.*, 2003; Aguirre *et al.*, 2011; Navarro, 2011; Navarro-Cerrillo, 2013; Cavers *et al.*, 2013).

Field sampling

Samples were randomly collected from 12 *C. fissilis* specimens in Concepción, from 30 *C. angustifolia* specimens in Postrervalle and from 11 *C. fissilis* specimens in Guarayos. Two to three increment cores at breast height (1.3 m above ground level) were taken from each specimen tree. It was not possible to obtain cross-sections for larger field observation

(López, 2003) since conservation actions or limited harvesting were taking place in the sample areas.

For additional analysis on the effect of other local specific conditions, complementary soil sampling was also taken in Postervalle for basic fertility components and texture analysis (Annex 1). For Concepción and Guarayos, we relied on the data soil analysis of previous studies (Peña-Claros *et al.*, 2012).

Dendrochronological data analysis

Samples were prepared using sandpaper using grit sizes ranging from 26.8 to 425 µm (Orvis and Grissino-Mayer, 2002). *Cedrela* annual ring formation has been proven in previous studies (Worbes, 1999; Dünisch *et al.*, 2002a; Brienen and Zuidema, 2005; Bräuning *et al.*, 2009) and tree-ring boundaries identification was conducted on increment cores and marked with lead pencil. *Cedrela* species from Postrervalle and Concepción sample sites (Tropical Andean and Brazilian-Paranean Regions, respectively) exhibited visible tree rings and they were composed by porous wood and parenchyma bands in the boundaries (Figure 3, B from Postrervalle and C from Concepción) as found by Worbes (2002). However, tree rings became more difficult to identify in Guarayos sample site (Amazon Region) as they were narrower and presented blurred bands of parenchyma in the boundaries (Figure 3, A).

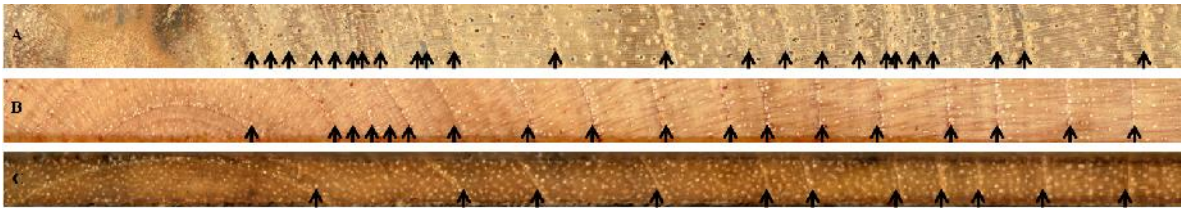

Figure 3: Visibility of tree rings and delimiting parenchyma indicated by arrows over the rings' transversal surface of samples from A) Guarayos, B) Postrervalle and C) Concepción.

As cross-dating involves cross-matching samples from different specimens based upon characteristic sequences of radial growth (Yamaguchi, 1991), we assigned each ring to the calendar year in which the growth of the tree rings started (from September of the current year to August of the following year; Schulman, 1956). According to the date of sample collection, the last year of growth measured in Concepción samples started in 2012, Postrervalle 2011 and Guarayos 2011.

Tree rings within each increment core were correctly compared and matched using WinDendro^{TM} (Regents Instruments Inc., Canada) with a 0.001 mm resolution. Missing and false rings, suggested by cross-dated samples, were also revised visually and using this software. The quality of inter-sample cross-dating was verified using COFECHA (Holmes, 1983) applying a cubic smoothing spline (Cook and Holmes, 1999) with a 50% frequency cut-off over 32 years to our measurement series for verification of cross-dating.

We used ARSTAN 40c (Cook and Krusic, 2006) to standardize and remove non-climatic environmental and age-related noise from tree-ring width series (Grissino-Mayer, 2001) and develop a tree-ring chronology from our verified data. We used a smoothing spline function with 50% frequency cut-off over 45 years for Concepción, 31 years for Postrervalle and 51 years for Guarayos series mean length. Autoregressive modeling was performed to remove autocorrelation from the tree-ring series and robust (biweight) mean was estimated to produce detrended chronologies of tree-ring width. The resulting STD, RES and ARS index were previously correlated with climate data to determine the best representing chronology. 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). The STD chronology was used in the following analysis as it contained the strongest climatic signal common to all trees during the cross-dated period.

In addition to the final chronology, we also calculated (a) the mean inter-series inter-correlation, which quantifies the similarity in residual width indices among trees (R_{bar};

Briffa, 1995), (b) mean sensitivity, which measures the year-to-year variability in width of consecutive rings (MS), (c) the annual growth trends of the chronology and (d) for the purpose of analyzing the site-species interactions, annual increments from *Cedrela* were compared between trees growing in different sites. Differences in growth were evaluated from common periods including the largest number of individuals in the compared sites based on the total number of individuals collected. A square root transformation was applied to the mean diameter growth and to the maximum mean growth increment (Rokal and Rohlf, 1995). Then, statistically significant differences ($p<00.5$) between sample populations were evaluated using a Tukey analysis of variance, assuming no-normal distribution of the variables (Tukey, 1977).

Radial growth – climate relationship

The meteorological data (temperature and rainfall) accessibility was limited, for this reason our periods of analysis varied for each study site. Based on the available climate data, we restricted our analysis to the 70-year window in Concepción, a 22-year window in Postrervalle and a 57-year window in Guarayos.

We analysed temperature and rainfall data for the 24 months spanning the previous and current growing periods (September$_{t-1}$ to May$_{t+1}$ in the southern hemisphere; Schulman, 1956). We also tested correlation between the STD indexed chronology and annual precipitations totals (Figure 6) to determine the influence of the different local climatic variables in *Cedrela* radial growth.

Finally, growth index were compared with monthly climate series of temperatures and precipitation during wet season for common period data 1985-2012 of mean temperature and 1943-2012 of precipitation measured in Concepción, 1990-2011 temperature and precipitation periods in Postrervalle and 1987-2011 and 1955-2011 temperature and precipitation periods respectively in Guarayos (Figure 7, 8 and 9).

Results

Tree-ring chronology

Cross-dating was verified for 20 radii in Concepción and Guarayos samples and 57 radii in Postrervalle. According to the year of the samples collection corresponding to the last year of tree-ring formation, the ring-width dataset spans between 1925-2012 (88 years) in Concepción, 1928-2011 (84 years) in Guarayos and 1936-2011 (76 years) in Postrervalle (Table 1) but for further analysis the dataset was restricted to 1931-2012 (82 years), 1931-2011 (81 years) and 1963-2011 (49 years) respectively (Figure 4). The difficulties in dating associated to areas of unclear tree-ring boundaries and wedging rings in the cross-sections restricted the chronologies and resulted in low series inter-correlations (R_{bar}) for *C. fissilis* species from Concepción and Guarayos with 0.261 and 0.284 respectively unlike the tree-rings boundaries exposed in *C. angustifolia* whose series inter-correlations was significant (0.374, $\alpha<0.01$). Mean sensitivity (MS) was 0.565 in Concepción, 0.579 in Guarayos and 0.526 in Postrervalle, indicating inter-annual variability in radial growth data in Postrervalle but with higher sensitivity in Guarayos and Concepción (Table 1).

Table 1: Site descriptions and characteristics of *Cedrela* chronologies in Bolivia. Series inter-correlations (R_{bar}) and Mean Sensitivity (MS).

Site	**Species**	**Number of series**	**Samples**	**Period**	(R_{bar})	**MS**
Concepción	*Cedrela fissilis*	20	12	1925-2012 (88 years)	0.261	0.565
Guarayos	*Cedrela fissilis*	20	11	1928-2011 (84 years)	0.284	0.579
Postrervalle	*Cedrela angustifolia*	57	30	1936-2011 (76 years)	0.374	0.526

Although the sample sites presented growth variation along the measured period, there was a common decrease of the growth trend during recent years. Specifically, common increasing growth was found during 1973, 1994, 2002, 2005 and 2009; and decreasing growth during 1969, 1972, 1978, 1984, 1993, 1997, 1999, 2004 and 2010 in all sites (Figure 4).

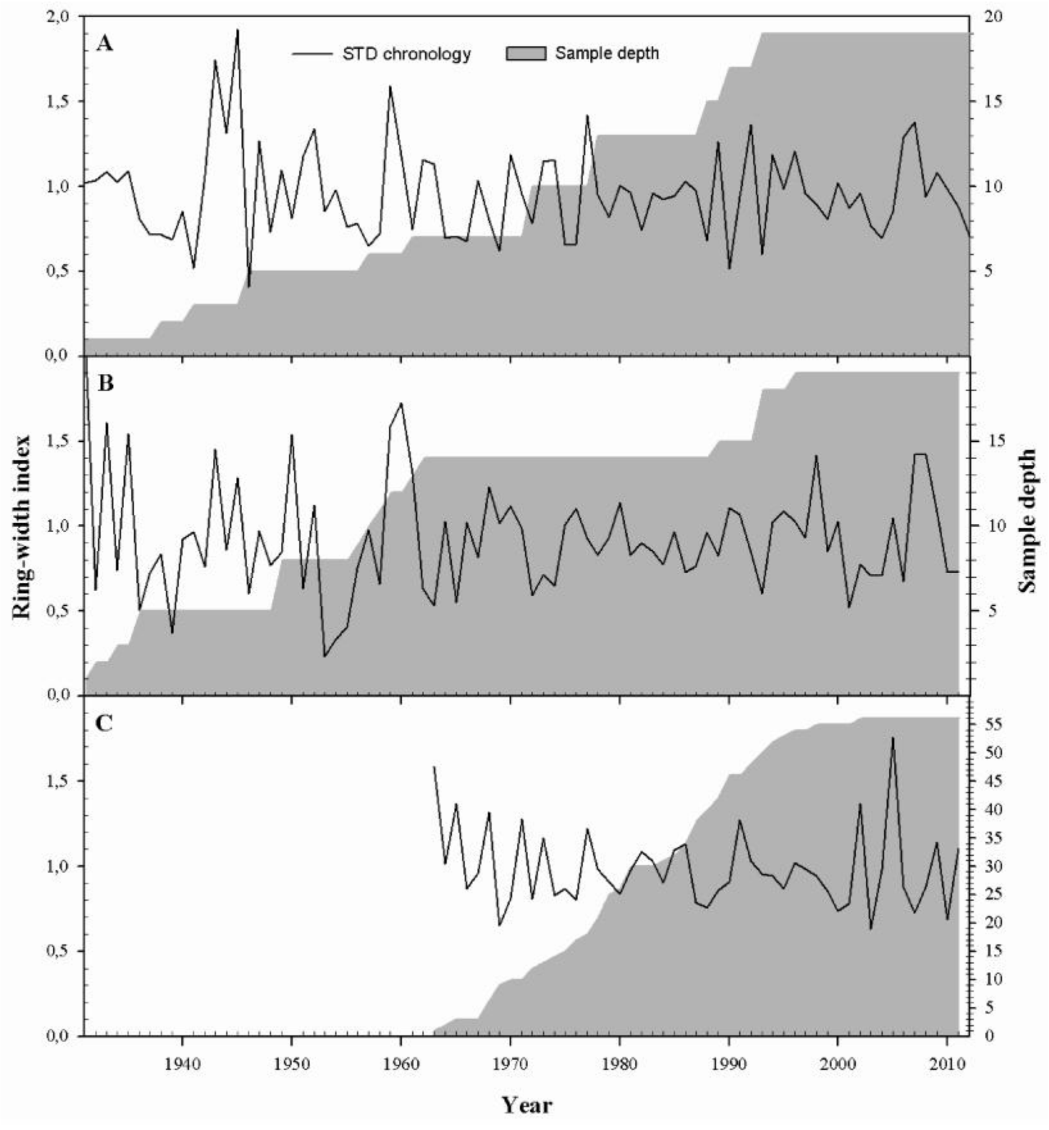

Figure 4: STD chronology and sample depth for A) *Cedrela fissilis* in Concepción, B) *Cedrela fissilis* in Guarayos and C) *Cedrela angustifolia* in Postrervalle.

As the Concepción and Guarayos chronologies extended 32 dated years more than Postrervalle, we found a common growth increase in 1940, 1943, 1945, 1952 and 1959 and decrease in 1936, 1946, 1953 and 1961 for these two sites during the common period. The outstanding years for all sites where 1973, 2002, 2005 and 2009 with high growth and 1969, 1972, 1978, 1999 and 2010 with the lowest growth.

In general, for the whole chronology period, between the Guarayos and Conception sites the growth was similar while in Postrervalle was different from the two other sites (Figure 5). Mean annual growth for *C. fissilis* in Concepción was 2.07 mm/year, 1.92 mm/year in Guarayos and for *C. angustifolia* 2.82 mm/year in Postrervalle.

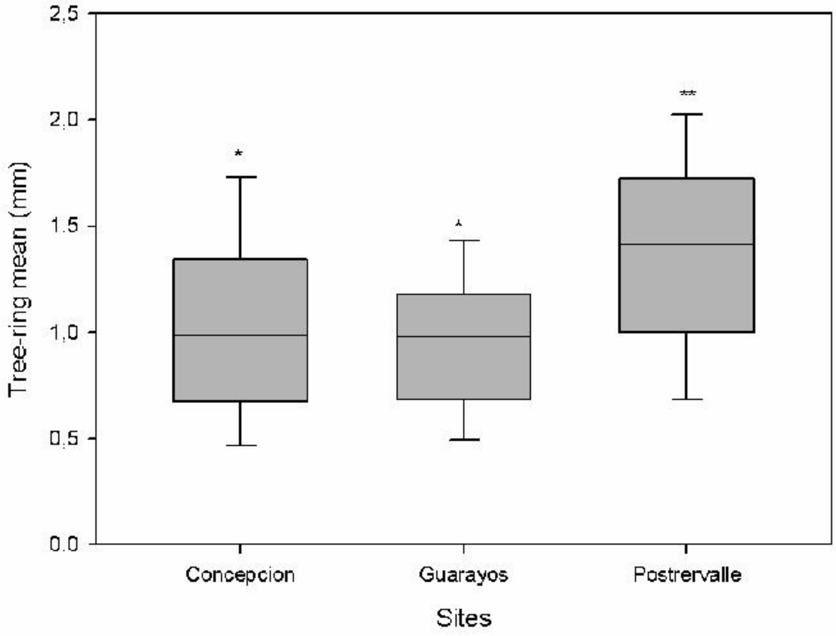

Figure 5: Site index and tree-ring mean in Concepción, Guarayos and Postrervalle.

Although growth differences may not seem outstanding, annual increment in Postrervalle showed to be statistically higher and with different response to environmental conditions. These results suggest that the same environmental variables would be controlling growth in Concepción and Guarayos. However growth in Postrervalle was different with a media value higher than the two previous sites indicating that climatic and site conditions are more favorable for growth.

Climate – growth relationship

Correlations of STD index with mean rainfall showed a general common trend although there were some points of significant divergence. For this reason, we performed specific periodic analysis for each site, taking into account the influence of wet and dry months (Figure 6).

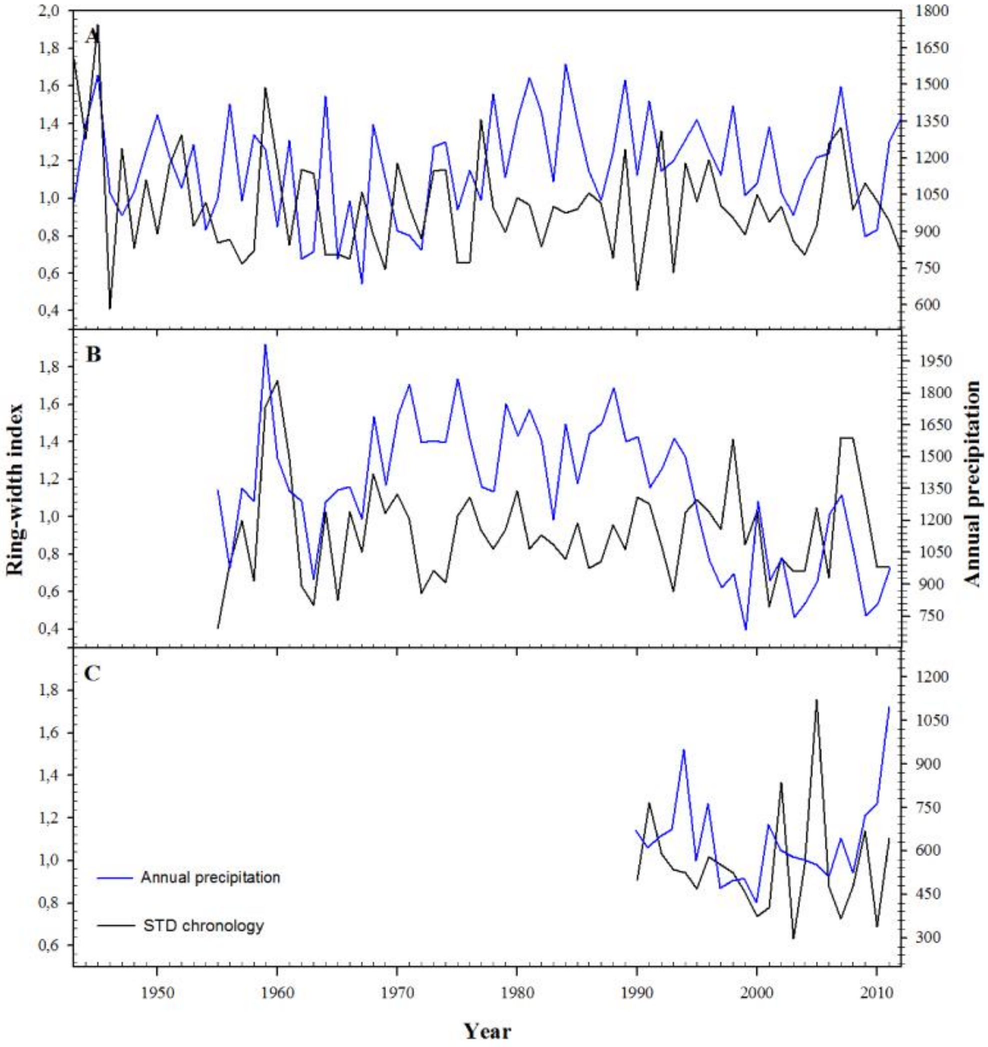

Figure 6: STD index and annual precipitation in A) Concepción, B) Guarayos and C) Postrervalle.

Array analysis was performed with the correlation of the *Cedrela* STD chronology and two variables, precipitation and temperature (Figure 7). After the comparison and correlation analysis, some of the sites gave significantly growth correlation with precipitation and temperature. The Concepción significantly correlation between the STD chronology and precipitation corresponded to the months of February, March and April of the current year plus December and January of the previous growth year (p-value = 0.5 to 95%). That is, when the amount of increasing water available (by the rainfall) appears stable. While significant negative correlations were evident between the STD chronology and precipitation during 1961, 1970 and 2000 for these months.

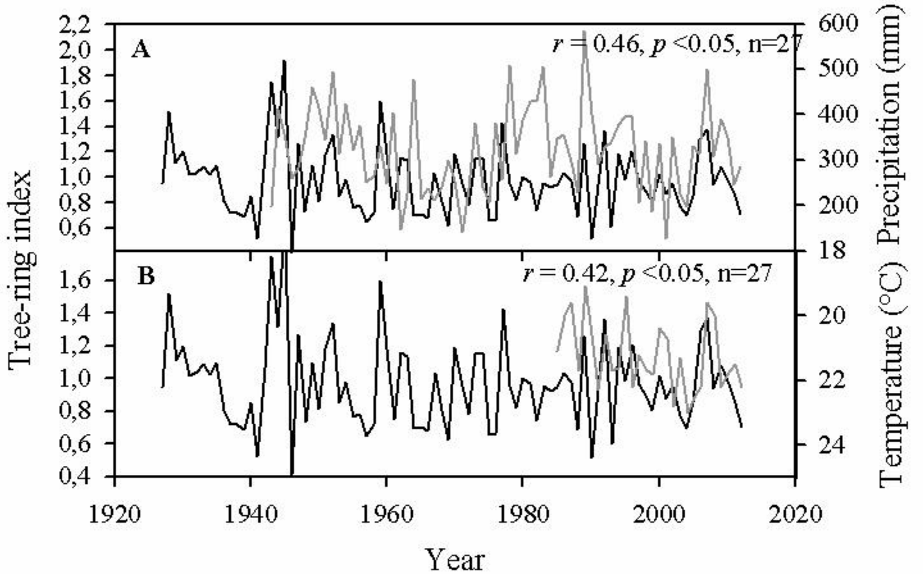

Figure 7: STD chronology and wet season climate in Concepción.

Moreover, the chronology was associated with the temperature during the months of May, June and July of the current year. This season, of mean temperature significantly associated to growth, is distinctly dry and belongs to the end of autumn and beginning of winter in the region (Figure 7).

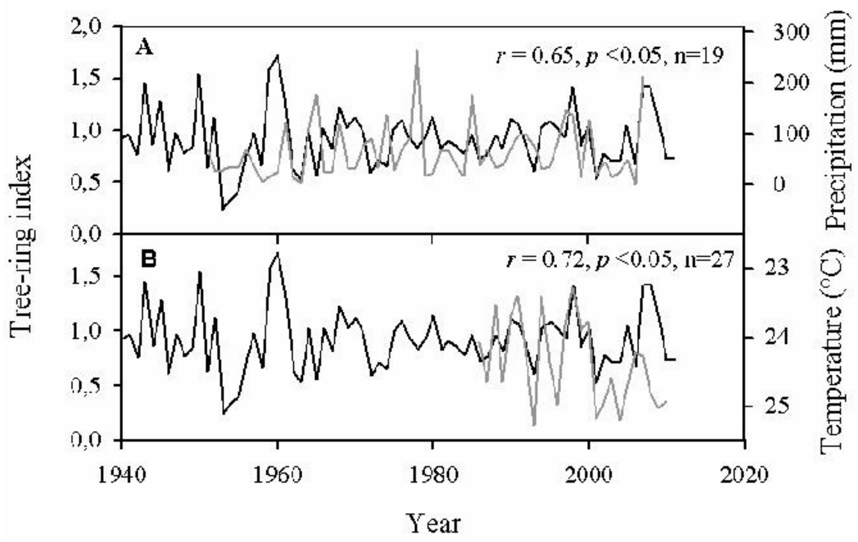

Figure 8: STD chronology and wet season climate in Guarayos.

While for the Guarayos chronology, the best correlation with precipitation was found on March, April and May of the current year, corresponding to the decrease of available water levels. Mean temperature from November to December of the current year plus June and July of the previous year, when it reaches the highest and lowest values respectively (Figure 8).

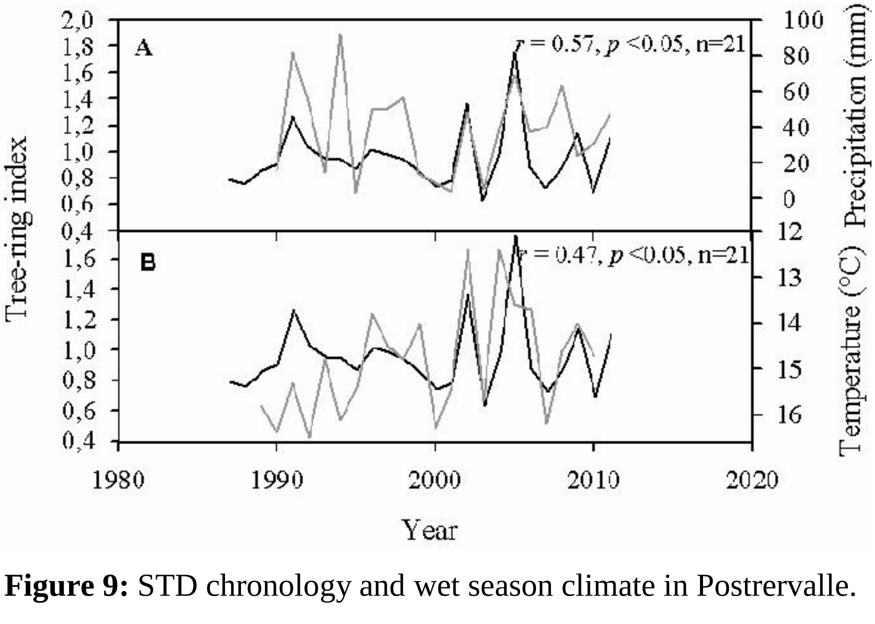

Figure 9: STD chronology and wet season climate in Postrervalle.

Furthermore, Postrervalle chronology best correlations were found with precipitation during October, November and December of the current year and with the temperature during May, June and July of the current year. This significantly correlations happened as soon as the monthly precipitation levels increased notably and the monthly mean temperature reached the lowest values along the year of growth.

Discussion

Tree-ring chronology

Having previously tested the annuity tree-ring formation in *Cedrela* species (Worbes, 1999; Dünisch *et al.*, 2002a; Brienen and Zuidema, 2005; Bräuning *et al.*, 2009), it was possible to crossdate samples from 3 different sites. *C. fissilis* from Concepción and *C. angustifolia* specimens from Postrervalle showed visible tree rings and presented mean inter-series correlation of 0.26 and 0.37 respectively; and despite of the tree rings were more difficult to identify in Guarayos sample site, due to narrower and blurred bands of delimiting parenchyma, it was also possible to crossdate them with a mean correlation of 0.28. Correlation values were similar to those observed for *Cedrela* species for the humid mountain rainforest in Southern Ecuador (0.30, Bräuning *et al.*, 2009) and for the central Amazon in Brazil (0.24, Dünisch *et al.*, 2003). The formation of missing and false rings hampered the synchronization among trees and may have caused weakness in their respective correlations. Samples from Postrervalle, in particular, showed distinct tree rings and well marked ring boundaries. This differentiation of tree rings visibility between samples from Postrervalle (*C. angustifolia*) and Concepción and Guarayos (*C. fissilis*) may be due to the wood anatomy structure which seems to be genetically controlled (Détienne, 1989; Worbes, 1995; Worbes, 1999).

The resulting tree-ring index chronologies of all sites presented common variation of growth along the period of analysis with remarkable increase during 1973, 2002, 2005 and 2009; and with lowest values during 1969, 1972, 1978, 1999 and 2010. Despite of the differences among environmental local conditions and sample site distances mean annual growth for *C. fissilis* in Concepción (Chiquitania region) and Guarayos (Chiquitano transitional Amazonian) were 2.07 mm/year and 1.92 respectively. This annual increment was less that those reported from the Permament Plots in the Chiquitania region with 2.99 mm/year for the same species and 3.89 mm/year averaged for all the species measured in the Permament Plots of the Chiquitano transitional Amazonian forest (Dauber *et al*., 2003). However, the growth in *C. angustifolia* of 2.82 mm/year in the Tucuman montane forest of Postrervalle estimated in this study seemed to be similar to those obtained for *C. fissilis* from Chiquitania region previously mentioned. Similar results were also obtained for *C. odorata* (2.95 mm/year) near Aripuanã, Mato Grosso, Brasil (Dünisch *et al.,* 2003). The difference of reported growth by permanent plots to those obtained in this study for Concepción and Guarayos may be due to the short period of measurement in the plots compared to the longer period offered by our tree-ring analysis. The latter also represents an advantage when providing growth data from Postrervalle where no permanent plots are installed to date.

In addition, the similarity of annual growth value in Concepción and Guarayos suggest that it may be not only for being the same species but also because the same environmental variables would be controlling *C. fissilis*'s trees development in both locations. On the other hand, mean growth in Postrervalle is higher indicating that weather and site conditions are more favorable for growth in this site.

Climate – growth relationship

In general, the climatic variation presented a common effect in *Cedrela*'s growth. There was a common sensitivity to precipitation along the rainy season in the three sites. Many studies have found that the rainfall is the most important variable related to water availability being the main limiting factor not only for species distribution and diversity (Peña-Claros *et al.,* 2012; Toledo *et al.,* 2011a, 2012; Amissah *et al.,* 2014) but also for growth (Borchert 1994a, 1994b, 1999) compare to other environmental factors (Dünisch *et* *al.*, 2002b; Toledo *et al.*, 2011b; Volland-Voigt *et al.*, 2011). Also, cambial cell divisions were found to be concentrated during the more humid months, stating that cambial growth is determined by water supply (Dünisch *et al.*, 2003). Worbes (1999) found that wood growth of *C. odorata* trees ceased when precipitation was <5mm. *Cedrela*'s root system was previously explained as a factor influencing common response of trees to precipitation (Dünisch *et al.*, 2003) as this is characterized for growing in the upper soil layers (Noldt *et al.*, 2001).

For Concepción and Postrervalle *Cedrela* species, the sensitivity period to precipitation extents from October to April which corresponds to the wettest season. These two study sites showed more sensitiveness to low temperatures during the driest months (from May to July). The significant relationship of growth to these opposite conditions seasons might be also explained by the direct relationship between water availability during these months and all seasonal processes (e.g. cambial activity) which are strongly inhibited by water stress (Borchert, 1994a, 1994b). Cambial growth periodicity and its relationship with the rainy season have been already evidenced by dendrometer measurements in previous studies with *C. montana* from humid mountain rainforest in Ecuador (Bräuning *et al.*, 2009) and *C. odorata* in an tropical rainforest of Aripuanã, Mato Grosso, Brazil (Dünisch *et al.*, 2003); and also by cambial wounding technique of consecutive years in *C. odorata* trees from a tropical plantation and forest reserve of Caraparo, Venezuela (Worbes, 1999). On the other hand, worth noting that even when different *Cedrela* species where analyzed in these two sites (*C. fissilis* in Concepción and *C. angustifolia* in Postrervalle), they showed similar growth response to local environmental conditions. The decreasing sensitivity in growth to precipitation later in the rainy season may be explained by the overpass of the critical levels needed to initiate growth and the gradually increase of water stored in the soil (Brienen and Zuidema, 2005).

Contrary to that, Guarayos samples seemed to be more sensitive to precipitation during late rainy season (March, April and May of the current year) and high temperatures also corresponding to the rainy months (November to December) plus dry season (June and

July) of the previous year. The difference of growth sensitiveness to high mean temperatures when the area presents the highest levels of water availability suggests inverse relationship between rainfall and maximum temperature. Maximum temperature, in addition to radiation, increases water pressure deficit and consequently tree transpiration (Bräuning *et al.*, 2008a) regulating water supply (i.e., the balance between precipitation and evapotranspiration) which in turn influenced annual variation in tree growth (López and Villalba, 2011). In addition, this location presents the highest mean monthly temperatures and rainfall levels during the period of analysis (SENAMHI, 2011).

The decreasing but still existing growth of *C. fissilis* in Guarayos (from March to May) may be due to the decreasing photosynthetic capacities of older leaves (Mooney *et al.*, 1981; Ackerly and Bazzas, 1995; Kitajima *et al.*, 1997), the proximity to the leafless period of this species (Bräuning *et al.*, 2008b) and changes in the hydrological status of the stem instead of cambial activity (Bräuning *et al.*, 2009; Dünisch *et al*., 2003). The shedding of leaves as a response to drought (Medway, 1972; Alvim and Alvim, 1976) and decreasing growth when soil water potential reaches its permanent wilting point (Franco, 1979) was also found in *C. odorata* among other species (Worbes, 1999). Although the phenological behaviour maybe an explanation of the decreasing radial growth for also the other study sites, *Cedrela* species are deciduous (Borchert, 1994a; Mostacedo *et al.*, 2003) and its medium density wood stores water in the stem (Worbes, 1999) are used in flowers and fruits during dry season (Reich and Borchert, 1984).

Different strategies of growth of our study species also may explain the differences of response to climatic variables; e.g. correlation of growth with precipitation (Concepción) and temperature (Guarayos) of the previous year. The response of Concepción tree growth to rainy season of previous year, unlike Postervalle, may be because as this site is drier, *C. fissilis* focus on long-term stem water storage (Borchert, 1994c) and formation of food reserves on wood when water is supplied, mobilizing them in the following year (current year of growth; Höll, 1985; Sauter, 2000). This storing and mobilization of reserves in the following year was also found in *C. odorata* species (Dünisch and Puls, 2002; Dünisch *et al.*, 2003).

The interaction of local climatic and micro site ecological conditions may play an important role of *Cedrela*'s tree growth variation at short term while long-term patterns may be influenced by the dynamic stage of the forest and life strategy of the species, i.e. the age and history of the forest and life strategy and light competition of the understorey species (Worbes, 1999; Brienen *et al.*, 2010). Canopy dynamics and light availability showed a great effect on *Cedrela*'s tree development (Brienen *et al.*, 2010) because it is a relatively light-demanding canopy tree (Brienen and Zuidema, 2006). Brienen *et al.* (2010) suggest that light is a stronger limiting factor and releases from low-light conditions are more important for trees in the moist forest compared to those in the dry forest where amount of direct light received in the forest floor may be higher. They also suggested that the bigger gaps, the longer time required for their closure, resulting in differences in light levels between gaps and understorey in moist forest, as those partially presented in the Chiquitano transitional Amazonian forest of Guarayos that may have influenced on growth variations. On the other hand, the correlation of growth rates and releases with the drop of maximum temperatures in the dry forest may suggest that releases are induced by periodic change in climatic conditions; as increased respiration or drought stress may affect more to photosynthesis rates (Clark *et al.*, 2003; Fichtler *et al.*, 2004; Feeley *et al.*, 2007) and hence cause a decrease in radial growth of moist forest trees (Brienen *et al.*, 2010).

Although as not as significant as rainfall, soil characteristic showed effect on tree growth (Toledo *et al.*, 2011b) on dry forest where soil water availability and nutrients seems to impact on growth (Medina, 1995; Mooney *et al.*, 1995; Oliveira-Fihlo *et al.*, 1998). This impact shows an spatial gradient (Murphy and Lugo, 1986; Mooney *et al.*, 1995; Ceccon *et al.*, 2006) that progressively shift in wetter forests where light variation is more important for growth specially in *Cedrela* species as it is a light-demanding canopy tree (Engelbrecht *et al.*, 2007; Brienen *et al.*, 2010). The importance of water availability and K content in the soil were also analysed for *Cedrela* species in the Amazon forest

(Dünisch *et al.*, 2002b), where photosynthesis showed that water uptake of the species decreased with decreasing K content of soil. Although this uptake of K per unit biomass decreased with increasing tree age; and its use efficiency for photosynthesis was of secondary importance during dry periods. Previous studies about soil effects on forest structure and diversity in Guarayos and Concepción (Peña-Claros *et al.*, 2012) suggest that the K content in the latest is higher (0.30 cmol/kg and 0.38 cmol/kg respectively). This is consistent with the differences of mean annual growth found in this study for *C. fissilis* with 1.92 mm/year in Guarayos and 2.07 mm/year in Concepción. However, although growth in Postrervalle was higher that the two other sites, with 2.82 mm/year, soil analysis during this study showed the lowest K value (0.026 cmol/kg). This inconsistency suggests a higher adaptation capacity of *C. angustifolia* to adverse environmental conditions or plasticity to site conditions. Some other species of the same genera as *C. odorata* was found to be less adapted to poorer soils and changing soil water contents than other species in Meliaceae family (Dünisch *et al.*, 2002b). It should be also taken into consideration that the low K rating can be due to a deficiency of this factor in relation to the excess of the other mineral elements.

Biochemical processes may also hold a strong relationship with temperature which in turn affects tree growth. During photosynthesis some mineral elements, like K and Mg, are indispensable for the synthesis of glucose (Küppers *et al.*, 1985; Marschner, 1995) and the velocity of their biochemical reactions are temperature dependant (Rosenthal and Camm, 1997). Although loss of assimilates by respiration varies in time and among species (Stockfors and Linder, 1997; Pathre *et al.*, 1998) the variation in response and growth of *C. fissilis* from both Concepción and Guarayos in this study may indicate the importance of the temperature role on tree development.

Dünisch *et al.* (2003) found that although *Swietenia macrophylla* belongs to the same family of *Cedrela* species, the former showed lower ecological amplitude and higher sensitivity to unfavourable micro site conditions which was attributed to the ecophysiology of the species, i.e. light, water and nutrients demand for the net photosynthesis and the biomass production (Dünisch *et al.*, 2002b). The ecophysiology and ecological amplitude may also explain the lower growth of *C. fissilis* in Chiquitano transitional Amazonian forest given that this site presented higher levels of annual rainfall in comparison to the other sample sites.

Although there was some ring width correlating with ENSO years, they were not significant (data not included). This is consistent with Bräuning *et al.* (2009) analysis which did not found any relationship of ENSO in local climate and of the latest to *C. montana* growth in the humid mountain rainforest. Worbes (1999) found also no significant correlations between *C. odorata* growth and ENSO.

These analyses together suggest that ecological processes and their interactions are complex and that the micro climatic and environmental factors must be taken into account for a more accurate information and management decision making. However, the role and importance of microclimate vary widely among forests, ecosystems over time and under different weather conditions (Reifsnyder *et al.*, 1971). Additionally, ecosystem structure and functions are scale dependent (Meentemeyer and Box, 1987) and have cumulative effects (Chen *et al.*, 1999) being needed to be considered when analyzing and interpreting growth response of *Cedrela* species at the local and management scales.

Conclusion

On this study, it was possible to crossdate *C. fissilis* and *C. angustifolia* samples from 3 different sites. *Cedrela* species showed significant mean inter-series correlations. The similar mean annual growth in Concepción (Chiquitania region) of 2.07 mm/year and Guarayos (Chiquitano transitional Amazonian) of 1.92 mm/year and the higher growth in *C. angustifolia* of 2.82 mm/year in the Tucuman montane forest of Postrervalle suggest that, although there was a common correlation with precipitation during rainy season, there are other local environmental factors affecting tree growth.

Concepción, Guarayos and Postrervalle *Cedrela* species presented sensitivity to precipitation and the common response to water availability showed to be linked to temperature variations. Postrervalle trees showed more increase in growth with the less water availability and minimum temperatures in comparison to those from Guarayos where rainfall values and temperatures were higher, suggesting that temperatures can highly influence tree growth through evapotranspiration processes. Growth of *Cedrela* species in Concepción, Guarayos and Postrervalle showed to be sensitive to local climatic conditions but there was not significant correlation between ring width and ENSO years which suggests that the micro climatic and environmental factors are playing an important role on *Cedrela*'s growth. For this reason, further analysis on these local-specific factors and their interaction at a spatial and temporal scale are required for a better understanding of the species ecology and pertinent management decisions taking. The results presented in this study showed the growth differences between sites and species and their response to climate variations hence also planning and management of each site should be handled with different guidelines.

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Chapter 5

General Discussion

Tropical forest are home of a wide diversity of wildlife and vegetation and millions of people depend on the goods and ecosystem services they provide (Myers, 1992). Forest management in Bolivia is based on a polycyclic system and Minimum Logging Diameter (MLD; García-Fernández *et al*., 2007). However, MLD values adopted are based on arbitrary assumptions of growth rather than profound ecological knowledge. Thus, populations of the most valuable timber species as morado (*Machaerium scleroxylon*), roble (*Amburana cearensis*) and cedro (*Cedrela sp*), have been reduced and degraded (Gullison *et al*., 1996; Killeen *et al*., 1993). For these reasons, a better understanding of the ecological dynamics of the target species is essential to establish truly sustainable management policies in tropical forests.

In this thesis, we used dendrochronology as a tool for assessing ecology and growth patterns of forest species through long-term tree rings dataset. We investigated the potential for some timber species for tree-ring analysis, growth estimations, climate reconstructions and their response to climatic variables such as rainfall, temperature and atmospheric circulation patterns (El Niño-Southern Oscillation). This chapter provides an overview of the application of dendrochronology in tree growth analysis in different environmental conditions and species and also an analysis of the strengths and limitations of this methodology. Finally, a review of the implications for forest management and climate adaptation are given together with some recommendations.

Dendrochronological potential of forest species and growth analysis

Tree rings of four different species have been analyzed in this thesis. One of the objectives of CHAPTER 2 was to develop the first chronology from *M. scleroxylon*, one of the most valuable and fragile timber species from the Chiquitano forest in Santa Cruz de la Sierra, Bolivia. Little dendrochronological analysis has been conducted on Bolivia's endemic species. It has long been argued that many woody species of the world's tropical and intra-tropical forests, such as Bolivia's, do not form distinct growth rings (Eckstein *et al.*, 1981). The rationale for this argument is the belief that cambial activity does not vary throughout the year (Dave and Rao, 1982; Borchert, 1999). However, previous studies have shown the dendrochronological potential of several tree species in Bolivia such as *Bertholletia excelsa*, *Cedrelinga catenaeformis*, *Tachigali vaquezii* and *Peltogine* cf. *heterophylla* (Brienen and Zuidema, 2006a, 2006b; López and Villalba, 2011), which specifies that these species develop annual rings clearly visible (Brienen and Zuidema 2005a). Although tree rings of *M. scleroxylon* (morado) were hardly distinguishable (Roig 2000) and presented lenses and false rings, fine marginal parenchyma lines defined their boundaries and facilitated their identification and cross dating was possible. In addition, we had to resort to alternative techniques for identifying tree rings as immersion of the disks in sodium hypochlorite. We found a high occurrence of wedging rings and lenses, which hampered the identification and measurement of tree rings (López, 2003). The wedding rings were found in places of buttresses formation on the trunk and lenses were recognized as growth in certain sectors of the circumference of a tree due to stimulus in cambial activity and/or vascular growth during the annual cycle (Villalba, 1997; López, 2003).

According to the difficulty of dating and timing of sample collection, we counted on entire cross sections of the species, which was basically opportunistic and taking advantage of logging activities that were taken place at the sample site. Complete *M. scleroxylon* cross sections permitted us to identify difficult areas for dating and correlate first among the radii of a single tree and later between different trees. We found significant correlation between radii of the same tree but the values decreased as we compared them with other trees which reflected the effect of the geometry in each of them.

Contrary to starting from scratch and having to develop technical alternatives for *M. scleroxylon* dating, for the analysis *Amburana cearensis* and *Cedrela* species, we count on previous studies that identified and proved their annual ring formation and their dendrochronological potential (Worbes, 1999; Dünisch *et al.,* 2002a; Brienen and Zuidema, 2005a; Bräuning *et al.,* 2009). Tree-ring boundaries were defined by a band of marginal parenchyma and annual tree rings of *A. cearensis* were clearly identified on the sample discs; *Cedrela* species also showed visible tree rings with the exception of that from the Chiquitano transitional Amazonian forest (*Cedrela fissilis* from Guarayos sample site), due to narrower and blurred bands of delimiting parenchyma. The low inter-radial correlation between and within trees as a consequence of growth eccentricities is not only common in tropical forest species (Sousa *et al.*, 2012; Paredes-Villanueva *et al.*, 2013) but is also evident in some temperate genera (Brookhouse and Brack, 2008). Our tree-ring analysis revealed that irregular diametric growth with wedging rings and lenses significantly affected crossdating and may have caused weakness in their respective correlations. However, despite the formation of missing and false rings (generally discontinuous around the circumference of the sample discs) hampered the synchronization among trees, further analysis were possible for climate reconstructions in CHAPTER 3 and even comparison among different site conditions was presented in CHAPTER 4.

We developed the first tree-ring chronology of *M. scleroxylon* and *C. angustifolia*, important timber species from the lowland tropical dry and montane forests in Bolivia and continue with further dendrochronological analysis in *A. cearensis* and *C. fissilis* which were previously studied (Worbes, 1999; Dünisch *et al.*, 2002a; Brienen and Zuidema, 2005a; Bräuning *et al.*, 2009). According to our results, all our species tree rings are annual in nature and chronologies showed a strong common signal between the individual series of each sample site. Based on measurements from permanent plots installed across different regions in Bolivia, it was estimated that *M. scleroxylon* has a general average diameter increment of 2.37 mm year^{-1}, *A. cearensis* increase 3.09 mm yr^{-1} and *C. fissilis* 2.99 mm yr^{-1} (Dauber *et al*., 2003). It has been found that the diameter is a poor indicator of tree age (Harper, 1977; Sarukhan *et al.*, 1984) and some studies used averages to eliminate bias caused by age-related long-term size and variations of short-term growth caused by climate (Nowacki and Abrams, 1997), but for the analysis of the growth rate, the use of the mean or median trends to overestimate the age of trees (Brienen and Zuidema, 2006a). According to our results, *M. scleroxylon* species has an annual increment of 1.43 mm year^{-1}, *A. cearensis* had 5.75 mm yr^{-1} and *C. fissilis* from 1.92 to 2.07 mm year^{-1} (Chiquitano transitional Amazonian and Chiquitania forests respectively). *M. scleroxylon* and *C. fissilis* annual increments were less that those reported from the measurements of the permanent plots and the *A. cearensis*' exceeded them. These variations maybe due to the number of measurements analyzed through permanent plots (4 years) and tree rings (68 years in *M. scleroxylon*, 223 years in *A. cearensis* and from 84 to 88 years in *Cedrela* species) data which clearly affected the averages. In line with our results of *A. cearensis*, Lopéz *et al.* (2013) reported a general growth of 5,8 mm yr^{-1} for the Chiquitania region and for *Cedrela* species Dünisch *et al.* (2003) reported an increment of 2.95 mm yr^{-1} near Aripuanã, Brasil through the analysis of tree rings.

Cedrela angustifolia chronologies and growth rates hadn't been studied previously; it presented an average annual increment of 2.82 mm yr^{-1} in the Tucuman montane based on the measurement of tree rings from 1936 to 2011 (76 years). Although we couldn't compare our obtained growth rates of this species with data of the permanent plots, tree rings analysis represented an advantage when providing annual growth data from Postrervalle where no permanent plots are installed to date.

As previously said, *M. scleroxylon* tree rings were possible to cross date but due to the complications presented (lenses, false rings and eccentricity) and the time consuming and much effort invested, further applications were not possible. However, the *A. cearensis* chronology presented consistent results for subsequent climate reconstructions; and due to the broad distribution, relatively less difficulty of dating and clear structure of tree rings presented on *Cedrela* species, we could cross date and compare samples from different sites.

Climate-growth relationship and potential for reconstruction

To support determination of sustainable forest harvesting guidelines and decision-making processes it is important to know forest growth response to climate variability (López *et al*., 2012; Brienen and Zuidema, 2005a, 2005b). Tree-ring data offers the opportunity to study growth and the effect of the variability in the physical environment throughout a tree's entire lifespan. Dendrochronology also allows modeling growth of each species in the future climate scenario. The phases of growth and relative inactivity in many plants are closely related to environmental changes i.e., water availability effect on the seasonal cambial activity (Borchert, 1994). Thus, to understand the behavior of Bolivian fragile ecosystems in a context of global climate change, this thesis offers a basis of knowledge on how species of *Machaerium scleroxylon*, *Amburana cearensis, Cedrela fissilis* and *Cedrela angustifolia* respond to precipitation and temperature to allow inferences about potential behavior of species under climate change in the long term (Zuidema *et al.*, 2013).

To quantify the changes in recent radial growth in response to climatic variables such as rainfall, temperature and atmospheric circulation patterns (El Niño-Southern Oscillation) we used chronologies of species that growth at different growth rates on different site conditions. Cross-dating was verified for 30 radii corresponding to 10 *M. scleroxylon* specimens from the dry Chiquitano forest (Roboré), 22 radii in 8 *A. cearensis* specimens from dry Chiquitano forest (San Ignacio), 20 radii in 12 *Cedrela fissilis* specimens from dry Chiquitano forest (Concepción), 57 radii in 30 *Cedrela angustifolia* specimens from Tucuman montane forest (Postrervalle) and 20 radii in 11 *Cedrela fissilis* specimens from Chiquitano transitional Amazonian forest (Guarayos). Although it was possible to estimate a regional moisture deficit or moisture index by integrating temperature and precipitation in a single parameter (López and Villalba, 2011), we assessed these parameters separately for a more detailed analysis of their local variations.

Rainfall

Tree growth variation was explained by rainfall in all the study species and was particularly strongly correlated with rainy season. This is in line with previous dendroecological researches on Bolivian forests (Brienen and Zuidema, 2005a; López and Villalba, 2011; López *et al.*, 2013) where a close relationship between interannual variations in tree growth and local-regional climate were found. Rainfall was also found to be the determinant for the species distribution and diversity in many types of forests (Peña-Claros *et al.*, 2012; Toledo *et al.*, 2011a, 2012; Amissah *et al.*, 2014) and water availability as the main limiting factor in tree growth (Borchert 1994a, 1994b, 1999) even in different forest types with different environmental conditions (Dünisch *et al.*, 2002b; Toledo *et al.*, 2011b; Volland-Voigt *et al.*, 2011).

In the dry Chiquitano forest, *M. scleroxylon* growth was significantly correlated to rainfall during December, January and February (Figure 5, Chapter 2); *A. cearensis* growth significantly correlated with rainfall during October, November and May of the current growth year as well as April of the previous growth year (Figure 6 and 7, Chapter 3); and *C. fissilis* during the rainy season from October to April (Figure 7, Chapter 4). Even *C. angustifolia* from the Tucuman montane forest showed a high correlation from October to April (Figure 9, Chapter 4). However, *C. fissilis* from Chiquitano transitional Amazonian forest showed more sensitivity at the end of the rainy season (March, April and May of the current year; Figure 8, Chapter 4). All seasonal processes, as reproductive period leaf shedding, shoot growth and cambial activity, are strongly inhibited by water stress and hence reflect changes of water within the trees (Borchert, 1994a, 1994b; 1999; Soriano, 2005).

Unfavorable climate conditions, i.e. dry periods of at least two months with rainfall below 50 mm (Worbes 1999), limit cambial activity (Kozlowski, 1971) so that when there is seasonality in rainfall (in alternating periods of dry and rainy seasons) this results in the formation of marginal parenchyma and tree rings boundaries (Eckstein *et al*., 1981; Jacoby, 1989).

Contrary to the findings in the Chiquitano transitional Amazonian forest, the significant positive correlation of *M. scleroxylon*, *A. cearensis*, *C. fissilis* and *C. angustifolia* growth as soon as the rainy season starts suggests that this early reaction may explain the high sensitivity of these species to the change of water availability in tropical dry forest. So that, the decreasing sensitivity in growth to precipitation later in the rainy season may be due to the variability of water stored in the soil (Markesteijn *et al*., 2010) as this gradually increases and critical levels needed to initiate growth are exceeded, hence growth will remain positive regardless of the subsequent amount of rainfall (Brienen and Zuidema, 2005a). The low correlation of growth during late rainy season was also explained by the decreasing photosynthetic capacities of older leaves (Mooney *et al*., 1981; Ackerly and Bazzas, 1995; Kitajima *et al*., 1997) and break of bud dormancy concurrent with rainy season. However, in our study species the latest may vary even in individual trees of the same species in the same sample site.

Variation in ring width related to conditions during the previous growing season of *A. cearensis* from the dry Chiquitano forest and *C. fissilis* from the Chiquitano transitional Amazonian forest (rainfall and temperature, respectively) is attributed to the ability of storing water (Dünisch *et al.*, 2003; Brienen and Zuidema, 2005a), long-term water-table depth or water storage in stem tissues (Borchert, 1994c; Borchert, 1999).

Temperature

Trees response to temperature presented more variation between sample sites than response to rainfall during rainy season. *M. scleroxylon* growth was negatively correlated with mean and minimum temperatures during February and March of the current growth year. Maximum temperatures showed positive significant correlation with previous February and current June; and negative significant correlation with October of the current growth year (Figure 5, Chapter 2). *A. cearensis* growth showed significant negative correlations with maximum temperature during March, April and September of the current growth year and June of the previous growth year (Figure 6, Chapter 3). Although evaluating the effect of a wide range of temperature values, there is a common response where all the above-average temperatures in spring and summer seem to increase water deficit and reduce tree growth; this was evident when findings showed the significant positive correlation of maximum values during autumn-winter (June). This was also the case of *C. fissilis* and *C. angustifolia* (from the dry Chiquitano and Tucuman montane forests, respectively), since growth was more sensitive to low temperatures from May to July, i.e. winter season (Figure 7 and 9, Chapter 4). On the other hand, *C. fissilis* from

Chiquitano transitional Amazonian forest showed more sensitiveness to the rainy months with high temperatures, November to December of the growth year plus the dry months of June and July in the previous year (Figure 8, Chapter 4). It is worth mentioning, that the causes of a positive correlation with maximum temperatures during summer and autumn of the previous year remains unclear as the most of the study species need to be studied more extensively. Fritz (1976) suggested that ring width maybe influenced by processes extending beyond the current growth season.

With all, in contrast to rainfall, tree growth showed a general negative correlation with temperature during the rainy season, these findings evidence the inverse relationship between maximum temperature and rainfall during rainy season, suggesting that inter-annual variation in tree growth is related to water supply which is largely regulated by temperature, i.e., the balance between precipitation and evapotranspiration (López and Villalba, 2011). High summer temperatures, in addition to radiation, increase water pressure deficit and consequently tree transpiration (Bräuning *et al.*, 2008a) which in turn inhibit tree growth (Borchert 1994, 1999; Ferrero and Villalba, 2009; Toledo *et al*. 2011b). This effect was evident in the Chiquitano transitional Amazonian forest, where monthly temperatures and rainfall levels presented the highest values during the period of analysis compared to the other dry Chiquitano sample sites (SENAMHI, 2011).

Our results indicate that trees response more to maximum temperatures, rather than mean and minimum values. Tree growth from dry Chiquitano forest was favored with maximum temperature during autumn-winter but this was hampered when maximum values surpass an apparent range of temperature tolerance as it was the case in the Chiquitano transitional Amazonian forest. The response to low temperatures in the dry season for the species in the dry Chiquitano and Tucuman montane forest do not play the same role as for individuals growing in the Chiquitano transitional Amazonian forest because in the latter, as it is the site with higher temperature values, lower temperatures could rather promote growth due to less stress caused by evapotranspiration.

ENSO

With *M. scleroxylon* we performed further analysis on climate and focused on the effect of ENSO to tree growth (Chapter 2). For this species tree rings, we evaluated the response of growth to El Niño-Southern Oscillation (ENSO) from 1978 to 2009, using two different regions in the Pacific Ocean: El Niño 3.4 (5°N-5°S, 170°-120°W), and El Niño 1.2 (0°-10°S, 90°-80°W); we also used monthly values of the Southern Oscillation Index (SOI).

In general, dry season has apparently been extended and intensified in the last 14 years in the dry Chiquitano forest and it is related with changes in SOI cycles (Figure 2, Chapter 2). With respect to the chronology of *M. scleroxylon*, it showed a general positive correlation with SOI indices during the dry periods of this species and the beginning of the growing season. Oppositely, the response to El Niño 3.4 and El Niño 1.2 regions (negative phase of SOI) for the ENSO in the Pacific Ocean was overall negative (Figure 6B and C, Chapter 2). Also, the analysis of climatic trends and radial growth variability (Figure 2 and 4, Chapter 2) shows that the years 1951-1952, 1963-1964, 1977 -1978, 1986-1988, 2004-2005 and 2006-2007 with high growth corresponds to that of El Niño years with high rainfall events and flooding; and the years 1954-1956, 1964-1965, 1989-1990, 1999-2000 and 2007-2008 characterized as very dry years correspond to that of low tree ring growth and La Niña events. These findings agree with previous affirmations that climate cycles, as ENSO, have influence on local climate (Ropelewski and Halpert, 1987; Grimm *et al.*, 2000) which in turn affects tree growth variability.

It is worth mentioning, that because of the difficulty of dating *M. scleroxylon* tree rings, time consuming and impossibility of dating pith due to the common presence of rot, further climate analysis as climate reconstruction was not possible. On the other hand, despite the correlation of *C. fissilis* and *C. angustifolia* ring width ENSO years, these were not significant hence no further climate analysis was possible. This is in line with previous studies on *Cedrela montana* and *Cedrela odorata* where no significant correlation of growth with climate and ENSO was found (Bräuning *et al.*, 2009; Worbes, 1999). From a broader perspective, differences in correlation between growth and climate suggest that the influence that ENSO exerts on climate and trees behaviors may vary locally (Holmgren *et al.*, 2001; Stenseth *et al.*, 2002; Bowman *et al.*, 2013).

Climate reconstructions

The potential for climate reconstructions was analysed in Chapter 3. For this analysis we counted on complete cross sections of *A. cearensis* and previous studies that confirmed the significant correlation of the species growth with climate (Brienen and Zuidema, 2005a). Although *A. cearensis* chronology spans 223 years for climate reconstruction analysis, we restricted our analysis to the 61-year window based on climate data available and we analysed rainfall data for the 24 months spanning the previous and current growing periods (Septembert-1 to Mayt+1 in the southern hemisphere). This species showed significant positive correlation with rainfall during October, November and May of the current growth year as well as April of the previous growth year but significant negative correlations with maximum temperature during March, April and September of the current growth year and June of the previous growth year (Figure 6, Chapter 3). These results indicate that *A. cearensis* tree rings hold potential for climate reconstruction of monthly rainfall and maximum temperature data during the rainy season but not for minimum temperature which is consistent with the statements about the prominence effect of water availability and maximum temperature (Borchert, 1999; Ferrero and Villalba, 2009; Toledo *et al*., 2011b) previously explained.

Effect of internal and external conditions on tree growth

Disentangle the degree of importance factors affecting tree growth is complex as many interactions of the variables are present (Reifsnyder *et al*., 1971; Meentemeyer and Box, 1987). These interactions and wide range of environmental influences within a forest stand could have resulted in high growth variations between our study species and individually.

For example, for assessment of climatological analysis on tree rings, during the cross dating of our species, eccentricities clearly affected not only the distribution of the tree rings in the transversal surface but also our measurements data. It is common in tropical forest species (Sousa *et al*., 2012; Paredes-Villanueva *et al*., 2013) as can also be present in some temperate genera (Brookhouse and Brack, 2008). Eccentricity can be caused by gravity compensation by trees on steep slopes and bending stresses caused by high wind (Gartner, 1995; Schweingruber, 1996) or landslides (Schmid and Schweingruber, 1995). This may be the cause of tree rings variation on *A. cearensis* and *Cedrela* species as they present cylindrical trunk in general (Mostacedo *et al.*, 2003). This may not be the case of *M. scleroxylon* as this species seems to intrinsically present spiny and usually fluted trunk halfway and cylindrical in the upper trunk (Justiniano and Fredericksen, 1998). However, the pit rot in *M. scleroxylon*, which also affected tree ring dating, was found to be caused by fungal infestations promoted by forest fires at early stages of young seedlings (Justiniano and Fredericksen, 1998). In all our study species in general, the irregular diametric of tree rings caused by eccentricities were manifested through wedging rings and lenses which hampered the cross dating and measurement of tree rings. Lenses are known as growth in certain sectors of the circumference of a tree due to the stimulus in cambial activity and/or vascular growth during the annual cycle (Villalba, 1997; López, 2003), this, for example, restricted us to analyze just 30%-70% of the radii from bark to pith in *M. scleroxylon* and discard 33% of the series of *A. cearensis* measured samples.

Phenological behaviour may partly explain growth correlation with climate for our deciduous species (Borchert, 1994a). *Cedrela* species and *A. cearensis* are deciduous and *M. scleroxylon* is considered of semi deciduous habit (Mostacedo *et al.*, 2003), and since the existence of annual rings is more common in deciduous species than those in semi deciduous or evergreen species (Borchert, 1999; Worbes, 1999) as a response to drought (Medway, 1972; Alvim and Alvim, 1976), the intermediate characteristic in dominance within the forest and abscission of leaves of the later species, may have affected the on formation of tree rings which in turn affected the inter-tree correlation and further relationship with climatic data. In addition, the deciduous species *A. cearensis* with bud dormancy break matching early rainfall (October-November) in our study confirmed this hypothesis.

On the other hand, if a decreasing growth along the rainy seasons is present, as *C. fissilis* decreasing growth from March to May in Chiquitano transitional Amazonian forest (Figure 8, Chapter 4), may be due to the gradually decreasing photosynthetic capacities of older leaves (Mooney *et al.*, 1981; Ackerly and Bazzas, 1995; Kitajima *et al.*, 1997) as the leafless period approaches (Bräuning *et al.*, 2008b) and changes in the hydrological status of the stem rather than cambial activity taking place (Bräuning *et al.*, 2009; Dünisch *et al.*, 2003).

Designating water availability for storing in stem and use it for flowering and fruiting during the coming dry season (Reich and Borchert, 1984), as the case of the medium density wood of *Cedrela* (Worbes, 1999) may not only affect the current gradual decreasing growth of correlation with rainfall but also express the relationship of the current with the previous growth year and vice versa. It has been found that the ability of the species to store water or photosynthates produced during the late growth season can affect growth of the following year earlywood so that climate signal may be mixed from one year to another (Jacoby and D'arrigo, 1990). Therefore, species specific growth strategies, as the storage of water reserves on stem (Brienen and Zuidema, 2005a; Dünisch *et al.*, 2003) and access to long-term water-table depth (Borchert, 1994c), may explain the differences of response to environmental conditions and the high correlation of growth with previous growth year rainfall in April for *A. cearensis* and December-January for *C. fissilis* growth from dry Chiquitano forest (Figure 6, Chapter 3 and Figure 7, Chapter 4 respectively) and previous growth year mean temperature in June and July for *C. fissilis* from the Chiquitano transitional Amazonian forest (Figure 8, Chapter 4). Thus response to previous rainy season in the dry Chiquitano forest may point the long-term stem water storage (Borchert, 1994c) and formation of food reserves on wood to mobilizing them in the following year (Höll, 1985; Sauter, 2000; Dünisch and Puls, 2002).

In addition to the variation of growth caused within trees, a wide range of non-climatic factors (Brookhouse, 2006) and their interaction in micro site ecological conditions may play an important role of our study species and may have influenced on growth variations. Light availability is also one of the most important factors for growth and establishment of our species from the dry forest of Chiquitanía (*A. cearensis*, *M. scleroxylon* and *C. fissilis*), since most species are codominant in relation to the position of the tree canopy (Killeen *et al*., 1998). The shade tolerance, eventual canopy emergence and high sensitivy along the first years of growth were expressed by the low correlation on trees of small diameters on *A. cearensis* and older tree rings in *Cedrela* samples (Figure 5, Chapter 3 and Figure 4, Chapter 4, respectively). Tree-specific light availability can largely limit tree development (Brienen *et al.*, 2010) and forest dynamics, especially for light-demanding canopy species (Brienen and Zuidema, 2006) and those from the moist forest, as our samples from the Chiquitano transitional Amazonian forest, where bigger gaps and longer time for their closure are required compared to those in the dry forest where amount of direct light received in the forest floor may be higher (Brienen *et al.*, 2010). However, the degree on positive growth responses to the clear openings may depend on climatic conditions, e.g. with decreasing temperature in dry and moist forests, since an increased respiration or drought stress caused by high temperatures may affect to photosynthesis rates (Clark *et al.*, 2003; Fichtler *et al.*, 2004; Feeley *et al.*, 2007) and consequently cause a decrease in tree growth (Brienen *et al.*, 2010).

Besides light and tree crown position, lianas infestation was found to be influencing tree growth (Putz, 1991). Growth from permanent plots in Bolivia showed increments when trees received more light and presented fewer lianas infestation (Mostacedo *et al.*, 2009). Previous studies have found that tropical dry forests in Bolivia presents from 50% to 80% of lianas infestation (Carse *et al*., 2000; Uslar *et al*., 2003; Toledo *et al*., 2008b) and that rainforest were below 50% (Toledo *et al*., 2008b) and that this values showed an increasing trend due to climate change that negatively impact on tree growth (Phillips *et al*., 2002;

van der Heijden and Phillips, 2009). Therefore, its great abundance in the dry Chiquitano forest where more of our samples were collected may have also affected growth variability.

The dynamic of water in the soil also contribute to growth which can start decreasing during dry season when soil water potential reaches its permanent wilting point (Franco, 1979; Worbes, 1999) or even during rainy season when water stored in the soil gradually increases and critical levels needed to initiate growth are exceeded (Brienen and Zuidema, 2005a). Furthermore, the topographical gradient with water in different soil layers may influence on how a species responds based on their root system since the surface of the dry Chiquitano forest soil is drier than the deep part during dry season but wet in rainy season (Markesteijn *et al*., 2010), suggesting that the surface layer is more vulnerable to extreme fluctuations, so if the tree roots were superficial these changes could also affect growth. This may be the case for *Cedrela* root system as they are characterized of being in the upper soil layers (Noldt *et al.*, 2001) and have previously demonstrated their prompt response to rainfall (Dünisch *et al*., 2003) when it was <5mm (Worbes, 1999). After rainfall (water availability), soil characteristic and nutrients seems to affect on growth (Medina, 1995; Mooney *et al.*, 1995; Oliveira-Fihlo *et al.*, 1998; Toledo *et al.*, 2011b) specially of the dry forest spatially progressing (Murphy and Lugo, 1986; Mooney *et al.*, 1995; Ceccon *et al.*, 2006) and shifting to light conditions in wetter forests, i.e. being *Cedrela* a light-demanding canopy tree (Engelbrecht *et al.*, 2007; Brienen *et al.*, 2010) this may explain the growth variation in the Chiquitano transitional Amazonian forest. With respect to nutrients, K content on soil showed to influence water uptake for photosynthesis process in *Cedrela* species from the Amazon forest (Dünisch *et al.*, 2002b), dry Chiquitano forest was found to have higher K content than Chiquitano transitional Amazonian forest (0.38 cmol/kg and 0.30 cmol/kg respectively; Peña-Claros *et al.*, 2012); this may support our findings with *C. fissilis*, with 2.07 mm/year and 1.92 mm/year for each region respectively. However the opposite situation was observed in Tucuman montane forest where K content was the lowest 0.026 cmol/kg but growth was the highest with 2.82 mm/year. Adaptation to poorer soils and changing soil water contents was found to vary among species of Meliaceae family (Dünisch *et al.*, 2002b).

Throughout this thesis, we have tried to disentangle the effect of each environmental and climatic variable on tree growth, however when trying to explain the effect of only one of them it has not been possible to avoid including the effect of other variables because they exhibit high interaction either directly or indirectly to influence tree growth.

Methodological aspects and interpretation of data

Dendrochronology offers the advantages to reconstruct and quantify climatic or ecological events even when millennia have passed (Esper *et al*., 2007; Cook *et al.*, 2010; Li *et al.*, 2013, Nehrbass-Ahles *et al.*, 2014). The presence of demarcated growth rings is a well-defined feature on the wood of most trees and shrubs that grow in temperate and cold regions (Villalba *et al.*, 1998). In regions with cold and temperate climates cambial activity is generally regulated by photoperiod (light hours) and temperature. In spring, there is a rapid flow of growth hormones which stimulates the production of early woody elements. As the growing season passes apical growth ceases, there are changes in the synthesis of hormones and the formation of characteristic elements of the late wood begins. At the end of the summer, cambial tissue enters dormancy and lies dormant until next spring (Jacoby, 1989).

Limitations of tree-ring analysis

Tree ring analysis was not commonly applied in the tropics due to general perception that many woody species of the world's tropical and intra-tropical forests, such as Bolivia's, do not form distinct growth rings (Eckstein *et al.*, 1981). The rationale for this argument is the belief that cambial activity does not vary throughout the year (Dave and Rao, 1982; Borchert, 1999; Lang and Knight, 1983). These assumptions discouraged and limited the application of dendrochronology to other type of forests (Lang and Knight, 1983). Nevertheless, in the last decade it has become clear that local climatic variability in tropical regions is sufficient to permit the formation of annual rings in endemic species (Worbes, 1999; Brienen and Zuidema, 2005; Ferreira *et al.*, 2009). Worbes (1995) identified rainfall, temperature and flooding as factors determining cambial activity in tropical forests. If well defined seasonality is not present this may also affect the distinction of annual tree rings (Jacoby, 1989). The climate sample sites in this thesis, presented seasonality which led us to assume that our species form annual rings. Dendrochronological methods used in this thesis were based on the tree ring analysis of four tropical species: *Machaerium scleroxylon* (Chapter 2), *Amburana cearensis* (Chapter 3), *Cedrela fissilis* and *Cedrela angustifolia* (Chapter 4). For *Amburana cearensis* and *Cedrela* species, we relied on previous studies that identified and proved the annual ring formation (Worbes; 1999; Dünisch *et al.,* 2002a; Brienen and Zuidema, 2005a; Bräuning *et al.*, 2009). However, for *Machaerium scleroxylon* we performed anatomical cross dating and tree rings/climate relationship analysis to confirm its annual nature.

The presence of false rings, wedging rings and lenses (López, 2003) were common in all species which besides hampering the identification and measurement of tree rings required more time and effort. In addition, missing rings could also affect tree ring identification and dating, when trees living near the environmental limit of their range, as *C. fissilis* from Chiquitano transitional Amazonian forest, form a partial ring during stressful years (Norton *et al.*, 1987), if only a radii/core is analyzed this rings may be missing. However, the use of complete cross sections or multiple radii across the stem my help to overcome this problem.

These variations on site’s correlations might be due to the number of samples as well as the specific site conditions. The role and significance of microclimate vary widely among forests, ecosystems over time and under different weather conditions (Reifsnyder *et al.*, 1971) as functions are scale dependent (Meentemeyer and Box, 1987) and have cumulative effects (Chen *et al.*, 1999). For assessing short-term growth variation, spatial variation in climate and elevational gradients should be taken into account (Corlett, 2011). On the other hand, for assessing long-term growth variation, the cumulative effects can be understood through the analysis of dynamic stage and stand history of a species (Brienen *et al.*, 2010) as recovery from past disturbance may lead to apparent growth trends over time (Vlam, 2014).

Growth trends

Understanding global change drivers and their relation with future dynamics of tropical forests is to date limited which prevents us to inform adaptation policies with reliable information to develop effective adaptation strategies (Corlett, 2011). For example, in a recent study through stable isotopes, van der Sleen (2014) found that elevated atmospheric CO_2 does not lead to a stimulation of tree growth opposite to the general assumptions that a CO_2 fertilization may be reflected in an increasing growth trend (Cox *et al.*, 2013; Huntingford *et al.*, 2013).

In addition, interpretation of observed growth trends in tropical trees should be made with caution as the real causes can be masked due to sampling biases resulting in misleading inferences about the effect of environmental global changes (Bowman *et al.*, 2013). The classical dendrochronology sampling includes only dominant individuals (Briffa *et al.*, 1998) which may cause the “slow grower survivorship bias” and “big-tree selection bias” and result in strong historical increases. The former is caused by differences in tree longevity of fast and slow growing trees within a population. If fast-growing trees live shorter, they are underrepresented in the oldest part of the chronology. The later is caused by sampling only the biggest tree in a population resulting in an underrepresentation of slow-growing small trees in recent times as they did not reach the minimum sample diameter (Brienen *et al.*, 2012a). However, the detrendings and standardizations used in this thesis are expected to remove the variations caused by age and size (Cook, 1985; Cook and Holmes, 1986; Brienen *et al.*, 2012a). STD version removes effects of endogenous stand disturbances to enhance the common signal contained in the data while ARS contains the persistence common and synchronous among a large proportion of series from the site, without including that found in only one or a very few series (Cook, 1985). It is intended to contain the strongest climatic signal possible or low frequency signal (Cook and Holmes, 1986).

Increasing the number of samples for each site may not be enough to improve the interpretation of long-term growth (Bowman *et al.*, 2013). By including long-term records with different ages and sizes of samples, we can minimize this effect (Cherubini *et al.*, 1998; Bowman *et al.*, 2013). In this regard, Brienen *et al.* (2012a) recommended trees sampling of smaller size classes, including samples from non-living trees and taking care in the interpretation of historical growth rate patterns based on tree rings, as the current living trees represent only a subset of the original in a population. For our study, the collection of dominant trees was limited by access and abundance of trees. However, because the co dominant trees are those with greater abundance in the dry Chiquitano forest, our results provide significant insights for the area. The causes of increasing growth trend of trees at longer time scales remains discussed but possibility of extending chronologies opens greater opportunity to analyze the long-term drivers.

Local availability of climate data

Not only irregularities and frequencies of measurement of data but also the accuracy of the given climatic data restricted the analysis of our chronologies. Many zones in Bolivia lack continuous, publicly-available meteorological data, however, once annual growth shows significant correlation with climate, like *A. cearensis*, tree rings hold high potential for the climate reconstructions offering an alternative source for climatological data to support ecological and forest management studies.

Longer chronologies and potential for climate reconstructions are also possible with *Cedrela* which can substantially become older (Brienen and Zuidema, 2005a) and can be found along different climatic and environmental gradients (Mostacedo *et al.*, 2003; Aguirre *et al.*, 2011; Navarro, 2011; Navarro-Cerrillo, 2013; Cavers *et al.*, 2013).

Permanent plots

Permanent plots offer limited possibilities to relate tree growth (biomass) changes with climatic variation because of the low frequency of measurements (aprox. each 5 years) and site changes in biomass are species specific and challenging when interactions with other species are present (Zuidema *et al.*, 2013). Despite the general high growth rate values presented by the permanent plots in comparison to our tree ring data. It is important not to detract from the valuable information they provide. An advantage is that interval of growth measurements are known precisely and provide growth rates from the time they are established (Bowman *et al.*, 2013) and could therefore well supplement to the lifetime-span information provided by tree rings.

Forest management and possible climatic changes in the region

Forest management implications

Since diameter is a poor indicator of tree age (Harper, 1977; Sarukhan *et al.*, 1984; Stahle *et al.*, 1999) many studies have tried to eliminate age-related long-term size and climate-related growth biases by using radial-growth averages (Nowacki and Abrams, 1997), but the use of the mean or median tends to overestimate the age of trees (Brienen and Zuidema, 2006a). This thesis covered a wide distribution of timber species, from tropical dry forest to montane forest providing insights into radial tree growth through the analysis of tree rings. As expected, growth varied among sites. *M. scleroxylon* species has an annual increment of 1.43 mm year^{-1} and *A. cearensis* had 5.75 mm yr^{-1} (dry Chiquitano forest); *C. fissilis* from 1.92 to 2.07 mm year^{-1} (Chiquitano transitional Amazonian and Chiquitania forests respectively) and *Cedrela angustifolia* of 2.82 mm yr^{-1} (Tucuman montane forest). Growth rates varied en relation to climate and site-specific environmental conditions. These results have important implications for forest management since the current Bolivian Forestry Law applies general estimations and rules for management of different species and sites that may have long-term consequences on the low growing species sustainability.

Based on age and cumulative ring-with data, the estimated growth rates indicate that a greater MLD and optimal cutting rotation are required. Bolivan forest regulations suggest a general MLD of 45 cm diameter for *Amburana cearensis* from dry Chiquitano forest, 60 cm for any *Cedrela* species in all type of forests and even *Machaerium scleroxylon* is mentioned as “other species” with 40 cm for dry Chiquitano forest (Normas Técnicas 136, 1997) at breast height (DBH) with a minimum cutting cycle (20 years) recommended by the Technical Standards of the Forestry Act 1700 in Bolivia (MDSP, 1998). However, the positive growth in diameters trends indicates that a greater MLD should be considered in forest management plans for our study species. The optimal period to harvest the trees is at the peak of the current volume increment (Schöngart *et al.*, 2007; López *et al.*, 2013), that is when *M. scleroxylon* trees have a biological rotation age greater than 140 years which corresponds to a DBH of 50 cm. López *et al.* (2012) also found that *Cedrela fissilis* from the transitional Amazonian forest initially presented a maximum rate of 2.91 cm año^{-1} during the first 40 years of growth but latter decreased to 0.51 cm año^{-1} and *Amburana cearensis* from the dry Chiquitano forest varied from 1.93 to 0.22 cm año^{-1} over a period of 100 years. Tree diameter at the maximum current volume increment seems to indicate the preferred time for logging (Stahle *et al.*, 1999; Brienen and Zuidema, 2006b).

The cutting cycle until the tree reaches the required MLD exceeded that recommended by the forest regulations depending on each individual tree (Brienen and Zuidema, 2006a, 2006b; López *et al.*, 2012, 2013). It is worth mentioning that, from an economic point of view, in addition to silvicultural treatments, pith rot should be taken into account for a more feasible MLD determination. Our results are based on the mean diameters of the samples of different sizes but in many cases it was not possible to date central rings, especially in the case of *M. scleroxylon* species which presented pith rot area (60% of samples), still they provide useful insights of growth rates and behavior across different sites. Given that tropical dry forests in Bolivia presents high lianas infestation (Carse *et al.*, 2000; Uslar *et al*., 2003; Toledo *et al*., 2008b), one specific-site silvicultural treatment for this region could be liana cutting (Peña-Claros *et al*., 2008; Verwer *et al*., 2008; Villegas *et al*., 2009; Toledo, 2010) to promote tree growth for future harvesting.

Climate change and local variability

In this thesis we also analyzed the annual variability of growth in relation to climate. Based on the Roboré climatological station and ombrothermic analysis alone, rainfall in the dry Chiquitano forest has showed an overall decline during the second half of the 20th century, whereas the temperature increased between 1°C to 2°C from the mean in the period 1978-2009 (Figure 2, Chapter 2) showing a trend towards aridification since the 1970s consistent with previous findings in different Bolivian types of forests (Brienen and Zuidema, 2006a; López and Villalba, 2011). Similar results were also found by Toledo (2010) with increasing trend of temperature and decreasing trend of precipitation during the last 30 years in the lowlands of Bolivia.

In addition, dendroclimatological analysis based on *A. cearensis* ring width demonstrated that climate reconstructions are possible for the dry Chiquitano forests and that this may contribute to fill the gaps of information caused by the lack of reliable climatological data obtained from instrumental measurements. Thus, the interannual and decadal variations in our analysis suggest that changes in climate are affecting tree growth; however, despite the clear local climate change showed by instrumental climatological data, to make long-term inferences by using tree ring data, the short span of our chronologies limits the conclusions that maybe drawn about climate change. For long-term inferences it is necessary to count on larger chronologies. In general, excluding the limiting effect of other environmental site-specific factors, if precipitation is decreasing, tree growth may also reflect decreasing trends. While, if long term changes are to be analyzed the influence of the dynamic stage of the forest and life strategy of the species, i.e. the age and history of the forest and life strategy and light competition of the understorey species

(Worbes, 1999; Brienen *et al.*, 2010) should be taken in to account; using the information of forest disturbances and isotopic composition on tree rings may contribute to this aim.

Transitional ecosystems, as our study sites, are more likely to be impacted by climate change as many species are at the extreme limits of their ecological requirements (Killeen *et al.*, 2006) and more when environmental complex interactions are present (Reifsnyder *et al.*, 1971; Meentemeyer and Box, 1987) which were clearly visible in Chiquitano transitional Amazonian forest through *Cedrela fissilis* tree-ring analysis. Given the high influence of climate on tree distribution (Peña-Claros *et al.*, 2012; Toledo *et al.*, 2011a, 2012; Amissah *et al.*, 2014) and growth assessed in this study, if rainfall trends change, the distribution of individual species will change (Toledo *et al.*, 2012).

The velocity of the biochemical reactions during photosystensis, like Mg and K indispensable for the synthesis of glucose (Küppers *et al.*, 1985; Marschner, 1995), is temperature dependant (Rosenthal and Camm, 1997). There is a variation on assimilates loss by respiration among species (Stockfors and Linder, 1997; Pathre *et al.*, 1998), although not significant differences were present, the variation in response and growth of the same species from the Chiquitania and Chiquitano transitional Amazonian forests (2.07 and 1.92 mm year^{-1}, respectively) this may indicate the importance of the temperature role on tree development. For example, *Swietenia macrophylla* (corresponding to the same family as *Cedrela* species) showed lower ecological amplitude and higher sensitivity to unfavourable micro site conditions which was attributed to the ecophysiology of the species, i.e. light, water and nutrients demand for the net photosynthesis and the biomass production (Dünisch *et al.*, 2002b; Dünisch *et al.*, 2003).

Tree ring analysis yield not only lifetime growth information but also physiological responses to environmental changes over long periods and at annual resolution (Zuidema *et al.*, 2012). Vulnerability to warming for a species depends to physiological limits (Deutsch *et al.*, 2008; Hoffmann, 2010). Therefore, the ecophysiology and ecological amplitude may also explain the lower growth of *Cedrela fissilis* in Chiquitano transitional Amazonian forest given that this site presented greater levels of annual rainfall and higher temperatures in comparison to the dry Chiquitano forest sites. Other plot and tree ring studies also reported reduced diameter growth with low rainfall and high temperatures (Clark *et al.*, 2003; Rozendaal and Zuidema, 2011; Dong *et al.*, 2012). It is also worth mentioning that *Cedrela angustifolia* samples were found in the altitudinal ranges between 1700-2200 m.a.s.l. On the other hand, although *Cedrela fissilis* is distributed over a wider range of ecosystems our results indicate that the growth and development of this species is restricted to 200-400 m.a.s.l. in the Chiquitano transitional Amazonian forest and 600 m.a.s.l. in the dry Chiquitano forest. This strongly supports our findings that the study species may have a thermal limit for performance and growth.

Temperature plays an important role in determining species' range limits (Grinnell, 1917; Crozier and Dwyer, 2006; Sheldon *et al.*, 2011). Sheldon *et al.* (2011) explained that "thermal tolerance, the range of temperatures over which an organism can function (Angilletta, 2009), should be strongly influenced by the variation in environmental temperatures species experience (Janzen, 1967; Gaston and Chown, 1999; Ghalambor *et al.*, 2006). Vapor pressure deficit increases water stress even when rainfall values remain constant (Corlett, 2011). Species that evolve in areas with little environmental temperature variation, such as the tropics, tend to be thermal specialists and have relatively narrow thermal tolerance. In contrast, species that evolve in areas with high environmental temperature variation, such as the temperate zones, are thermal generalists with broad thermal tolerance (Sunday *et al.*, 2011). Thermal specialists should be especially vulnerable to climate change (Ghalambor *et al.*, 2006)". They also suggested that tropical forests may have limited shift of their thermal tolerance since temperature rate changes are shorter with elevational gradient than latitudinal, as may be the case of the lowland forests in Bolivia. With all, given the greater specialization, biotic closer interactions (Schemske *et al.*, 2009) and competition (Worbes, 1999; Brienen *et al.*, 2010) in the tropics, a unique response by species may also be possible according to the multiple stressors (or limiting factors) to which trees are exposed varying in time and space at different scales (Helmuth, 2009). That the same species (*Cedrela fissilis*) have reacted different (growth) in different sites can be a sign of their vulnerability due to their physiological limits in relation to temperature.

Areas for future research

If global temperatures continue to rise, as projected under most climate scenarios (IPCC, 2007), even high-latitude species will experience decreased performance as temperature exceed their optimum ranges but the shift response may be constrained by physiological and ecological tradeoffs (Davis *et al.*, 1998; Deutsch *et al.*, 2008). The analysis of growth for specific forest types gives us insights into the effect of local climatic variables on growth and the analysis on *Cedrela* allowed us to consider in this range of variables the physiological sensitivity of this species to temperature changes and it suggests possible tolerance ranges. From the *Cedrela*'s low growth in the Chiquitano transitional Amazonian forest we could deduce a negative impact of increasing temperatures; however deeper analysis is required to that respect. Through the analysis on this thesis, we have tried to mention the possible causes of variation in tree growth, however, determining which factor is more important and when requires more specific analysis for each site.

Climate and growth relationship were investigated using tree rings of hard and soft valuable timber. Clearly site-specific conditions affected growth further demonstrated by low inter-tree growth and inter-site correlations. Combining tree rings with ecophysiological analysis to assess climate-induced range shifts across different type of forests in Bolivia will be useful to link species sensitivity with geographic patterns of the temperature change magnitude.

Annual nature of *Machaerium scleroxylon* and *Cedrela angustifolia* were confirmed through tree rings analysis. For those species on sample sites where climatic data is not available, by matching ^{14}C measurements in dated tree rings, the annual nature of tree rings can be evaluated. The use of stable isotopes can also help when non clear tree ring boundaries or difficulties on tree dating (false, wedging rings, lenses and missing rings) are present.

The high visibility of *A. cearensis* and *Cedrela* species hold a great potential for longer climate reconstructions. On the other hand, although *M. scleroxylon* analyzes limited 30%-70% of the dated radii from bark to pith, this shows the long lifespan of the species and hence the potential for constructing larger series and chronologies. However, if we are to prioritize, the relationship between ecological variables and growth are urgently needed for an appropriate management planning. The harvesting taking place at a managed forest may increase the opportunities to obtain complete cross sections. So, the findings about annual nature on many tropical species may be encouraging to continue exploring the dendrochronology potential to meet the need of knowledge on the ecology and growth of timber species which can contribute to establishing more accurate guidelines and best execution of forest management. Our findings suggest that careful studies of tree age, size, and environmental conditions could produce useful volume and yield information for species ecological settings and may contribute to sustainable forest management.

Chapter 6

General Conclusions

The outstanding conclusions for our study species and their relationship with climate and environmental factors are as follows:

1. Annual temperature has increased and rainfall has decreased in southeastern of Chiquitano forests during the twentieth century, leading to a long-term reduction in water availability and water stress in trees, which is expressed in the variation of tree-rings width.

2. The annuity formation of tree rings were confirmed for two new species: *Machaerium scleroxylon* and *Cedrela angustifolia*; and their first chronology were successfully developed. *Machaerium scleroxylon* had an annual increment of increment of 2.37 mm year^{-1} and *Cedrela angustifolia* of 2.82 mm yr^{-1} which unlike the former took less time and effort when identifying and dating tree rings.

3. All the samples analyzed in this thesis presented lenses, false and wedging rings due to eccentricities in tree growth.

4. Despite the dating difficulties, the chronologies for each species and site showed a common signal. Growth was mainly explained by precipitation during rainy season which was regulated by variations of temperature.

5. The growth response to atmospheric circulation patterns varied across study sites. *Machaerium scleroxylon* showed significant correlation with El Niño-Southern Oscillation while *Cedrela* species showed not significant correlations.

6. The further analysis on climate-growth relationship in *Amburana cearensis* revealed a potential for climate reconstruction especially for monthly rainfall and maximum temperature during rainy season in Chiquitania region.

7. The relatively low correlations between different individuals of the same species and sites and between growth and climate suggest there may be other important factors influencing tree growth.

8. Local environmental conditions may play an important role on the growth variations of the study species. The variations in response to climate and environmental conditions suggest that forest guidelines and management should be appropriate to the species and local context.

9. Tree-ring analysis provided insights into the ecology of *Machaerium scleroxylon*, *Amburana cearensis*, *Cedrela fissilis* and *Cedrela angustifolia*. The dendrochronological potential of many tropical species offers an opportunity of the determination of Minimum Cutting Diameter and cutting cycle adequate for each species.

10. The growth-climate relationships observed in tree rings also represents an opportunity to reconstruct climate data especially for those areas in Bolivia where publicly- meteorological information are limited.

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Anexes

Annex 1: Complemmentary physico-chemical analysis of soil done for the Tucuman montane forest in Postrervalle, Bolivia.

Soil texture characteristics	
Sand (%)	72
Silt (%)	21
Clay (%)	7
Humus (%)	8.71
Soil chemical characteristics	
pH	5.7
Cation exchange capacity (meq/100g)	2.59
Electrical conductivity (mmohos/cm)	0.372
N (ppm)	4616
P (ppm)	11
K (ppm)	10
Ca (ppm)	300
Mg (ppm)	61
Na (ppm)	20
Sum. Cat. (meq/100g)	2
Sat. Bases (%)	82