UNIVERSITAT DE BARCELONA

Impacts of climate and drought on tree radial growth in Neotropical dry forests: scaling up from short to long time-scales

Impactos del clima y las sequías en el crecimiento radial de los árboles en los bosques secos Neotropicales: Evaluación de sus efectos a diferentes escalas temporales

Hooz Angela Chaparro Mendivelso

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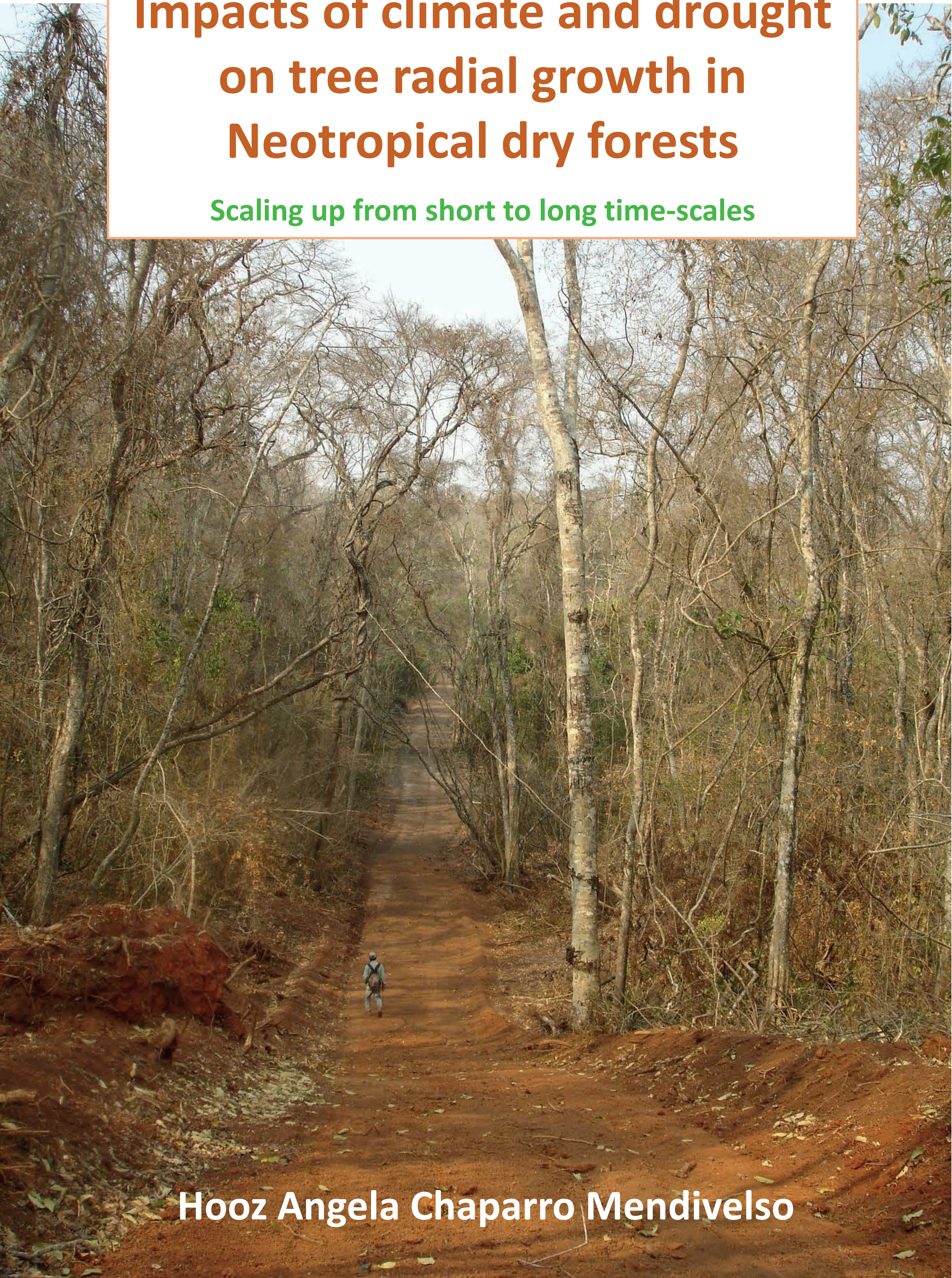

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Impactos del clima y las sequías en el crecimiento radial de los árboles en los bosques secos Neotropicales:

Evaluación de sus efectos a diferentes escalas temporales

Memoria presentada por Hooz Angela Chaparro Mendivelso para optar al grado de doctora por la Universidad de Barcelona.

Programa de Doctorado: Ecología Fundamental y Aplicada.

Este trabajo se realizó en el Instituto Pirenaico de Ecología (IPE-CSIC) bajo la dirección del Dr. Jesús Julio Camarero (Instituto Pirenaico de Ecología, IPE-CSIC) y del Dr. Pieter A. Zuidema (Wageningen University) y la tutoría de la Dra. Emilia Gutiérrez Merino (Universidad de Barcelona).

Doctoranda	Director	Codirector	Tutora
Hooz A. Chaparro M.	J. Julio Camarero	Pieter A. Zuidema	Emilia Gutiérrez

A mis cuatro amores:
Osana, Angel, Jeffer y Chema

Contents

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Al finalizar el trabajo de laboratorio en el IPE y con dos artículos publicados bajo el brazo, migré de Zaragoza a Barcelona para terminar de escribir la tesis. En esta última ciudad, fui bien recibida por la Universidad de Barcelona gracias a las gestiones realizadas por mi tutora. Durante esa época, tuve la oportunidad de realizar una estancia con el grupo de investigación “Forest Ecology and Forest Management” en la Univesidad de Wageningen (Países Bajos). Agradezco al programa COST Action, FP1106, STREeSS, por la financiación de mi estancia, como también al director del grupo, Dr. Frits Mohren, y a todos sus miembros por hacerme sentir, desde mi llegada, como uno de los suyos. Doy gracias a mis dos supervisores, la Dra. Ute Sass-Klaassen y el codirector de esta tesis, por todo el conocimiento trasmitido sobre la dendrocronología y la demografía de especies tropicales, respectivamente. A Merel Jansen (estudiante de doctorado), por su asesoría en la construcción de modelos demográficos en R. Además de todo el conocimiento que recibí por parte de ellos, el participar en las múltiples actividades académicas organizadas por este grupo de investigación, hizo que mi estancia fuera muy productiva para mi vida académica.

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Hooz Angela Chaparro Mendivelso,
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Chapter 1


Sunset of the Chiquitano tropical dry forest during dry season (Bolivia)

General Introduction

Tropical dry forests: global distribution, socio-ecological importance and threats

Tropical dry forests (hereafter TDFs) are a type of vegetation dominated by tree species with leaf habits from deciduous to evergreen (Eamus, 1999); TDFs grow in the lowlands of the intertropical zone of America, Africa and Southeast Asia, and in countries such as Australia and India (Miles et al., 2006), where the mean annual temperature is > 20 °C (Murphy and Lugo, 1986), the total annual precipitation is ≤ 2000 mm, and there is a strong dry season (≤ 8 months) with a monthly precipitation < 100 mm (Table 1). The latitudinal distance to the equator determines the duration of dry season. Thus, TDFs near to the equator show the shortest and least severe dry season than TDFs next to both Tropic of Cancer and Capricorn (Murphy and Lugo, 1986). In general, TDFs have smaller trees (height and diameter) that leave an open canopy, and tree richness is lower than in tropical rain forests (Murphy and Lugo, 1986).

As a whole, TDFs and other kind of forests belonging to the tropics, play a key role in the global carbon cycle. Specifically, Pan et al. (2011) estimated that almost 50% of the global forest biomass C sink for the period 1990-2007 is from relatively undisturbed tropical forests (2.4 ± 0.4 Pg C year^{-1}). Furthermore, TDFs provide several ecosystem services, such as water and climate regulation, nutrient cycling and soil stabilization (Pizano and García, 2014). On the other hand, TDFs offer numerous products to millions of people that depend directly or indirectly on this ecosystem, such as wild fruits, nuts, edible insects, bushmeat, beeswax, honey, wood for timber export and charcoal making (Blackie et al., 2014).

TDFs cover almost 105 Mha (c. 0.7%) of the Earth's landmass (Miles et al., 2006), this correspond to less than 50% of their original extent (Hoekstra et al., 2005), as consequence of widespread deforestation and degradation by human activity (Janzen, 1988), and limited habitat protection (Hoekstra et al., 2005). Miles et al. (2006) estimated that almost 97% of the TDFs are at risk from one or more of the following threats: climate change, habitat fragmentation, fire, human settlement and its transformation into cropland. Thus, TDFs are considered the most threatened major type of tropical forest (Janzen, 1988). Given this negative panorama, researchers have proposed establishing new protected areas for TDFs as well as finding ways to mitigate human impact and protecting the remaining TDFs and their biodiversity (Janzen, 1988; Miles et al., 2006; Songer et al., 2009). Historically, large TDF areas have been deforested, transforming them into farmlands and grasslands, while other TDF areas has been degraded through logging of valuable timber species, firewood extraction and fires (Fig. 2). For instance, the selective logging of *Amburana cearensis* and *Cedrela fissilis* (two of the 14 species studied in this thesis) has caused a critical reduction of their populations. Currently, both tree species are endangered (IUCN, 2016).

Table 1. Climatic conditions in tropical dry forests (TDFs) around the world registered by several authors. Empty cells mean that there is no information about the variable.

Total annual precipitation (mm)	Dry season (months)	Monthly precipitation in dry season (mm)	Reference
250 - 2000	1-8		Murphy and Lugo (1986)
<1600	5-6	<100	Gentry (1995)
600-1700	2-7		Eamus (1999)
<2000	≥ 4	<100	Dirzo et al. (2011)

This thesis focus on Neotropical TDFs, which represent the largest area of TDFs, with almost 52 Mha (Portillo-Quintero and Sánchez-Azofeifa, 2010). Nevertheless, the deforestation and degradation in some of their regions and countries have caused a critical state of fragmentation. For instance, Venezuelan TDFs occupy almost 10% of their potential extent coverage (Fajardo et al., 2005), and Mesoamerican TDFs (southern Mexico and Central America) occupy less than 2% of their original area existing when Spaniards arrived in the Americas (Janzen, 1988).

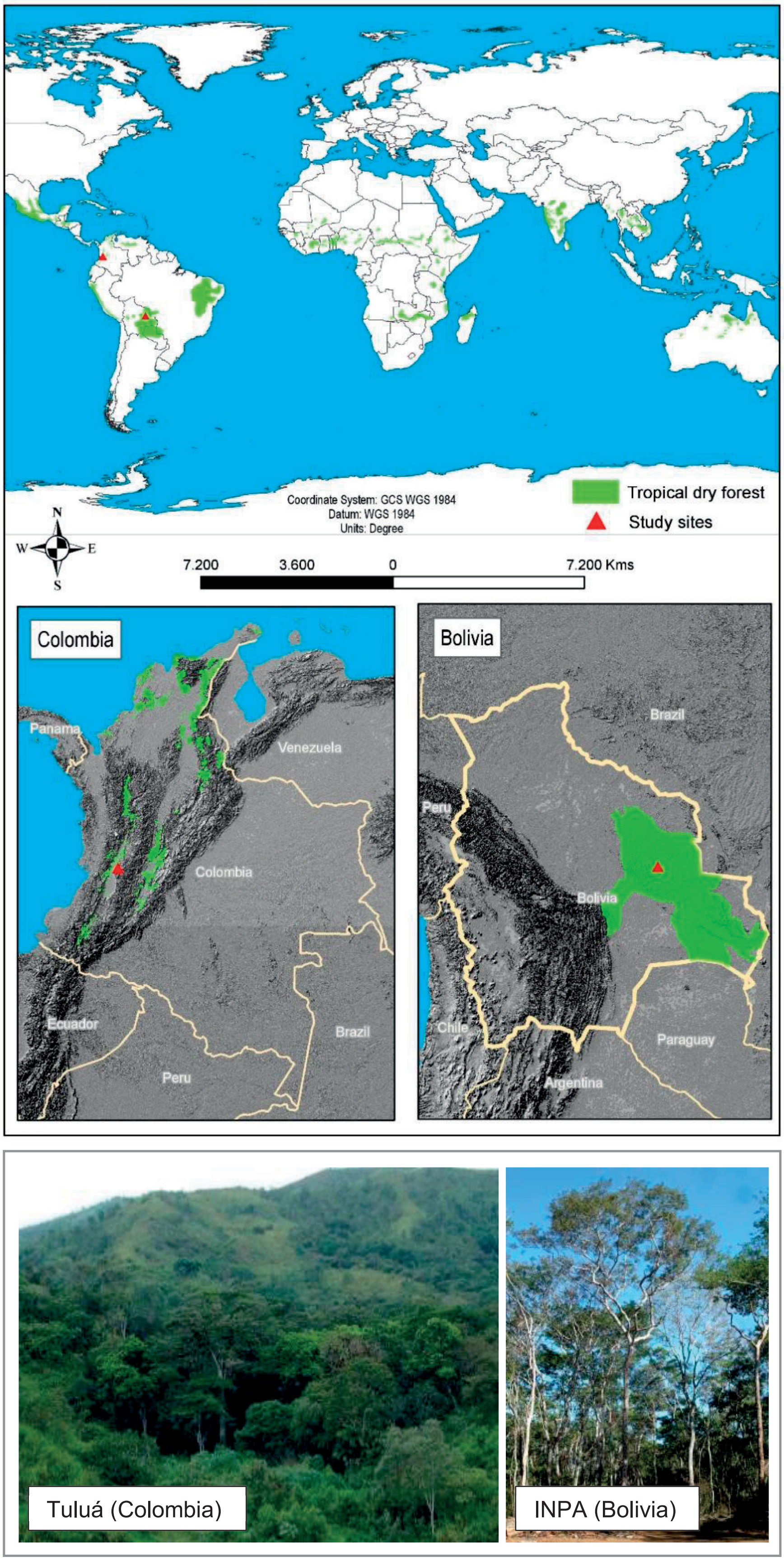

Figure 1. Global distribution of TDFs (top panel) and their location in Colombia (middle left panel) and Bolivia (middle right panel). Views of the two TDFs studied are displayed at the bottom panels. Maps were modified from Miles et al. (2006), Pizano and García (2014) and Seiler et al. (2015).

Figure 2. Some anthropogenic threats on Bolivian TDFs. The indiscriminate use of fire as a method for preparing farmlands generate multiple forest fires each year (top panels). Legal and illegal logging reduces the population size of timber tree species (bottom panels) as *Amburana cearensis* and *Cedrela fissilis*, which belong to the red list of threatened tree species (IUCN, 2016).

In Colombia, where one of the two study sites of this thesis (Tuluá) is located (Fig. 1), TDFs have lost more than 90% of their original extension. Thus, its biodiversity is under serious threaten (Pizano and García, 2014). In particular, 60% of TDF deforested areas are used for agriculture and livestock and many of the relict TDFs are privately owned (Pizano and García, 2014). In contrast, Mexico, Brazil and Bolivia have the largest and best-preserved TDFs from America (Portillo-Quintero and Sánchez-Azofeifa, 2010) (Fig. 1). Particularly, the Chiquitano TDF is one of the largest TDFs that currently exist in South America with about 14 Mha (Portillo-Quintero and Sánchez-Azofeifa, 2010), where the other study site (INPA) of this thesis is located (Fig. 1). The Chiquitano TDF is situated among Brazil, Bolivia and Paraguay, but it is better preserved areas are located in Bolivia and Paraguay, because in Brazil the complete forest cover was eliminated for agricultural or ranching purposes (Vides-Almonacid et al., 2007).

In addition to the pressures exerted by human impact on TDFs, droughts are also a big threat to them. More severe and longer droughts have been observed since the 1970s, linked to higher temperatures and increased evaporation, in the tropical and subtropical areas of the globe (IPCC, 2007). A plausible warmer world with longer and more severe droughts could lead to rapid collapse of tropical forest communities converting them into a large carbon source with cascading ecosystem effects, which affect global climate-vegetation feedbacks (Lewis, 2006). For instance, severe droughts during the 2000s reduced the net primary production (NPP) of most neotropical forests (Phillips et al., 2009; Zhao and Running, 2010), being the wood production the most sensitive component of above-ground NPP to the water availability reduction (Brando et al., 2008). To resolve part of the uncertainty linked to the climate-drought-forest feedbacks we must advance on the understanding of the long-term impacts of climate and droughts on the productivity, growth and functioning of TDFs.

Evaluating intra-annual growth patterns in TDF trees

To understand the impact of climate and droughts on tree growth at long-term is necessary to understand their effects at short-term scales. Currently, it is known that the annual xylem growth in tropical tree species is delimited by cambial dormancy, which is induced by three environmental factors: (i) the presence of an annual dry season associated with a decrease or absence of precipitation, (ii) annual periods of flooding as occur in some areas of the

Amazon Basin and (iii) annual fluctuations of soil water salinity in the case of mangroves (Borchert, 1999; Chowdhury et al., 2008; Schöngart et al., 2002). In particular, the seasonality of precipitation in the TDFs generates the alternation between favorable (wet season) and unfavorable (dry season) periods for cambium activity (Borchert, 1999). These two contrasting seasons make TDFs a valuable system to disentangle climate- leaf phenology-xylogenesis relationships, since they host many tree species showing different tolerances to water deficit during the dry season (Bullock et al., 1995; Eamus, 1999). In particular, these tree species respond to water deficit with: (i) contrasting leaf phenologies (Borchert, 1994, 1999; Eamus and Prior, 2001), (ii) contrasting seasonal patterns of stem hydraulic conductivity (Brodribb et al., 2002), and (iii) contrasting stem and bark water storage strategies (Poorter et al., 2014; Rosell et al., 2014). On the other hand, Worbes et al. (2013) registered differences in the length of the xylem growth period among tree species with different leaf phenology from a TDF. Furthermore, they recorded that in deciduous tree species the onset of xylem growth may occur simultaneously or after the leaf flushing. Considering these findings, a detailed description of how and when the xylem is formed at species level is of utmost importance; i.e. determining its association with leaf phenology, and identifying which climatic variables are the main constraints of both xylogenesis and leaf phenology. This information may improve our understanding of how wood formation and carbon uptake occur in TDFs. Furthermore, it would allow understanding the mechanisms of long-term growth responses of TDFs to climate warming and drought. In this thesis, we evaluated intra-annual patterns of xylogenesis and radial increment at hourly to monthly scales in 10 coexisting tree species from Colombian and Bolivian TDFs and we determined their relationships with climate and leaf phenology.

Detecting long-term growth trends in tree species: permanent sample plot vs. dendrochronology

Long-term data on tropical tree growth have been mostly obtained from permanent sample plots (PSPs). Particularly, PSPs have provided data for growth and yield models which can be used to assist forest management (Alder and Synnott, 1992; Priyadi et al., 2005). PSPs have also allowed to evaluate the effects on tree growth of several environmental factors such as climate (e.g. Toledo et al., 2011). Regarding this, PSPs have allowed to identify a decelerating growth in some tropical forests over the past decades. This response has been associated to altered temperature and precipitation regimes, which may modify the amount of water available for trees (Feeley et al., 2007). In contrast, other PSP-based studies from relatively undisturbed tropical forests have registered an increment in both biomass and tree growth associated to an increase in atmospheric CO_2 levels (Baker et al., 2004; Phillips et al., 1998). These studies were based on re-measurements of tree diameter changes every 5 to 10 years, which limited its temporal resolution and span. Furthermore, such re-censuses studies are usually shorter than 25 years and may render erratic results when the aim is to decipher how tree growth responds to climate variability and drought severity at a long-time scale (Clark and Clark, 2010).

Dendrochronology (tree-ring analysis) has been used as an alternative tool to analyze the variability of radial growth at yearly resolution and at a long-term scale from individual trees. Specifically, the periodic tree growth identified as annual growth rings in numerous tropical tree species (Brienen et al., 2016; Giraldo-Jiménez, 2011; Mendivelso et al., 2016a; Rozendaal and Zuidema, 2011; Tomazello F^{o} et al., 2009; Worbes, 2002) has allowed dendrochronology to provide reliable, annually resolved, retrospective and much longer growth records of stem wood production (a reliable surrogate of carbon uptake) than PSPs studies do in tropical forests (Zuidema et al., 2012, 2013; Zuidema and Frank, 2015). Although it is difficult to identify the annual growth rings in tropical tree species due to their complex wood anatomy (Stahle, 1999; Worbes and Fichtler, 2010), the recent publication by Brienen et al. (2016) confirmed the annual ring formation in 230 tropical tree species. This number is very low compared to the number of tropical tree species estimated by Slik et al. (2015) of at least ∼40,000 and possibly more than ∼53,000 species. Nevertheless, tree-ring analysis is contributing to better understand climate effects on tropical forests and thus, it will allow to improve predictions of long-term forest responses to global change (Zuidema et al., 2013; Zuidema and Frank, 2015). Several methods to evaluate the climate effect on growth trends using tree-ring analyses can be accessed in Peters et al. (2015).

Specifically, the information recorded in tree rings from TDFs has allowed quantifying how tree growth responds to climatic variables and determining if growth variability is related to large-scale atmospheric patterns, such as El Niño-Southern Oscillation (Table 2). Furthermore, in several tropical tree species tree-ring analysis using stable carbon isotopes has allowed determining an intrinsic water-use efficiency increment over the past 150 years as atmospheric CO_2 concentrations increased, but not an acceleration of individual tree growth when analyzing the width of growth rings (van der Sleen et al., 2015). On the other hand, tree-ring analysis has allowed to evaluate the effect of the precipitation on long-term growth of TDF trees (Table 2), since water availability is one of the most important factors driving growth and productivity of tropical forests (Toledo et al., 2011; Wagner et al., 2012, 2014, 2016). In contrast, few dendrochronological studies have evaluated the long-term growth responses to temperature in tropical forests (Brienen et al., 2016), and particularly in TDFs (Table 2). This might be due to the low intra-annual temperature variability in the tropics compared with areas from higher latitudes. The growth responses to temperature should be considered as an additional component to understand the future responses of the tree species in TDFs to climate warming. Particularly, the exploration of new variables that integrate precipitation and temperature in one single parameter, such as climate water balance or moisture and drought indexes (e.g. López and Villalba, 2011; Vicente-Serrano et al., 2013) can offer a major understanding of the environmental control on radial growth. In this dissertation I apply tree-ring analysis in seven deciduous tree species from a Bolivian TDF to evaluate the radial growth responses to climate (precipitation and temperature), water balance (P-PET, differences between precipitation and potential evapotranspiration) and drought events using the Standardized Precipitation Evapotranspiration Index (SPEI), which explicitly considers the effect of temperature on water availability (Vicente-Serrano et al., 2010). Both water balance and drought index have not been used until now in tropical dendrochronological studies.

Study sites

Two TDFs subjected to different drought severity were chosen for this study. The first site is located in the "Juan María Céspedes" botanical garden which is located 7 km away from Tuluá (hereafter Tuluá) in an inter-Andean valley in south-western Colombia (3° 59´ N, 76° 6´ W, 1050-1430 m a.s.l.). It is a 154 ha secondary forest situated over hilly terrain with acid soils (pH = 6.3) containing abundant organic matter (3.1%) in the upper soil layer (depth of 15 cm), where soils are of sandy and sandy-loam textures. This TDF has been undisturbed for the past 44 years. Most of the tree species are semi-deciduous and evergreen. Fabaceae is the dominant family, and the most abundant tree species are *Guazuma ulmifolia* Lam, *Cupania americana* L. and *Guarea guidonia* (L.) Sleumer. The studied forest has 31 tree species ha^{-1} and basal area of 12.4 m^2 ha^{-1} (Adarve et al., 2013).

The second site is a lowland and deciduous TDF located 32 km away from Concepción in the eastern region of Bolivia (16° 07´ S, 61° 43´ W, 380 m a.s.l.). It is a private property of INPA PARKET Ltda (hereafter INPA). This site belongs to the Chiquitano forest formation, which is considered one of the largest and most diverse TDF. It is located in the transition between the Amazonian lowland evergreen rain forest in the north and the Chaco dry scrubland southwards (Killeen et al., 1998) and occupies about 14 Mha (Portillo-Quintero and Sánchez-Azofeifa, 2010). INPA is situated on the Precambrian Brazilian shield and the soils are acid (pH = 5.8), present low organic matter contents (1.4%) in the upper soil layer, and have a sandy-loam texture. The study area is generally flat to gently sloping. Most of the tree species are deciduous. The studied forest has 98 canopy tree species, with a mean of 34 tree species ha^{-1} and basal area of 21 m^2 ha^{-1} (Villegas et al., 2009).

Table 2. Tree species with dendrochronological potential in TDFs. Legend: leaf habit, De, deciduous; Sd, semi deciduous; Ev, evergreeen; ring anatomy, Rp, ring porous; Srp, semi-ring porous; Bpf, alternating bands of parenchyma and fibers; Mp, marginal parenchyma band; Vvd, variation in vessel density; Tr, tracheids with thick cell walls. Columns abbreviated by P, T and SOI indicate if the corresponding study found positive, negative or no significant correlation (+, -, ns) between radial growth and precipitation (P), mean temperature (T) or the Southern Oscillation Index (SOI), respectively. An empty cell means that the climate variable was not tested. (*) unpublished data.

Family **Tree species**	**Leaf habit**	**Ring anatomy**	**Relationship with radial growth**			**Latitude, Longitude**	**Reference**
			P	**T**	**SOI**		
Apocynaceae							
Aspidosperma tomentosum	D	Mp	(+)	(-)		16° 07´ S, 61° 43´ W	Mendivelso et al. (2014)
Bignoniaceae							
Tabebuia chrysantha	D	Mp	(+)	ns	(-)	04° 21' S, 80° 15' W	C.I. Espinosa-J.J. Camarero (*)
Tabebuia impetiginosa	D	Mp	(+)	(-)		16° 07´ S, 61° 43´ W	Mendivelso et al. (2014)
Zeyheria tuberculosa	D	Mp	(+)	ns		16° 07´ S, 61° 43´ W	Mendivelso et al. (2014)
Burseraceae							
Bursera graveolens	D		(+)		(-)	04° 35´ S, 80° 13´ W	Rodríguez et al. (2005)
Bursera graveolens	D		(+)		(-)	04° 41´ S, 80° 27´ W	Rodríguez et al. (2005)
Bursera graveolens	D		(+)		(-)	05° 09´ S, 80° 10´ W	Rodríguez et al. (2005)
Capparidaceae							
Capparis indica	E		(+)	ns	ns	10°45´ N, 85° 30´ W	Enquist and Leffler (2001)
Capparis odoratissima	E	Mp	(+)	(-)	(+)	11° 30´ N, 72° 20' W	Ramírez and del Valle (2011)
Combretaceae							
Anogeissus leiocarpus	D	Vvd	(+)		ns	09° 12´ N, 01° 90´ E	Schöngart et al. (2006)
Anogeissus leiocarpus	D	Vvd	(+)		ns	08° 41´ N, 03° 47´E	Schöngart et al. (2006)
Terminalia guianensis	E	Mp	(+)			07° 20' N, 70° 30' W	Worbes (1999)
Cupressaceae							
Juniperus procera	E	Tr	(+)	ns		06° 50´N, 30° 07´ E	Sass-Klaassen et al. (2008)
Juniperus procera	E	Tr	(+)	ns		08° 97´ N, 38° 35´ E	Sass-Klaassen et al. (2008)
Ebenaceae							
Diospyros abyssinica	E	Bpf	(+)		ns	08° 41´ N, 03° 47´E	Schöngart et al. (2006)
Fabaceae							
Acacia senegal	D	Mp	(+)		(+)	07° 51´N, 38° 42´ E	Gebrekirstos et al. (2008)
Acacia seyal	D	Mp	(+)		(+)	07° 51´N, 38° 42´ E	Gebrekirstos et al. (2008)
Acacia tortilis	D	Mp	(+)		(+)	07° 51´N, 38° 42´ E	Gebrekirstos et al. (2008)
Acosmium cardenasii	D	Mp	(+)	(-)		16° 07´ S, 61° 43´ W	Mendivelso et al. (2014)
Afzelia africana	D	Mp	(+)		ns	09° 12´ N, 01° 90´ E	Schöngart et al. (2006)
Afzelia xylocarpa	D	Mp	(+)	(-)		15º 36' N, 99º 12' E	Vlam et al. (2013)
Amburana cearensis	D	Mp	(+)	(-)		16° 09´ S, 60° 47´ W	Paredes-Villanueva (2015)
Anadenanthera macrocarpa	D	Mp	(+)	(-)		16° 07´ S, 61° 43´ W	Mendivelso et al. (2014)
Caesalpinia pluviosa	D	Mp	(+)	(-)		16° 07´ S, 61° 43´ W	Mendivelso et al. (2014)
Centrolobium microchaete	D	Mp	(+)	(-)		16° 07´ S, 61° 43´ W	Mendivelso et al. (2014)
Centrolobium microchaete	S	Mp	(+)	(-)		16° 22´ S, 61° 41´ W	López and Villalba (2011)
Centrolobium microchaete	S	Mp	(+)	(-)		15° 58´ S, 62° 22´ W	López and Villalba (2011)
Daniellia oliveri	D	Mp	(+)		ns	09° 12´ N, 01° 90´ E	Schöngart et al. (2006)
Daniellia oliveri	D	Mp	(+)		ns	08° 41´ N, 03° 47´E	Schöngart et al. (2006)
Geoffroea spinosa	D	Mp	(+)			04° 21' S, 80° 15' W	C.I. Espinosa-J.J. Camarero (*)
Isoberlinia doka	S	Mp	(+)			09° 12´ N, 01° 90´ E	Schöngart et al. (2006)
Machaerium scleroxylon	S	Mp	(+)	(-)	(+)	18° 19´S, 59° 46´ W	Paredes-Villanueva et al. (2013)
Mimosa acantholoba	D	Srp	(+)	(-)	(+)	16° 39´ N, 95° 00' W	Brienen et al. (2010b)
Mimosa tenuiflora	D	Mp	(+)			08° 04' S, 37° 12' W	Mattos et al. (2015)
Parkinsonia praecox	D	Mp	(+)	(-)	(+)	11° 46´ N, 72° 47´ W	Ramírez and del Valle (2012)
Prosopis pallida		Mp	(+)		(-)	05° 10' S, 80° 38' W	López et al. (2005)
Prosopis sp.	E		(+)			04° 41´ S, 80° 27´ W	Rodríguez et al. (2005)
Pterocarpus erinaceus	D	Vvd	(+)			09° 12´ N, 01° 90´ E	Schöngart et al. (2006)

Table 2. Tree species with dendrochronological potential in TDFs. Legend: leaf habit, De, deciduous; Sd, semi deciduous; Ev, evergreeen; ring anatomy, Rp, ring porous; Srp, semi-ring porous; Bpf, alternating bands of parenchyma and fibers; Mp, marginal parenchyma band; Vvd, variation in vessel density; Tr, tracheids with thick cell walls. Columns abbreviated by P, T and SOI indicate if the corresponding study found positive, negative or no significant correlation (+, -, ns) between radial growth and precipitation (P), mean temperature (T) or the Southern Oscillation Index (SOI), respectively. An empty cell means that the climate variable was not tested. (*) unpublished data.

Family Tree species	Leaf habit	Ring anatomy	Relationship with radial growth			Latitude, Longitude	Reference
			P	T	SOI		
Lamiaceae							
Tectona grandis	D	Rp	(+)	(-)			Pumijumnong et al. (1995)
Meliaceae							
Cedrela fissilis	D		(+)	(-)		16° 08´ S, 62° 01´ W	Paredes-Villanueva et al. (2016)
Cedrela odorata	D	Mp	(+)			19°03´ N, 90° 00' W	Brienen et al. (2010a)
Chukrasia tabularis	E - S	Mp	(+)	(-)		15º 36’ N, 99º 12’ E	Vlam et al. (2013)
Melia azedarach	D	Rp	(+)	(-)		15º 36’ N, 99º 12’ E	Vlam et al. (2013)
Toona ciliata	D	Rp	(+)	(-)		15º 36’ N, 99º 12’ E	Vlam et al. (2013)
Rubiaceae							
Genipa americana	D		(+)	ns	ns	10° 45´ N, 85° 30´ W	Enquist and Leffler (2001)
Rutaceae							
Zanthoxylum rhoifolium	S - D	Mp	(+)	ns		04° 02’ N, 76° 10’ W	H.A. Mendivelso et al. (*)
Zygophyllaceae							
Balanites aegyptiaca	E	Mp	(+)		(+)	07° 51´N, 38° 42´ E	Gebrekirstos et al. (2008)

According to climatic data from Tuluá-Farfán (4° 06´ N, 76° 14´ W, 955 m a.s.l) and Concepción (16° 15´ S, 62° 06´ W, 410 m a.s.l) meteorological stations, the mean annual precipitation in Tuluá (1317 mm) and INPA (1226 mm) did not significantly differ for the 1984-2011 period (t = -1.49, P = 0.14; see Fig. 3). In contrast, INPA shows a mean temperature (24.0 °C) significantly higher (t = 7.25, P < 0.001) than Tuluá (22.6 °C) (Fig. 3). Tuluá shows low rainfall records (<60 mm) and negative water balance from June to August, whilst in INPA the driest period normally goes from June to September but the potential evapotranspiration exceeds precipitation from April to October (Fig. 3). The relationship between monthly precipitation and temperature is significantly positive in INPA, but it is negative in Tuluá (Fig. 3).

Study tree species

In total 14 tree species were selected in this study, four species were sampled in Tuluá (Colombia) and 10 species were sampled in INPA (Bolivia). They belong to seven different families, display contrasting crown positions and leaf habit (Table 3). According to the electronic database published by Tropicos® (2016), the tree species from Tuluá are widespread tropical taxa [*Cordia alliodora* (Ruiz & Pav.) Oken, *Cupania americana* L., *Pithecellobium dulce* (Roxb.) Benth., *Zanthoxylum rhoifolium* Lam.]. The INPA tree species *Acosmium cardenasii* H.S. Irwin & Arroyo is restricted to the Chiquitano TDF. The remaining tree species of INPA are also found either only in countries neighboring Bolivia [*Amburana cearensis* (Allemão) A.C. Sm., *Anadenanthera macrocarpa* (Benth.) Brenan, *Aspidosperma cylindrocarpon* Müll. Arg., *Aspidosperma tomentosum* Mart., *Centrolobium microchaete* (Mart. ex Benth.) H.C. Lima, *Zeyheria tuberculosa* (Vell.) Bureau], or they are widespread across the neotropics [*Caesalpinia pluviosa* DC., *Cedrela fissilis* Vell., *Tabebuia impetiginosa* (Mart. ex Dc.) Standl.]. IUCN (2016) reports that two of the 10 tree species studied in INPA are endangered (*Amburana cearensis* y *Cedrela fissilis*), and one is vulnerable (*Zeyheria tuberculosa*).

Institutional context, funding and project team

This thesis is part of the two larger projects: “Análisis retrospectivos mediante dendrocronología para profundizar en la ecología y mejorar la gestión de los bosques tropicales secos” (DENTROPICAS, financed by Fundación BBVA) and “Regeneración, crecimiento y modelos dinámicos de bosques tropicales secos: herramientas para su conservación y para el uso sostenible de especies maderables" (AECID 11-CAP2-1730, financed by Spanish Ministry of Foreign Affairs). Both research projects were led by Dr. J. Julio Camarero (Instituto Pirenaico de Ecología, IPE-CSIC, Spain). Furthermore, these projects were conducted in cooperation with the Instituto Boliviano de Investigación Forestal (IBIF, Bolivia), the Jardín Botánico "Juan María Céspedes" (INCIVA, Colombia), the Univ. Técnica Particular de Loja (Loja, Ecuador) the Dept. d' Ecologia (Universitat de Barcelona), and the Dept. of Forest Ecology and Forest Management (University of Wageningen).

The project team who contributed in some way to this thesis was formed by Dr. J. Julio Camarero (principal investigator, IPE-CSIC), Robin Corrià Ainslie (PhD student, IPE-CSIC), Hooz Angela Chaparro Mendivelso (PhD student, IPE-CSIC and Universidad de Barcelona), Dr. Emilia Gutiérrez (co-investigator, Universidad de Barcelona), Dr. Pieter A. Zuidema and Dr. Ute Sass-Klassen (co-investigators, Wageningen Universtity), Dr. Marisol Toledo (co-investigator, Instituto Boliviano de Investigación Forestal, IBIF) and MSc. Alejandro Castaño-Naranjo (co-investigator, INCIVA). Further collaborators were two biologists (Liseth Castellanos, Oriol Royo), five undergraduate students (Luisa Velásquez, Luz Natalia Mercado, Camila Castilla, Juan Moigue Chamo, Oscar Romero), two laboratory technicians (Elena Lahoz, Dr. María Carmen Sancho) and several field assistants (Juan Adarve, Wilson Devia, Vincent Vroomans).

Table 3. Characteristics of the 14 tree species sampled in two tropical dry forests (TDFs) located in Tuluá (Colombia) and INPA (Bolivia). The last column shows the chapters in which they are included.

Study site	Species	Family	Crown position	Leaf habit	Chapter
Tuluá	*Cordia alliodora*	Boraginaceae	Canopy	Semi-deciduous / deciduous	2
	Cupania americana	Sapindaceae	Emergent	Semi-deciduous	2
	Pithecellobium dulce	Fabaceae	Canopy	Semi-deciduous	2
	Zanthoxylum rhoifolium	Rutaceae	Canopy	Semi-deciduous / deciduous	2
INPA	*Acosmium cardenasii*	Fabaceae	Sub-canopy	Deciduous	2-4
	Amburana cearensis	Fabaceae	Canopy	Deciduous	2
	Anadenanthera macrocarpa	Fabaceae	Emergent	Deciduous	3-4
	Aspidosperma cylindrocarpon	Apocynaceae	Sub-canopy	Semi-deciduous	2
	Aspidosperma tomentosum	Apocynaceae	Sub-canopy	Deciduous	2-4
	Caesalpinia pluviosa	Fabaceae	Canopy	Deciduous	3-4
	Cedrela fissilis	Meliaceae	Canopy	Deciduous	2
	Centrolobium microchaete	Fabaceae	Canopy	Deciduous	2-4
	Tabebuia impetiginosa	Bignoniaceae	Canopy	Deciduous	3-4
	Zeyheria tuberculosa	Bignoniaceae	Canopy	Deciduous	3-4

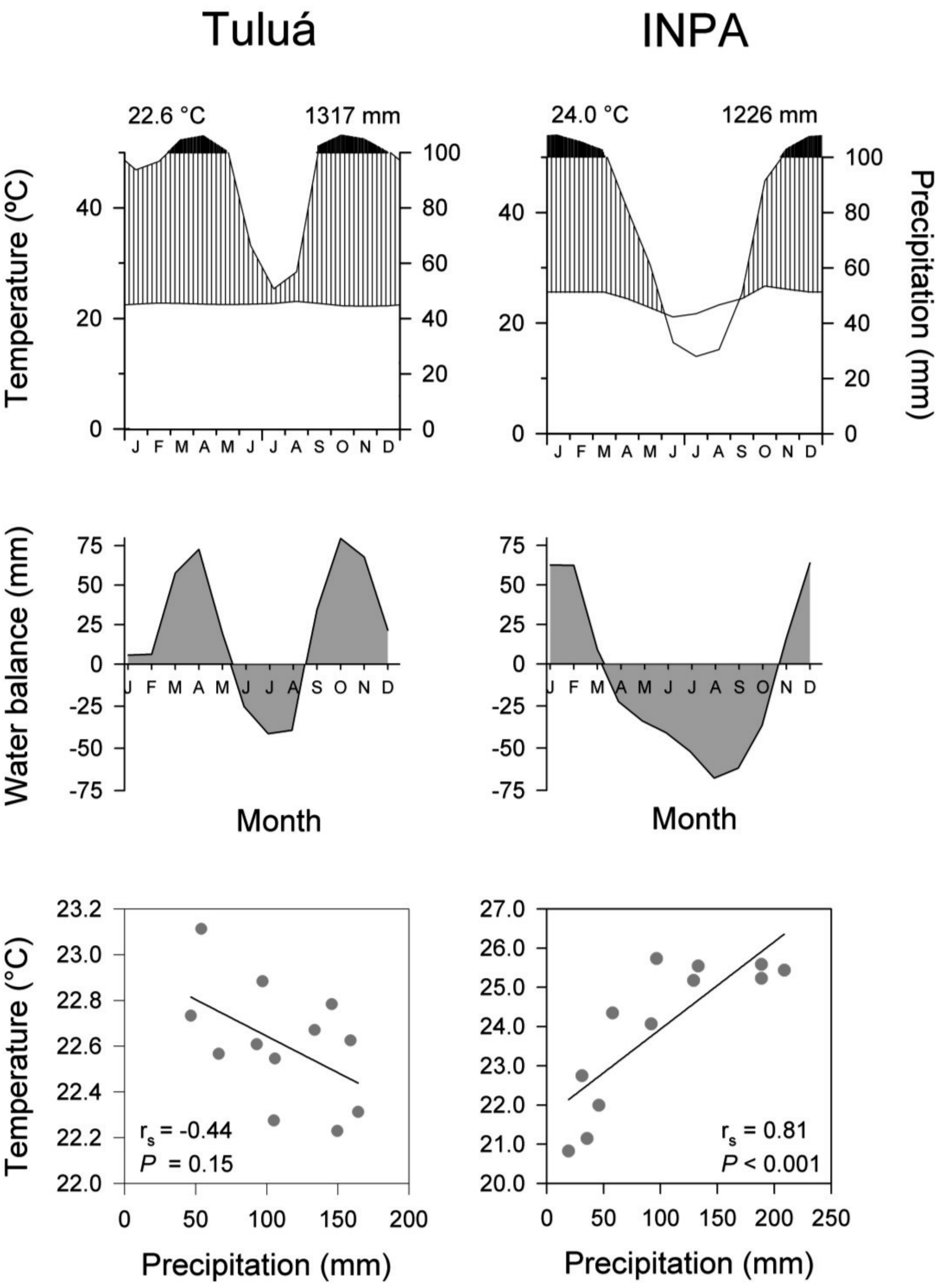

Figure 3. Climatic diagrams and estimated monthly climate water balance (difference between precipitation and potential evapotranspiration, P-PET) at two study sites (data correspond to nearby climatic stations for to the 1984-2011 period). The lowermost plots show the relationships between monthly precipitation and temperature values at two study sites (r_S, Spearman coefficients).

Objectives

This research aims to determine the dynamics of radial growth at different time-scales in relation to climate and drought in tropical dry forests (TDFs) from Colombia and Bolivia.

The specific objectives are:

1. To assess intra-annual patterns of radial growth (radial-increment dynamics and xylogenesis) in 10 coexisting tree species from Colombian and Bolivian TDFs and determine their relationship with climate and leaf phenology (Mendivelso *et al.* 2016b).

2. To analyze the effects of climate and drought on long-term radial growth at different time-scales using dendrochronology in seven coexisting deciduous tree species from a Bolivian TDF (Mendivelso *et al.* 2014).

3. To evaluate the long-term radial growth responses to changes in climate water balance and determine their relationship with sapwood density in seven coexisting deciduous tree species from a Bolivian TDF (Mendivelso *et al.* 2013).

To achieve the first objective, the intra-annual radial growth and leaf phenology as related to climate in two TDFs with different drought seasonality and severity were quantified (Chapter 2). In total 10 tree species were selected, four and six species were sampled in the Tuluá (Colombia) and INPA (Bolivia) sites, respectively. On the one hand, the leaf phenology and radial-increment dynamics were monthly registered using manual band dendrometers. Additionally, hourly and daily radial-increment dynamics were recorded in eight species using automatic band dendrometers, whilst the dynamics of xylem growth (xylogenesis) were evaluated in six species by taking wood microcores (Fig. 4). A better understanding of the effects of climate on xylem development and its relation with leaf phenology will improve our understanding of how wood formation and carbon uptake occur in tropical tree species.

Regarding the second objective, the effects of climate and drought on inter-annual radial growth of deciduous tree species coexisting in a Bolivian TDF (INPA site) were analyzed (Chapter 3). Tree-ring data from the seven deciduous tree species collected in the INPA site were used (Fig. 4). Multi-species analyses of radial growth in TDFs are necessary to understand expected community growth responses to climate warming and increased drought stress. The assessment of the time-dependency of growth responses to drought should be explicitly considered as an additional constraint of the community dynamics in evaluations of the future responses of TDFs to climate warming.

Finally, to achieve the third objective, it was determined how coexisting deciduous tree species respond to the climate water balance (P-PET, difference between precipitation and potential evapotranspiration) in a Bolivian TDF (INPA site) by analyzing long-term climate-growth relationships (Chapter 4). Basal area increment data from the seven most abundant tree species collected in this site were used (Fig. 4). The evaluation of the long-term growth responses to changes in the water balance is expected to provide an understanding of how and when coexisting tree species in TDFs respond to water deficit.

In Chapter 5 the main findings of this thesis are discussed. In particular, the first part discusses about intra-annual patterns of radial growth in tree species coexisting in the two TDFs and shows their relationship with climate and leaf phenology. The second part discusses about the effects of precipitation, temperature, climate water balance and drought on inter-annual radial growth of seven deciduous tree species coexisting in a Bolivian TDF. In the third and last part an outlook for further research is discussed, and the main conclusions are shown at both intra- and inter-annual scales and focusing on the differences among the tree species studied.

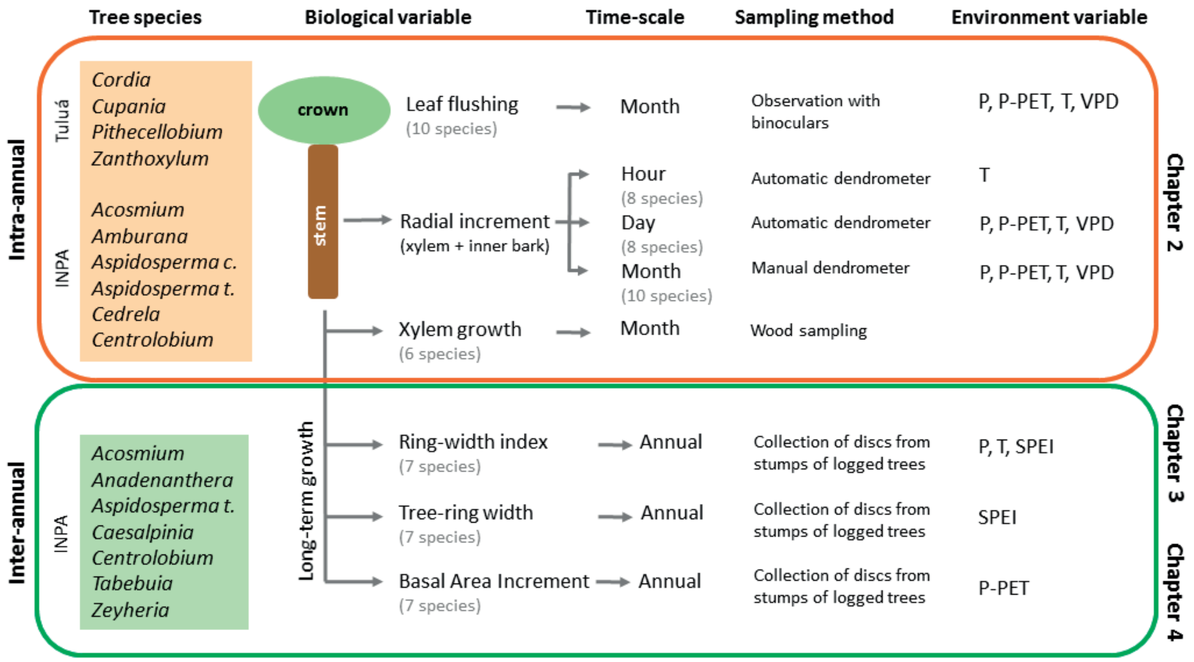

Figure 4. Biological variables used to evaluate the effect of environmental variables on radial increment, xylem growth and leaf phenology, at different time scales in two TDFs located in Colombia (Tuluá) and Bolivia (INPA). Abbreviations of climate variables: P, precipitation; P-PET, climate water balance; T, temperature; VPD, vapor pressure deficit; SPEI, Standardized Precipitation Evapotranspiration Index (drought index). See the complete scientific name per each species in Table 1 of the General Introduction.

Chapter 2


View of the Inter-Andean dry forest during wet season (Colombia)

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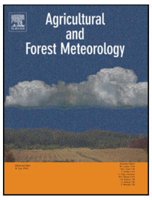

Climatic influences on leaf phenology, xylogenesis and radial stem changes at hourly to monthly scales in two tropical dry forests

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ABSTRACT

Assessing the effects of climate on leaf phenology and xylem development will improve our understanding of how wood formation and carbon uptake occur in tropical tree species. Wood formation depends on how tree stems enlarge, shrink or swell at multiple temporal scales. To address these issues we analyzed climate data, leaf phenology, xylogenesis and radial increment at hourly to monthly scales of ten tree species in two tropical dry forests with different drought seasonality and severity (the wet Tuluá site is located in Colombia and the dry INPA site is situated in Bolivia). Leaf flushing and radial growth occurred during the wet season at both sites, reflecting the influence of high precipitation, a positive water balance and low vapor pressure deficit on the development of new leaves and xylem cells. In Tuluá, the xylem growing season was associated with low air temperatures, while in INPA it was related to high air temperatures. At both sites, the high air temperatures registered throughout the day negatively affected radial-increment rates at hourly scales, probably by rising vapor pressure deficit and enhancing evapotranspiration rates. Tree species could face adverse dry conditions by growing in periods of the day when temperatures decrease and water loss due to evapotranspiration is reduced, particularly at dry INPA site. Stem shrinkage and swelling were observed at hourly to daily scales in all tree species, but most INPA species also registered strong reversible shrinkage at monthly scales. The strength of the positive association between leaf flushing and radial-increment rates was species-specific and it related to sapwood density. Thus, *Cedrela fissilis*, a pioneer deciduous species with low sapwood density showed the strongest associations between leaf flushing and radial-increment rates, whereas *Acosmium cardenasii*, a shade-tolerant deciduous species showed the reverse characteristic. The time-dependent growth responses of tree species to water availability should be explicitly considered to properly forecast their responses to climate warming and to evaluate their relevance as carbon sinks under warmer and drier conditions.

1. Introduction

The temporal variability of tree growth occurs at different temporal scales and thus can be utilized as an indicator of environmental impacts on tropical forests (Bräuning et al., 2008). However, most of the long-term assessments of growth responses to climate in tropical forests are based on annual tree rings (Rozendaal and Zuidema, 2011; Worbes, 2002). Integrated approaches comparing leaf phenology and radial growth assessed at multiple time scales should allow better understanding how coupled climate and leaf phenology and radial growth are in tropical trees (Camarero et al., 2013; Yáñez-Espinosa et al., 2006).

Tropical dry forests (hereafter TDF) constitute a valuable system to disentangle climate–phenology–growth relationships because (i) they host many coexisting tree species showing different tolerances to water deficit, and (ii) these species experience seasonally contrasting soil moisture availability but respond to water deficit with contrasting phenologies (Bullock et al., 1995; Eamus, 1999).

Abbreviations: DOY, day of the year; Md, manual band dendrometer; Ma, automatic band dendrometer; Mc, microcore; P, precipitation; PET, potential evapotranspiration; P-PET, water balance; T, temperature; TDF, tropical dry forest; VPD, vapor pressure deficit.

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Several mechanisms of drought tolerance have been identified in TDF tree species as different leaf fall behaviors (Borchert, 1999, 1994; Eamus and Prior, 2001) and contrasting seasonal patterns of stem hydraulic conductivity (Brodribb et al., 2002). Changes in stem and bark water storage are also prominent among TDF tree species and depend on wood anatomical features (Poorter et al., 2014; Rosell et al., 2014), which are possibly related to xylem phenology (xylogenesis).

In tropical forests, only few studies have explicitly dealt with the links between leaf phenology and radial growth at intra-annual scales (Coster, 1927; Lisi et al., 2008; Schöngart et al., 2002; Worbes et al., 2013). Particularly, the leaf phenology is tightly coupled to changing water availability and stem water content in TDFs (Borchert, 1994). Therefore, seasonal water deficit should modulate leaf development and senescence in TDF tree species and this influence should translate into different radial-growth rates and xylogenesis. A better knowledge of these relationships would allow understanding long-term growth responses of TDFs to climate warming and drought (Rozendaal and Zuidema, 2011; Worbes, 2002, 1995).

Xylogenesis in tropical trees is determined by seasonal cambial dormancy induced by several environmental stressors including a dry season, flooding or fluctuations in salinity in the case of mangroves (Borchert, 1999; Chowdhury et al., 2008; Schöngart et al., 2002). Usually, the transition from the dormant season to the growing season represents a critical period for understanding the dynamics of stem wood formation in tropical tree species. In the case of TDFs, the duration of the transition from the dry to the rainy season affects xylem growth rates, whilst the onset of xylem growth is related to leaf emergence (Mendivelso et al., 2014).

Here we quantify intra-annual tree growth (xylogenesis) and leaf phenology as related to climate at two TDFs. We analyze if growth and leaf phenology relate to tree species traits (e.g., leaf habit, wood porosity, sapwood density) and drought severity. Our objectives were: (i) to evaluate climate effects on monthly leaf phenology and xylogenesis, (ii) to determine the relationship between four climatic variables (precipitation, temperature, water balance and vapor pressure deficit) and radial-increment dynamics from hourly to monthly scales, and (iii) to assess if leaf phenology, radial increment and tree species traits are linked.

2. Material and methods

2.1. Study sites

Two TDFs subjected to different drought severity were chosen for this study. The wettest site is situated in the "Juan María Céspedes" botanical garden which is located 7 km away from Tuluá (hereafter Tuluá) in an inter-Andean valley in south-western Colombia (4°02′ N, 76°10′ W, 1050–1430 m a.s.l.). It is a 154 ha secondary forest situated over hilly terrain with acid soils (pH = 6.3) containing abundant organic matter (3.1%) in the upper soil layer (depth of 15 cm), where soils are of sandy and sandy-loam textures. This TDF has been undisturbed for the past 44 years. Most of the tree species are semi-deciduous and evergreen. Fabaceae is the dominant family, and the most abundant tree species are *Guazuma ulmifolia* Lam, *Cupania americana* L. and *Guarea guidonia* (L.) Sleumer. The studied forest has 31 tree species ha^{-1} and basal area of 12.4 m^2 ha^{-1} (Adarve et al., 2013).

The driest site is a lowland and deciduous TDF located 32 km away from Concepción in eastern Bolivia (16°07′ S, 61°43′ W, 380 m a.s.l.). It is a private property of INPA PARKET Ltda (hereafter INPA). This site belongs to the Chiquitano forest formation, which is considered one of the largest and most diverse TDF occupying about 16.4 millions of ha in the transition between the Amazonian lowland evergreen rain forest in the north and the Chaco dry scrubland southwards (Killeen et al., 1998). INPA is situated on the Precambrian Brazilian shield and the soils are acid (pH = 5.8), present low organic matter contents (1.4%) in the upper soil layer, and have a sandy-loam texture. The study area is flat to gently sloping. Most of the tree species are deciduous. The studied forest has 34 tree species ha^{-1} and basal area of 19.7 m^2 ha^{-1} (Villegas et al., 2009).

According to climatic data from Tuluá-Farfán (4°06′ N, 76°14′ W, 955 m a.s.l) and Concepción (16°15′ S, 62°06′ W, 410 m a.s.l) meteorological stations, the mean annual precipitation in Tuluá (1317 mm) and INPA (1226 mm) did not significantly differ for the 1984–2011 period ($t = -1.49$, $P = 0.14$; see Fig. A1). In contrast, INPA shows a mean temperature (24.0 °C) significantly higher ($t = 7.25$, $P < 0.001$) than Tuluá (22.6 °C; see Fig. A1). Therefore, the seasonal distribution of rainfall, drought severity and the relationship between monthly precipitation and temperature differ between sites. Tuluá shows low rainfall records (<60 mm) and negative water balance from June to August, whilst in INPA the driest period normally goes from June to September but the potential evapotranspiration exceeds precipitation from April to October (Fig. A1). The relationship between monthly precipitation and temperature is significantly positive in INPA, but it is negative in Tuluá (Fig. A1). Precipitation in Tuluá was more than twice that recorded in INPA during the study period (July 2010–September 2011) with 42% and 21% of rainy days in the former and latter sites, respectively (Fig. 1).

2.2. Tree species

In total 10 tree species were selected in this study, four species were sampled in Tuluá and six species were sampled in INPA. They belong to six different families and display contrasting crown positions, leaf habit, wood porosity and sapwood density (Table 1). The tree species from Tuluá are widespread tropical taxa [*Cordia alliodora* (Ruiz & Pav.) Oken, *Cupania americana* L., *Pithecellobium dulce* (Roxb.) Benth. and *Zanthoxylum rhoifolium* Lam.]. Two of the six species studied in INPA [*Amburana cearensis* (Allemão) A.C. Sm. and *Cedrela fissilis* Vell.] belong to the red list of threatened tree species (see http://www.iucnredlist.org), whilst one species (*Acosmium cardenasii* H.S. Irwin & Arroyo) is restricted to the Bolivian Chiquitano TDF. The remaining three species are found in other TDFs [*Aspidosperma cylindrocarpon* Müll. Arg., *Aspidosperma tomentosum* Mart., *Centrolobium microchaete* (Mart. ex Benth.) H.C. Lima].

2.3. Links between leaf phenology, radial increment and sapwood density

To reduce the effects of tree size on growth, all trees selected for recording leaf phenology, stem radius variation and xylem formation had similar diameter at 1.3 m (Table 1). Leaf phenology data were registered monthly for 10 individuals per species using binoculars and by calculating the percentage of trees presenting the crown covered by swelling buds, mature leaves or without leaves. We quantified the changes in stem perimeter of the same individuals using manual band dendrometers (DB20, EMS Brno, Czech Republic). In addition, automatic band dendrometers (DRL26, EMS Brno, Czech Republic) were installed in one individual per species to record perimeter changes and air temperatures near the stem at hourly scales. In *Amburana* and *Aspidosperma t.* only 2–3 individuals were monitored using manual band dendrometers. All dendrometers were installed at breast height (1.3 m). A total of 84 individuals were considered in these analyses (Table 1).

Before installing the dendrometers the outer layer of dead bark was carefully removed and then we measured the tree perimeter and diameter at 1.3 m. Manual band dendrometers were read

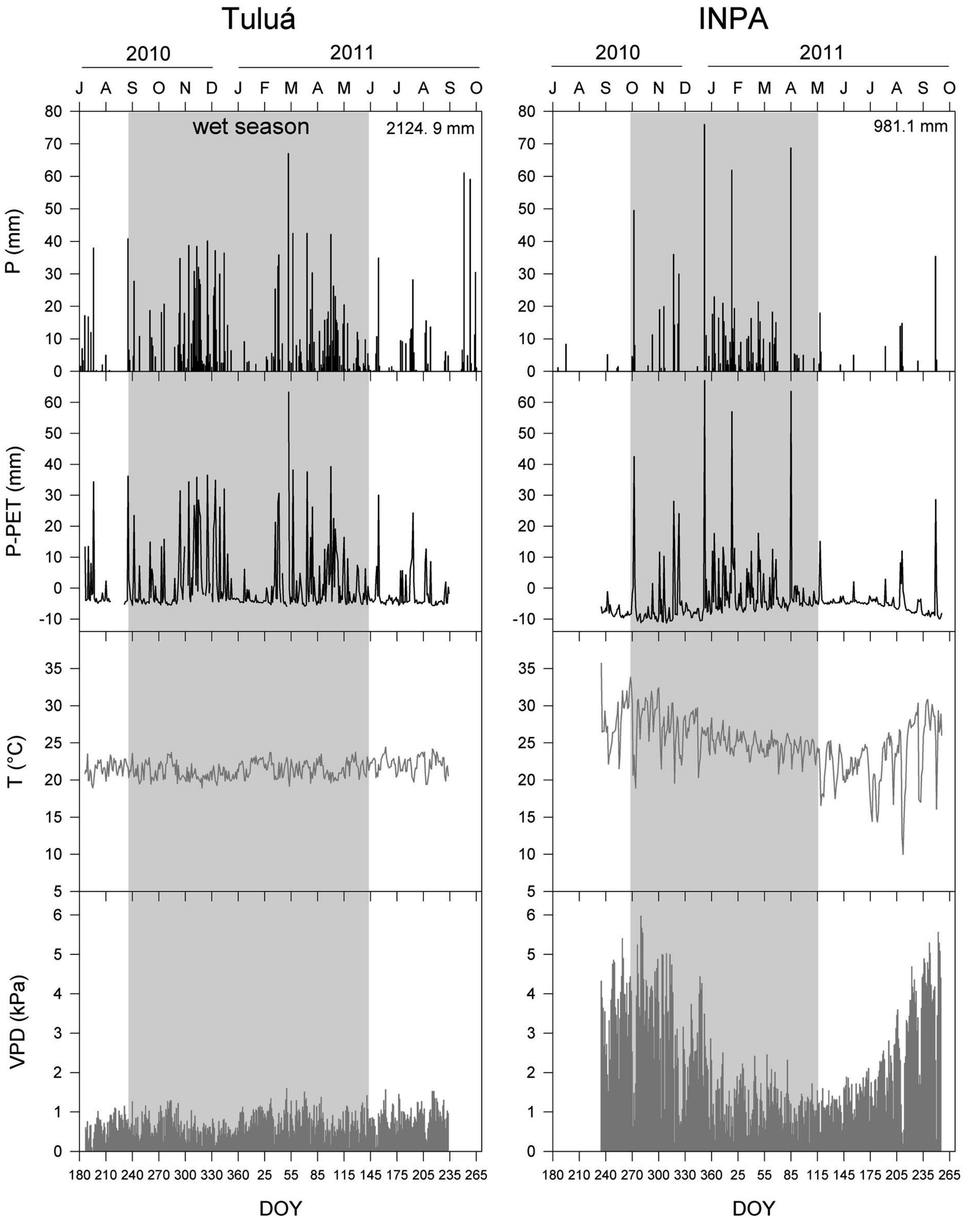

Fig. 1. Daily climatic conditions in the two studied tropical dry forests located in Tuluá (Colombia) and INPA (Bolivia). Abbreviations: *P*, total precipitation; P-PET, water balance; *T*, mean air temperature; VPD, vapor pressure deficit.

monthly to the nearest 0.1 mm over a period of 13 months, from July 2010 to August 2011 in Tuluá, and from August 2010 to September 2011 in INPA. All measurements were recorded in the early morning to reduce diurnal bias because daytime transpiration causes stem shrinkage (Zweifel et al., 2001). The changes in perimeter were converted to radial increment assuming that tree stems were circular. Radial increment data are presented at several temporal scales (month, day and hour). In addition, the volumetric soil water content in the upper soil layer (15 cm) and around each adult tree base was measured once per month using a Time Domain Reflectometry probe (Theta Probe Soil Moisture Sensor, Delta-T, Cambridge, UK). Finally, to estimate the sapwood density for each species we collected radial cores (5-mm wide, 30-mm long) from five trees per species using a Pressler increment borer (see more details on sampling methods in Mendivelso et al., 2013).

Table 1
Characteristics of sampled individuals for each tree species. Abbreviations: Md, manual band dendrometer; Ad, automatic band dendrometer; Mc, microcore. Values are means ± 1 SE. The letters represent comparisons of the same variable among tree species for each study site. Means sharing the same letter were not significantly different using Tukey and Games-Howell post hoc tests for those cases with or without homoscedasticity, respectively ($P > 0.05$).

Study site	Species (family)	Crown position	Leaf habit	Diameter at 1.3 m (cm)	Height (m)	Wood porosity	Sapwood density (g cm^{-3})	No. of sampled trees		
								Md	Ad	Mc
Tuluá	*Cordia alliodora* (Boraginaceae)	Canopy	Semi-deciduous/ deciduous	23.6 ± 1.6a	18.0 ± 1.1b	Diffuse porous	0.49 ± 0.03a	10	1	3
	Cupania americana (Sapindaceae)	Emergent	Semi-deciduous	18.7 ± 1.1a	15.1 ± 1.4ab	Diffuse porous	0.62 ± 0.03b	10	1	3
	Pithecellobium dulce (Fabaceae)	Canopy	Semi-deciduous	19.5 ± 1.6a	13.6 ± 0.9ab	Diffuse porous	0.56 ± 0.02ab	10	1	3
	Zanthoxylum rhoifolium (Rutaceae)	Canopy	Semi-deciduous/ deciduous	20.5 ± 2.1a	12.2 ± 0.9a	Diffuse porous	0.53 ± 0.02ab	10	1	3
INPA	*Acosmium cardenasii* (Fabaceae)	Sub-canopy	Deciduous	14.5 ± 0.5a	11.9 ± 0.8a	Diffuse porous	0.69 ± 0.02c	10	1	5
	Amburana cearensis (Fabaceae)	Canopy	Deciduous	15.5 ± 4.3a	10.3 ± 2.1a	Diffuse porous	0.52 ± 0.02ab	3	–	–
	Aspidosperma cylindrocarpon (Apocynaceae)	Sub-canopy	Semi-deciduous	14.8 ± 0.6a	11.1 ± 0.5a	Diffuse porous	0.67 ± 0.03c	8	1	–
	Aspidosperma tomentosum (Apocynaceae)	Sub-canopy	Deciduous	16.2 ± 2.6a	9.3 ± 1.3a	Diffuse porous	0.66 ± 0.01bc	2	–	–
	Cedrela fissilis (Meliaceae)	Canopy	Deciduous	19.2 ± 1.9a	11.5 ± 1.1a	Semi-ring porous	0.42 ± 0.01a	11	1	–
	Centrolobium microchaete (Fabaceae)	Canopy	Deciduous	14.7 ± 1.1a	13.0 ± 0.6a	Semi-ring porous	0.59 ± 0.02bc	10	1	5

2.4. Xylogenesis

The dynamics of xylem growth (xylogenesis) were characterized by doing repeated wood sampling taking wood microcores (15-mm long and 2-mm thick wood samples) extracted monthly using a Trephor puncher (Rossi et al., 2006). We studied xylogenesis in six tree species (all Tuluá species and *Acosmium* and *Centrolobium* from INPA) by sampling 3–5 individuals per species (Table 1). Microcores were collected monthly at 5–10 cm apart from each other following a zigzag down or up the stem from dendrometers site, to avoid disturbance reactions caused by cambium wounds. Microcores were placed in Eppendorf tubes containing fixative (formalin–ethanol–acetic acid 5:90:5).

In the laboratory, microcores were dehydrated with ethanol and limonene and then embedded in paraffin blocks (Rossi et al., 2006). Then, several transversal sections per microcore were cut at 10–15 μm thickness with a semi-automatic rotary microtome (Leica RM2255). Each section was stained with safranin (0.5 g in 100 ml 96% ethanol), which stains lignified secondary cell walls, and astra blue (0.5%), which dyes primary cell walls, to identify mature and growing tissues, respectively (Cutler et al., 2008). Mounted cross sections were examined under a light microscope (Olympus BH2, Olympus, Tokyo, Japan) to detect recently formed vessels and fibers and to quantify the radial increment of the most recently formed tree ring. Cambial reactivation was determined by detecting the firstly differentiated xylem cells formed after the cambial zone, which was characterized by flattened cells with thin blue-stained walls. During xylogenesis, enlarging vessels also presented thin and green-stained walls, while lignification of vessel walls was detected by their characteristic red staining.

2.5. Analyses of radial increment dynamics based on automatic band dendrometers

High-precision automatic band dendrometers inform on variation in stem water storage and are also useful as indirect monitors of xylogenesis (Bouriaud et al., 2005; Deslauriers et al., 2007, 2003; King et al., 2013; Köcher et al., 2012; Mäkinen et al., 2003; Tardif et al., 2001; Urrutia-Jalabert et al., 2015). To extract the nature of stem radius variation during the growing period, the stem cycle approach was used following algorithms developed by Downes et al. (1999) and Deslauriers et al. (2003). This approach uses stem shrinking and swelling dynamics to split radial increment in three phases: contraction, recovery or expansion and increment (Deslauriers et al., 2003). This last phase has been considered as an estimate of actual growth, i.e. it has been linked to the production of new xylem cells (Deslauriers et al., 2003). We calculated the duration of contraction, recovery and increment phases in hours. We also used the daily mean increment rates to identify the three phases at daily scales. Each phase was related with climatic variables calculated at the same time scales (air temperature, precipitation, water balance, and vapor pressure deficit). We estimated the water balance as the difference between precipitation (*P*) and potential evapotranspiration (PET) following (Hargreaves and Samani, 1982), and the vapor pressure deficit (VPD) was calculated as the difference between saturation vapor pressure and actual vapour pressure. The latter was derived from dewpoint temperature (Allen et al., 1998).

2.6. Statistical analyses

All the variables measured (tree diameter and height, sapwood density, radial increment and soil moisture) were compared among tree species for each study site using one-way ANOVAs. Differences between species were assessed using Tukey and Games-Howell post hoc tests for those cases with or without homoscedasticity, respectively. The relationships between monthly leaf flushing and radial-increment rates and climate data were assessed using Spearman correlations coefficients. Climatic data were summed (precipitation) or averaged (air temperature, water soil and VPD) for the 1, 2, 3, 5, 10, 15 and 20 days before each sampling date and between consecutive samplings. These intervals were selected to detect delayed responses of leaf flushing and radial increment to climate. Kruskal–Wallis tests were performed to compare daily climate variables between the three radial phases (contraction, recovery and increment) for each tree species, and the differences between stem phases for each species were assessed using Mann–Whitney tests (Guisande et al., 2006). The relationships between mean hourly air temperature and the occurrence of each stem phase were analyzed by computing Kendall correlation coefficients (Guisande et al., 2006). All statistical analyses were done using the statistical package SPSS ver. 17.0 (SPSS Inc., Chicago, USA).

3. Results

3.1. Monthly climate, leaf phenology and radial-increment rates

In Tuluá, semi-deciduous species showed leaf flushing and shedding at the same time during most of the study period. However, more than half of study trees in Tuluá formed new leaves during the rainiest period from September to May (wet season), while a low or null production of new leaves was associated with the sharp decline in rainfall recorded during the early dry season in June (Fig. 2a). In INPA, deciduous species started leaf flushing in the early wet season (October), excepting *Amburana*, and showed maximum canopy cover during the wet season (from October to April). Leaf shedding of these species started in the early dry season (May), whilst the semi-deciduous *Aspidosperma c.* hold green foliage during the whole study period (Fig. 2b). The radial increment rate was always positive during the wet season in the two study TDFs, but a severe decrease in the precipitation during the wet season (December in INPA, and January in Tuluá) caused a sharp decline in radial-increment rates leading to negative values in most tree species from INPA (Fig. 2a and b).

In general, high precipitation and a positive water balance were positively related to leaf flushing and radial increment (Fig. 3), indicating that both growth components are limited by water availability. In contrast, both air temperature and VPD showed negative associations with the production of new leaves (excepting in the case of *Amburana*), and radial increment (Fig. 3).

The ways leaf production and radial-increment rates responded to climate were species-specific and time-dependent characteristics. For instance, in *Pithecellobium* and *Zanthoxylum* the production of new leaves responded to all climatic variables evaluated at time-scales shorter than 10 days, whereas *Cedrela* was sensitive to precipitation in almost all analyzed time scales (Fig. 3). Regarding the radial-increment rates, all species responded to precipitation, excepting *Cordia* and *Zanthoxylum* (Fig. 3). In INPA, the radial-increment rate of tree species did not respond significant to temperature and VPD regardless the analyzed time scales, whereas in Tuluá, *Cordia* and *Zanthoxylum* were sensitive to temperature at time scales longer than 20 days (Fig. 3).

The associations between leaf flushing and radial-increment rates were positive for all tree species (Fig. 2a and b). However, the species differed in the strength of these associations as a function of the sapwood density ($r_s = -0.71$, $P = 0.023$, Fig. 2c). For instance, *Cedrela* showed the strongest leaf-stem association and the lowest sapwood density, whilst *Acosmium* presented the opposite characteristics (Table 1, Fig. 2).

3.2. Annual radial increment and monthly growth patterns

Similar cumulative radial-increment patterns were registered based on records from the manual and automatic band dendrometers (Fig. 4; see also Fig. A3a). The radial increment measurements based on dendrometers were always higher than those based on microcores measurements (Fig. 4b, e, g and j; see also Fig. A3b). This confirms that dendrometers did not capture the actual xylem growth detected by microcores. However, in some *Zanthoxylum* individuals we registered similar increment measurements based either on dendrometers or microcores data (Fig. A3b).

The annual radial increment (obtained from manual band dendrometers) and the annual xylem growth (based on microcore data), differed between the two study sites being significantly higher in Tuluá than in INPA (Tuluá, 4.2 ± 0.4 mm year^{-1}; INPA, 1.7 ± 0.2 mm year^{-1}; $t_{\mathrm{dendrometer}} = 5.48$, $P < 0.001$; Tuluá, 2.4 ± 0.4 mm year^{-1}; INPA, 0.8 ± 0.1 mm year^{-1}; $t_{\mathrm{microcore}} = 3.71$, $P = 0.017$). We also found significant differences in both annual radial increment and xylem growth among species (Table 2). The cumulative radial increment always showed an ascending sigmoid tendency in all tree species from Tuluá (Fig. 4a). However, in INPA we detected patterns corresponding to shrinking and swelling processes corresponding to dry and wet periods, respectively (Fig. 4f). At this site the magnitude of the shrinking–swelling patterns was almost as large as half the annual radial increment (Fig. 4f). The most intense shrinking events were registered on late December 2010 (wet season) and July 2011 (dry season), being these two events preceded by at least 20 days with low precipitation values (Fig. 1). In contrast, the majority of the tree species showed the highest swelling event in early April (final of the wet season) after a short but strong rainy period (Figs. 1 and 4f).

3.3. Daily radial-increment dynamics and their relationships with leaf phenology and xylogenesis

The shrinking and swelling processes were also recorded by the automatic band dendrometers at daily scales at both TDFs (Fig. 4b–e, g–j). The increment phase was the most conspicuous in Tuluá trees as compared with the recovery and contraction phases (Fig. 4b–e). At this site, the increment phase occurred when temperature and VPD decreased but precipitation and water balance increased, whilst the contraction phase was characterized by the reverse climatic conditions (Fig. 5). Overall, trees did not show leaf flushing during the contraction and recovery phases (Fig. 4b–e). The increment phase detected since September 2010 corresponded to the formation of new xylem observed in the microcores (Fig. 4b and e). Stem contraction and no leaf flushing coincided with the end of xylem growth in June 2011. Despite we were not able to measure xylem growth in *Phitecellobium* its xylogenesis was similar to that observed in *Zanthoxylum* (Fig. 4d and e). Lastly, we could not detect the onset and final phases of xylem growth in *Cupania* (Fig. 4c).

In contrast with the dominance of the increment phase in Tuluá, the contraction and recovery phases were the most conspicuous in INPA (Fig. 4g–j). Here, the contraction phase was associated to dry periods with elevated VPD, whilst the increment phase occurred during wet periods with low VPD (Fig. 5). The recovery phase was linked to colder periods, while the warmer periods dominated contraction and increment phases. In INPA, the leaf flushing, cambial reactivation and xylem growth occurred during the wet season. The two first increment phases were associated to strong rainy periods in October and November (early wet season). In these periods, leaf flushing began but no xylem growth was detected (Fig. 4g and j). In late December, *Acosmium* and *Centrolobium* showed fully covered crowns and a small xylem growth (Fig. 4g and j). Nevertheless, a strong stem contraction without leaf shedding, associated to a previous short dry period, preceded that first xylem growth (Figs. 1 and 4g and j). During the second half of the wet season (January to March) and late wet season (April) we recorded a third increment phase in *Centrolobium*, which was the most intense and long increment phase and coincided with xylem growth (Fig. 4j). A similar process was also observed in *Acosmium* (Fig. 4g). Since the

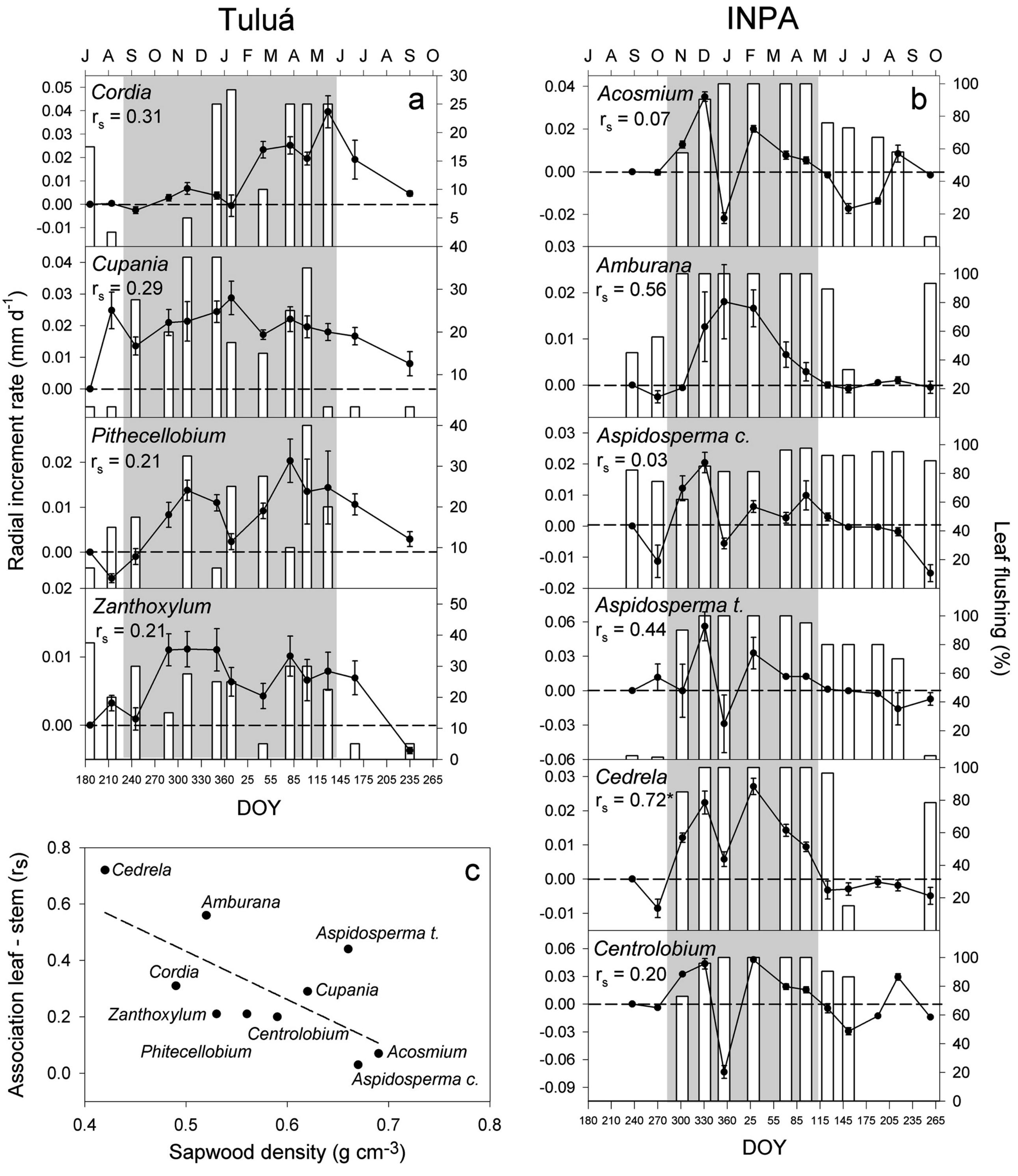

Fig. 2. Monthly leaf flushing (white bars) and radial-increment rates (black lines, values are means ± 1 SE) recorded in two tropical dry forests ((a) Tuluá and (b) INPA) during the study period. The relationships between leaf flushing and radial-increment rate are indicated for each species (r_s, Spearman coefficients; $^*P < 0.05$). These relationships (association leaf-stem) are negatively linked to the stem sapwood density as is shown at the bottom right figure (c). The gray area corresponds to the wet season. DOY stands for the day of the year.

beginning of the dry season (May), we detected the longest contraction phase associated with the end of xylem growth in both *Acosmium* and *Centrolobium* (Fig. 4g and j). During the dry season, foliage was completely lost by deciduous species but leaf shedding was asynchronous. In *Cedrela* the complete leaf loss was very fast (1 month) whilst leaf shedding was gradual in *Acosmium* taking up to 4 months (Fig. 2b).

3.4. Hourly radial-increment dynamics

All tree species showed a daily cycle of stem radius variation (Fig. 6). Species from Tuluá and INPA showed the increment, recovery and contraction phases during the wet season, and two Tuluá species (*Cordia* and *Cupania*) also showed those three phases during the dry season. The three phases aforementioned were

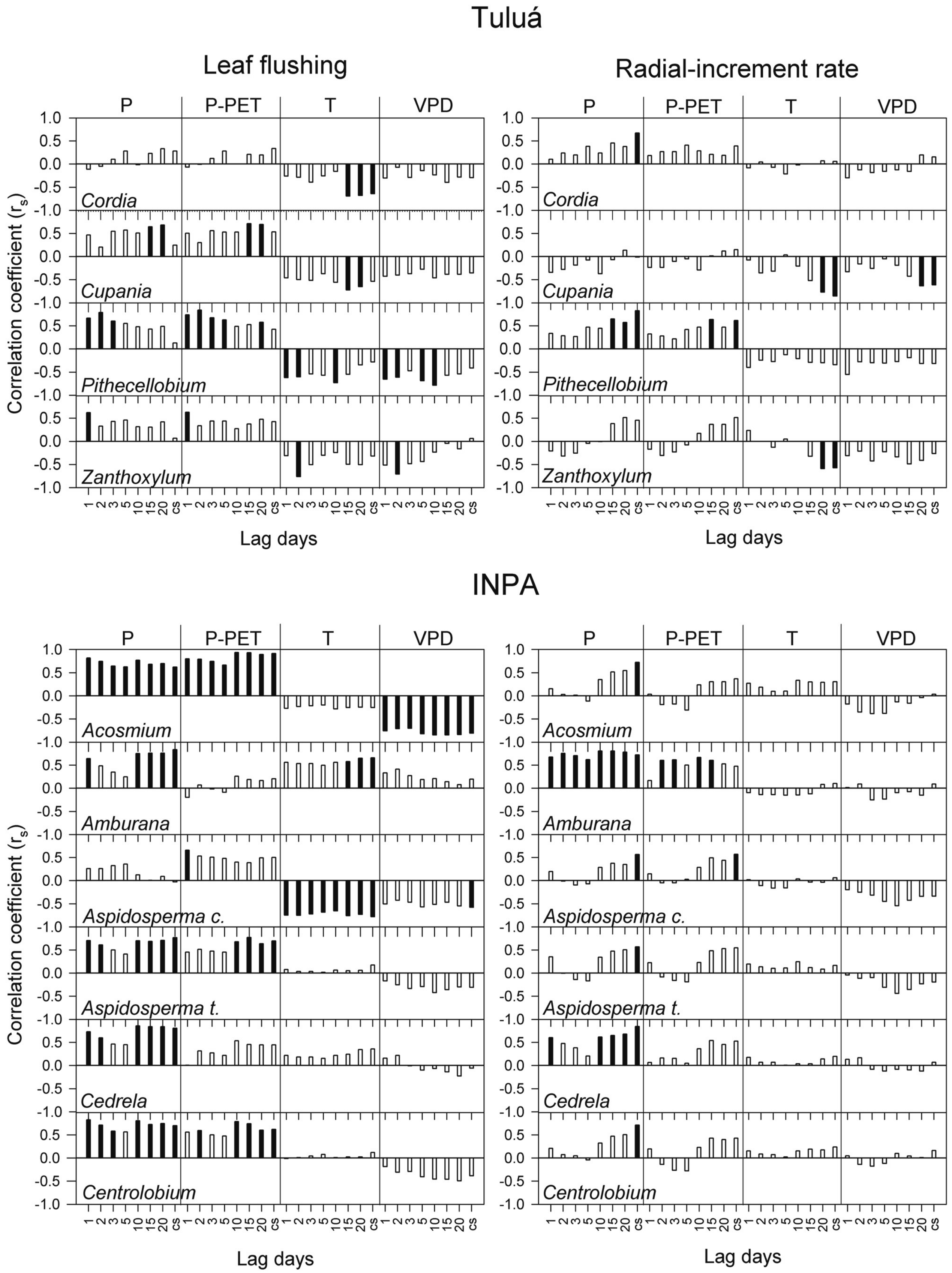

Fig. 3. Relationships calculated (r_s, Spearman coefficients) between leaf flushing, radial-increment rates and lagged climatic variables (*P*, precipitation; P-PET, water balance; *T*, air temperature; VPD, vapor pressure deficit). Lagged climatic data were averaged (*T*, P-PET, and VPD) or summed (*P*) for the 1, 2, 3, 5, 10, 15 and 20 days before each sampling and between consecutive samplings (cs). Significant correlations are indicated by black bars ($P < 0.05$).

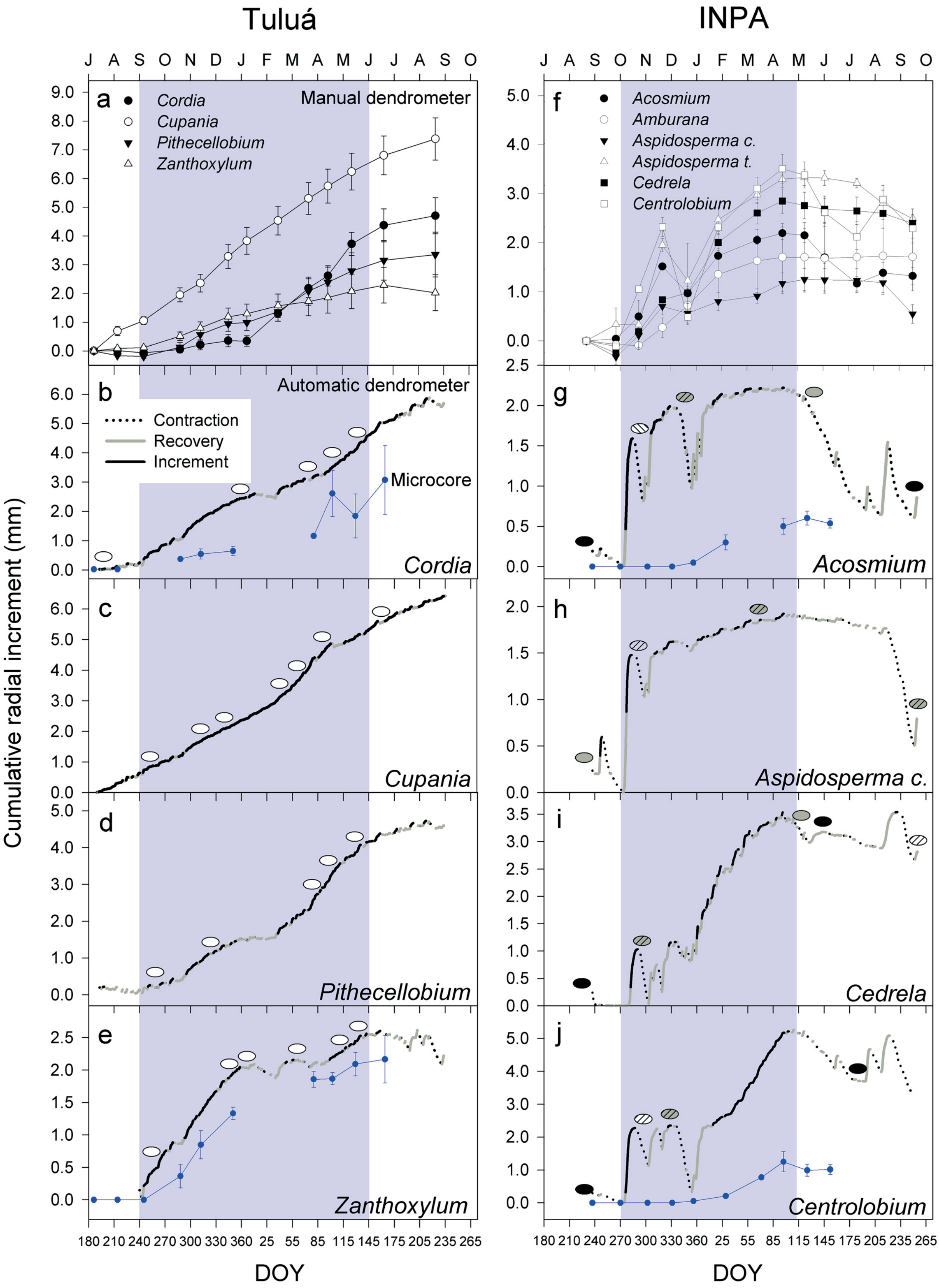

Fig. 4. Cumulative radial increment variations based on manual and automatic band dendrometers and microcores as compared with leaf phenology (ovals). Empty ovals represent production of new leaves in the semi-deciduous tree species from Tuluá, whilst in deciduous tree species from INPA the striped white ovals show the start of leaf production, striped gray ovals represent the crowns fully covered with foliage, gray ovals show the beginning of leaf shedding, and filled ovals indicate total foliage loss. The gray area corresponds to the wet season. Values are means ± 1 SE. DOY stands for the day of the year.

Table 2
Annual radial increment and xylem growth of tree species based on data of manual band dendrometers and microcores, respectively. Values are means ± 1 SE. Means sharing the same letter were not significantly different among tree species of each site (Tukey post hoc tests, $P > 0.05$).

Site	Species	Radial increment (mm year^{-1})	Xylem growth (mm year^{-1})
Tuluá	*Cordia*	4.37 ± 0.57ab	2.85 ± 1.10a
	Cupania	6.81 ± 0.68b	–
	Pithecellobium	3.15 ± 0.69a	–
	Zanthoxylum	2.29 ± 0.63a	2.17 ± 0.37a
INPA	*Acosmium*	1.27 ± 0.19ab	0.54 ± 0.06a
	Amburana	1.71 ± 0.69ac	–
	Aspidosperma c.	0.55 ± 0.19a	–
	Aspidosperma t.	2.49 ± 0.04bc	–
	Cedrela	2.39 ± 0.30c	–
	Centrolobium	2.29 ± 0.29bc	1.02 ± 0.15b

time- and temperature-dependent (Fig. 6). During the wet months the contraction-phase peak was associated to high temperatures in all tree species, except *Cupania* (Tuluá) and *Aspidosperma c.* (INPA), who showed the lowest correlation coefficients between occurrence of the contraction phase and temperature (Table 3). Specifically, the common period of contraction phase time occurred between 9 and 14 h in Tuluá, with temperatures being above 21 °C (Fig. 6). In INPA, the contraction phase during the wet season was more delayed as compared with Tuluá, but it was also associated to high temperatures (Fig. 6). The shrinking of the stems occurred when the temperatures were above 28 °C, except in *Cedrela* which showed a threshold of 34 °C. At this site the contraction-phase time lengthened during the dry season, and it was not associated to high temperatures in deciduous species (Table 3, Fig. 6).

In tree species from Tuluá, the increment phase mainly occurred from predawn until early morning and it was associated with low temperatures (Table 3, Fig. 6). In general, tree species showed the increment phase between 1 and 8 h with temperature values ranging between 17 °C and 19 °C. In contrast, INPA tree species showed a less strong negative association between temperature and the occurrence of the increment phase than Tuluá species, being not significant in *Aspidosperma c.* (Table 3). Specifically, most INPA tree species showed the increment phase from morning until afternoon (7–15 h) with temperatures ranging between 21 °C and 27 °C, excepting *Cedrela* with temperatures reaching 32 °C (Fig. 6).

4. Discussion

4.1. Climate controls on leaf phenology and xylogenesis in TDFs

The leaf flushing and xylem growth occurred during the wet season at both TDFs, reflecting the influence of high precipitation and a positive water balance on the development of new leaves and xylem cells. In Tuluá the leaf flushing and xylem growth of the semi-deciduous tree species were overlapped with the wet season, whereas in INPA the xylem growth of deciduous tree species started at the mid wet season, when their crowns were fully covered (Fig. 4). Several studies on radial growth periodicity of tropical tree species have shown that rainfall variation drives the seasonal periodicity of xylem formation (Volland-Voigt et al., 2010; Worbes, 1995). Dendrochronological studies performed in INPA confirm that long-term radial growth of coexisting deciduous tree species is enhanced by high precipitation values and positive water balances, mainly during the wet season (López and Villalba, 2011; Mendivelso et al., 2014, 2013).

In the deciduous *Acosmium* and *Centrolobium* INPA tree species, xylem growth started in December when their crowns were completely covered by new foliage (Fig. 4). Leaf development before xylem growth starts has also been observed in other tropical deciduous tree species (Krepkowski et al., 2011; Marcati et al., 2007, 2006). The relationship among leaf development, xylem growth and wood porosity from temperate forests support our observations, because the cambial activity in ring-porous species begins before or during bud break (Suzuki et al., 1996), whereas in diffuse-porous and semi-ring-porous species, as *Acosmium* and *Centrolobium*, respectively (Table 1), vessel initiation and leaf development coincide (Aloni, 1991; Frankenstein et al., 2005; Sass-Klaassen et al., 2011; Savidge, 2001). All tree species stop growing when the dry season starts at both sites (Fig. 4). Usually tree species from TDFs show a reduced or absent cambial activity after the beginning of the dry period regardless their leaf habits (Worbes et al., 2013). This observation suggests that a pause in cambial activity during the dry season because of low moisture availability and high VPD probably drives ring boundary formation (Lisi et al., 2008; Volland-Voigt et al., 2010; Worbes et al., 2013). The leaf development previous to xylem growth observed in *Acosmium* and *Centrolobium* suggests they use the previous-year xylem layers to transport water to the crown for the formation of new foliage. The previously formed xylem could be functional during the next wet season because diffuse-porous (*Acosmium*) and semi-ring porous xylem (*Centrolobium*) are less vulnerable to cavitation than ring-porous xylem (Suzuki *et al.*, 1996).

4.2. Climate controls on reversible stem changes observed at multiple temporal scales

In all species, air temperatures at hourly scales showed a positive and negative relationship with the stem contraction and increment phases, respectively (Table 3). However, the analyzed data do not allow confirming a direct link between temperature and radial-increment dynamics. Air temperature can modulate plant water use through its effects on VPD, evapotranspiration rates and soil water availability. The alternating contraction (shrinkage) and increment (swelling) phases registered at hourly scales during the wet season (Fig. 6) could be related to two main periods of utilization and refilling of sapwood water stores. These stem-increment phases fluctuate according to diurnal changes of environmental conditions (Goldstein et al., 1998; King et al., 2013; Krepkowski et al., 2011; Turcotte et al., 2009). During the early hours of the day, the studied tree species probably use firstly water stored in branches (Goldstein et al., 1998; Schulze et al., 1985). Then, once water stored in branches is finished up, the high transpiration rates associated with rising VPD values at midday force trees to use the remaining water stored in the stem. The synchronization between the contraction phase and high temperatures in most study tree species indicates that evapotranspiration and water loss through the canopy trigger stem shrinkage (Fig. 6). Later, the internal water stores in the stem are recharged during late afternoon in Tuluá species (Goldstein et al., 1998) and during the night in INPA species as has been suggested in other tropical forests (Bräuning et al., 2009). During the dry season, only semi-deciduous species from Tuluá and INPA exhibited similar patterns of contraction to those recorded during the wet season (Table 1, Fig. 6). The partial leaf coverage of these species during the dry season may allow them following similar patterns of stem water storage and use as those aforementioned.

The studied tree species showed reversible stem shrinkage at hourly to daily scales (Figs. 4 and 6), but most INPA species also registered reversible stem shrinkage at monthly scales (Fig. 4f), which caused negative radial-increment rates (Fig. 2b). Chitra-Tarak et al. (2015) have shown that at least a part of the temporal variability in annual tree-growth rates arise from reversible, water-induced fluctuations in TDFs. The climate controls on radial-increment dynamics varied between daily and monthly scales. At daily scales, there is a positive effect of high precipitation and a positive water

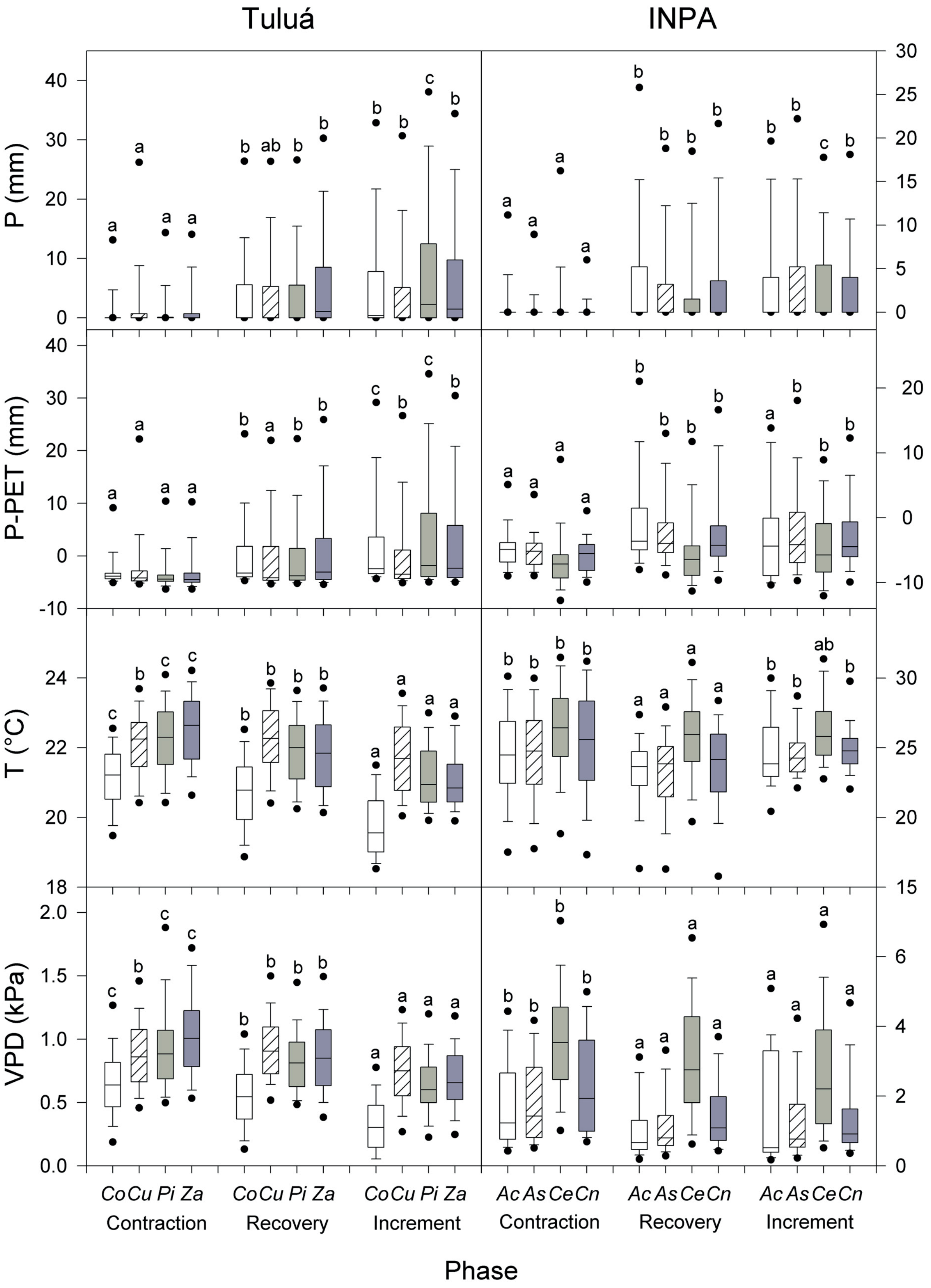

Fig. 5. Variation in climatic variables (*P*, precipitation; P-PET, water balance; *T*, air temperature; VPD, vapor pressure deficit) at different daily stem phases (contraction, recovery and increment) for different tree species (Co, *Cordia*; Cu, *Cupania*; Pi, *Pithecellobium*; Za, *Zanthoxylum*; Ac, *Acosmium*; As, *Aspidosperma c.*; Ce, *Cedrela*; Cn, *Centrolobium*). The letters represent comparisons of the same climate variable among growth phases for each tree species. Values sharing the same letter were not significantly different based on Mann–Whitney tests ($P > 0.05$). The box plots show the median (horizontal line), 5th and 95th percentiles, and outliers.

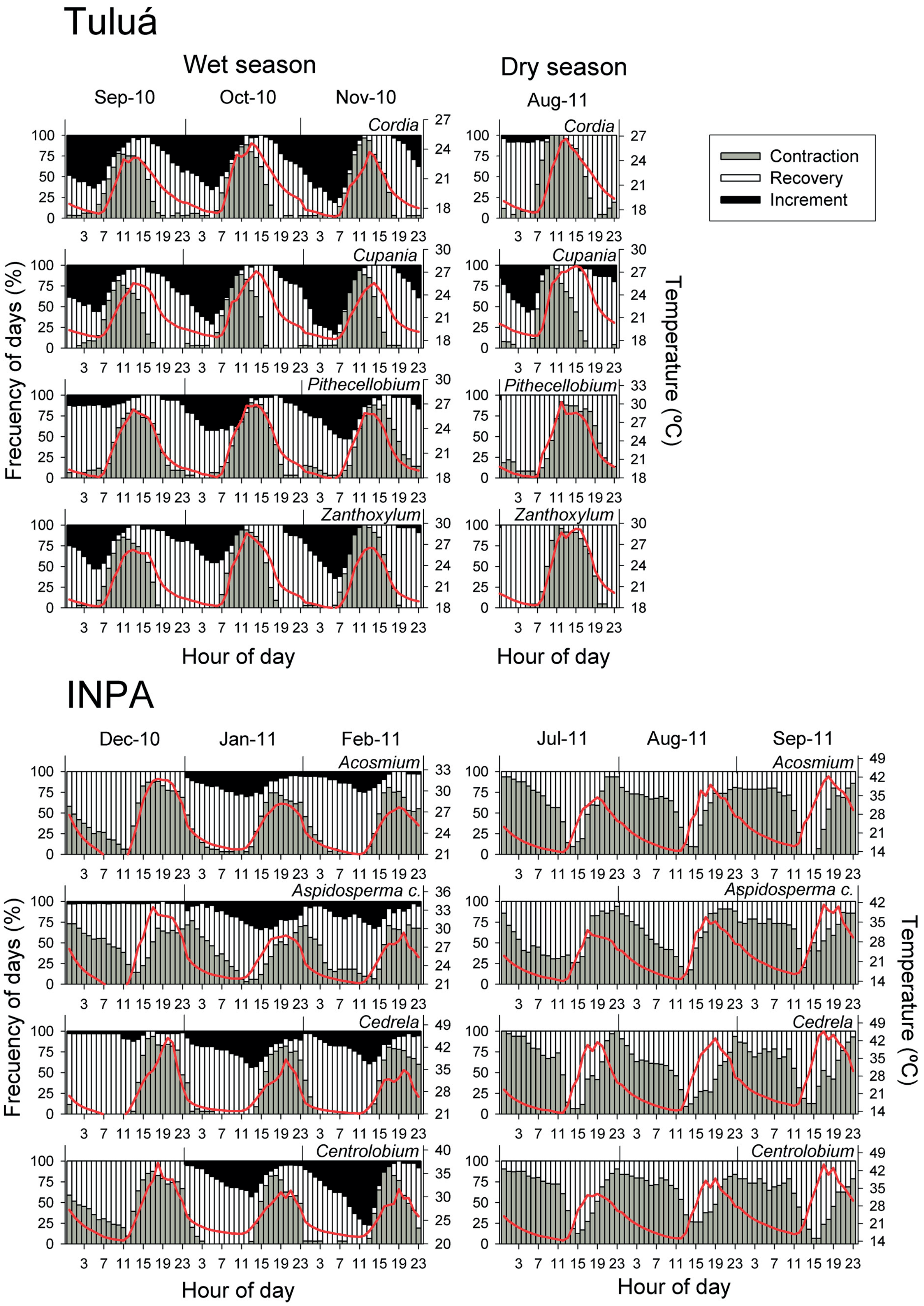

Fig. 6. Hourly changes in stem radius are related to air temperatures during the wet and dry seasons. Plots show daily cycles of stem radius registered by automatic band dendrometers in tree species studied. The three different fills indicate the percentage of days corresponding to the three stem phases (contraction, recovery, increment) inferred from automatic band dendrometer recordings. The red lines show mean hourly temperature (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

Table 3
Relationships observed between mean hourly air temperature and the occurrence of stem contraction, recovery and increment. Values are Kendall correlation coefficients for the wet and dry seasons (see also Fig. 6). Bold coefficients are significant ($P < 0.05$).

Site	Species	Wet season			Dry season		
		Contraction	Recovery	Increment	Contraction	Recovery	Increment
Tuluá	*Cordia*	**0.44**	−0.02	−**0.74**	**0.49**	−**0.36**	−**0.65**
	Cupania	**0.26**	**0.17**	−**0.82**	0.21	0.19	−**0.78**
	Pithecellobium	**0.69**	−**0.47**	−**0.40**	**0.81**	−**0.81**	–
	Zanthoxylum	**0.54**	−**0.19**	−**0.71**	**0.62**	−**0.62**	–
INPA	*Acosmium*	**0.76**	−**0.78**	−**0.44**	0.06	−0.06	
	Aspidosperma	**0.30**	−**0.38**	0.04	**0.42**	−**0.42**	–
	Cedrela	**0.79**	−**0.64**	−**0.32**	0.08	−0.08	–
	Centrolobium	**0.62**	−**0.41**	−**0.68**	−0.17	0.17	–

balance and a negative effect of VPD on the increment phase (Fig. 5), whilst at monthly scales the precipitation was the main variable that positively affecting radial increment (Fig. 3). Accordingly, the differences found in the monthly increment patterns between the wet Tuluá site (persistent increase) and the dry INPA site (reversible swelling; cf. Figs. 2 and 4) appeared to be mainly associated to precipitation variability. Bark could also modulate the large stem fluctuations observed in INPA tree species. In general, the bark has lower density than the sapwood and it is able to store more water in their tissues (Poorter et al., 2014; Rosell et al., 2014; Stahl et al., 2010). We argue that bark traits should be explicitly considered as key features to understand the diverse mechanisms used by trees species to tolerate the adverse effects of drought on radial growth in TDFs.

4.3. Phenological leaf-stem relationships are linked to the stem sapwood density

The positive associations detected between leaf flushing and radial-increment rates differed between species (Fig. 2). This may be related to a different coupling response of leaf and stem to climate (Fig. 3). Thus, in *Cedrela* the high correlation observed between leaf flushing and radial-increment rate can be related to a synchronous response of both processes to precipitation, which was mainly detected at timescales longer than 10 days (Fig. 3). In contrast, the lowest leaf-stem association showed in *Acosmium*, may be linked to the differential response to climate of both processes since leaf flushing responded to precipitation, water balance and VPD at all analyzed time scales, whereas the radial-increment rate was sensitive to changes in precipitation at time scales longer than 20 days (Fig. 3).

Cedrela, a pioneer deciduous species with low sapwood density (Table 1), showed the highest correlation value between leaf flushing and radial-increment rates (Fig. 2). The pioneer and deciduous species with low wood density are more vulnerable to cavitation than shade-tolerant and deciduous species with opposite xylem density values (Markesteijn et al., 2011; Méndez-Alonzo et al., 2012), Thus, *Cedrela* can buffer its vulnerability to cavitation losing rapidly the foliage at the start of the dry season (see in Fig. 2 the sharp decline in leaf flushing in the early dry season). It could be also hypothesized that *Cedrela* counteracts its xylem vulnerability to embolism-induced cavitation by growing in microsites with high soil moisture (Fig. A2), but these ideas should be better evaluated in more tree species and TDFs.

4.4. Annual radial increment and xylem growth in TDFs

The annual radial increment and xylem growth were site- and species-specific. In general, Tuluá tree species showed higher values than INPA tree species (Table 2, Fig. 4). Tuluá shows a shorter and less severe dry season than INPA (Fig. A1). Therefore, tree species in Tuluá display a longer growing season than in INPA. Accordingly, the stem increment phase at daily scales was associated with high rainfall and low temperatures in Tuluá, whilst that phase corresponded to both high rainfall and high temperatures in INPA (Fig. 5). Consequently, an increase of the evapotranspiration rates and VPD during the growing season associated with high temperatures would negatively affect the radial increment of INPA tree species. We also speculate that INPA species could face these adverse environmental conditions by growing during the increment phase identified at hourly scales (Fig. 6), i.e. by restricting growth to periods of the day when temperatures are low and water losses due to evapotranspiration decrease (see Steppe et al., 2015). The negative effect of temperature on tree growth has also been noted in several tropical forests (Clark et al., 2003; Dong et al., 2012; Mendivelso et al., 2014; Pumijumnong and Buajan, 2013). In fact, warming-induced growth decline is more widespread among tropical tree species than in tree species from temperate or boreal forests (Way and Oren, 2010).

5. Conclusions

Leaf flushing, cambium reactivation and xylem growth of tree species occurred during the wet season at both sites, reflecting the influence of high precipitation, a positive water balance and low VPD on the development of new leaves and xylem cells. In the semi-deciduous tree species from the wet Tuluá site the growing period overlapped with the wet season, whereas in deciduous tree species from the dry INPA site the growing period started at the mid wet season, when their crowns were fully covered. Stem shrinkage and swelling were observed at hourly to daily scales in all tree species, but most INPA species also registered strong reversible shrinkage at monthly scales. The strength of the positive association between leaf flushing and radial-increment rates was species-specific and it related to sapwood density. For instance, *Cedrela*, a pioneer deciduous species with low sapwood density, showed the strongest associations between leaf flushing and radial-increment rates, whereas *Acosmium*, a shade-tolerant deciduous species showed the reverse characteristic. In Tuluá the growing season was associated with low air temperatures, while in INPA it was related to high air temperatures. Nevertheless, at both TDFs the high air temperatures registered throughout the day negatively affected radial increment at hourly scales. Tree species could face the adverse dry conditions by growing during the increment phase detected by automatic band dendrometer, i.e. by restricting radial growth to periods of the day when temperatures are low and water loss due to evapotranspiration is reduced. The time-dependent growth responses of TDF tree species to water availability should be explicitly considered to properly forecast their responses to climate warming.

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Appendix A.

Figs. A1–A3.

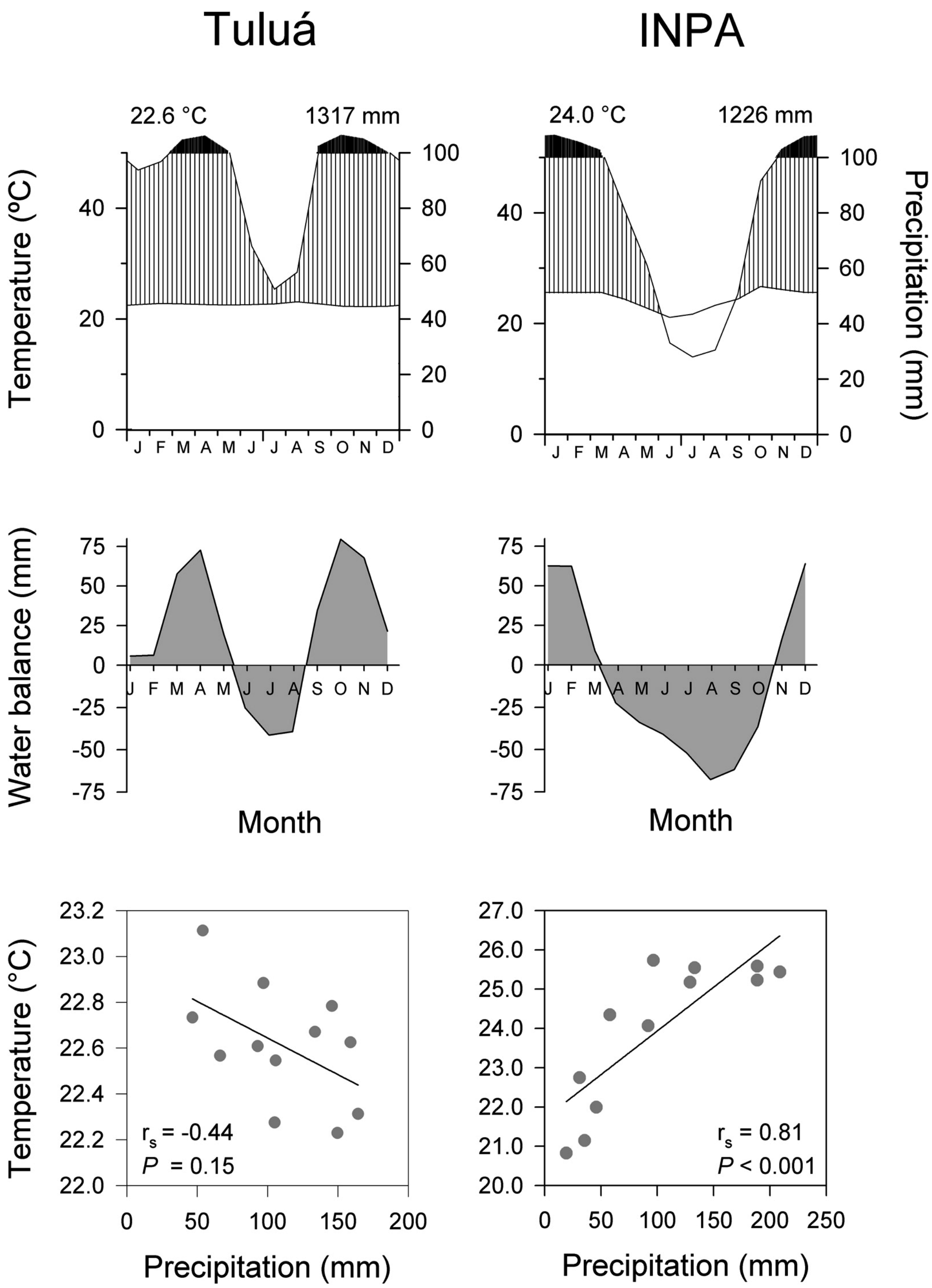

Fig. A1. Climatic diagrams and estimated monthly water balance (P-PET) at two study sites (data correspond to nearby climatic stations for to the 1984–2011 period). The lowermost plots show the relationships between monthly precipitation and temperature values at two study sites (r_s, Spearman coefficients).

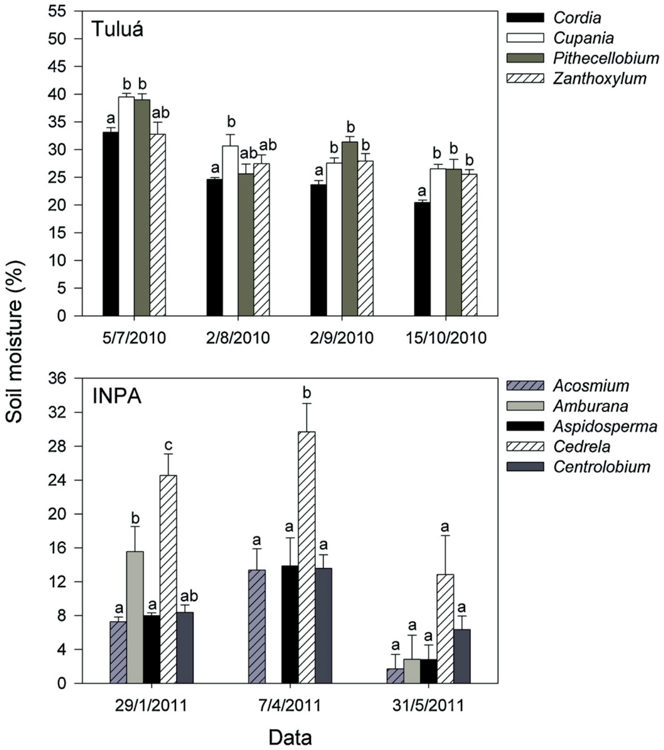

Fig. A2. Soil moisture values measured in the upper 15-cm soil layer at two study sites. The letters represent comparisons of soil moisture values between species during the same day. Values are means ± 1 SE. Means sharing the same letter were not significantly different using Tukey and Games-Howell post hoc tests for those cases with or without homoscedasticity, respectively ($P > 0.05$).

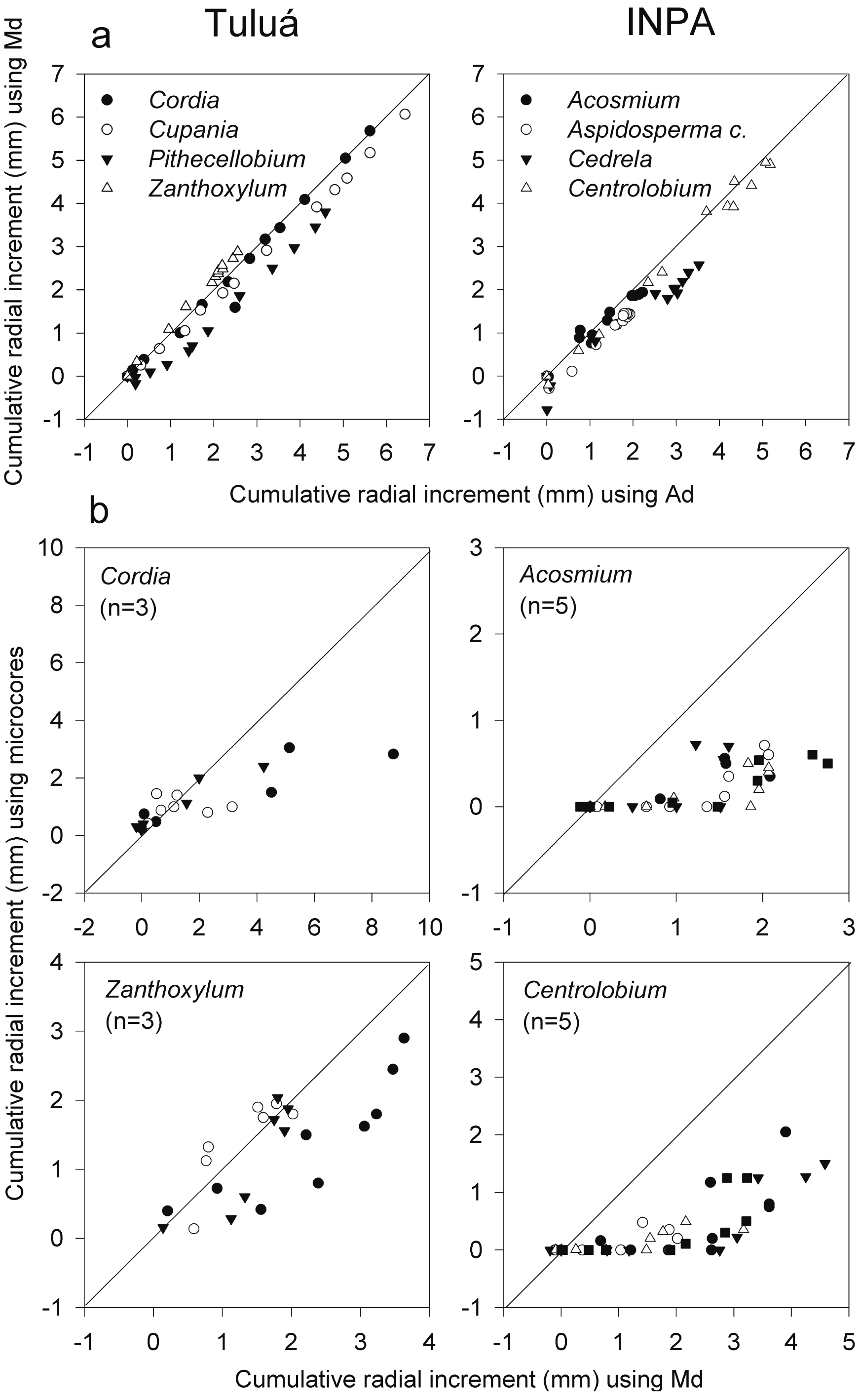

Fig. A3. Relationships between cumulative radial increments estimated (a) using both manual dendrometers (Md, *y* axis) and automatic band dendrometers (Ad, *x* axis), and (b) using microcores (*y* axes) and manual band dendrometers (Md, *x* axes). The diagonal lines show the *x* = *y* relationship. Each symbol corresponds to a different tree.

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Chapter 3

Chiquitano tropical dry forest next to the Precambrian Brazilian shield (Bolivia)

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Time-dependent effects of climate and drought on tree growth in a Neotropical dry forest: Short-term tolerance vs. long-term sensitivity

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ABSTRACT

We analyzed the effects of climate and drought on radial growth using dendrochronology in seven deciduous tree species coexisting in a Bolivian tropical dry forest subjected to seasonal drought. Precipitation, temperature and a multiscalar drought index were related to tree-ring width data at different time-scales (from one month to 42 years). Precipitation affected positively tree growth in all species, mainly during the wet season, while temperature affected it negatively in five species. Tree growth responses to precipitation and temperature were species-specific and peaked at short-time scales, specifically from one to nine months. At inter-annual scales tree growth always responded positively to less dry conditions at short-time scales, particularly from two to seven months, and also at long-time scales from six to 30 years. Tree growth was mainly sensitive to multi-annual droughts and such sensitivity differed among species. Our findings suggest that tree species of the studied tropical dry forest are predominantly sensitive in terms of growth reduction to long-lasting droughts. This time-dependency of growth responses to drought should be explicitly considered as an additional constraint of the community dynamics in evaluations of the future responses of tropical dry forests to climate warming.

1. Introduction

More severe and longer droughts have been observed since the 1970s over tropical and subtropical areas according to the IPCC (2007), and such drying trend has been linked to higher temperatures and increased evaporation. A plausible warmer world with longer and more severe droughts could lead to rapid collapse of tropical forest communities converting them from a net carbon sink into a large carbon source with cascading ecosystem effects affecting global climate-vegetation feedbacks (Lewis, 2006). For instance, severe droughts during the 2000s reduced the net primary production (NPP) in most Neotropical forests (Phillips et al., 2009; Zhao and Running, 2010), being the wood production the most sensitive component of above-ground NPP to the water deficit reduction (Brando et al., 2008). To resolve part of the uncertainty linked to the climate-drought-forest feedbacks we should advance on the understanding of the long-term impacts of droughts on the functioning of tropical forest communities.

Decelerating growth in some tropical forests over the past decades has been associated to altered temperature and precipitation regimes which may modify the amount of water available to trees and consequently drought severity (Feeley et al., 2007). However, the latter study was based on re-measurements of tree diameter changes which limited its retrospective analyses. Such re-censuses studies are usually shorter than 25 years and may render erratic results when the aim is to decipher how tree growth responds to drought severity (Clark and Clark, 2010). Dendrochronology may provide reliable, annually resolved, retrospective and much longer growth records of stem wood production (a reliable surrogate of carbon uptake) in diverse tropical forests than monitoring studies do (Zuidema et al., 2013). Yet obtaining such datasets requires sampling adult canopy-level trees of coexisting tree species responding to water deficit, using appropriate tree-ring proxies and successfully cross-dating (assigning a calendar year to each annual ring) those wood samples (Brienen and Zuidema, 2005; Stahle et al., 1999; Worbes, 2002).

Abbreviations: TDF, tropical dry forest; SPEI, Standardized Precipitation Evapotranspiration Index; AC1, first-order autocorrelation of tree-ring width series; MSx, mean sensitivity; R-bar, mean interseries correlation; EPS, expressed population signal.

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Tropical dry forests (hereafter abbreviated as TDFs) are subjected to annual seasonal drought (Bullock et al., 1995) so they might face more climatic risks related to warming-driven drought stress than wet rainforests, such as rapid aridification transitions toward savanna woodlands (Dirzo et al., 2011). TDFs also constitute one the most endangered tropical ecosystem because they have been intensively converted into farmlands and grasslands (Janzen, 1988). Furthermore, TDFs are diverse ecosystems dominated by drought-tolerant species with varied strategies to tolerate water scarcity (Markesteijn et al., 2011), but there is scarce information on how these species grow in response to drought at multiple temporal scales (Phillips et al., 2010). For example, growth responses to drought change depending on the analyzed time scale in Mediterranean forests with species from xeric sites usually responding to drought at short-time scales (Pasho et al., 2011). Do also tree species from TDFs show contrasting growth responses to drought at different time scales?

Multi-species analyses of tree-rings in TDFs are rare but necessary to understand expected community growth responses to warming and increased aridification. Consequently, we analyzed the effects of climate and drought at different time scales on the radial growth of seven deciduous tree species coexisting in a Bolivian TDF (*Acosmium cardenasii* H.S. Irwin & Arroyo, *Anadenanthera macrocarpa* (Benth.) Brenan, *Aspidosperma tomentosum* Mart., *Caesalpinia pluviosa* DC., *Centrolobium microchaete* (Mart. ex Benth.) H.C. Lima, *Tabebuia impetiginosa* (Mart. ex DC.) Standl., *Zeyheria tuberculosa* (Vell.) Bureau). We related temperature, precipitation, drought severity to indexed tree-ring width chronologies of these species at different time scales ranging from months to decades. The drought severity was quantified using a multiscalar drought index, the Standardized Precipitation Evapotranspiration Index, which explicitly considers the effect of temperature on water availability (Vicente-Serrano et al., 2010). Our specific objectives were: (1) to determine the main climatic variables related to radial tree growth and (2) to evaluate the effects of drought on tree growth at different time scales. We expect that the studied species will show contrasting growth responses to climate and drought at characteristic time scales.

2. Materials and methods

2.1. Study site

The study site is a lowland and seasonally deciduous TDF located 32 km away from Concepción in eastern Bolivia (Fig. 1). The study site (16°07′ S, 61°43′ W, mean elevation of 380 m) is found in a private property of a certified timber company (INPA Parket). This site is also included within the network of long-term research sites of the Instituto Boliviano de Investigación Forestal. The study site belongs to the Chiquitano forest formation, which is considered one of the largest and most diverse TDFs occupying ca. 16.4 millions of ha in Bolivia. Chiquitano forests are located in the transition of the Amazonian lowland evergreen rain forest in the north and the Chaco shrub dry formations toward the south (Killeen et al., 1998). The study site is situated on the Precambrian Brazilian shield and the soils are acid (pH = 5.8), present low organic matter contents (1.42%), and have a sandy-loam texture. The studied forest has an average tree richness of 34 species ha^{-1}, a mean stem density of 437 trees ha^{-1}, and a mean basal area of 19.7 m^2 ha^{-1}, while average canopy height ranges between 20 and 25 m (Mostacedo, 2007; Villegas et al., 2009).

Monthly climatic data (mean air temperature, total precipitation) were obtained from the Concepción station (16°15′ S, 62°06′ W; 410 m a.s.l., period 1949–2009), located about 35 km from the study site. At this station the mean annual temperature is 24.3 °C and the mean total precipitation is 1160 mm. The wet period goes from November to March but the highest rainfall amount is recorded between December and February. The driest period normally goes from June to September but the potential evapotranspiration exceeds precipitation from April to October (Fig. A1).

2.2. Tree species

We sampled the seven most abundant deciduous tree species, they presented well-defined tree ring boundaries delimited by bands of marginal parenchyma (see Mendivelso et al., 2013). The selected species belong to three different families and display contrasting crown positions, shade tolerances and traits such as the leafless period, wood density and sapwood area (Table 1). One of the studied species is restricted to the Bolivian Chiquitano TDF (*Acosmium cardenasii*), whereas the others are found in other Bolivian tropical forests (*Aspidosperma tomentosum*, *Centrolobium microchaete*, *Zeyheria tuberculosa*), or are widespread across the Neotropics (*Anadenanthera macrocarpa*, *Caesalpinia pluviosa*, *Tabebuia impetiginosa*). Because none of the species sampled are congeneric, we used genus names henceforth.

2.3. Field sampling and sample preparation

Wood discs were collected from 7 to 14 living and dominant trees per species with diameters at 1.3 m bigger than 20 cm (Table 2), which were felled for timber collection in 2010 and 2011 (see more details on sampling methods in Mendivelso et al., 2013). In the laboratory, the wood discs were air-dried and polished using sandpapers with increasing grit until the tree rings were clearly visible.

2.4. Dendrochronological methods

Tree-ring series were visually cross-dated by comparing and detecting characteristic rings among radii of the same tree and then by matching the series from different trees of the same species. We measured the ring widths from the most recent ring up to the pith along three to four radii per disk, separated by 90–120° to account for: (i) the eccentric growth of most discs and (ii) the within-tree (among radii) growth variability. Hence, the mean value of the ring widths measured along different radii was considered to represent an average radial-growth series of each tree. We assigned to each ring the calendar year in which ring formation began according to the dating convention for the southern hemisphere (Schulman, 1956). Tree rings were measured with a precision of 0.01 mm under a binocular scope using a LINTAB measuring device (RinnTech, Heidelberg, Germany) associated with the program TSAP (Rinn, 1996). The previous visual cross-dating was checked using the COFECHA program which calculates the correlation between individual ring-width series and a master series for each species (Holmes, 1983). Tree-ring chronologies for the seven species were constructed following a standard dendrochronological protocol. Each raw series was standardized using a Friedman super smoother function (Friedman, 1984) preserving 50% of the variance contained in the measurement series at a wavelength of 20 years and removing non-climatic trends in growth like those related tree aging. This smoothing function is more appropriate than deterministic fixed functions (e.g., negative exponential) for trees whose tree-ring width series are subjected to the influence of forest dynamics such as the case of TDFs (Drew et al., 2012). Standardization involved transforming the measured values into a dimensionless index by dividing the raw values by the expected values given by the smoother function. Autoregressive modeling was carried out on each standardized series to remove part of the temporal autocorrelation. The indexed residual ring-width series were

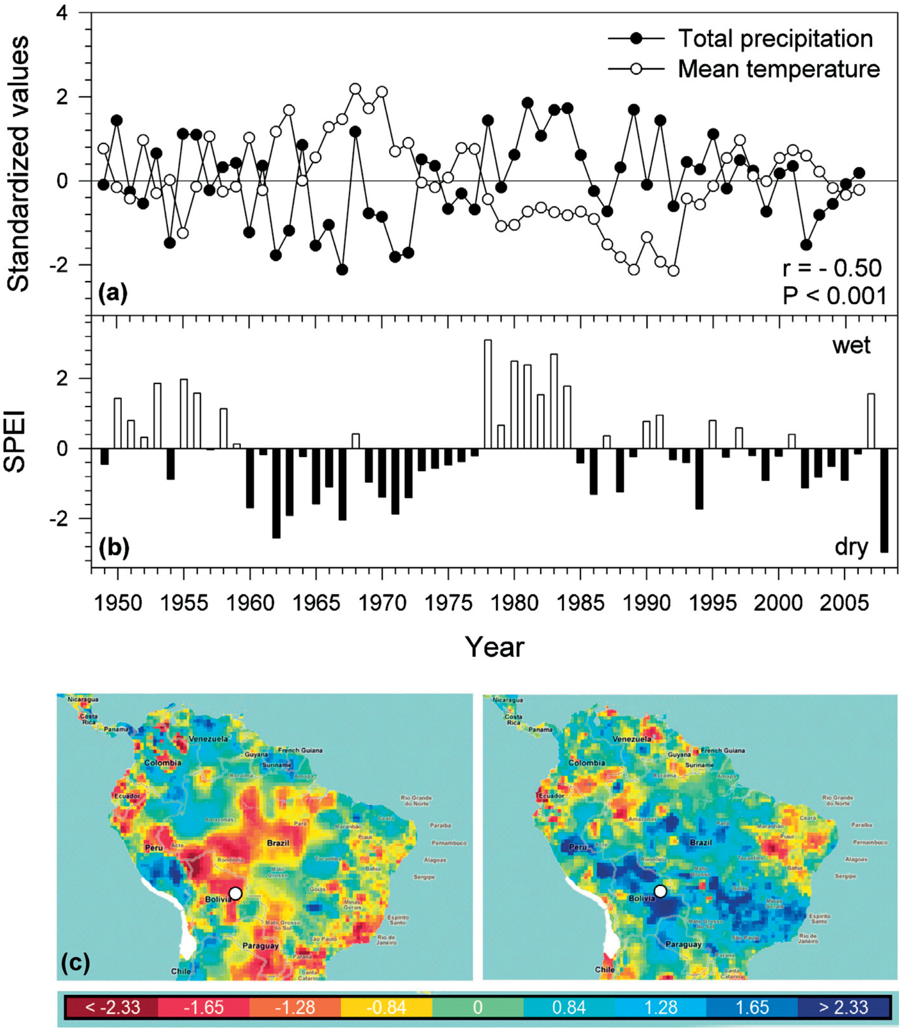

Fig. 1. Temporal (a and b) and spatial (c) patterns of climatic and drought variability in the study area. In the upper graph the relationship between the standardized temperature and precipitation values is indicated with its corrected probability value. The lower maps (obtained from http://sac.csic.es/spei/map/maps.html) show the drought intensity as assessed by the Standardized Precipitation Evapotranspiration Index (SPEI) for a dry (1962, left map) and a wet (1981, right map) year across southern America (the white circle indicates the location of the study area). The lower color scale shows the SPEI classes with red and blue colors corresponding to negative (dry conditions) and positive SPEI values (wet conditions), respectively. The maps and the time series show the 12-months SPEI calculated for September. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

Table 1
Characteristics of the seven tree species studied in a Bolivian tropical dry forest. Values are means ± 1SE.

Species (family)	Crown position	Functional group	Leafless period (months)	Onset of leaf expansion	Diameter at 1.3 m (cm)	Wood density (g cm^{-3})	Sapwood area (%)
Centrolobium microchaete (Fabaceae)	C	LLP	Jun–Oct (5)	Nov	36.0 ± 3.2	0.59 ± 0.02	29.7 ± 2.0
Acosmium cardenasii (Fabaceae)	Sc	TST	Aug–Sep (2)	Oct	29.2 ± 3.9	0.69 ± 0.02	26.6 ± 0.7
Caesalpinia pluviosa (Fabaceae)	C	PST	Aug–Sep (2)	Oct	46.5 ± 3.7	0.79 ± 0.01	23.2 ± 2.4
Aspidosperma tomentosum (Apocynaceae)	Sc	PST	Jul–Sep (3)	Oct	26.9 ± 4.6	0.66 ± 0.01	28.1 ± 1.2
Zeyheria tuberculosa (Bignoniaceae)	C	LLP	Oct–Nov (2)	Dec	38.2 ± 3.6	0.61 ± 0.01	42.6 ± 2.2
Anadenanthera macrocarpa (Fabaceae)	E	LLP	Jun–Oct (5)	Nov	42.1 ± 2.9	0.71 ± 0.05	25.3 ± 3.4
Tabebuia impetiginosa (Bignoniaceae)	C	LLP	Jul–Sep (3)	Oct	43.3 ± 3.4	0.74 ± 0.04	26.8 ± 1.2

Crown position, functional group and some leafless period data were taken from Mostacedo (2007) and Villegas et al. (2009), whereas the leafless period, wood density and sapwood area were taken from Mendivelso et al. (2013). *Abbreviations*: C. Canopy; Sc, Sub canopy; E, Emergent; LLP, long-lived pioneers; TST totally shade-tolerant, PST, partially shade-tolerant.

Table 2
Dendrochronological statistics of the seven tree species studied in a Bolivian tropical dry forest. Values are means ± 1 SE while in the case of age the range is displayed.

Species	Tree variables		Raw data		Residual chronologies		
	No. trees/radii	Age (years)	Tree-ring width (mm)	AC1	MSx	R-bar	EPS
Centrolobium	14/42	71–109	1.50 ± 0.08	0.47	0.34	0.26	0.94
Acosmium	11/38	71–128	1.93 ± 0.10	0.54	0.25	0.24	0.92
Caesalpinia	8/31	91–176	1.56 ± 0.09	0.15	0.50	0.15	0.84
Aspidosperma	8/24	56–96	1.16 ± 0.05	0.51	0.26	0.23	0.86
Zeyheria	7/21	65–137	1.70 ± 0.14	0.51	0.40	0.20	0.83
Anadenanthera	8/24	80–155	1.36 ± 0.07	0.39	0.33	0.19	0.85
Tabebuia	7/24	59–129	2.37 ± 0.11	0.47	0.30	0.17	0.83

Statistics: AC1, the first-order autocorrelation of ring-width series; MSx, mean sensitivity; R-bar, mean interseries correlation; EPS, expressed population signal.

then averaged to obtain mean site chronologies with 95% bootstrapped confidences limits for each species. We used the program ARSTAN 41d (Cook and Krusic, 2007) to obtain the chronologies of ring-width indices (Cook, 1985), which were used in all subsequent analysis.

The characteristics of the tree ring chronologies were evaluated for the common period 1949–2008 using several dendrochronological statistics (Briffa and Jones, 1990): the first-order autocorrelation (AC1) of raw ring-width series which measures the year-to-year growth similarity; the mean sensitivity of indexed ring-width series (MSx) which quantifies the year-to-year variability in width of consecutive rings; the, mean inter-series correlation (R-bar), and the expressed population signal (EPS) which assess the among-trees coherence in growth and the statistical quality of the mean site chronology as compared with an infinitely replicated chronology, respectively (Table 2). The period of the residual chronologies showing EPS ≥ 0.80 (1949–2008) was considered to be well replicated and used in further analyses, despite the 0.85 threshold is usually employed for non-tropical tree species (Wigley et al., 1984). Lastly, we summarized the growth variability among species by performing a Principal Components Analysis based on the covariance matrix built using the residual ring-width series for the common period 1949–2008.

2.5. Statistical analyses

The climate–growth relationships were evaluated at time scales ranging from 1 to 12 months to assess the effect of changes in the total precipitation and mean temperature on the annual variation of tree-ring width indices. To relate growth to climate first we defined the biological growth year of the tree species from October to September (Fig. A1) based on previous phenological studies (Mostacedo, 2007) and dendrometer records of radial increments (H.A. Mendivelso & J.J. Camarero, unpublished results). This characterization agrees with the definition of the hydrological year in the study area (Ronchail, 1995). Bootstrapped correlation analyses were performed to evaluate the relationships between residual ring-width chronologies of each species and 78 climatically different periods using the software Dendroclim2002 (Biondi and Waikul, 2004). We used Pearson correlation coefficients and performed 999 permutations of the data. Each period was based on different months and time scales (1–12 months), and climatic variables were either averaged (temperature) or summed (precipitation). Since we were not concerned with the simultaneous testing of all correlations no Bonferroni correction was applied to significant levels (Perneger, 1998).

To quantify the impact of drought on tree growth we employed the multiscalar Standardized Precipitation Evapotranspiration Index (SPEI; Vicente-Serrano et al., 2010). The use of the SPEI is relevant to quantify the effects of droughts on growth at different time scales (Vicente-Serrano et al., 2013). For instance, in drought-stressed periods (negative SPEI values) tree growth would decline, whereas in humid periods (positive SPEI values) tree growth would be enhanced. The SPEI data were obtained from the SPEIbase (http://sac.csic.es/spei/database.html), with a 0.5° spatial resolution.

First, to analyze short-term growth responses to drought we carried out Pearson correlation analyses by relating ring-width indices and SPEI considering different months and time-scales (1–24 months). The SPEI time-scale showing the highest correlation to growth indices was kept for the following analyses. Second, to analyze the multi-year responses to droughts we related the raw tree-ring width chronologies to the SPEI time-scale selected in the first step. Smoothed SPEI and growth were obtained through a locally weighted polynomial regression (LOESS) (Cleveland, 1979). The first order polynomial (linear) and bandwidth methods (nearest neighbors) were used for LOESS fits. A wide range of the α smoothing parameter ($0.1 \leq \alpha \leq 0.7$), which determines the proportion of observations that is used in each LOESS fit, was used for capturing different time-scales corresponding to different smoothing intensities. Correlation analyses were performed to determine the smoothed growth scale most tightly related to the SPEI, i.e., that showing the highest and significant correlation (Fig. A2). Since the probability values (P) of these Pearson coefficients are affected by temporal autocorrelation we calculated corrected P values using the Correltool software (available at http://oxlel.zoo.ox.ac.uk/reconstats) which estimates and models the temporal autocorrelation present in the compared time series (Macias-Fauria et al., 2012).

Finally, we divided the study period (1949–2008) in four different long-periods with contrasting multi-year water-availability conditions and SPEI values (ANOVA, $F = 17.62$, $P < 0.001$): two wet long-periods (1949–1959 and 1978–1984) and two dry long-periods (1960–1977 and 1985–2008) (see Fig. 1). SPEI and ring-width values for each species were compared between long-climatic periods using one-way ANOVAs, and differences between long-periods were assessed using Tukey post hoc tests. The first wet long-period (1949–1959, SPEI = 0.7 ± 0.3) was less wet (Tukey $t = 1.38$, $P = 0.014$) than the second one (1978–1994, SPEI = 2.1 ± 0.3), while the first dry long-period (1960–1977, SPEI = −1.0 ± 0.2) was not significantly drier than the last one (1985–2008, SPEI = −0.7 ± 0.2). On average, the wet long-periods were shorter (7–11 years) than the dry long-periods (18–24 years). All statistical analyses were done with SPSS 17.0 (SPSS Inc., Chicago, USA).

3. Results

3.1. Growth characteristics and dendrochronological statistics

Considering the common period 1949–2008, the mean ring width of the study species ranged between 1.16 mm in *Aspidosperma* (partially shade-tolerant) and 2.37 mm in *Tabebuia* (long-lived pioneers) (Table 2). *Acosmium*, *Aspidosperma* and

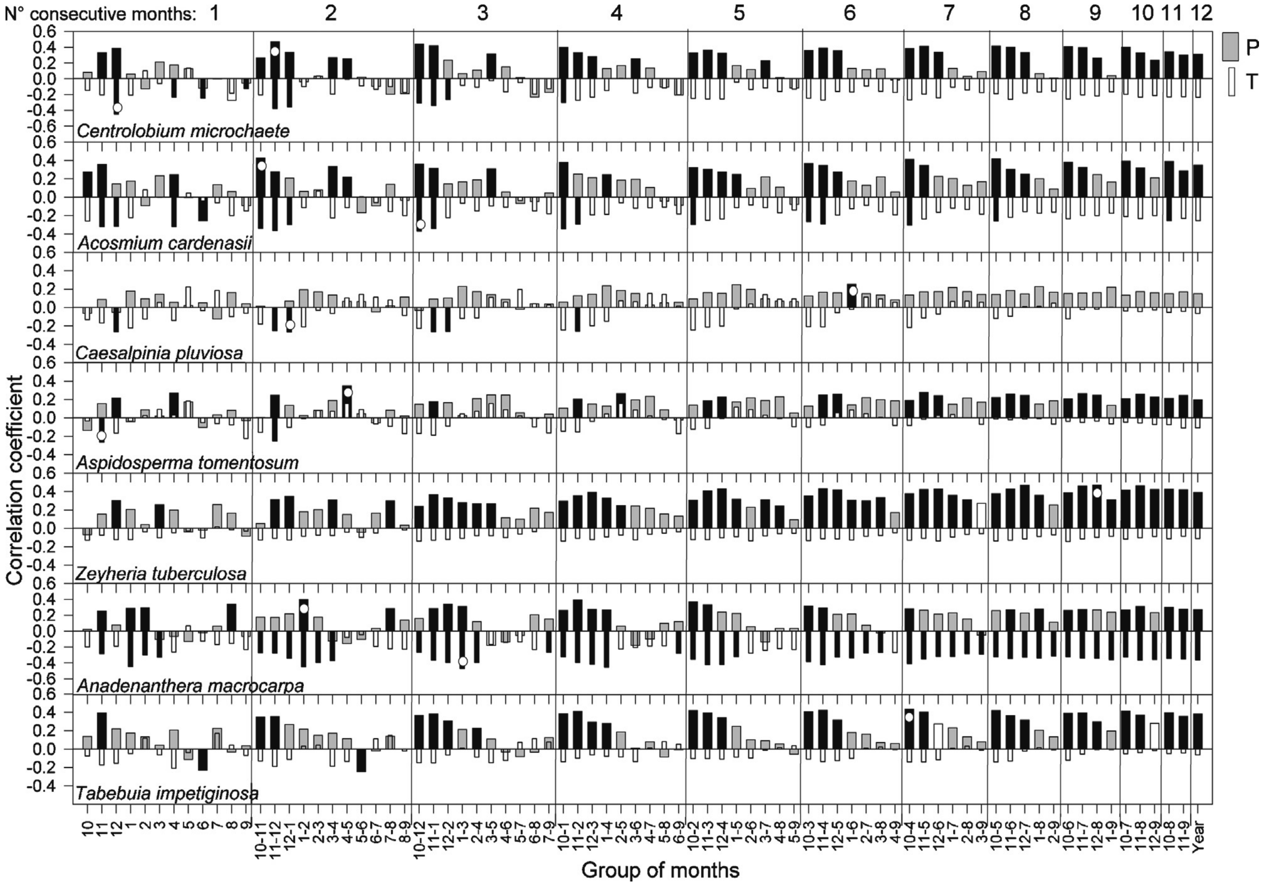

Fig. 2. Correlations (Pearson coefficients) calculated between climatic variables (P, total precipitation, wide gray bars; T, mean temperature, thin empty bars) and residual tree-ring width chronologies for the common period 1949–2008. The month or group of months used for computing climate data are indicated by numbers in the lowermost *x* axis and they are arranged considering consecutive months (from 1 to 12 months, see uppermost *x* axis). Climatic variables were summed (P) or averaged (T). Significant bootstrapped correlations are indicated by black columns and the highest correlations are highlighted by white circles.

Zeyheria had the highest first-order correlation values in ring-width, whereas the highest mean sensitivity was observed in *Caesalpinia* and *Zeyheria*. The mean correlation between the individual series of each species varied from 0.15 in *Caesalpinia* to 0.26 in *Centrolobium*. The first two components of the Principal Components Analysis accounted for 40.3% and 16.0% of the total growth variance (Fig. A3). All species had positive values in the first component indicating that they share high common growth variability in response to climate.

3.2. Relationships between climate and growth

In all studied species the precipitation was positively related to growth, while temperatures showed negative associations in five species (Fig. 2). Overall, the precipitation explained from 6.4% (*Caesalpinia*) to 22.0% (*Centrolobium* and *Zeyheria*) of the inter-annual variation in growth indices, while temperature accounted for 7.1% (*Aspidosperma* and *Caesalpinia*) to 22.5% (*Anadenanthera*) of that variation. In particular, *Caesalpinia* and *Aspidosperma* showed the lowest number of significant correlation coefficients between climatic variables and ring-width indices. All tree species showed time-dependent responses of growth indices to precipitation. Specifically, *Acosmium*, *Anadenathera*, *Aspidosperma* and *Centrolobium* showed the highest correlation coefficients at bimonthly scales, while *Caesalpinia*, *Tabebuia* and *Zeyheria* showed the highest coefficients at longer scales (from six to nine months). In general, the strongest growth responses to precipitation were observed for those months included within the wet season from November to March, except in *Aspidosperma* where the highest correlation between growth indices and precipitation occurred from April to May, i.e., during the transition from the wet to the dry season.

Regarding air temperature, *Tabebuia* and *Zeyheria* did not respond to temperature at any analyzed time scale, while the emergent *Anadenathera* responded to temperature changes at monthly to annual scales. The remaining species showed negative growth-index responses to temperature from one to three months scales (Fig. 2). The highest correlations, in absolute terms, were detected at monthly or trimonthly scales, mainly during the wet season, i.e., from November and December (*Acosmium*, *Aspidosperma*, *Caesalpinia* and *Centrolobium*) up to January and March (*Anadenathera*) (Fig. 2).

3.3. Relationships between the drought index and growth

The strongest relationships observed between the SPEI and growth indices were always positive irrespective of the analyzed time scale indicating that growth is severely limited by water deficit (Fig. 3). The highest correlations were recorded at bimonthly scales in *Aspidosperma* ($r = 0.54$) and *Acosmium* ($r = 0.48$), while *Tabebuia* presented the highest correlation ($r = 0.42$) at seven-month scales (Fig. 3). The SPEI-growth correlations were usually observed for months of the wet season (*Acosmium*, *Centrolobium*, *Caesalpinia*, *Anadenanthera*, *Tabebuia*) or during the transition from the wet to the dry season (*Aspidosperma*, *Zeyheria*).

At long-time scales, the highest correlations between smoothed SPEI and growth data were observed in *Anadenanthera* ($r = 0.94$)

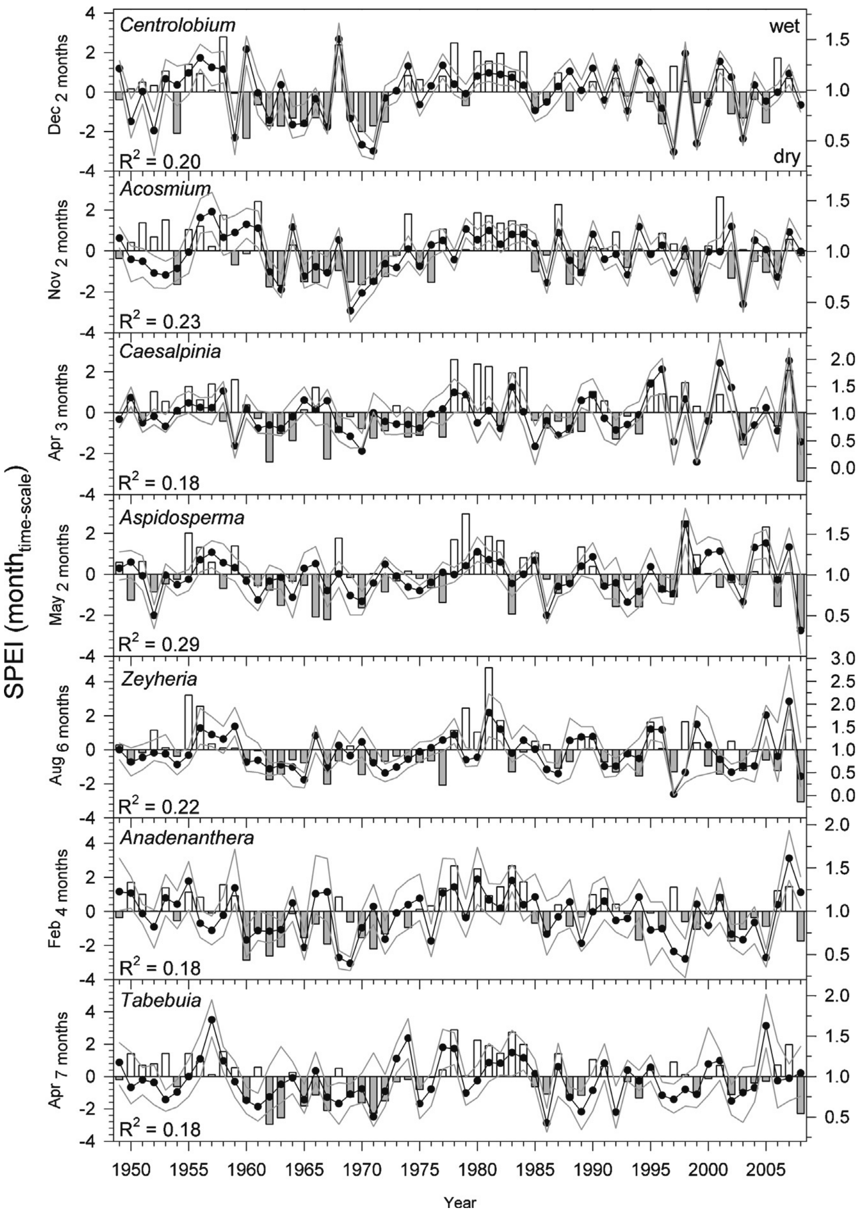

Fig. 3. Highest correlations found between residual ring-width chronologies (lines with symbols and bootstrapped 95% confidence limits) and SPEI (bars). The month and time-scales (subscripts) where the highest correlation was found is shown on the *y*-axis labels for each species. Positive and negative SPEI values correspond to wet (empty bars) and dry (filled bars) conditions, respectively. All presented coefficients of determination have $P < 0.05$.

and *Aspidosperma* ($r = 0.83$) with smoothing parameters (α) corresponding to 30- ($\alpha = 0.5$) and 18-years ($\alpha = 0.3$) long scales (Fig. 4). The remaining species presented significant growth responses to SPEI at 12- ($\alpha = 0.2$) and 6-years ($\alpha = 0.1$) long scales, excepting *Caesalpinia* which did not show any significant response (Fig. A2). The SPEI explained from 17.5% (*Anadenanthera*) to 28.9% (*Aspidosperma*) of the growth variance at short-time scales (from two to seven months) while at long time scales (from six to 30 years) from 44.8% (*Tabebuia*) to 87.9% (*Anadenathera*) of the growth variance was explained by that drought index (Figs. 3 and 4).

There were statistically differences in tree-ring width for all species when comparing the four long sub-periods with different SPEI values, excepting in the case of *Caesalpinia* ($F = 2.64$, $P = 0.058$). Lower tree-ring width values were observed in the two dry sub-periods (1960–1977, 1985–2008), while the highest growth values occurred during the wettest and longest sub-period (1978–1994) (Fig. 5).

4. Discussion

4.1. The inter-annual precipitation partially explains the variation of the tree growth

The different growth responses of the study species to precipitation can be quantified by considering either (i) the timing or period when the strongest response to precipitation is observed or (ii) the magnitude of that response, i.e., the value of the precipitation-growth correlation which can be regarded as a surrogate of growth sensitivity to precipitation. We found that the strongest responses of growth indices to precipitation and drought were observed in the wet season or during the transition from the wet to the dry season, which implies that growth was constrained by water availability. In TDFs, deciduous tree species show maximum rates of photosynthesis and hydraulic conductivity during the wet season which agrees with our findings (Eamus and Prior, 2001). However, we found diverse growth responses to water availability among coexisting

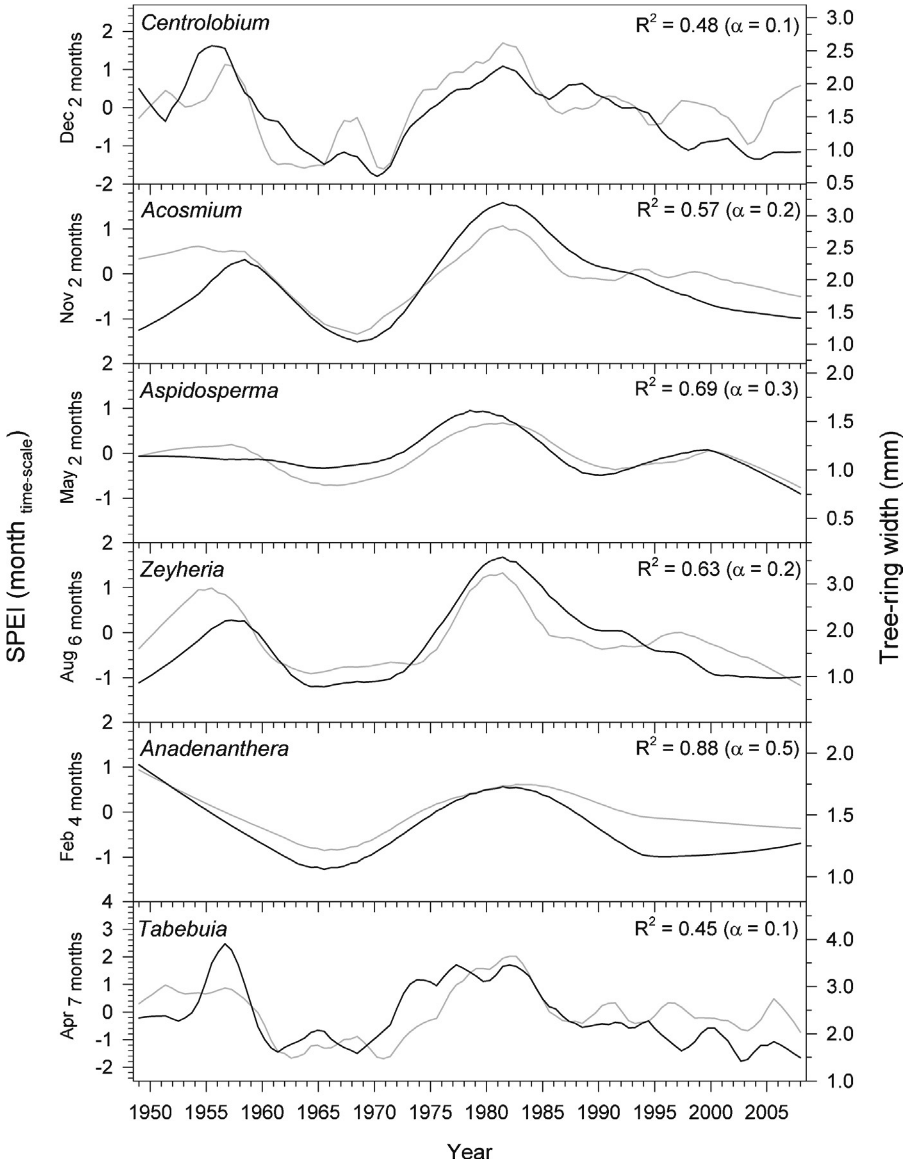

Fig. 4. Highest long-term relationship found between tree-ring widths (black lines) and drought severity assessed through the SPEI (gray lines). All presented coefficients of determination have $P < 0.05$. The smoothing parameter (α) gives the proportion of the displayed period (1949–2008, 59 years) considered by the LOESS smoother (e.g., $\alpha = 0.5$ is equivalent to a 30-year long period). *Caesalpinia* is not shown because it was not observed any statistically significant long-term association between growth and the SPEI drought index (see Fig. A2).

tree species indicating species-specific responses of wood formation to water availability in TDFs (Borchert, 1999, 1994; Enquist and Leffler, 2001; Rozendaal and Zuidema, 2011; Worbes, 1999).

Several species' growth reacted to water availability during the early wet season from November to December (*Acosmium*, *Centrolobium*, *Tabebuia*, *Zeyheria*) indicating a rapid growth increment in response to the increase of water availability. This could be related to efficient root and hydraulic systems which rapidly capture and transport water to the buds triggering the flush of new leaves and the beginning of the production of new xylem cells. In the other species studied, growth indices responded to precipitation in the mid to late wet season or even in the transition to the dry season despite they flushed in October (*Aspidosperma*, *Caesalpinia*) or November (*Anadenanthera*). This lagged response suggests a long process to rehydrate the xylem and reactivate cambial activity (Borchert, 1999). The rapid production of new leaves in the early wet season suggests the existence of efficient shallow roots. In TDFs the upper soil layers are the main source of water captured by root systems of adult trees (Meinzer et al., 1999; Goldsmith et al., 2012) which indicates that rooting depth may not be a major trait determining growth responses to precipitation.

The most and least responsive species in terms of growth-index associations with precipitation were *Centrolobium* and *Zeyheria*, and *Caesalpinia*, respectively. The most sensitive species responding to precipitation require more water and a more efficient water transport for growth than less sensitive species. In TDFs deciduous tree species show more variable hydraulic-conductivity patterns than brevi-deciduous or evergreen species (Brodribb et al., 2002). According to these authors, during the transition from the dry to the wet season, a first group of deciduous species exhibit huge changes in their stem hydraulic conductivity, while a second group of deciduous and evergreen species show minor changes. We consider that *Centrolobium* and *Zeyheria*, species showing the highest growth sensitivity to precipitation, can exhibit hydraulic patterns

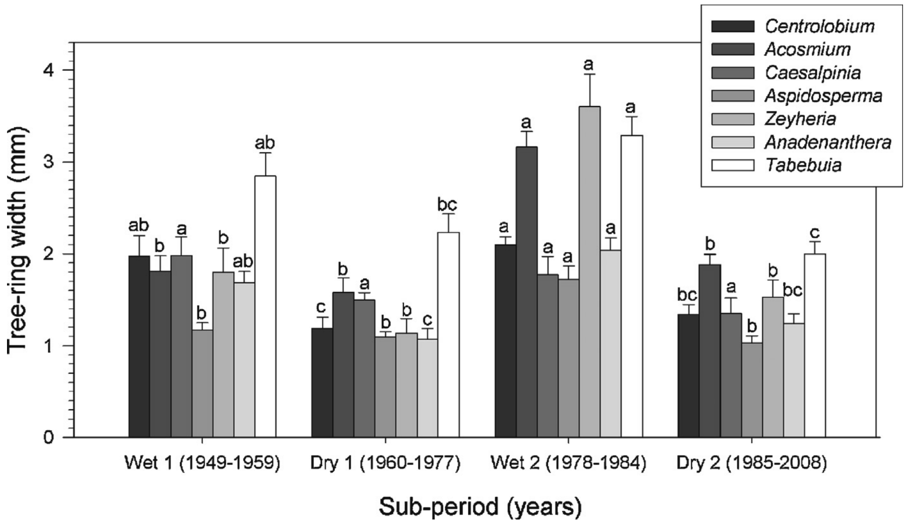

Fig. 5. Comparison of mean tree-ring widths (mean ± 1SE) obtained for the four sub-periods with contrasting drought severity (two wet sub-periods and two dry sub-periods) as assessed by the SPEI. Columns with different letters correspond to means showing significantly differences in tree-ring width between sub-periods for the same species ($P < 0.05$).

similar to those reported by Brodribb et al. (2002) for the first deciduous tree species, whereas the least sensitive species (*Caesalpinia*) could behave similarly to the second group of species. In fact, the wood densities of *Centrolobium* and *Zeyheria* are within the optimum range for hydraulic efficiency reported by Kallarackal et al. (2013). Moreover, the different sensitiveness to precipitation can be related to traits determining water use and storage. TDF tree species which have a less dense wood and produce more sapwood (p.e. *Zeyheria*) may store more water in their stems, therefore these species should show a high sensitivity in terms of growth changes to water availability (compare Table 1 and Fig. 2; see also Mendivelso et al., 2013). Species showing the reverse characteristics (denser wood and less sapwood) could store less water therefore should be the least responsive to water availability (p.e. *Caesalpinia*).

Despite precipitation was the climatic variable most strongly related to growth, it only accounted for a low amount of growth variance ranging from 6.4% in *Caesalpinia* to 22.0% in *Zeyheria*. Similar results were observed in other TDFs (Enquist and Leffler, 2001; López and Villalba, 2011; Paredes-Villanueva et al., 2013). This finding may be explained by the different strategies used by tree species to tolerate drought in TDFs and to buffer the negative effects of the dry season on growth (Worbes et al., 2013). For instance, the loss of leaves in response to dry conditions reduces the transpiration rates and rehydrates stems as has been observed in the group of "deciduous softwood" trees species defined by Borchert (1994), which included all the study species. In this respect, *Zeyheria* was drought tolerant species being able to keep its leaves during the whole dry season, while the rest of species avoid drought by losing their leaves during most of the dry season (*Anadenanthera*, *Centrolobium*) or during the driest months (*Acosmium*, *Caesalpinia*, *Aspidosperma*, *Tabebuia*). Of course, unusual dry or wet periods occurring during the wet or dry seasons, respectively, could alter these patterns indicating a high phenological plasticity of TDF tree species (Borchert et al., 2002).

4.2. Relationships between growth and temperature in TDFs: a latitudinal effect

We observed negative responses of growth indices to air temperature in five species mainly at monthly or trimonthly scales during the wet season, when the highest mean temperatures are registered (Fig. A1). Despite some of these growth responses to temperature may be caused by indirect effects on evaporative forcing our analyses based on the SPEI drought index already accounted for those effects. In terms of growth responsiveness *Anadenanthera* was the most sensitive species to temperature which may be related to the fact that it is an emergent species whose crowns are usually completely exposed to elevated radiation levels.

Few studies have evaluated the long-term growth responses to temperature in tropical forests (Clark and Clark, 2010; Dong et al., 2012) and particularly in TDFs. Perhaps this is due to the low intra-annual variability of temperature in the tropics compared with extratropical areas. The latitudinal distance to the equator determines the intra-annual variability of thermal conditions in TDFs (Eamus, 1999). Apparently, species that grow near the equator do not respond to temperature, probably because of the low inter-monthly variability of temperature (<3 °C) in those areas. For example, *Juniperus procera* located at 9° N in Ethiopian TDFs (Sass-Klaassen et al., 2008) and *Zanthoxylum rhoifolium* located at 4° N in Colombian TDFs (H.A. Mendivelso, personal observations) showed no responsiveness of radial growth to temperature variability. However, in the studied Bolivian TDFs located at 16° S, showing an inter-monthly variability of temperature of about 5 °C, six out of the seven study species showed negative growth responses to temperature mainly during the wet season. This was also reported for nearby *Centrolobium microchaete* and *Machaerium scleroxylon* stands (López and Villalba, 2011; Paredes-Villanueva et al., 2013) and *Mimosa acantholoba* occurring in Mexican TDF at 16° N (Brienen et al., 2010a). This suggests that rising temperatures and increased evapotranspiration would negatively affect tree growth of TDFs subjected to more temperature variability within (increased seasonality) and between years (Clark et al., 2010).

4.3. Drought-growth associations at different time scales: short-term tolerance vs. long-term sensitivity?

The drought index (SPEI) explained up to 28.9% of the year-to-year growth variance, which suggests that the study species can buffer the negative effects of drought on radial growth at short time scales. As mentioned before, TDF tree species may alleviate the negative effects of water shortage on growth through induced or altered leafless period but they can also uptake water from deep soils sources, increase their xylem resistance to cavitation or enhance water storage in the stem and branch wood (Markesteijn, 2010). Our results suggest that these functional responses may be rapid and translate into significant SPEI-growth associations recorded at relatively short time scales (from two to seven months). This finding is concurrent with a global study which evidenced that in arid biomes vegetation activity and growth mainly responded to drought at short-time scales (Vicente-Serrano et al., 2013).

This short-time buffering and responses to drought contrast with the sensitivity to long-term droughts as evidenced the notable increase in growth variance explained by SPEI at times scales varying from six to 30 years, excepting *Caesalpinia*. In other drought-prone areas such as Mediterranean forests it has been argued that these long-time growth responses to precipitation and drought are linked to different accessibility of roots to soil water reserves located at different depths (Sarris et al., 2007). Water located at deeper depths would be only readily accessible after long and severe droughts for tree species with deep and efficient root systems. However, the high sensitivity of wood formation to long-term droughts in most of the studied species suggests that they cannot access the water from these deep layers to form wood or that there is a low availability of water in those layers during consecutive dry years. Accordingly, in all species, excepting *Caesalpinia*, we observed the lowest growth values during the two dry sub-periods (1960–1977, 1985–2008) whereas the highest ring widths were observed during the wettest sub-periods (1978–1984). This indicates that the long-term temporal variability of water availability drive the community growth dynamics of TDFs, probably to a higher extent than in humid rainforests where radiation is the major environmental driver of tree growth (Brienen et al., 2010b; Brienen and Zuidema, 2006). Tree species may tolerate short-term annual droughts by using the same ecophysiological mechanisms and traits to withstand the dry season (see Markesteijn et al., 2011), which is a main characteristic of the TDFs (Bullock et al., 1995). However, these mechanisms seem not be very efficient in terms of radial growth and productivity to deal with long-term droughts. In fact, long-lasting droughts have been shown to negatively affect growth of the tree community in TDFs (Leigh Jr. et al., 1990) and also in humid rainforests (Feeley et al., 2007; Phillips et al., 2009).

Among the study species, *Anadenanthera* was that showing a highest long-term growth sensitivity to SPEI since this drought index explained almost 90% of growth variance. This would indicate a high sensitivity of this species to long-term atmospheric water demand. In contrast, *Caesalpinia* growth did not respond to long-term SPEI variability, suggesting that this species may tolerate severe and lasting droughts. Further, the low production of sapwood of the latter species, which is also observed in other Fabaceae (Reyes-García et al., 2012), could also be related with a low water demand. The dense wood of *Caesalpinia* also confers it a low potential hydraulic conductance (cf., Kallarackal et al., 2013). The low sensitivity to long-term droughts of *Caesalpinia* is consistent with observations done in lowland Amazonian forests where species with denser wood were less vulnerable to drought and may become dominant after long periods of water deficit (Phillips et al., 2010).

5. Conclusions

Precipitation enhanced tree growth of all TDF study species, mainly when water availability increased during the wet season, while temperature was negatively related to growth in five out of seven species. Tree growth responses to precipitation peaked at short time scales (from two to nine months). Species with low-density wood and high production of sapwood (e.g., *Zeyheria*) were the most sensitive in terms of growth responses to precipitation variability, whereas species with the opposite characteristics (e.g., *Caesalpinia*) were the least sensitive ones. The emergent *Anadenanthera* responded to temperature changes at monthly to annual scales, while the rest of species showed negative growth responses to temperature at short-time scales (from one to three months), again chiefly during the wet season. Growth responded positively to less dry conditions at short (from two to seven months) and long-time scales (from six to 30 years). Temporal variability in water availability drives growth community dynamics of the study TDF at different time scales. Tree species tolerate short-term droughts while growth is particularly sensitive to long-lasting droughts, excepting *Caesalpinia*. The time-dependent growth response to climate and drought should be treated as an additional constraint of community growth dynamics to properly forecast the responses of TDFs to climate warming.

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Appendix A.

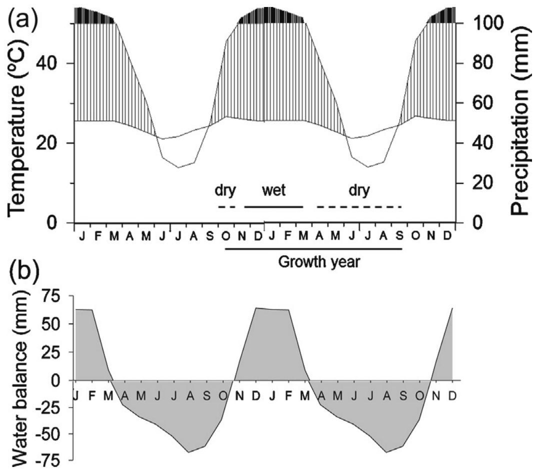

Fig. A1. Climate diagram and estimated monthly water balance of the study area considering the period 1949–2008.

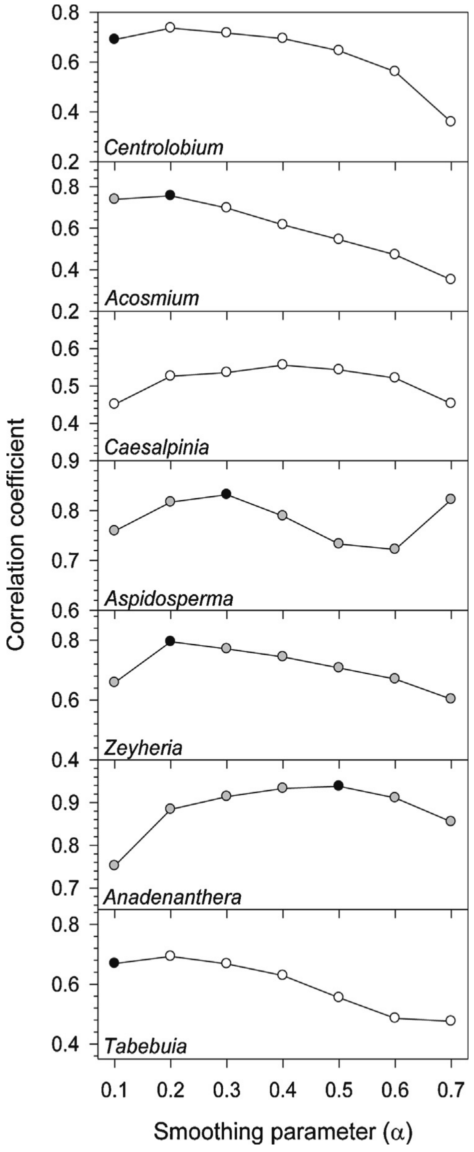

Fig. A2. Relationships (Pearson correlation coefficients) calculated between smoothed tree-ring width and drought index (SPEI) series considering the seven study species and the period 1949–2008.

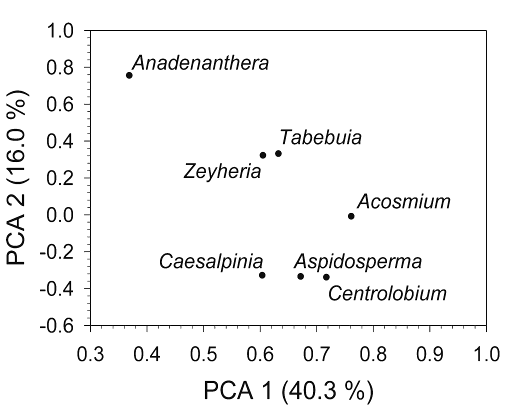

Fig. A3. Graphical summary of the seven tree species' scores considering the first two components of a Principal Component Analysis calculated on the residual tree-ring width chronologies.

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Chapter 4

Wood discs collected from stumps in the Chiquitano tropical dry forest (Bolivia)

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Differential Growth Responses to Water Balance of Coexisting Deciduous Tree Species Are Linked to Wood Density in a Bolivian Tropical Dry Forest

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Abstract

A seasonal period of water deficit characterizes tropical dry forests (TDFs). There, sympatric tree species exhibit a diversity of growth rates, functional traits, and responses to drought, suggesting that each species may possess different strategies to grow under different conditions of water availability. The evaluation of the long-term growth responses to changes in the soil water balance should provide an understanding of how and when coexisting tree species respond to water deficit in TDFs. Furthermore, such differential growth responses may be linked to functional traits related to water storage and conductance. We used dendrochronology and climate data to retrospectively assess how the radial growth of seven coexisting deciduous tree species responded to the seasonal soil water balance in a Bolivian TDF. Linear mixed-effects models were used to quantify the relationships between basal area increment and seasonal water balance. We related these relationships with wood density and sapwood production to assess if they affect the growth responses to climate. The growth of all species responded positively to water balance during the wet season, but such responses differed among species as a function of their wood density. For instance, species with a strong growth response to water availability averaged a low wood density which may facilitate the storage of water in the stem. By contrast, species with very dense wood were those whose growth was less sensitive to water availability. Coexisting tree species thus show differential growth responses to changes in soil water balance during the wet season. Our findings also provide a link between wood density, a trait related to the ability of trees to store water in the stem, and wood formation in response to water availability.

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Introduction

Tropical dry forests (TDFs) cover almost 17% of the Earth's tropical landmass and constitute one of the most diverse forest ecosystems in the world [1,2]. TDFs are also among the most threatened lowland tropical forests types, with habitat loss mainly caused by human-induced forest removal due to logging and farming [3]. Therefore we need a better knowledge of the main climatic factors driving forest recovery and tree growth in TDFs to inform the conservation of the forests that remain.

The existence of a dry season, which may last from two up to seven months, causes sharp temporal and spatial changes in soil water balance and tree phenology [4,5,6]. In TDFs many tree species are deciduous for two to four months during the dry season [7]. Leaf phenology has also been linked to contrasting growth rates and water transport efficiency [8,9,10]. Such varied patterns in aboveground phenology are also linked to the cambium activity through the tree water status which mainly depends on water uptake through the root system, water loss though the leaves, and water storage in the wood [4]. The variations in the leafless periods of TDF tree species have been also correlated with different functional features, such as wood density and water content, which could explain diverse responses to drought and contrasting growth responses to the soil water balance in TDFs [11,12]. These observations suggest that the seasonal changes in the soil water balance may act as the main driver of tree growth in TDFs.

In TDFs coexisting tree species may show differential growth responses to the seasonal changes in the soil water balance, but within-species variation also provides fundamental information to understand how growth responds to climate [13]. In fact, variability levels in species' traits, both inter-specific (*e.g.*, wood hydraulic properties; cf. Markesteijn *et al.* [12]) and intra-specific (*e.g.*, temporal autocorrelation in radial growth; cf. Zuidema *et al.* [14]), explain different responses to the changing water balance in TDFs. The seasonality imposed by a dry period causes an annual rhythm in cambial activity, and this leads to the formation of annual tree rings in many tree species [15]. Therefore, TDFs constitute a good study system to evaluate how coexisting tree species respond to varying levels of the soil water balance by showing differential growth responses. These responses represent long-term growth information recorded in annual tree-ring widths, which can be recovered using dendrochronology methods [16].

Here, we aim to determine how coexisting deciduous tree species respond to the soil water balance in TDFs by analyzing long-term climate-growth relationships. We studied seven tree species in a TDF located in the Chiquitana region of eastern Bolivia, where most tree species shed their leaves in the dry season [17]. We hypothesize that coexisting tree species will show contrasting growth patterns and differential responses to the soil water balance linked to different traits (*e.g.*, leafless period duration), particularly those related to their ability to store water in the stem (*e.g.*, wood density, sapwood production).

Materials and Methods

Ethics Statements

All field sampling was carried out with permission from the national authority (Autoridad Bosques y Tierra, Bolivia). Wood samples were collected from previously felled trees.

Study site

The study site is a seasonally deciduous lowland TDF located 32 km from Concepción (department of Santa Cruz) in eastern Bolivia (Fig. 1). The study site (16°07′S, 61°43′W, mean elevation of 380 m) is found in a private property of a certified timber company (INPA Parket) and it is included within the network of long-term research sites of the Instituto Boliviano de Investigación Forestal (IBIF; see http://www.ibifbolivia.org.bo/index.php/Monitoreo/INPA). The study site belongs to the Chiquitano forest formation, situated on the Precambrian Brazilian shield, and is considered one of the largest (occupying ca. 16.4 millions of ha.) and most diverse TDFs in Bolivia. Chiquitano forests are located in the transition of the Amazonian lowland evergreen rain forest in the north and the Chaco shrub dry formations towards the south [18]. The studied forest has an average tree richness of 34 species ha^{-1}, mean stem density of 437 trees ha^{-1}, basal area of 19.7 m^{2} ha^{-1}, average canopy height between 20 and 25 m, and 19 out of the 59 tree species have timber value [17,19]. In the study area the soils are acid (pH = 5.8), contain low organic matter contents (1.42%), and have a sandy-loam texture.

Meteorological data were obtained from the Concepción station (16°15′S, 62°06′W; period 1949–2009), located about 35 km from the study site. At this station the mean annual temperature was 24.3°C and the recorded total precipitation was 1160 mm. The driest period normally occurs from June to September but the dry season may last up to seven months, from April to October, in which the potential evapotranspiration exceeds precipitation, *i.e.* the water balance is negative (Fig. 2).

Tree species

We sampled the seven most abundant deciduous tree species forming distinct growth rings (Table 1). All are considered timber tree species, with the exception of *A. cardenasii* which has not been exploited in INPA. Nomenclature of sampled tree species (Table 1) follows the Tropicos webpage [20]. The selected species belong to three different families and display contrasting crown positions, shade tolerances and leafless periods (Table 1). One of the studied species is restricted to the Bolivian Chiquitano TDF (*Acosmium cardenasii*), whereas the others are found in other Bolivian tropical forests (*Aspidosperma tomentosum*, *Centrolobium microchaete*, *Zeyheria tuberculosa*), or are widespread across the Neotropics (*Anadenanthera macrocarpa*, *Caesalpinia pluviosa*, *Tabebuia impetiginosa*).

Field sampling

Wood samples (discs) were collected from living and healthy trees felled for timber in 2010 and 2011 and evaluated for growth and sapwood area. Each wood disc was taken at heights ranging from 0.2 to 2.5 m above the ground and discs were always collected above buttresses. In order to reduce spatial autocorrelation in growth patterns, we selected trees that were more than 20 m apart. Additionally, for each species we collected radial cores including sapwood (5-mm wide, 30-mm long) from five trees per species using a Pressler increment borer. The sampled individuals were located in the same stands where the wood discs were collected.

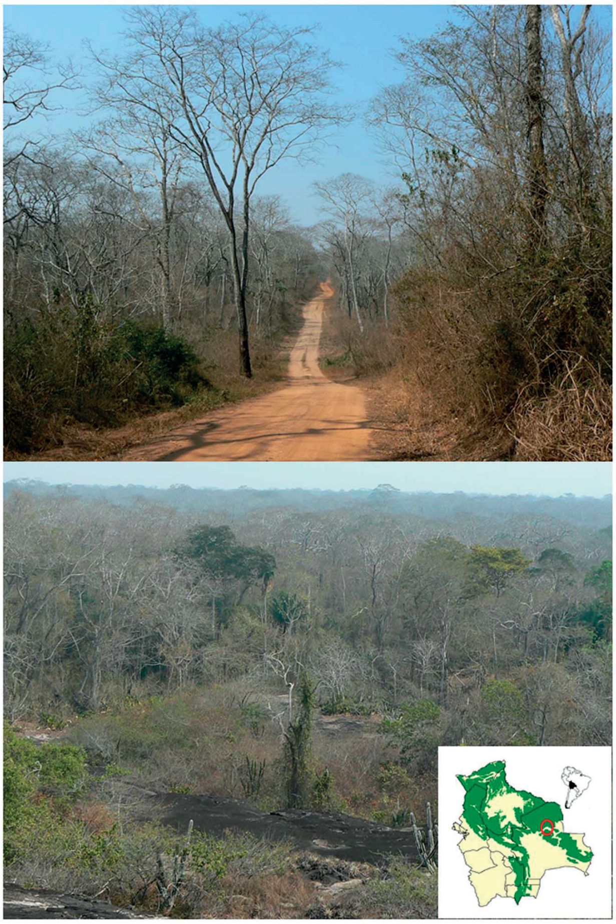

Figure 1. Views of the Bolivian Chiquitano tropical dry forest during the dry season. The inset shows the location of the study site (circle) within Bolivia (green areas correspond to forests).
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Wood density and sapwood area

To estimate the potential water storage capacity of the stems we calculated wood density (D) and sapwood area using radial cores and wood discs, respectively. The volume of the radial core (V) was estimated as the volume of a perfect cylinder. The radial cores were oven-dried at 60°C for 48 hours and weighed to obtain the dry weight (DW). Wood density (in g cm^{-3}) was calculated according to Borchert [4] as follows:

$$D = DW/V \tag{1}$$

In the laboratory, the wood discs ($n = 63$) were air-dried and sanded using successively finer grained sandpapers up to 600 grit

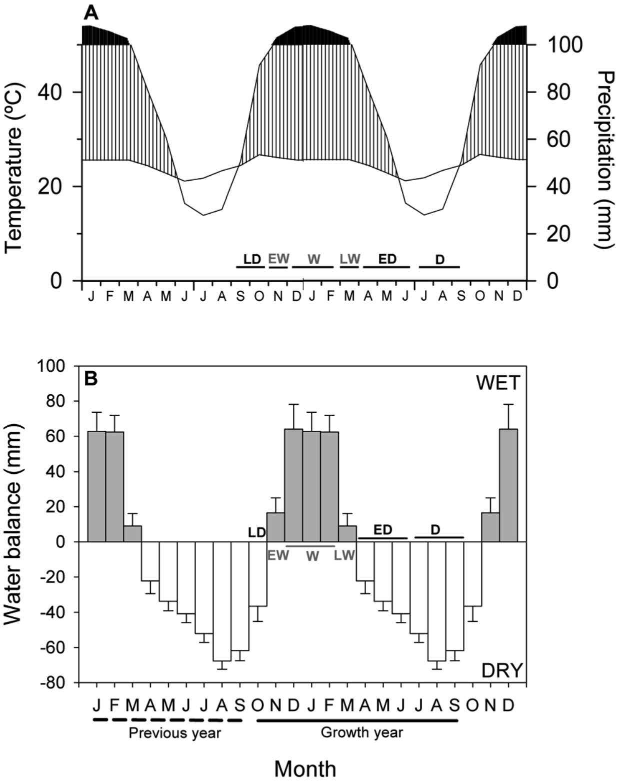

Figure 2. Climatic conditions of the study area. Data from a nearby Concepción meteorological station (A), and estimated monthly water balance (B). The previous (dashed line) and current (continuous line) growth years correspond to the years when the tree ring formation started and ended, respectively. Abbreviations: LD, late dry season; EW, early wet season; W, wet season; LW, late wet season; ED, early dry season; D, dry season. Values of water balance are means ± 1SE.
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until the tree rings were clearly visible. A digital picture of each wood disc was taken to calculate the relative stem wood area occupied by sapwood using the ImageJ image analysis software [21]. The distinction between heartwood and sapwood was visually determined by colour differences, which were very evident in five species (*A. macrocarpa*, *C. microchaete*, *C. pluviosa*, *T. impetiginosa*, and *Z. tuberculosa*; see Fig. S1), and the other two species (*A. tomentosum* and *A. cardenasii*) were checked by applying bromocresol green stain on the wood [22]. We assumed that the contraction of dried sapwood in the laboratory would be similar among the seven tree species. All measured samples corresponded to wood discs with areas varying between 1000 and 2000 cm^2. This size range is similar to those of previous analyses on sapwood area in tropical tree species [23].

Dendrochronological methods

Tree-ring series were visually cross-dated by comparing and detecting characteristic rings among radii of the same tree and then by matching the series from different trees of the same species. We measured the ring widths from the most recent ring up to the pith along three to four radii per disc, separated by 90–120° to account for: (*i*) the eccentric growth of most discs and (*ii*) the within-tree (among radii) growth variability (see Fig. S1). Hence, the mean value of the ring widths measured along different radii was considered to represent an average radial-growth series of each tree. We assigned to each ring the calendar year in which ring formation began according to the dating convention for the southern hemisphere [24]. Tree rings were measured under a binocular scope using a LINTAB measuring device (Rinntech, Heidelberg, Germany). Then, the previous visual cross-dating was checked using the COFECHA program which calculates the correlation between individual ring-width series and a master series for each species [25]. Only those trees which had established before 1949 were used in further analyses. For each of the seven species, we successfully cross-dated and measured from 7 to 14 trees (Table 2).

Growth patterns

We used basal area increment (BAI) to describe growth patterns because this variable removes the variation in growth attributable to increasing stem circumference and captures changes in growth better than linear measures such as tree-ring width [26]. BAI series for dominant healthy trees usually show an early suppression phase before a rapid increase and a stable phase once trees reach maturity [27]. BAI was calculated as follows:

$$\mathrm{BAI} = \pi\left(R_t^{\,2} - R_{t-1}^{\,2}\right) \qquad (2)$$

where R_t and R_{t-1} are the stem radius in years *t* and *t*-1.

Considering the first 70 years of tree life, we calculated BAI trends for each tree as a function of age by using three-parameter logistic functions with information of the following three parameters: maximum BAI (asymptote), maximum growth rate and age when the maximum growth rate is reached. Considering the period 1949–2009, when the maximum number of growth series was available, we also evaluated BAI trends for the mature phase when BAI stabilizes, calculated mean correlations among individual tree BAI series (based on Pearson coefficients), and obtained BAI means and coefficients of variation.

Definition of the biological growth year and seasonal soil water balances

We defined the biological growth year of the investigated species from October to September (Fig. 2) based on previous phenological studies [17] and dendrometer records of radial increments (Mendivelso & Camarero, *unpublished data*).

We divided the growth year, when tree ring formation starts and ends, in six sub-periods based on their contrasting climatic characteristics and soil water balances (see Fig. 2): (*i*) late dry season (LD, October), (*ii*) early wet season (EW, November), (*iii*) wet season (W, from December to February) when the maximum values of water balance were recorded, (*iv*) late wet season (LW, March), (*v*) early dry season (ED, from April to June), and (*vi*) dry season (D, from July to September) when very low soil water potentials were recorded [6]. We calculated the soil water balance as the difference between the precipitation and the potential evapotranspiration (PET). The PET was calculated from monthly values of minimum, maximum, and mean temperatures using the Hargreaves-Samani method [28].

Linear mixed-effects models of growth

We fitted linear mixed-effects models to evaluate the relationships between BAI residuals and the six defined climatic sub-periods in the biological growth year (plus the same sub-periods lagged by 1 year) taking into account the variability among individuals (within species) and among species. We calculated BAI residuals as the differences between the observed and the predicted BAI values, where the predicted BAI was obtained by fitting a logistic to growth data as a function of cambial age. We designated

Table 1. Characteristics of the seven tree species studied in the INPA site, a tropical dry forest located in the Chiquitana region of Bolivia.

Family	Species	Crown position	Shade tolerance	Leafless period (months)	Basal area (m^2 ha^{-1})	Density (stems ha^{-1})
Bignoniaceae	*Zeyheria tuberculosa* (Vell.) Bureau	Canopy	Intolerant	October–November (2)	0.04	2.75
Bignoniaceae	*Tabebuia impetiginosa* (Mart. ex DC.) Standl.	Canopy	Intolerant	July–September (3)	0.27	1.83
Fabaceae	*Centrolobium microchaete* (Mart. ex Benth.) H.C.de Lima *ex* G. P. Lewis	Canopy	Intolerant	June–October (5)	0.55	11.42
Fabaceae	*Anadenanthera macrocarpa* (Benth.) Brenan	Emergent	Intolerant	June–October (5)	2.00	13.67
Fabaceae	*Acosmium cardenasii* H.S. Irwin & Arroyo	Sub-canopy	Tolerant	August–September (2)	6.89	159.25
Fabaceae	*Caesalpinia pluviosa* DC	Canopy	Partially tolerant	August–September (2)	1.18	15.17
Apocynaceae	*Aspidosperma tomentosum* Mart.	Sub-canopy	Partially tolerant	July–September (3)	0.40	12.92

Leaf phenology data were based on field observations and on data presented by Mostacedo [17].
Basal area and density data (considering only stems with diameter at 1.3 m>10 cm) were taken from Mostacedo [17].
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both individual tree and biological growth year as random effects and the climatic sub-periods as fixed effects. The response variable was normalized using logarithms, because the distribution of BAI values was left-skewed. We used growth and climate data for the period 1953–2006 (53 years) considering the previous (*t*-1) and current (*t*) years. The fitted model can be summarized as follows:

$$\log(\mathrm{BAI}_{ij}) = \beta_0 + \gamma_{0i} + \alpha\ \mathrm{year}_j + \beta_1\ \mathrm{WB}_1 + \ldots + \beta_{12}\ \mathrm{WB}_{12} + \varepsilon_{ij} \quad (3)$$

where β_0 is the intercept, γ_{0i} is the random effect related to tree (i), α is a parameter adjusting the year (j) fixed effect, $\beta_1 \ldots \beta_{12}$ are parameters controlling the fixed effects related to water balance (WB) of different sub-periods ($\mathrm{WB}_1 \ldots \mathrm{WB}_{12}$), and ε_{ij} is the error term. We accounted for temporal autocorrelation by using an AR(1) correlation structure, *i.e.* by considering a first-order autoregressive model, since BAI usually presents temporal persistence at a one-year lag. We fitted 43 models for each species to evaluate which combinations of climatic variables best explained BAI. Our models ranged from null (only intercept) and single-variable models to more complicated models (see Table S1). The 43 models we fitted constitute only a subset of all possible models, because we excluded unrealistic models and those including highly correlated ($P \leq 0.01$) pairs of explanatory climatic variables (Table S2). Accordingly, in all of the selected models the variance inflation factor of all fixed factors was <3. The parameters were estimated using the restricted maximum likelihood method [29].

We considered models with substantial support to be those in which we obtained minimum values of the Akaike Information Criterion (AIC), which combines the measure of goodness of fit with a penalty term based on the number of parameters used [30]. We also considered supported models those in which the difference of AIC between the best and following models, *i.e.* those ranked with lowest AIC values, was less than 2. We calculated the Akaike weight (W_i) which is the relative likelihood that the selected i model is the best-fitting model for the observed data. The explained variance (R^2) of the selected models was estimated using a likelihood ratio statistic for each individual tree in all species [31]. Then, we compared the mean R^2 values among species. The linear mixed-effects models were carried out using the *nlme* package [32] in the R statistical software [33].

Results

Growth features of tree species

The studied species formed diffuse-porous wood and they presented well-defined tree ring boundaries formed by marginal parenchyma (Fig. 3). Wedging rings were sporadically observed in *A. cardenasii* and *C. pluviosa* (Fig. S1). The mean ages of sampled trees varied from 84 (*A. tomentosum*) to 149 years (*C. pluviosa*), whereas the sapwood area reached minimum and maximum

Table 2. Characteristics of trees and species sampled in a Bolivian tropical dry forest.

Species	No. trees/No. radii	Diameter at 1.3 m (cm)	Age (years)	Wood density (g cm^{-3})	Sapwood area (%)
Z. tuberculosa	7/21	38.17±3.60	112±11	0.61±0.01 (a)	42.63±2.15 (d)
T. impetiginosa	7/24	43.29±3.39	97±10	0.74±0.04 (bc)	26.79±1.15 (bc)
C. microchaete	14/42	36.03±3.15	89±3	0.59±0.02 (a)	29.70±2.03 (c)
A. macrocarpa	8/24	42.06±2.85	112±9	0.71±0.05 (bcd)	25.26±3.42 (bc)
A. cardenasii	11/38	29.16±3.90	92±5	0.69±0.02 (bd)	16.58±0.69 (a)
C. pluviosa	8/31	46.54±3.74	149±10	0.79±0.01 (c)	23.24±2.42 (b)
A. tomentosum	8/24	26.89±4.62	84±5	0.66±0.01 (d)	28.07±1.15 (c)

Values are means ± 1SE. Means sharing a letter were not significantly different using paired Mann-Whitney *U* tests ($P \leq 0.05$).
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values in *A. cardenasii* (13.6%) and *Z. tuberculosa* (42.6%), respectively (Table 2). The wood density varied between 0.59 and 0.79 g cm^{-3}. *C. microchaete* and *Z. tuberculosa* exhibited the lowest wood density values while *C. pluviosa* presented the highest.

During the first 70 years of life, *A. tomentosum* (a sub-canopy partially shade-tolerant species) and *T. impetiginosa* (a canopy shade-intolerant pioneer species) had the respective lowest (10.7 cm^2) and highest (30.3 cm^2) mean BAI values (Table 3; Fig. 4). *A. tomentosum* also showed the lowest BAI rate, whereas the highest rate corresponded to *C. pluviosa* (canopy partially shade-tolerant species). The estimated ages to reach such maximum rate were within a narrow range and varied from 23 (*A. macrocarpa*) to 41 years (*A. tomentosum*).

During the common period 1949–2009, *A. tomentosum* (6.8 cm^2) presented the lowest BAI values while *T. impetiginosa* showed the highest ones (25.1 cm^2), *i.e.* more than a threefold rise as compared with the former species (Table 3; Fig. 4). *Z. tuberculosa* presented the highest variability in BAI as assessed by the coefficient of variation (90.3%), followed by *A. macrocarpa* (73.7%), while *A. tomentosum* presented the lowest growth variability (63.4%). Finally, the highest within-species coherence among individual BAI tree series (mean correlation values >0.50) was found for *A. cardenasii* followed by *Z. tuberculosa*, while the lowest coherences (mean correlation values <0.30) were observed for *A. macrocarpa*, *C. pluviosa*, and *T. impetiginosa*.

Relationships between seasonal water variability, BAI, and species traits

The associations between water balance and BAI were positive for all species during the wet season. However, the species differed in the strength of relationships between growth and water balance during this season (Table 4, Fig. 5; see also Fig. S2). In general, *Z. tuberculosa* was the species that showed the strongest responses to the wettest sub-periods (early wet, wet, and late wet seasons) during the previous and growth years, whereas *A. tomentosum* exhibited moderate responses (early wet season).

From the BAI variance explained by the best model fits (see mean R^2 values, Table 4), the growth of *Z. tuberculosa* (29%) and *A. cardenasii* (20%) was most responsive to water availability, while *C. pluviosa* (6%) and *T. impetiginosa* (6%) were least responsive. The variability of growth explained by water balance was negatively related to wood density ($r = -0.76$, $P = 0.04$) but unrelated to sapwood area ($r = 0.36$, $P = 0.43$). *Zeyheria tuberculosa* was the most sensitive species to water balance and had low wood density values, while, at the other extreme, *C. pluviosa* and *T. impetiginosa* were the least responsive to water balance and had the highest wood density values (Tables 2 and 4, Fig. 6).

Discussion

Growth is strongly but differentially related to water balance during the wet season

Our main finding is that radial growth is strongly but differentially related to the wet season water balance in tree species coexisting in a TDF. We discuss the potential mechanisms of such contrasting growth responses to the water balance and how these responses may be linked to functional traits such as wood density.

We found that the studied tree species formed cross-datable annual rings, delimited by marginal parenchyma, a type of parenchyma which is a common anatomical feature in tropical tree species [34]. Such wood anatomy appears to be particularly

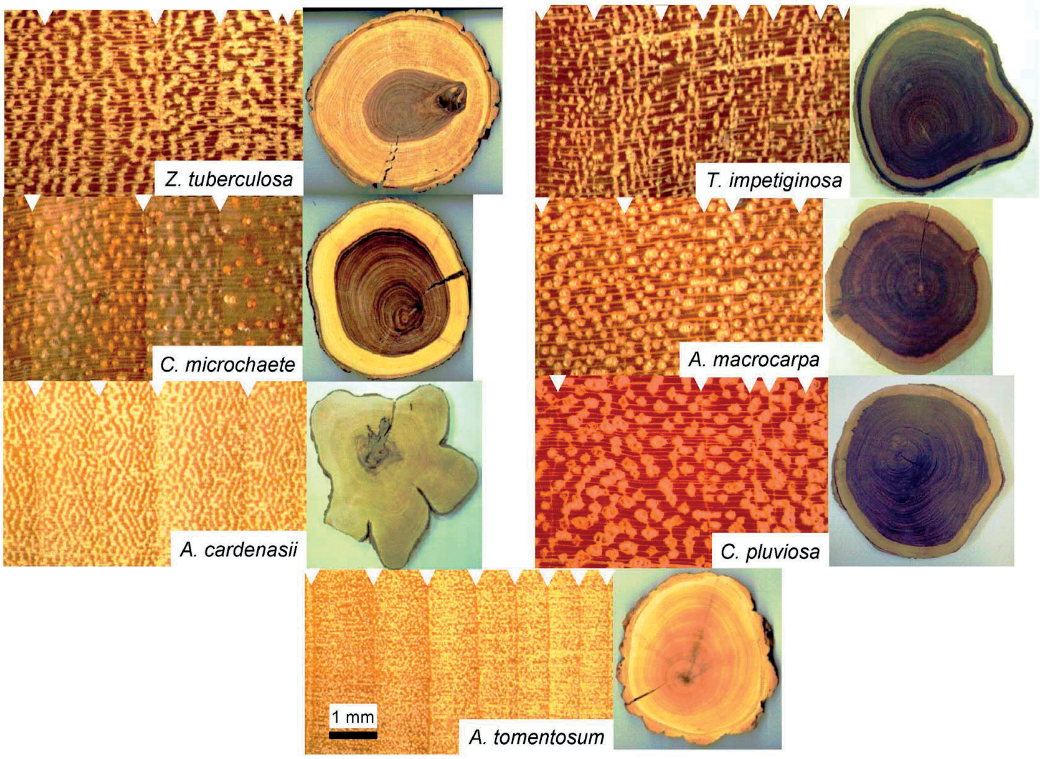

Figure 3. Wood cross-sections with distinct annual rings of studied tree species. The white triangles mark the annual boundaries corresponding to marginal parenchyma. In the rings the growth direction is from left (pith) to right (bark).
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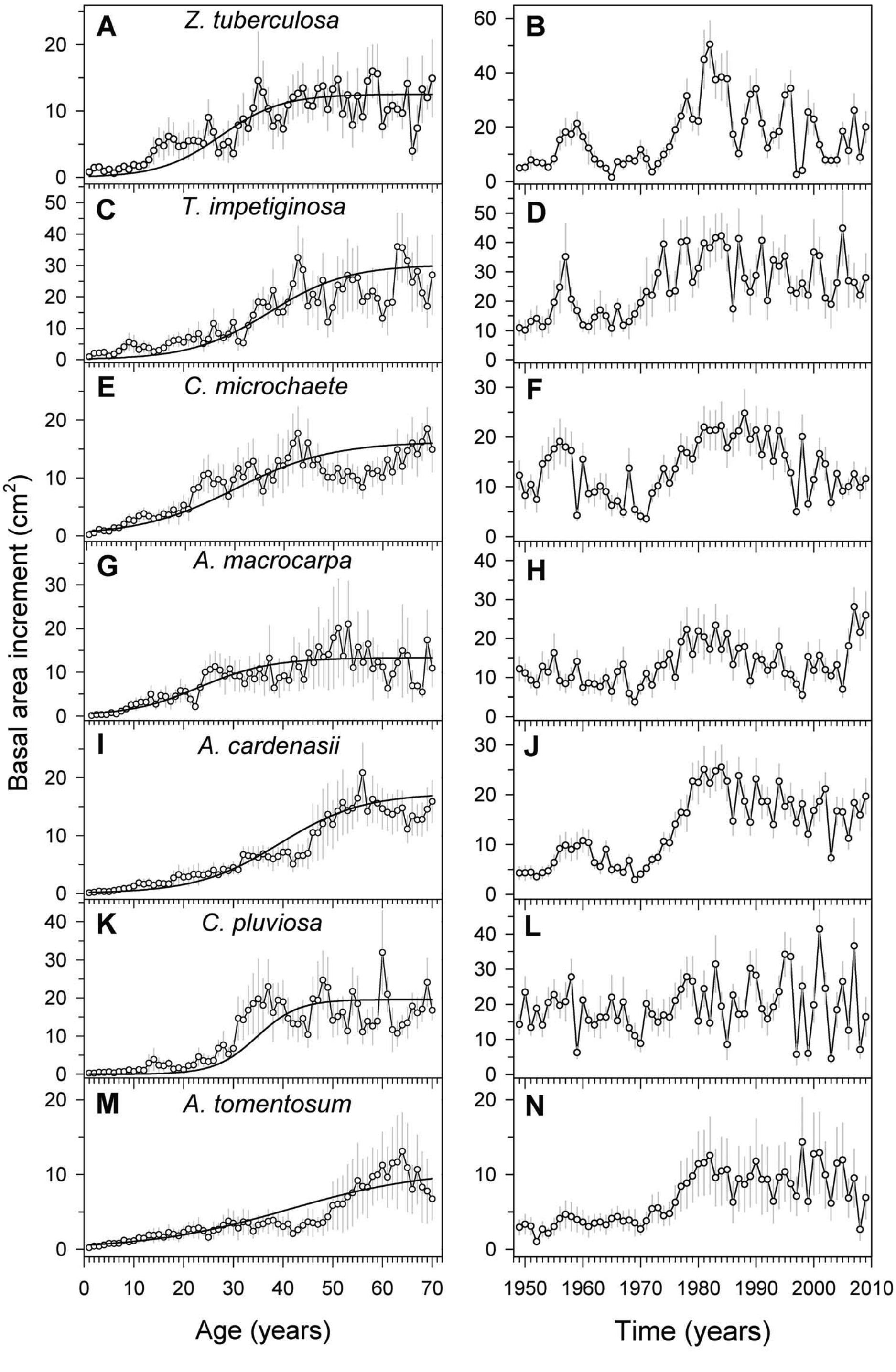

Figure 4. Basal-area increment patterns for the seven tree species from a Bolivian tropical dry forest. Basal area increments (means ± 1SE) are displayed as a function of tree age (A, C, E, G, I, K, M) and calendar year (B, D, F, H, J, L, N). See also the comparisons among tree species displayed in Table 3.
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widespread among deciduous tree species from TDFs [35,36]. This observation suggests that a pause in cambial activity during the dry season because of low moisture availability probably drives ring boundary formation [37].

The soil water balance is a much stronger driver of tropical tree growth than other factors such as atmospheric CO_2 concentration, soil type, or disturbance [38,39]. This finding agrees with other studies from TDFs [40–42]. In all studied species, basal area increment increased most during the wettest period of the year, suggesting that the maximum growth rates occur when soil humidity is the highest and probably when carbon uptake also reaches the highest rates [9,43]. Our findings reveal that growth

Table 3. Growth-related characteristics of the seven tree species studied in a Bolivian tropical dry forest.

Species	First seventy years of tree life (see Figs. 4 A, C, E, G, I, K, M)			Period 1949–2009 (see Figs. 4 B, D, F, H, J, L, N)		
	Maximum BAI (cm^2)	Maximum growth rate (cm^2 yr^{-1})	Age at maximum growth rate (yrs)	BAI (cm^2)	CV BAI (%)	Correlation between tree BAI series
Z. tuberculosa	12.51±1.84 (ab)	1.34±0.47 (b)	27.44±3.72 (ab)	16.41±2.06 (bc)	90.35±5.28 (b)	0.54±0.03 (c)
T. impetiginosa	30.26±6.76 (c)	1.59±0.56 (b)	37.28±9.28 (ab)	25.06±3.56 (d)	65.13±3.72 (a)	0.27±0.02 (a)
C. microchaete	16.27±3.02 (ab)	0.76±0.20 (b)	30.44±5.88 (ab)	13.63±2.29 (ab)	67.51±2.35 (a)	0.41±0.02 (b)
A. macrocarpa	13.29±5.16 (ab)	0.93±0.35 (b)	23.02±5.91 (a)	13.36±2.17 (ab)	73.68±6.82 (ab)	0.23±0.04 (a)
A. cardenasii	17.30±3.54 (ab)	1.12±0.62 (b)	41.35±3.99 (b)	13.20±1.87 (ab)	65.99±3.91 (a)	0.62±0.02 (d)
C. pluviosa	19.59±2.31 (bc)	2.32±0.75 (c)	34.70±7.18 (ab)	19.34±2.69 (cd)	66.50±3.22 (a)	0.26±0.03 (a)
A. tomentosum	10.66±4.47 (a)	0.19±0.08 (a)	39.09±7.85 (b)	6.81±2.60 (a)	63.40±5.46 (a)	0.45±0.04 (b)

Abbreviations note: BAI, Basal area increment; CV, Coefficient of variation. Values are means ± 1SE. Means sharing a letter were not significantly different using Tukey (BAI and growth-rate variables) and Games-Howell (age) *post hoc* tests for those cases with or without homoscedasticity, respectively ($P \leq 0.05$).

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mainly responds to wet season conditions and species' sensitivty to drought are thus not dependent on dry season conditions, which probably control the late phases of wood formation [37]. However, the variability of growth explained by water balance and maximum juvenile growth rates were not related at all, confirming that these variables are not correlated in the long term.

Wood density is linked to growth responses to water balance

Based on the best linear-mixed effect models, species were ranked from most to least sensitive according to growth response to water balance,: *Z. tuberculosa*, *A. cardenasii*, *C. microchaete*, *A. macrocarpa*, *A. tomentosum*, *T. impetiginosa*, and lastly *C. pluviosa*. The most responsive species also had a high intra-specific coherence in growth among individuals, possibly mediated by climatic stress. The species with lowest wood density, *i.e.*, a high potential to store water in the sapwood, were those with the highest growth responsiveness to water balance during the wettest sub-periods of both the previous and the year of growth. A good example is *Z. tuberculosa* which showed a strong growth response to water balance during the previous and current-growth years. *Z. tuberculosa* also exhibited a low wood density and a high sapwood area which gives it a higher potential to store water in the stem. Furthermore, this species is able to tolerate drought and keeps its leaves during the driest period. However, there is no relationship between the duration of leaf shedding in the dry season to either wood density or the variability of growth explained by soil water balance when considering all species. Although there was no significant correlation between sapwood area and growth variability explained by the availability of water, *Z. tuberculosa*, the most sensitive species to water balance, exhibited the highest sapwood area (43%), while *C. pluviosa*, the least sensitive species, had one of the lowest sapwood areas (23%). Finally, Fabaceae species (*A. cardenasii*, *A. macrocarpa*, *C. pluviosa*) also had low values of sapwood area which may be related to a strategy for heartwood production in this family [44].

During the short wet season, TDF deciduous tree species maximize photosynthesis, hydraulic conductivity, and growth rate [45,46]. Deciduous hardwood species with a very dense wood ($D > 0.8$ g cm^{-3}) and a low storage ability of water in their stems uptake and deplete water from the shallow soil layers. These species are unable to fully rehydrate their stems after leaf fall during the dry season. Conversely, deciduous softwood tree species usually have less dense wood ($D = 0.5$–0.8 g cm^{-3}) and a high water storage capacity and they reduce water loss during the dry season by leaf shedding [4]. Our study species may be included in this last group which is characterized by a high ability to rehydrate their tissues after the first rainfalls [47]. This fast rehydration ability allows them to quickly reactivate cambial activity [48]. At seasonal scales, the water content of the sapwood and the inner bark also help to explain seasonal changes in girth increment [49]. Lastly, wood density and the ability of deciduous trees from TDFs to store water could explain the mechanisms they use to escape from water stress [50].

Nevertheless, further analyses should consider the multiple roles played by wood density with respect to the water status and the growth responsiveness to climate (hydraulic conductivity, vulnerability to xylem embolism and vessel collapse, water storage) [50]. For instance, tree species with low wood density may also have the largest xylem diameters and thus the highest capacity for water transport and possibly elevated photosynthetic and growth rates under conditions of high water availability, *i.e.* during the wet season. However, in this study, wood density and the maximum growth rates during the first 70 years of life were positively but non-significantly related ($r = 0.66$, $P = 0.11$). Hence, species with denser wood presented the highest juvenile growth rates. This suggests that the increased ability to conduct water provided by a less dense wood likely comes at the expense of a high vulnerability to xylem embolism [50], which requires a tight regulation of stomatal conductance and may reduce growth rates. These potential trade-offs may also contribute to explain the increasing sensitivity of variation of growth rates with decreasing wood densities.

The wide range in wood density of TDF tree species suggests that tree water status and cambium phenology may be related to soil water balance. Perhaps, tree species in TDFs may be able to tap increasingly deeper sources of soil water as the dry season progresses [51]. To test whether stem water storage drives changes in growth responsiveness to water balance we need additional data on the actual water status of trees and how they take up water during the dry and wet seasons [52]. We speculate that contrasting rooting depths of coexisting tree species might explain different time-dependent growth responses to drought. Species with deep roots might access additional sources of soil water as the dry season progresses and thus show growth responses to drought at longer time lags than species with shallow roots.

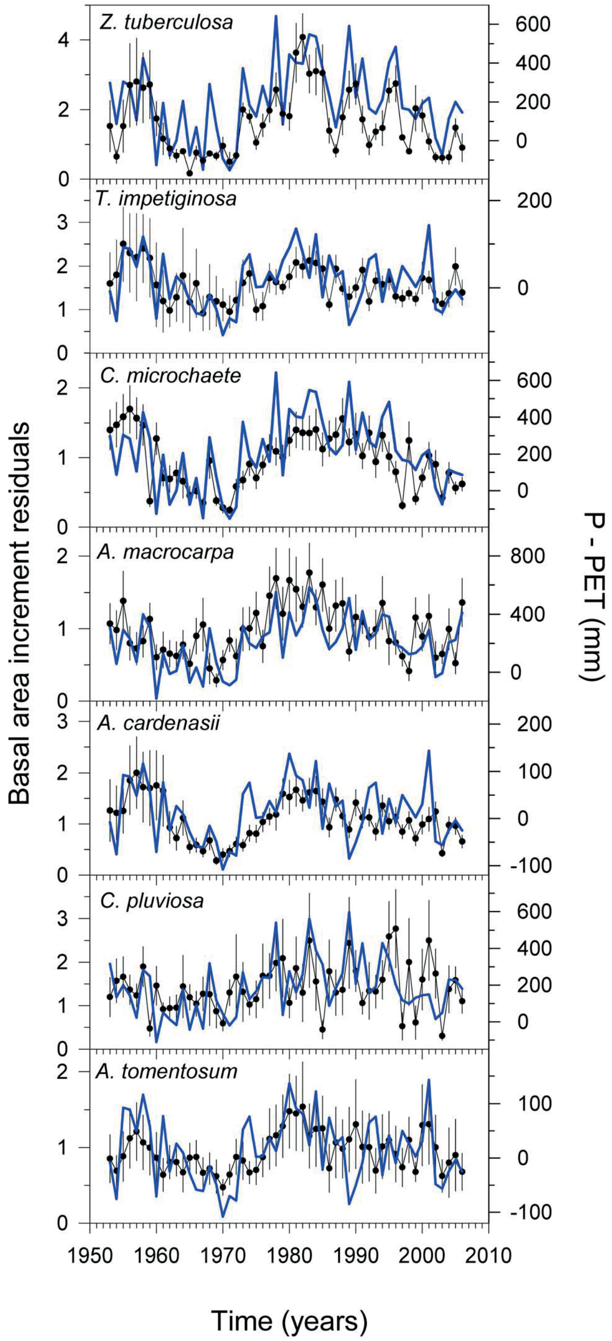

Figure 5. Relationship between basal area increment and soil water balance during the most influential period for growth. Basal area increments (means ± 1SE) residuals and seasonal water balances (those selected as the most influential for tree growth during the current year; see Table 4) are displayed as black and blue lines, respectively. The soil water balance was calculated as the difference between the precipitation (P) and the potential evapotranspiration (PET).
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Shade tolerance is not related to juvenile growth patterns

Soil water balance seems also to drive growth during the juvenile life stage since shade tolerance was not related at all with growth rates during the first 70 years of life. The maximum growth rates during that life stage were observed in partially shade tolerant and shade-intolerant pioneer species (e.g., *C. pluviosa*), which may grow rapidly to reach the canopy. Conversely, sub-canopy partially shade tolerant species showed the lowest growth rates (e.g., *A. tomentosum*) and, consequently, took more time to attain high growth rates. Overall, the reported studied species presented similar maximum juvenile growth rates which partially agree with results based on repeated measurements of permanent plots reported by Villegas *et al.* [19] for the same forest. Their observations suggested that species partially tolerant to shade show the highest growth rates.

In moist tropical forests shade-intolerant species should grow more rapidly than shade-tolerant ones in light and open conditions [53]. In TDFs growth differences among sub-canopy juveniles persist over longer time than in rainforests due to higher spatial heterogeneity in soil water availability than in moist forests [54]. This reinforces the potential role played by soil water balance as major driver of growth even in early life stages, and could explain the high intra-specific variability observed in basal area increment values during the establishment process of TDF tree species.

Searching for links between growth and functional traits

Recently, there has been an intense effort to link functional traits and secondary growth in diverse TDFs (*e.g.*, Poorter *et al.* [55]). Growth seems to be related to several functional xylem traits such as wood density [56] or vessel lumen diameter and hydraulic conductance [57]. Hérault *et al.* [58] concluded that stem traits such as wood density and water content largely explained interspecific differences in growth trajectories of tropical tree species. Growth responses to climate may also depend on additional or unmeasured traits such as water-use efficiency or rooting depth. The relative importance of wood density, compared with other traits for controlling the response of growth to water availability, could not be quantified with the available data in this study. Further support for our ideas may come from field studies characterizing seasonal changes in stem and soil water storage and relating them to cambial dynamics. Nonetheless, to the best of our knowledge, this is one of the few studies providing a link between a key functional trait, wood density, and differential growth responsiveness to water balance in TDFs. Finally, we are confident that our approach reduced the effects of several biases which can influence growth estimates: namely, tree ontogeny, size, and competition [59]. First, sampled trees were of similar ages and diameters and they were sampled in the same site from nearby stands subjected to comparable levels of competition between trees. Second, the use of relative basal area increment made it easier to compare the variability in growth, regardless of tree age and size, among conspecific trees [26].

Conclusions

We found that soil water balance during the wet season strongly and differentially drives radial growth of coexisting tree species in TDFs. The differences in growth explained by water balance varied among species. The strength of the relationship between water balance and growth varied among species as a function of the wood density. *Zeyheria tuberculosa* was the most sensitive species to water balance, exhibited low wood density values, and high sapwood area which is associated with high stem water storage. These traits are likely related to drought tolerance, which might explain its capacity to retain leaves throughout most of the dry season. The species presenting the opposite characteristics (*e.g.*, high wood density) were those whose growth was the least

Table 4. Statistics of the best linear mixed-effects models fitted to basal area increment as a function of soil water balance.

		Previous year						Growth year							
Species	**Intercept**	**LD**	**EW**	**W**	**LW**	**ED**	**D**	**LD**	**EW**	**W**	**LW**	**ED**	**D**	***Wi***	**R^2**
Z. tuberculosa	**1.55**		**0.25**	**0.23**	**0.22**				0.14	**0.31**	**0.22**			0.77	0.29±0.05 (a)
T. impetiginosa	**1.37**								**0.20**					0.38	0.06±0.01 (b)
C. microchaete	**0.96**		**0.09**	**0.08**					**0.13**	**0.09**				0.33	0.19±0.04 (ac)
A. macrocarpa	**0.99**								**0.10**	**0.16**				0.79	0.11±0.02 (bc)
A. cardenasii	**1.10**		**0.19**						**0.16**					0.96	0.20±0.03 (a)
C. pluviosa	**1.43**			**0.14**						**0.12**				0.29	0.06±0.02 (b)
A. tomentosum	**0.97**		**0.08**						**0.09**					0.59	0.09±0.04 (bc)

Abbreviations: LD, late dry season; EW, early wet season; W, wet season; LW, late wet season; ED, early dry season; D, dry season. Note the relative probability that the selected model is the best one (*Wi*) and the basal area increment variance (R^2) explained by the models. Bold coefficients are significant ($P \leq 0.05$). Means sharing a letter were not significantly different using paired Mann-Whitney *U* tests.

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responsive to water balance (*e.g.*, *C. pluviosa*). Our findings thus provide a link between wood density, a proxy of the tree's ability to store water in the stem, and differential growth responses to water balance.

Supporting Information

Figure S1 Images of the radii that were cross-dated and measured in *A. cardenasii* (A) and *A. macrocarpa* (B). Note that *A. macrocarpa* shows a clear distinction between sapwood and heartwood. The scale bars correspond to 10 cm.
(DOC)

Figure S2 Relation of basal area increment residual to water balance for the different species. The lines show linear regressions (black lines) and related 95% confidence intervals (gray lines). The Pearson correlation coefficients (*r*) between growth and water balance are indicated for each species with its associated probability level (*, $P<0.05$; **$P<0.01$).
(DOCX)

Table S1 Comparison of the 43 linear mixed-effects models fitted to basal area increment as a function of several variables related to water balance of the previous and current growth years. The first reported model is the null one which only considers an intercept. Abbreviations: BAI, basal area increment; *t*, current growth year; *t*-1, previous growth year; LD, late dry season; EW, early wet season; W, wet season; LW, late wet season; ED, early dry season; D, dry season.
(DOCX)

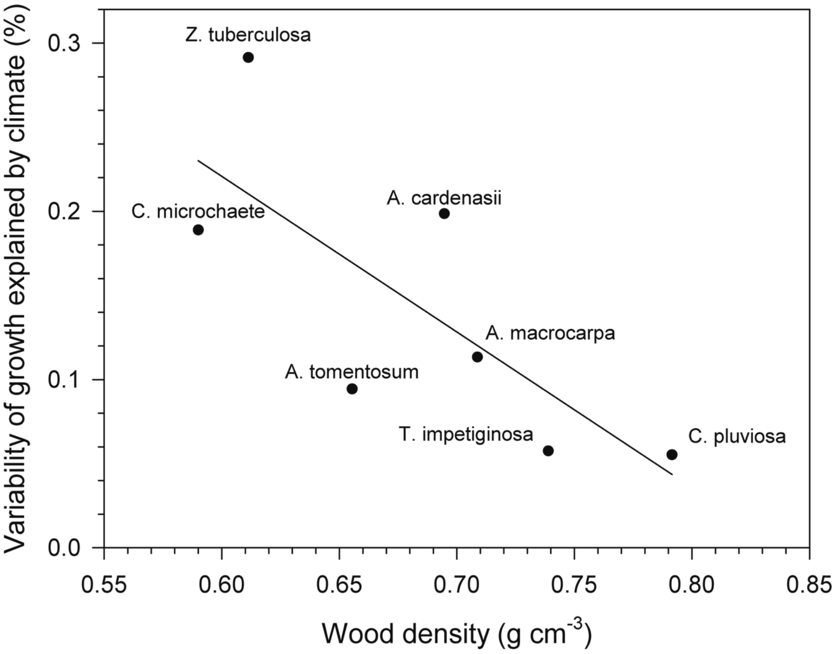

Figure 6. Wood density is negatively related to growth variability driven by water balance. The amount of basal area increment variance (R^2) explained by the best linear mixed-effects models fitted as a function of soil water balance is shown in the *y* axis (see Table 4).

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Table S2 Relationships between the water availability calculated for six sub-periods during the previous and current growth years. Abbreviations: LD, late dry season; EW, early wet season; W, wet season; LW, late wet season; ED, early dry season; D, dry season. The asterisk indicates high significance levels of Pearson correlation coefficients ($P \leq 0.01$).
(DOCX)

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Author Contributions

Conceived and designed the experiments: HAM JJC EG MT. Performed the experiments: HAM JJC ORO. Analyzed the data: HAM JJC EG. Wrote the paper: HAM JJC. Obtained permission for sampling: MT.

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Chapter 5

Ants on a felled tree in the Chiquitano tropical dry forest (Bolivia)

General Discussion

This thesis analyzed the dynamics of radial growth at different time scales in relation to climate and drought in two tropical dry forests (TDFs) located in Colombia (Tuluá site) and Bolivia (INPA site). Several tree species were studied from each TDF to have a better understanding about the growth responses to climate and drought at community level. This chapter summarizes the main findings of the three core chapters and integrates the presented findings with results from other studies on tropical forests. In particular, the first two sections provide insight into climate and drought controls on intra- and inter-annual patterns of radial growth in tree species coexisting at TDFs.

Climate controls on intra-annual patterns of radial growth in TDFs

The climatic controls on intra-annual patterns of radial growth and their relationship with leaf phenology were quantified in two TDFs with different drought seasonality and severity (Chapter 2). Specifically, the intra-annual patterns of growth were evaluated by quantifying: (i) the radial-increment dynamics (xylem and inner bark) from hourly to monthly scales using manual and automatic band dendrometers and, (ii) the xylem growth dynamics (xylogenesis) at monthly scales taking repeated wood samples (microcores). The climate control on both radial-increment dynamics and xylogenesis and their relationship with leaf phenology are discussed below.

Climatic control on radial-increment dynamics and their association with leaf phenology

Automatic band dendrometer data allowed splitting the daily cycle of stem radius variation in three phases: contraction, recovery and increment (Chapter 2). This last phase has been considered as an estimate of actual growth, i.e. the production of new xylem cells (Deslauriers et al., 2003). Furthermore, it was possible to identify those three phases at a daily scale using radial-increment rates (Chapter 2). The identification of contraction, recovery and increment phases at hourly and daily time-scales allowed evaluating the climate effect on radial-increment dynamics.

All tree species showed a daily cycle of stem radius variation during the wet season (Fig. 1). In contrast, only contraction and recovery phases were recorded during the dry season in most tree species (Fig. 1). During the wet season, the three phases aforementioned were time- and temperature-dependent in all species (Fig. 1). The air temperatures at hourly scales showed positive and negative relationships with the stem contraction and recovery-increment phases, respectively (Chapter 2). Nevertheless, the current results do not show a direct link between temperature and radial-increment dynamics. Air temperature can modulate plant water use through its effects on vapor pressure deficit (VPD), evapotranspiration rates and soil water availability. The alternating contraction (shrinkage) and recovery (swelling) phases occurring at hourly scales during the wet season (Fig. 1) could be related to two main periods of utilization and refilling of sapwood water stores. These stem-increment phases fluctuate according to diurnal changes of environmental conditions (Goldstein et al., 1998; King et al., 2013; Krepkowski et al., 2011; Turcotte et al., 2009). During the early hours of a day, the trees are likely to firstly use water stored in branches (cf. Goldstein et al., 1998; Schulze et al., 1985). Then, once water stored in branches is depleted, the high transpiration rates associated with rising VPD values at midday force trees to use the remaining water stored in the stem or roots. The synchronization between the contraction phase and warm temperatures in most tree species indicates that evapotranspiration and water loss through canopy evaporation trigger stem shrinkage (Fig. 1). Thereafter, the internal stem water stores is recharged during late afternoon in Tuluá species (cf. Goldstein et al., 1998), and during the night in INPA species as has been suggested in other tropical forests (Bräuning et al., 2009).

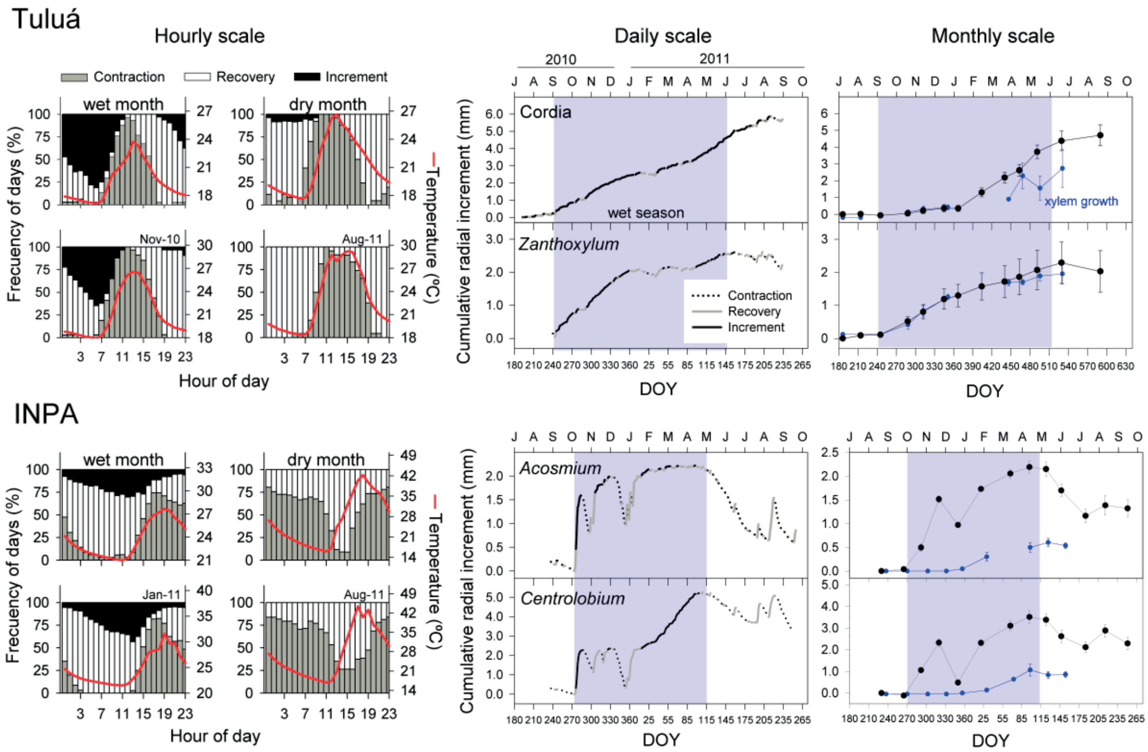

Figure 1. Radial increment dynamics at hourly, daily and monthly scales in four tree species from Colombian (Tuluá site) and Bolivian (INPA site) TDFs based on data from manual and automatic band dendrometers. Xylem growth dynamics are shown in blue lines and they were quantified by taking wood microcores. See information about other tree species in Chapter 2.

The stem-increment phase detected at daily scales by the automatic dendrometers overlapped with the xylem growth in semi-deciduous tree species from Tuluá, whereas in deciduous tree species from INPA only the last one of the three identified stem-increment phases was associated to xylem growth (Fig. 1).

Particularly, the stem-increment phase was associated with high rainfall, positive water balances and low temperatures and hence, low VPD in Tuluá, whereas this phase corresponded to both high rainfall and warm temperatures in INPA (Chapter 2). Nevertheless, at both TDFs the warm air temperatures noted throughout the day negatively affected radial increment at hourly scales (Chapter 2). Tree species could face the adverse dry conditions by growing during the increment phase, i.e. by restricting radial growth to periods of the day when temperatures are low and water loss due to evapotranspiration is reduced, i.e. during the night (Chapter 2). In tree species from Tuluá, the increment phase at hourly scales mainly occurred from predawn until early morning with temperatures ranging between 17° and 19 °C. In contrast, most INPA tree species showed an increment phase from the morning until the afternoon with temperatures ranging between 21° and 27 °C (Chapter 2). These findings show that the high water availability during the wet season plays an important role favoring radial growth, and temperature is determinant by driving the hourly fluctuations of both the VPD and the evapotranspiration rate.

In addition, the studied tree species showed reversible stem shrinkage from hourly to daily scales (Fig. 1), but most species from the INPA site also displayed reversible stem shrinkage at monthly scales (Fig. 1), which produced negative radial-increment rates (Chapter 2). Chitra-Tarak et al. (2015) have shown that at least part of the temporal variability in annual growth rates arise from reversible, water-induced fluctuations in TDFs. Particularly, the climate controls on radial-increment dynamics varied between daily and monthly scales. At daily scales, there is a positive effect of high precipitation and a positive water balance and a negative effect of VPD on the increment phase (Chapter 2), whilst at monthly scales the precipitation was the main variable that positively affected radial increment (Chapter 2). Accordingly, the differences found in the monthly increment patterns between Tuluá (persistent increase) and INPA sites (reversible swelling; Fig. 1) appeared to be mainly associated with precipitation variability. Bark could also modulate the large stem fluctuations observed in INPA tree species. In general, the bark has lower density than the sapwood and is able to store more water in its tissues (Poorter et al., 2014; Rosell et al., 2014; Stahl et al., 2010). Consequently, bark traits should be explicitly considered as key features to understand the diverse mechanisms used by trees species to tolerate the adverse effects of drought on radial growth in TDFs.

Lastly, the relationship between leaf flushing and radial-increment rates at monthly scales was positive for all TDF tree species. Nevertheless, the strength of relationship among tree species differed as a function of the sapwood density (Fig. 2). Specifically, *Cedrela* showed a strongest leaf-stem relationship and a lowest sapwood density, whilst *Acosmium* showed a reverse pattern (Fig. 2). In the case of *Cedrela* (pioneer species), the high correlation observed between leaf flushing and radial-increment rate may be related to a synchronous response of both processes to precipitation, which was mainly detected at time scales longer than 10 days (see Fig. 3 in Chapter 2). In contrast, the lowest leaf-stem association shown by *Acosmium* (shade-tolerant species), may be linked to the differential response to climate of both processes since leaf flushing responded to precipitation, water balance and VPD at all analyzed time-scales, whereas the radial-increment rate was sensitive to changes in precipitation at time-scales longer than 20 days (see Fig. 3 in Chapter 2). In particular, the pioneer and deciduous species with low wood density, such as *Cedrela*, are more vulnerable to cavitation than shade-tolerant and deciduous species with opposite xylem density values, such as *Acosmium* (Markesteijn et al., 2011a; Méndez-Alonzo et al., 2012). Thus, *Cedrela* can buffer its vulnerability to cavitation losing rapidly the foliage at the start of the dry season (Chapter 2), whereas *Acosmium* slowly loses its leaves during the dry season. It could be also hypothesized that *Cedrela* counteracts its xylem vulnerability to embolism-induced cavitation by growing in microsites with high soil moisture (Chapter 2), but this idea should be better evaluated in more TDFs.

Climatic control on the xylem growth period and its relationship with leaf phenology

Water availability is one of the most important factors that determine growth and productivity of tropical forests (Toledo et al., 2011; Wagner et al., 2012, 2014, 2016). In particular, the annual precipitation seasonality in TDFs generates alternating favorable (wet season) and unfavorable (dry season) periods for cambium activity (Borchert, 1999). Therefore, the activation of cambium and radial tree growth are seasonal in TDFs (Worbes et al., 2013). The results of this thesis agree with these findings, since the xylem growth occurred during the wet season at both deciduous and semi-deciduous tree species in both studied TDFs, reflecting the influence of high precipitation and positive water balance on the development of new xylem cells (Chapter 2). Several studies on tropical tree species have shown that rainfall variation drives the seasonal periodicity of xylem formation. Particularly, an active growth during wet season is often reported in TDFs (Krepkowski et al., 2011; Volland-Voigt et al., 2010; Worbes et al., 2013). Nevertheless, the xylem growth period can be as long as or shorter than the wet season. In semi-deciduous tree species from the Tuluá site the xylem growth occurred during the wet season, whilst in the INPA site the xylem growth of deciduous tree species started at the mid wet season, when their crowns were completely covered by new foliage (Fig. 3).

The main occurrence of xylem growth throughout the wet season recorded in Tuluá may be explained by the elevated precipitation recorded in this TDF caused by a “La Niña” event occurred between 2010 and 2011. In Tuluá, *Cordia* and *Zanthoxylum* are deciduous trees during dry years but their leaf habit can change in wet years, becoming semi-deciduous trees. I suggest that during years with unusual increase in rainfall and, therefore, presence of leaves during the transition from the dry to the wet season, the xylem growth could start at the beginning of the wet season.

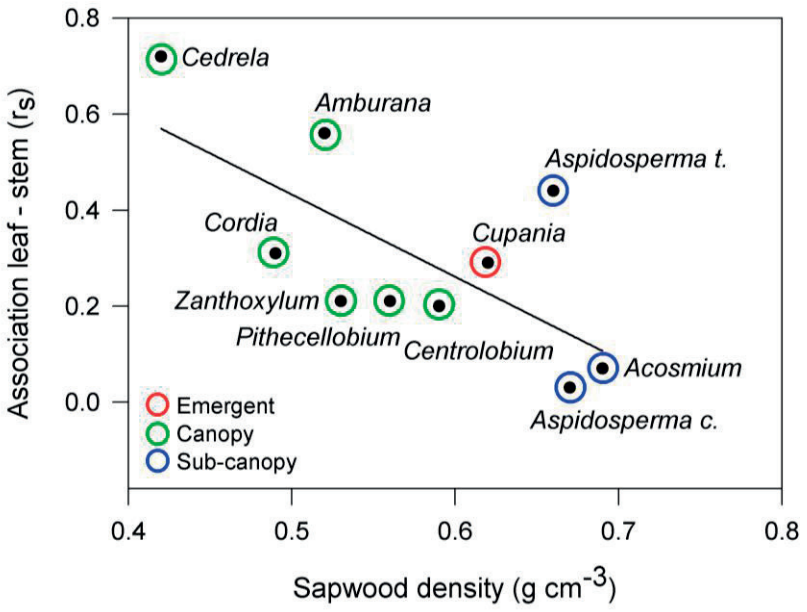

Figure 2. The relationships between leaf flushing and radial-increment rate is negatively linked to the stem sapwood density. Circles show the crown position of each tree species. See more details in Chapter 2.

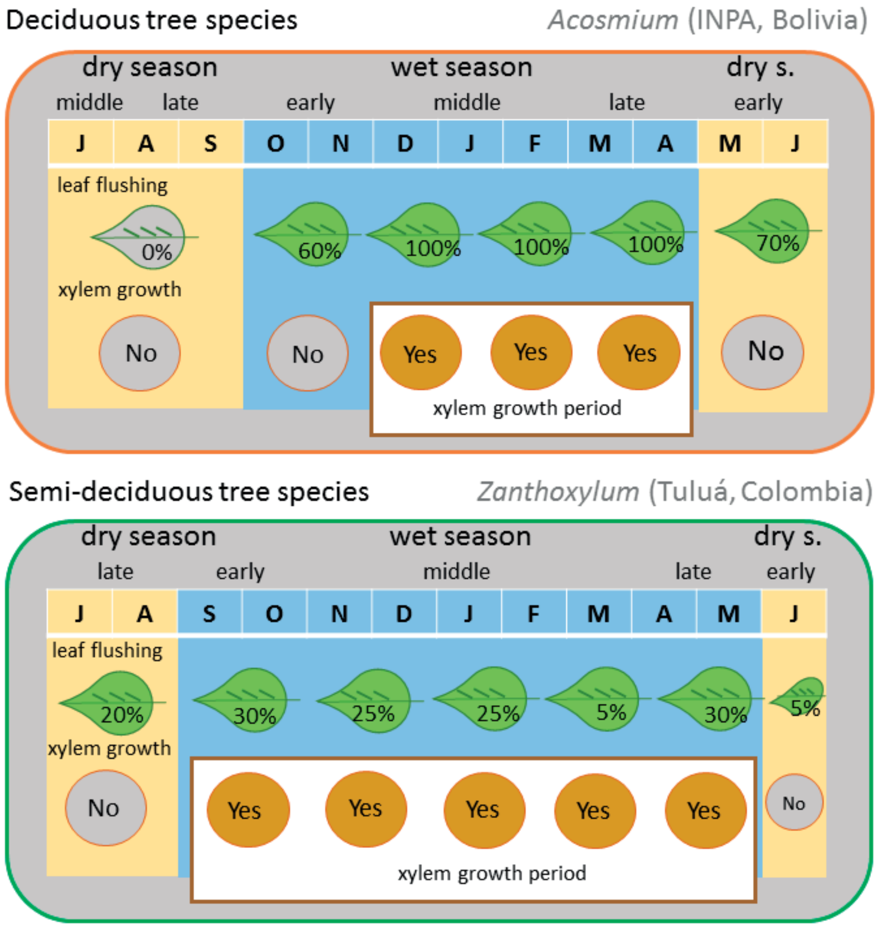

Figure 3. Xylem growth period in two tree species with different leaf habit from Colombian and Bolivian tropical dry forests and its association with leaf flushing during wet (blue) and dry season (yellow). See information about other tree species in Chapter 2.

On the other hand, leaf development before xylem growth recorded in deciduous tree species from the INPA site (*Acosmium* and *Centrolobium*) has also been observed in other tropical deciduous and brevi-deciduous tree species (Krepkowski et al., 2011; Marcati et al., 2006, 2007; Worbes et al., 2013). Nevertheless, the beginning of leaf production and xylem growth are simultaneous in some deciduous, semi-deciduous and stem succulent tree species (Dié et al., 2012; Worbes et al., 2013). In the deciduous tree species studied from INPA, the development of new xylem after full-leaf crown agrees with the fact that these tree species use the previous-year xylem layers to transport water to the crown to allow for new foliage formation. The previously formed xylem could be functional during the next wet season because diffuse-porous (*Acosmium*) and semi-ring porous xylem (*Centrolobium*) are less vulnerable to cavitation than ring-porous xylem (Suzuki et al., 1996). This idea is reinforced by Brodribb et al. (2002), who found that some deciduous tree species from TDFs do not change significantly their conductivity of branches from wet to dry season, indicating that a large proportion of xylem remains functional during the dry season, despite of leaf shedding. Apparently, in these kind of deciduous tree species leaf senescence occurs without embolism. Therefore, the xylem can remain hydrated but inactive until resumption of rainfall in the next wet season. In addition, the beginning of xylem development occurring after the leaves were fully expanded, suggests that deciduous tree species, such as *Acosmium* and *Centrolobium*, can assimilate new photosynthates and thus, they do not depend on internal carbon stores to grow. In other words, radial growth could depend less on the availability of carbohydrates than on water availability. This hypothesis is supported by findings related to the inter-annual patterns of long-term growth registered in coexisting tree species from the INPA site. During the last six decades two multi-annual droughts alternated with a multi-annual wet period in this site (Chapter 3). Specifically, in INPA the lowest growth rates were recorded during the two multi-annual droughts in 1960-1977 and 1985-2008, whereas the highest growth rates were registered during the multi-annual wet period occurring between those two droughts (1978-1984) (Chapter 3). Nevertheless, this growth plasticity associated to water availability is mediated by functional traits as sapwood density. Deciduous tree species with the highest sapwood densities did not show a significant increase in long-term growth associated with increased water availability, i.e. there were no differences between multi-annual wet and dry periods (Chapter 3).

At both TDF sites, all tree species cease growing when the dry season starts (Figs. 1 and 3). Specifically, stem contraction registered from dendrometers and no leaf flushing coincided with the end of xylem growth in semi-deciduous tree species from the Tuluá site (Chapter 2). In deciduous tree species from the INPA site, the end of xylem growth was associated to longest contraction phase and the beginning of leaf shedding, but the total loss of foliage asynchronously occurred among tree species (Chapter 2). Tree species from TDFs do not show cambial activity after the beginning of the dry period regardless of their leaf habits (Worbes et al., 2013). This observation suggests that a pause in cambial activity during the dry season takes place because of low moisture availability and high VPD and these dry conditions drive ring-boundary formation (Lisi et al., 2008; Volland-Voigt et al., 2010; Worbes et al., 2013).

Climate and drought effects on inter-annual patterns of radial growth in TDFs

Here, I discuss the effects of the two main climatic variables used in previous dendrochronological studies, i.e. precipitation and temperature (see Table 2 in General Introduction), on radial growth of seven coexisting deciduous tree species from the INPA site, by analyzing long-term climate-growth relationships. Furthermore, I discuss about the radial growth responses to climate and drought using two additional environmental variables (Fig. 4): (i) the climate water balance (P-PET, differences between precipitation and potential evapotranspiration) and, (ii) the Standardized Precipitation Evapotranspiration Index (SPEI), which explicitly considers the effect of temperature on water availability (Vicente-Serrano et al., 2010). Both variables have not been previously used in tropical dendrochronological studies. Lastly, as multi-species analyses of tree-rings were used to understand the community growth responses to climate and drought, this discussion also focuses on the differences among coexisting tree species.

Climate control on xylem-growth variability: the role of precipitation and temperature

As discussed earlier, precipitation exerts a huge positive influence on xylem growth at intra-annual scales (see also Chapter 2). As expected, this positive effect of the precipitation on radial growth was also registered in long-term tree growth responses in all studied tree species from INPA using residual tree-ring width chronologies (Fig. 5, see also Chapter 3). Several studies have shown that inter-annual tree growth variability responds positively to precipitation in TDFs (see Table 2 in General Introduction), which implies that xylem growth is constraint by water availability. Specifically, the tree growth responses to precipitation were more intense at short-time scales (from 2 to 9 months) mainly during the wet season in the INPA site (Fig. 5, see also Chapter 3). This suggests that radial growth does not occur throughout the year, but it is concentrated in a few months. This hypothesis is supported by xylogenesis studies developed in both study sites, which showed that xylem growth of coexisting tree species occurred during the wet season (Figs. 1 and 3, see also Chapter 2). The seasonality in precipitation annual at TDFs generates favorable and unfavorable periods for the cambium activity during wet and dry seasons, respectively (Borchert, 1999; Worbes et al., 2013).

The review done by Brienen et al. (2016) showed that tree growth sensitivity to precipitation fluctuations is similar among tropical forest, where 24% and 32% of the ring-width variability are explained by the year-to-year variation in precipitation from wet forests and TDFs, respectively. Specifically, this thesis shows that the sensitivity of xylem growth to rainfall fluctuations was species-specific in the INPA site (Chapter 3), as it has been recognized in other TDFs (e.g. Enquist and Leffler, 2001; Vlam et al., 2013). It has been suggested that trees have different strategies to grow and use water, as this has been reported in other TDFs (Borchert 1994, 1999; Worbes 1999). In fact, this thesis shows that the variance of the radial growth associated to precipitation can range from 6% to 22% in the INPA site depending on the study species (Fig. 5). Although these percentages are low, they are within the recorded values in other TDFs (e.g. Enquist and Leffler, 2001; López and Villalba, 2011; Paredes-Villanueva et al., 2013). The wide range of this growth variance explained by rainfall might be caused by the different strategies used by TDF tree species to tolerate or avoid drought (Worbes et al., 2013). For instance, in several tree species from TDFs a high leaf phenological plasticity associated to unusual dry or wet periods within the wet or dry seasons, respectively, has been registered (Borchert et al., 2002).

Regarding temperature, a negative effect on tree growth has been observed in several tropical forests using permanent sample plots at long time-scales (Clark and Clark, 2010; Dong et al., 2012), but this has also been inferred from dendrochronological studies carried out in tropical forest (Brienen et al., 2016), including several tree species considered in this thesis (Fig. 5, see more details in Chapter 3). Particularly, coexisting tree species from a Thai TDF showed that the relationships between growth and temperature were generally stronger than those between growth and precipitation (Vlam et al., 2013). In fact, warming-induced growth decline is more widespread among tropical tree species than in tree species from temperate or boreal forests (Way and Oren, 2010). Nevertheless, it remains unclear whether the indirect negative effect of temperature on stem growth in tropical tree species is mainly due to reduced growth rates caused by higher evapotranspiration rates and amplified drought stress due to water loss through stomata, or because of an indirect effect due to the increase in respiration (Schippers et al., 2015; Vlam et al., 2013) or the decrease in photosynthesis rates (Seiler et al., 2015).

In contrast, other dendrochronological studies showed that radial growth does not respond to temperature fluctuations in TDFs (see Table 2 in General Introduction). The amplitude of the intra-annual temperature variability among TDFs, associated to the latitudinal distance to the Equator (Eamus, 1999), could partially explain these contrasting findings.

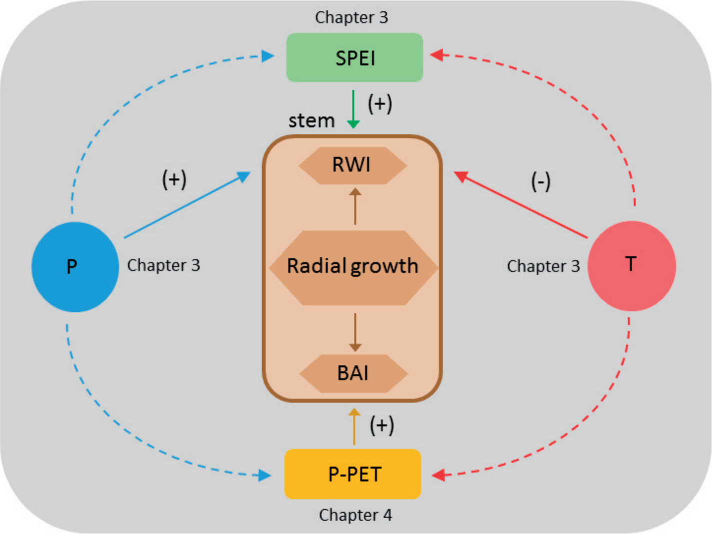

Figure 4. Environmental effects on radial growth measured as ring-width index (RWI) and basal area increment (BAI). The effects of total precipitation (P) and mean temperature (T) were first separately evaluated and then considered together through the calculation of the climatic water balance (P-PET, differences between precipitation and potential evapotranspiration) and a drought index (Standardized Precipitation Evapotranspiration Index, SPEI; positive and negative SPEI values indicate wet and dry conditions, respectively). The positive (+) and negative (-) effects of each environmental variable on growth are shown and the corresponding chapter where they appear are indicated.

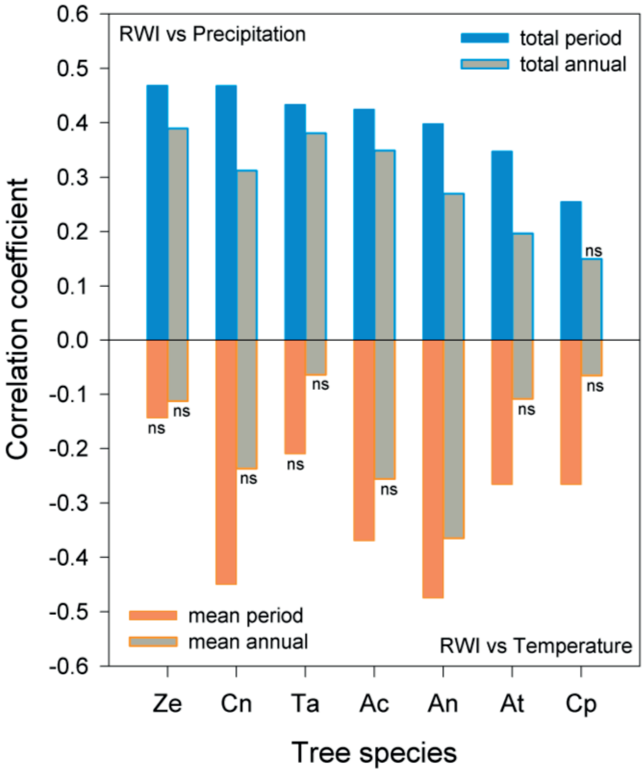

Figure 5. Correlations (Pearson coefficients) calculated between residual tree-ring width chronologies (RWI) and climatic variables at annual and monthly scales for the common period 1949–2008. Significance was calculated through bootstrapping and not significant correlations are indicated (ns). The specific month or group of months (period) in which the highest correlations were recorded can be seen in Chapter 3. Tree species' abbreviations: Ze, *Zeyheria tuberculosa*; Cn, *Centrolobium microchaete*; Ta, *Tabebuia impetiginosa*; Ac, *Acosmium cardenasii*; An, *Anadenanthera macrocarpa*; At, *Aspidosperma tomentosum*; Cp, *Caesalpinia pluviosa*.

Apparently, species that grow near the Equator do not respond to temperature, probably because of the low intra-annual temperature variability (<3 °C) in those areas. In this regard, tree species showed no responsiveness of radial growth to temperature variability (see Table 2 in General Introduction). In contrast, tree species from TDFs show negative growth responses to temperature mainly during the wet season at latitudes ≥ 11° where the inter-monthly temperature variability is ca. 5 °C (see Table 2 in General Introduction).

On the other hand, the negative relationship between temperature and growth in the majority of INPA tree species, contrasts with the positive precipitation-growth associations (Fig. 5). This may be due to the negative co-linearity between precipitation and temperature at inter-annual scales (Fig. 6), which has been recorded in other tropical forests (Brienen et al., 2016). Therefore, and as expected, years with high rainfall and low temperature enhanced growth (Chapter 3). Nevertheless, the tree growth responses to temperature were more intense at short-time scales (from one to three months) during the wet season, when the highest mean temperatures in INPA are registered (Chapter 3). Therefore, an increase of the evapotranspiration rates during the growing season associated with high temperatures would negatively affect the radial increment of INPA tree species, since the leaf stomata tend to close to minimize water loss, which leads to a lower CO_2-uptake and thus, lower carbon assimilation rates. Nevertheless, tree species could face those adverse conditions by growing during the hours with the lowest temperatures, i.e. when the water loss due to evapotranspiration is reduced (e.g., night and dawn periods), as mentioned above.

Tree growth responses to temperature were also species-specific. In particular, negative responses of ring-width indices to air temperature in five out of the seven tree species studied were recorded (Fig. 5). The temperature explained 7% to 22% of the inter-annual growth variability, being *Anadenanthera* the most sensitive tree species to temperature changes at monthly to annual scales (Fig. 5). This finding may be related to the fact that it is an emergent species whose crowns are usually completely exposed to elevated radiation levels and thus, air temperature fluctuations.

Besides, the temperatures are expected to rise between 2.5° and 6.0 °C for the period 2070 - 2099 in the Bolivian lowlands (where the INPA site is located), according to climate models forced by different CO_2-emission scenarios (Seiler et al., 2013). This suggests a trend towards drier conditions, mainly due to a higher atmospheric water demand because of a high evapotranspiration rates associated to rising temperatures. These potential new climatic conditions in the INPA site could lead to a decrease in growth rates in the future, due to the indirect negative effect of the temperature on radial growth that was found in this thesis, but the growth decline could be species-specific with tree species most sensitive to temperature being probably the most negatively affected. Nevertheless, a physiological species-specific trait acclimation could occur in order to maximize carbon gain and thus, increase the resilience of tropical trees to climate warming (Sterck et al., 2016). Therefore, it is not entirely correct to affirm that the most temperature-sensitive tree species will be the most vulnerable to climate warming in the INPA site.

Differential radial growth responses to water balance among tree species are linked to sapwood density

Precipitation data offer a coarse approximation of water availability to TDF trees. In this regard, the atmospheric water balance (Fig. 4) allows a better estimate of water available for the trees, since it takes into account water loss to the atmosphere through evaporation and transpiration.

Nevertheless, growth responses to both climate variables should present similar patterns. According to that, all tree species from the INPA site showed a positive effect of a high water balance on growth. Specifically, the radial-growth responses (measured as basal area increment, BAI) peaked at short-time scales during the wet season (Chapter 4), as happened with the precipitation. This suggests that the xylem growth is concentrated during this season, which is supported by xylogenesis data (Figs. 1 and 3). During the short wet season, TDF deciduous tree species maximize photosynthesis, hydraulic conductivity, and growth rate (Borchert, 1999; Brodribb et al., 2002; Eamus, 1999). Nevertheless, the strength of the relationships observed between the water balance and growth during the wet season varied among species. In particular, the variability of growth explained by water balance was negatively related to sapwood density (Fig. 7).

Zeyheria was the most sensitive species to precipitation and water balance (Figs. 5 and 7), exhibited low sapwood density values and a high sapwood area (43%) (Fig. 7), which can be associated with a strategy towards high stem water storage. In contrast, *Caesalpinia*, the least sensitive species showed the opposite characteristics, high wood density and low (23%) sapwood area (Fig. 7). Hypothetically, *Zeyheria* is able store more water in their stems that *Caesalpinia* and thus, *Zeyheria* shows a high sensitivity in terms of growth changes to water availability in comparison with *Caesalpinia* (Chapters 3, 4). This idea is supported by the results presented in Chapter 3, which shows that between 1949 and 2008 two multi-annual wet periods alternated with two multi-annual droughts were recorded. In particular, low tree-ring width values were observed in the two multi-annual droughts (1960–1977, 1985–2008), while the highest growth values occurred during the wettest and longest period (1978-1984) in all species, excepting in tree species with the highest wood density, i.e. *Caesalpinia*. On the other hand, *Zeyheria* was the most sensitive deciduous tree species responding to the water balance (Fig. 7), and it could require more water to grow and thus, a more efficient water transport than less sensitive deciduous tree species. In fact, the wood density of *Zeyheria* is within the optimum range for hydraulic efficiency reported by Kallarackal et al. (2013) (Fig. 7).

The hypothetical high stem water storage showed by *Zeyheria* might also explain its capacity to retain leaves throughout most of the dry season (Chapter 4) and thus, to be considered drought tolerant. In contrast, *Caesalpinia* may avoid drought by losing their leaves during the driest months. Although *Zeyheria* was one of the species that showed the lowest density of wood (Fig. 7), other INPA species may also present low wood density as *Cedrela* (0.42 g cm^{-3}) (Fig. 2). Unlike *Zeyheria*, *Cedrela* does not retain their leaves for most of the dry season (drought-tolerant species), on the contrary it could avoid drought by losing their complete foliage at the beginning of the dry season (Chapter 2). This suggests that *Cedrela* rapidly reduces the flow of water to the crown as a precaution for avoiding cavitation.

Currently, there has been an intense effort to link functional traits and radial growth in several TDFs (e.g. Poorter et al., 2010). In particular, the radial growth seems to be related to several functional xylem traits, such as, wood density or vessel lumen diameter and hydraulic conductance (Fan et al., 2012; Iida et al., 2012). Hérault et al. (2011) concluded that stem traits, such as, wood density and water content largely explained interspecific differences in growth trajectories of tropical tree species. Growth responses to climate may also depend on additional or unmeasured traits, such as, water-use efficiency or rooting depth. The relative importance of wood density, compared with other traits for controlling the response of growth to water availability, could not be quantified with the available data in this study. Nonetheless, this is one of the few studies providing a link between a key functional trait, i.e. wood density (a proxy of the tree's ability to store water in the stem), and differential growth responsiveness to water balance in TDFs.

Impact of drought on tree radial growth

A recent study on drought variability and trends across Bolivia during the period 1955-2012 showed that the mean drought conditions across the country had a temporal behavior mainly characterized by decadal variations (Vicente-Serrano et al., 2014). Specifically, this thesis registered how two multi-annual wet periods alternated with multi-annual droughts in the INPA site over the past 60 years by using the SPEI, a multiscale drought index (Fig. 6b, see more details in Chapter 3). Overall, years with low rainfall and high temperatures were identified as dry years (see negative SPEI values in Fig. 6). This finding suggests that INPA tree species have to face intra-annual (dry season) and multi-annual or long-lasting droughts.

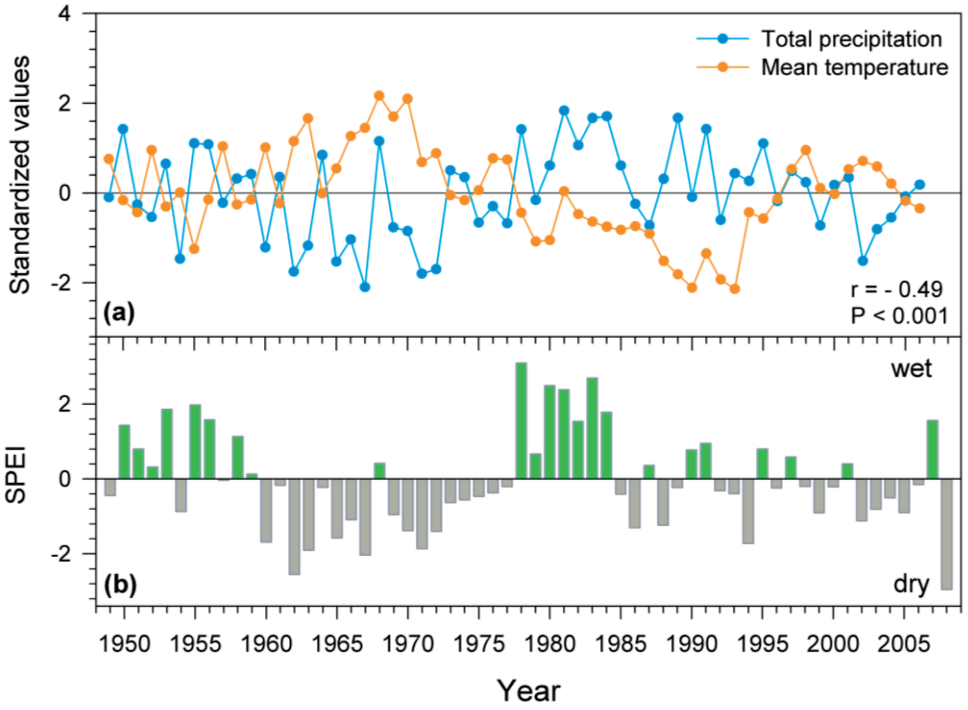

Figure 6. Temporal patterns of climatic (a) and drought variability (b) in INPA (Bolivia). In the upper plot the relationship between the standardized temperature and precipitation values is indicated with its corrected probability value. In the bottom plot the time series show the 12-months long Standardized Precipitation Evapotranspiration Index - SPEI (drought index) calculated for September. Note that positive and negative SPEI values indicate wet and dry conditions, respectively. See more details in Chapter 3.

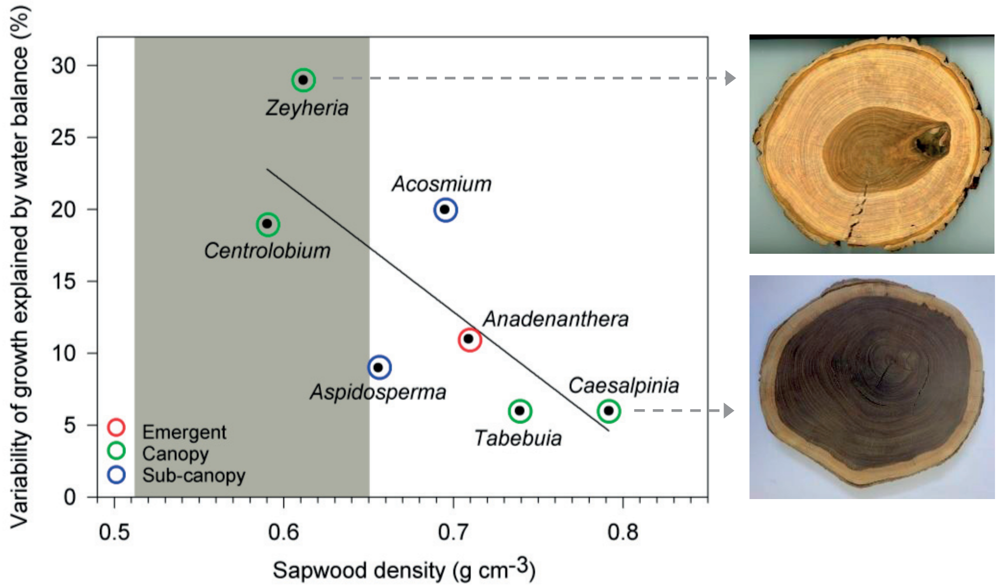

Figure 7. Sapwood density is negatively related to the growth variability explained by climate water balance. The amount of growth (basal area increment) variance (R^2) explained by the best fitted linear mixed-effects models as a function of water balance is shown in the y axis (see Table 4 in Chapter 4). Wood cross-sections show the difference in the proportion of sapwood (light outer wood) and heartwood (dark inner wood) between *Zeyheria tuberculosa* (top right) and *Caesalpinia pluviosa* (bottom right). The circles show the crown position of each tree species. The gray area corresponds to the optimum range for hydraulic efficiency reported by Kallarackal et al. (2013).

The strongest relationships observed between the SPEI and ring-width indices were always positive irrespective of the analyzed time-scale, indicating that growth is severely limited by water deficit. At inter-annual scales, the SPEI explained from 17% to 29% of the year-to-year growth variance (Fig. 8). These values suggest that the tree species studied can buffer the negative effects of drought on growth. In particular, the functional responses to cope with droughts may be rapid and translate into significant SPEI-growth associations, since the highest correlations were recorded at relatively short-time scales, i.e. from two to seven months (Chapter 3). Thus, this thesis confirmed the finding from a global study, which evidenced that vegetation activity and growth mainly responded to drought at short-time scales in drought-prone biomes (Vicente-Serrano et al., 2013). This short-time buffering and responses to drought contrast with the sensitivity to long-term droughts, as evidenced by the notable increase in growth variance explained by the SPEI, with values ranging from 45% to 88% at time-scales varying from six to 30 years (Fig. 8, see more details in Chapter 3). Tree species may tolerate a dry year by using the same ecophysiological mechanisms and traits to withstand the dry season (cf. Markesteijn et al., 2011b), which is a main characteristic of the TDFs (Bullock et al., 1995). Nevertheless, these mechanisms seem not to be very efficient to deal with long-term droughts in terms of growth and probably forest productivity. In fact, long-lasting droughts have been shown to negatively affect growth of TDFs tree species (Leigh Jr. et al., 1990) and also in humid rainforests (Feeley et al., 2007; Phillips et al., 2009). This indicates that the long-term temporal variability of water availability drives the community growth dynamics of TDFs, probably to a higher extent than in humid rainforests, where radiation is the major environmental driver of tree growth (Brienen et al., 2010a; Brienen and Zuidema, 2006).

The emergent *Anadenanthera,* which was the most temperature-sensitive tree species (Fig. 5), also showed a highest long-term growth sensitivity to SPEI since this drought index explained almost 90% of the growth variance (Fig. 8). This would indicate a high sensitivity of this species to long-term atmospheric water demand. In contrast, *Caesalpinia* growth did not respond to long-term SPEI variability, suggesting that this species may tolerate severe and lasting droughts. Furthermore, the high density and low production of sapwood of the latter species (Fig. 7), which is also observed in other Fabaceae (Reyes-García et al., 2012), could be also related with a low water demand. The dense wood of *Caesalpinia* also implies a low potential hydraulic conductance (cf., Kallarackal et al., 2013). The low sensitivity to long-term droughts of *Caesalpinia* is consistent with observations from lowland Amazonian forests, where species with denser wood were less vulnerable to drought and may become dominant after long periods of water deficit (Phillips et al., 2010).

In conclusion, the temporal variability in water availability drives growth community dynamics of the TDF species studied at different time scales. Specifically, the radial growth responded positively to less dry conditions at short (from two to seven months) and long-time scales (from six to thirty years). Tree species are resilient to short-term droughts while growth is particularly sensitive to long-lasting droughts, except in those species with a high sapwood density (e.g., *Caesalpinia*).

Outlook for further research

Several questions arose during the development of this thesis, which can give rise to several research lines. Here are three of the most important lines of further research:

Selecting potential tree species to dendroclimatological reconstructions in TDFs

The radial growth in the tree species studied showed that is positively related to precipitation and water balance and negatively to temperature (Chapter 3), indicating that they share high common growth variability in response to local climate. Nevertheless, the strongest response of growth to climate was species-specific, indicating that there is a differential sensitivity among tree species to these climate variables (Chapter 3). This finding is very important, since the most sensitive tree species to climate will be the best proxies to reconstruct the climatic conditions in the Chiquitano TDF. As this TDF only has a small set of climate data (from 1950) due to scarcity of instrumental records, proxy-based climatic reconstructions will be highly valuable. I suggest using *Zeyheria tuberculosa* and *Centrolobium microchaete* ring-width data as precipitation and water balance proxies, while *Anadenanthera macrocarpa* ring-width data may be suitable temperature proxies, since they were the most sensitive species to the mentioned climate variables (Chapters 3 and 4).

Evaluating the role played by drought as a driver of tree population dynamics in TDFs

This thesis showed that radial growth of tree species responded differently to short- and to long-term droughts in a Bolivian TDF. In particular, these tree species are more sensitive to multi-annual droughts and that such sensitivity differs among species (Chapter 3). This finding raises the following general question: How can these multi-annual droughts drive TDF dynamics? Specifically, what are the consequences of persistent droughts for population dynamics in long-lived TDF species?

In order to scale up the drought effects on population level it is necessary to combine the information gained from dendrochronology with those from permanent sample plots (PSPs), using demographic modelling, such as, Integral Projection Models - IPMs (Zuidema *et al.*, 2010). In regard to the drought severity, it could be quantified using the Standardized Precipitation Evapotranspiration Index - SPEI, a multiscalar drought index, which explicitly considers the effect of temperature on water availability (Vicente-Serrano et al., 2010). The inclusion of this drought index in IPMs could be a big challenge, but the valuable information that could be obtained would allow evaluating the effects of droughts on population growth rates and the stable population structures, and to determine if this effect is species-specific. In particular, evaluations are needed for drought effects on: tree growth, tree survival, and tree recruitment and thus, the activities to be carried out to answer those questions are:

- To assess the drought-growth relationships at a short-time scale in individuals of different sizes and tree species using dendrochronological data.
- To determine if the number of new recruits is related to drought intensity using PSP data.
- To evaluate the drought-survival relationship for each tree species using PSP data.

Assessing differences among TDFs as carbon sinks

According to climatic data from Tuluá and INPA study sites for the 1984-2011 period, the relationship between monthly precipitation and temperature is significantly positive in INPA, but it is negative in Tuluá (Fig. 3 in General Introduction). This suggests that during growing season, high rainfall can be associated to high or low temperature in different TDFs, such as, INPA and Tuluá, respectively. These two climate scenarios, negative or positive relationship between precipitation and temperature, could determine differences in annual growth rates of tree species among TDFs and thus, generate differences among them as carbon sinks. Particularly, an increase of the evapotranspiration rates and vapor pressure deficit during the growing season associated with high temperatures would negatively affect the radial increment of INPA tree species due to water stress, while Tuluá tree species could be growing under more favorable weather conditions. In fact, the annual xylem growth (based on microcore data), differed between the two study sites being significantly higher in Tuluá than in INPA (Chapter 2). However, the low number of tree species studied (two per site) and the very short period of this study (one year), do not allow to test the hypothesis proposed above. It is necessary to conduct a specific study to properly evaluate this question considering also functional traits of tree species as sapwood density.

Conclusions

In this thesis I assessed the dynamics of radial growth at different time-scales in relation to climate and drought of deciduous and semi-deciduous tree species coexisting in two TDFs located in Bolivia (INPA site) and Colombia (Tuluá site). In this way, the main conclusions are shown at both intra- and inter-annual scales and focusing on the differences among the tree species studied.

Climate control on intra-annual patterns of radial growth in Colombian and Bolivian TDF tree species

- Cambium reactivation and xylem growth of tree species occurred during the wet season at both study sites, reflecting the influence of high **precipitation** and a positive **water balance** on the development of new xylem cells.
- In the semi-deciduous tree species from the Tuluá site the xylem growth period overlapped with the wet season, whereas in deciduous tree species from the INPA site the growth period started at the mid wet season, when the tree crowns were fully developed.
- High water availability during the wet season plays an important role enhancing radial growth. **Temperature**, as a determinant factor in the hourly fluctuations of both the vapor pressure deficit and the evapotranspiration rate, could exert a huge influence on tree radial growth dynamics during the growing season. Particularly, in the Tuluá site the growing season was associated with low temperatures and hence low **vapor pressure deficit** (VPD), while in the INPA site the growing season was related to high temperatures and VPD. Nevertheless, at both TDFs the high temperatures registered throughout the day negatively affected radial increment at hourly scales. Tree species could face the adverse dry conditions by restricting growth to periods of the day when temperatures are low, since water loss due to evapotranspiration are low too.
- Stem shrinkage and swelling occurred at hourly to daily scales in all tree species, and most INPA tree species displayed strong reversible shrinkage at monthly scales. Particularly, the climate controls on radial-increment dynamics varied between daily and monthly scales. At daily scales, there was a positive effect of high precipitation and a positive water balance and a negative effect of VPD on the increment phase, while at monthly scales the precipitation was the main variable that positively affected radial increment.
- The relationship between radial-increment rates and leaf flushing recorded at monthly scales was positive for all tree species. Nevertheless, the tree species differed in the strength of these stem-leaf associations as a function of the sapwood density. Thus, *Cedrela*, a pioneer deciduous tree species, showed the highest stem-leaf association and the lowest sapwood density, while *Acosmium,* a shade-tolerant deciduous species, showed the lowest stem-leaf association and the highest sapwood density.

Climate and drought effects on inter-annual patterns of radial growth in Bolivian tree species

- The radial growth in the tree species studied showed a positive relationship with precipitation and climate water balance and a negative association with temperature, indicating that they share high common growth variability in response to local climate. Nevertheless, the strongest response of growth to climate was species-specific, indicating that there was a differential sensitivity among tree species to these climate variables.
- **Precipitation** enhanced tree radial growth of all TDF study species at short time scales (from two to nine months), mainly when water availability increased during the wet season.

- The radial growth of all tree species responded positively to **water balance** during the wet season, but such responses differed among species as a function of their stem sapwood density. Specifically, sapwood density was negatively related to the growth variability explained by the water balance. Tree species with low-density wood and high production of sapwood, such as *Zeyheria*, were the most sensitive to water balance, whereas species with the opposite characteristics, such as *Caesalpinia*, were the least sensitive ones.
- Radial growth was negatively related to **temperature** in five out of seven tree species from the INPA site. *Anadenanthera*, an emergent tree species, was the most sensitive tree species to monthly and annual temperature changes, whereas the rest of species showed negative growth responses to temperature at short-time scales (from one to three months), again mainly during the wet season.
- Growth responded positively to wetter conditions at short (from two to seven months) and long-time scales (from six to thirty years). Specifically, tree species tolerated **short-term droughts** while they were particularly sensitive to **long-lasting droughts**, with the exception of *Caesalpinia.* This indicates that the tree species from the INPA site are predominantly sensitive in terms of growth reduction to long-lasting droughts. The emergent *Anadenanthera*, which was the most temperature-sensitive tree species, also showed the highest growth sensitivity to long-lasting droughts. In contrast, the growth of the canopy tree species *Caesalpinia*, which showed the lowest sensitivity to the water balance, did not respond to long-term drought variability.

Resumen

Urania fulgens (Walker, 1854) a day-flying highly migratory moth (Bolivia)

1. INTRODUCCIÓN

1.1. Los bosques secos tropicales: distribución espacial, importancia socio-ecológica y amenazas

Los bosques secos tropicales (BsTs) son formaciones vegetales dominadas por árboles con hábitos foliares desde caducifolios hasta perennes (Eamus, 1999); crecen en las tierras bajas de la zona intertropical de América, África y el Sureste asiático, y en países como Australia e India (Miles et al., 2006), bajo un régimen de precipitación anual ≤ 2000 mm, temperaturas promedio anuales > 20 °C, y una época seca hasta de 8 meses, que registra precipitaciones mensuales < 100 mm (Dirzo et al., 2011; Eamus, 1999; Gentry, 1995; Murphy y Lugo, 1986). En general, los BsTs presentan un dosel más abierto, con árboles de menor tamaño (altura y diámetro), y una menor riqueza de especies arbóreas que los bosques húmedos tropicales (Murphy y Lugo, 1986).

Los BsTs junto a los otros tipos de bosques ubicados en la franja intertropical, desempeñan un papel clave en el ciclo global del carbono. En particular, Pan et al. (2011) estimaron que los bosques tropicales mejor conservados, son los sumideros de carbono de casi el 50% de la biomasa forestal global acumulada durante 1990-2007 (2,4 ± 0,4 Pg C year^{-1}). Al igual que otros tipos de bosques, los BsTs suministran diversos servicios ecosistémicos, tales como: la regulación hídrica y climática, el ciclado de nutrientes y la estabilización de los suelos (Pizano y García, 2014). A su vez, los BsTs ofrecen diversos productos a millones de personas que dependen directa o indirectamente de este tipo de bosques, tales como: frutos silvestres, insectos comestibles, productos derivados de las abejas (miel y cera), madera como producto de exportación y para fabricar carbón (Blackie et al., 2014).

Los BsTs abarcan cerca de 105 millones de ha, equivalente al 0.7% de la superficie terrestre del planeta (Miles et al., 2006). Esta área corresponde a menos del 50% de la extensión original que tuvieron los BsTs (Hoekstra et al., 2005), como consecuencia de la amplia deforestación y degradación producto de la actividad antrópica (Janzen, 1988) y la limitada protección de sus hábitats (Hoekstra et al., 2005). Miles et al. (2006) estimaron que al menos un 97% de los BsTs están en riesgo, por una o más de las siguientes amenazas: cambio climático, fragmentación del hábitat, fuegos, asentamientos humanos y transformación a tierras de cultivo. Por lo tanto, los BsTs son considerados como los bosques más amenazados de toda la zona intertropical (Janzen, 1988). Teniendo en cuenta este panorama tan adverso, diversos investigadores han propuesto crear nuevas áreas protegidas y definir mecanismos para mitigar el impacto negativo de la actividad antrópica, con el fin de proteger los fragmentos que quedan de los BsTs y por ende, su biodiversidad (Janzen, 1988; Miles et al., 2006; Songer et al., 2009).

Históricamente, extensas áreas de los BsTs fueron deforestadas, transformándolas en tierras de cultivo y ganadería, mientras otras áreas fueron degradadas mediante la tala de especies de árboles maderables, extracción de leña y la realización de incendios forestales. Por ejemplo, la tala selectiva de *Amburana cearensis* y *Cedrela fissilis* (dos de las 14 especies de árboles estudiadas en esta tesis) ha causado una reducción drástica de sus poblaciones. En la actualidad, ambas especies están en peligro de extinción (IUCN, 2016).

Esta tesis se centra en los BsTs del Neotrópico, donde se encuentra la mayor extensión de este tipo de bosques, con alrededor de 52 millones de ha (Portillo-Quintero y Sánchez-Azofeifa, 2010). Sin embargo, la deforestación y degradación han causado un estado crítico de fragmentación en muchos países. Por ejemplo, los BsTs venezolanos ocupan cerca del 10% de su extensión original (Fajardo et al., 2005), y en Mesoamérica (Sureste de México y América Central) ocupan menos del 2% del área que fue registrada cuando los españoles llegaron a América (Janzen, 1988). En Colombia, donde está ubicado uno de los sitios de muestreo de esta tesis (Tuluá), los BsTs cubrían más de 9 millones de ha. Actualmente, ha perdido más del 90% de su extensión original. Por lo tanto, su biodiversidad está en un riesgo inminente de desaparecer (Pizano y García, 2014). En particular, el 60% de los remanentes de los BsTs en Colombia son usados para la agricultura y la ganadería (Pizano y García, 2014). En contraste, México, Brasil y Bolivia presentan las extensiones más grandes y mejor conservadas de los BsTs en el Neotrópico (Portillo-Quintero y Sánchez-Azofeifa, 2010). Específicamente, el BsT Chiquitano, donde se está ubicado el otro sitio de muestreo de esta tesis (INPA), es uno de los BsTs más extensos que existen actualmente en América del Sur, con cerca de 14 millones de ha (Portillo-Quintero y Sánchez-Azofeifa, 2010). El BsT Chiquitano está localizado entre Brasil, Bolivia y Paraguay. Actualmente, las áreas mejor conservadas están en Bolivia y Paraguay, ya que en Brasil la cobertura forestal de este bosque fue eliminado por completo para fines agrícolas y ganaderos (Vides-Almonacid et al., 2007).

Además de las presiones antrópicas que se han ejercido históricamente sobre los BsTs, las sequías son una amenaza adicional para ellos. En particular, sequías más intensas y de mayor duración, vinculadas a un incremento de la temperatura y la evaporación, se han observado desde los años 1970 sobre las áreas tropicales y subtropicales del planeta (IPCC 2007). Un posible escenario en el futuro estaría caracterizado por la presencia de sequías más intensas y duraderas, las cuales podrían conllevar al colapso de las comunidades forestales tropicales, convirtiéndolas de sumideros a fuentes de carbono y esto a su vez, generando un efecto cascada afectando la retro-alimentación clima-vegetación a escalas globales (Lewis, 2006). Por ejemplo, las sequías intensas registradas a inicios del siglo XXI, causaron una disminución de la productividad primaria neta (PPN) en la mayoría de los bosques Neotropicales (Phillips et al., 2009; Zhao y Running, 2010), donde la producción de la madera fue el componente más sensible de la PPN aérea a la disminución de la disponibilidad de agua (Brando et al., 2008). Con el fin de resolver parte de esta incertidumbre vinculada a la retro-alimentación clima-sequía-bosques debemos avanzar en el entendimiento de los impactos del clima y de las sequías en la productividad, el crecimiento y el funcionamiento de los bosques, en general, y de los BsTs, en particular.

1.2. Evaluación de los patrones del crecimiento intra-anual en los árboles de los BsTs

Con el fin de entender el impacto del clima y de las sequías en el crecimiento de los árboles a largo plazo, es necesario entender sus efectos a escalas temporales más cortas. Actualmente, se conoce que el crecimiento anual del xilema de los árboles en las zonas tropicales está limitado por la dormancia del cambium, la cual es inducida por tres factores ambientales: (i) la presencia de una estación seca anual asociada a una disminución pronunciada o a la ausencia de precipitaciones, (ii) períodos de inundación anuales, tal como ocurre en la cuenca del Amazonas y (iii) fluctuaciones anuales en el incremento de la salinidad del agua contenida en el suelo de los manglares (Borchert, 1999; Chowdhury et al., 2008; Schöngart et al. 2002).

En particular, la estacionalidad de la precipitación en los BsTs genera una alternancia entre períodos favorables (estación húmeda) y desfavorables (estación seca) para la actividad del cambium (Borchert, 1999). Estas dos estaciones contrastantes sumadas a la presencia de numerosas especies de árboles que exhiben diferentes estrategias para tolerar el déficit hídrico durante la estación seca (Bullock et al., 1995; Eamus, 1999), hacen que los BsTs sean un sistema interesante para entender las relaciones clima - fenología de las hojas - crecimiento del xilema. En particular, la respuesta especie-específica de los árboles al déficit hídrico en los BsTs se evidencia por la presencia de: (i) diferentes comportamientos en la fenología de las hojas (Borchert, 1994, 1999; Eamus y Prior, 2001), (ii) diversos patrones estacionales de la conductividad hidráulica del tronco (Brodribb et al., 2002), y (iii) diferentes estrategias de almacenamiento de agua en el xilema y la corteza (Poorter et al., 2014; Rosell et al., 2014). Por su parte, Worbes et al. (2013) registraron en un BsT diferencias en la longitud del período de crecimiento del xilema entre especies de árboles con diferentes hábitos foliares. Además, observaron que en las especies caducifolias el comienzo del crecimiento del xilema puede ocurrir simultáneamente o después del inicio de la producción de hojas. Teniendo en cuenta esta valiosa información, resulta importante conocer de manera detallada cómo y cuándo el xilema es formado en cada una de las especies de árboles, es decir, determinar su asociación con la fenología de las hojas e identificar cuáles variables climáticas son las principales limitantes tanto de la xilogénesis (formación de la madera) como de la fenología de las hojas. Esta información puede mejorar nuestro entendimiento de cómo la formación de la madera y, por ende, la captura de carbono ocurre en los BsTs. Además, permitiría entender las respuestas del crecimiento a largo plazo frente a las sequías y al calentamiento climático.

1.3. *Identificación de las tendencias del crecimiento radial a largo plazo: parcelas permanentes de muestreo vs. dendrocronología*

Los datos sobre el crecimiento a largo plazo en especies de árboles tropicales son obtenidos, principalmente, a partir de parcelas permanentes de muestreo (PPMs). En particular, las PPMs suministran datos para la elaboración de modelos de crecimiento y rendimiento de especies arbóreas, los cuales ayudan a la gestión forestal (Alder y Synnott, 1992; Priyadi et al., 2005). Además, las PPMs permiten evaluar el efecto de varias variables ambientales sobre el crecimiento radial de los árboles (cf. Toledo et al., 2011). Al respecto, la información obtenida de las PPMs ha permitido identificar una disminución del crecimiento radial en algunos bosques tropicales durante las últimas décadas. Esta respuesta fue asociada a una alteración en los regímenes de la temperatura y la precipitación, los cuales pueden modificar la cantidad de agua disponible para los árboles y, por ende, afectar el crecimiento de los árboles (Feeley et al., 2007). Sin embargo, en otros estudios que han utilizado datos provenientes de PPMs instaladas en bosques tropicales con un disturbio bajo, registraron un incremento de la biomasa y del crecimiento de los árboles, lo cual fue asociado a un incremento de los niveles del CO_2 atmosférico (Baker et al., 2004; Phillips et al., 1998). Todos los estudios anteriormente mencionados, están basados en remediciones de los cambios del diámetro de los árboles cada 5 o 10 años, lo cual limita la resolución temporal. Además, éstas remediciones son usualmente inferiores a 25 años y, por ende, pueden generar datos errados cuando el propósito es descifrar cómo el crecimiento de los árboles responde a la variabilidad climática y a la severidad de la sequía a escalas de tiempo largas (Clark y Clark, 2010).

La dendrocronología (análisis de los anillos de crecimiento) se ha utilizado como una herramienta alternativa para analizar la variabilidad del crecimiento radial a escalas temporales largas a partir de árboles individuales. En particular, el crecimiento periódico del xilema de los árboles, identificado como anillos de crecimiento anual, es observado en numerosas especies tropicales (Brienen et al., 2016; Giraldo-Jiménez, 2011; Mendivelso et al., 2016a; Rozendaal and Zuidema, 2011; Tomazello F^{o} et al., 2009; Worbes, 2002). Esto ha permitido que la dendrocronología en la zona intertropical proporcione registros fiables sobre el crecimiento retrospectivo de los árboles, con una resolución anual, y por un período de tiempo mucho más largo que los registros obtenidos desde las PPMs (crecimiento prospectivo) en los bosques tropicales (Zuidema et al., 2012, 2013; Zuidema y Frank, 2015).

Aunque es difícil identificar los anillos anuales de crecimiento en las especies de árboles tropicales debido a la complejidad de la anatomía de la madera (Stahle, 1999; Worbes y Fichtler, 2010), la reciente publicación realizada por Brienen et al. (2016) confirma la formación de anillos de crecimiento anual en 230 especies de árboles tropicales. Aunque este número es bajo comparado con el número de especies arbóreas estimado por Slik et al. (2015), entre ∼40,000 y ∼53,000 especies, el análisis de los anillos de crecimiento está contribuyendo a una mejor comprensión de los efectos del clima en los bosques tropicales y por ende, permitirá mejorar las predicciones de las respuestas de los bosques a largo plazo al cambio global (Zuidema et al., 2013; Zuidema y Frank, 2015). Varios métodos para evaluar el efecto del clima en las tendencias del crecimiento usando el análisis de los anillos de crecimiento, pueden ser consultados en la publicación realizada por Peters et al. (2015).

Específicamente, la información registrada en los anillos de crecimiento anual de los árboles de los BsTs ha permitido cuantificar cómo los árboles responden a las variables climáticas y determinar si la variabilidad del crecimiento está relacionada con los patrones atmosféricos a gran escala, tales como El Niño - Oscilación del Sur (ENSO, por sus siglas en inglés). Además, en varias especies de árboles tropicales el análisis de los anillos de crecimiento anual utilizando isótopos estables de carbono permitió determinar que existe un incremento de la eficiencia en el uso del agua en los últimos 150 años, asociado a un incremento de las concentraciones de CO_2 atmosférico, pero no permitió identificar un incremento del crecimiento de los árboles cuando fue analizado el grosor (anchura) de los anillos (van der Sleen et al., 2015).

El análisis de los anillos de crecimiento anual ha permitido evaluar, principalmente, el efecto de la precipitación sobre el crecimiento a largo plazo en los árboles de los BsTs, ya que la disponibilidad hídrica es uno de los factores más importantes que determinan el crecimiento y la productividad de los bosques forestales (Toledo et al., 2011; Wagner et al., 2012, 2014, 2016).

Por el contrario, pocos estudios dendrocronológicos han evaluado el efecto de la temperatura en el crecimiento a largo plazo en los bosques tropicales (Brienen et al., 2016). Esto puede estar asociado a la baja variabilidad de la temperatura a escalas intra-anuales en los trópicos con relación a las zonas de mayor latitud. Sin embargo, la respuesta del crecimiento a la temperatura debería ser considerada como un componente adicional para entender las respuestas de las especies de árboles al calentamiento climático en los BsTs. La exploración de nuevas variables que integren la precipitación y la temperatura en un simple parámetro, tal como el balance hídrico atmosférico o los índices de humedad o de sequía (p.e. López y Villalba, 2011; Vicente-Serrano et al., 2013), pueden ayudar a mejorar nuestra comprensión sobre el efecto del clima en el crecimiento radial de los árboles.

2. OBJETIVOS

El objetivo general de esta tesis fue evaluar la dinámica del crecimiento radial a diferentes escalas temporales y determinar su relación con el clima y la sequía en dos BsTs de Colombia y Bolivia.

Los objetivos específicos fueron:

2.1. Evaluar los patrones intra-anuales del crecimiento radial (dinámica del incremento radial y la xilogénesis) en 10 especies de árboles que coexisten en los BsTs de Colombia y Bolivia, y determinar su relación con el clima y la fenología de las hojas.

2.2. Analizar los efectos del clima y la sequía en el crecimiento radial inter-anual a diferentes escalas temporales, usando datos dendrocronológicos, en siete especies de árboles caducifolios que coexisten en un BsT boliviano.

2.3. Evaluar la respuesta del crecimiento radial inter-anual a los cambios en el balance hídrico atmosférico y determinar su relación con la densidad de la albura en siete especies de árboles caducifolios que coexisten en un BsT boliviano.

3. MATERIALES Y MÉTODOS

3.1. Sitios de estudio

Se seleccionaron dos BsTs del Neotrópico que presentan diferencias en la duración e intensidad de la estación seca. El primer sitio de estudio se encuentra ubicado en el Jardín Botánico Juan María Céspedes, a 7 km de Tuluá en un valle inter-andino (Valle del Cauca), al Suroeste de Colombia (3° 59′ N, 76° 6′ W, 1050-1430 m de altitud). Este sitio, que en adelante se llamará Tuluá, corresponde a un bosque secundario de 154 ha que crece sobre terrenos ondulados, suelos ácidos (pH = 6.3), de textura arenosa y limo-arenosa, y con abundante materia orgánica (3.1%) en los primeros 15 cm de profundidad. Este bosque lleva 44 años de recuperación, es decir, sin ninguna actividad antropogénica. Presenta una densidad de 31 especies de árboles por ha^{-1} y un área basal de 12.4 m^2 ha^{-1} (Adarve et al., 2013). La mayoría de las especies de árboles son semi-caducifolias a perennifolias. La familia Fabaceae es la más abundante, y las especies de árboles dominantes son *Guazuma ulmifolia* Lam, *Cupania americana* L. y *Guarea guidonia* (L.) Sleumer.

El segundo sitio es un BsT caducifolio de tierras bajas, localizado a 32 km al sureste de Concepción, en el departamento de Santa Cruz, al Este de Bolivia (16° 07´ S, 61° 43´ W, 380 m de altitud). Este sitio que en adelante se llamará INPA, es una propiedad privada de 30 mil ha, que pertenece a la compañía maderera INPA PARKET Ltda. Este sitio se encuentra inmerso en el BsT de la Chiquitanía, el cual es considerado uno de los más extensos y con mayor diversidad de árboles entre los BsTs del mundo. Está ubicado entre Bolivia, Brasil y Paraguay. En Bolivia, ocupa cerca de 14 millones de ha (Portillo-Quintero y Sánchez-Azofeifa, 2010) y está localizado entre la selva tropical del Amazonas y los matorrales secos del Chaco (Killeen et al., 1998). Este bosque crece sobre suelos ácidos (pH = 5.8) de textura limo-arenosa y con bajo contenido de materia orgánica (1.4%) en los primeros 15 cm de profundidad. El terreno es principalmente plano a poco inclinado. En este BsT se han identificado 98 especies de árboles, con un promedio de 34 especies de árboles por ha^{-1}, la mayoría de ellas caducifolias, y un área basal de 21 m^2 ha^{-1} (Villegas et al., 2009).

Según los datos climáticos de las estaciones metereológicas Tuluá-Farfán (4° 06´ N, 76° 14´ W, 955 m de altitud) y Concepción (16° 15´ S, 62° 06´ W, 410 m de altitud) para el período 1984-2011, la precipitación promedio anual en Tuluá (1317 mm) e INPA (1226 mm) fueron similares (t = -1.49, P = 0.14). Sin embargo, INPA registró temperaturas promedio anuales (24.0 °C) más altas (t = 7.25, P < 0.001) que Tuluá (22.6 °C). La relación entre la precipitación y la temperatura mensual es positiva en INPA (r_s = 0.81, P < 0.001), pero negativa en Tuluá (r_s = -0.44, P < 0.15). Esto, junto a una diferente distribución estacional las precipitaciones entre los sitios, determina las diferencias encontradas en la longitud y magnitud de la época seca anual entre Tuluá e INPA. En particular, Tuluá presenta precipitaciones bajas (<60 mm) y un balance hídrico negativo (es decir, el potencial de evapotranspiración excede a la precipitación) entre junio y agosto, mientras que en INPA el período seco va desde junio hasta septiembre con un balance hídrico negativo entre abril a octubre. Durante los años 2010 y 2011, la precipitación registrada en Tuluá (2125 mm) duplicó el valor registrado en INPA (981 mm), debido al fenómeno de "La Niña". Este evento se presentó en Colombia durante el período anteriormente mencionado, y se caracterizó por generar un incremento anormal de las precipitaciones en todo el territorio del país.

3.2. Especies estudiadas

Se seleccionaron 14 especies de árboles, cuatro de ellas en Tuluá (Colombia) y 10 en INPA (Bolivia). Estas especies pertenecen a siete familias y presentan diferentes hábitos foliares y posiciones de la copa con respecto al dosel del bosque (Tabla 1). Según Tropicos® (2016), las cuatro especies de Tuluá son taxones de amplia distribución en el trópico [*Cordia alliodora* (Ruiz & Pav.) Oken, *Cupania americana* L., *Pithecellobium dulce* (Roxb.) Benth., *Zanthoxylum rhoifolium* Lam.]. En cuanto a las especies de INPA (Bolivia), *Acosmium cardenasii* H.S. Irwin & Arroyo es una especie endémica del BsT de la Chiquitanía. Las especies restantes también están presentes en los países limítrofes con Bolivia [*Anadenanthera macrocarpa* (Benth.) Brenan, *Amburana cearensis* (Allemão) A.C. Sm., *Aspidosperma cylindrocarpon* Müll. Arg., *Aspidosperma tomentosum* Mart., *Centrolobium microchaete* (Mart. ex Benth.) H.C. Lima, *Zeyheria tuberculosa* (Vell.) Bureau], o están ampliamente distribuidas en el Neotrópico [*Caesalpinia pluviosa* DC., *Cedrela fissilis* Vell., *Tabebuia impetiginosa* (Mart. ex Dc.) Standl.]. La IUCN (2016) reporta que dos de las 10 especies estudiadas en INPA están en peligro de extinción (*Amburana cearensis* y *Cedrela fissilis*) y que una es altamente vulnerable (*Zeyheria tuberculosa*).

Teniendo en cuenta que las especies estudiadas pertenecen a diferentes géneros (excepto *Aspidosperma cylindrocarpon* y *Aspidosperma tomentosum*), de aquí en adelante, serán nombradas por su género.

3.3. Seguimiento del crecimiento radial mensual con dendrómetros y de la fenología de la copa de los árboles en Tuluá e INPA

Se realizó un seguimiento mensual del crecimiento radial y de la fenología de la copa a cuatro especies de árboles en Tuluá (*Zanthoxylum*, *Pithecellobium*, *Cordial* y *Cupania*) y a seis especies en Inpa (*Acosmium*, *Amburana*, *Aspidosperma c.*, *Aspidosperma t.*, *Cedrela* y *Centrolobium*). El seguimiento fue realizado entre julio de 2010 y agosto de 2011.

Tabla 1. Características de las 14 especies estudiadas en los dos BsTs de Colombia (Tuluá) y Bolivia (INPA).

Sitio de estudio	Especie	Familia	Posición de la copa	Hábito foliar
Tuluá	*Cordia alliodora*	Boraginaceae	Dosel	Semi-caducifolia / caducifolia
	Cupania americana	Sapindaceae	Emergente	Semi-caducifolia
	Pithecellobium dulce	Fabaceae	Dosel	Semi-caducifolia
	Zanthoxylum rhoifolium	Rutaceae	Dosel	Semi-caducifolia / caducifolia
INPA	*Acosmium cardenasii*	Fabaceae	Sub-dosel	Caducifolia
	Amburana cearensis	Fabaceae	Dosel	Caducifolia
	Anadenanthera macrocarpa	Fabaceae	Emergente	Caducifolia
	Aspidosperma cylindrocarpon	Apocynaceae	Sub-dosel	Semi-caducifolia
	Aspidosperma tomentosum	Apocynaceae	Sub-dosel	Caducifolia
	Caesalpinia pluviosa	Fabaceae	Dosel	Caducifolia
	Cedrela fissilis	Meliaceae	Dosel	Caducifolia
	Centrolobium microchaete	Fabaceae	Dosel	Caducifolia
	Tabebuia impetiginosa	Bignoniaceae	Dosel	Caducifolia
	Zeyheria tuberculosa	Bignoniaceae	Dosel	Caducifolia

Para tal fin, fueron instalados dendrómetros de banda manuales a 10 árboles por especie (Fig. 1a), y a uno de ellos le fue instalado, adicionalmente, un dendrómetro de banda automático (registra los cambios en el crecimiento y la temperatura del aire cada hora, Fig. 1b), excepto en *Aspidosperma t.* y *Amburana*. La fenología de la copa fue registrada mensualmente en todos los árboles mediante la observación directa de sus copas con binoculares (ver más detalles en el Capítulo 2). Para estimar la densidad de la albura (parte joven del xilema que es funcional para el transporte de agua), fueron colectados cores radiales que incluían esta parte del xilema (5 mm ancho, 30 mm longitud), en cinco árboles por especie usando la barrena de *Pressler* (Fig. 1g-h).

3.4. Seguimiento del crecimiento mensual del xilema a través de mini-cores en los árboles de Tuluá e INPA

A los árboles mencionados en la sección anterior (3-5 individuos por especie), se les extrajo mensualmente una muestra pequeña del tronco (mini-core) utilizando un extractor *Trephor* (Fig. 1c-d). A cada mini-core (Fig. 1e) se le realizó cortes histológicos utilizando dos tipos de micrótomos y se realizaron montajes permanentes de las secciones, las cuales fueron previamente teñidas para evaluar el proceso de formación de la madera (xilogénesis) a una escala intra-anual (Fig. 1f).

3.5. Evaluación del crecimiento radial a largo plazo en INPA

Aunque en Bolivia se trabajó en un área de explotación maderera, todas las muestras fueron recolectadas en zonas donde se realizó por primera vez la extracción de árboles con valor comercial. En particular, se recolectaron rodajas (discos) a partir de tocones de árboles (parte del tronco que queda unida a la raíz cuando se tala) recientemente aprovechados (7 y 14 individuos por especie), entre 0.2 y 0.5 m del suelo (Fig. 2a). En el caso de *Acosmium* las muestras fueron recolectadas entre 0.5 y 2.5 m, siempre evitando los contrafuertes. Con el fin de reducir la autocorrelación espacial en el crecimiento, los árboles seleccionados estuvieron separados, entre sí, más de 20 m. Todas las muestras fueron pulidas con lijas de grano sucesivamente más fino hasta que los anillos de crecimiento se distinguieron y fueron visibles (Fig. 2b-c).

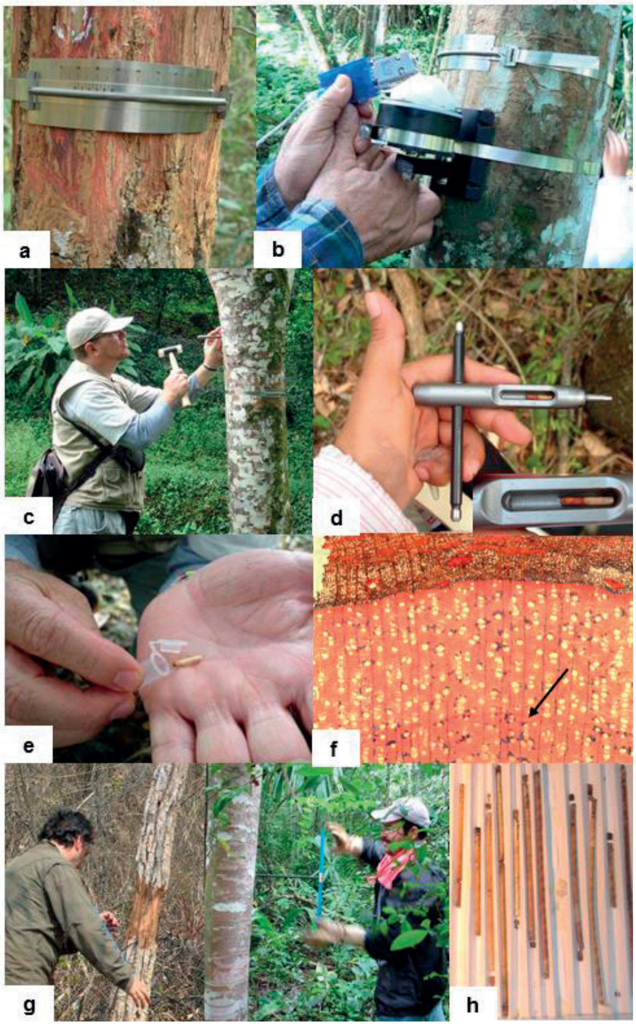

Figura 1. Métodos utilizados para evaluar el crecimiento radial de los árboles a una escala intra-anual y determinar la densidad de la madera. Las figuras superiores muestran dendrómetros de banda manual (a) y automático (b) colocados respectivamente en *Aspidosperma cylindrocarpon* ubicado en el BsT de la Chiquitanía (INPA) y en *Cordia alliodora* localizado en un bosque seco interandino de Colombia (Tuluá) mostrando la descarga de datos. Obtención de un mini-core con el extractor *Trephor* (c-e), aspecto de un corte histológico (f) mostrando un límite de un anillo de crecimiento (flecha) en *Acosmium cardenasii,* una especie arbórea endémica del BsT de la Chiquitanía (Bolivia). Extracción de muestras de madera con la barrena de *Pressler* (g), testigos cilíndricos de madera recolectados para cuantificar la densidad de la albura (h).

Adicionalmente, para determinar la densidad de la albura fueron colectados cores radiales que incluían esta parte del xilema, en cinco árboles por especie usando la barrena de *Pressler* (ver más detalles en el Capítulo 4).

3.6. Elaboración de cronologías y su utilidad en este estudio

Una vez las rodajas de madera estuvieron bien pulidas, fueron observadas con un estereoscopio (Fig. 2c). En particular, se realizó la datación visual cruzada o sincronización de la anchura de los anillos de cada individuo se realizó con relación a los otros individuos de la misma especie. A cada anillo se le asignó el año calendario en el cual se formó (datación de la muestra) según lo propuesto Schulman (1956) para el hemisferio sur. Posteriormente, se midió la anchura de los anillos en tres o cuatro radios por individuo datado. La validación estadística de las dataciones se llevó a cabo determinando

Figura 2. Métodos de campo y laboratorio para evaluar el crecimiento radial a largo plazo. Muestras recolectadas a partir de tocones, usando una motosierra, en zonas de aprovechamiento forestal (a), lijado de las rodajas de madera (b), datación cruzada o sincronización visual y medición de los anillos de crecimiento anual (c).

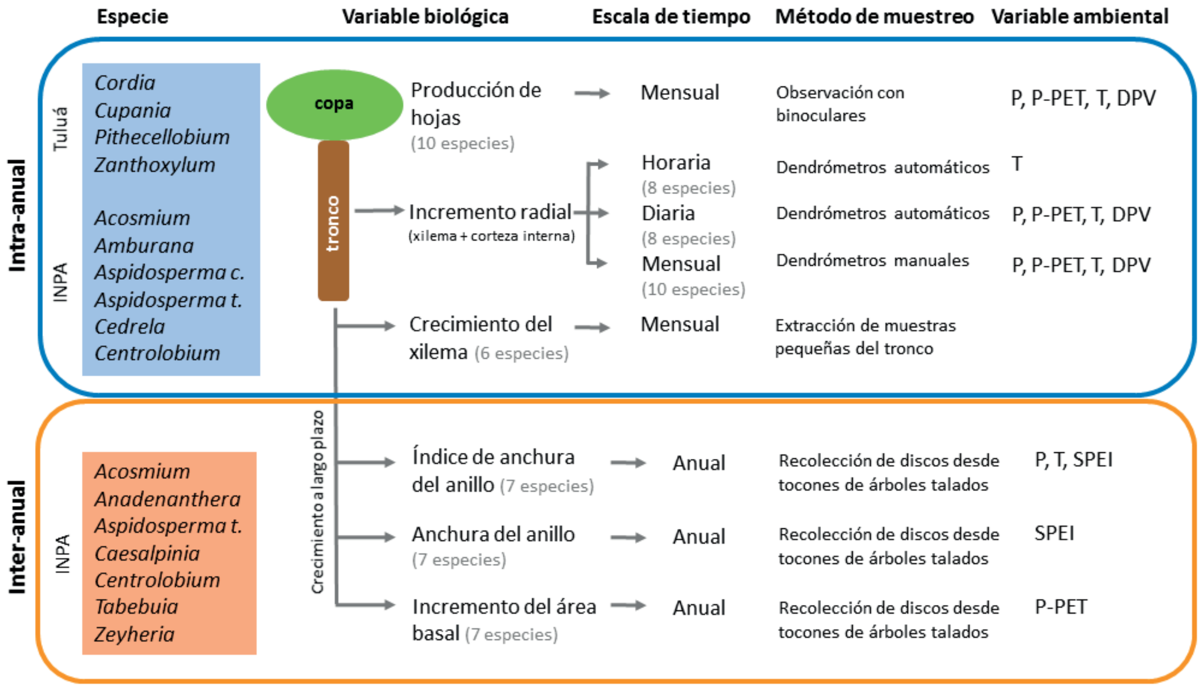

Figura 3. Variables biológicas utilizadas para evaluar el efecto de diferentes variables ambientales en el incremento radial, crecimiento del xilema y la producción de hojas a diferentes escalas temporales en los dos sitios de estudio, Tuluá (Colombia) e INPA (Bolivia). Abreviaturas: P, precipitación; P-PET, balance hídrico atmosférico; T, temperatura; DPV, déficit de presión del vapor; SPEI, índice de sequía (SPEI, por sus siglas en inglés de “Standardized Precipitation Evapotranspiration Index”). El nombre científico completo de cada especie puede ser consultado en la Tabla 1.

el grado de sincronía entre las muestras mediante estadísticos como el coeficiente de correlación. El objetivo final de la datación de las muestras fue la obtención de una serie media o cronología para cada especie. Esta cronología fue utilizada después para analizar las relaciones entre el clima y el crecimiento. Ver más detalles sobre la construcción de las cronologías en los Capítulos 3 y 4.

3.7. Evaluación del efecto climático y de la sequía en el crecimiento radial a diferentes escalas temporales

Se evaluó el efecto de la precipitación, el balance hídrico atmosférico (P-PET, precipitación menos el potencial de evapotranspiración), la temperatura y el déficit de presión del vapor (DPV) en la producción de hojas y el incremento radial a escalas intra-anuales (Fig. 3). Adicionalmente, se evaluó el efecto de las mismas variables ambientales (excepto DPV) sobre el crecimiento a largo plazo (Fig. 3). Para tal fin se utilizaron las cronologías obtenidas para cada especie. Todo lo referente a las pruebas estadísticas utilizadas en cada uno de los casos, puede ser consultado en los Capítulos 2, 3 y 4.

4. RESULTADOS Y DISCUSIÓN

4.1. Control climático en los patrones intra-anuales del crecimiento radial de los árboles en Tuluá e INPA

4.1.1. Control climático en la dinámica del incremento radial intra-anual y su asociación con la fenología de las hojas

Los dendrómetros de banda automáticos permitieron dividir los cambios en el grosor de los troncos a lo largo del día (ciclo diario) en tres fases: contracción, recuperación e incremento. La última fase se considera como un estimativo del crecimiento real, es decir, la producción de nuevas células del xilema (Deslauriers et al., 2003). Además, fue posible identificar éstas tres fases a escalas diarias usando las tasas de incremento radial. La identificación de las tres fases, tanto a escalas horarias como diarias, permitió evaluar el efecto del clima en la dinámica del incremento radial.

A escalas horarias, todas las especies mostraron las tres fases (contracción, recuperación e incremento) durante la estación húmeda (Fig. 4), mientras que sólo las fases de contracción y recuperación fueron registradas durante la estación seca en la mayoría de las especies de árboles (Fig. 4). Durante la estación húmeda, las tres fases anteriormente mencionadas fueron dependientes del tiempo y de la temperatura del aire en todas las especies (Fig. 4). La temperatura del aire a escalas horarias mostró una relación positiva y negativa con las fases de contracción y recuperación-incremento del tronco, respectivamente. Sin embargo, los datos analizados no permitieron confirmar un vínculo directo entre la temperatura del aire y la dinámica del incremento radial. La temperatura del aire puede modular el uso del agua del árbol a través de su efecto en el déficit de presión del vapor (DPV), las tasas de evapotranspiración y la disponibilidad de agua en el suelo. En particular, la alternación entre las fases de contracción (encogimiento) y recuperación (hinchazón) registradas a escalas horarias durante la estación húmeda (Fig. 4), podría estar relacionada con los principales períodos de utilización del agua almacenada en la albura y su posterior llenado. Varias investigaciones han demostrado que esas fluctuaciones del diámetro del tronco están asociadas a los cambios diurnos de las condiciones ambientales (Goldstein et al., 1998; King et al., 2013; Krepkowski et al., 2011; Turcotte et al., 2009). Durante las primeras horas del día, las especies estudiadas probablemente usan primero el agua almacenada en las ramas (ver Goldstein et al., 1998; Schulze et al., 1985). Una vez el agua almacenada en las ramas es utilizada por completo, las altas tasas de transpiración asociadas a un aumento del DPV al medio día obliga a los árboles a usar el agua almacenada en el tronco y raíces. Luego, el agua interna almacenada en el tronco es recargada al final de la tarde en las especies de Tuluá (ver Goldstein et al., 1998), y durante la noche en las especies de INPA, lo cual ha sido sugerido para otras especies de los bosques tropicales (Bräuning et al., 2009).

La fase de incremento detectada a escalas diarias por los dendrómetros automáticos coincidió con el período de crecimiento del

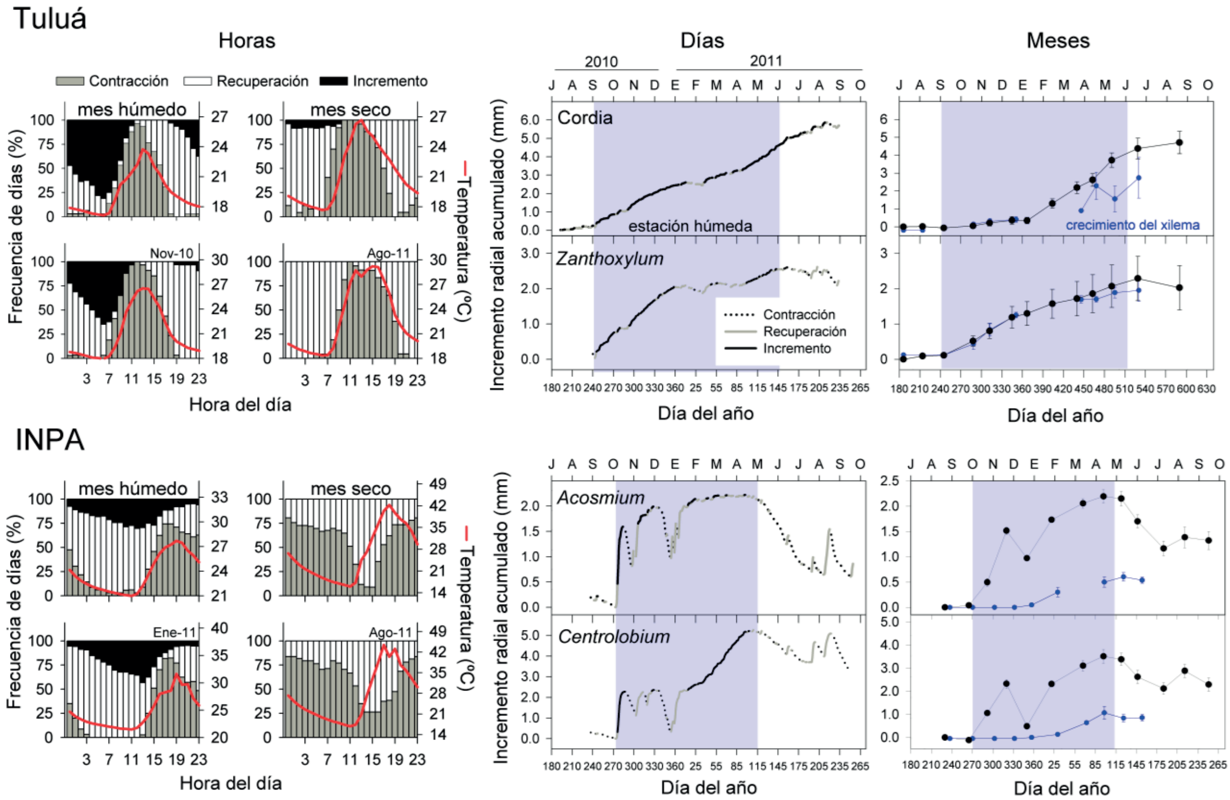

Figura 4. Dinámica del incremento radial a escalas horarias, diarias y mensuales en cuatro especies de los BsTs de Colombia (Tuluá) y Bolivia (INPA), con base en los datos de los dendrómetros de banda manuales y automáticos. La dinámica del crecimiento del xilema fue cuantificada a partir de mini-cores y es representada por las líneas azules. Ver información sobre las otras especies en el Capítulo 2.

xilema en las especies semi-caducifolias de Tuluá, mientras que en las especies caducifolias de INPA sólo la última de las tres fases de incremento identificadas por los dendrómetros automáticos coincidió con el período del crecimiento del xilema (Fig. 4).

Particularmente, la fase de incremento del tronco a escalas diarias estuvo asociada con valores altos de las precipitaciones, balances hídricos positivos y temperaturas bajas y, por ende, valores bajos del DPV en las especies de Tuluá, mientras que esta fase correspondió tanto a precipitaciones altas como temperaturas cálidas en las especies de INPA (Capítulo 2). Por su parte, en los dos BsTs las temperaturas cálidas del aire registradas a lo largo del día afectaron negativamente el incremento radial a escalas horarias (Capítulo 2). Las especies pueden enfrentar esta situación adversa creciendo durante la fase de incremento identificada por los dendrómetros automáticos, es decir, limitando el crecimiento radial a los períodos del día cuando las temperaturas son bajas y la pérdida de agua debida a la evapotranspiración es reducida (Capítulo 2). En las especies de Tuluá, la fase de incremento a escalas horarias principalmente ocurrió desde el amanecer hasta tempranas horas de la mañana, cuando se alcanzaron temperaturas entre 17° y 19 °C. Por su parte, la mayoría de especies de INPA mostraron la fase de incremento desde la mañana hasta las primeras horas de la tarde, con temperaturas entre 21° y 27 °C (Capítulo 2). Estos resultados muestran que la disponibilidad de agua durante la estación húmeda juega un papel importante, favoreciendo el crecimiento radial. Sin embargo, la temperatura del aire determina las fluctuaciones horarias del DPV y las tasas de evapotranspiración y, por ende, los momentos favorables a lo largo del día para crecer.

Las especies estudiadas mostraron un proceso de contracción reversible de los troncos a escalas horarias y diarias (Fig. 4). Sin embargo, la mayoría de especies de INPA se registraron contracciones reversibles de los troncos a escalas mensuales (Fig. 4), lo cual generó tasas de incremento radial negativa en algunos meses (Capítulo 2). Chitra-Tarak et al. (2015) han mostrado que al menos una parte de la variabilidad temporal en las tasas de crecimiento anual es determinada por las fluctuaciones reversibles inducidas por el agua en los BsTs. En particular, el control climático en la dinámica del incremento radial fue diferente a escalas diarias y mensuales. A escalas diarias, se registró un efecto positivo de las precipitaciones y del balance hídrico y un efecto negativo del DPV en la fase de incremento (Capítulo 2), mientras que a escalas mensuales la precipitación fue la principal variable climática que afectó el incremento radial (Capítulo 2). En consecuencia, las diferencias encontradas en los patrones de incremento mensual entre Tuluá (incremento persistente) e INPA (hinchazón reversible; Fig. 4), parecen estar principalmente asociadas a las diferencias en la variabilidad de la precipitación entre los sitios de muestreo. Además, la corteza de los árboles en las especies de INPA pueden estar contribuyendo a modular las grandes fluctuaciones observadas a escalas mensuales. No obstante, los datos obtenidos en esta tesis no permiten evaluar esa hipótesis. En general, la corteza tiene una menor densidad que la albura y, por ende, una mayor capacidad de almacenar agua en sus tejidos (Poorter et al., 2014; Rosell et al., 2014; Stahl et al., 2010). Por lo tanto, las características de la corteza de los árboles deberían ser explícitamente considerada como una característica clave para entender los mecanismos usados por las especies de árboles para tolerar los efectos adversos de la sequía en el crecimiento radial de los árboles en los BsTs.

Por último, las asociaciones entre la producción de hojas y las tasas de incremento radial registradas a escalas mensuales fueron positivas para todas las especies. Sin embargo, las especies mostraron diferencias en la fuerza de estas asociaciones en función de la densidad de la albura (Fig. 5). Específicamente, *Cedrela* mostró la asociación más fuerte y la densidad de la albura más baja, mientras que *Acosmium* presentó las características opuestas (Fig. 5). En el caso de *Cedrela* (especie demandante de luz), la alta correlación que fue observada entre la producción de hojas y las tasas de incremento radial puede estar relacionada con la respuesta sincrónica de ambos procesos a la precipitación; los cuales fueron detectados a escalas temporales iguales o superiores a 10 días (ver Fig. 3 en el Capítulo 2). Por su parte, la baja correlación mostrada por *Acosmium* (especie tolerante a la sombra), estuvo asociada a la respuesta diferencial de la producción de hojas y del incremento radial a las variables climáticas evaluadas. Mientras que la producción de las hojas respondió a la precipitación, balance hídrico y DPV a todas las escalas temporales analizadas, las tasas de incremento radial fueron sensibles a cambios en la precipitación a escalas temporales superiores a 20 días (ver Fig. 3 en el Capítulo 2). En particular, las especies pioneras y caducifolias con baja densidad de la madera, tal como *Cedrela*, son más vulnerables a la cavitación que las especies caducifolias tolerantes a la sombra con altas densidades de la madera, tal como *Acosmium* (Markesteijn et al., 2011a; Méndez-Alonzo et al., 2012). Por lo tanto, *Cedrela* puede amortiguar su vulnerabilidad a la cavitación perdiendo rápidamente el follaje al comienzo de la estación seca (Capítulo 2), mientras *Acosmium* pierde sus hojas lentamente durante la estación seca.

4.1.2. Control climático en el crecimiento del xilema a escalas intra-anuales y su asociación con la fenología de las hojas

La disponibilidad de agua es el factor más importante que determina el crecimiento y la productividad de los bosques tropicales (Toledo et al., 2011; Wagner et al., 2012, 2014, 2016). Específicamente, la estacionalidad de la precipitación anual en los BsTs genera períodos alternativos favorables (estación húmeda) y desfavorables (estación seca) para la actividad del cambium (Borchert, 1999). Por lo tanto, la activación del cambium y el crecimiento radial de los árboles son estacionales en los BsTs (Worbes et al., 2013). Los resultados de esta tesis apoyan esos hallazgos previos, ya que el crecimiento del xilema ocurrió durante la estación húmeda, tanto en las especies caducifolias y semi-caducifolias en los dos BsTs estudiados, reflejando la influencia de las

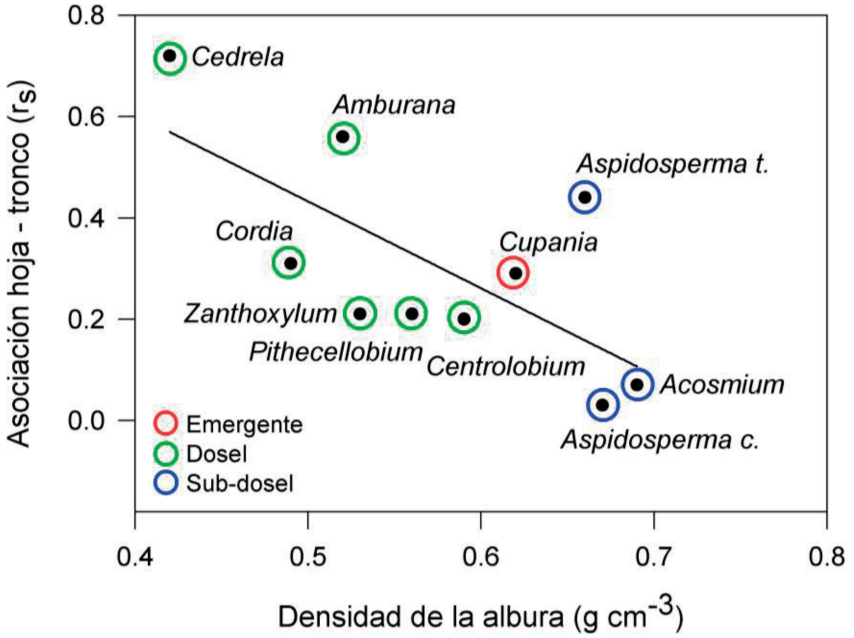

Figura 5. La relación entre la producción de las hojas y las tasas de incremento radial (indicado en el eje *y* como asociación hoja - tronco) está negativamente asociada a la densidad de la albura. Los círculos muestran la posición de las copas de cada especie con respecto al dosel del bosque. Ver más detalles en el Capítulo 2.

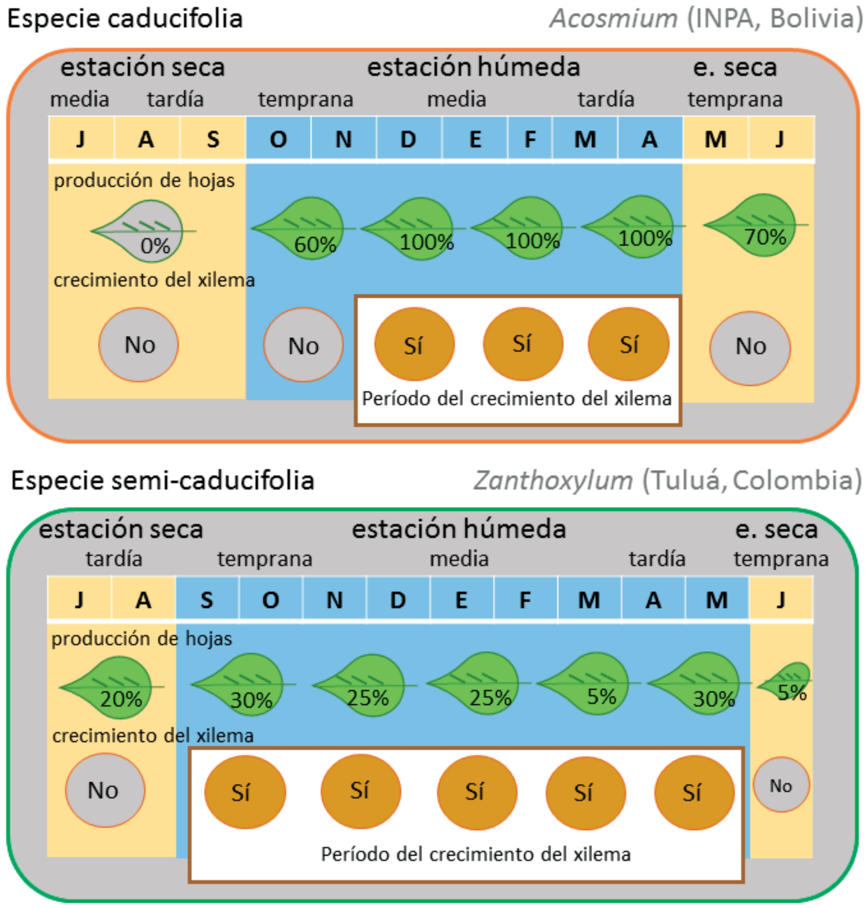

Figura 6. Período del crecimiento del xilema en dos especies con diferente hábito foliar en los BsTs de Colombia y Bolivia, y su asociación con la producción de las hojas durante la estación húmeda (azul) y la estación seca (amarillo). Ver información de las otras especies en el Capítulo 2.

precipitaciones altas y el balance hídrico positivo en el desarrollo de nuevas células del xilema (Capítulo 2). Varios estudios en especies de árboles tropicales han mostrado que la variación anual de la precipitación determina la estacionalidad en la formación del xilema. Particularmente, un crecimiento activo durante la época húmeda es frecuentemente reportado en los BsTs (Krepkowski et al., 2011; Volland-Voigt et al., 2010; Worbes et al., 2013). Sin embargo, el período de crecimiento del xilema puede ser igual de largo o más corto que la estación húmeda. En las especies semi-caducifolias de Tuluá, el crecimiento ocurrió durante toda la estación húmeda, mientras que en INPA, el crecimiento del xilema de las especies caducifolias comenzó a mediados de la época húmeda, cuando las copas de los árboles estuvieron completamente cubiertas por el nuevo follaje (Fig. 6). La formación del xilema durante toda la estación húmeda registrada en Tuluá, pudo estar asociada a la elevada precipitación registrada en este BsT durante el período de estudio, causado por el evento de “La Niña” que se presentó entre 2010 y 2011. En Tuluá, *Cordia* y *Zanthoxylum* son especies caducifolias durante años secos, pero su hábitat foliar puede cambiar en años húmedos, cuando las especies pasan a ser semi-caducifolias. En años con un inusual incremento de las precipitaciones, tal como lo ocurrido en el período de estudio, la presencia de hojas durante la transición de la estación seca a la húmeda, puede permitir que el crecimiento del xilema comience al inicio de la estación húmeda. Sin embargo, para comprobar esta hipótesis sería importante evaluar, en estas mismas especies, la asociación entre la fenología de las hojas y la xilogénesis en los años secos.

Por su parte, el desarrollo de las hojas antes del crecimiento del xilema registrado en las especies caducifolias de INPA (Fig. 6), se ha observado en otras especies de árboles caducifolios y brevi-caducifolios (Krepkowski et al., 2011; Marcati et al., 2006, 2007; Worbes et al., 2013). Sin embargo, el comienzo de la producción de hojas y el crecimiento del xilema pueden ser simultáneos en algunas especies de árboles caducifolios, semi-caducifolios y de troncos suculentos (Dié et al., 2012; Worbes et al., 2013). En las especies caducifolias estudiadas en INPA, el desarrollo del nuevo xilema después del desarrollo completo del follaje sugiere que esas especies usan el xilema formado en el año previo para transportar agua hacia la copa y permitir la formación del nuevo follaje. El xilema formado en el año previo podría ser funcional durante la próxima estación húmeda, ya que el xilema con poro difuso y poro semi-difuso, como es el caso de *Acosmium* y *Centrolobium*, respectivamente, es menos vulnerable a la cavitación que el xilema con poro en anillo (Suzuki et al., 1996). Esta idea es apoyada adicionalmente por Brodribb et al. (2002), quienes encontraron que algunas especies caducifolias de los BsTs no cambian significativamente la conductividad en sus ramas, entre la estación húmeda y la seca, indicando que una gran proporción del xilema puede permanecer funcional durante la estación seca, a pesar de que sus copas pierdan el follaje. Aparentemente, en este tipo de especies caducifolias la senescencia de las hojas ocurre sin embolismo. Por lo tanto, el xilema puede permanecer hidratado pero inactivo hasta la reanudación de las precipitaciones en la próxima estación húmeda. Adicionalmente, el comienzo del desarrollo del xilema después de que las hojas están completamente desarrolladas, sugiere que las especies caducifolias tales como *Acosmium* y *Centrolobium*, pueden asimilar nuevos fotosíntatos y, por ende, estas especies pueden no depender del almacenamiento interno de carbono para crecer. En otras palabras, el crecimiento radial podría depender menos de la disponibilidad de carbohidratos que de la disponibilidad de agua. Esta hipótesis es soportada por los resultados de los patrones inter-anuales del crecimiento a largo plazo registrado en especies de árboles coexistentes en INPA. Durante las últimas seis décadas dos sequías multi-anuales se alternaron con dos períodos húmedos multi-anuales en INPA (Capítulo 3). Específicamente, se registraron tasas de crecimiento bajas durante las dos sequías multi-anuales en 1960-1977 y 1985-2008, mientras que las tasas de crecimiento fueron altas durante el período húmedo multi-anual (1978-1984), ocurrido entre estas dos sequías multi-anuales (Capítulo 3). Sin embargo, esa plasticidad en el crecimiento asociada a la disponibilidad de agua está mediada por rasgos funcionales, tal como, la densidad del xilema. En particular, las especies caducifolias con densidades altas del xilema no mostraron una plasticidad en el crecimiento asociado a un incremento en la disponibilidad de agua, es decir, no se evidenciaron diferencias del crecimiento entre los períodos húmedos multi-anuales y las sequías multi-anuales (Capítulo 3).

En ambos BsTs estudiados, el crecimiento del xilema finalizó al inicio de la estación seca (Figs. 4 y 6). Específicamente, la contracción del tronco registrada por los dendrómetros automáticos y la ausencia en la producción de hojas, coincidió con la finalización del crecimiento del xilema en las especies semi-caducifolias de Tuluá (Capítulo 2). En las especies caducifolias de INPA, la finalización del crecimiento del xilema estuvo asociada a una fase larga de la contracción del tronco, la cual fue registrada por los dendrómetros automáticos, y al inicio de la caída de hojas. Sin embargo, la pérdida total del follaje ocurrió de manera asincrónica entre las especies (Capítulo 2). Estos resultados coinciden con los reportado por Worbes et al. (2013) para otro BsT. Ellos encontraron que todas las especies arbóreas no muestran una actividad del cambium después del comienzo de la época seca, independientemente de su hábito foliar (Worbes et al., 2013). Esta observación sugiere que una pausa en la actividad del cambium ocurre durante la estación seca a causa de la baja disponibilidad de agua y a un DPV alto. Varios estudios han demostrado que estas condiciones de sequía intra-anual conducen a la formación del límite del anillo en los BsTs (Lisi et al., 2008; Volland-Voigt et al., 2010; Worbes et al., 2013).

4.2. Efectos del clima y las sequías en los patrones inter-anuales del crecimiento radial en los BsTs

4.2.1. Control climático en la variabilidad del crecimiento radial de los árboles a largo plazo: el papel de la precipitación y la temperatura

Como era de esperarse, el efecto positivo de la precipitación en el crecimiento radial de los árboles a escalas intra-anuales, fue además registrado en las respuestas del crecimiento a largo plazo en todas las especies de INPA (Capítulo 3). Varios estudios muestran que la variabilidad inter-anual del crecimiento responde positivamente a la precipitación en los BsTs (ver Tabla 2 del Capítulo 1), lo cual implica que el crecimiento del xilema está limitado por la disponibilidad de agua. En particular, las respuestas del crecimiento fueron más intensas a escalas de tiempo cortas (de dos a nueve meses), principalmente, durante la estación húmeda (Capítulo 3). Esto sugiere que el crecimiento no ocurre durante todo el año, sino que está restringido a ciertos meses. Esta hipótesis es soportada por los estudios de la xilogénesis realizados en los dos BsTs estudiados (Tuluá e INPA), los cuales mostraron que el crecimiento del xilema ocurre durante la estación húmeda (Figs. 4 y 6, ver además el Capítulo 2).

El trabajo de revisión realizado por Brienen et al. (2016) mostró que la sensibilidad del crecimiento de los árboles a las fluctuaciones de la precipitación fue similar en diferentes tipos de bosques tropicales. Específicamente, entre el 24% y el 32% de la variabilidad de la anchura de los anillos fue explicada por la variación anual de la precipitación en los bosques húmedos y secos, respectivamente. Por su parte, esta tesis demostró que la sensibilidad del crecimiento del xilema a las fluctuaciones de la precipitación fue especie-específica en INPA (Capítulo 3), tal como se ha registrado en otros BsTs (p.e. Enquist y Leffler, 2001; Vlam et al., 2013). Esto sugiere que las especies de árboles tienen diferentes estrategias para crecer y usar el agua, como se ha reportado en otros BsTs (Borchert 1994, 1999; Worbes 1999). De hecho, esta tesis encontró que la varianza del crecimiento radial asociada a la precipitación varió del 6% al 22% entre las especies estudiadas en INPA (Fig. 7). Aunque estos porcentajes son bajos, están dentro de los valores registrados en otros BsTs (p.e. Enquist y Leffler, 2001; López y Villalba, 2011; Paredes-Villanueva et al., 2013). La amplitud del rango de la varianza del crecimiento explicada por la precipitación puede ser causada por diferentes estrategias usadas por las especies del BsT para tolerar o evitar la sequía (Worbes et al., 2013). Por ejemplo, en varias especies de árboles del BsT se ha registrado una alta plasticidad en la fenología de las hojas, asociada a un inusual

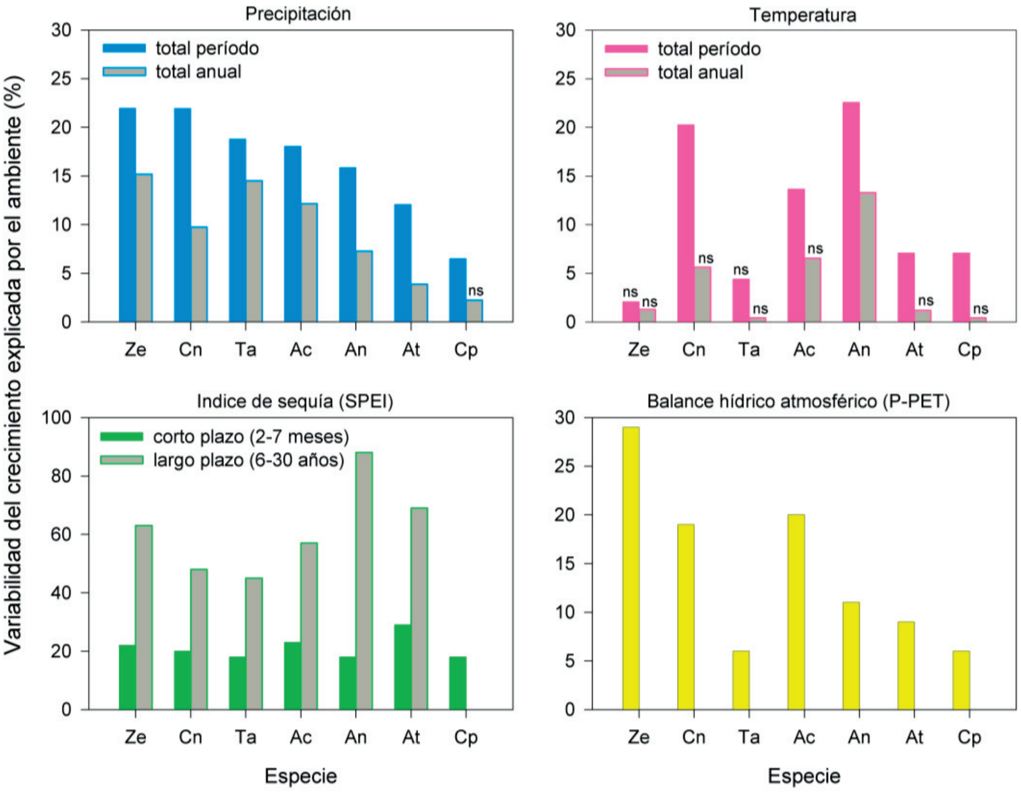

Figura 7. Variabilidad del crecimiento explicada (R^2) por cada una de las variables ambientales analizadas durante el período 1949–2008 en siete especies de INPA (Bolivia). El mes o grupos de meses (período) en los cuales se registraron las correlaciones más altas pueden ser vistos en los Capítulos 3 y 4. Las correlaciones no significativas son indicadas (ns). Abreviaturas de los nombres de las especies: Ze, *Zeyheria tuberculosa*; Cn, *Centrolobium microchaete*; Ta, *Tabebuia impetiginosa*; Ac, *Acosmium cardenasii*; An, *Anadenanthera macrocarpa*; At, *Aspidosperma tomentosum*; Cp, *Caesalpinia pluviosa*.

período seco o húmedo dentro de la estación húmeda o seca, respectivamente (Borchert et al., 2002).

En cuanto a la temperatura, su efecto negativo en el crecimiento radial a largo plazo, ha sido registrado en diversos bosques tropicales usando parcelas permanentes de muestreo (Clark y Clark, 2010; Dong et al., 2012). Por su parte, esta asociación negativa también se ha inferido desde estudios dendrocronológicos realizados en bosques tropicales (Brienen et al., 2016), incluyendo varias especies consideradas en esta tesis (Capítulo 3). En particular, varias especies que coexisten en un BsT tailandés mostraron una asociación más fuerte entre el crecimiento y la temperatura que entre el crecimiento y la precipitación (Vlam et al., 2013). De hecho, la disminución del crecimiento inducido por el calentamiento climático es más severo entre las especies tropicales que entre las especies de bosques templados o boreales (Way y Oren, 2010). Sin embargo, aún no es claro si la reducción en las tasas de crecimiento asociadas a un aumento de la temperatura, son causadas por un incremento en las tasas de evapotranspiración y un estrés hídrico maximizado por la pérdida de agua a través de los estomas, por el efecto indirecto debido al incremento en la respiración (Schippers et al., 2015; Vlam et al., 2013), o por una disminución de las tasas fotosintéticas (Seiler et al., 2015). Por el contrario, otros estudios dendrocronológicos muestran que el crecimiento radial no responde a las fluctuaciones de la temperatura en los BsTs (ver Tabla 2 del Capítulo 1). La amplitud de la variabilidad de la temperatura a escalas intra-anuales entre BsTs, asociada a la distancia al ecuador (Eamus, 1999), podría explicar parcialmente estos resultados contrastantes.

Al parecer, las especies que crecen cerca de la línea ecuatorial no responden a la temperatura, probablemente debido a la baja variabilidad intra-anual (<3 °C) en aquellas regiones, es decir, que el crecimiento radial de las especies no muestra una respuesta a la variabilidad de la temperatura (ver Tabla 2 del Capítulo 1). Por el contrario, las especies que crecen en BsTs ubicados a latitudes ≥ 11°, donde la variabilidad entre meses es cercana a 5 °C (ver Tabla 2 del Capítulo 1), registran una relación negativa entre el crecimiento radial y la temperatura.

Por otra parte, la relación negativa entre la temperatura y el crecimiento, registradas en la mayoría de las especies de INPA, contrasta con la asociación positiva precipitación-crecimiento. Esto puede estar relacionado con la colinealidad negativa entre la precipitación y la temperatura a escalas inter-anuales, tal como se ha registrado en otros bosques tropicales (Brienen et al., 2016). Por lo tanto, como era de esperarse, en años con precipitaciones altas y temperaturas bajas el crecimiento aumentó (Capítulo 3). Sin embargo, en INPA las respuestas del crecimiento de los árboles a la temperatura fueron máximas a escalas temporales cortas (de uno a tres meses) dentro de la estación húmeda, esto significa que las especies arbóreas crecen en la época de año que registra las temperaturas mensuales más altas (Capítulo 3). Por lo tanto, un incremento de las tasas de evapotranspiración durante la estación de crecimiento asociado a temperaturas altas podría afectar negativamente el crecimiento radial de las de especies de INPA, ya que el cierre de los estomas para minimizar la pérdida de agua, conlleva a una disminución de la captura de CO_2 atmosférico y, por ende, las tasas de asimilación de carbono disminuyen. Sin embargo, las especies pueden contrarrestar esas condiciones adversas creciendo durante las horas del día en las que se registran temperaturas bajas, es decir, cuando la pérdida del agua debida a la evapotranspiración se minimiza (p.e., en la noche y el amanecer), como fue mencionado en la parte inicial de esta discusión.

Además, las respuestas del crecimiento a la temperatura fueron especie específicas. En cinco de las siete especies estudiadas en INPA, se registró una respuesta negativa del crecimiento radial a la temperatura del aire (Fig. 7). Específicamente, la temperatura explicó del 7% al 22% de la variabilidad inter-anual del crecimiento radial, donde *Anadenanthera* fue la especie más sensible a los cambios de la temperatura, tanto a escalas mensuales como anuales (Fig. 7). La alta sensibilidad de esta especie puede estar relacionada con la posición de las copas de los árboles. Al ser una especie emergente, las copas de los árboles están completamente expuestas a niveles de radiación elevados y, por ende, a las fluctuaciones de la temperatura del aire.

4.2.2. Respuesta diferencial del crecimiento radial al balance hídrico atmosférico entre especies arbóreas y su relación con la densidad de la albura

Aunque los datos de precipitación ofrecen una primera aproximación acerca de la disponibilidad de agua para los árboles, el balance hídrico atmosférico permite una mejor estimación, ya que incluye la pérdida de agua hacia la atmósfera a través de los procesos de evaporación y transpiración. Sin embargo, las respuestas del crecimiento a la precipitación y al balance hídrico atmosférico pueden presentar patrones similares. En todas las especies de INPA se registró un efecto positivo del balance hídrico atmosférico sobre el crecimiento (medido como el incremento del área basal, BAI) durante la estación húmeda (Capítulo 4), tal como se observó con la precipitación. Esto sugiere que el crecimiento del xilema está concentrado a esta estación, lo cual es soportado por los datos de la xilogénesis (Figs. 1 y 3). Varios estudios han reportado que durante la corta estación húmeda, las especies caducifolias de los BsTs maximizan la fotosíntesis, la conductividad hidráulica y las tasas de crecimiento (Borchert, 1999; Brodribb et al., 2002; Eamus, 1999). Sin embargo, la fuerza de la relación observada entre el balance hídrico atmosférico y el crecimiento durante la estación húmeda varió entre especies. En particular, la variabilidad del crecimiento explicada por el balance hídrico atmosférico estuvo negativamente relacionado con la densidad de la albura (Fig. 8).

Zeyheria fue la especie más sensible a la precipitación y al balance hídrico atmosférico

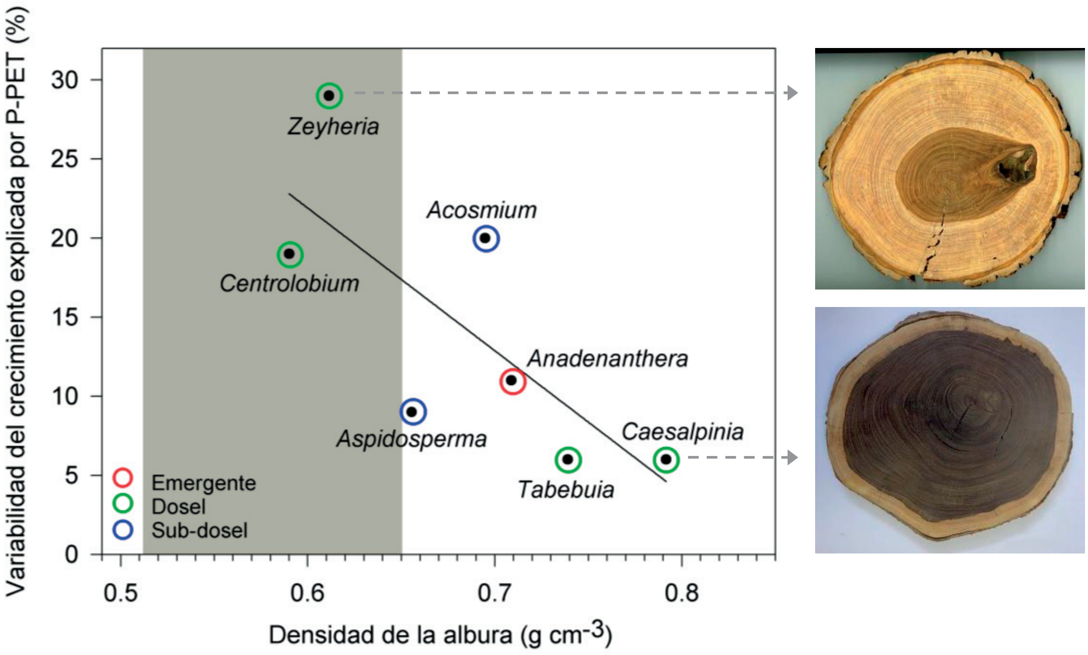

Figura 8. La densidad de la albura está negativamente relacionada a la variabilidad del crecimiento (área de incremento basal) explicada por el balance hídrico atmosférico (P-PET). La cantidad de la varianza del crecimiento explicada (R^2) por el mejor modelo-mixto lineal ajustado como función del balance hídrico atmosférico es mostrado en el eje y (ver Tabla 4 del Capítulo 4). Las secciones transversales del tronco muestran las diferencias en la proporción de albura (madera clara hacia el exterior del tronco) y el duramen (madera oscura hacia el interior del tronco) entre *Zeyheria tuberculosa* (arriba-derecha) y *Caesalpinia pluviosa* (abajo-derecha). Los círculos muestran la posición de las copas de cada especie con respecto al dosel del bosque. El área gris corresponde al rango óptimo de eficiencia hidráulica reportado por Kallarackal et al. (2013).

(Fig. 7); además, registró la densidad más baja del xilema y una alta producción de albura (43% del área total del xilema) (Fig. 8). Estas dos últimas características pueden estar asociadas a una alta capacidad de almacenamiento de agua en el tronco. Por el contrario, *Caesalpinia*, fue la especie menos sensible y presentó las características opuestas, es decir, una densidad alta del xilema y un bajo porcentaje de albura (23%) (Fig. 8). Hipotéticamente, *Zeyheria* es capaz de almacenar más agua en su tronco que *Caesalpinia* y, por ende, *Zeyheria* muestra una alta sensibilidad en términos de cambios del crecimiento asociados a la disponibilidad de agua en comparación con *Caesalpinia* (Capítulos 3 y 4). Esta idea es soportada por los resultados presentados en el Capítulo 3, donde se muestra que entre 1949 y 2008 existieron dos períodos húmedos multi-anuales alternados con dos sequías multi-anuales. Particularmente, el crecimiento más bajo fue registrado durante las dos sequías multi-anuales (1960–1977, 1985–2008), mientras que el crecimiento más alto se registró durante el período multi-anual más húmedo (1978-1984) en todas las especies, excepto en *Caesalpinia,* quien presentó la densidad de la albura más alta. Por su parte, *Zeyheria* fue la especie caducifolia más sensible al balance hídrico atmosférico (Fig. 7), y podría requerir más agua para crecer y, por ende, un sistema de transporte de agua más eficiente que las especies caducifolias menos sensibles. Específicamente, la densidad de la madera de *Zeyheria* está dentro del rango óptimo de eficiencia hidráulica (Fig. 7) reportado por Kallarackal et al. (2013).

Actualmente, se evidencia un esfuerzo intenso por vincular los rasgos funcionales al crecimiento radial en varios BsTs (p.e. Poorter et al., 2010). En particular, el crecimiento radial parece estar relacionado con varios rasgos funcionales, tales como: la densidad del xilema, el diámetro del lumen de los vasos y la conductividad hidráulica (Fan et al., 2012; Iida et al., 2012). Específicamente, Hérault et al. (2011) concluyeron que los rasgos la densidad de la madera y el contenido de agua en los troncos explican mayormente las diferencias en las trayectorias de crecimiento de las especies tropicales. Aunque las respuestas del crecimiento al clima pueden depender de rasgos adicionales que no tuvimos en cuenta en esta tesis, tales como la eficiencia en el uso del agua o la profundidad de las raíces, este es uno de los pocos estudios que proporciona un vínculo entre un rasgo funcional clave, tal como la densidad del xilema (un proxy de la capacidad del árbol para almacenar agua en el tronco), y la respuesta diferencial del crecimiento al balance hídrico atmosférico en los BsTs.

4.2.3. Impacto de las sequías en el crecimiento radial a largo plazo

Un estudio reciente sobre la variabilidad y las tendencias de las sequías en Bolivia durante el período 1955-2012, mostró que las sequías en ese país han tenido un comportamiento temporal caracterizado, principalmente, por variaciones entre décadas (Vicente-Serrano et al., 2014). Al respecto, esta tesis identificó en los últimos 60 años, dos períodos húmedos multi-anuales alternados con dos sequías multi-anuales en INPA, utilizando el SPEI, un índice de sequía multi-escalar (Capítulo 3). En general, los años que registraron precipitaciones bajas y temperaturas altas fueron identificados por este índice como años secos (valores negativos del SPEI). Estos hallazgos sugieren que las especies de INPA deben enfrentar sequías intra-anuales (estación seca anual) y también sequías multi-anuales o sequías de larga duración.

La fuerza de la asociación observada entre el SPEI y el índice de la anchura de los anillos fue siempre positiva, independientemente, de la escala de tiempo analizada. Esto indica que el crecimiento es drásticamente limitado por el déficit hídrico. A escalas inter-anuales, el SPEI explicó del 17% al 29% de la varianza del crecimiento anual (Fig. 7). Estos valores sugieren que las especies estudiadas pueden amortiguar los efectos negativos de la sequía en el crecimiento. Al parecer, las respuestas funcionales para afrontar las sequías son rápidas, ya que las correlaciones más altas entre el SPEI y el crecimiento fueron registradas a escalas temporales cortas, es decir, de dos a siete meses (Capítulo 3). Este resultado confirma el hallazgo de un estudio global, el cual evidencia que la actividad de la vegetación y el crecimiento de las especies que habitan los biomas secos responden a la sequía a escalas temporales cortas (Vicente-Serrano et al., 2013). Esta amortiguación y respuesta a corto plazo del crecimiento a la variación de las sequías a escalas inter-anuales contrasta con la sensibilidad del crecimiento de las especies a las sequías de largas duración (multi-anuales); como se evidencia en el notable incremento de la varianza explicada por el SPEI, con valores que fluctuaron del 45% al 88% (Fig. 7), a escalas de tiempo que variaron entre seis a 30 años (Capítulo 3). Las especies pueden tolerar un año seco utilizando los mismos mecanismos eco-fisiológicos para sobrevivir a la estación seca anual (ver Markesteijn et al., 2011b). Sin embargo, estos mecanismos parecen no ser muy eficientes para contrarrestar las sequías de larga duración en términos del crecimiento radial de los árboles y probablemente de la productividad forestal. De hecho, varios estudios han demostrado que las sequías de larga duración tienen un efecto negativo en las especies de árboles de los BsTs (Leigh Jr. et al., 1990) y de los bosques húmedos (Feeley et al., 2007; Phillips et al., 2009). No obstante, es probable que la variabilidad en la disponibilidad de agua a escalas temporales largas, afecte en mayor medida la dinámica del crecimiento en los BsTs, con respecto a los bosques húmedos, ya que en estos últimos la radiación es el principal factor ambiental que limita el crecimiento de los árboles (Brienen et al. 2010a; Brienen y Zuidema, 2006).

Anadenathera, una especie emergente, fue la más sensible a la temperatura (Fig. 7), y además, mostró una alta sensibilidad del crecimiento al SPEI a escalas temporales largas. Específicamente, este índice de sequía explicó casi el 90% de la varianza en el crecimiento (Fig. 7). Esto indica que *Anadenathera* podría presentar una alta sensibilidad a la demanda atmosférica de agua a largo plazo. Por el contrario, el crecimiento de *Caesalpinia* no respondió a la variabilidad del SPEI a escalas temporales largas, lo que sugiere que esta especie puede tolerar sequías intensas y duraderas. En particular, la densidad alta del xilema y la baja producción de la albura registradas en esta especie (Fig. 8), pueden estar relacionadas con una baja demanda de agua. Específicamente, la baja sensibilidad de *Caesalpinia* a las sequías de larga duración, es consistente con las observaciones obtenidas en la Amazonía, donde se encontró que las especies de árboles con densidades del xilema bajas son menos vulnerables a las sequías y por lo tanto, pueden llegar a ser las especies dominantes en estos bosques (Phillips et al., 2010).

5. CONCLUSIONES

Las conclusiones principales de esta tesis están agrupadas en dos escalas temporales (intra- e inter-anual). Además, se resaltan las diferencias encontradas entre las especies estudiadas.

5.1. Control climático en los patrones intra-anuales del crecimiento radial en las especies de los BsTs de Colombia y Bolivia

- La reactivación del cambium y el crecimiento de la xilema se registró durante la época húmeda del año en ambos sitios de estudio. Esto refleja la influencia de las precipitaciones y los valores positivos del balance hídrico en el desarrollo de las nuevas células del xilema.
- El período de crecimiento del xilema coincidió con la época húmeda en las especies semi-caducifolias de Tuluá (Colombia), mientras que en las especies caducifolias de INPA (Bolivia) el período de crecimiento comenzó a mediados de la estación húmeda, cuando las hojas de las copas de los árboles estaban totalmente desarrolladas.
- El período de crecimiento en Tuluá (Colombia) estuvo asociado a temperaturas bajas y, por ende, a un déficit de presión de vapor (DPV) bajo, mientras que en INPA estuvo asociado a valores altos de temperatura y DPV. Sin embargo, en ambos sitios de estudio se evidenció un efecto negativo de la temperatura en el incremento radial de los árboles durante las horas del día más cálidas. Las especies pueden hacer frente a esta condición adversa, por ejemplo, restringiendo el crecimiento a períodos del día cuando las temperaturas son bajas, ya que la pérdida de agua asociada a la evapotranspiración también sería baja.
- La contracción reversible de los troncos se registró a escalas horarias y diarias en las especies de Tuluá e INPA. Sin embargo, la mayoría de las especies de INPA registraron además contracciones reversibles fuertes a escalas mensuales. En particular, el control climático sobre la dinámica del incremento radial varió entre escalas diarias y mensuales. A escalas diarias, existió un efecto positivo de las precipitaciones y del balance hídrico, y un efecto negativo del DPV en la fase de incremento, mientras a escalas mensuales, la precipitación fue la variable más importante que afectó positivamente al incremento radial.
- La asociación entre las tasas de incremento radial y la producción de hojas a escalas mensuales fue positiva en todas las especies. Sin embargo, las especies presentaron diferencias en la fuerza de esa asociación en función de la densidad de la albura. De esta manera, *Cedrela*, una especie pionera y caducifolia, presentó la asociación tronco-hoja más fuerte y la densidad de la albura más baja, mientras que *Acosmium*, una especie tolerante a la sombra y caducifolia, presentó las características opuestas, es decir, una asociación tronco-hoja menos fuerte y la densidad de la albura más alta.

5.2. Efectos del clima y las sequías en los patrones inter-anuales del crecimiento radial en las especies del BsT boliviano

- El crecimiento radial en todas las especies estudiadas presentó una relación positiva con la precipitación y el balance hídrico atmosférico y una relación negativa con la temperatura. Esto indica que todas las especies comparten una señal común de la variabilidad del crecimiento en respuesta al clima local. No obstante, la fuerza de la respuesta fue especie-específica. Esto indica que existe una sensibilidad diferencial entre las especies al clima.

- La **precipitación** tuvo un efecto positivo en el crecimiento radial de todas las especies a escalas de tiempo cortas (de dos a nueve meses), principalmente, cuando la disponibilidad hídrica se incrementó durante la época húmeda.
- El crecimiento radial de todas las especies respondió positivamente al **balance hídrico** atmosférico durante la estación húmeda, pero la fuerza de esa respuesta fue diferente entre las especies, en función de la densidad de la albura. En particular, la densidad de la albura fue negativamente relacionada a la variabilidad del crecimiento explicada por el balance hídrico. Las especies con una densidad baja de la albura, tal como *Zeyheria*, fueron las más sensibles al balance hídrico, mientras que las especies que presentaron una densidad alta de la albura, tal como *Caesalpinia*, fueron las menos sensibles.
- El crecimiento radial se relacionó de manera negativa a la **temperatura** en cinco de las siete especies evaluadas en INPA. *Anadenanthera*, una especie emergente, fue la más sensible a los cambios de la temperatura a escalas mensuales y anuales, mientras que el resto de especies mostraron una respuesta negativa del crecimiento a la temperatura a escalas temporales cortas (de dos a tres meses), principalmente, durante la época húmeda.
- Las especies de INPA fueron resilientes a las **sequías de corto plazo** (estación seca anual), mientras que el crecimiento fue particularmente sensible a las **sequías de larga duración** (sequías multi-anuales), excepto en las especies con alta densidad de la albura. En particular, *Anadenanthera* (especie emergente), aparte de ser la especie más sensible a la temperatura, fue la más sensible a las sequías de larga duración. Por el contrario, *Caesalpinia* (especie del dosel), quien no fue sensible a las sequías de larga duración, fue la que mostró la densidad más alta de la albura y la menor sensibilidad al balance hídrico atmosférico.

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INFORME FIRMADO DE LOS DIRECTORES DE TESIS SOBRE EL FACTOR DE IMPACTO DE ARTÍCULOS PUBLICADOS

La tesis titulada "Impacts of climate and drought on tree radial growth in Neotropical dry forests: Scaling up from short to long time-scales" que presenta la Sta. Hooz Angela Chaparro Mendivelso en la Facultat de Biologia de la Universitat de Barcelona consta de los siguientes artículos científicos ya publicados en revistas de las áreas de ecológica y ciencias forestales:

1-Mendivelso, H.A., Camarero, J.J., Royo Obregón, O., Gutiérrez, E. and Toledo, M. 2013. Differential growth responses to water balance of coexisting deciduous tree species are linked to wood density in a Bolivian tropical dry forest. Plos ONE 8: e73855 (capítulo 4 de la tesis; el factor de impacto de la revista en el año de la publicación fue de 3.534).

2-Mendivelso, H.A., Camarero, J.J., Gutiérrez, E. and Zuidema, P.A. 2014. Time-dependent effects of climate and drought on tree growth in a Neotropical dry forest: Short-term tolerance vs. long-term sensitivity. Agricultural and Forest Meteorology 188: 13-23 (capítulo 3 de la tesis; el factor de impacto de la revista en el año de la publicación fue de 3.762).

3-Mendivelso, H.A., Camarero, J.J., Gutiérrez, E. and Castaño-Naranjo, A. 2016. Climate influences on leaf phenology, xylogenesis and radial stem changes at hourly to monthly scales in two tropical dry forests. Agricultural and Forest Meteorology 216: 20-36 (capítulo 2 de la tesis; factor de impacto de la revista en el año 2015 fue de 4.461).

Atentamente,

Fdo.: J. Julio Camarero Martínez (Director)　　Fdo.: Pieter A. Zuidema (Codirector)

21 de septiembre de 2016

INFORME FIRMADO DE LOS DIRECTORES DE TESIS ESPECIFICANDO LA PARTICIPACIÓN DE LA DOCTORANDA EN CADA ARTÍCULO

La tesis titulada “Impacts of climate and drought on tree radial growth in Neotropical dry forests: Scaling up from short to long time-scales” que presenta la Sta. Hooz Angela Chaparro Mendivelso en la Facultat de Biologia de la Universitat de Barcelona consta de los siguientes artículos científicos ya publicados en revistas de las áreas de ecológica y ciencias forestales. A continuación, detallamos la participación de la doctoranda en cada artículo:

1- Mendivelso, H.A., Camarero, J.J., Royo Obregón, O., Gutiérrez, E. and Toledo, M. 2013. Differential growth responses to water balance of coexisting deciduous tree species are linked to wood density in a Bolivian tropical dry forest. Plos ONE 8: e73855 (capítulo 4 de la tesis): la doctoranda participó en el muestreo y en su diseño, en la recogida y análisis de datos y en la elaboración y discusión del manuscrito final.

2- Mendivelso, H.A., Camarero, J.J., Gutiérrez, E. and Zuidema, P.A. 2014. Time-dependent effects of climate and drought on tree growth in a Neotropical dry forest: Short-term tolerance vs. long-term sensitivity. Agricultural and Forest Meteorology 188: 13-23 (capítulo 3 de la tesis): la doctoranda participó en el muestreo y en su diseño, en la recogida y análisis de datos y en la elaboración y discusión del manuscrito final.

3- Mendivelso, H.A., Camarero, J.J., Gutiérrez, E. and Castaño-Naranjo, A. 2016. Climate influences on leaf phenology, xylogenesis and radial stem changes at hourly to monthly scales in two tropical dry forests. Agricultural and Forest Meteorology 216: 20-36 (capítulo 2 de la tesis): la doctoranda participó en el muestreo y en su diseño, en la recogida y análisis de datos y en la elaboración y discusión del manuscrito final.

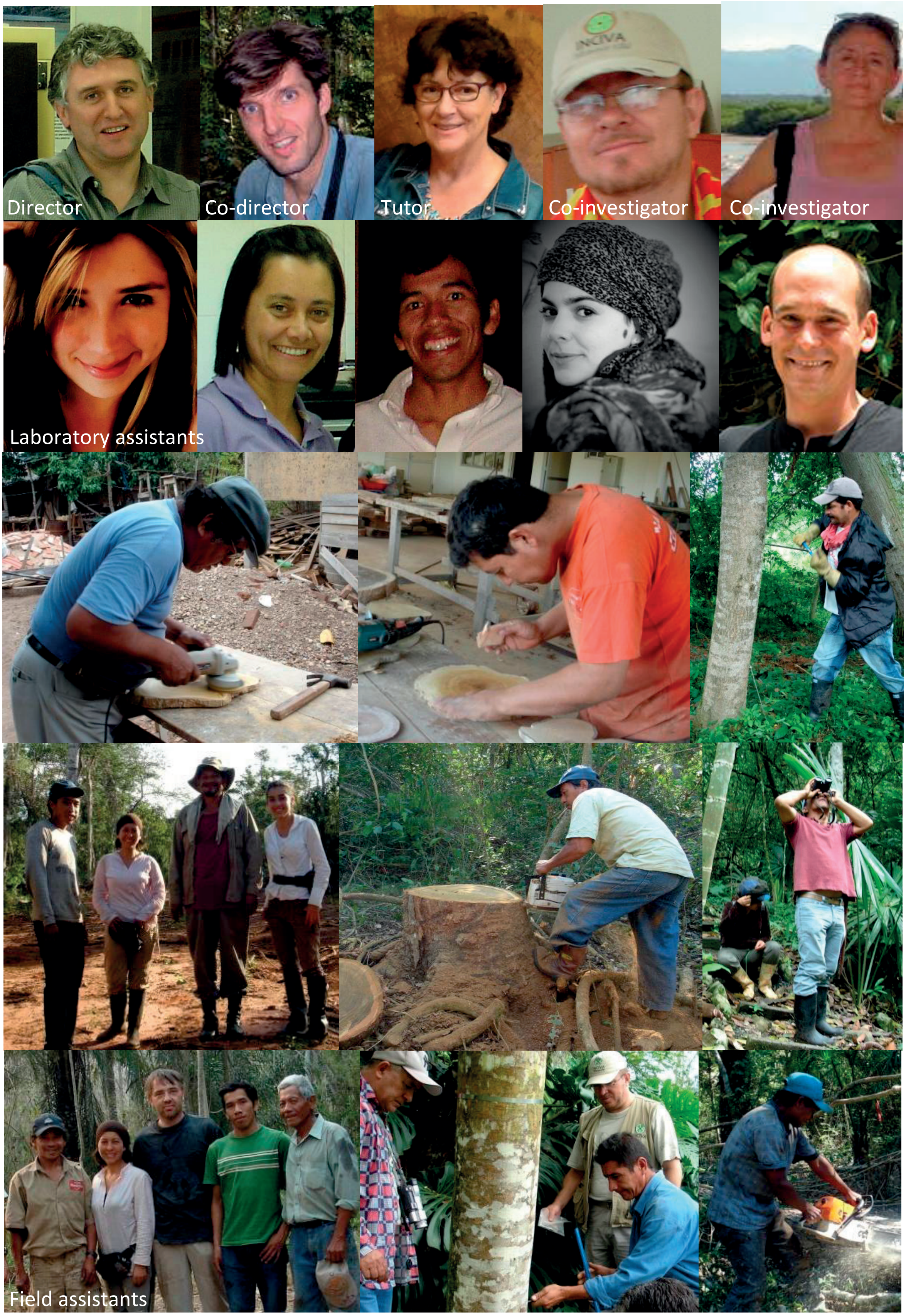
Finalmente, hacemos también constar que ninguno de los coautores de los artículos citados y presentados en esta tesis doctoral ha utilizado esos trabajos para la elaboración de otras tesis doctorales.

Atentamente,

Fdo.: J. Julio Camarero Martínez (Director)   Fdo.: Pieter A. Zuidema (Codirector)

21 de septiembre de 2016

Project team



Tropical dry forests are distributed throughout the tropical regions of America, Africa and Southeast Asia, and in countries, such as Australia and India. As a whole, the tropical dry forests and other kind of forests belonging to the tropics, play a key role in the global carbon cycle.

Historically, large tropical dry forest areas have been deforested, transforming them into farmlands and grasslands, while other tropical dry forest areas has been degraded through logging of valuable timber species, firewood extraction and fires. In addition to the pressures exerted by human impact on tropical dry forests, droughts are also a big threat to them.

A plausible warmer world with longer and more severe drought could lead to rapid collapse of tropical forest communities converting them into a large carbon source with cascading ecosystem effects, which affect global climate-vegetation feedbacks. To resolve part of the uncertainty linked to the climate-drought-forest feedbacks we must advance on the understanding of the long-term impacts of climate and drought on the productivity, growth and functioning of tropical dry forests.

This research aims to determine the dynamics of radial growth at different time-scales in relation to climate and drought in Neotropical dry forests from Colombia and Bolivia.

Inter-Andean tropical dry forest
in the Cauca valley (Tuluá, Colombia)

Chiquitano tropical dry forest
(Concepción, Bolivia)