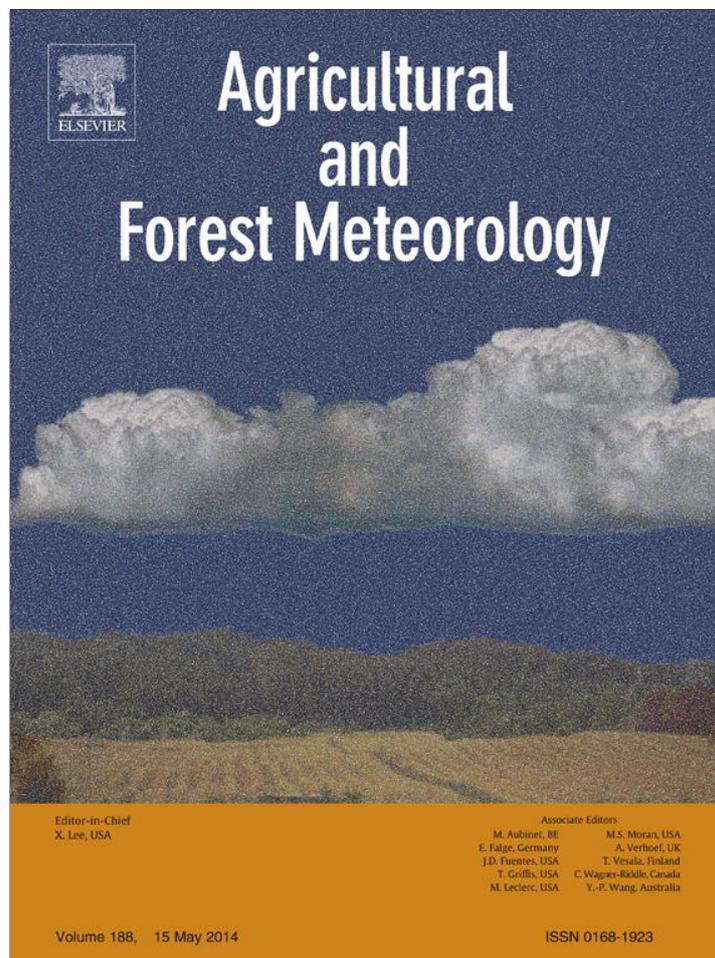


Provided for non-commercial research and education use.
Not for reproduction, distribution or commercial use.



This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

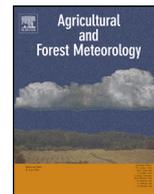
In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

<http://www.elsevier.com/authorsrights>



Contents lists available at ScienceDirect

Agricultural and Forest Meteorology

journal homepage: www.elsevier.com/locate/agrformet

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

Hooz A. Mendivelso^{a,b,c,*}, J. Julio Camarero^{b,c,d}, Emilia Gutiérrez^b, Pieter A. Zuidema^e^a Instituto Pirenaico de Ecología (CSIC), Avda. Montañana 1005, 50059 Zaragoza, Spain^b Departament d'Ecologia, Universitat de Barcelona, Avda. Diagonal 643, 08028 Barcelona, Spain^c Instituto Boliviano de Investigación Forestal (IBIF), PO Box 6204, Santa Cruz de la Sierra, Bolivia^d ARAID, Instituto Pirenaico de Ecología (CSIC), Avda. Montañana 1005, 50059 Zaragoza, Spain^e Forest Ecology and Forest Management Group, Wageningen University, PO Box 47, 6700 AA Wageningen, The Netherlands

ARTICLE INFO

Article history:

Received 29 August 2013

Received in revised form

20 December 2013

Accepted 23 December 2013

Keywords:

Climate

Drought

Secondary growth

Standardized Precipitation

Evapotranspiration Index (SPEI)

Time scales

Tropical dry forest

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 multiscale 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.

© 2014 Elsevier B.V. All rights reserved.

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.

* Corresponding author at: Instituto Pirenaico de Ecología, CSIC, Avda. Montañana 1005, 50059 Zaragoza, Spain. Tel.: +34 697752388; fax: +34 974363222.

E-mail addresses: hangelachaparro@gmail.com (H.A. Mendivelso), jjcamarero@ipe.csic.es (J.J. Camarero), emgutierrez@ub.edu (E. Gutiérrez), pieter.zuidema@wur.nl (P.A. Zuidema).

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 of the most endangered tropical ecosystems 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 m² 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

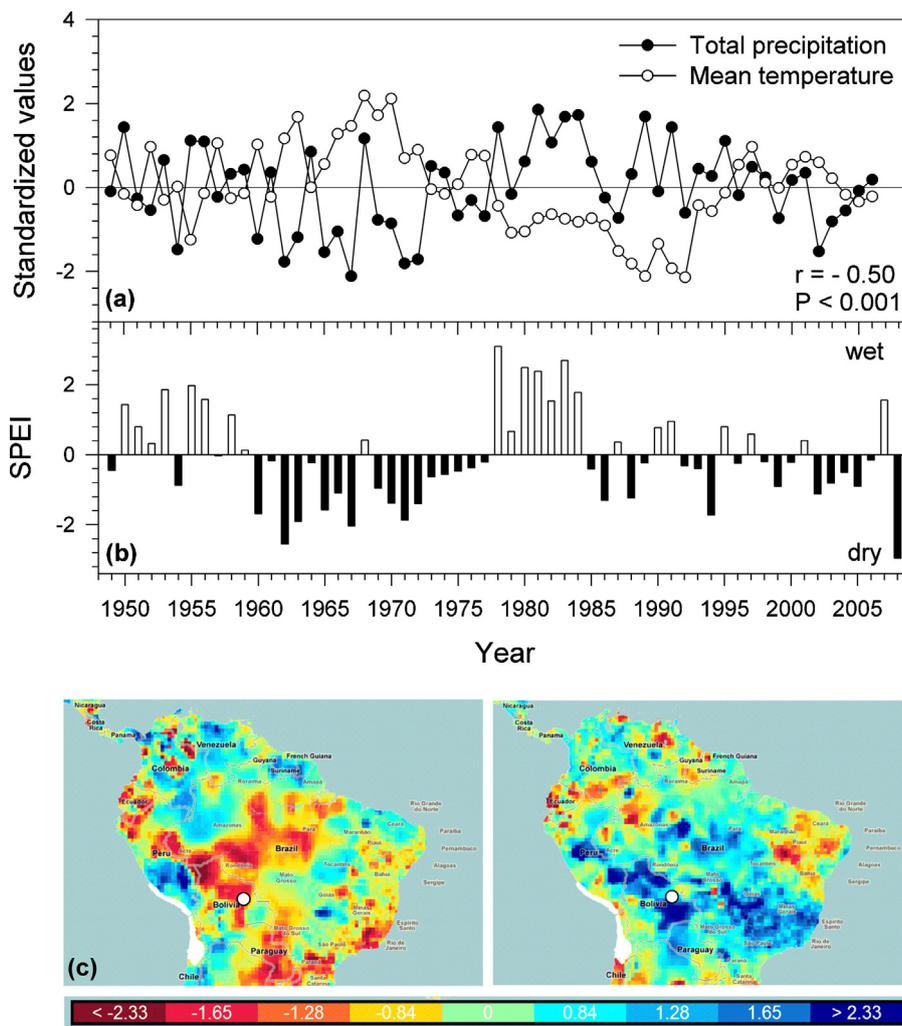


Fig. 1. Temporal (a and b) and spatial (c) patterns of climatic and drought variability in the study area. In the upper graph the relationship between the standardized temperature and precipitation values is indicated with its corrected probability value. The lower maps (obtained from <http://sac.csic.es/spei/map/maps.html>) 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 \pm 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 (%)
<i>Centrolobium microchaete</i> (Fabaceae)	C	LLP	Jun–Oct (5)	Nov	36.0 \pm 3.2	0.59 \pm 0.02	29.7 \pm 2.0
<i>Acosmium cardenasii</i> (Fabaceae)	Sc	TST	Aug–Sep (2)	Oct	29.2 \pm 3.9	0.69 \pm 0.02	26.6 \pm 0.7
<i>Caesalpinia pluviosa</i> (Fabaceae)	C	PST	Aug–Sep (2)	Oct	46.5 \pm 3.7	0.79 \pm 0.01	23.2 \pm 2.4
<i>Aspidosperma tomentosum</i> (Apocynaceae)	Sc	PST	Jul–Sep (3)	Oct	26.9 \pm 4.6	0.66 \pm 0.01	28.1 \pm 1.2
<i>Zeyheria tuberculosa</i> (Bignoniaceae)	C	LLP	Oct–Nov (2)	Dec	38.2 \pm 3.6	0.61 \pm 0.01	42.6 \pm 2.2
<i>Anadenanthera macrocarpa</i> (Fabaceae)	E	LLP	Jun–Oct (5)	Nov	42.1 \pm 2.9	0.71 \pm 0.05	25.3 \pm 3.4
<i>Tabebuia impetiginosa</i> (Bignoniaceae)	C	LLP	Jul–Sep (3)	Oct	43.3 \pm 3.4	0.74 \pm 0.04	26.8 \pm 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 \pm 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
<i>Centrolobium</i>	14/42	71–109	1.50 \pm 0.08	0.47	0.34	0.26	0.94
<i>Acosmium</i>	11/38	71–128	1.93 \pm 0.10	0.54	0.25	0.24	0.92
<i>Caesalpinia</i>	8/31	91–176	1.56 \pm 0.09	0.15	0.50	0.15	0.84
<i>Aspidosperma</i>	8/24	56–96	1.16 \pm 0.05	0.51	0.26	0.23	0.86
<i>Zeyheria</i>	7/21	65–137	1.70 \pm 0.14	0.51	0.40	0.20	0.83
<i>Anadenanthera</i>	8/24	80–155	1.36 \pm 0.07	0.39	0.33	0.19	0.85
<i>Tabebuia</i>	7/24	59–129	2.37 \pm 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 confidence 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 $EPS \geq 0.80$ (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, $SPEI=0.7 \pm 0.3$) was less wet (Tukey $t=1.38$, $P=0.014$) than the second one (1978–1994, $SPEI=2.1 \pm 0.3$), while the first dry long-period (1960–1977, $SPEI=-1.0 \pm 0.2$) was not significantly drier than the last one (1985–2008, $SPEI=-0.7 \pm 0.2$). 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

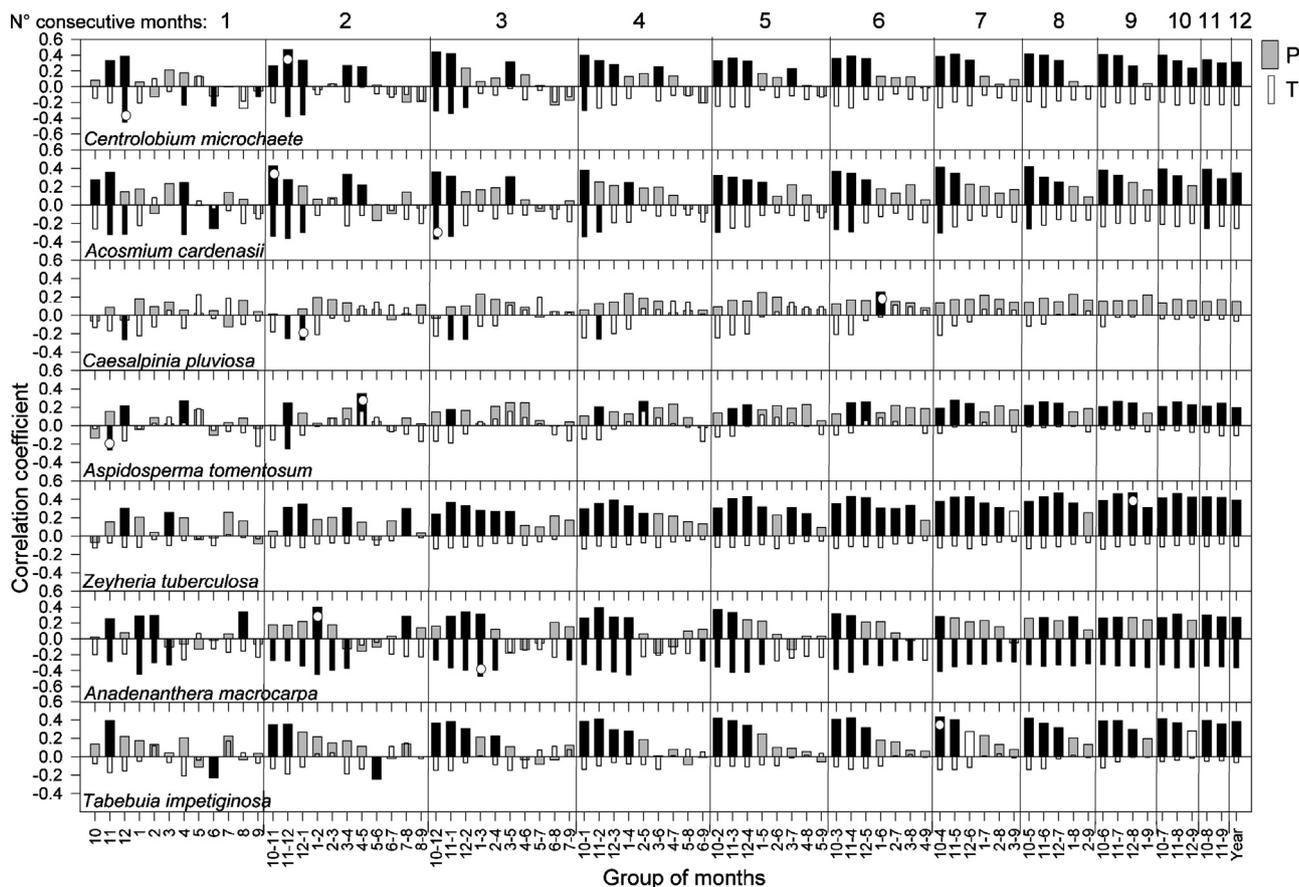


Fig. 2. Correlations (Pearson coefficients) calculated between climatic variables (P, total precipitation, wide gray bars; T, mean temperature, thin empty bars) and residual tree-ring width chronologies for the common period 1949–2008. The month or group of months used for computing climate data are 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*, *Anadenanthera*, *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 was obtained during 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 *Anadenanthera* 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 (*Anadenanthera*) (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* ($r=0.94$)

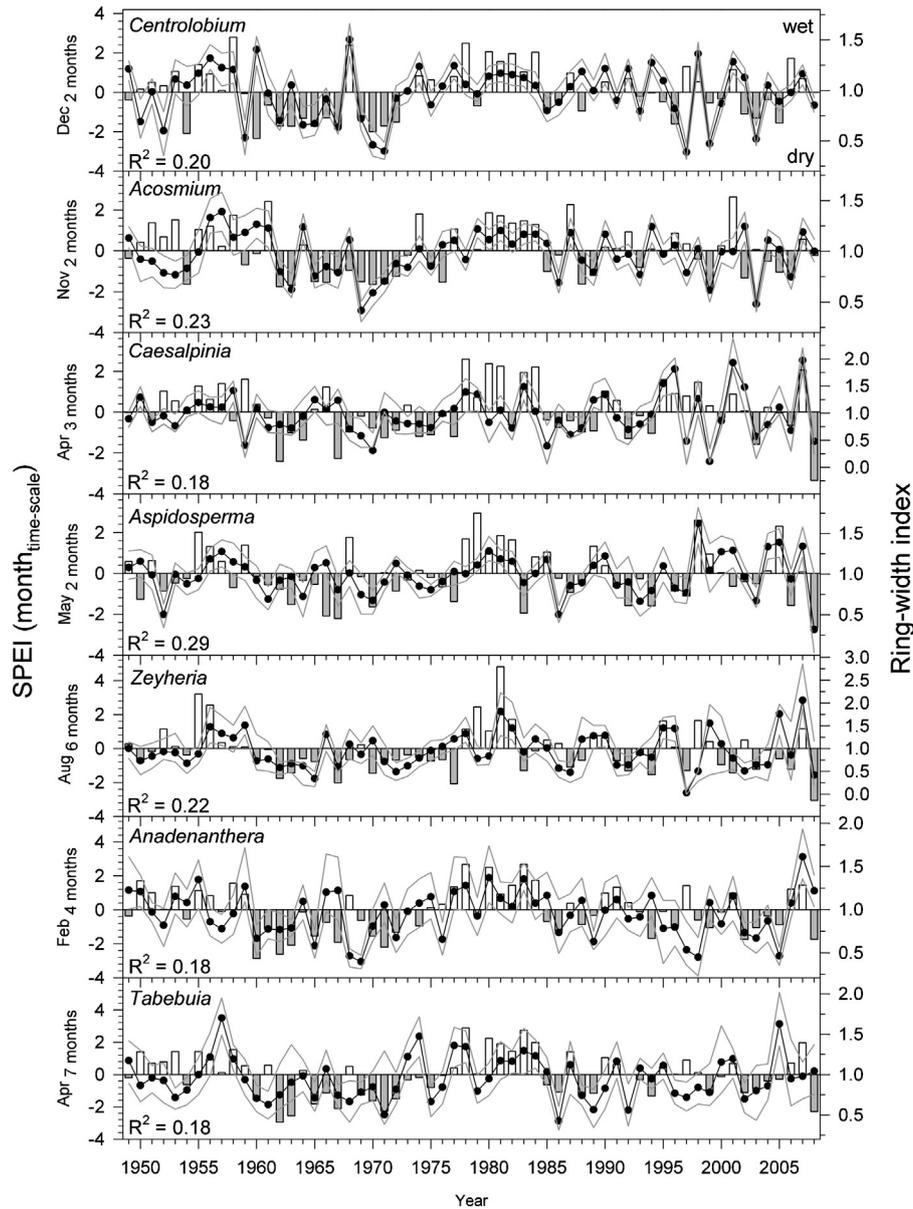


Fig. 3. Highest correlations found between residual ring-width chronologies (lines with symbols and bootstrapped 95% confidence limits) and SPEI (bars). The month and time-scales (subscripts) where the highest correlation was found is shown on the y-axis labels for each species. Positive and negative 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% (*Anadenanthera*) 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

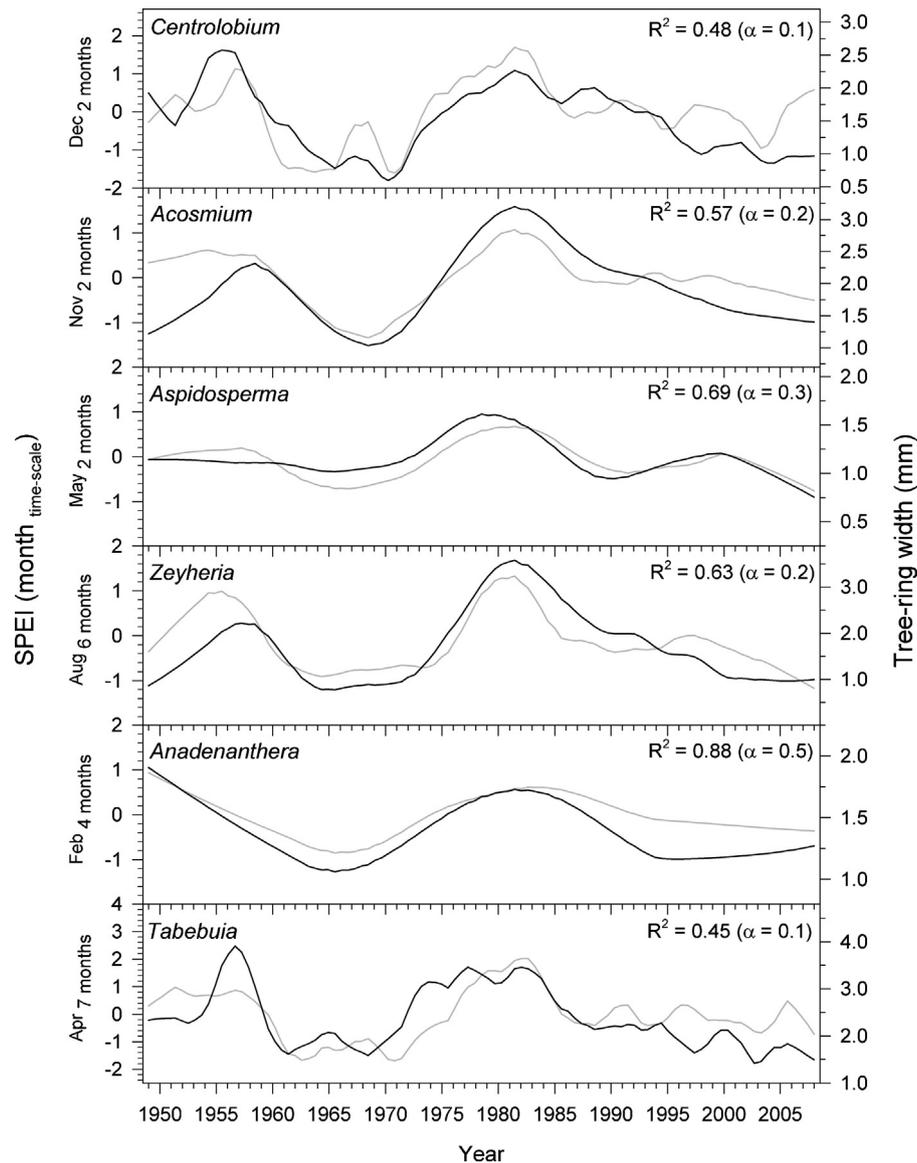


Fig. 4. Highest long-term relationship found between tree-ring widths (black lines) and drought severity assessed through the SPEI (gray lines). All presented coefficients of determination have $P < 0.05$. The smoothing parameter (α) gives the proportion of the displayed period (1949–2008, 59 years) 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 (Brodrribb 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

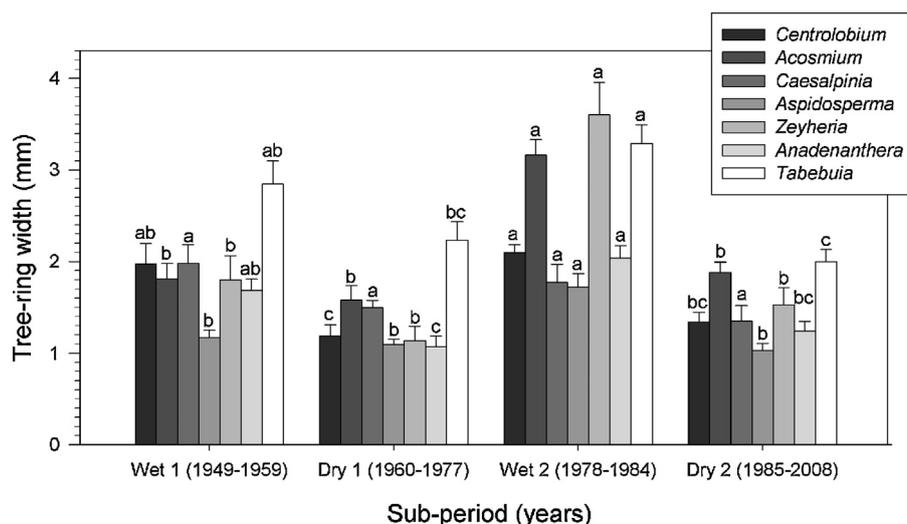


Fig. 5. Comparison of mean tree-ring widths (mean \pm 1 SE) obtained for the four sub-periods with contrasting drought severity (two wet sub-periods and two dry sub-periods) as assessed by the SPEI. Columns with different letters correspond to means showing significant differences in tree-ring width 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.

Acknowledgements

We thank all the staff and students of the Instituto Boliviano de Investigación Forestal for their support, particularly M. Toledo and V. Vroomans. We sincerely acknowledge P. Roosenboom (INPA Co.) and his staff at Concepción (G. Urbano) for their help to sample and work on their property. We thank O. Royo for his help in the laboratory work. We are grateful to two anonymous reviewers and the editor for their constructive comments on an earlier version of this manuscript. This study was supported by the projects “Análisis retrospectivos mediante dendrocronología para profundizar en la ecología y mejorar la gestión de los bosques tropicales secos (Dentropicas)” (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). JJC sincerely acknowledges funding by ARAID. PAZ acknowledges funding by an ERC Grant (#242955).

Appendix A.

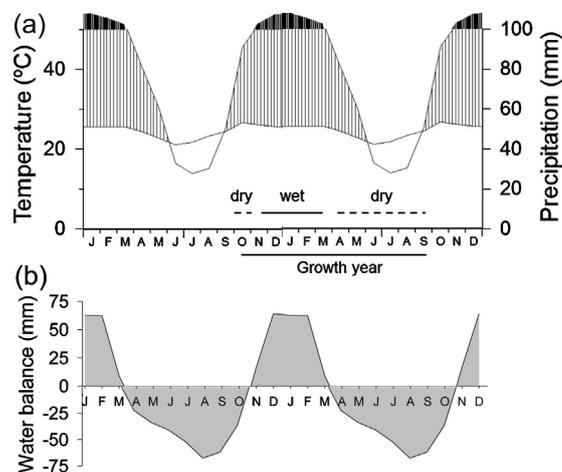


Fig. A1. Climate diagram and estimated monthly water balance of the study area considering the period 1949–2008.

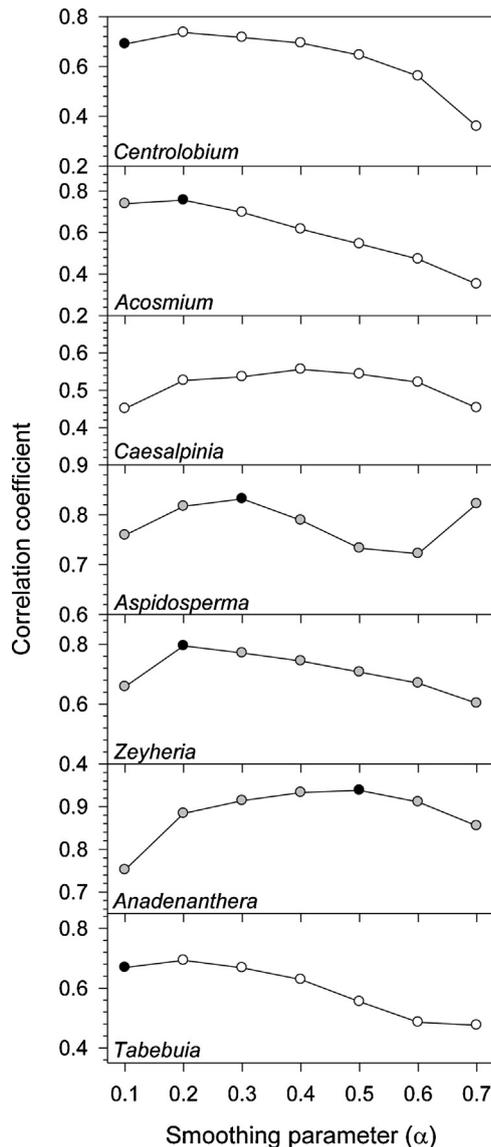


Fig. A2. Relationships (Pearson correlation coefficients) calculated between smoothed tree-ring width and drought index (SPEI) series considering the seven study species and the period 1949–2008.

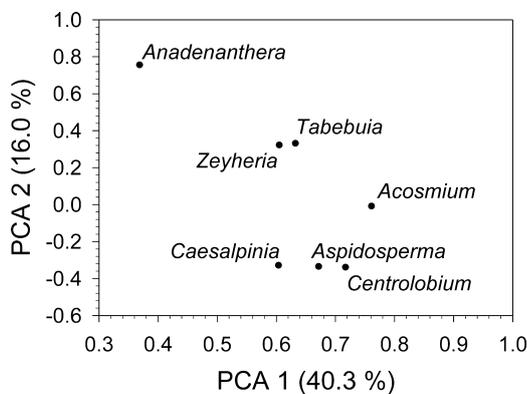


Fig. A3. Graphical summary of the seven tree species' scores considering the first two components of a Principal Component Analysis calculated on the residual tree-ring width chronologies.

References

Biondi, F., Waikul, K., 2004. DENDROCLIM2002: a C++ program for statistical calibration of climate signals in tree-ring chronologies. *Comput. Geosci.* 30, 303–311.

Borchert, R., 1994. Soil and stem water storage determine phenology and distribution of tropical dry forest trees. *Ecology* 75, 1437–1449.

Borchert, R., 1999. Climatic periodicity, phenology, and cambium activity in tropical dry forest trees. *IAWA J.* 20, 239–247.

Borchert, R., Rivera, G., Hagnauer, W., 2002. Modification of vegetative phenology in a tropical semi-deciduous forest by abnormal drought and rain. *Biotropica* 34, 27–39.

Brando, P.M., Nepstad, D.C., Davidson, E.A., Trumbore, S.E., Ray, D., Camargo, P., 2008. Drought effects on litterfall, wood production and belowground carbon cycling in an Amazon forest: results of a throughfall reduction experiment. *Philos. Trans. R. Soc. B: Biol. Sci.* 363, 1839–1848.

Brienen, R.J.W., Lebrija-Trejos, E., Zuidema, P.A., Martínez-Ramos, M., 2010a. Climate-growth analysis for a Mexican dry forest tree shows strong impact of sea surface temperatures and predicts future growth declines. *Glob. Change Biol.* 16, 2001–2012.

Brienen, R.J.W., Zuidema, P.A., 2005. Relating tree growth to rainfall in Bolivian rain forests: a test for six species using tree ring analysis. *Oecologia* 146, 1–12.

Brienen, R.J.W., Zuidema, P.A., 2006. Lifetime growth patterns and ages of Bolivian rain forest trees obtained by tree ring analysis. *J. Ecol.* 94, 481–493.

Brienen, R.J.W., Zuidema, P., Martínez-Ramos, M., 2010b. Attaining the canopy in dry and moist tropical forests: strong differences in tree growth trajectories reflect variation in growing conditions. *Oecologia* 163, 485–496.

Briffa, K.R., Jones, P.D., 1990. Basic chronology statistics and assessment. In: Cook, E.R., Kairiukstis, L.A. (Eds.), *Methods of Dendrochronology: Applications in the Environmental Sciences*. Kluwer Academic Publishers, Dordrecht, pp. 137–152.

Brodribb, T.J., Holbrook, N.M., Gutierrez, M.V., 2002. Hydraulic and photosynthetic co-ordination in seasonally dry tropical forest trees. *Plant Cell Environ.* 25, 1435–1444.

Bullock, S.H., Mooney, H.A., Medina, E., 1995. *Seasonally Dry Tropical Forest*. Cambridge University Press, Cambridge.

Clark, D.A., Clark, D.B., 2010. Assessing tropical forests' climatic sensitivities with long-term data. *Biotropica* 43, 31–40.

Clark, D.B., Clark, D.A., Oberbauer, S.F., 2010. Annual wood production in a tropical rain forest in NE Costa Rica linked to climatic variation but not to increasing CO₂. *Glob. Change Biol.* 16, 747–759.

Cleveland, W.S., 1979. Robust locally weighted regression and smoothing scatterplots. *J. Am. Stat. Assoc.* 74, 829–836.

Cook, E.R., (Ph.D. thesis) 1985. *A time series approach to tree-ring standardization*. University of Arizona, Tucson.

Cook, E.R., Krusic, P., 2007. ARSTAN 41d. A Tree-ring standardization program based on detrending and autoregressive time series modeling, with interactive graphics. <https://www.ldeo.columbia.edu/tree-ring-laboratory/resources/software> (accessed 20.08.13).

Dirzo, R., Young, H.S., Monney, H.A., Ceballos, G., 2011. *Seasonally Dry Tropical Forest: Ecology and Conservation*. Island Press, Washington.

Dong, S.X., Davies, S.J., Ashton, P.S., Bunyavejchewin, S., Supardi, M.N.N., Kassim, A.R., Tan, S., Moorcroft, P.R., 2012. Variability in solar radiation and temperature explains observed patterns and trends in tree growth rates across four tropical forests. *Proc. R. Soc. B: Biol. Sci.* 279, 3923–3931.

Drew, D.M., Allen, K., Downes, G.M., Evans, R., Battaglia, M., Baker, P., 2012. Wood properties in a long-lived conifer reveal strong climate signals where ring-width series do not. *Tree Physiol.* 33, 37–47.

Eamus, D., 1999. Ecophysiological traits of deciduous and evergreen woody species in the seasonally dry tropics. *Trends Ecol. Evol.* 14, 11–16.

Eamus, D., Prior, L., 2001. Ecophysiology of trees of seasonally dry tropics: comparisons among phenologies. In: Caswell, H. (Ed.), *Advances in Ecological Research*, 32. Academic Press, London, pp. 113–197.

Enquist, B.J., Leffler, A.J., 2001. Long-term tree ring chronologies from sympatric tropical dry-forest trees: individualistic responses to climatic variation. *J. Trop. Ecol.* 17, 41–60.

Feeley, K.J., Joseph Wright, S., Nur Supardi, M.N., Kassim, A.R., Davies, S.J., 2007. Decelerating growth in tropical forest trees. *Ecol. Lett.* 10, 461–469.

Friedman, J.H., 1984. A variable span smoother. *Lab. Comput. Stat. Stanf. Univ. Tec. Rep. No 5*.

Goldsmith, G.R., Muñoz-Villers, L.E., Holwerda, F., McDonnell, J.J., Asbjornsen, H., Dawson, T.E., 2012. Stable isotopes reveal linkages among ecohydrological processes in a seasonally dry tropical montane cloud forest. *Ecohydrology* 5, 779–790.

Holmes, R.L., 1983. Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bull.* 43, 69–78.

IPCC, 2007. *Climate change 2007: the physical science basis*. In: Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M., Miller, H.L. (Eds.), *Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge and New York.

Janzen, D.H., 1988. Tropical dry forest: the most endangered major tropical ecosystem. In: Wilson, E.O. (Ed.), *Biodiversity*. National Academy Press, Washington, pp. 130–137.

- Kallarackal, J., Otieno, D.O., Reineking, B., Jung, E.-Y., Schmidt, M.W.T., Granier, A., Tenhunen, J.D., 2013. Functional convergence in water use of trees from different geographical regions: a meta-analysis. *Trees* 3, 787–799.
- Killeen, T.J., Jardim, A., Mamani, F., Rojas, N., 1998. Diversity, composition and structure of a tropical semideciduous forest in the Chiquitania region of Santa Cruz, Bolivia. *J. Trop. Ecol.* 14, 803–827.
- Leigh Jr., E.G., Windsor, D.M., Rand, A.S., Foster, R.B., 1990. The impact of the El Niño drought of 1982–83 on a Panamanian semideciduous forest. *Elsevier Oceanogr. Ser.* 52, 473–486.
- Lewis, S.L., 2006. Tropical forests and the changing earth system. *Philos. Trans. R. Soc. B: Biol. Sci.* 361, 195–210.
- López, L., Villalba, R., 2011. Climate influences on the radial growth of *Centrolobium microchaete*, a valuable timber species from the tropical dry forests in Bolivia. *Biotropica* 43, 41–49.
- Macias-Fauria, M., Grinsted, A., Helama, S., Holopainen, J., 2012. Persistence matters: estimation of the statistical significance of paleoclimatic reconstruction statistics from autocorrelated time series. *Dendrochronologia* 30, 179–187.
- Markesteyn, L., (Ph.D. thesis) 2010. Drought tolerance of tropical tree species: functional traits, trade-offs and species distribution. Wageningen University, Wageningen.
- Markesteyn, L., Poorter, L., Bongers, F., Paz, H., Sack, L., 2011. Hydraulics and life history of tropical dry forest tree species: coordination of species' drought and shade tolerance. *New Phytol.* 191, 480–495.
- Meinzer, C., Andrade, J.L., Goldstein, G., Holbrook, N.M., Cavelier, J., Wright, S.J., 1999. Partitioning of soil water among canopy trees in a seasonally dry tropical forest. *Oecologia* 121, 293–301.
- Mendivelso, H.A., Camarero, J.J., Royo, O., Gutierrez, E., 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*, <http://dx.doi.org/10.1371/journal.pone.0073855>.
- Mostacedo, B., (Ph.D. thesis) 2007. Natural regeneration of canopy trees in a tropical dry forest in Bolivia. University of Florida, Gainesville.
- Paredes-Villanueva, K., Sánchez-Salguero, R., Manzanedo, R.D., Quevedo-Sopepi, R., Palacios, G., Navarro-Cerrillo, R.M., 2013. Growth rate and climatic response of *Machaerium scleroxylon* in a dry tropical forest in southeastern Santa Cruz, Bolivia. *Tree-Ring Res.* 69, 63–79.
- Pasho, E., Camarero, J.J., de Luis, M., Vicente-Serrano, S.M., 2011. Impacts of drought at different time scales on forest growth across a wide climatic gradient in north-eastern Spain. *Agric. For. Meteorol.* 151, 1800–1811.
- Perneger, T.V., 1998. What's wrong with Bonferroni adjustments. *Br. Med. J.* 316, 1236–1238.
- Phillips, O.L., Aragão, L.E.O.C., Lewis, S.L., Fisher, J.B., Lloyd, J., López-González, G., Malhi, Y., Monteagudo, A., Peacock, J., Quesada, C.A., van der Heijden, G., Almeida, S., Amaral, I., Arroyo, L., Aymard, G., Baker, T.R., Bánki, O., Blanc, L., Bonal, D., Brando, P., Chave, J., Alves de Oliveira, Á.C., Dávila Cardozo, N., Czimczik, C.I., Feldpausch, T.R., Freitas, M.A., Gloor, E., Higuchi, N., Jiménez, E., Lloyd, G., Meir, P., Mendoza, C., Morel, A., Neill, D.A., Nepstad, D., Patiño, S., Peñuela, M.C., Prieto, A., Ramírez, F., Schwarz, M., Silva, J., Silveira, M., Sota Thomas, A., ter Steege, H., Stropp, J., Vázquez, R., Zelazowski, P., Alvarez Dávila, E., Andelman, S., Andrade, A., Chao, K.-J., Erwin, T., Di Fiore, A., Honorio, C.E., Keeling, H., Killeen, T.J., Laurance, W.F., Peña Cruz, A., Pitman, N.C.A., Núñez Vargas, P., Ramírez-Angulo, H., Rudas, A., Salamão, R., Silva, N., Terborgh, J., Torres-Lezama, A., 2009. Drought sensitivity of the Amazon rainforest. *Science* 323, 1344–1347.
- Phillips, O.L., van der Heijden, G., Lewis, S.L., López-González, G., Aragão, L.E.O.C., Lloyd, J., Malhi, Y., Monteagudo, A., Almeida, S., Alvarez Dávila, E., Amaral, I., Andelman, S., Andrade, A., Arroyo, L., Aymard, G., Baker, T.R., Blanc, L., Bonal, D., Alves de Oliveira, Á.C., Chao, K.-J., Dávila Cardozo, N., da Costa, L., Feldpausch, T.R., Fisher, J.B., Fyllas, N.M., Freitas, M.A., Galbraith, D., Gloor, E., Higuchi, N., Honorio, E., Jiménez, E., Keeling, H., Killeen, T.J., Lovett, J.C., Meir, P., Mendoza, C., Morel, A., Núñez Vargas, P., Patiño, S., Peh, K.S.-H., Peña Cruz, A., Prieto, A., Quesada, C.A., Ramírez, F., Ramírez, H., Rudas, A., Salamao, R., Schwarz, M., Silva, J., Silveira, M., Ferry, Slik, J.W., Sonké, B., Sota Thomas, A., Stropp, J., Taplin, J.R.D., Vázquez, R., Vilanova, E., 2010. Drought–mortality relationships for tropical forests scales. *New Phytol.* 187, 631–646.
- Reyes-García, C., Andrade, J.L., Simá, J.L., Us-Santamaría, R., Jackson, P.C., 2012. Sapwood to heartwood ratio affects whole-tree water use in dry forest legume and non-legume trees. *Trees* 26, 1317–1330.
- Rinn, F., 1996. *TSAP (Time Series Analysis and Presentation)*. Version 3.0. RinnTech, Heidelberg.
- Ronchail, J., 1995. Variabilidad interanual de las precipitaciones en Bolivia. *Bull. Inst. Fr. Études Andin.* 24, 369–378.
- Rozendaal, D.M.A., Zuidema, P.A., 2011. Dendroecology in the tropics: a review. *Trees* 25, 3–16.
- Sarris, D., Christodoulakis, D., Körner, C., 2007. Recent decline in precipitation and tree growth in the eastern Mediterranean. *Glob. Change Biol.* 13, 1187–1200.
- Sass-Klaassen, U., Couralet, C., Sahle Sterck, F.J., 2008. Juniper from Ethiopia contains a large-scale precipitation signal. *Int. J. Plant Sci.* 169, 1057–1065.
- Schulman, E., 1956. *Dendroclimatic Change in Semiarid America*. University of Arizona Press, Tucson.
- Stahle, D.W., Mushove, P.T., Cleaveland, M.K., Roig, F., Haynes, G.A., 1999. Management implications of annual growth rings in *Pterocarpus angolensis* from Zimbabwe. *For. Ecol. Manage.* 124, 217–229.
- Vicente-Serrano, S.M., Beguería, S., López-Moreno, J.I., 2010. A multiscalar drought index sensitive to global warming: the standardized precipitation evapotranspiration index. *J. Clim.* 23, 1696–1718.
- Vicente-Serrano, S.M., Gouveia, C., Camarero, J.J., Beguería, S., Trigo, R., López-Moreno, J.I., Azorín-Molina, C., Pasho, E., Lorenzo-Lacruz, J., Revuelto, J., Morán-Tejeda, E., Sanchez-Lorenzo, A., 2013. Response of vegetation to drought time-scales across global land biomes. *Proc. Natl. Acad. Sci. U.S.A.* 110, 52–57.
- Villegas, Z., Peña-Claros, M., Mostacedo, B., Alarcón, A., Licona, J.C., Leño, C., Pariona, W., Choque, U., 2009. Silvicultural treatments enhance growth rates of future crop trees in a tropical dry forest. *For. Ecol. Manage.* 258, 971–977.
- Wigley, T.M.L., Briffa, K.R., Jones, P.D., 1984. On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. *J. Clim. Appl. Meteorol.* 23, 201–213.
- Worbes, M., 1999. Annual growth rings, rainfall-dependent growth and long-term growth patterns of tropical trees from the Caparo Forest Reserve in Venezuela. *J. Ecol.* 87, 391–403.
- Worbes, M., 2002. One hundred years of tree-ring research in the tropics – a brief history and an outlook to future challenges. *Dendrochronologia* 20, 217–231.
- Worbes, M., Blanchart, S., Fichtler, E., 2013. Relations between water balance, wood traits and phenological behavior of tree species from a tropical dry forest in Costa Rica – a multifactorial study. *Tree Physiol.* 33, 527–536.
- Zhao, M., Running, S.W., 2010. Drought-induced reduction in Global Terrestrial Net Primary Production from 2000 through 2009. *Science* 329, 940–943.
- Zuidema, P.A., Baker, P.J., Groenendijk, P., Schippers, P., van der Sleen, P., Vlam, M., Sterck, F., 2013. Tropical forests and global change: filling knowledge gaps. *Trends Plant Sci.* 18, 413–419.