1 Time-dependent effects of climate and drought on tree growth in a

2 Neotropical dry forest: short-term tolerance vs. long-term sensitivity

3

4

5 Hooz A. Mendivelso[a,b,c*], J. Julio Camarero[b,c,d], Emilia Gutiérrez[b] and Pieter A. Zuidema[e]

6

7

8 [a]Instituto Pirenaico de Ecología (CSIC). Avda. Montañana 1005, 50059 Zaragoza, Spain.

9 [b]Departament d'Ecologia, Universitat de Barcelona. Avda. Diagonal 643, 08028 Barcelona,

10 Spain. emgutierrez@ub.edu

11 [c]Instituto Boliviano de Investigación Forestal (IBIF), PO Box 6204, Santa Cruz de la Sierra,

12 Bolivia.

13 [d]ARAID, Instituto Pirenaico de Ecología (CSIC). Avda. Montañana 1005, 50059 Zaragoza,

14 Spain.

15 [e]Forest Ecology and Forest Management Group, Wageningen University, PO Box 47, 6700

16 AA Wageningen, the Netherlands.

17

18

19 *Corresponding author:

20 Hooz A. Mendivelso

21 Instituto Pirenaico de Ecología, CSIC.

22 Avda. Montañana 1005, 50059 Zaragoza, Spain

23 Tel: +34 697752388

24 Fax: +34 974363222

25

26 E-mail addresses: hangelachaparro@gmail.com (H.A. Mendivelso), jjcamarero@ipe.csic.es

27 (J.J. Camarero), emgutierrez@ub.edu (E. Gutiérrez), pieter.zuidema@wur.nl (P. Zuidema)

28   **Abstract**

29   We analyzed the effects of climate and drought on radial growth using dendrochronology in

30   seven deciduous tree species coexisting in a Bolivian tropical dry forest subjected to seasonal

31   drought. Precipitation, temperature and a multiscalar drought index were related to tree-ring

32   width data at different time-scales (from one month to 42 years). Precipitation affected

33   positively tree growth in all species, mainly during the wet season, while temperature affected

34   it negatively in five species. Tree growth responses to precipitation and temperature were

35   species-specific and peaked at short-time scales, specifically from one to nine months. At

36   inter-annual scales tree growth always responded positively to less dry conditions at short-

37   time scales, particularly from two to seven months, and also at long-time scales from six to 30

38   years. Tree growth was mainly sensitive to multi-annual droughts and such sensitivity

39   differed among species. Our findings suggest that tree species of the studied tropical dry

40   forest are predominantly sensitive in terms of growth reduction to long-lasting droughts. This

41   time-dependency of growth responses to drought should be explicitly considered as an

42   additional constraint of the community dynamics in evaluations of the future responses of

43   tropical dry forests to climate warming.

44

45   **Key words**: climate; drought; secondary growth; Standardized Precipitation

46   Evapotranspiration Index (SPEI); time scales; tropical dry forest.

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).

72   Tropical dry forests (hereafter abbreviated as TDFs) are subjected to annual seasonal drought

73   (Bullock et al., 1995) so they might face more climatic risks related to warming-driven drought

74   stress than wet rainforests, such as rapid aridification transitions towards savanna woodlands (Dirzo

75   et al., 2011). TDFs also constitute one the most endangered tropical ecosystem because they have

76   been intensively converted into farmlands and grasslands (Janzen, 1988). Furthermore, TDFs are

77   diverse ecosystems dominated by drought-tolerant species with varied strategies to tolerate water

78   scarcity (Markesteijn et al., 2011), but there is scarce information on how these species grow in

79   response to drought at multiple temporal scales (Phillips et al., 2010). For example, growth

80   responses to drought change depending on the analyzed time scale in Mediterranean forests with

81   species from xeric sites usually responding to drought at short-time scales (Pasho et al., 2011). Do

82   also tree species from TDFs show contrasting growth responses to drought at different time scales?

83   Multi-species analyses of tree-rings in TDFs are rare but necessary to understand expected

84   community growth responses to warming and increased aridification. Consequently, we analyzed

85   the effects of climate and drought at different time scales on the radial growth of seven deciduous

86   tree species coexisting in a Bolivian TDF (*Acosmium cardenasii* H.S. Irwin & Arroyo,

87   *Anadenanthera macrocarpa* (Benth.) Brenan, *Aspidosperma tomentosum* Mart., *Caesalpinia*

88   *pluviosa* DC., *Centrolobium microchaete* (Mart. ex Benth.) H.C. Lima, *Tabebuia impetiginosa*

89   (Mart. ex DC.) Standl., *Zeyheria tuberculosa* (Vell.) Bureau). We related temperature, precipitation,

90   drought severity to indexed tree-ring width chronologies of these species at different time scales

91   ranging from months to decades. The drought severity was quantified using a multiscalar drought

92   index, the Standardized Precipitation Evapotranspiration Index, which explicitly considers the effect

93   of temperature on water availability (Vicente-Serrano et al., 2010). Our specific objectives were: (1)

94   to determine the main climatic variables related to radial tree growth, and (2) to evaluate the effects

95   of drought on tree growth at different time scales. We expect that the studied species will show

96   contrasting growth responses to climate and drought at characteristic time scales.

97

4

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 (16º 07' S, 61º 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 towards 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. A.1).

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 7-14 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 disc, separated by 90-120º 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

150 assigned to each ring the calendar year in which ring formation began according to the dating

151 convention for the southern hemisphere (Schulman, 1956). Tree rings were measured with a

152 precision of 0.01 mm under a binocular scope using a LINTAB measuring device (RinnTech,

153 Heidelberg, Germany) associated with the program TSAP (Rinn, 1996). The previous visual cross-

154 dating was checked using the COFECHA program which calculates the correlation between

155 individual ring-width series and a master series for each species (Holmes, 1983). Tree-ring

156 chronologies for the seven species were constructed following a standard dendrochronological

157 protocol. Each raw series was standardized using a Friedman super smoother function (Friedman,

158 1984) preserving 50% of the variance contained in the measurement series at a wavelength of 20

159 years and removing non-climatic trends in growth like those related tree aging. This smoothing

160 function is more appropriate than deterministic fixed functions (e.g., negative exponential) for trees

161 whose tree-ring width series are subjected to the influence of forest dynamics such as the case of

162 TDFs (Drew et al., 2012). Standardization involved transforming the measured values into a

163 dimensionless index by dividing the raw values by the expected values given by the smoother

164 function. Autoregressive modeling was carried out on each standardized series to remove part of the

165 temporal autocorrelation. The indexed residual ring-width series were then averaged to obtain mean

166 site chronologies with 95% bootstrapped confidences limits for each species. We used the program

167 ARSTAN 41d (Cook and Krusic, 2007) to obtain the chronologies of ring-width indices (Cook,

168 1985), which were used in all subsequent analysis.

169   The characteristics of the tree ring chronologies were evaluated for the common period 1949-

170 2008 using several dendrochronological statistics (Briffa and Jones, 1990): the first-orden

171 autocorrelation (AC1) of raw ring-width series which measures the year-to-year growth similarity;

172 the mean sensitivity of indexed ring-width series (MSx) which quantifies the year-to-year

173 variability in width of consecutive rings; the, mean inter-series correlation (R-bar), and the

174 expressed population signal (EPS) which assess the among-trees coherence in growth and the

175 statistical quality of the mean site chronology as compared with an infinitely replicated chronology,

176 respectively (Table 2). The period of the residual chronologies showing EPS ≥ 0.80 (1949-2008)

177 was considered to be well replicated and used in further analyses, despite the 0.85 threshold is

178 usually employed for non-tropical tree species (Wigley et al., 1984). Lastly, we summarized the

179 growth variability among species by performing a Principal Components Analysis based on the

180 covariance matrix built using the residual ring-width series for the common period 1949-2008.

181

182 *2.5. Statistical analyses*

183

184   The climate-growth relationships were evaluated at time scales ranging from 1 to 12 months to

185 assess the effect of changes in the total precipitation and mean temperature on the annual variation

186 of tree-ring width indices. To relate growth to climate first we defined the biological growth year of

187 the tree species from October to September (Fig. A.1) based on previous phenological studies

188 (Mostacedo, 2007) and dendrometer records of radial increments (H.A. Mendivelso & J.J.

189 Camarero, unpublished results). This characterization agrees with the definition of the hydrological

190 year in the study area (Ronchail, 1995). Bootstrapped correlation analyses were performed to

191 evaluate the relationships between residual ring-width chronologies of each species and 78

192 climatically different periods using the software Dendroclim2002 (Biondi and Waikul, 2004). We

193 used Pearson correlation coefficients and performed 999 permutations of the data. Each period was

194 based on different months and time scales (1-12 months), and climatic variables were either

195 averaged (temperature) or summed (precipitation). Since we were not concerned with the

196 simultaneous testing of all correlations no Bonferroni correction was applied to significant levels

197 (Perneger, 1998).

198   To quantify the impact of drought on tree growth we employed the multiscalar Standardized

199 Precipitation Evapotranspiration Index (SPEI; Vicente-Serrano et al., 2010). The use of the SPEI is

200 relevant to quantify the effects of droughts on growth at different time scales (Vicente-Serrano et

201 al., 2013). For instance, in drought-stressed periods (negative SPEI values) tree growth would

202   decline, whereas in humid periods (positive SPEI values) tree growth would be enhanced. The SPEI

203   data were obtained from the SPEIbase (http://sac.csic.es/spei/database.html), with a 0.5° spatial

204   resolution.

205   First, to analyze short-term growth responses to drought we carried out Pearson correlation

206   analyses by relating ring-width indices and SPEI considering different months and time-scales (1-24

207   months). The SPEI time-scale showing the highest correlation to growth indices was kept for the

208   following analyses. Second, to analyze the multi-year responses to droughts we related the raw tree-

209   ring width chronologies to the SPEI time-scale selected in the first step. Smoothed SPEI and growth

210   were obtained through a locally weighted polynomial regression (LOESS) (Cleveland, 1979). The

211   first order polynomial (linear) and bandwidth methods (nearest neighbors) were used for LOESS

212   fits. A wide range of the α smoothing parameter ($0.1 \leq \alpha \leq 0.7$), which determines the proportion of

213   observations that is used in each LOESS fit, was used for capturing different time-scales

214   corresponding to different smoothing intensities. Correlation analyses were performed to determine

215   the smoothed growth scale most tightly related to the SPEI, i.e. that showing the highest and

216   significant correlation (Fig. A.2). Since the probability values (P) of these Pearson coefficients are

217   affected by temporal autocorrelation we calculated corrected P values using the Correltool software

218   (available at http://oxlel.zoo.ox.ac.uk/reconstats) which estimates and models the temporal

219   autocorrelation present in the compared time series (Macias-Fauria et al., 2012).

220   Finally, we divided the study period (1949-2008) in four different long-periods with contrasting

221   multi-year water-availability conditions and SPEI values (ANOVA, $F = 17.62$, $P < 0.001$): two wet

222   long-periods (1949-1959 and 1978-1984) and two dry long-periods (1960-1977 and 1985-2008)

223   (see Fig. 1). SPEI and ring-width values for each species were compared between long-climatic

224   periods using one-way ANOVAs, and differences between long-periods were assessed using Tukey

225   post-hoc tests. The first wet long-period (1949-1959, SPEI = 0.7 ± 0.3) was less wet (Tukey $t =$

226   1.38, $P = 0.014$) than the second one (1978-1994, SPEI =2.1 ± 0.3), while the first dry long-period

227   (1960-1977, SPEI = -1.0 ± 0.2) was not significantly drier than the last one (1985-2008, SPEI = -0.7

228   ± 0.2). On average, the wet long-periods were shorter (seven-11 years) than the dry long-periods

229   (18-24 years). All statistical analyses were done with SPSS 17.0 (SPSS Inc., Chicago, USA).

230

231   **3. Results**

232

233   *3.1. Growth characteristics and dendrochronological statistics*

234

235   Considering the common period 1949-2008, the mean ring width of the study species ranged

236   between 1.16 mm in *Aspidosperma* (partially shade-tolerant) to 2.37 mm in *Tabebuia* (long-lived

237   pioneers) (Table 2). *Acosmium*, *Aspidosperma* and *Zeyheria* had the highest first-order correlation

238   values in ring-width, whereas the highest mean sensitivity was observed in *Caesalpinia* and

239   *Zeyheria*. The mean correlation between the individual series of each species varied from 0.15 in

240   *Caesalpinia* to 0.26 in *Centrolobium*. The first two components of the Principal Components

241   Analysis accounted for 40.3% and 16.0% of the total growth variance (Fig. A.3). All species had

242   positive values in the first component indicating that they share high common growth variability in

243   response to climate.

244

245   *3.2. Relationships between climate and growth*

246

247   In all studied species the precipitation was positively related to growth, while temperatures

248   showed negative associations in five species (Fig. 2). Overall, the precipitation explained from

249   6.4% (*Caesalpinia*) to 22.0% (*Centrolobium* and *Zeyheria*) of the inter-annual variation in growth

250   indices, while temperature accounted for 7.1% (*Aspidosperma* and *Caesalpinia*) to 22.5%

251   (*Anadenanthera*) of that variation. In particular, *Caesalpinia* and *Aspidosperma* showed the lowest

252   number of significant correlation coefficients between climatic variables and ring-width indices. All

253   tree species showed time-dependent responses of growth indices to precipitation. Specifically,

10

254 *Acosmium*, *Anadenathera, Aspidosperma* and *Centrolobium* showed the highest correlation

255 coefficients at bimonthly scales, while *Caesalpinia*, *Tabebuia* and *Zeyheria* showed the highest

256 coefficients at longer scales (from six to nine months). In general, the strongest growth responses to

257 precipitation were observed for those months included within the wet season from November to

258 March, except in *Aspidosperma* where the highest correlation between growth indices and

259 precipitation occurred from April to May, i.e. during the transition from the wet to the dry season.

260 Regarding air temperature, *Tabebuia* and *Zeyheria* did not respond to temperature at any

261 analyzed time scale, while the emergent *Anadenathera* responded to temperature changes at

262 monthly to annual scales. The remaining species showed negative growth-index responses to

263 temperature from one to three months scales (Fig. 2). The highest correlations, in absolute terms,

264 were detected at monthly or trimonthly scales, mainly during the wet season, i.e. from November

265 and December (*Acosmium*, *Aspidosperma*, *Caesalpinia* and *Centrolobium*) up to January and March

266 (*Anadenathera*) (Fig. 2).

267

268 ***3.3. Relationships between the drought index and growth***

269

270 The strongest relationships observed between the SPEI and growth indices were always

271 positive irrespective of the analysed time scale indicating that growth is severely limited by water

272 deficit (Fig. 3). The highest correlations were recorded at bimonthly scales in *Aspidosperma* (r =

273 0.54) and *Acosmium* (r = 0.48), while *Tabebuia* presented the highest correlation (r = 0.42) at

274 seven-month scales (Fig. 3). The SPEI-growth correlations were usually observed for months of the

275 wet season (*Acosmium*, *Centrolobium, Caesalpinia*, *Anadenanthera*, *Tabebuia*) or during the

276 transition from the wet to the dry season (*Aspidosperma*, *Zeyheria*).

277 At long-time scales, the highest correlations between smoothed SPEI and growth data were

278 observed in *Anadenanthera* (r = 0.94) and *Aspidosperma* (r = 0.83) with smoothing parameters (α)

279 corresponding to 30- (α= 0.5) and 18-years (α= 0.3) long scales (Fig. 4). The remaining species

280　presented significant growth responses to SPEI at 12- (α= 0.2) and 6-years (α= 0.1) long scales,

281　excepting *Caesalpinia* which did not show any significant response (Fig. A.2). The SPEI explained

282　from 17.5% (*Anadenanthera*) to 28.9% (*Aspidosperma*) of the growth variance at short-time scales

283　(from two to seven months) while at long time scales (from six to 30 years) from 44.8% (*Tabebuia*)

284　to 87.9% (*Anadenathera*) of the growth variance was explained by that drought index (Figs. 3, 4).

285　　　There were statistically differences in tree-ring width for all species when comparing the four

286　long sub-periods with different SPEI values, excepting in the case of *Caesalpinia* ($F = 2.64$, $P =$

287　0.058). Lower tree-ring width values were observed in the two dry sub-periods (1960-1977, 1985-

288　2008), while the highest growth values occurred during the wettest and longest sub-period (1978-

289　1994) (Fig. 5).

290

291　**4. Discussion**

292

293　*4.1. The inter-annual precipitation partially explains the variation of the tree growth*

294　　　The different growth responses of the study species to precipitation can be quantified by

295　considering either (*i*) the timing or period when the strongest response to precipitation is observed

296　or (*ii*) the magnitude of that response, i.e. the value of the precipitation-growth correlation which

297　can be regarded as a surrogate of growth sensitivity to precipitation. We found that the strongest

298　responses of growth indices to precipitation and drought were observed in the wet season or during

299　the transition from the wet to the dry season, which implies that growth was constrained by water

300　availability. In TDFs, deciduous tree species show maximum rates of photosynthesis and hydraulic

301　conductivity during the wet season which agrees with our findings (Eamus and Prior, 2001).

302　However, we found diverse growth responses to water availability among coexisting tree species

303　indicating species-specific responses of wood formation to water availability in TDFs (Borchert,

304　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 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

13

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. A.1). Despite some of these growth responses to temperature may be caused by

14

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 (< 3ºC) in those areas. For example, *Juniperus procera* located at 9º N in Ethiopian TDFs (Sass-Klaassen et al., 2008) and *Zanthoxylum rhoifolium* located at 4º 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 16º S, showing an inter-monthly variability of temperature of about 5 ºC, 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 16º 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?

382   The drought index (SPEI) explained up to 28.9% of the year-to-year growth variance, which

383   suggests that the study species can buffer the negative effects of drought on radial growth at short

384   time scales. As mentioned before, TDF tree species may alleviate the negative effects of water

385   shortage on growth through induced or altered leafless period but they can also uptake water from

386   deep soils sources, increase their xylem resistance to cavitation or enhance water storage in the stem

387   and branch wood (Markesteijn, 2010). Our results suggest that these functional responses may be

388   rapid and translate into significant SPEI-growth associations recorded at relatively short time scales

389   (from two to seven months). This finding is concurrent with a global study which evidenced that in

390   arid biomes vegetation activity and growth mainly responded to drought at short-time scales

391   (Vicente-Serrano et al., 2013).

392   This short-time buffering and responses to drought contrast with the sensitivity to long-term

393   droughts as evidenced the notable increase in growth variance explained by SPEI at times scales

394   varying from six to 30 years, excepting *Caesalpinia*. In other drought-prone areas such as

395   Mediterranean forests it has been argued that these long-time growth responses to precipitation and

396   drought are linked to different accessibility of roots to soil water reserves located at different depths

397   (Sarris et al., 2007). Water located at deeper depths would be only readily accessible after long and

398   severe droughts for tree species with deep and efficient root systems. However, the high sensitivity

399   of wood formation to long-term droughts in most of the studied species suggests that they cannot

400   access the water from these deep layers to form wood or that there is a low availability of water in

401   those layers during consecutive dry years. Accordingly, in all species, excepting *Caesalpinia*, we

402   observed the lowest growth values during the two dry sub-periods (1960-1977, 1985-2008) whereas

403   the highest ring widths were observed during the wettest sub-periods (1978-1984). This indicates

404   that the long-term temporal variability of water availability drive the community growth dynamics

405   of TDFs, probably to a higher extent than in humid rainforests where radiation is the major

406   environmental driver of tree growth (Brienen et al., 2010b; Brienen and Zuidema, 2006). Tree

407   species may tolerate short-term annual droughts by using the same ecophysiological mechanisms

16

408   and traits to withstand the dry season (see Markesteijn et al., 2011), which is a main characteristic

409   of the TDFs (Bullock et al., 1995). However, these mechanisms seem not be very efficient in terms

410   of radial growth and productivity to deal with long-term droughts. In fact, long-lasting droughts

411   have been shown to negatively affect growth of the tree community in TDFs (Leigh Jr. et al., 1990)

412   and also in humid rainforests (Feeley et al., 2007; Phillips et al., 2009).

413   Among the study species, *Anadenanthera* was that showing a highest long-term growth

414   sensitivity to SPEI since this drought index explained almost 90% of growth variance. This would

415   indicate a high sensitivity of this species to long-term atmospheric water demand. In contrast,

416   *Caesalpinia* growth did not respond to long-term SPEI variability, suggesting that this species may

417   tolerate severe and lasting droughts. Further, the low production of sapwood of the latter species,

418   which is also observed in other Fabaceae (Reyes-García et al., 2012), could also be related with a

419   low water demand. The dense wood of *Caesalpinia* also confers it a low potential hydraulic

420   conductance (cf., Kallarackal et al., 2013). The low sensitivity to long-term droughts of *Caesalpinia*

421   is consistent with observations done in lowland Amazonian forests where species with denser wood

422   were less vulnerable to drought and may become dominant after long periods of water deficit

423   (Phillips et al., 2010).

424

425   **5. Conclusions**

426

427   Precipitation enhanced tree growth of all TDF study species, mainly when water availability

428   increased during the wet season, while temperature was negatively related to growth in five out of

429   seven species. Tree growth responses to precipitation peaked at short time scales (from two to nine

430   months). Species with low-density wood and high production of sapwood (e.g., *Zeyheria*) were the

431   most sensitive in terms of growth responses to precipitation variability, whereas species with the

432   opposite characteristics (e.g., *Caesalpinia*) were the least sensitive ones. The emergent

433   *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.

455   **References**

456   Biondi, F., Waikul, K., 2004. DENDROCLIM2002: A C++ program for statistical calibration of

457   climate signals in tree-ring chronologies. Comput. Geosci. 30, 303–311.

458   Borchert, R., 1994. Soil and stem water storage determine phenology and distribution of tropical

459   dry forest trees. Ecology 75, 1437–1449.

460   Borchert, R., 1999. Climatic periodicity, phenology, and cambium activity in tropical dry forest

461   trees. IAWA J. 20, 239–247.

462   Borchert, R., Rivera, G., Hagnauer, W., 2002. Modification of vegetative phenology in a tropical

463   semi-deciduous forest by abnormal drought and rain. Biotropica 34, 27–39.

464   Brando, P.M., Nepstad, D.C., Davidson, E.A., Trumbore, S.E., Ray, D., Camargo, P., 2008.

465   Drought effects on litterfall, wood production and belowground carbon cycling in an

466   Amazon forest: results of a throughfall reduction experiment. Philos. Trans. R. Soc. B

467   Biol. Sci. 363, 1839–1848.

468   Brienen, R.J.W., Lebrija-Trejos, E., Zuidema, P.A., Martínez-Ramos, M., 2010a. Climate-growth

469   analysis for a Mexican dry forest tree shows strong impact of sea surface temperatures

470   and predicts future growth declines. Global Change Biol. 16, 2001–2012.

471   Brienen, R.J.W., Zuidema, P.A., 2005. Relating tree growth to rainfall in Bolivian rain forests: a

472   test for six species using tree ring analysis. Oecologia 146, 1–12.

473   Brienen, R.J.W., Zuidema, P.A., 2006. Lifetime growth patterns and ages of Bolivian rain forest

474   trees obtained by tree ring analysis. J. Ecol. 94, 481–493.

475   Brienen, R.J.W., Zuidema, P., Martínez-Ramos, M., 2010b. Attaining the canopy in dry and

476   moist tropical forests: strong differences in tree growth trajectories reflect variation in

477   growing conditions. Oecologia 163, 485–496.

478 Briffa, K.R., Jones, P.D., 1990. Basic chronology statistics and assessment, in: Cook, E.R.,

479   Kairiukstis, L.A. (Eds.), Methods of Dendrochronology: Applications in the

480   Environmental Sciences. Kluwer Academic Publishers, Dordrecht, pp. 137–152.

481 Brodribb, T.J., Holbrook N.M., Gutierrez M.V. 2002 Hydraulic and photosynthetic co-ordination

482   in seasonally dry tropical forest trees. Plant Cell Env. 25, 1435–1444.

483 Bullock, S.H., Mooney, H.A., Medina, E., 1995. Seasonally dry tropical forest. Cambridge

484   University Press, Cambridge.

485 Clark, D.A., Clark, D.B., 2010. Assessing tropical forests' climatic sensitivities with long-term

486   data. Biotropica 43, 31–40.

487 Clark, D.B., Clark, D.A., Oberbauer, S.F., 2010. Annual wood production in a tropical rain forest

488   in NE Costa Rica linked to climatic variation but not to increasing CO_2. Global Change

489   Biol. 16, 747–759.

490 Cleveland, W.S., 1979. Robust locally weighted regression and smoothing scatterplots. J. Am.

491   Stat. Assoc. 74, 829–836.

492 Cook, E.R., 1985. A time series approach to tree-ring standardization. PhD Thesis. University of

493   Arizona,Tucson.

494 Cook, E.R., Krusic, P., 2007. ARSTAN 41d. A Tree-ring standardization program based on

495   detrending and autoregressive time series modeling, with interactive graphics. URL

496   https://www.ldeo.columbia.edu/tree-ring-laboratory/resources/software. [accessed 20

497   August 2013].

498 Dirzo, R., Young, H.S., Monney, H.A., Ceballos, G., 2011. Seasonally dry tropical forest:

499   Ecology and conservation. Island Press, Washington.

500 Dong, S.X., Davies, S.J., Ashton, P.S., Bunyavejchewin, S., Supardi, M.N.N., Kassim, A.R., Tan,

501   S., Moorcroft, P.R., 2012. Variability in solar radiation and temperature explains observed

502   patterns and trends in tree growth rates across four tropical forests. Proc. R. Soc. B Biol.

503   Sci. 279, 3923–3931.

504 Drew, D.M., Allen, K., Downes, G.M., Evans, R., Battaglia, M., Baker, P., 2012. Wood

505   properties in a long-lived conifer reveal strong climate signals where ring-width series do

506   not. Tree Physiol. 33, 37–47.

507 Eamus, D., 1999. Ecophysiological traits of deciduous and evergreen woody species in the

508   seasonally dry tropics. Trends Ecol. Evol. 14, 11–16.

509 Eamus, D., Prior, L., 2001. Ecophysiology of trees of seasonally dry tropics: Comparisons among

510   phenologies, in: Caswell H. (Ed), Advances in Ecological Research, Volume 32.

511   Academic Press, London, pp. 113–197.

512 Enquist, B.J., Leffler, A.J., 2001. Long-term tree ring chronologies from sympatric tropical dry-

513   forest trees: Individualistic responses to climatic variation. J. Trop. Ecol. 17, 41–60.

514 Feeley, K.J., Joseph Wright, S., Nur Supardi, M.N., Kassim, A.R., Davies, S.J., 2007.

515   Decelerating growth in tropical forest trees. Ecol. Lett. 10, 461–469.

516 Friedman, J.H., 1984. A variable span smoother. Lab. Comput. Stat. Stanf. Univ. Tec. Rep. N° 5.

517 Goldsmith, G.R., Muñoz-Villers, L.E., Holwerda, F., McDonnell, J.J., Asbjornsen, H., Dawson,

518   T.E., 2012. Stable isotopes reveal linkages among ecohydrological processes in a

519   seasonally dry tropical montane cloud forest. Ecohydrol. 5, 779–790

520 Holmes, R.L., 1983. Computer-assisted quality control in tree-ring dating and measurement.

521   Tree-Ring Bull. 43, 69–78.

522 IPCC, 2007. Solomon, S., Qin D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor,

523   M., Miller H.L. (Eds.), Climate change 2007: the physical science basis. Contribution of

524   Working Group I to the fourth assessment report of the Intergovernmental Panel on

525   Climate Change. Cambridge University Press. Cambridge & New York.

526   Janzen, D.H., 1988. Tropical dry forest: the most endangered major tropical ecosystem, in:

527   Wilson, E.O. (Ed.), Biodiversity. National Academy Press, Washington, pp. 130–137.

528   Kallarackal, J., Otieno, D.O., Reineking, B., Jung, E.-Y., Schmidt, M.W.T., Granier, A.,

529   Tenhunen, J.D., 2013. Functional convergence in water use of trees from different

530   geographical regions: a meta-analysis. Trees 3, 787–799.

531   Killeen, T.J., Jardim, A., Mamani, F., Rojas, N., 1998. Diversity, composition and structure of a

532   tropical semideciduous forest in the Chiquitanía region of Santa Cruz, Bolivia. J. Trop.

533   Ecol. 14, 803–827.

534   Leigh Jr., E.G., Windsor, D.M., Rand, A.S., Foster, R.B., 1990. The impact of the "El Niño"

535   drought of 1982-83 on a Panamanian semideciduous forest. Elsevier Ocean. Ser. 52, 473–

536   486.

537   Lewis, S.L., 2006. Tropical forests and the changing earth system. Philos. Trans. R. Soc. B Biol.

538   Sci. 361, 195–210.

539   López, L., Villalba, R., 2011. Climate influences on the radial growth of *Centrolobium*

540   *microchaete*, a valuable timber species from the tropical dry forests in Bolivia. Biotropica

541   43, 41–49.

542   Macias-Fauria, M., Grinsted, A., Helama, S., Holopainen, J., 2012. Persistence matters:

543   Estimation of the statistical significance of paleoclimatic reconstruction statistics from

544   autocorrelated time series. Dendrochronologia 30, 179–187.

545   Markesteijn, L., 2010. Drought tolerance of tropical tree species: Functional traits, trade-offs and

546   species distribution. PhD Thesis, Wageningen University, Wageningen.

547   Markesteijn, L., Poorter, L., Bongers, F., Paz, H., Sack, L., 2011. Hydraulics and life history of

548   tropical dry forest tree species: coordination of species' drought and shade tolerance. New

549   Phytol. 191, 480–495.

550 Meinzer, C., Andrade, J.L., Goldstein, G., Holbrook, N.M., Cavelier, J., Wright, S. J. 1999.

551 Partitioning of soil water among canopy trees in a seasonally dry tropical forest.

552 Oecologia 121: 293–301.

553 Mendivelso, H.A., Camarero, J.J., Royo, O., Gutierrez, E., Toledo, M., 2013. Differential growth

554 responses to water balance of coexisting deciduous tree species are linked to wood density

555 in a Bolivian tropical dry forest. PLoS ONE DOI: 10.1371/journal.pone.0073855.

556 Mostacedo, B., 2007. Natural regeneration of canopy trees in a tropical dry forest in Bolivia. PhD

557 Thesis, University of Florida, Gainesville.

558 Paredes-Villanueva, K., Sánchez-Salguero, R., Manzanedo, R.D., Quevedo-Sopepi, R., Palacios,

559 G., Navarro-Cerrillo, R.M., 2013. Growth rate and climatic response of *Machaerium*

560 *scleroxylon* in a dry tropical forest in southeastern Santa Cruz, Bolivia. Tree-Ring Res.

561 69, 63–79.

562 Pasho, E., Camarero, J.J., de Luis, M., Vicente-Serrano, S.M., 2011. Impacts of drought at

563 different time scales on forest growth across a wide climatic gradient in north-eastern

564 Spain. Agric. For. Meteorol. 151, 1800–1811.

565 Perneger, T.V., 1998. What´s wrong with Bonferroni adjustments. Br. Med. J. 316, 1236–1238.

566 Phillips, O.L., Aragão, L.E.O.C., Lewis, S.L., Fisher, J.B., Lloyd, J., et al., 2009. Drought

567 sensitivity of the Amazon rainforest. Science 323, 1344–1347.

568 Phillips, O.L., van der Heijden, G., Lewis, S.L., López-González, G., Aragão, L.E.O.C., et al.,

569 2010. Drought–mortality relationships for tropical forests scales. Preprints, Eighth Conf.

570 on Applied Climatology. New Phytol. 187, 631–646.

571 Reyes-García, C., Andrade, J.L., Simá, J.L., Us-Santamaría, R., Jackson, P.C., 2012. Sapwood to

572 heartwood ratio affects whole-tree water use in dry forest legume and non-legume trees.

573 Trees 26, 1317–1330.

574   Rinn, F., 1996. TSAP (Time Series Analysis and Presentation). Version 3.0. RinnTech,

575   Heidelberg.

576   Ronchail, J., 1995. Variabilidad interanual de las precipitaciones en Bolivia. Bull. Inst. Fr. Études

577   Andin. 24, 369–378.

578   Rozendaal, D.M.A., Zuidema, P.A., 2011. Dendroecology in the tropics: a review. Trees 25, 3–

579   16.

580   Sarris, D., Christodoulakis, D., Körner, C., 2007. Recent decline in precipitation and tree growth

581   in the eastern Mediterranean. Global Change Biol. 13, 1187–1200.

582   Sass-Klaassen, U., Couralet, C., Sahle, Sterck, F.J., 2008. Juniper from Ethiopia contains a large-

583   scale precipitation signal. Int. J. Plant Sci. 169, 1057–1065.

584   Schulman, E., 1956. Dendroclimatic change in semiarid America. University of Arizona Press,

585   Tucson.

586   Stahle, D.W., Mushove, P.T., Cleaveland, M.K., Roig, F., Haynes, G.A., 1999. Management

587   implications of annual growth rings in Pterocarpus angolensis from Zimbabwe. For. Ecol.

588   Manag. 124, 217–229.

589   Vicente-Serrano, S.M., Beguería, S., López-Moreno, J.I., 2010. A multiscalar drought index

590   sensitive to global warming: The standardized precipitation evapotranspiration index. J.

591   Clim. 23, 1696–1718.

592   Vicente-Serrano, S.M., Gouveia, C., Camarero, J.J., Beguería, S., Trigo, R., López-Moreno, J.I.,

593   Azorín-Molina, C., Pasho, E., Lorenzo-Lacruz, J., Revuelto, J., Morán-Tejeda, E.,

594   Sanchez-Lorenzo, A., 2013. Response of vegetation to drought time-scales across global

595   land biomes. Proc. Natl. Acad. Sci. USA 110, 52–57.

596 Villegas, Z., Peña-Claros, M., Mostacedo, B., Alarcón, A., J.C.Licona, Leaño, C., Pariona, W.,

597   Choque, U., 2009. Silvicultural treatments enhance growth rates of future crop trees in a

598   tropical dry forest. For. Ecol. Manag. 258, 971–977.

599 Wigley, T.M.L., Briffa, K.R., Jones, P.D., 1984. On the average value of correlated time series,

600   with applications in Dendroclimatology and Hydrometeorology. J. Clim. Appl. Meteorol.

601   23, 201–213.

602 Worbes, M., 1999. Annual growth rings, rainfall-dependent growth and long-term growth

603   patterns of tropical trees from the Caparo Forest Reserve in Venezuela. J. Ecol. 87, 391–

604   403.

605 Worbes, M., 2002. One hundred years of tree-ring research in the tropics - a brief history and an

606   outlook to future challenges. Dendrochronologia 20, 217–231.

607 Worbes, M., Blanchart, S., Fichtler, E., 2013. Relations between water balance, wood traits and

608   phenological behavior of tree species from a tropical dry forest in Costa Rica - a

609   multifactorial study. Tree Physiol. 33, 527–536.

610 Zhao, M., Running, S.W., 2010. Drought-induced reduction in Global Terrestrial Net Primary

611   Production from 2000 through 2009. Science 329, 940–943.

612 Zuidema, P.A., Baker, P.J., Groenendijk, P., Schippers, P., van der Sleen, P., Vlam, M., Sterck,

613   F., 2013. Tropical forests and global change: filling knowledge gaps. Trends Plant Sci.

614   18, 413–419.

Table legends

617　**Table 1.** Characteristics of the seven tree species studied in a Bolivian tropical dry forest. Values

618　are means ± 1 SE.

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

619　Crown position, functional group and some leafless period data were taken from Mostacedo
620　(2007) and Villegas et al. 2009, whereas the leafless period, wood density and sapwood area were
621　taken from Mendivelso et al. (2013). Abbreviations: C. Canopy; Sc, Sub canopy; E, Emergent;
622　LLP, long-lived pioneers; TST totally shade-tolerant, PST, partially shade-tolerant.

630   **Table 2.** Dendrochronological statistics of the seven tree species studied in a Bolivian tropical

631   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

632

633   Statistics: AC1, the first-order autocorrelation of ring-width series; MSx, mean sensitivity; R-bar,

634   mean interseries correlation; EPS, expressed population signal.

635   **Figure legends**
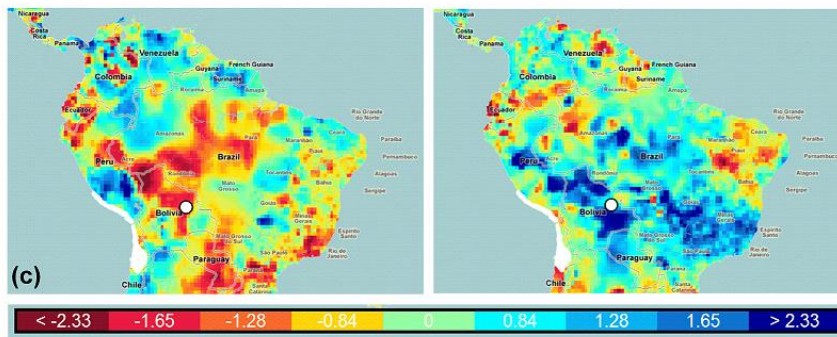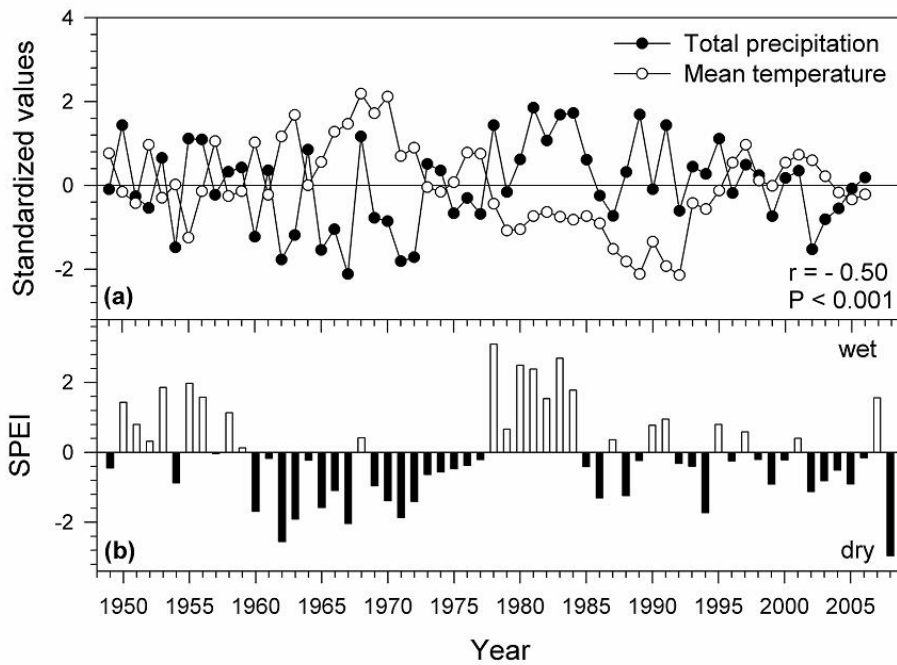
636

637   **Fig. 1.** Temporal (a and b) and spatial (c) patterns of climatic and drought variability in the study

638   area. In the upper graph the relationship between the standardized temperature and precipitation

639   values is indicated with its corrected probability value. The lower maps (obtained from

641   Standardized Precipitation Evapotranspiration Index (SPEI) for a dry (1962, left map) and a wet

642   (1981, right map) year across southern America (the white circle indicates the location of the

643   study area). The lower color scale shows the SPEI classes with red and blue colors corresponding

644   to negative (dry conditions) and positive SPEI values (wet conditions), respectively. The maps

645   and the time series show the 12-months SPEI calculated for September (for interpretation of the

646   references to color in this figure legend, the reader is referred to the web version of the article).

647
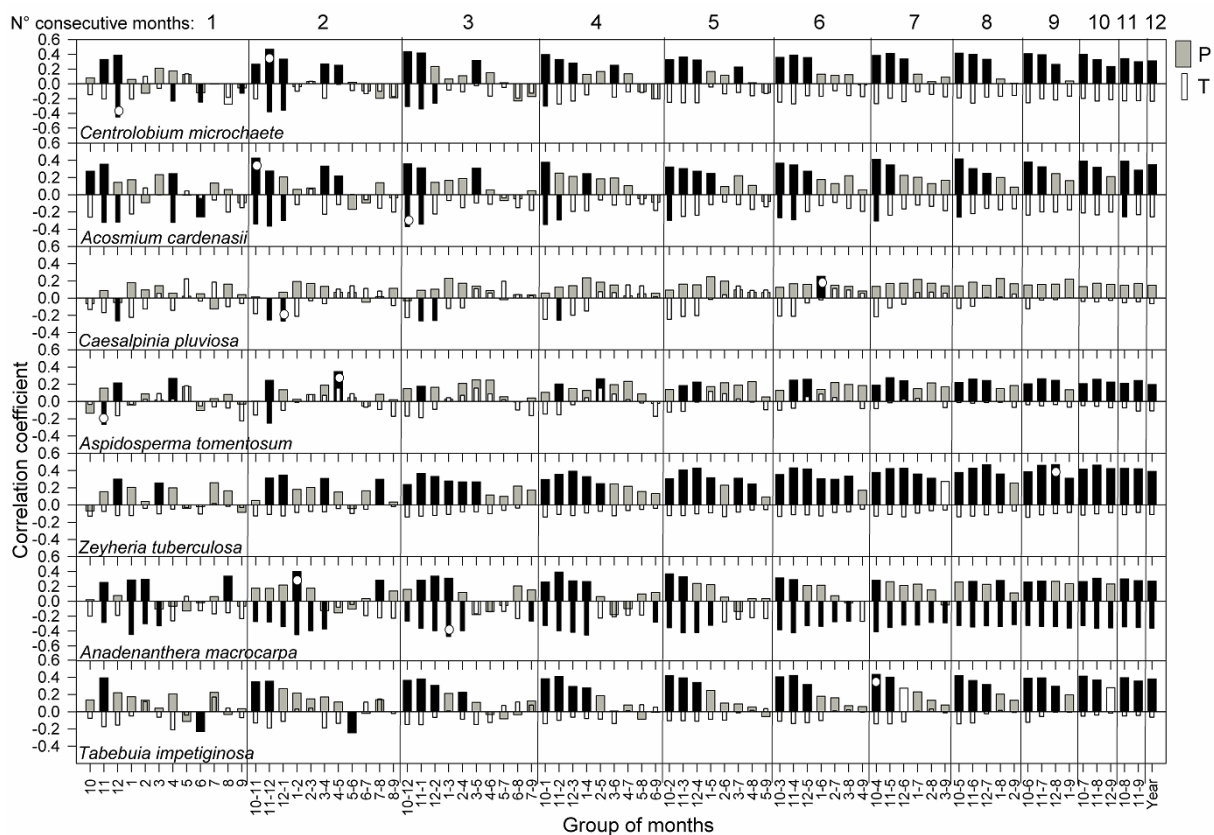
Fig. 2. Correlations (Pearson coefficients) calculated between climatic variables (P, total

649   precipitation, wide grey bars; T, mean temperature, thin empty bars) and residual tree-ring width

650   chronologies for the common period 1949-2008. The month or group of months used for

651   computing climate data are indicated by numbers in the lowermost *x* axis and they are arranged

652   considering consecutive months (from 1 to 12 months, see uppermost *x* axis). Climatic variables

653   were summed (P) or averaged (T). Significant bootstrapped correlations are indicated by black

654   columns and the highest correlations are highlighted by white circles.
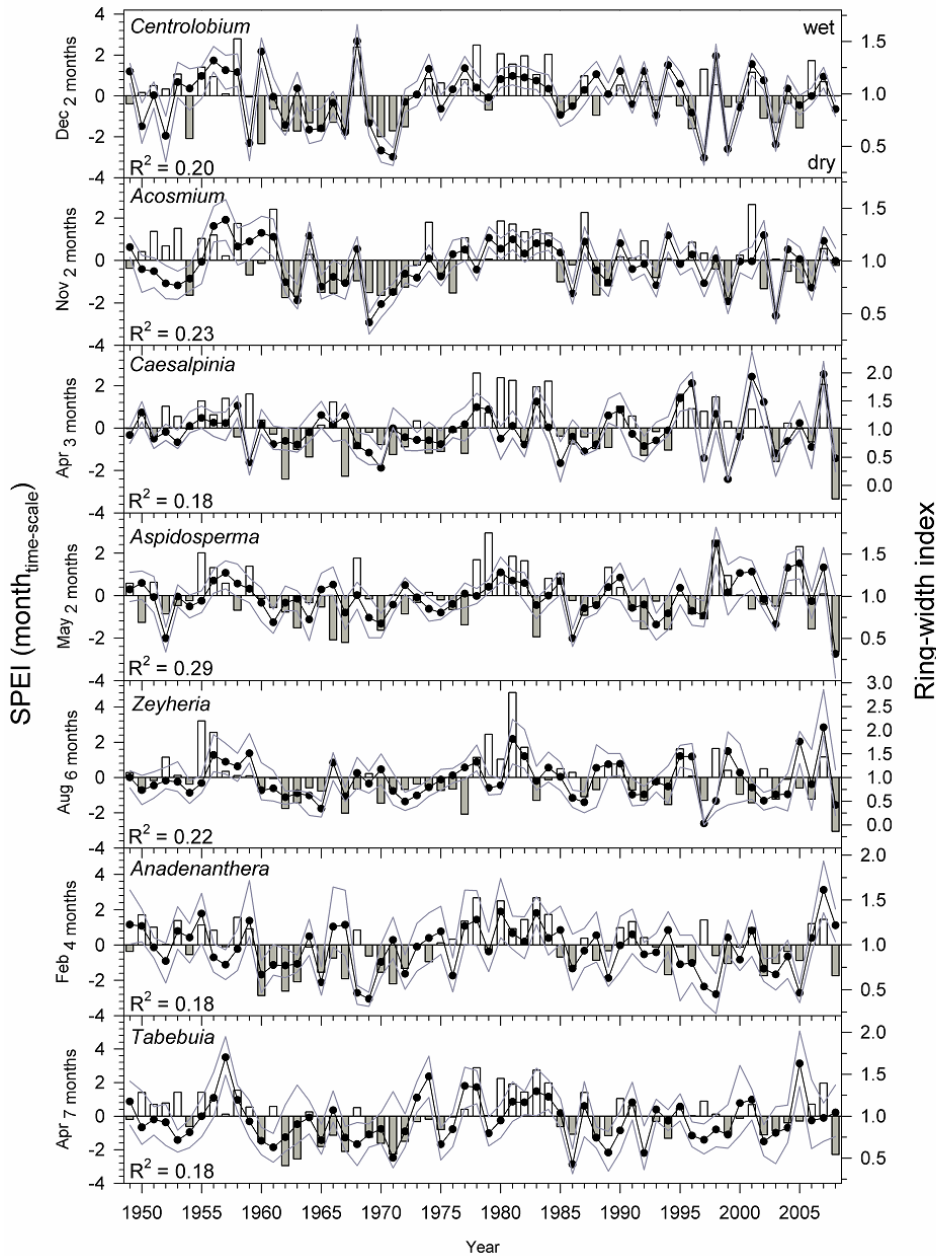

655

656   **Fig. 3.** Highest correlations found between residual ring-width chronologies (lines with symbols

657   and bootstrapped 95% confidence limits) and SPEI (bars). The month and time-scales

658   (subscripts) where the highest correlation was found is shown on the y axis labels for each

659　species. Positive and negative SPEI values correspond to wet (empty bars) and dry (filled bars)

660　conditions, respectively. All presented coefficients of determination have $P < 0.05$.
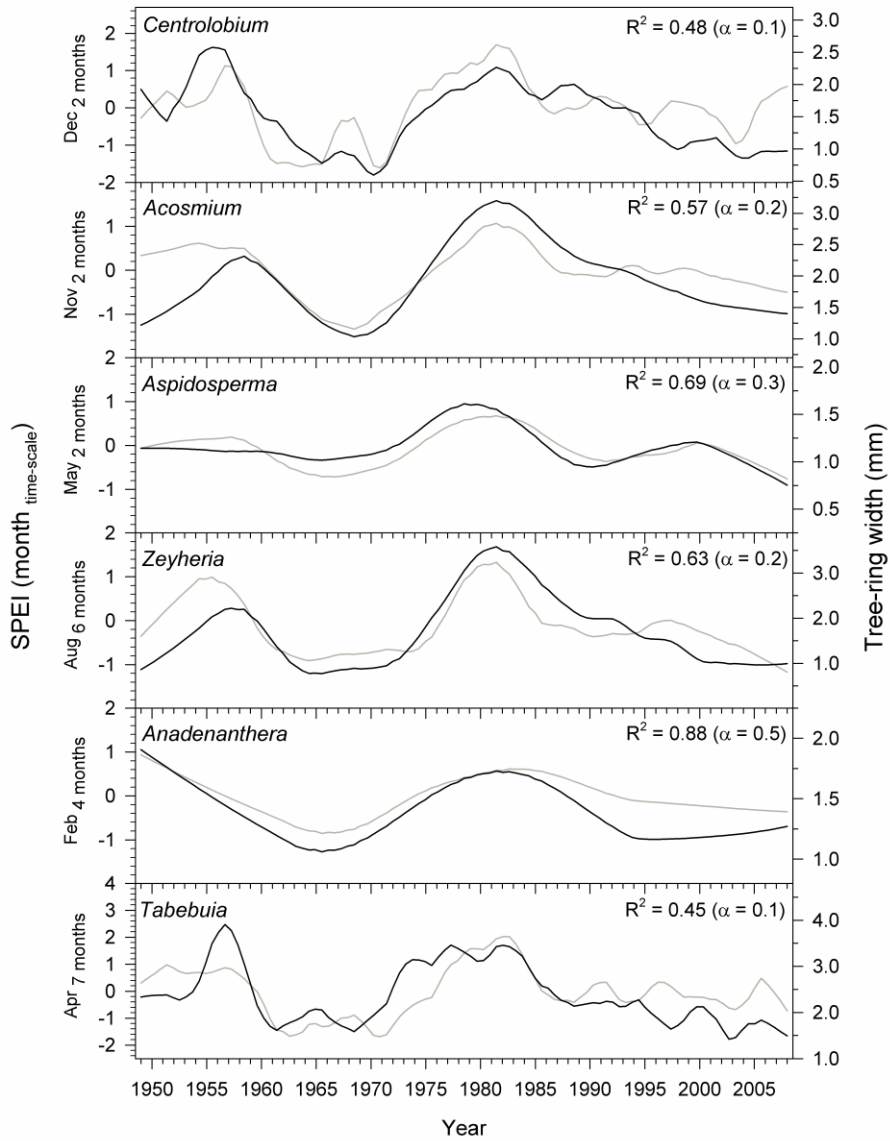
661

662　**Fig. 4.** Highest long-term relationship found between tree-ring widths (black lines) and drought

663　severity assessed through the SPEI (gray lines). All presented coefficients of determination have

664     $P < 0.05$. The smoothing parameter (α) gives the proportion of the displayed period (1949-2008,

665   59 years) considered by the LOESS smoother (e.g., $\alpha = 0.5$ is equivalent to a 30-year long

666   period). *Caesalpinia* is not shown because it was not observed any statistically significant long-

667   term association between growth and the SPEI drought index (see Fig. A2).
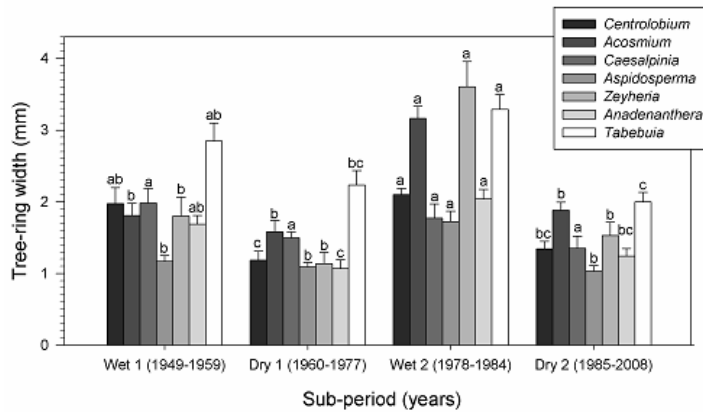
668

669   **Fig. 5.** Comparison of mean tree-ring widths (mean ± 1SE) obtained for the four sub-periods with

670   contrasting drought severity (two wet sub-periods and two dry sub-periods) as assessed by the

671   SPEI. Columns with different letters correspond to means showing significantly differences in

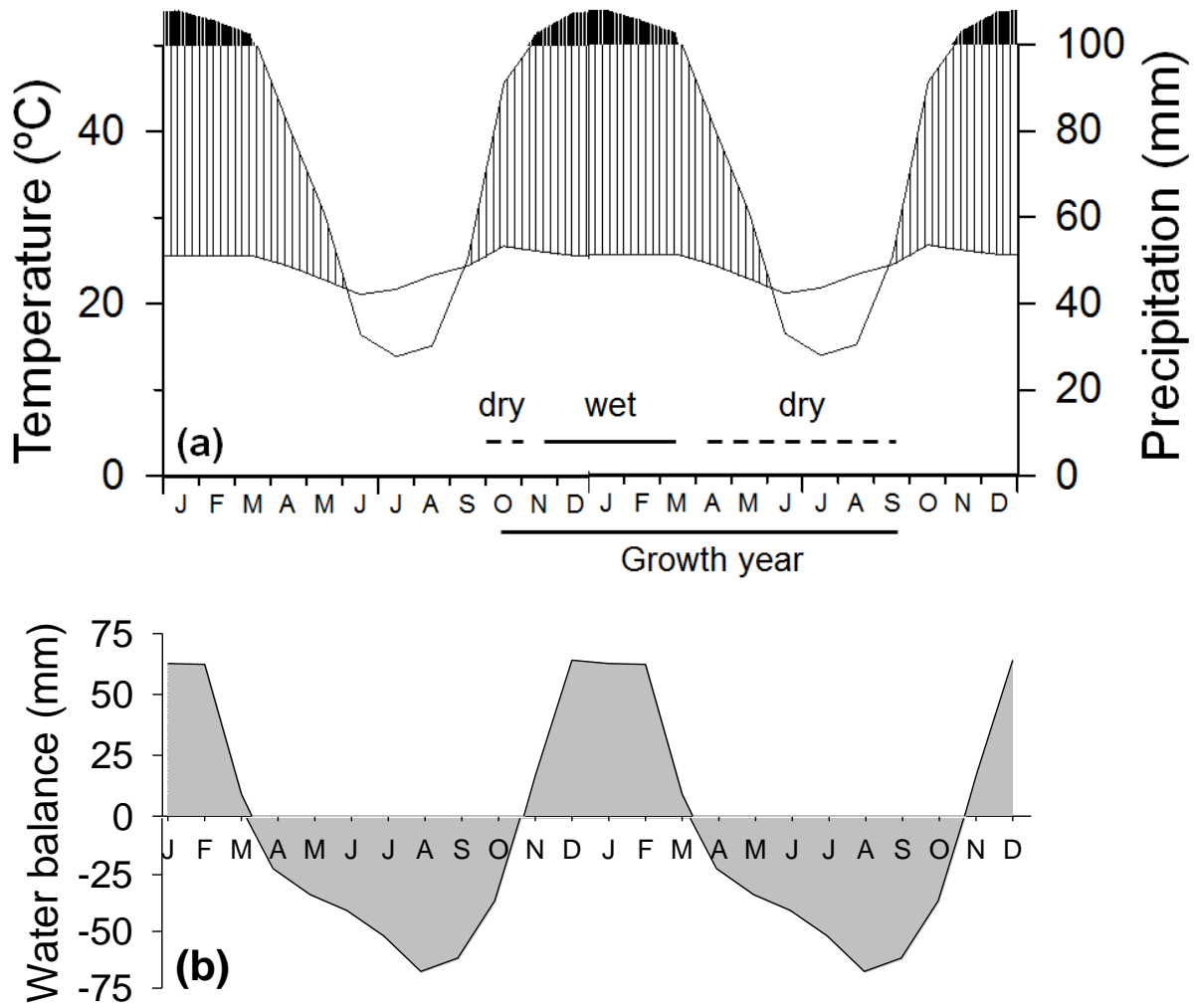672   tree-ring width between sub-periods for the same species ($P < 0.05$).

Figure A1. Climate diagram of the study area (a) and estimated monthly water balance (b), i.e. the difference between precipitation and potential evapotranspiration. Data were obtained for Concepción station (16° 15' S, 62° 06' W) considering the period 1949-2008. Tree growth year goes from October to September. The wet season is indicated by solid line and dry season by dotted lines.
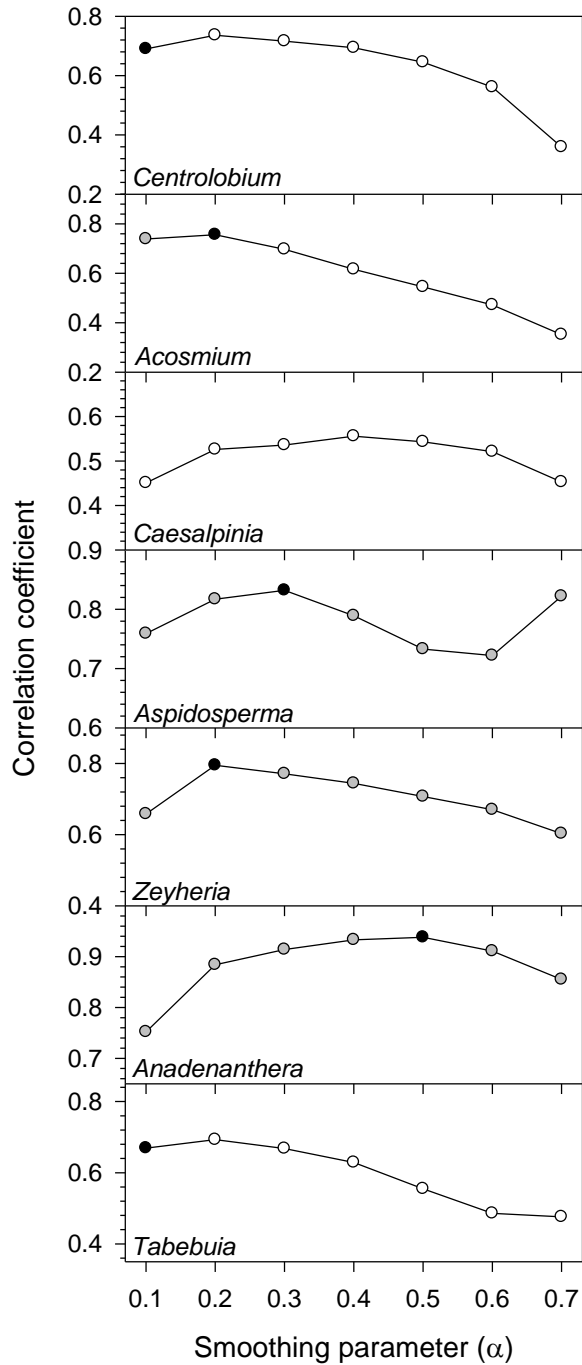
Figure A2. Relationships (Pearson correlation coefficients) calculated between smoothed tree-ring width and drought index (SPEI) series considering the seven study species and the period 1949-2008. Correlations were obtained for different smoothing parameters ($\alpha = 0.1, 0.2, 0.3, 0.4, 0.5, 0.6$ and 0.7, which are equivalent to 6, 12, 18, 24, 30, 36 and 42-year long scales). Significant correlations ($P < 0.05$) are indicated by gray symbols and the highest correlation is indicated by a black symbol.

1
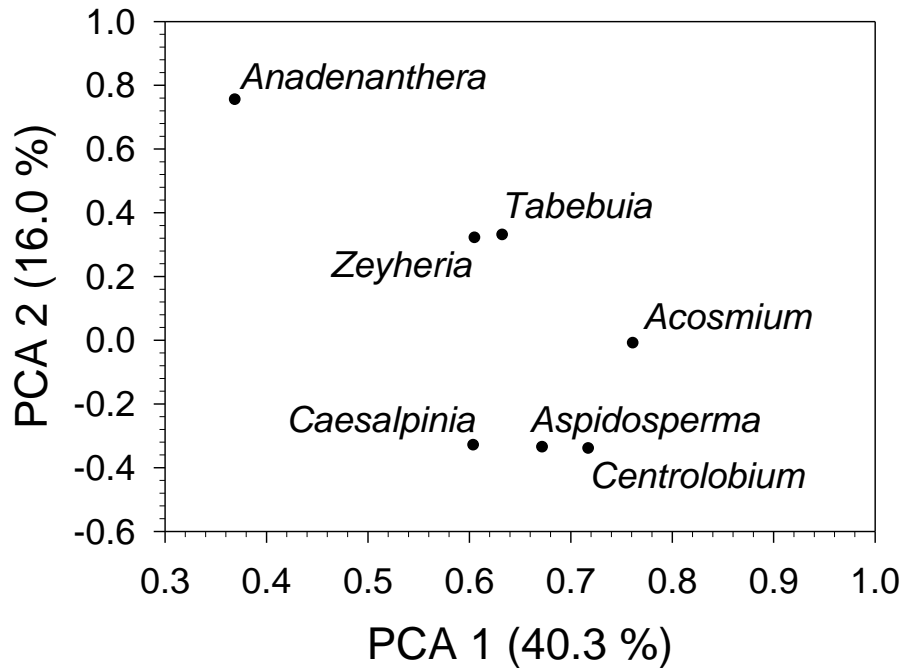
Figure A3. Graphical summary of the seven tree species' scores considering the first two components of a Principal Component Analysis calculated on the covariance matrix of the residual ring-width series for the common period 1949-2008.

Abbreviations

6 TDF   Tropical dry forest

7 SPEI   Standardized Precipitation Evapotranspiration Index

8 AC1   First-order autocorrelation of tree-ring width series

9 MSx   Mean sensitivity

10 R-bar Mean interseries correlation

11 EPS   Expressed Population Signal