

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

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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 multiscale 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.

47 **1. Introduction**

48

49 More severe and longer droughts have been observed since the 1970s over tropical and
50 subtropical areas according to the IPCC (2007), and such drying trend has been linked to higher
51 temperatures and increased evaporation. A plausible warmer world with longer and more severe
52 droughts could lead to rapid collapse of tropical forest communities converting them from a net
53 carbon sink into a large carbon source with cascading ecosystem effects affecting global climate-
54 vegetation feedbacks (Lewis, 2006). For instance, severe droughts during the 2000s reduced the net
55 primary production (NPP) in most Neotropical forests (Phillips et al., 2009; Zhao and Running,
56 2010), being the wood production the most sensitive component of above-ground NPP to the water
57 deficit reduction (Brando et al., 2008). To resolve part of the uncertainty linked to the climate-
58 drought-forest feedbacks we should advance on the understanding of the long-term impacts of
59 droughts on the functioning of tropical forest communities.

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

98 **2. Materials and methods**

99

100 **2.1. Study site**

101

102 The study site is a lowland and seasonally deciduous TDF located 32 km away from
103 Concepción in eastern Bolivia (Fig. 1). The study site (16° 07' S, 61° 43' W, mean elevation of 380
104 m) is found in a private property of a certified timber company (INPA Parket). This site is also
105 included within the network of long-term research sites of the Instituto Boliviano de Investigación
106 Forestal. The study site belongs to the Chiquitano forest formation, which is considered one of the
107 largest and most diverse TDFs occupying ca. 16.4 millions of ha. in Bolivia. Chiquitano forests are
108 located in the transition of the Amazonian lowland evergreen rain forest in the north and the Chaco
109 shrub dry formations towards the south (Killeen et al., 1998). The study site is situated on the
110 Precambrian Brazilian shield and the soils are acid (pH = 5.8), present low organic matter contents
111 (1.42%), and have a sandy-loam texture. The studied forest has an average tree richness of 34
112 species ha⁻¹, a mean stem density of 437 trees ha⁻¹, and a mean basal area of 19.7 m² ha⁻¹, while
113 average canopy height ranges between 20 and 25 m (Mostacedo, 2007; Villegas et al., 2009).

114 Monthly climatic data (mean air temperature, total precipitation) were obtained from the
115 Concepción station (16° 15' S, 62° 06' W; 410 m a.s.l., period 1949-2009), located about 35 km
116 from the study site. At this station the mean annual temperature is 24.3° C and the mean total
117 precipitation is 1160 mm. The wet period goes from November to March but the highest rainfall
118 amount is recorded between December and February. The driest period normally goes from June to
119 September but the potential evapotranspiration exceeds precipitation from April to October (Fig.
120 A.1).

121

122 **2.2. Tree species**

123

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

133

134 **2.3. Field sampling and sample preparation**

135

136 Wood discs were collected from 7-14 living and dominant trees per species with diameters at
137 1.3 m bigger than 20 cm (Table 2), which were felled for timber collection in 2010 and 2011 (see
138 more details on sampling methods in Mendivelso et al., 2013). In the laboratory, the wood discs
139 were air-dried and polished using sandpapers with increasing grit until the tree rings were clearly
140 visible.

141

142 **2.4. Dendrochronological methods**

143

144 Tree-ring series were visually cross-dated by comparing and detecting characteristic rings
145 among radii of the same tree and then by matching the series from different trees of the same
146 species. We measured the ring widths from the most recent ring up to the pith along three to four
147 radii per disc, separated by 90-120° to account for: (i) the eccentric growth of most discs and (ii) the
148 within-tree (among radii) growth variability. Hence, the mean value of the ring widths measured
149 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 confidence 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-order
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 (\bar{R}), 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 $EPS \geq 0.80$ (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://oxlcl.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, $\text{SPEI} = 0.7 \pm 0.3$) was less wet (Tukey $t =$
226 1.38 , $P = 0.014$) than the second one (1978-1994, $\text{SPEI} = 2.1 \pm 0.3$), while the first dry long-period
227 (1960-1977, $\text{SPEI} = -1.0 \pm 0.2$) was not significantly drier than the last one (1985-2008, $\text{SPEI} = -0.7$

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,

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- ($\alpha = 0.5$) and 18-years ($\alpha = 0.3$) long scales (Fig. 4). The remaining species

280 presented significant growth responses to SPEI at 12- ($\alpha= 0.2$) and 6-years ($\alpha= 0.1$) 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% (*Anadenanthera*) 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).

305 Several species' growth reacted to water availability during the early wet season from
306 November to December (*Acosmium*, *Centrolobium*, *Tabebuia*, *Zeyheria*) indicating a rapid growth
307 increment in response to the increase of water availability. This could be related to efficient root
308 and hydraulic systems which rapidly capture and transport water to the buds triggering the flush of
309 new leaves and the beginning of the production of new xylem cells. In the other species studied,
310 growth indices responded to precipitation in the mid to late wet season or even in the transition to
311 the dry season despite they flushed in October (*Aspidosperma*, *Caesalpinia*) or November
312 (*Anadenanthera*). This lagged response suggests a long process to rehydrate the xylem and
313 reactivate cambial activity (Borchert, 1999). The rapid production of new leaves in the early wet
314 season suggests the existence of efficient shallow roots. In TDFs the upper soil layers are the main
315 source of water captured by root systems of adult trees (Meinzer et al., 1999; Goldsmith et al.,
316 2012) which indicates that rooting depth may not be a major trait determining growth responses to
317 precipitation.

318 The most and least responsive species in terms of growth-index associations with precipitation
319 were *Centrolobium* and *Zeyheria*, and *Caesalpinia*, respectively. The most sensitive species
320 responding to precipitation require more water and a more efficient water transport for growth than
321 less sensitive species. In TDFs deciduous tree species show more variable hydraulic-conductivity
322 patterns than brevi-deciduous or evergreen species (Brodribb et al., 2002). According to these
323 authors, during the transition from the dry to the wet season, a first group of deciduous species
324 exhibit huge changes in their stem hydraulic conductivity, while a second group of deciduous and
325 evergreen species show minor changes. We consider that *Centrolobium* and *Zeyheria*, species
326 showing the highest growth sensitivity to precipitation, can exhibit hydraulic patterns similar to
327 those reported by Brodribb et al. (2002) for the first deciduous tree species, whereas the least
328 sensitive species (*Caesalpinia*) could behave similarly to the second group of species. In fact, the
329 wood densities of *Centrolobium* and *Zeyheria* are within the optimum range for hydraulic
330 efficiency reported by Kallarackal et al. (2013). Moreover, the different sensitiveness to

331 precipitation can be related to traits determining water use and storage. TDF tree species which
332 have a less dense wood and produce more sapwood (p.e. *Zeyheria*) may store more water in their
333 stems, therefore these species should show a high sensitivity in terms of growth changes to water
334 availability (compare Table 1 and Fig. 2; see also Mendivelso et al. 2013). Species showing the
335 reverse characteristics (denser wood and less sapwood) could store less water therefore should be
336 the least responsive to water availability (p.e. *Caesalpinia*).

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

351

352 ***4.2. Relationships between growth and temperature in TDFs: a latitudinal effect***

353

354 We observed negative responses of growth indices to air temperature in five species mainly at
355 monthly or trimonthly scales during the wet season, when the highest mean temperatures are
356 registered (Fig. A.1). Despite some of these growth responses to temperature may be caused by

357 indirect effects on evaporative forcing our analyses based on the SPEI drought index already
358 accounted for those effects. In terms of growth responsiveness *Anadenanthera* was the most
359 sensitive species to temperature which may be related to the fact that it is an emergent species
360 whose crowns are usually completely exposed to elevated radiation levels.

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

378

379 ***4.3. Drought-growth associations at different time scales: short-term tolerance vs. long-term***
380 ***sensitivity?***

381

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 (Markestijn, 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

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

434 species showed negative growth responses to temperature at short-time scales (from one to three
435 months), again chiefly during the wet season. Growth responded positively to less dry conditions at
436 short (from two to seven months) and long-time scales (from six to 30 years). Temporal variability
437 in water availability drives growth community dynamics of the study TDF at different time scales.
438 Tree species tolerate short-term droughts while growth is particularly sensitive to long-lasting
439 droughts, excepting *Caesalpinia*. The time-dependent growth response to climate and drought
440 should be treated as an additional constraint of community growth dynamics to properly forecast the
441 responses of TDFs to climate warming.

442

443 **Acknowledgements**

444 We thank all the staff and students of the Instituto Boliviano de Investigación Forestal for their
445 support, particularly M. Toledo and V. Vroomans. We sincerely acknowledge P. Roosenboom
446 (INPA Co.) and his staff at Concepción (G. Urbano) for their help to sample and work on their
447 property. We thank O. Royo for his help in the laboratory work. We are grateful to two anonymous
448 reviewers and the editor for their constructive comments on an earlier version of this manuscript.
449 This study was supported by the projects “Análisis retrospectivos mediante dendrocronología para
450 profundizar en la ecología y mejorar la gestión de los bosques tropicales secos (Dentropicas)”
451 (Fundación BBVA) and "Regeneración, crecimiento y modelos dinámicos de bosques tropicales
452 secos: herramientas para su conservación y para el uso sostenible de especies maderables" (AECID
453 11-CAP2-1730). JJC sincerely acknowledges funding by ARAID. PAZ acknowledges funding by
454 an ERC grant (#242955).

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615 **Table legends**

616

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

618 are means \pm 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 (%)
<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

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.

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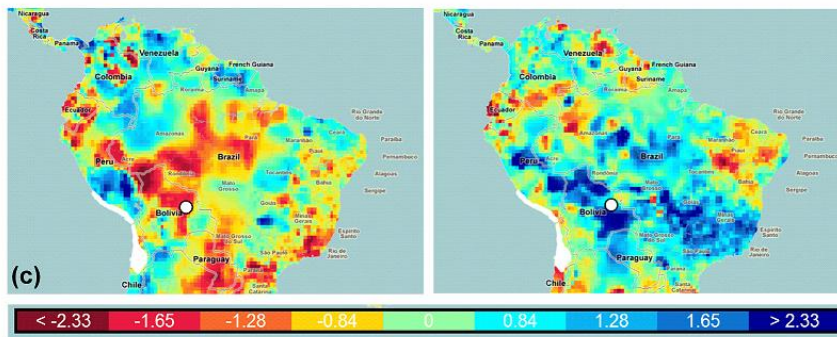
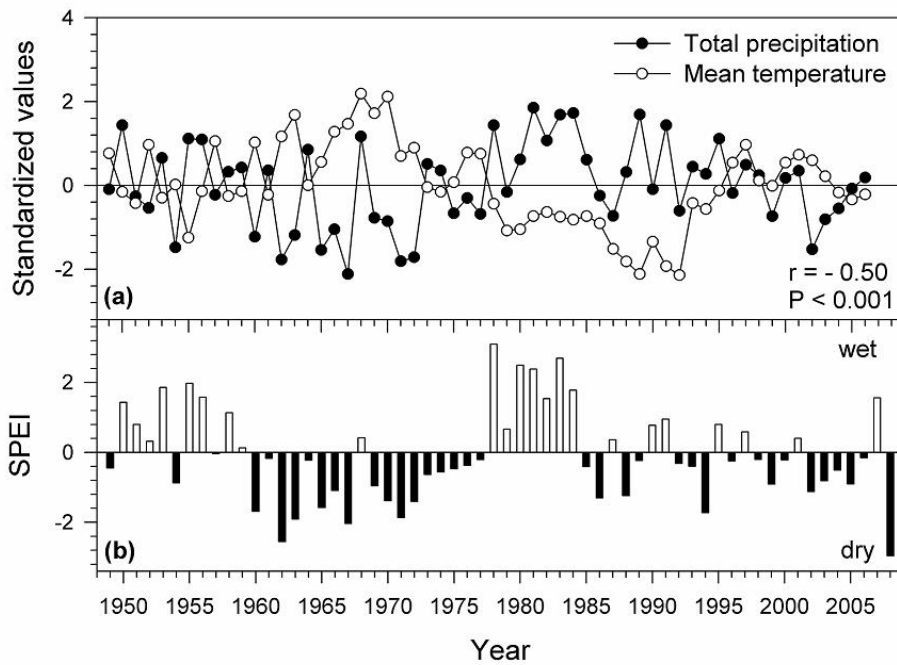
628

629

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

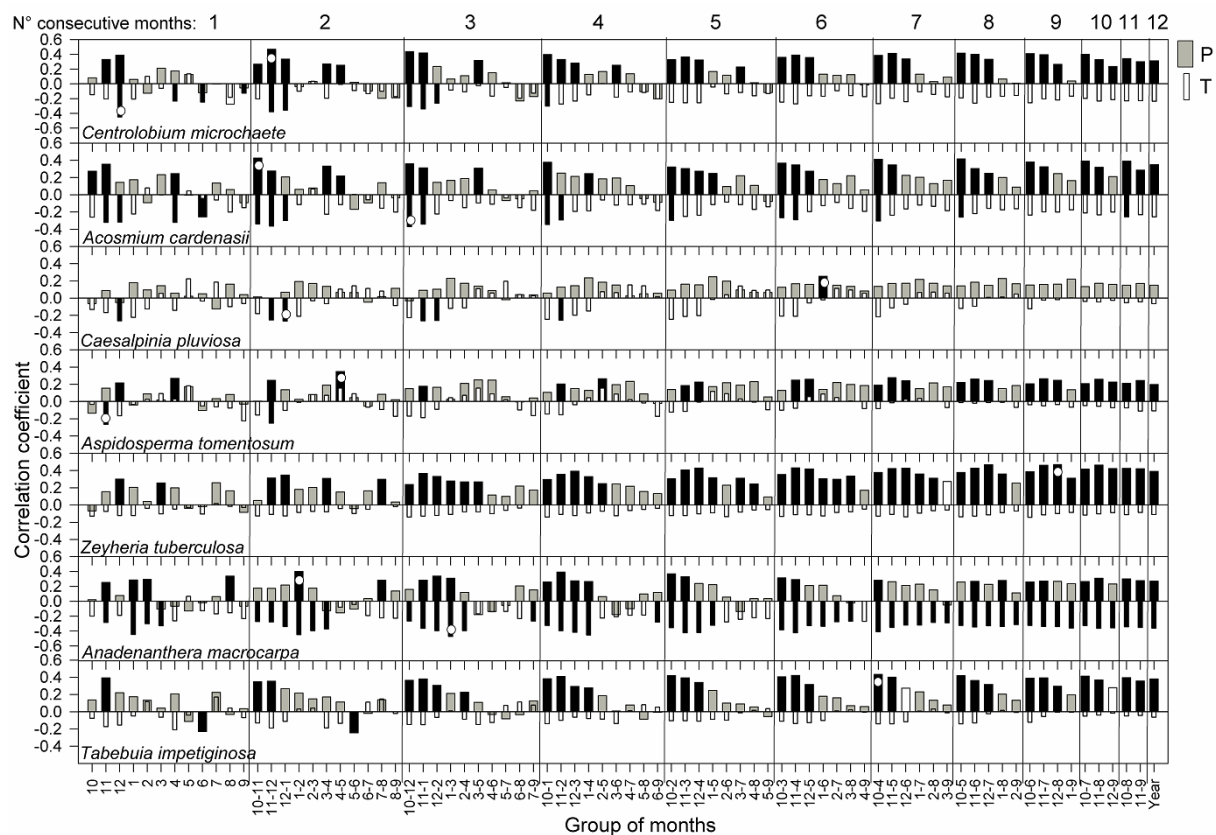
Species	Tree variables		Raw data		Residual chronologies		
	No. trees / radii	Age (years)	Tree-ring width (mm)	AC1	MSx	R-bar	EPS
<i>Centrolobium</i>	14 / 42	71 - 109	1.50 \pm 0.08	0.47	0.34	0.26	0.94
<i>Acosmium</i>	11 / 38	71 - 128	1.93 \pm 0.10	0.54	0.25	0.24	0.92
<i>Caesalpinia</i>	8 / 31	91 - 176	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

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.



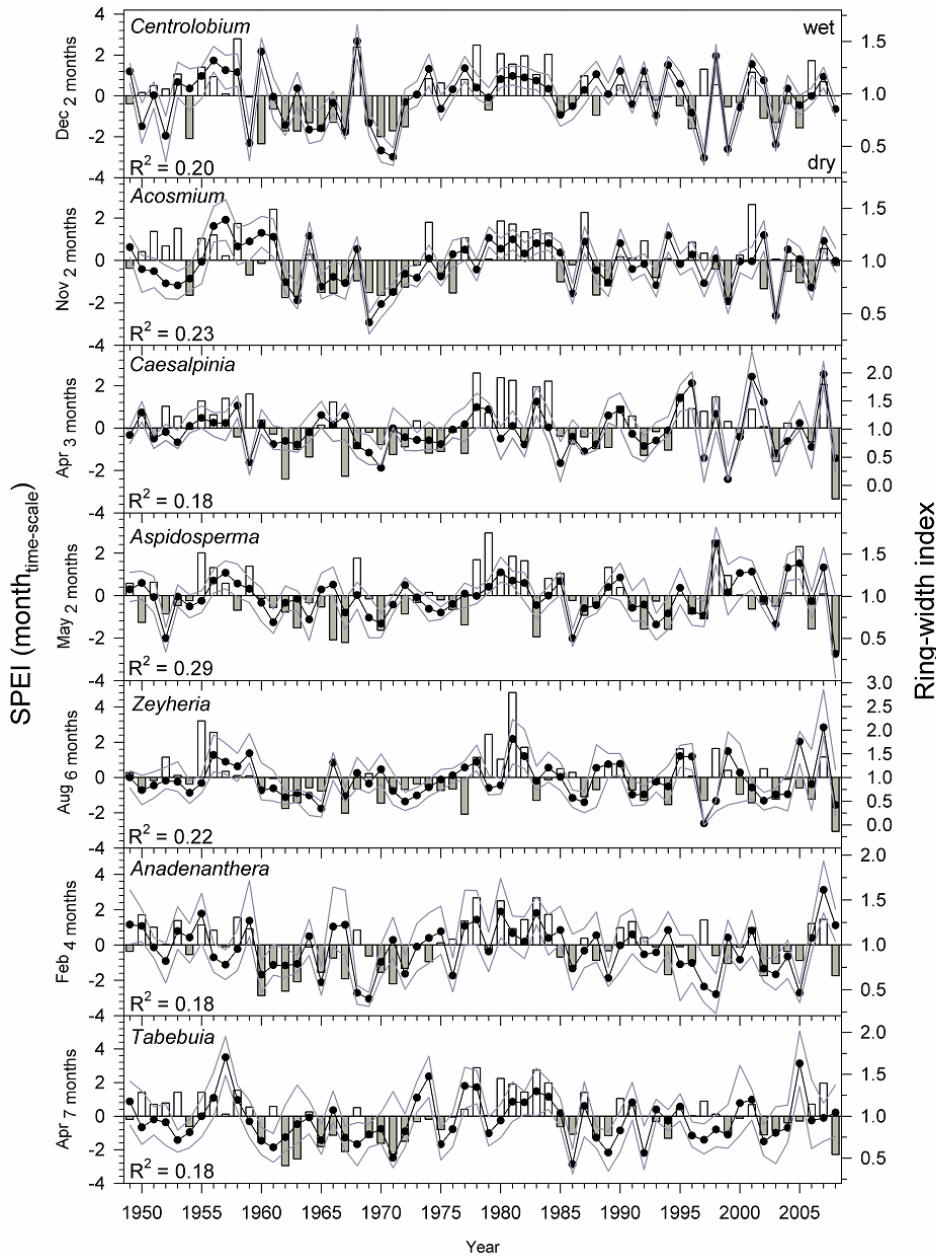
636
 637 **Fig. 1.** Temporal (a and b) and spatial (c) patterns of climatic and drought variability in the study
 638 area. In the upper graph the relationship between the standardized temperature and precipitation
 639 values is indicated with its corrected probability value. The lower maps (obtained from

640 <http://sac.csic.es/spei/map/maps.html>) show the drought intensity as assessed by the
 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).



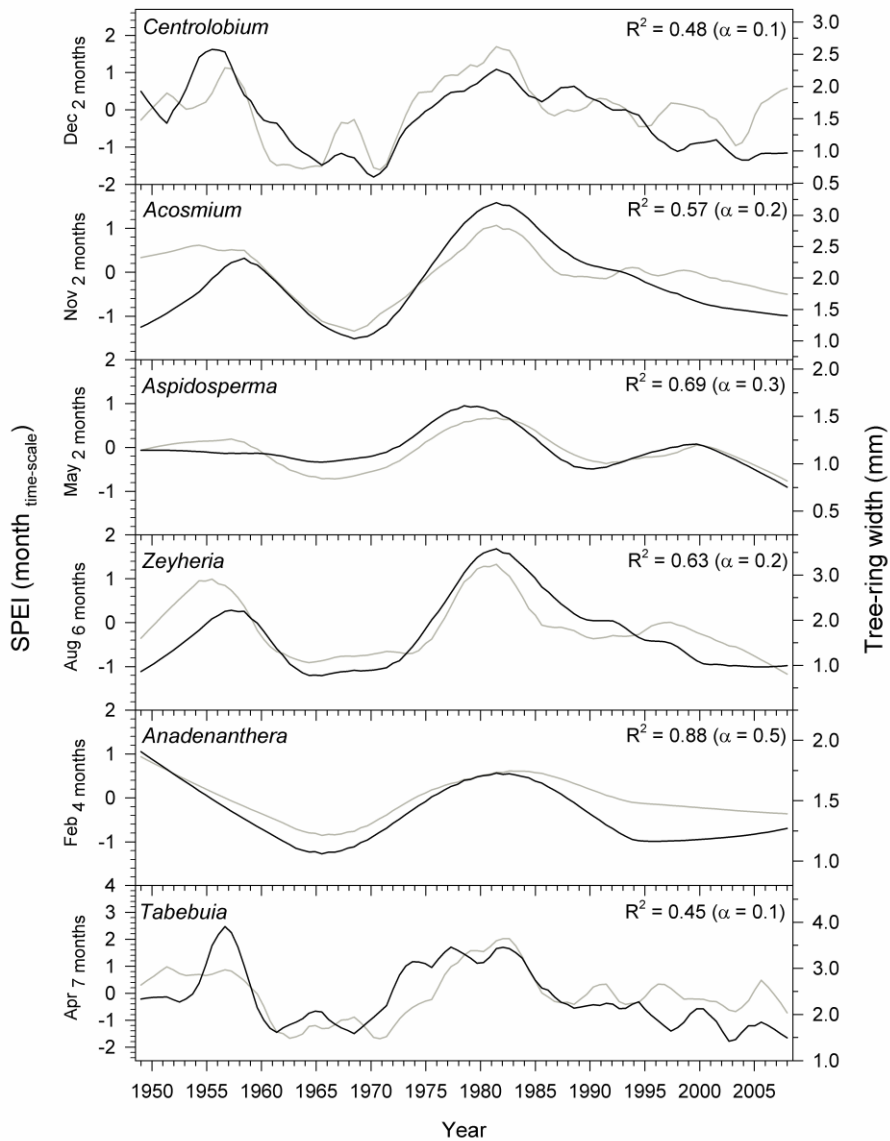
647
 648 **Fig. 2.** Correlations (Pearson coefficients) calculated between climatic variables (P, total
 649 precipitation, wide grey bars; T, mean temperature, thin empty bars) and residual tree-ring width
 650 chronologies for the common period 1949-2008. The month or group of months used for
 651 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.



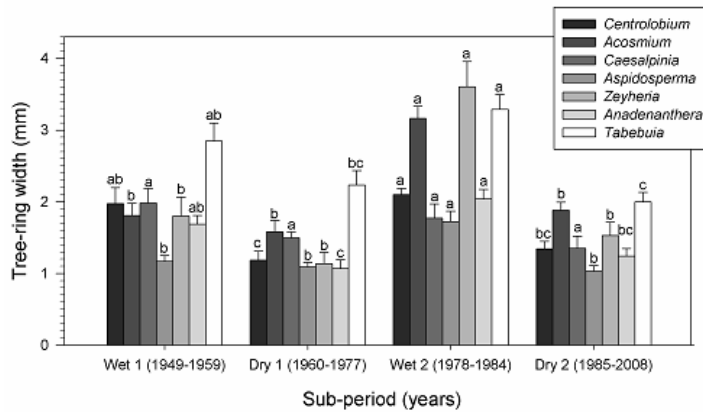
655
 656 **Fig. 3.** Highest correlations found between residual ring-width chronologies (lines with symbols
 657 and bootstrapped 95% confidence limits) and SPEI (bars). The month and time-scales
 658 (subscripts) where the highest correlation was found is shown on the y axis labels for each

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 \pm 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 significant differences in
 672 tree-ring width between sub-periods for the same species ($P < 0.05$).

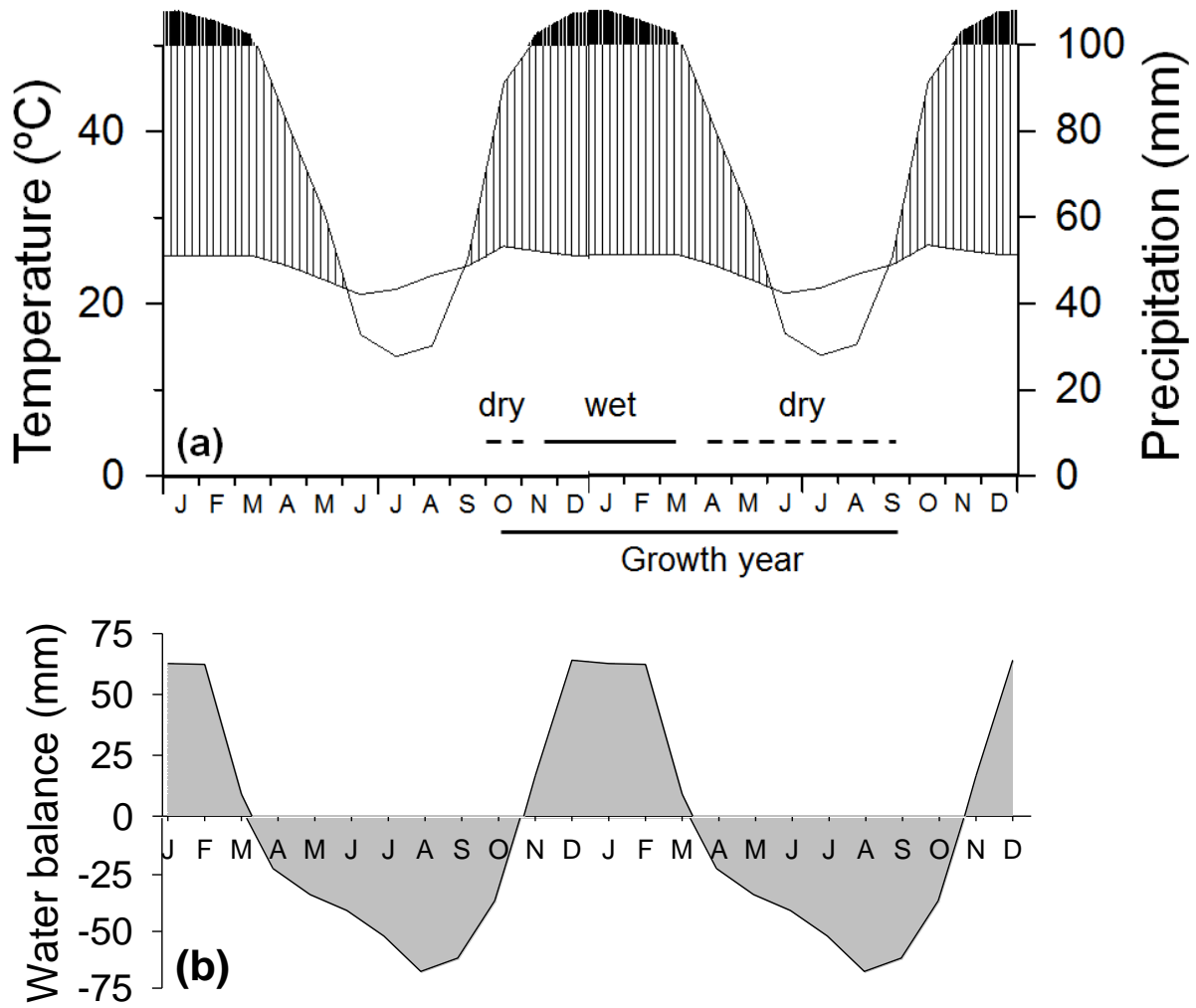


Figure A1. Climate diagram of the study area (a) and estimated monthly water balance (b), i.e. the difference between precipitation and potential evapotranspiration. Data were obtained for Concepción station (16° 15' S, 62° 06' W) considering the period 1949-2008. Tree growth year goes from October to September. The wet season is indicated by solid line and dry season by dotted lines.

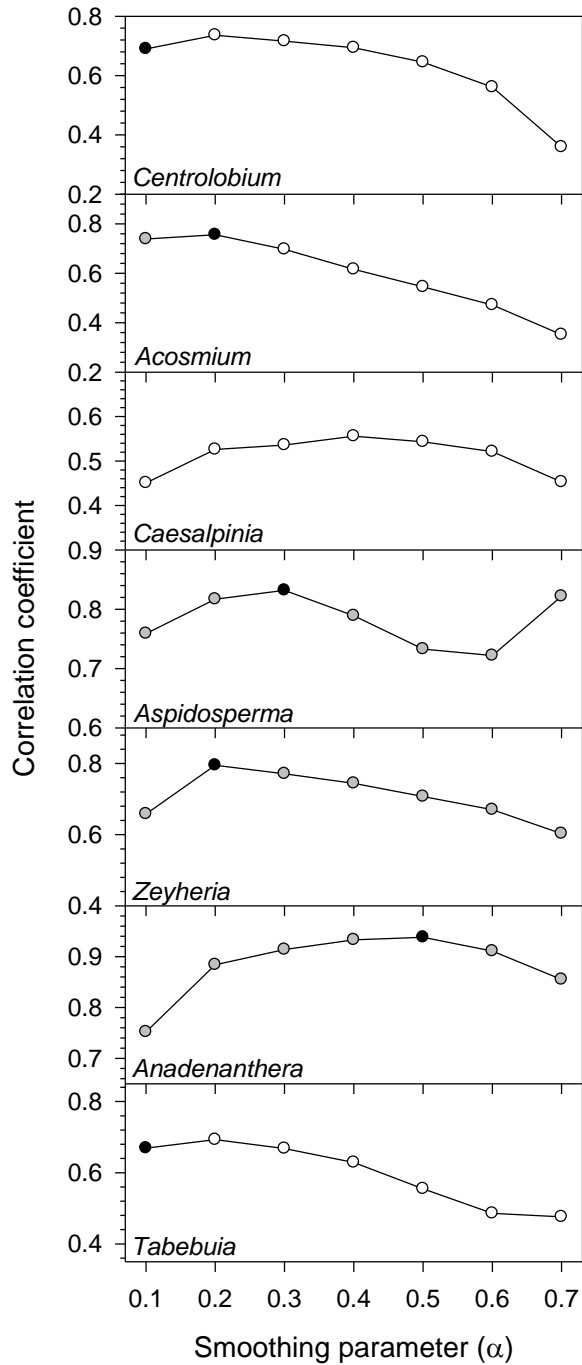
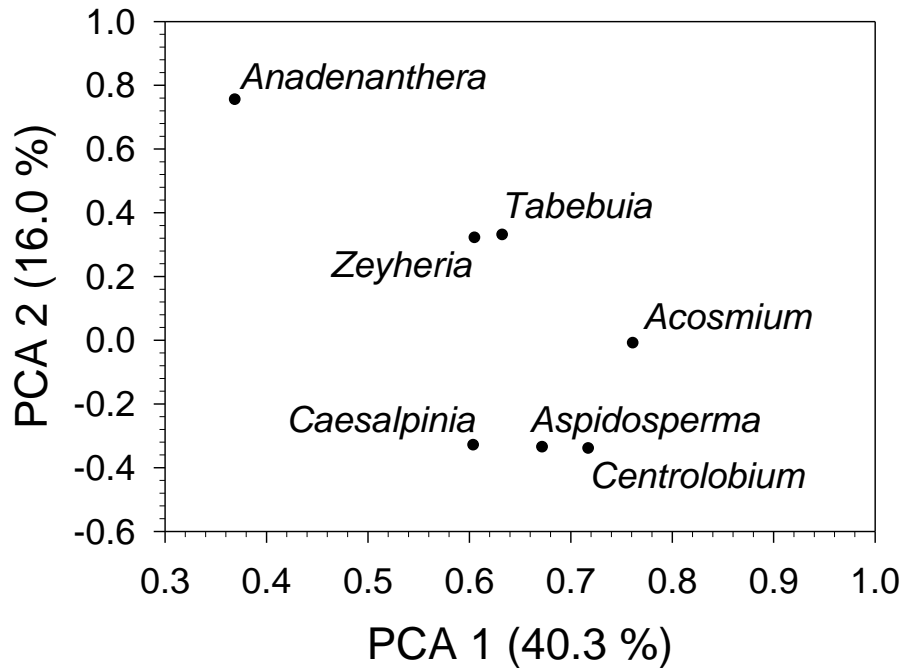


Figure A2. Relationships (Pearson correlation coefficients) calculated between smoothed tree-ring width and drought index (SPEI) series considering the seven study species and the period 1949-2008. Correlations were obtained for different smoothing parameters ($\alpha = 0.1, 0.2, 0.3, 0.4, 0.5, 0.6$ 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
 2 **Figure A3.** Graphical summary of the seven tree species' scores considering the first two
 3 components of a Principal Component Analysis calculated on the covariance matrix of the
 4 residual ring-width series for the common period 1949-2008.

5 **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