Hydroclimatic variations reveal differences in carbon capture in two concurrent conifers in northern Mexico

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Background. Forest ecosystems are considered among the largest terrestrial carbon sinks. The dynamics of forest carbon depend on where the carbon is stored and its responses to environmental factors, as well as the physiology of the trees. Thus, threatened forest regions with high biodiversity have great scientific importance, such as the Sierra Madre Occidental in Mexico. A comparative analysis of tree species can expand the knowledge of the carbon cycle dynamics and ecological processes in this region. Here, we examined the growth, wood density, and carbon accumulation of two threatened species (*Pseudotsuga menziesii* and *Cupressus lusitanica*) to evaluate their hydroclimatic responsiveness.

Methods. The temporal variations in the carbon accumulation patterns of two co-occurring species (*P. menziesii* and *C. lusitanica*) and their sensitivity to the local climate were studied using dendroecological techniques, X-ray densitometry, and allometric equations.

Results. The results show that the annual carbon accumulation in *C. lusitanica* is positively associated with the temperature during the current fall, while the carbon accumulation in *P. menziesii* is correlated with the rainfall during the winter of the previous year. The climatic responses are associated with the intra-annual variations of wood density and ring widths for each species. The ring width was strongly correlated with carbon accumulation in *C. lusitanica*, while the mean wood density was linked to carbon accumulation in *P. menziesii.*

Discussion. This study has implications for the carbon accumulation rates of both species, revealing differences in the carbon capture patterns in response to climatic variations. Although the species coexist, there are variation in the hydroclimatic sensitivity of the annual carbon sequestered by trunks of trees, which would be associated with tree-ring width and/or wood density, i.e. directly by anatomical features. The results are relevant to analyze the response to the variability of climatic conditions expected in the near future of the tree communities of Sierra Madre Occidental. Therefore, this study provides a basis for modeling the long-term carbon budget projections in terrestrial ecosystems in northern Mexico.

1 **Hydroclimatic Variations Reveal Differences in Carbon**

2 **Capture in Two Concurrent Conifers in Northern Mexico**

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20   **Abstract**

21   **Background**. Forest ecosystems are considered among the largest terrestrial carbon sinks. The

22   dynamics of forest carbon depend on where the carbon is stored and its responses to environmental

23   factors, as well as the physiology of the trees. Thus, threatened forest regions with high biodiversity

24   have great scientific importance, such as the Sierra Madre Occidental in Mexico. A comparative

25   analysis of tree species can expand the knowledge of the carbon cycle dynamics and ecological

26   processes in this region. Here, we examined the growth, wood density, and carbon accumulation

27   of two threatened species (*Pseudotsuga menziesii* and *Cupressus lusitanica*) to evaluate their

28   hydroclimatic responsiveness.

29

30   **Methods.** The temporal variations in the carbon accumulation patterns of two co-occurring species

31   (*P. menziesii* and *C. lusitanica*) and their sensitivity to the local climate were studied using

32   dendroecological techniques, X-ray densitometry, and allometric equations.

33

34   **Results.** The results show that the annual carbon accumulation in *C. lusitanica* is positively

35   associated with the temperature during the current fall, while the carbon accumulation in *P.*

36   *menziesii* is correlated with the rainfall during the winter of the previous year. The climatic

37   responses are associated with the intra-annual variations of wood density and ring widths for each

38   species. The ring width was strongly correlated with carbon accumulation in *C. lusitanica*, while

39   the mean wood density was linked to carbon accumulation in *P. menziesii.*

40

41   **Discussion.** This study has implications for the carbon accumulation rates of both species*,*

42   revealing differences in the carbon capture patterns in response to climatic variations. Although

43   the species coexist, there are variation in the hydroclimatic sensitivity of the annual carbon

44   sequestered by trunks of trees, which would be associated with tree-ring width and/or wood

45   density, i.e. directly by anatomical features. The results are relevant to analyze the response to the

46   variability of climatic conditions expected in the near future of the tree communities of Sierra

47   Madre Occidental. Therefore, this study provides a basis for modeling the long-term carbon budget

48   projections in terrestrial ecosystems in northern Mexico.

49   **1. Introduction**

50

51   Many of the world's forest ecosystems are negatively responding to climate change,

52   including changes in biodiversity, high mortality of tree communities, and increases in plagues

53   and diseases (Allen et al., 2010). These phenomena are related mainly to the global increase in the

54   intensity and severity of mega droughts in many regions, which have caused an acceleration in

55   foliar senescence and forest decline in many tree species (Bigler et al., 2007; Sánchez-Salguero,

56   2010; Zeppel, Anderegg & Adams, 2012; Périé & De Blois, 2016; Venegas-González et al., 2018).

57   Tree growth in forest ecosystems is the most important terrestrial process associated with

58   carbon dynamics. The total terrestrial carbon sink by forests is currently estimated at 2.4 ± 0.4 PgC

59   per year (global net sink = 1.1 ± 0.8 PgC per year), being the temperate forests the second most

60   important sink after tropical forest (Pan et al. 2011). However, the sequestration carbon by forest

61   ecosystem depend on different factors, such as extreme weather events, land use change, stand

62   age, forest disturbances, management practices and competition, among other ecological processes

63   (IPCC, 2013). Thus, tree-ring growth dynamics contribute to the understanding of annual carbon

64   uptake in forest ecosystems, allowing proposal of management actions for mitigation and

65   adaptation to climate change (Babst et al., 2014a).

66   The Sierra Madre Occidental is the most extensive mountainous system in Mexico, and its

67   forests represent the largest terrestrial oxygen- and biomass-producing ecosystems that remain in

68   southwestern North America (González-Elizondo et al., 2012). The great biodiversity of this

69   region allows for studies of concurrent species of great ecological importance, such as *Cupressus*

70   *lusitanica* (Mill.), which grows in areas with high water availability, and *Pseudotsuga menziesii*

71   (Mirb.) Franco, which represents a southern populations, with a limited distribution in Mexico.

72   Dendrochronology has been widely used in Mexico to study forest ecology and climate

73   reconstructions (e.g. Acosta-Hernández et al., 2017). Some studies have been conducted with the

74   intent to reconstruct precipitation (Cleaveland et al., 2003, Villanueva et al., 2011), teleconnections

75   with El Niño–Southern Oscillation (Cleaveland et al., 2003), drought occurrence (Cerano et al.,

76   2011), evaporation data (Pompa-García & Camarero, 2015),and analyze the seasonal climatic

77   variations through early and latewood (Carlón-Allende et al., 2018). Tree-ring analyses (associated

78   with other methods) have proven that the accumulation of carbon in different species (*Pinus*

79   *arizonica* and *Pinus cembroides*) can be influenced by specific hydroclimatic conditions, site

80   conditions, or the functional characteristics of each species (Pompa-García et al., 2018). However,

81   this information is unknown in some threatened species of the Sierra Madre Occidental, such as

82   *Cupressus lusitanica* and *Pseudotsuga menziesii.* As a result of their distributions along

83   biogeographic gradients, these concurrent species can be used to evaluate the effects of limited

84   water resources and the different conservation statuses on their growth dynamics, wood density,

85   and carbon accumulation, as well as to assess the influence of hydroclimatic variability.

86   Several methods are used to estimate carbon content, such as total organic carbon (TOC;

87   Houghton, 2005), X-ray densitometry (Taki et al., 2014; Pompa-García & Venegas-González,

88   2016), and allometric equations based on time series of tree diameters (Návar, 2009). These

89   nondestructive methods can be used to analyze the temporal variations in carbon fixation of trees

90   (Pompa-García et al., 2018).

91   In general, biomass evaluations assume that wood density is constant, ignoring the

92   interannual variation caused by the climate and tree age (Babst et al., 2014b). The calculation of

93   tree biomass can be obtained as a product of the volume and density of the wood. Current biometric

94   studies rely on stem diameter growth estimated from tree rings (Babst et al., 2014b).

95   As tree growth responds differently to environmental conditions across tree species in

96   Sierra Madre Occidental (Pompa-García et al., 2017a), there will also be variation in the total

97 carbon accumulation by species. We used tree rings, allometric equations and wood density (WD)

98 to examine the growth and carbon accumulation of *C. lusitanica* and *P. menziesii* trees located in

99 the Sierra Madre Occidental and to evaluate their hydroclimatic response. We hypothesized that

100 the variations in carbon accumulation reflect climatic conditions, according to the specific

101 sensitivity of each species.

102

103 **2. Materials and Methods**

104 *2.1. Area of Study*

105 The study was conducted in the Sierra Madre Occidental, in the state of Durango, northwestern

106 Mexico (Figure 1). This mountainous system of volcanic origin has an average elevation of 2000

107 masl, reaching 3000 masl in some areas, and it extends from the south of the Tropic of Cancer to

108 the west of Durango, ending in southern Arizona (Aguirre-Díaz & Labarthe-Hernández, 2003).

109 **Figure 1.** Study site location and local climate diagram. **(a)** The map shows the study area where
110 *Cupressus lusitanica* and *Pseudotsuga menziesii* trees were sampled. **(b,c)** The climate diagrams
111 illustrate the distribution of monthly precipitation (P) and mean temperature (T) for 1946–2015
112 (El Salto meteorological station; located 10 km from the study site, at coordinates 23° 41' 25", -
113 105° 21' 10", at an altitude of 2,538 m).
114

115   This region has a temperate subhumid climate with a wet and cool summer due to the

116 influence of the North American Monsoon (NAM). The region also has two characteristic dry

117 seasons during spring and winter. The precipitation ranges from 1000 to 1200 mm annually. The

118 main rainy season begins with the start of the NAM in late June or early July and ends in late

119 September. Further low-intensity precipitation falls during the cold season (November-February).

120 The maximum values of monthly temperatures occur from May to June; with minimum mean

121 temperature of 7 °C, and a maximum mean temperature of 17 °C (CNA, 2016). The dominant soils

122 in the area are cambisols, lithosols, regosols, and phaeozems (Aguirre-Díaz & Labarthe-

123 Hernández, 2003), while in the study sites, we found mainly luvisol, regosol and cambisol.

124 *2.2. Study Species and Sampling*

125 We selected two coniferous species from Sierra Madre Occidental, *Cupressus lusitanica* and

126 *Pseudotsuga menziesii,* due to their dendrochronological potential and importance for

127 conservation and management (e.g. Pompa-García, Sánchez-Salguero & Camarero, 2017).). *C.*

128 *lusitanica* is located in humid sites while that *P. menziesii* is found in semihumid sites. Fifteen

129 dominant individuals of each species were selected and sampled (diameter ≥10 cm at breast height

130 (DBH), approximately 1.30 m above ground level). From each of these trees, two radial growth

131 cores were collected at a height of 1.3 m with a nondestructive method using a Pressler borer (Ø

132 = 5.1 mm). *P. menziesii* was collected at 2,747 masl and shows an average DBH and height of

133 36.3 cm and 18.1 m, respectively. *C. lusitanica* was collected at 2,651 masl and shows an average

134 DBH and height of 31.5 cm and 16.4 m, respectively (Table 1). The field permit approval was

135 granted by the Mexican Federal Government agency SEMARNAT (i.e. Secretariat of Environment

136 and Natural Resources, N° SGPA/DGVS 09456/16).

137 *2.3. Annual Density of Wood*

138 Radial wood cores were cut in the transverse direction, maintaining a thickness of 1.7 ± 0.2 mm,

139 and these cores were kept in a room temperature (20 °C) and 50% relative humidity until they

140 reached a stable moisture content of 12% (Tomazello et al., 2008). To determine the ring widths

141 and wood densities, the samples were scanned from bark to pith using an X-ray densitometer

142 QTRS01X Tree-Ring Scanner (Quintek Measurement Systems, Knoxville, TN, USA) at 0.08 mm

143 intervals. The demarcation zone between the rings was automatically configured by the device and

144 checked manually for each ring that was analyzed. For each year, the ring width (RW), mean wood

145   density (MeanD), maximum wood density (MXD), and minimum wood density (MND) were

146   determined. These four variables were used to analyze the response to local climate variability.

147   The MeanD value was used to estimate the increase in aerial biomass and carbon.

148   *2.4. Development of Chronologies*

149   We developed chronologies using the ring width obtained from the X-ray densitometer. Visual

150   dating was then statistically validated by using the COFECHA program, which compares each

151   series with a master chronology for each species (Holmes, 1983). For the construction of

152   chronologies, the natural long-term growth trends (age and tree geometry) were eliminated using

153   a negative exponential function to obtain standardized ring widths. Subsequently, an

154   autoregressive model was applied to each of the standardized series to eliminate most of the

155   temporal autocorrelation related to the growth of the previous year. Finally, a robust biweight

156   average was used to obtain the chronologies of the residual indices for each species (mean = 1).

157   This procedure was performed using the *dendrochronology* program library in R (dplR; Bunn,

158   2008) of the free statistical software R (R Development Core Team, 2015).

159   *2.5. Aerial Biomass and Carbon Estimation*

160   The annual RW values were used to reconstruct the historical diameters of the trees and their

161   increases in basal area. These values were then combined with the MeanD values to estimate

162   biomass and, subsequently, the carbon allocated in that particular year. To estimate the biomass,

163   we used the following allometric equation (1), which was proposed to estimate the carbon stocks

164   in the forests of northwestern Mexico (Návar, 2009):

$$AWB = 0.0752 * D^{2.4448} * 2.0331^{p} \qquad (1)$$

166   where AWB = aerial biomass; D = normal diameter; and p = wood density. Different percentages

167   of carbon concentrations in the biomass were used according to specific laboratory analyses

168   (Yerena-Yamallel et al., 2012), as follows: *C. lusitanica*, 45.57%, and *P. menziesii,* 47.78%

169   (Pompa-García et al., 2017b).

170   *2.6. Statistical Analyses*

171   Statistical analyses were performed using the Mann-Whitney-Wilcoxon test, with $p<0.05$

172   considered significant in the evaluation of differences in radial growth, density, and carbon

173   accumulation between species. This nonparametric test was used because the values of the

174   variables did not comply with the basic assumptions of a normal distribution, according to a

175   Shapiro-Wilks test (Zar, 2010).

176   The influences of climate (precipitation and temperature) on RW and WD were evaluated by

177   analyzing the Pearson correlation coefficients, which were estimated for each species using

178   residual chronologies. Autoregressive models were used to eliminate any temporal autocorrelation

179   (Cook, 1985). Chronologies were compared with parameters of local climatic variability:

180   Maximum temperature (Tmax), minimum temperature (Tmin), average temperature (Tmean), and

181   precipitation (Pp). In addition, we evaluated the relationship between carbon accumulation and

182   internal variables (RW and WD) and climatic influences (precipitation and temperature) by

183   principal component analysis. Climatic data sets (1946–2014) were obtained from the "El Salto"

184   meteorological station, located at coordinates 23° 41' 25", –105° 21' 10", which is less than 10 km

185   from the study site at an altitude of 2,538 m (CNA, 2016).

186   **3. Results**

187   *3.1. Growth, Density and Carbon Accumulation*

188   Table 1 shows the descriptive statistics of RW, density, and carbon accumulation for both tree

189   species that were analyzed. The lengths of the chronologies, which included at least five trees,

190   ranged from 113 (*P. menziesii*) to 159 (*C. lusitanica*) years, and the longest chronologies (with

191   less than five trees) were those of *C. lusitanica* (244 years). The values of the expressed population

192   signal (EPS) for *P. menziesii* were ≥0.85 over the entire period (estimated with at least five trees),

193   mainly since 1920, showing that replication of the sampling was adequate. In the case of *C.*

194   *lusitanica*, the usual EPS threshold of 0.85 was not reached (EPS = 0.78), but this does not mean

195   that the samples were not adequately cross-dated. Rather, this means that the climate signal is

196   lower in comparison to the sites where *Pseudotsuga menziesii* thrives (Wigley, Briffa & Jones,

197   1984). This sampling strategy has yielded good results for quantifying carbon accumulation

198   through tree rings (Pompa-García et al., 2018). In this sense, before 1920, higher variability in the

199   ring width series was observed (Figure 2). The mean sensitivity was 0.25 for both species, showing

200   that the trees react to the environment through their annual growth variability (Grissino-Mayer,

201   2001).

202   **Table 1.** Descriptive statistics of chronologies. Time span (TS), mean sensitivity (MS), expressed
203   signal of the population (EPS), density (WD), carbon accumulation (C).

204   **Figure 2.** Tree-ring chronologies of the two study species. Residual chronologies (black lines) and

205   series (gray lines) of ring widths of the two study species for the best cross-dated period. (**a**)

206   *Cupressus lusitanica*, (**b**) *Pseudotsuga menziesii*.

207

208   Both species had similar growth rates per year (1.24 mm for *C. lusitanica* and 1.58 mm for

209   *P. menziesii*). However, *P. menziesii* had a higher mean wood density (550.5 kg m^3 yr^{-1}) (Table 1).

210   In general, there was variation in the wood density measured since 1920, especially in *P. menziesii*

211   (Figure 3), where the three variables (maximum, minimum, and mean) exhibited negative trends.

212 In contrast, *C. lusitanica* trees showed positive trends in mean wood density (MeanD) and

213 minimum wood density (MND).

214

215 **Figure 3.** Mean values of wood density of the two study species. Mean ± SE values of maximum

216 density (MXD), minimum density (MND), and mean density (MeanD) of the two study species,

217 for the period 1920–2014 (five trees per species). Positive (+) and negative (-) trends of density

218 values are shown in right graphics. **(a,b)** *Cupressus lusitanica*, **(c,d)** *Pseudotsuga menziesii*.

219

220 *3.2. Climatic Influence on Radial Growth and Wood Density*

221 The influences of climate variables on the RW and the WD variables (MND, MXD and MeanD)

222 are shown in Figures 4 and 5 for the period 1946–2014. Overall, *P. menziesii* showed more climatic

223 sensitivity than *C. lusitanica*. For accumulated precipitation, the RW of *P. menziesii* trees was

224 positively correlated with the rainfall during the winter or cold season (from October to April, $r =$

225 0.60, $p<0.001$), while MND and MeanD exhibited negative correlations with the rainfall during

226 winter and spring (from December to May, $r <-0.36$, $p<0.01$). For *C. lusitanica*, the general pattern

227 was that all the variables negatively reacted to the increase in rainfall during all months, with the

228 change in MXD being significant throughout the year ($r <-0.26$, $p<0.05$) (Figure 4). Regarding the

229 mean temperature, the RW and MXD of *P. menziesii* trees showed negative correlations with

230 temperature during the previous and current growth years, which were significant for spring

231 (March to May, $r <-0.35$, $p<0.01$) and for annual mean temperature ($r <-0.30$, $p<0.05$) in relation

232 to RW, as well as for the temperature of the previous fall (September to November, $r <-0.35$,

233 $p<0.01$) related to MXD. For *C. lusitanica*, we observed a positive association between MND and

234 MeanD and the mean temperature of the previous and current fall ($r <-0.32$, $p<0.01$) (Figure 5).

235 **Figure 4.** Relationships between residual chronologies (growth ring width (RW), maximum
236 density (MXD), minimum density (MND), and mean density (MeanD) and accumulated
237 precipitation. The left and right columns represent the analysis by month and by season,
238 respectively; that is, summer, fall, winter, spring, annual, and cold (October–April). Letters
239 indicate growth periods (PY and lowercase = previous year, CY and uppercase = current year).
240 Dashed horizontal lines indicate statistical significance at the 95% confidence level. (**a**) *Cupressus*
241 *lusitanica*, (**b**) *Pseudotsuga menziesii*.

242

243 **Figure 5.** Relationships between residual chronologies (growth ring width (RW), maximum
244 density (MXD), minimum density (MND), and mean wood density (MeanD) and mean
245 temperature. The left and right columns represent analysis by month and by season, respectively;
246 that is, summer, fall, winter, spring, annual, and cold (October–April). Letters indicate growth
247 periods (PY and lowercase = previous year, CY and uppercase = current year). Dashed horizontal
248 lines indicate statistical significance at the 95% confidence level. (**a**) *Cupressus lusitanica*, (**b**)
249 *Pseudotsuga menziesii*.

250

251 *3.3. Local and Climatic Influence in Carbon Accumulation*

252 The annual carbon accumulation for 1920–2014 is represented in Figure 6, which shows a higher

253 carbon accumulation in *P. menziesii* trees (3.7 kg yr^{-1}) than in *C. lusitanica* (2.2 kg yr^{-1}) (Table 1).

254 Since 1975, an increase in carbon accumulation in *P. menziesii* but a decrease in *C. lusitanica*

255 (which has recovered since 2005) has been observed (Figure 6a). This difference could be

256 explained by the climatic influences (temperature and precipitation) and internal influences (radial

257 growth and wood densities). These results seem to correspond to the high correlation between

258 carbon and mean wood density of the first species ($r = 0.48$, $p < 0.01$) (Figure 6b) and carbon and

259 ring width in the second species ($r = 0.45$, $p < 0.01$) (Figure 6c). Regarding climatic influences,

260 we observed that carbon accumulation in *C. lusitanica* is linked to the temperature of the fall

261 season ($r = 0.40$, $p=0.02$), while carbon accumulation in *P. menziesii* is strongly associated with

262 the precipitation during the previous winter ($r = 0.58$, $p=0.0002$) (Figure 7).

263 **Figure 6.** Temporal variation of carbon capture. (**a**) Carbon accumulation per year in the two
264 studied conifers. Gray lines indicate the standard error. (**b**) Relationship between carbon

265 accumulation per year and ring width in *Cupressus lusitanica*. (**c**) Relationship between carbon
266 accumulation per year and mean wood density in *Pseudotsuga Menziesii*. (**d**) Data trend of mean
267 annual temperature and total precipitation per year

268
269 **Figure 7.** Principal component analysis between carbon capture and internal influences (radial
270 growth and wood density variables) and seasonal climatic influences (precipitation and
271 temperature) for 1975–2014. The yellow, green, blue and red circles indicate radial growth, the
272 wood density variables, the precipitation variables, and the temperature variables, respectively.
273 Win = winter, Fall = autumn, Spr = spring, Sum = summer. The dashed circle represents the
274 maximum correlation with carbon accumulation. (**a**) *Cupressus lusitanica* (cophenetic correlation
275 = 0.79), (**b**) *Pseudotsuga menziesii* (cophenetic correlation = 0.81).

276
277 **4. Discussion**

278 The dendrochronological statistics were adequate for *P. menziesii*; however, *C. lusitanica* had a
279 low EPS (0.78; Wigley, Briffa & Jones, 1984), which is consistent with previous studies carried
280 out in the study area (Pompa-García et al., 2017a). This result is attributed to the fact that *C.*
281 *lusitanica* is considered a species with low sensitivity to climatic variability because it inhabits
282 areas near water bodies; however, it also responded to local climatic variability (Figures 4, 5 and
283 7). The results indicate a strong relationship between the internal variables (RW and WD) and
284 external factors (climatic variables) in the carbon accumulation capacity of the two species; this
285 demonstrates the vulnerability of these ecosystems to global warming and environmental changes
286 in northern Mexico.

287   The application of allometric equations associated with wood density and its response to
288 climatic variability constitutes a reliable methodology that allows for the understanding of the
289 variability in carbon accumulation under specific climatic conditions (Pompa-García & Venegas-
290 González, 2016). This approach offers a temporal perspective of carbon accumulation and allows

291   us to appreciate the intra-annual variation in woody biomass and consequently the carbon content

292   (Pompa-García et al., 2018).

293   The inclusion of wood density as an indicator of climate variability improves the carbon

294   capture estimates. Several studies carried out in the area have evaluated the responses to climatic

295   conditions (González-Elizondo et al., 2005; González-Cásares, Pompa-García & Camarero, 2017;

296   Pompa-García et al., 2017a), while others have used density for biometric purposes (González-

297   Cásares, Yerena-Yamallel & Pompa-García, 2016; Pompa-García & Venegas-González, 2016). It

298   has also been reported that the wood density of a species (*Abies durangensis*) that coexists with

299   the species evaluated in the present study is more sensitive to temperature than the tree-ring width

300   (González-Cásares, Pompa-García & Venegas-González, 2018). In this study, density was used to

301   improve the estimation of carbon capture and its response to climate and thus facilitate a reliable

302   and valuable comparative analysis to broaden the knowledge of the carbon accumulation in forest

303   ecosystems.

304   The ring width of *P. menziesii* was positively correlated with the precipitation from the

305   previous winter through March of the current year. Precipitation during the cold season positively

306   affects tree growth because it recharges the soil water and triggers tree growth (Pompa-García &

307   Venegas-González, 2016), while it also improves the photosynthetic activity of trees during the

308   early growth season (Kerhoulas, Kolb & Koch, 2013). These results are consistent with those

309   obtained for other conifers from nearby regions (Carlón-Allende et al., 2018, Cleaveland et al.,

310   2003; González-Elizondo et al., 2005; Pompa-García & Camarero, 2015; Pompa-García &

311   Venegas-González, 2016). The RW and MXD values of *P. menziesii* showed a negative response

312   to temperature, which is consistent with the results of another study in the region that reported a

313   negative correlation between maximum temperature and WD in *Pinus cooperi* (Pompa-García &

314 Venegas-González, 2016). This result could be attributed to the fact that the wood density of some

315 conifers of the Sierra Madre Occidental is sensitive to high temperatures, which increases the cell

316 wall thickness of the tracheids of latewood. In contrast, temperature has a positive influence on

317 the MeanD and MND of *C. lusitanica* but not on the tree-ring width, which suggests that

318 temperature controls the size of the cell (the lumen and the cell wall of the tracheids) but not the

319 quantity (Thomas, Montagu & Conroy, 2007). In this species, it should be noted that the carbon

320 accumulation is more associated with ring width than wood density (Figure 7).

321 There is evidence that the increase in the global mean temperature is causing increased tree

322 mortality due in water stress and attack by biotic agents (Allen, Breshears & McDowell, 2015).

323 We observed a variation in carbon accumulation between the two species (Figure 6a), that could

324 be attributed to an increase in mean temperature and a decrease in rainfall in the region since 1980

325 (Figure 6d, CNA, 2016). *For P. menziesii*, results showed that ring width and maximum density

326 are negatively affected by temperature (Figure 5). In addition, a high association with carbon

327 accumulation was observed with mean wood density, which is strongly related to the rainfall

328 during the cold season (Figure 7a). All these findings would be affecting the growth of this species

329 in northern Mexico. In western North America, an outstanding increase in mortality triggered by

330 drought and high temperatures has been documented in *P. menziesii*, (Bentz et al., 2009).

331 In contrast for *C. lusitanica*, we observed a positive correlation with mean temperature that

332 would positively affect carbon accumulation, especially during the fall (September–November)

333 (Figure 5a, 7b). A recent study found that tree growth of this species increased with temperature

334 and did not seem respond to negatively to drought. Hence, it could be potentially favored with

335 projections of global warming (Pompa-García, Sánchez-Salguero & Camarero, 2017). However,

336 in other conifers from wet sites, if they are drought sensitivity and would be affected by the

337 increase in temperatures by 2100 (González-Cásares, Pompa-García & Camarero, 2017; Pompa-

338 García, Sánchez-Salguero & Camarero, 2017), so we believe that the response to climate varies

339 between species.

340 As climate change progresses, there is evidence of global temperature increases being

341 linked to an increasing frequency and duration of drought throughout much of the world (IPCC,

342 2013). The predicted climate changes are represented as an increase in the global average

343 temperature, with an increase in aridity in some areas as well as in the frequency and severity of

344 extreme droughts (Allen et al., 2010). In the projections of changes in vegetation caused by climate

345 change, tree mortality becomes a central issue (Allen, Breshears & McDowell, 2015). When

346 studying carbon capture in forests, it is important to have a general perspective on the effects of

347 the climate on these ecosystems.

348 Combined with other methods, the calculation of biomass using growth rings provides

349 more accurate estimations of carbon capture and improves the temporal resolution of periodic

350 forest inventories (Babst et al., 2014c). The use of wood density for estimating biomass improves

351 our understanding of the dynamics of carbon capture in these ecosystems (González-Cásares,

352 Yerena-Yamallel & Pompa-García, 2016; Pompa-García & Venegas-González, 2016; Pompa-

353 García et al., 2018). In general, the results show that low precipitation and high temperatures lead

354 to substantial effect on carbon accumulation over the last 30 years. The increase in the mean annual

355 temperature in the study area (CNA, 2016) that has taken place over the last years seems to have

356 had a positive impact on carbon accumulation in some tree species, such as *Cupressus lusitanica*.

357 Moreover, the negative trends of annual precipitation will cause reduced carbon uptake in some

358 species, such as *Pseudotsuga menziesii* (Figure 6d).

359 **5. Conclusion**

360   *Cupressus lusitanica* and *Pseudotsuga menziesii* exhibit different rates of carbon

361   accumulation. This difference is attributed to the specific responses of each species to climatic

362   conditions. *C. lusitanica* and *P. menziesii* showed different responses to seasonal climatic

363   variability. In general, the carbon accumulation of *P. menziesii* responded significantly to the

364   precipitation during the previous winter, while the temperature of the autumn season influenced

365   carbon sequestration by *C. lusitanica*. In this sense, the negative and positive trends in precipitation

366   and temperature in this region have caused negative and positive carbon accumulation trends in *P.*

367   *menziesii* and *C. lusitanica*, respectively. The results of this study provide a basis for modeling the

368   long-term carbon budget projections in terrestrial ecosystems in northern Mexico. Therefore, these

369   results are of value for the evaluation of dynamic models of the global carbon balance.

370   **Acknowledgments**

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523

Figure 1

Study site location and local climate diagram.

(**a**) The map shows the study area where *Cupressus lusitanica* and *Pseudotsuga menziesii* trees were sampled. (**b,c**) The climate diagrams illustrate the distribution of monthly precipitation (P) and mean temperature (T) for the time period 1946–2015 (El Salto meteorological station; located at coordinates 23° 41' 25'', -105° 21' 10'', at an altitude of 2,538 m).
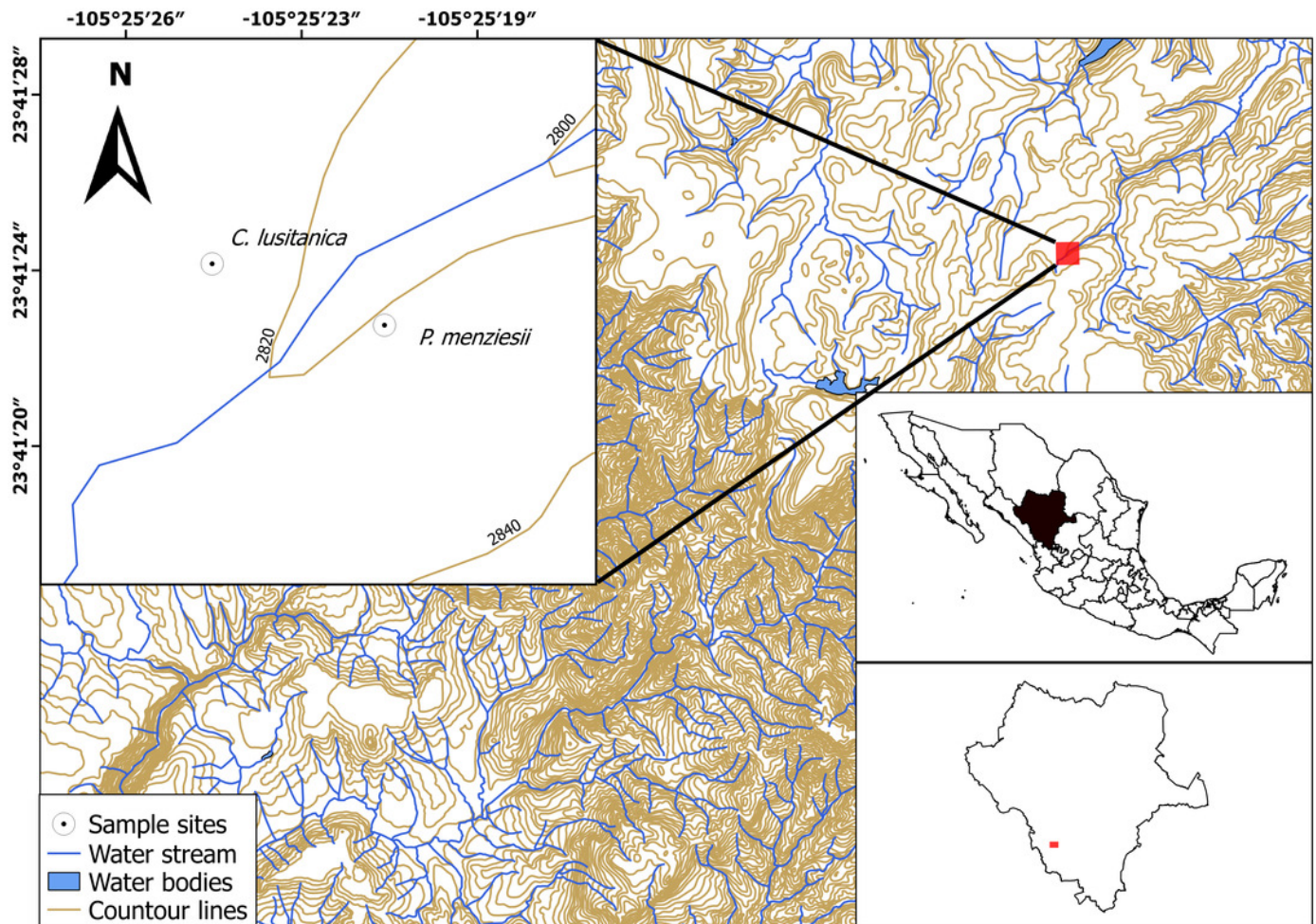
Figure 2

Tree-ring chronologies of the two study species

Residual chronologies (black lines) and series (gray lines) of ring widths of the two study species for the best cross-dated period. (**a**) *Cupressus lusitanica*, (**b**) *Pseudotsuga menziesii*.
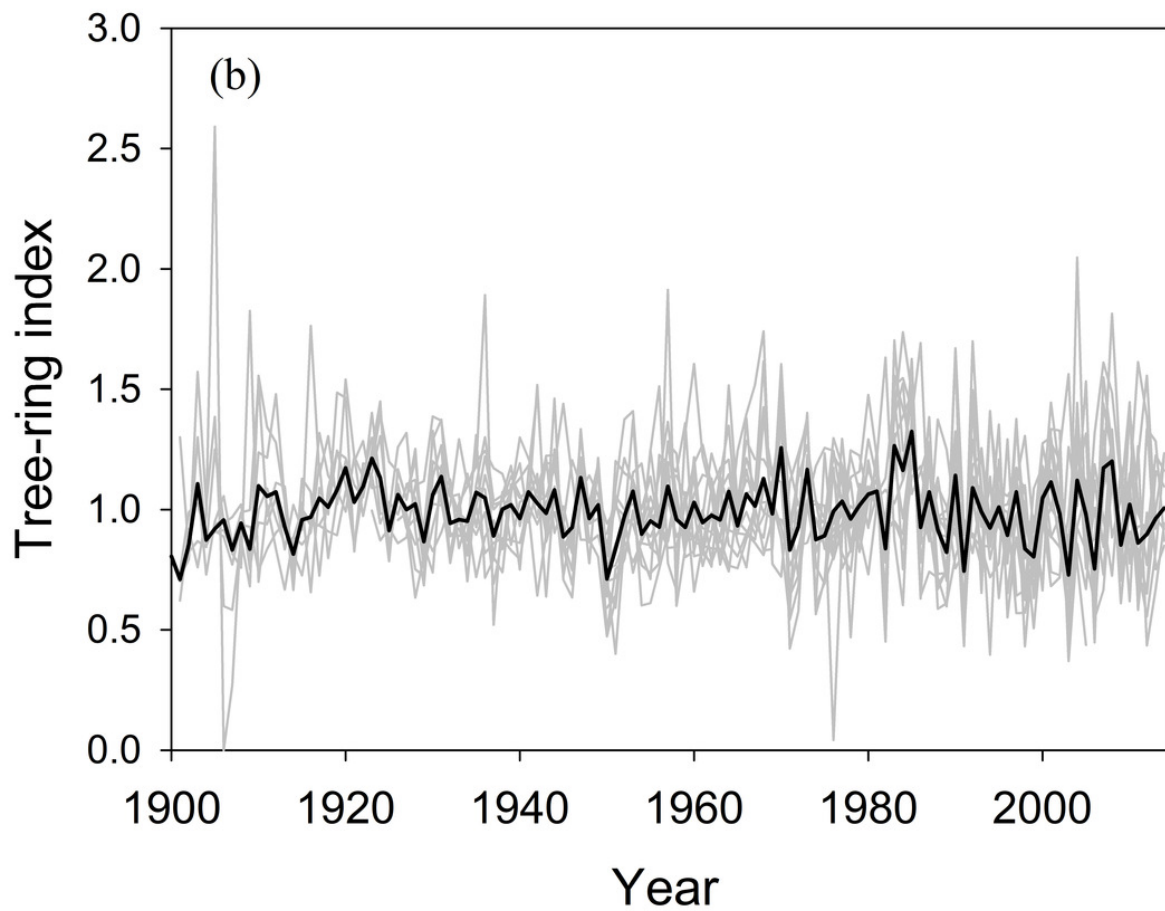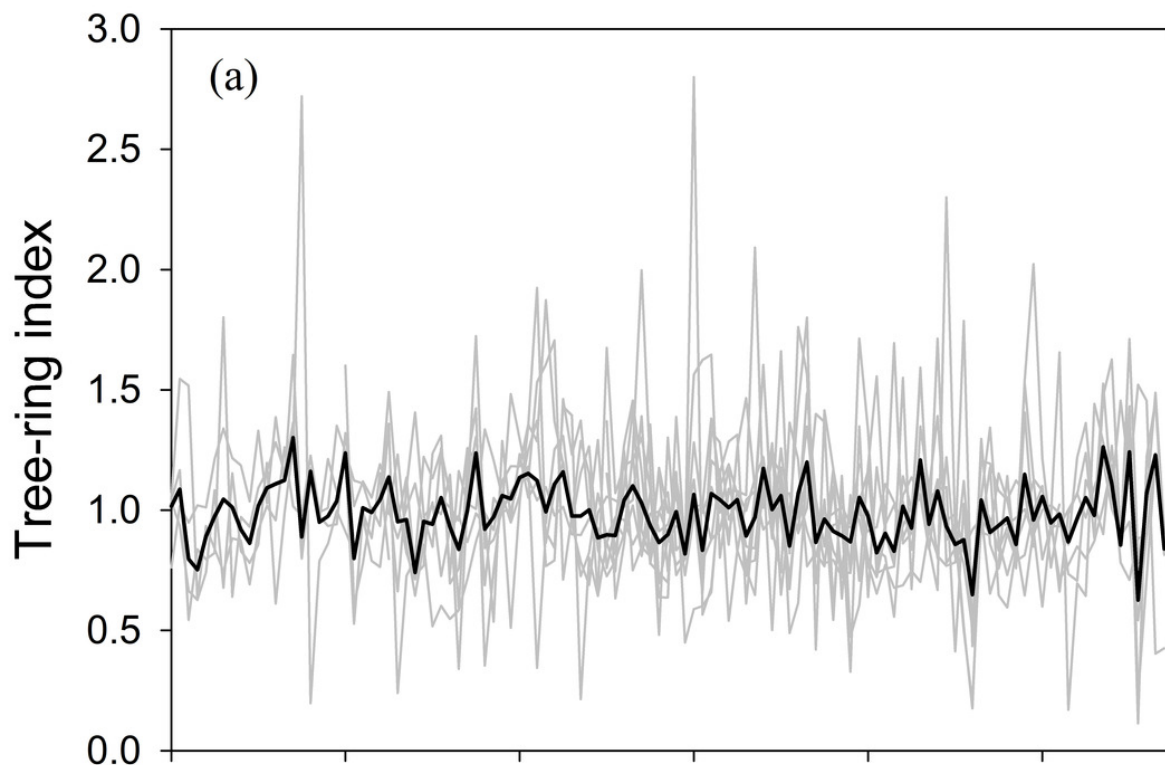
Figure 3

Mean values of wood density of the two study species

Mean ± SE values of maximum density (MXD), minimum density (MND), and mean density (MeanD) of the two study species, for the period 1920–2014 (five trees per species). Positive (+) and negative (-) trends of density values are shown in right graphics. (**a,b**) *Cupressus lusitanica,* (**c,d**) *Pseudotsuga menziesii*.
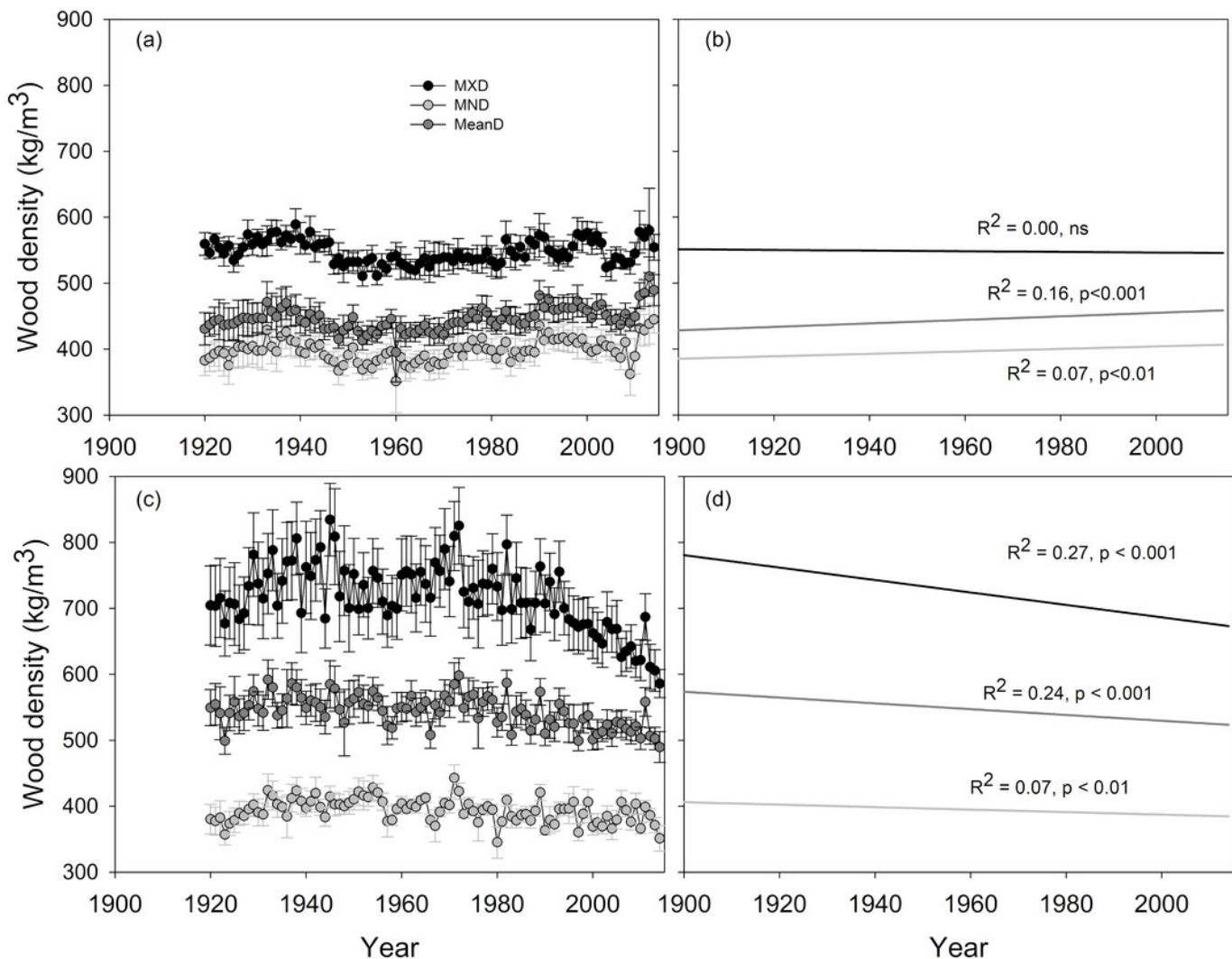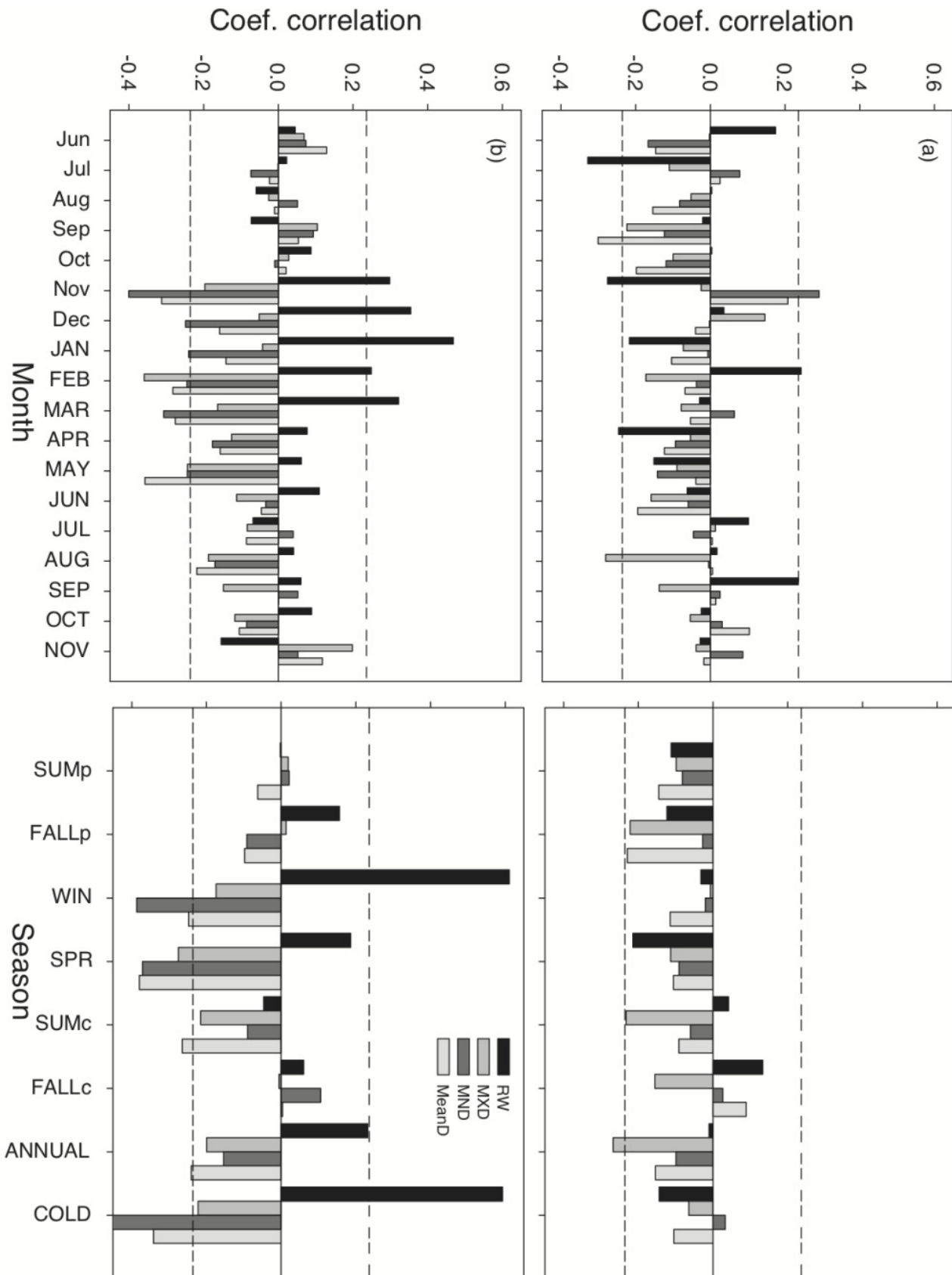
Figure 4

Relationships between residual chronologies (growth ring width (RW), maximum density (MXD), minimum density (MND), and mean density (MeanD) and accumulated precipitation.

The left and right columns represent the analysis by month and by season, respectively; that is, summer, fall, winter, spring, annual, and cold (October–April). Letters indicate growth periods (PY and lowercase = previous year, CY and uppercase = current year). Dashed horizontal lines indicate statistical significance at the 95% confidence level. (**a**) *Cupressus lusitanica*, (**b**) *Pseudotsuga menziesii*.

Figure 5

Relationships between residual chronologies (growth ring width (RW), maximum density (MXD), minimum density (MND) and mean density (MeanD)) and mean temperature.

The left and right columns represent analysis by month and by season, respectively; that is, summer, fall, winter, spring, annual, and cold (October–April). Letters indicate growth periods (PY and lowercase = previous year, CY and uppercase = current year). Dashed horizontal lines indicate statistical significance at the 95% confidence level. (**a**) *Cupressus lusitanica*, (**b**) *Pseudotsuga menziesii*.
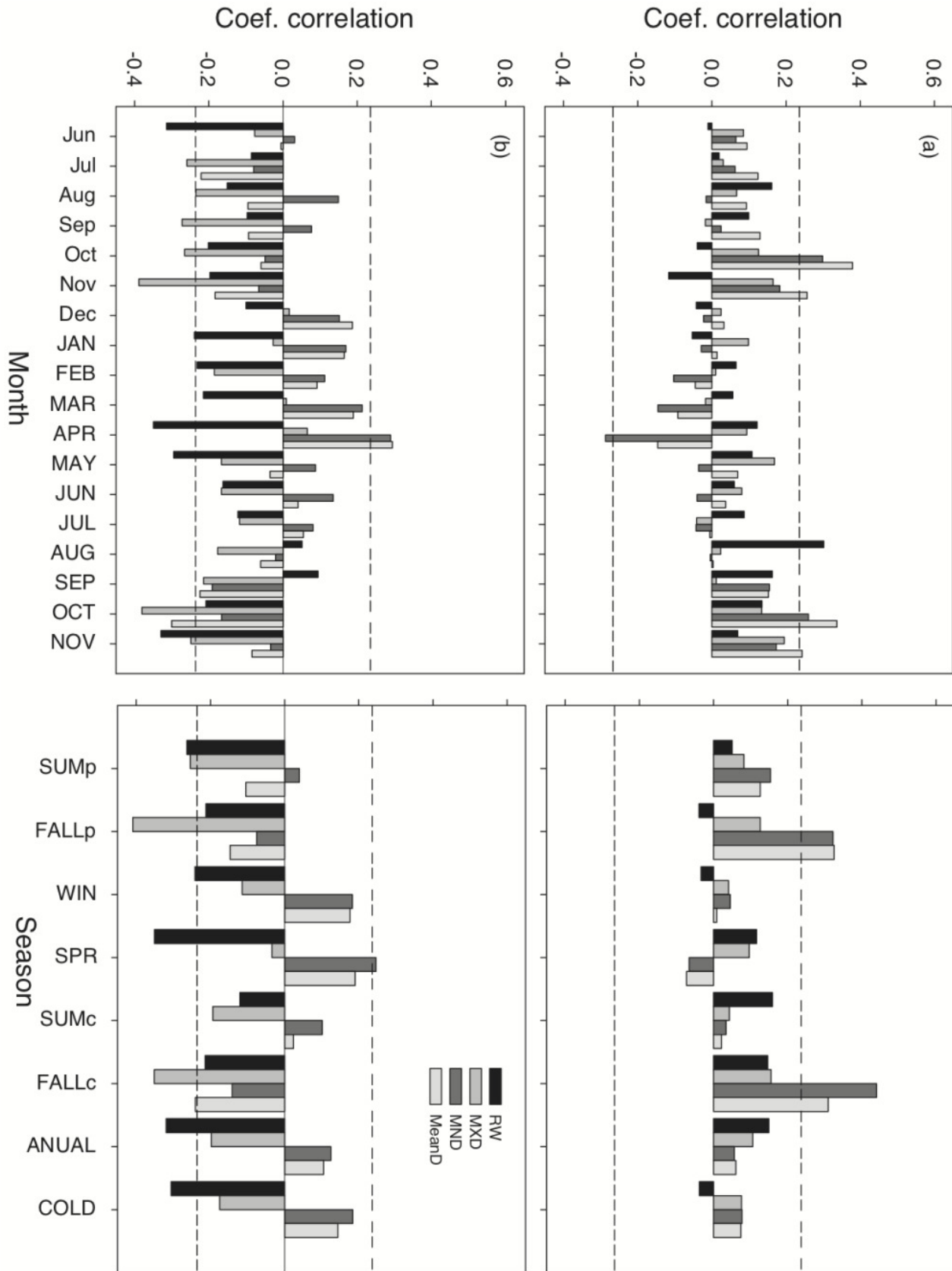
Figure 6

Temporal variation of carbon capture

(**a**) Carbon accumulation per year in the two studied conifers. Gray lines indicate the standard error. (**b**) Relationship between carbon accumulation per year and ring width in *Cupressus lusitanica*. (**c**) Relationship between carbon accumulation per year and mean wood density in *Pseudotsuga Menziesii.* **(d)** Data trend of mean annual temperature and total precipitation per year
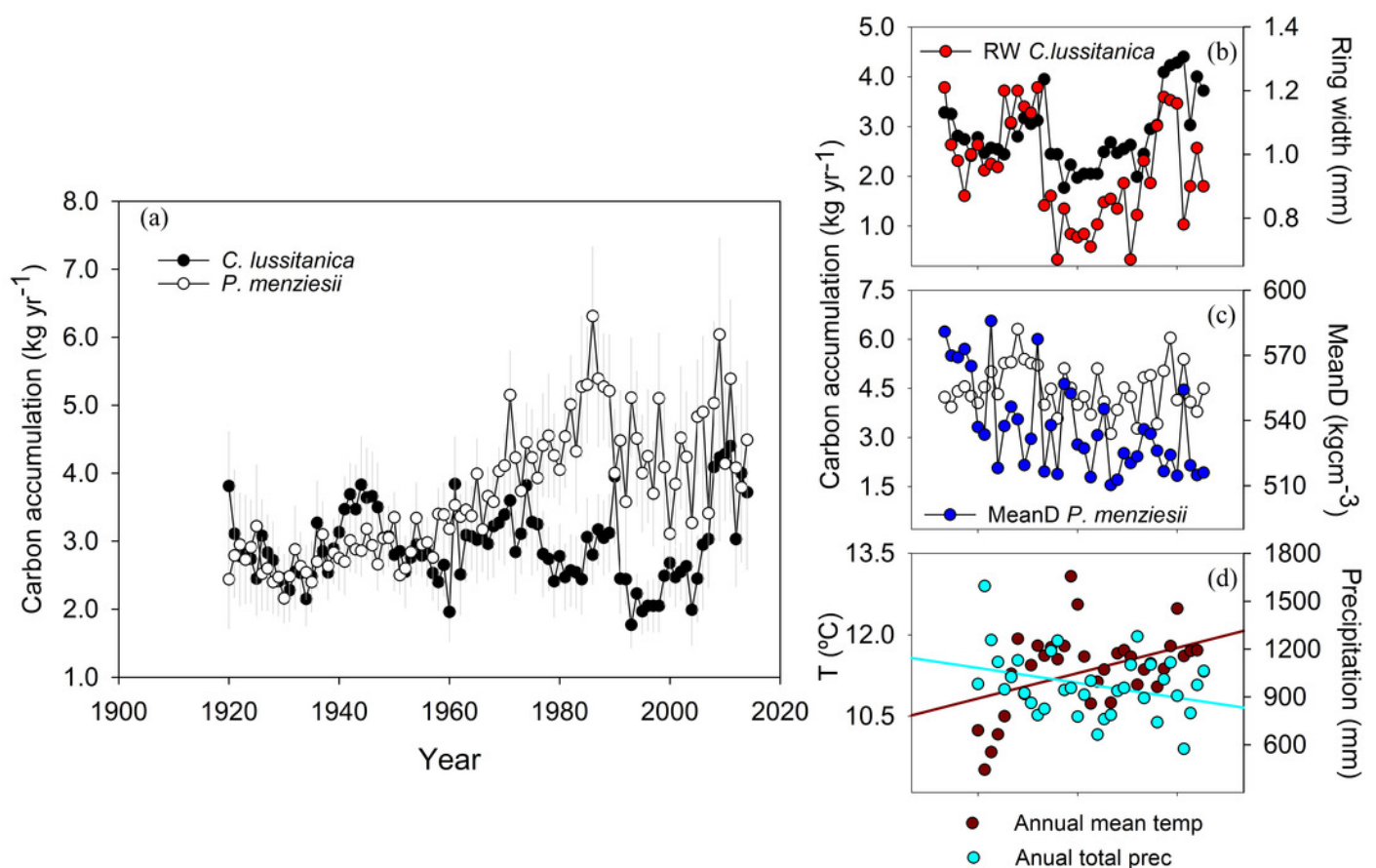
Figure 7

Principal component analysis between carbon capture and internal influences (radial growth and wood density variables) and seasonal climatic influences (precipitation and temperature) for 1975–2014

The yellow, green, blue and red circles indicate radial growth, the wood density variables, the precipitation variables, and the temperature variables, respectively. Win = winter, Fall = autumn, Spr = spring, Sum = summer. The dashed circle represents the maximum correlation with carbon accumulation. (**a**) *Cupressus lusitanica* (copheneticcorrelation = 0.79), (**b**) *Pseudotsuga menziesii* (copheneticcorrelation = 0.81).
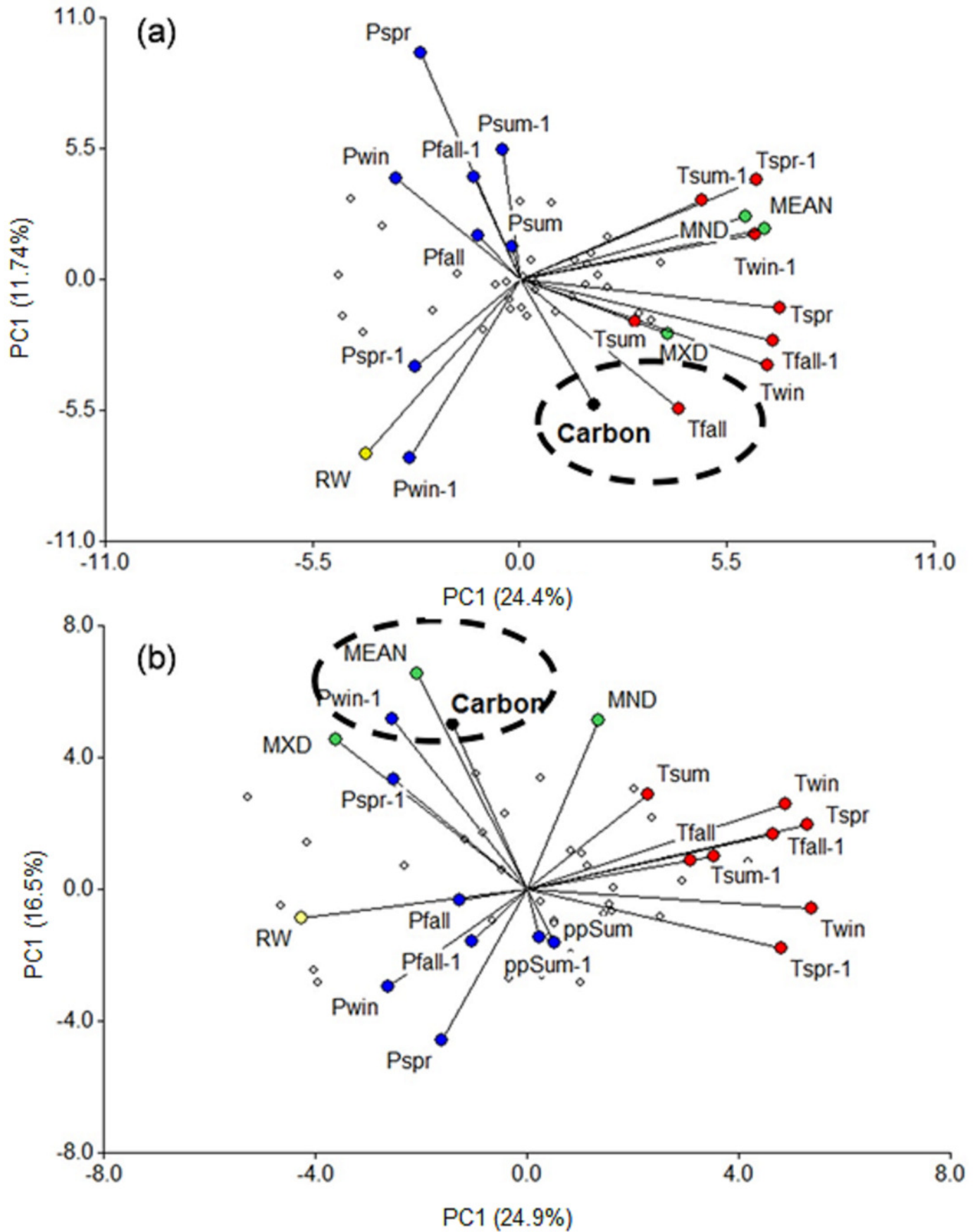
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Table 1(on next page)

Descriptive statistics of chronologies

Time span (TS), mean sensitivity (MS), expressed signal of the population (EPS), density (WD), carbon accumulation (C).

1 Table 1. Characteristics of the species studied. Period of time (TS), mean sensitivity (MS),
2 expressed signal of the population (EPS), density (WD), carbon accumulation (C).

3

Species	Trees (Cores)	TS	MS*	EPS	RW	WD (Kg m^{-3})	C (Kg yr^{-1})
C. lusitanica	15(12)	1855-2014	0.25	0.78	1.24 ± 0.35	462.3 ± 0.45(a)	2.2 ± 0.13(a)
P. menziesii	14(13)	1901-2014	0.25	0.89	1.58 ± 0.33	550.5 ± 0.78(b)	3.7 ± 0.24(b)

4 Values are annual means $\pm$ SE. Means sharing a letter were not significantly different ($p < 0.05$) using a Mann-
5 Whitney-Wilcoxon test. RW did not show significant differences

6

7

8