1 **Temporal interactions among throughfall, type of canopy and thinning drive**

2 **radial growth in an Iberian mixed pine-beech forest**

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20   **Abstract**

21   Many factors can influence tree growth over time such as different forest management

22   practices, climate or tree-to-tree interactions, especially in mixed forests. We show in

23   this work how the temporal growth patterns for Scots pine and European beech depend

24   on thinning intensity (0 %, 20 % and 40 % extraction of basal area), canopy type (pine–

25   beech vs. pine patches), throughfall and their interactions. To fulfill this objective we

26   monitored radial growth of both species using band dendrometers during a 6-year long

27   period including two very dry years. Temporal growth patterns differed between both

28   species. Whereas Scots pine showed two main peaks of growth in May-June and

29   October, European beech mainly grew from May to early September when throughfall

30   was very limited. Effects of thinning on growth generally increased for both species

31   during dry periods both at the seasonal and annual scales. The treatment with 20 % of

32   thinning intensity was the most effective at the annual scale for enhancing growth of

33   both species. However, increases in growth due to thinning were much higher in beech

34   than in pine and lasted longer. Thinning effects on pine were higher in mixed canopy

35   than in pure canopy and appeared to be modulated by throughfall. Global differences in

36   pine growth between canopy types as a function of throughfall increased during the

37   main growing season as beech canopy developed. Growth of Scots pine, but not that of

38   European beech, generally increased with throughfall which suggests that pine might be

39   more dependent for its growth on water from the soil surface layer while beech would

40   depend more on water from deeper soil layers. Our findings have implications to select

41   the most convenient thinning treatments and canopy type under a potential climate

42   change scenario characterized by warmer conditions, more severe droughts and less

43   throughfall.

44   Keywords: Dendrometer; Forest management; Growth; Mixed forest; Water

45   availability; Throughfall

46

1. Introduction

Forest researchers and managers consider that a conversion of pure coniferous forests into a mixed conifer-hardwood forest, is greatly meaningful from an ecological and economic point of view (Knoke et al., 2005; Spiecker, 2003). Mixed conifer-hardwood woodlands may provide multiple benefits such as higher biodiversity, protection from disease or stability (resilience) to disturbances including climate extremes as droughts (Knoke et al., 2005; Pretzsch et al., 2015). Additionally, mixed forests may increase stand productivity when inter-specific processes are not dominated by competition (Kelty, 1992). Nevertheless, empirical data on these topics is often nonexistent in mixed conifer-hardwood forests (Forrester and Tang, 2016), particularly long-term data are needed to elucidate mechanisms underlying observed patterns.

The growth dynamics in mixed conifer-hardwood forests are often difficult to predict due to a high number of interactions among coexisting tree species as well as to the fact that resource availability and climatic conditions change temporally and from site to site (Forrester and Tang, 2016). Although many studies have been carried out on the growth of Scots pine (*Pinus sylvestris* L.) or European beech (*Fagus sylvatica* L.) forests (Camarero et al., 1998; Ježík et al., 2011), relatively few scientific literature is available about inter-specific processes in mixed Scots pine and European beech forests (but see Pretzsch et al., 2015; Pretzsch et al., 2016 and references therein). This is one of the most widespread and economically relevant mixed forest type in Europe (Pretzsch et al., 2015b), with a high ecological amplitude spanning from mesic conditions in central Europe up to drought-prone conditions in sub-Mediterranean sites (del Río et al., 2014; Primicia et al., 2016, 2013). A more severe drought stress due to warmer conditions, higher evapotranspiration rates and more frequent heat waves (Cardil et al., 2014) are one of the major climatic concerns negatively impacting forest productivity and vitality, particularly in the Mediterranean Basin (Camarero et al., 2015). Indeed, temperature and water availability during the summer are the main climatic drivers of Scots pine (Martínez-Vilalta et al., 2008; Sánchez-Salguero et al., 2015) and European beech (Rozas et al., 2015) long-term growth in Mediterranean populations. In this respect, ongoing long-term increases in drought frequency and intensity in the Iberian Peninsula (Andreu et al., 2007; Candel-Pérez et al., 2012) are reducing the productivity and increasing the incidence of canopy dieback and mortality in Scots pine (Camarero et al., 2015; Gea-Izquierdo et al., 2014; Martínez-Vilalta and Piñol, 2002). In NE Spain

80 increased summer drought stress is impacting negatively on Scots pine growth, although

81 so far the magnitude of such punctual growth declines is not enough to counteract the

82 overall increase of growth during the 20th century (Martínez-Vilalta et al., 2008). In this

83 region, summer drought increase has even caused an upward shift (Peñuelas and Boada,

84 2003) and a dramatic growth decline of beech over the last half-century (Jump et al.,

85 2006). However, the beech populations are expanding across the mostly humid and

86 temperate areas of NW Spain, particularly in lowlands, and stand growth is expected to

87 show similar positive trends (Sánchez de Dios et al., 2016).

88 Drought-stress release of beech may be enhanced in mixed forests or stands relative to

89 pure ones (Mölder and Leuschner, 2014). However, mixing may not fully compensate

90 for lower field capacities or frequent lack of precipitation as shown by Metz et al.

91 (2016) when beech was admixed with Scots pine. Furthermore, mixing of Scots pine

92 and European beech may result in a reduction of throughfall (Primicia et al., 2013)

93 affecting tree growth negatively. Another strategy for minimizing forest drought

94 vulnerability in temperate forests (D'Amato et al., 2013; Elkin et al., 2015; Sohn et al.,

95 2016a) and also in drought-prone Mediterranean forests (Martín-Benito et al., 2010) is

96 thinning. Thinning has been recommended as a short-term solution to reduce drought

97 vulnerability by increasing resilience in mixed forests, albeit the initial enhancement of

98 resilience may be reversed as stands mature and bigger trees increase water demand

99 (D'Amato et al., 2013). Heavy thinning has been shown to improve resistance and

100 particularly resilience of Scots pine to drought events in Germany, but these benefits

101 diminish with time since the last intervention (Sohn et al., 2016a). In this case,

102 progressive decreases in growth recovery apparently resulted from decreased

103 throughfall and increased transpiration rather than from tree ageing. With regard to

104 beech, thinning can increase its growth during wet and also in dry years (Diaconu et al.,

105 2015; van der Maaten, 2013) but also affect growth negatively during dry periods by

106 reducing soil water availability layer (Geβler et al., 2004). Sohn et al., (2016a)

107 suggested that long-lasting effects on growth recovery are related to relatively larger

108 leaf area and fine-root biomass in thinned mixed stands. Consequently, they predicted

109 that European beech would recover faster from drought than Scots pine given its faster

110 expansion of crown and root systems. However, to our knowledge no single study has

111 dealt with the relationship between thinning intensity and growth response to drought in

112 mixed pine-beech forests. This is important because synergies between pine and beech

113 may result in different growth responses to thinning and drought relative to
114 monospecific stands. Furthermore, growth responses to thinning are typically studied at
115 an annual scale, but studying seasonal scales (Aldea et al., 2017; Primicia et al., 2013)
116 may be important to elucidate the mechanisms implied and the long-term effects on
117 growth. For instance, temporal patterns of rainfall and leaf phenology may interact and
118 modulate the effects of thinning on tree growth.

119 In this work we analyze whether temporal interactions among throughfall, canopy type
120 and thinning affected radial growth of Scots pine and European beech during a 6-year
121 long period (2009-2014) which included two very dry years. The research site, Aspurz,
122 is a thinned pine-beech forest located in the western Spanish Pyrenees, close to the
123 southern European limit of Scots pine and European beech. Previous research has
124 shown that throughfall is the most important growth limiting factor for Scots pines at
125 this site (Primicia et al., 2013). Aspurz can be considered as a transitional site between
126 the Eurosiberian and Mediterranean regions, respectively characterized by cool-wet and
127 warm-dry climate conditions, in which since 1920 mean annual temperatures have risen
128 +0.020 ºC year^{-1} and water surplus has significantly decreased (González de Andrés et
129 al., 2017).

130 Linear mixed models are a valuable statistical tool for describing and predicting the
131 radial-growth patterns in relation to different factors such as thinning and canopy type
132 in mixed forests (Pretzsch et al., 2015). Therefore, these models were used in this study
133 in order to fulfill the following objectives: (1) To compare intra-annual and inter-annual
134 basal-area growth patterns of Scots pine and European beech in a mixed forest; (2) To
135 evaluate the effects of canopy type and thinning on Scots pine basal-area growth
136 dynamics, and of thinning on basal area growth dynamics of European beech; and (3)
137 To assess the effects of throughfall and its interactions with other factors (i.e., month,
138 year, type of canopy and thinning) or combinations of these factors on basal-area
139 growth dynamics of Scots pine and European beech.
140
141 2. Methods
142   2.1. Study area

143 The study area is located in Aspurz (42º42'31''N, 1º08'40''W), a forest situated in the
144 western Spanish Pyrenees, Navarre. Plots are North-oriented, located at a mean altitude

145   of 642 m, a mean slope of 7 % and on a soil classified as Haplic Alisol (Blanco, 2004).

146   The climate is considered as a cold wet Mediterranean type with water deficit usually in

147   July and August with frequent frosts from winter to early spring. In the 1984-2014

148   period, mean annual precipitation was 921 mm and mean annual temperature 12.0 ºC

149   (data from Navascués weather station located at 2.7 km from the plots, 42º 43' 06'' N,

150   1º 06' 55'' W, 615 m). The forest is an even-aged mixed stand dominated by *Pinus*

151   *sylvestris L.* (Scots pine), naturally regenerated in the mid-1960s after strip-like clear-

152   cutting, with a mean dominant tree height of 20.4 m in 2014, being one of the most

153   productive Scots pine forests in Spain (Primicia et al., 2016). *Fagus sylvatica* L.

154   (European beech) is the second most abundant tree species, with a mean crown cover of

155   ca. 38 % and mean age of 35–40 years. Most beech trees were codominant or dominant,

156   although they covered all strata from suppressed to dominant ones.

157   2.2. Experimental design

158   A complete randomized block design (Andrew, 1986) was used in this study, including

159   nine plots (30 m x 40 m) installed by the Servicio Forestal del Gobierno de Navarra.

160   The experimental design can be thus specified as a split-plot (von Ende, 2001). Three

161   different thinning intensities (3 thinning intensities with 3 replicates) were applied in

162   November 1999 (0 %, 20 % and 30 % basal area removed) and March 2009 (0 %, 20 %

163   and 40 %) in the plots and in a buffer zone of 5-10 m around them. The first thinning

164   was carried out removing mainly suppressed or intermediate trees, and some dominant

165   or codominant trees with malformed stems. However, during the second thinning,

166   mainly subdominant or dominant trees were removed. The highest thinning intensity

167   was increased up to the 40 % of the basal area during the second thinning in accordance

168   to the silvicultural trends applied on similar surrounding stands at that moment.

169   Similarly, following the silvicultural guidelines applied in Navarre on mixed stands

170   with beech as secondary species, only Scots pine trees were thinned.

171   Within each plot, two discontinuous subplots can be distinguished: mixed beech-

172   pine and pure pine subplots (hereafter abbreviated as MC and PC sub-plots). To

173   establish the subplots, first we divided each plot into 300 2 m x 2 m quadrats by using

174   banderoles. Then, we delimitated the projection on the ground of beech canopy taller

175   than 2 m by using plastic bands. Lastly we used plot maps with georeferenced trees and

176   a grid of 2 m x 2 m quadrats to draw the contours of each type of subplot. In each plot,

177   we randomly selected three Scots pines in PC sub-plots, three Scots Pines and three

178 beeches in MC subplots. Only dominant or codominant trees were selected. Six

179 treatments are thus determined for pines (P) and three for beeches (B): BMT0 (beeches

180 in unmanaged mixed beech-pine), PMT0 (pines in unmanaged mixed beech-pine),

181 PPT0 (pines in unmanaged pure pine), BMT20 (beeches in mixed beech-pine in

182 moderate thinning), PMT20 (pines in mixed beech-pine in moderate thinning), PPT20

183 (pines in pure pine in moderate thinning), BMT40 (beeches in mixed beech-pine in

184 severe thinning), PMT40 (pines in mixed beech-pine in severe thinning) and PPT40

185 (pines in pure pine in severe thinning).

186 2.2.1. Seasonal dynamics of radial increment

187 In total, 54 Scots pine trees (6 per plot) and 27 beeches (3 per plot) were selected to

188 assess seasonal patterns of radial increments considering thinning intensities, canopy

189 type, throughfall, date and their interactions. Band manual dendrometers (DB20

190 Environmental Measuring Systems, Brno, Czech Republic) were placed at about 1.3 m

191 height around the stem after removing carefully the rhytidome (dead bark) to quantify

192 cumulative radial growth. We read them from March 2009 to November 2014 with a

193 biweekly frequency from March to June, when most growth occurs in the study species

194 (Camarero et al., 2010) and monthly from July to November. To avoid biases during

195 recording, all measures were always taken before midday, and they were never taken

196 after a rainy day. Finally, the cumulative radial growth data was converted to basal area

197 increment assuming a circular shape of the stems. These data were substracted from the

198 previous data measured and the result divided by the days elapsed between

199 measurements to calculate growth rates as daily basal-area increment (hereafter BAIr, in

200 $cm^2 \ day^{-1}$).

201 2.3. Throughfall

202 We measured throughfall monthly using 54 collectors placed in the plots (3 per subplot)

203 in mixed and pure areas. Each collector consisted of a plastic funnel (diameter 23.5 cm)

204 mounted onto a 25 L opaque polyethylene collection container. A filter of fiber-glass

205 coated with polyethylene (1.5 mm mesh size) was placed into the neck of the funnel to

206 avoid the entrance of coarse debris. Throughfall data were regressed with monthly

207 precipitation data obtained from the nearby Navascués station in the nine plots

208 considering mixed and pure patches within each plot (18 regressions) to estimate daily

209 throughfall in each container (r^2= 0.88 - 0.99, $p < 0.001$).

210   2.4. Xylogenesis

211 The cambium generates tracheids passing through different developmental stages. The

212 xylem differentiation process is called xylogenesis and can be studied by repeatedly

213 taking and observing wood samples (Fukuda, 1996). Two dominant or codominant

214 Scots pines (n = 18) and one European beech per plot (n = 9) were randomly selected

215 for this purpose. Xylogenesis was monthly monitored from April to December 2011 by

216 sampling wood microcores (2 mm in diameter, 1 - 2 cm in length) at a height of 1.3 m

217 following a spiral around the stem using a Trephor borer (Rossi et al., 2006).

218 Microcores were always collected in areas apart from dendrometers to avoid distorting

219 dendrometer records. The methods of processing, sectioning and staining micro-core

220 wood sections are described with more detail elsewhere (Antonova et al., 1983;

221 Primicia et al., 2013). For both species, we measured the intra-annual radial growth in

222 wood microcores. Microcore data were used to validate the dendrometer recordings and

223 to justify its use for representing radial growth and not swelling-shrinking dynamics of

224 the trunk (Sheil, 2003). Lastly, correlations between radial-increment measurements

225 taken by dendrometers and those obtained from microcores were calculated to justify

226 the accuracy and reliability of the growth measurements recorded by dendrometers.

227

228   2.5. Statistical analyses

229 All models and the statistical analyses were carried out using R 3.2.4 (R core

230 development team, 2017). Linear mixed-effects models were used to assess the effects

231 of type of canopy (pure pine, mixed beech-pine), thinning intensity (0%, 20%, 40%),

232 throughfall (continuous variable), month (April-October), year (2009-2014) and their

233 interactions on Scots pine and beech growth (BAIr) using the "nlme" package (Pinheiro

234 and Bates, 2000), following a split-plot design with repeated measures. Thinning

235 intensity, canopy type, throughfall, month and year were included in the model as fixed

236 effects, and tree nested in plot, as random effect. Additionally, we included an

237 autoregressive correlation structure of first order to account for the repeated measures

238 on the same tree, and a variance structure, if the residual spread differed per month

239 (Pinheiro and Bates, 2000). Thus, the proposed model was stated as follows:

240

241      $BAIr = I +$ thinning * canopy * throughfall + month + year + tree:plot +

242   corAR(tree:plot) + varIdent (month)   (1)

243

244   where: BAIr represents the daily basal area increment measured with dendrometers; *I* is

245   the intercept; thinning, canopy and throughfall represent the study treatments; month

246   and year are the sampled month and year for which BAIr has been estimated; tree:plot, a

247   random term specifying the effect of individual trees nested within each plot;

248   corAR(tree:plot), the autoregressive correlation structure to account for the repeated

249   measures on each tree within each plot; varIdent (month), variance structure to account

250   for the different spread of residuals per month. Throughfall was included in the model

251   as a continuous variable considering the sum of 10 days before each dendrometer

252   sampling date to take into account potentially lagged climate-growth responses

253   (Camarero et al., 1998; Primicia et al., 2013).

254   We compared nested models with and without the random and the correlation and

255   variance structures to analyse their appropriateness calculating the likelihood ratio test

256   using the restricted maximum likelihood estimation procedure. Similarly, the

257   significance of the fixed effects was determined by comparing nested models with and

258   without the fixed terms, but using the maximum likelihood estimation procedure (Zuur

259   et al., 2009). When interpretable, significant three- and two-way interactions where

260   described. If there was no evidence for dependence between factors, main factors were

261   analyzed (Underwood, 1997).

262   Throughfall intervals were delimeted in the graphs in order to highlight the growth

263   patterns, to show significant differences in growth between different levels of thinning,

264   canopy type or month for each throughfall interval by using Helmert contrasts

265   (Chambers and Hastie, 1992), and to describe the results more clearly. Five throughfall

266   intervals ([0-10], [10-20], [20-40], [40-80], >80 mm) were selected by using histograms

267   to provide the most uniform distribution of measurements.

268

269   3. Results

270   3.1. Relationships between radial-increment dynamics and xylogensis

271   Similar values of radial increment for Scots pine and European beech were recorded

272   using dendrometers and xylogenesis during 2011 as shown in Figure 1. Measurements

273   between the two methods were highly correlated (r=0.905 for Scots pines and r=0.951

274   for European beeches). Therefore, measurements of radial growth based on

275   dendrometers allow interpreting and discussing adequately the results of this work.

276   3.2. Annual and seasonal trends of tree growth

277   Month and year significantly influenced BAIr in both Scots pine and European beech

278   (Table 1, $p < 0.001$). Intra-annual growth patterns differed between both species (Figure

279   2). BAIr in Scots pine showed two main peaks in the year, a major peak in late spring

280   from the beginning of May (Day of the Year, DOY 105) to the middle of July (DOY

281   192), centered in mid May and June, and the other in early autumn (October,

282   specifically from DOY 285 to 303). However, the temporal growth pattern was different

283   for European beeches with a peak from late spring (DOY 130) to early autumn (DOY

284   255) from May to early September, centered in June and July (Figure 2), being

285   throughfall very limited in the latter. The highest growth rates were observed in late

286   May and late June in the case of Scots pine (2.4 cm^2 day^{-1}) and European beech (7.0

287   cm^2 day^{-1}), respectively. The growing period during the six study years took around 105

288   days considering the two main peaks for Scots pines and 125 days for European beech.

289   In 2011, the onset of xylogenesis was 60-90 and 122-152 DOY, and the cessation

290   occurred in 270 and 276 DOY for Scots pine and European beech, respectively.

291   3.3. Type of canopy and thinning

292   A significant interaction (p= 0.011) between type of canopy and month was found for

293   Scots pine (Table 1). Thus, except for August, BAIr in Scots pines was significantly

294   higher in pure patches during the months when most growth occurred (May to July and

295   October) but no significant differences between pure and mixed patches were found at

296   low BAIr values (i.e., April and September) (Figure 3a). On an annual basis, BAIr in

297   pure pine patches was on the average 22.1 % (range 17.3 to 28.2%) higher than in

298   mixed pine-beech patches, being these differences significant ($P < 0.05$) for all years

299   excepting 2012 (Figure 3b).

300   Thinning interacted significantly with month and year in Scots pine and with month in

301   European beech (Table 1, Figure 4). Thinning effects on Scots pine were only

302   significant ($P < 0.01$) in May (Figure 4a) but for European beech significant differences

303   ($P < 0.01$) were observed from May to September (Figure 4c). In Scots pine, growth

304   differences in moderately (20% of removed basal area) and severely (40% of removed

305   basal area) thinned plots relative to unthinned plots diminished from almost 50% in

306   April to about 10% in June. Then, in July and August differences remained at 10% for

307   moderate thinning but increased to 25-30 % in severe thinning (Figure 4a). In contrast,

308 beech differences relative to unthinned plots were almost constant from May to

309 September (around 40%) in severe thinning, being the effects of moderate thinning

310 much higher especially from June (80%) to August (120%) (Figure 4c). On an annual

311 basis, significant differences for pine occurred only in 2011 ($P < 0.001$) and for beech

312 from 2009 to 2012 ($P < 0.001$), and in 2013 (p < 0.01) and 2014 ($P < 0.05$) (Figures

313 4b,d). Growth of pine in thinned plots relative to that of unthinned plots showed a

314 unique positive peak in 2011 for both moderate (58%) and severe thinning (40%); by

315 2014, five years after thinning, the effect diminished until 20% and -5% under severe

316 and moderate thinning, respectively (Figure 4b). In contrast, beech exhibited a

317 progresive growth increase under moderate thinning from 2009 (83%) until 2012

318 (123%), to decrease afterwards to a minimum in 2014 (60%); under severe thinning

319 relative growth increased from 20% in 2009 to a plateau from 2010 to 2012 (around

320 48%) decreasing subsequently to 24% in 2014 (Figure 4d).

321   3.4. Throughfall influences tree growth dynamics

322 Throughfall significantly influenced BAIr in both Scots pine and European beech and it

323 was included in most of the significant interactions with other variables (Table 1).

324   3.4.1. Scots pine

325 The interaction between throughfall and type of canopy changed monthly as no

326 significant effects of canopy on BAIr at different throughfall levels were found in April

327 and November, but significant effects were found for the other months, particularly

328 during the months with highest tree growth ($P = 0.017$; Table 1; Figure 5). Thus, global

329 canopy effects (pure > mixed) on pine growth increased from May to July. Significant

330 effects between canopy types were found in May, June (0-10 mm and 10-20 mm) and

331 July (0-10 mm and 20-40 mm). It is also interesting to point out that no canopy effects

332 on BAIr were detected above 20-40 mm.

333 The interaction between throughfall and thinning changed depending on the type of

334 canopy (Figure 6). Thus, in pure patches, thinning significantly affected BAIr at 0-10

335 mm in pure (0% > 20% = 40%, $P = 0.01$) and mixed patches (20% > 0%, 20% = 40%,

336 0% = 40%, $P = 0.05$), but the effects were relatively small. However, thinning did

337 significantly ($P = 0.001$) affect BAIr in mixed patches at throughfall intervals 20-40

338   mm (20% > (40% = 0%)) and 40-80 mm ((20% =40%) > 0%) being the effects bigger

339   than at 0-10 mm .

340   The interaction between thinning and throughfall also changed monthly ($P < 0.046$;

341   Table 1) and annually ($P < 0.001$; Table 1). The monthly change is not shown as the

342   pattern is difficult to interpret. Significant relationships between throughfall and

343   thinning were detected in 2010 and 2013 (40-80 mm throughfall) and especially in

344   2011, the driest year of the study period (10-20 mm, 20-40mm and 80-160 mm)

345   (Appendix, Figure A.1a). Normally, higher values of throughfall were linked to greater

346   growth for Scots pine, in most years except for 2011 (Table 1, throughfall * year, $P <$

347   0.001, Figure A.1a), and especially during the growing season (i.e., May-July) (Table 1,

348   throughfall * month, $P < 0.01$; Figure 7). Particularly, BAIr increased concomitantly

349   with throughfall in May, June, August and October, whereas generally no matching was

350   found in relation to throughfall in April, July,September and November.

351   3.4.2. European beech

352   Unlike for pine, the interaction between throughfall, thinning and year was not

353   significant for beech ($P = 0.987$; Table 1). However, significant thinning effects were

354   observed in 2011 (0-10, 10-20 mm) and 2012 (0-10, 10-20, 20-40 mm), the two driest

355   years, and in 2010 (40-80 mm) and 2013 (20-40 mm) (Figure A.1b). Also differently to

356   pine, monthly BAIr generally did not increase concomitantly with throughfall , being

357   the interaction between throughfall and month not significant ($P =0.309$; Table 1;

358   Figure 7B).

359   3.4.3. Canopy and thinning influence throughfall

360   Moderate and severe thinning presented the highest values of throughfall at annual scale

361   (Appendix, Figure A2.) . Significant differences were found in the mean annual

362   amounts of throughfall as a function of canopy type ($P < 0.01$). Containers placed in

363   mixed patches received less amount of throughfall than those in pure patches, especially

364   in unmanaged mixed beech-pine plots. Thinning increased average throughfall only in

365   mixed patches, 29.2% and 21.5% in moderate and severe thinning, respectively.

366   4. Discussion

367   4.1. Temporal and seasonal trends of tree growth

368 Tree growth and cambial resumption in both Scots pine and European beech started

369 from April to May coinciding with a raise in air temperatures and with enough soil

370 humidity as occur in other boreal, temperate and Mediterranean forests (Camarero et al.,

371 2010; Čufar et al., 2008; Deslauriers et al., 2008; Schmitt et al., 2004). However,

372 differences in daily basal area increments patterns were found between both species

373 which presented the main growth peaks in May (pine) and June (beech) (Fig. 2). These

374 different growth peaks agree with xylogenesis studies carried out in nearby sites

375 (Martinez del Castillo et al., 2016). Scots pine exhibited a sharp reduction in growth in

376 mid-July, similarly to a previous study at this site (Primicia et al., 2013), whereas

377 European beech showed high growth until early September. This growth of beech

378 during summer might be related in part to the creation of parenchyma as the temperature

379 was raised (Morris et al., 2016). The reduction in BAIr in Scots pine matched with the

380 summer drought (i.e., low amounts of throughfall and high evapotranspiration rates) and

381 was probably caused by a decline in the cambial activity (Camarero et al., 2010, Gruber

382 et al., 2010), and possibly stem shrinkage (Zweifel et al., 2001). Relatively high growth

383 of beech during the summer dry period, as compared with pine, appears to be caused by

384 tapping of water by beech roots from deep soil horizons despite fine roots of pine and

385 beech reach highest densities at the upper soil layers (Curt and Prévosto, 2003).

386 However, as stands mature beech roots become predominant throughout the soil profile.

387 This seems to be the case at our experimental plots as sampled beech trees are dominant

388 or codominant. Furthermore, beech fine roots may shift deeper within the soil profile in

389 response to drought (Meier and Leuschner, 2008), and even show highest surface area

390 in deeper soil horizons in mixed stands (Bolte and Villanueva, 2006). Taken altogether

391 these patterns would explain the high growth rates of beech during the dry period linked

392 to its greater capacity to uptake soil water, but more research needs to be carried out to

393 link root functioning with wood formation. In contrast, Martinez et al. (2016) and

394 Michelot et al. (2012), found a severe reduction of beech cambial activity in mid-

395 August. A second growing peak was found for Scots pine from September to October;

396 and this bimodal pattern has been previously observed by analysing wood microcores in

397 the study site (Primicia et al., 2013) and elsewhere (Linares et al., 2009). However,

398 under colder conditions, Scots pine, that has a Euro-Siberian distribution, may show a

399 unimodal pattern (Camarero et al., 1998) suggesting an interaction of climate with other

400 factors to drive xylogenesis plasticity. In this context, unimodal patterns have been

401 reported for European beech, which has mainly an Euro-Siberian distribution.

402

403   4.2. Effects of canopy type and thinning on tree growth dynamics

404 Beech presence in Aspurz has caused an increase in average yearly reduction of BAIr

405 for Scots pine in mixed relative to pure patches from 17% in 2007-2008 (Primicia et al.,

406 2013) to 27% in 2014. This reduction is expected to increase as more beeches reach the

407 upper part of the canopy. Scots pine growth reduction resulting from competition with

408 beech has also been documented in other Pyrenean mixed forests (del Río et al., 2014).

409 The fact that this growth reduction pattern occurred from May to October suggests that

410 Scots pine and beech may be competing for different types of resources (i.e., light,

411 water and nutrients) or a combination of resources along the year. Competition may be

412 particularly intense in May when Scots pine shows its highest growth and sprouting and

413 accelerated expansion of beech leaves occurs, and in June when pines reach its second

414 highest growth value and beech its maximum growth (Fig. 2). During this period

415 competition for water and nutrients needed for shoot, leaf and flower production may be

416 important. Indeed, significantly lower soil $N-NH_4^+$ content in mixed than in pure

417 patches was detected in the same plots in 2007 and 2008 which suggests higher

418 ammonium uptake in mixed patches due to beech presence (Primicia, 2012). Beech may

419 have also outcompete pine by decreasing throughfall in mixed patches by 11.4% during

420 the leafless season and 20.5 % during the leafed season (Primicia, 2012). This effect on

421 growth was apparently higher in July and August, the driest months, when throughfall

422 reduction was higher (see figure 2 and A.1.). On a longer timescale, light was probably

423 the most limiting factor for suppressed pine trees growing nearby dominant or

424 codominant beech trees, whose leaves sprouted in April-May and were fully expanded

425 in September (Arretxe, 2010).

426

427   Thinning usually leads to improved growth in the short term (Elkin et al., 2015;

428 Linares et al., 2009; Primicia et al., 2016), an effect which can be explained by an

429 increase in soil water and nutrients availability to competing trees (Blanco et al., 2005),

430 and by an improved growth and photosynthetic capacity due to the increment of the

431 foliar mass of the crown (Aussenac, 2000). Absolute and relative increases in growth

432 due to thinning were much higher in beech than in Scots pine and lasted longer (Fig. 4).

433 This is not surprising given the fact that cover of beech at this site is increasingly

434 expanding relative to that of pine (Primicia et al., 2013) by taking advantage of its high

435   efficiency in space occupation (Pretzsch and Schütze, 2005). Additionally, based on

436   mean temperature and annual precipitation for Aspurz, conditions appear to be more

437   favorable for European beech than for Scots pine (Pretzsch et al., 2016).

438

439   Scots pine and beech showed different monthly and annual responses to thinning

440   (Fig. 4, Table 1). Positive growth differences between thinned and unthinned plots for

441   both species increased in July and August, the two driest months, indicating the efficacy

442   of thinning to mitigate drought stress. However, while severe thinning allowed Scots

443   pine to maintain relatively higher growth rates during the drought period, in the case of

444   beech the highest growth rates were achieved with moderate thinning. Wind speed

445   within the stand and evaporation may have increased following tree reduction, more so

446   at severe thinning, enhancing transpiration rates (Aussenac, 2000). Additionally, larger

447   crown surface area (Sohn et al., 2016b) and increases in understory vegetation cover

448   (unpublished results) under severe thinning may have also contributed to increase

449   transpirational demand. This would explain the more positive effect of moderate

450   thinning on beech growth, as less transpiration in this treatment than under severe

451   thinning could have resulted in a water balance more favorable. In this context, thinning

452   intensity probably did not affect so much between different thinning intensities in

453   transpiration of Scots pine, a drought-avoider species (Zweifel et al., 2001). Pine

454   probably reduced its stomata conductance at critical periods during the daytime as

455   indicated by low relative growth rates because of low surface soil water potential

456   (unpublished results). Consequently, severe thinning might have been more effective

457   than moderate thinning to mitigate growth reduction especially if root system

458   development of pines increased (Kneeshaw et al., 2002) and/or average fine-root depth

459   decreased (Giuggiola et al., 2016) with thinning intensity. The latter would be a

460   response to increased soil water availability in shallower soil depths resulting from an

461   increase in throughfall with thinning intensity

462

463   On an annual basis growth in thinned plots relative to that of unthinned plots showed a

464   positive peak in 2011 under moderate and to a less extent under severe thinning for

465   Scots pine, and a positive maximum in 2011 and 2012 under moderate thinning for

466   beech. These were the driest years during the study period, especially 2011 (663 mm of

467   rainfall; 1,042 mm of mean in 2009-2014 period; data from Navascués weather station;

468   Appendix, Figure A.3.). Therefore, thinning also mitigated growth reduction during

469 drought of Scots pine and European beech at an annual scale as it has been shown for

470 Scots pine in Switzerland (Giuggiola et al., 2013) and Central Europe (Sohn et al.,

471 2016a) and for beech in southwestern Germany (van der Maaten, 2013). Thus, if mean

472 annual temperature continues increasing and water surplus continues decreasing over

473 the long term at this region (González de Andrés et al., 2017), a 20 % thinning intensity

474 treatment could be the more efficient management option in terms of maximizing

475 growth.

476

477   4.3. Throughfall influences growth dynamics

478 Monitoring both intra-annual and inter-annual growth dynamics is a necessary approach

479 for characterizing the tree growth responses to different forest management treatments

480 such as thinning intensity and canopy type (Michelot et al., 2012). However, to

481 elucidate some mechanisms underlying the observed patterns it can be very relevant

482 looking at throughfall changes in relation to these treatments.

483 Global differences in pine BAIr between canopy types (pure > mixed, see Fig. 5) as a

484 function of throughfall increased from May to July, when most pine growth occurred.

485 Shoot elongation and leaf expansion of beech during this period apparently resulted in

486 less light (Pretzsch et al., 2016) and water (Primicia, 2012; Primicia et al., 2013)

487 reaching pine needles and roots, respectively, which could have lead to reduced growth

488 in mixed patches. Significant differences between canopy types were mainly observed

489 at low throughfall (0-10 mm) due in part to lower growth variability, and to a less extent

490 at medium flow (20-40 mm). No significant differences between canopy types were

491 found at high throughfall (40-80 mm, 80-160 mm) suggesting a throughfall threshold to

492 trigger these differences. These patterns may imply an increase in growth differences

493 between canopy types if the frequency of high throughfall events decreases, and that of

494 low-medium throughfall events increases. Furthermore, unlike in pure-canopy patches,

495 rainfall interception in mixed-canopy patches caused the reduction of maximum

496 throughfall input (i.e., the disappearance of throughfall interval 80-160 mm) into the

497 soil in May and October, and consequently a direct reduction of pine growth occurred

498 given the positive relationships between growth and throughfall amounts (see Fig. 7).

499 This pattern may strenghten as more beeches reach the upper canopy level, contributing

500 further to growth differences between canopy types. However, growth reduction over

501 time in mixed patches in response to decreasing throughfall probably will increase faster

502 in pine than in beech. This is because, at this site, water use efficiency (iWUE, i.e. the

503 ratio of assimilated carbon to water lost through stomata) of beech has increased more

504 (ca +22%) than that of pine (ca +12%) from 1980 to 2013 apparently as an adaptation to

505 increasing dryness (González de Andrés et al., 2017).

506 Although the double interaction thinning* canopy and the triple interactions

507 thinning*canopy* month or year were not significant for pine growth, the interaction

508 thinning* canopy changed significantly as a function of throughfall. This effect was

509 especially noticeable in mixed patches with throughfall of 20-40 mm and 40-80 mm in

510 which average growth was higher under moderate thinning than in severely thinned or

511 unthinned plots. In other words, the throughfall changed the thinning effects in mixed

512 patches but not in pure patches. This effect may have been caused by nutrients,

513 especially nitrates (Primicia, 2012), washed away by throughfall from the beech canopy

514 and the forest floor which is thicker in mixed patches. The higher effect of thinning on

515 pine growth in mixed patches under moderate thinning might be related to the lower

516 basal area of beech at these plots (Primicia et al., 2016) which would have resulted in

517 less competition on pines. A similar pattern was observed for the interaction between

518 thinning and type of canopy for throughfall (Figure A.2) indicating that the above

519 response of pine growth to thinning in mixed patches can also be generated by

520 differences in throughfall amounts among thinning intensities. Furthermore, in normal

521 or wet years significant thinning effects on pine and beech as a function of throughfall

522 were scarce. However, their frequency considerably increased in 2011 and 2012 in

523 beech for low-medium throughfall, and in 2011 in pine for low, medium and high

524 throughfall. The 2011 and 2012 years were especially dry, therefore these patterns

525 confirm that thinning treatments were effective to reduce some of the negative effects of

526 drought on growth, and that the main limiting resource during these years was water.

527 Growth of Scots pine generally increased with throughfall, especially in those months

528 when BAIr was higher. This confirms the role played by precipitation to enhance radial

529 growth in similar forests subjected to Mediterranean seasonal droughts (Bogino et al.,

530 2009; Camarero et al., 2010; Gutiérrez, 1989; Primicia et al., 2013)(Bogino et al., 2009;

531 Camarero et al., 2010; Gutiérrez, 1989; Primicia et al., 2013). However, monthly beech

532 growth was not generally related to throughfall. These two distinct patterns suggest that

533 pine might be more depending for its growth on water recently incorporated into the soil

534 (i., soil surface layer) while beech might depend relatively more on water from previous

535   rainfall events (i.e., deeper soil layers). These difference strategies could be further

536   investigated analyzing the isotope discrimination of oxygen and hydrogen in xylem and

537   soil water to identify the isotopic signature of water sources.

538   5.   Conclusions

539   Scots pine and beech showed bimodal and unimodal temporal growth patterns,

540   respectively, but the spring growth peak was the most important in both species The

541   relatively high growth of beech during the summer dry period, as compared with pine,

542   could be explained by tapping of water by beech roots from deep soil horizons.

543   Competition between Scots pine and beech appeared to be high in May and June

544   coinciding with their respective peaks of growth. As beech competition for light

545   intensifies, pine growth is progressively diminishing in mixed patches relative to pure

546   patches. Absolute and relative increase in growth due to thinning were much higher in

547   beech than in Scots pine, providing to beech a high efficiency in space occupation in

548   sites with favorable growing conditions (e.g., drought stress). Differences in growth

549   between thinned and control plots for both species increased during the driest months

550   and years indicating the efficacy of thinning to mitigate drought stress. On an annual

551   basis moderate thinning appeared to be the most efficient treatment to maximize

552   growth. Finally, interactions between throughfall and the analyzed factors explain

553   mechanisms underlying pine growth reduction in mixed patches relative to pure

554   patches, differences in thinning effects on pine growth in pure and mixed patches,

555   higher efficiency of thinning during drought periods, and why beech trees were capable

556   of growing during the dry months.

564

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802   Table 1. Likelihood ratio test (LRT) and significance of treatments (thinning intensity,
803   canopy type, throughfall, month and year) on daily basal area increments of Scots pine
804   and European beech considering the 2009-2014 period. Bold LRT values indicate
805   significant effects ($P < 0.05$).

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| Variable	Scots pine		European beech	
	LRT	*P* value	LRT	*P* value
Thinning (TH)	1.837	0.39	5.599	0.061
Canopy type (C)	**4.056**	**0.044**	Not applicable	Not applicable
Throughfall (T)	**860.829**	**<0.001**	**69.709**	**<0.001**
Month (M)	**1,406.414**	**<0.001**	**983.442**	**<0.001**
Year (Y)	**139.301**	**<0.001**	**99.588**	**<0.001**
TH*C	1.651	0.43	Not applicable	Not applicable
TH*T	**6.707**	**0.034**	1.989	0.370
TH*M	**33.283**	**0.006**	**134.203**	**<0.001**
TH*Y	**25.383**	**0.005**	10.16	0.426
C*T	2.552	0.11	Not applicable	Not applicable
C*M	**19.864**	**0.011**	Not applicable	Not applicable
C*Y	8.561	0.13	Not applicable	Not applicable
T *M	**188.626**	**<0.001**	7.135	0.309
T *Y	**120.568**	**<0.001**	**32.464**	**<0.001**
TH*C* T	**6.059**	**0.041**	Not applicable	Not applicable
TH*C* M	10.851	0.82	Not applicable	Not applicable
TH*C* Y	10.160	0.43	Not applicable	Not applicable
TH* T *M	**6.152**	**0.046**	8.179	0.771
TH* T *Y	**73.419**	**<0.001**	2.697	0.987
C* T *M	**18.659**	**0.017**	Not applicable	Not applicable
C* T *Y	9.715	0.084	Not applicable	Not applicable

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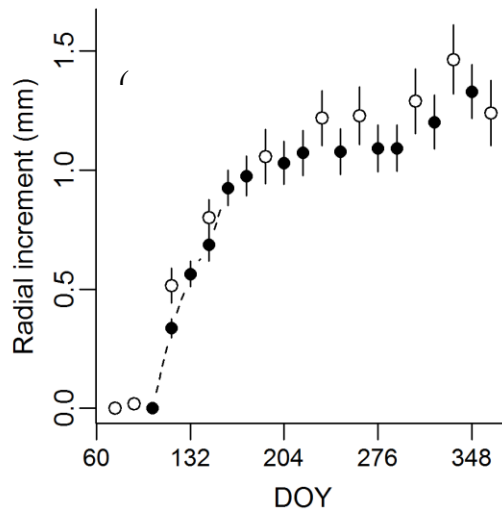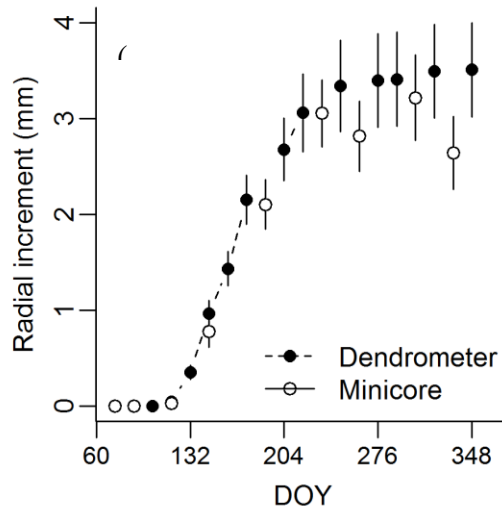
Figures

811   Figure 1. Cumulative radial increment for European beech (a) and Scots pine (b) from
812   April to December in 2011 using micro-cores and band dendrometers. DOY stands for
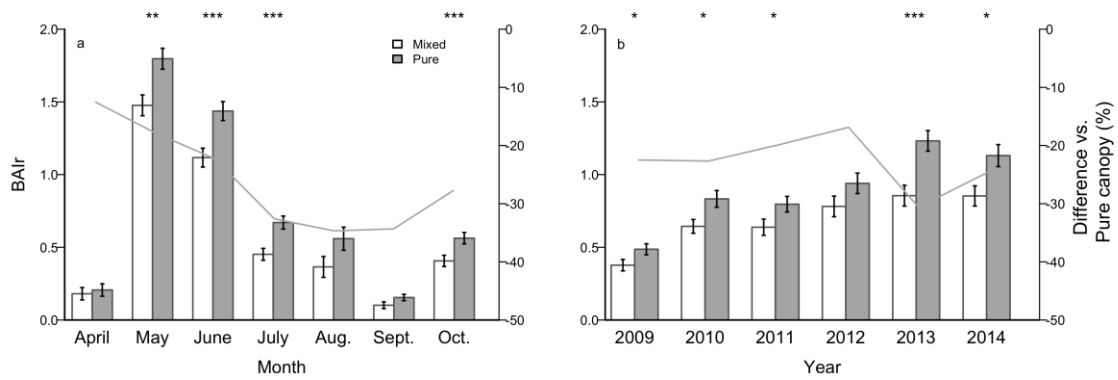813   day of the year.
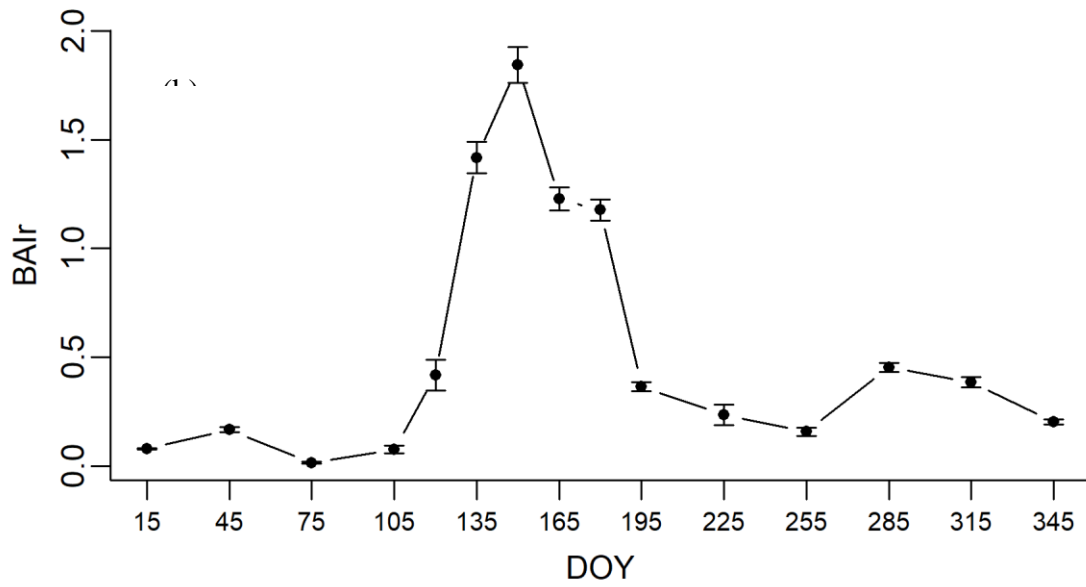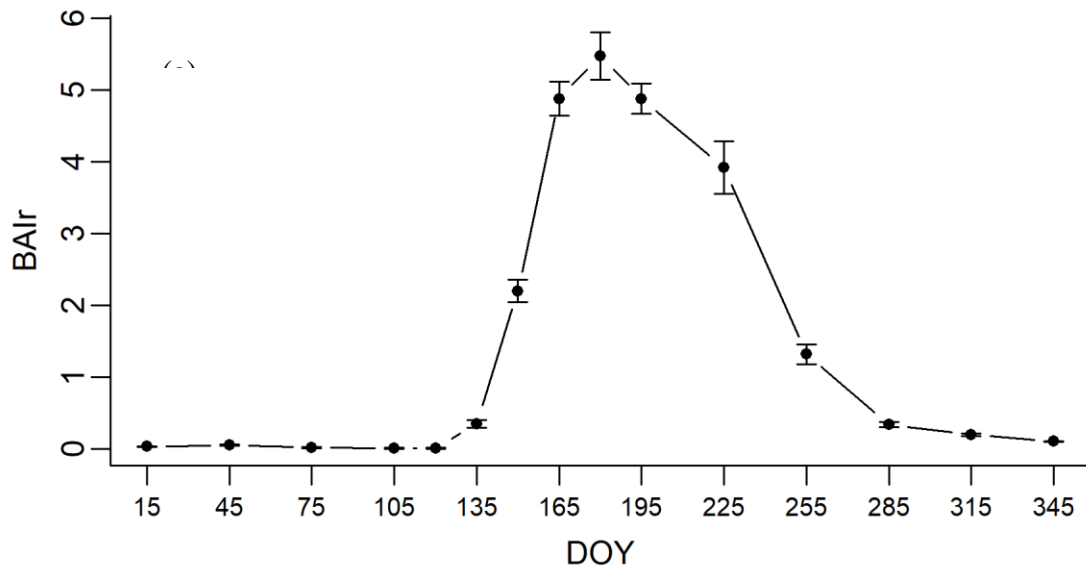
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816   Figure 2. Daily basal area increment (BAIr, cm^2 day^{-1}; values are means ± SE) for

817   European beech (a) and Scots pine (b) and from 2009 to 2014. DOY stands for day

818   of the year.

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820

821   Figure 3. Monthly (a) and yearly (b) basal area increment rates (BAIr, cm^2 day^{-1}) of

822   Scots pine as a function of type of canopy (pure pine patches, mixed pine-beech

823   patches) for the growing-season months during the 2009-2014 period. Significant

824   differences in BAIr between types of canopy are indicated as follows: * $P<0.05$; **

825    $P<0.01$; *** $P<0.001$. Percentage pine growth reductions of mixed patches relative to

826   pure patches (light lines) are shown on the right y axis.

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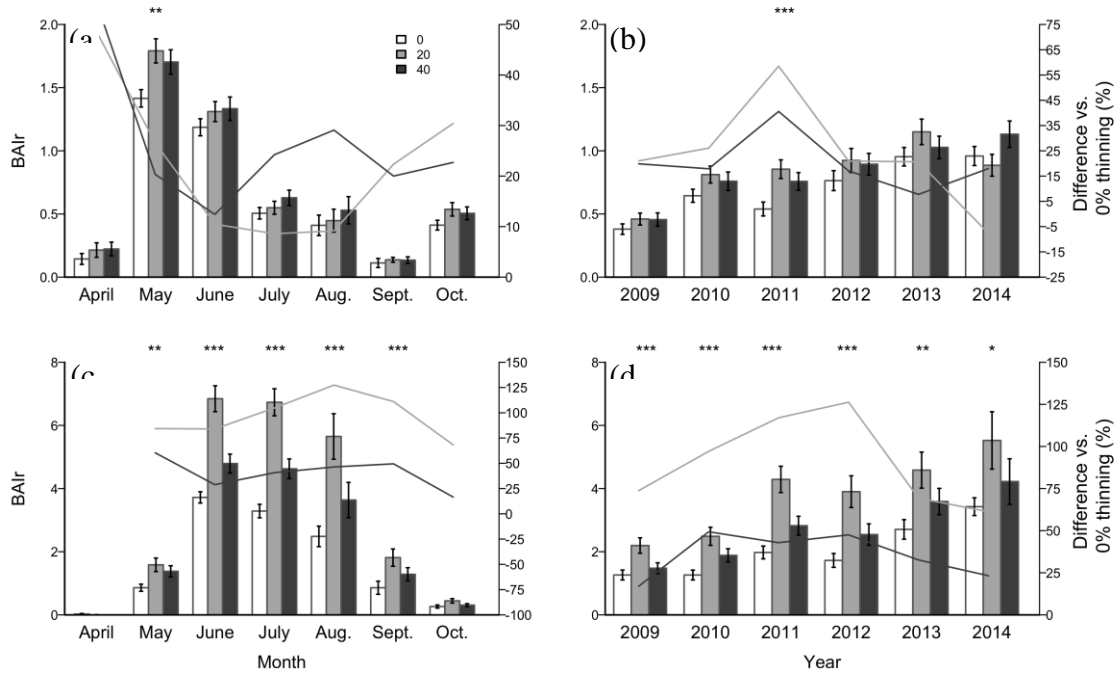
Figure 4. Monthly and yearly basal area increment rates (BAIr, cm^2 day^{-1}; means ± SE) of Scots pine (a and b, respectively) and European beech (c and d, respectively) as a function of thinning intensity (0%, 20% and 40% of basal reduction) for the growing-season months during the 2009-2014 period. Significant differences in BAIr among thinning treatments are indicated as follows: * $P<0.05$; ** $P<0.01$; *** $P<0.001$. Percentage growth differences of moderate (20%, light line) and severe (40%, dark line) thinning relative to unthinned plots are shown on the right y axes.

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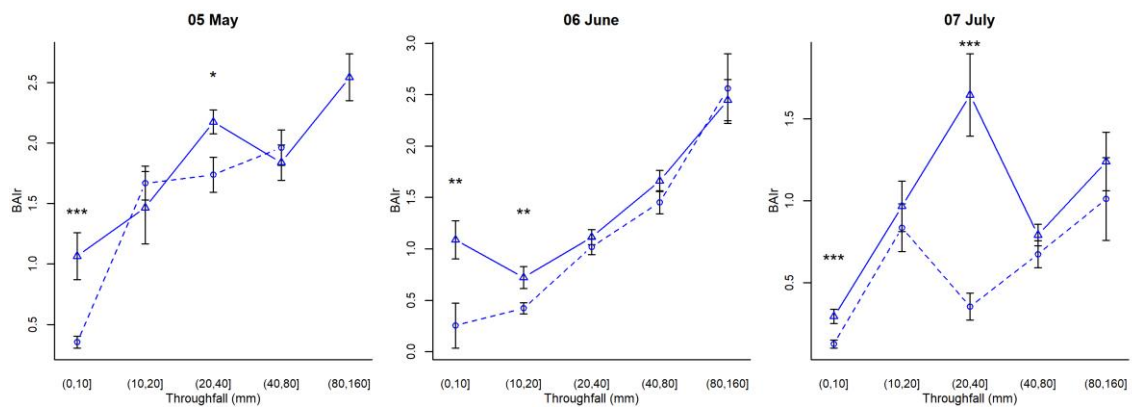
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849   Figure 5. Growth rates (daily basal area increment, BAIr in cm^2 day^{-1}; means ± SE) for
850   Scots pine in relation to throughfall, canopy type (triangles, pure forest; circles, mixed
851   forest) during the months with highest tree growth in the 2009-2014 period. Significant
852   differences in BAIr between canopy treatments are indicated as follows: * $P<0.05$; **
853 $P<0.01$; *** $P<0.001$. Note the different scales in the "y" axes.

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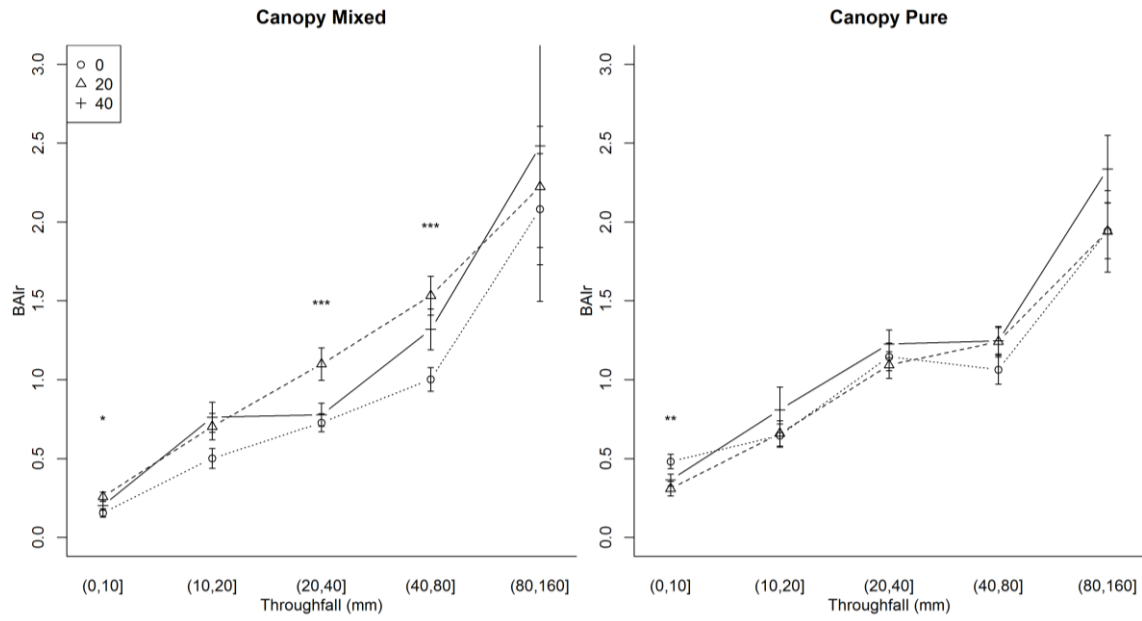
Figure 6. Growth rates (daily basal area increment, BAIr, in cm^2 day^{-1}; means $\pm$ SE) for Scots pine in relation to throughfall, thinning (0 %, 20 % and 40 % basal area removed) and canopy type from April to November and for the 2009-2014 period. Significant differences among thinning treatments in year month for BAIr are indicated above: * $P<0.05$; ** $P<0.01$; ***
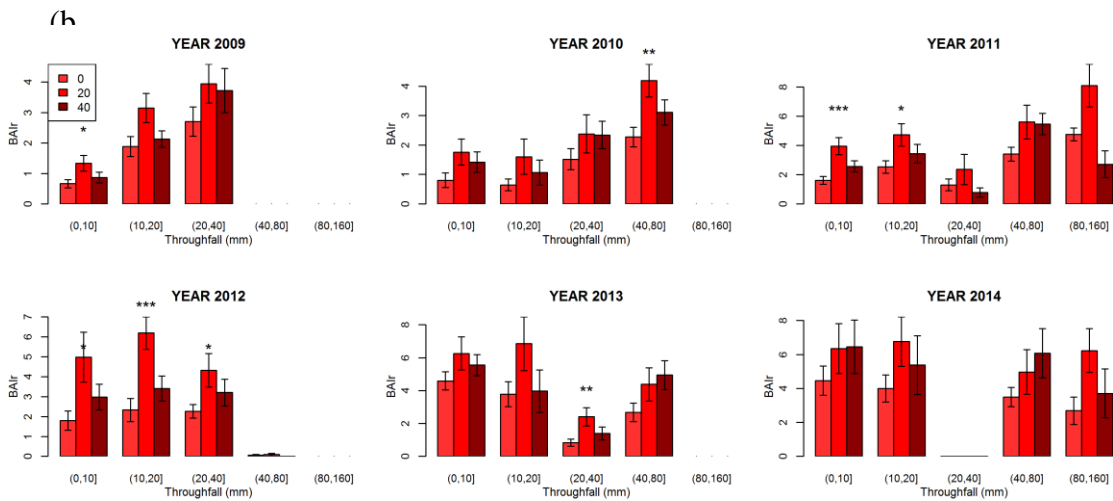
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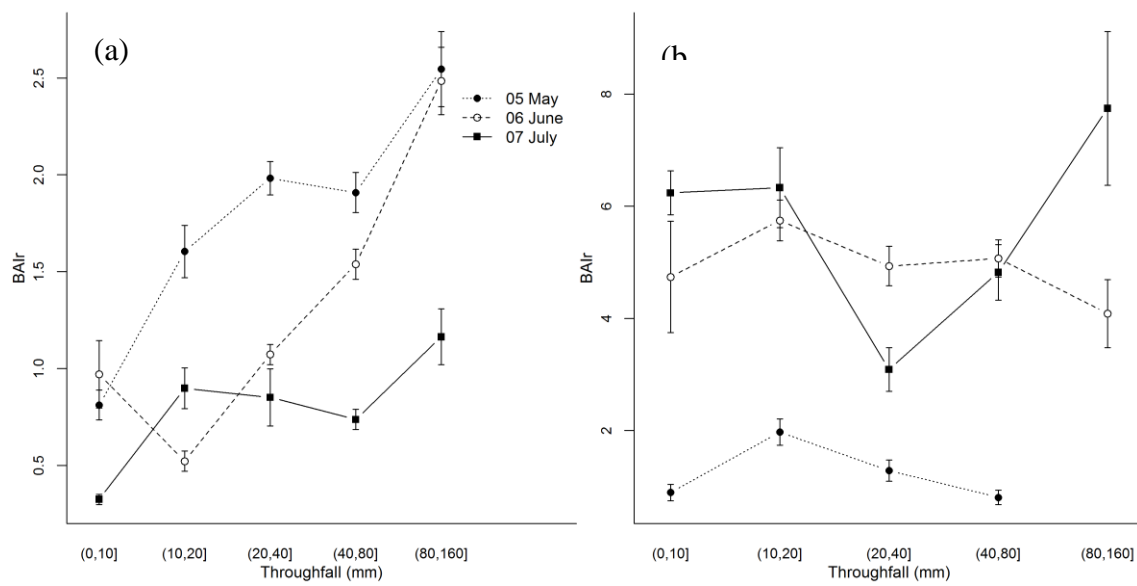
Figure 7. Growth rates (daily basal area increment, BAIr, in cm^2 day^{-1}; means $\pm$ SE) as a function of throughfall for Scots pine (a) and European beech (b) during the months with highest tree growth in the 2009-2014 period.

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866   APPENDICES

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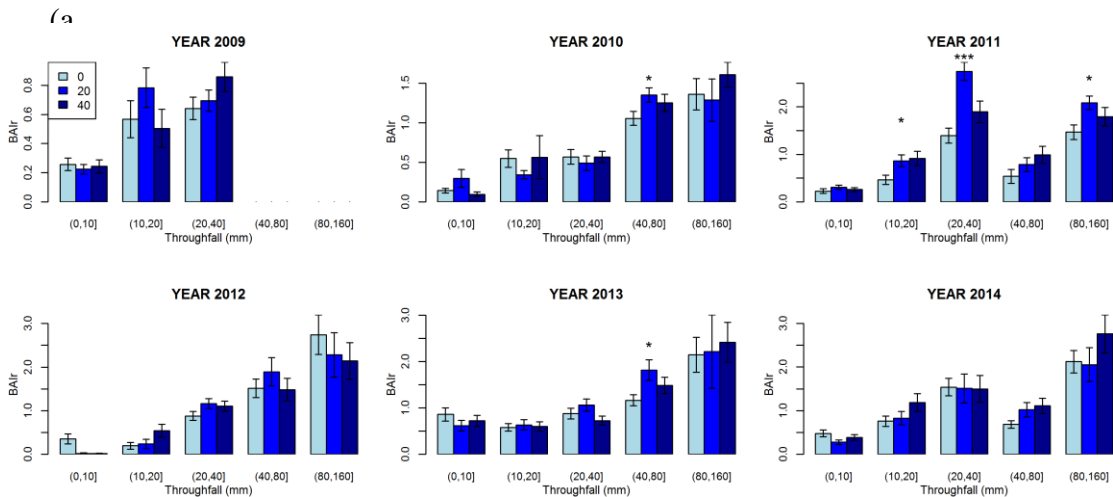
Figure A.1. Growth rates (daily basal area increment, BAIr, in cm^2 day^{-1}; means $\pm$ SE) as a function of throughfall and thinning severity (0 %, 20 % and 40 % of basal area removed) during different years for Scots pine (a; blue bars) and European beech (b; red bars) considering the 2009-2014 period. Significant differences between thinning treatments in each year for BAIr are indicated above: * $P<0.05$; ** $P<0.01$; *** $P<0.001$
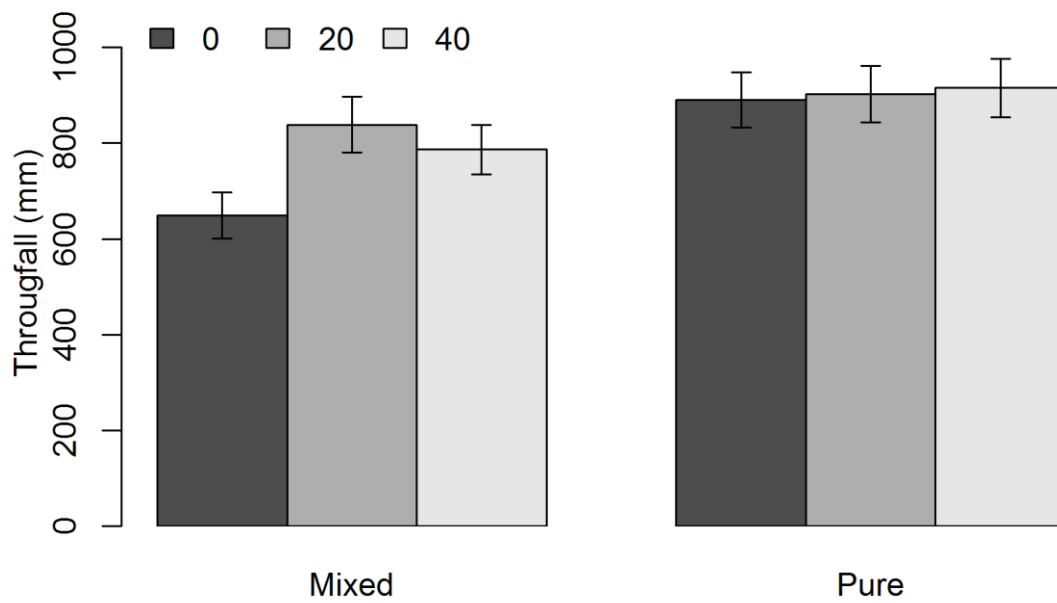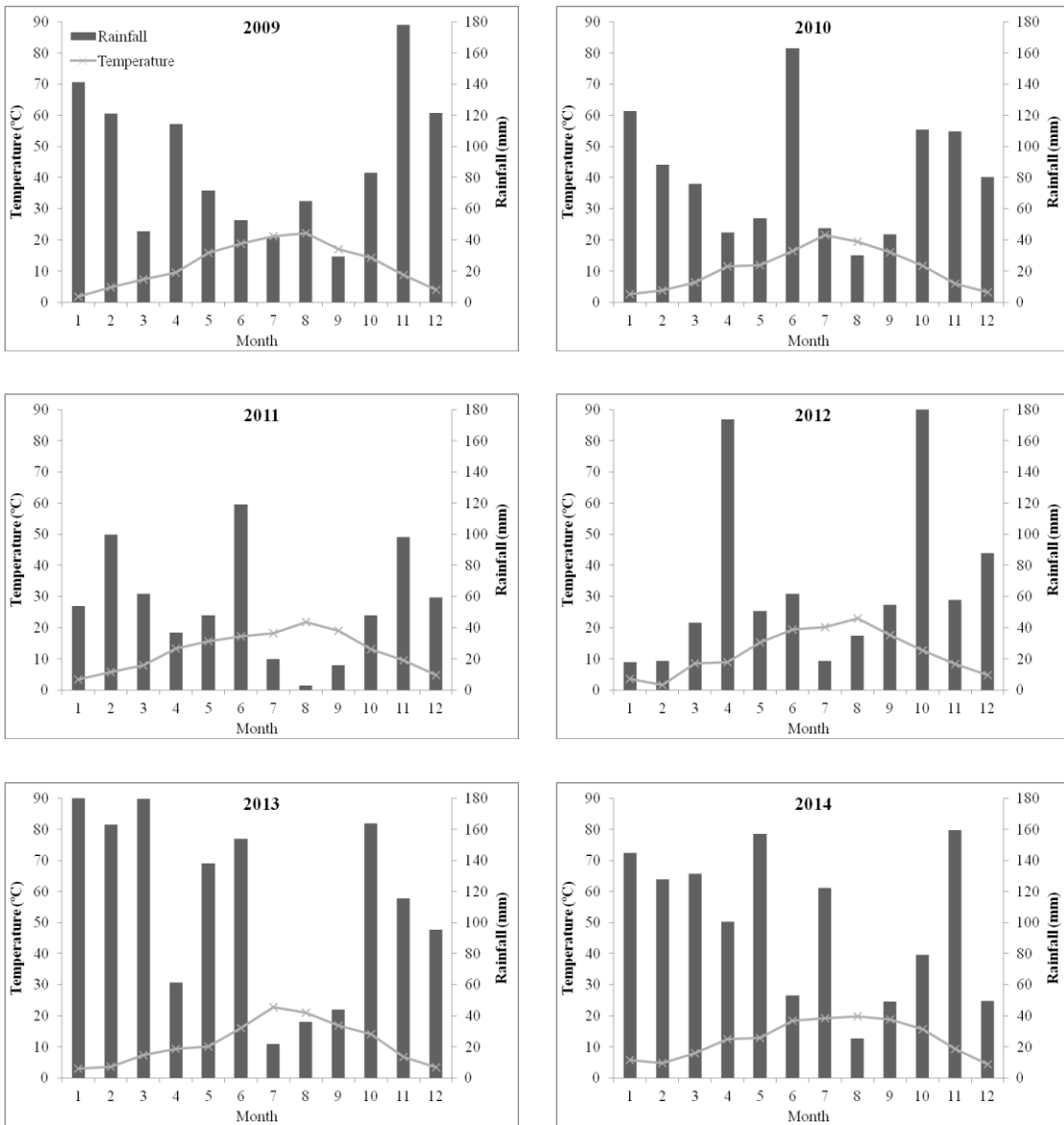
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877   Figure A.2. Mean annual amount of throughfall (means ± SE) considering thinning

878   intensity (0 %, 20 and 40% of basal area removed) and type of canopy from 2009 to

879   2014.

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882 Figure A.3. Climographs for the Aspurz study site (Navascués weather station) from
883 2009 to 2014

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