

**Disparate effects of global-change drivers on mountain conifer forests:
warming-induced growth enhancement in young trees vs. CO₂ fertilization
in old trees from wet sites**

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1 **Abstract**

2 Theory predicts that the post-industrial rise in the concentration of CO₂ in the atmosphere (c_a)
3 should enhance tree growth either through a direct fertilization effect or indirectly by
4 improving water use efficiency in dry areas. However, this hypothesis has received little
5 support in cold-limited and subalpine forests where positive growth responses to either rising
6 c_a or warmer temperatures are still under debate. In this study we address this issue by
7 analyzing an extensive dendrochronological network of high-elevation *Pinus uncinata* forests
8 in Spain (28 sites, 544 trees) encompassing the whole biogeographical extent of the species.
9 We determine if the basal-area increment (BAI) trends are linked to climate warming and
10 increased c_a by focusing on region- and age-dependent responses. The largest improvement in
11 BAI over the past six centuries occurred during the last 150 years affecting young trees and
12 being driven by recent warming. Indeed, most studied regions and age classes presented BAI
13 patterns mainly controlled by temperature trends, while growing-season precipitation was
14 only relevant in the driest sites. Growth enhancement was linked to rising c_a in mature (151-
15 300 years old trees) and old mature trees (301–450 years old trees) from the wettest sites only.
16 This finding implies that any potential fertilization effect of elevated c_a on forest growth is
17 contingent on tree features that vary with ontogeny and it depends on site conditions (for
18 instance water availability). Furthermore, we found widespread growth decline in drought-
19 prone sites probably indicating that the rise in c_a did not compensate for the reduction in water
20 availability. Thus, warming-triggered drought stress may become a more important direct
21 driver of growth than rising c_a in similar subalpine forests. We argue that broad approaches in
22 biogeographical and temporal terms are required to adequately evaluate any effect of rising c_a
23 on forest growth.

24 *Keywords:* basal area increment, climate warming, dendroecology, Generalized Additive
25 Mixed Models, subalpine forests, *Pinus uncinata*.

26 **Introduction**

27 The post-industrial planet has experience a steep increase in c_a which is linked to warmer air
28 temperatures (IPCC, 2013). However, current c_a does not suffice to saturate photosynthesis of
29 C_3 tree species (Norby & Zak, 2011). Therefore, future growth trends of those tree species
30 will depend on how forests respond to a rapidly CO_2 -enriched and warmer world (Bonan,
31 2008). Short-term experiments based on young trees growing under high c_a levels do not
32 allow a full understanding how mature trees will respond to elevated c_a in the field where
33 growth is mediated by ontogeny and limited by temperature oscillations and water availability
34 (Körner, 2013). For example, rising c_a stimulates photosynthesis and decreases stomatal
35 conductance through an improved intrinsic water-use efficiency (iWUE), i.e. the carbon gain
36 per unit of water lost (Norby *et al.*, 1999). However, such improved iWUE does not
37 necessarily translate into enhanced growth in the field (Peñuelas *et al.* 2008, 2011; Linares &
38 Camarero, 2012).

39 The questions of whether, where, and when tree growth is influenced by post-
40 industrial c_a still remain open and controversial. Numerous field studies performed in
41 different biome and forest types worldwide have found either positive (e.g., LaMarche *et al.*,
42 1984; Hari & Arovaara, 1988; Graybill & Idso, 1993; Idso & Kimball, 1993; Nicolussi *et al.*,
43 1995; Soulé & Knapp, 2006; Voelker *et al.*, 2006, Wang *et al.*, 2006; Martinez-Vilalta *et al.*,
44 2008; Cole *et al.*, 2010, Koutavas, 2013), or neutral to negative (Kienast & Luxmoore, 1988;
45 Graumlich, 1991; Tognetti *et al.*, 2000, Gedalof & Berg, 2010; Andreu-Hayles *et al.*, 2011;
46 Girardin *et al.*, 2011; Nock *et al.*, 2011; Lévesque *et al.*, 2014) growth responses to higher c_a .
47 A possible explanation for these contrasting findings can be that the influence of c_a on tree
48 growth depends either on local site conditions or on tree ontogeny.

49 Local conditions modulate the effect of recent rising temperature on growth since
50 post-industrial temperature trends vary in space (Hättenschwiler *et al.*, 1997; Rolland *et al.*,

51 1998, Hember *et al.*, 2012). Such spatial variability of long-term climate warming may be a
52 more important driver of tree growth than changing c_a in cold mountain forests (Salzer *et al.*,
53 2009). Direct warming effects on growth could thus confound indirect effects due to rising c_a
54 *per se* since growth is more sensitive to temperature than photosynthesis across the expected
55 range of temperatures in montane environments (Körner, 2003). Several authors speculate that
56 such fertilization effect of rising c_a on growth would happen in dry sites where iWUE should
57 be mainly improved (Huang *et al.*, 2007), whereas others regard mesic sites with high N
58 deposition rates as being the most sensitive sites to any c_a -enhanced growth (Knapp *et al.*,
59 2001; McMahon *et al.*, 2010; Silva & Anand, 2013).

60 The consideration of ontogeny is also critical to detect any fertilization effect on
61 growth since trees are organisms continuously adjusting to changing environmental
62 conditions (c_a and climate) through aging and changing size (Luysaert *et al.*, 2008; Phillips *et*
63 *al.*, 2008; Voelker, 2011). Under experimental conditions, trees subjected to warming allocate
64 more carbon to primary than to secondary growth being taller and skinnier than control trees
65 (Way & Oren, 2010). Such allocation rules can shift through ontogeny because young trees
66 tend to display growth stimulation under controlled CO_2 concentrations while mature trees do
67 not (Körner *et al.*, 2005; Norby *et al.*, 1999, 2010; Battipaglia *et al.*, 2013). Consequently, it is
68 essential to consider the individual responses of trees to changing c_a across wide climatic and
69 biogeographical gradients and encompassing long temporal frameworks (Johnson & Abrams,
70 2009; Carrer *et al.*, 2010). Dendrochronology may allow tackling these questions, once its
71 shortcomings are adequately treated. First, the ability to detect potential influences of rising c_a
72 on tree growth may be limited by the use of detrending techniques that remove long-term
73 growth trends (Briffa & Melvin, 2011; Bowman *et al.*, 2013). Second, a biased sampling of
74 big or fast-growing (small or slow-growing) trees could produce spurious rising (declining)
75 growth rates (Cherubini *et al.*, 1998; Brien *et al.*, 2012). Therefore, it is important to sample

76 coexisting trees of diverse sizes, growth rates and ages. Finally, rising c_a and temperatures
77 may also exert nonlinear influences on growth (Lloyd *et al.*, 2013) by stimulating them up to
78 certain site- or age-dependent thresholds (Fig. 1).

79 Here we evaluate these ideas by quantifying the long-term growth responses of *Pinus*
80 *uncinata* trees to rising c_a and air temperature. These trees were sampled in 28 forests
81 subjected to different climatic conditions across the entire distribution area of the species in
82 Spain. Specifically, we test two hypotheses: (i) pre-industrial trees (age > 150 years) present
83 lower juvenile growth rates than post-industrial trees (age ≤ 150 years) established later and
84 subjected to higher c_a , and (ii) tree growth will be enhanced in the driest sites where iWUE is
85 improved and growth is not so constrained by low temperatures. Thus, we expect growth
86 stimulation by rising c_a being more noticeable either in young trees (cf. Voelker *et al.*, 2006)
87 or in relatively dry and mild sites (cf. Huang *et al.*, 2007).

88

89 **Material and methods**

90 *Study site and species*

91 *Pinus uncinata* Ram. is a long-lived and shade intolerant conifer occurring in subalpine
92 forests from the Alps, the Vosges, the Pyrenees and the Iberian System. Across the study area
93 in NE Spain, *P. uncinata* is subjected to a wide range of topographical and soil conditions and
94 the southernmost limit of its distribution is located in this area (Ceballos & Ruiz de la Torre,
95 1979). In this species wood formation mainly occurs from May to October (Camarero *et al.*,
96 1998). We used data of 544 *P. uncinata* trees with complete topographic and size data (see
97 below) selected among 642 living trees sampled from 1994 to 2010 (see details in Galván *et*
98 *al.*, 2012, 2014). These trees were sampled in 28 forests located throughout the entire
99 geographic range of the species in northern Spain (Supporting Information, Table S1; for a
100 complete description of the studied regions see Galván *et al.*, 2012, 2014). Most sampled sites

101 (25 out of 28) were located in the Pyrenees where the species is dominant and forms the
102 alpine treeline ecotone, while 2 sites were sampled in the Iberian System and another one in
103 the Pre-Pyrenees. The climate of the sampled populations is continental but varied from sub-
104 Mediterranean (relatively dry summers) to temperate conditions (wet-cool summer)
105 (Supporting Information, Fig. S1). The macroclimate of the study area is strongly influenced
106 by east–west and north–south gradients with increasing warmer conditions eastwards and
107 southwards, whereas dry and continental conditions prevail in the Central Pyrenees (Galván *et*
108 *al.*, 2012). In the Central Pyrenees mean annual temperatures range between 3.0 and 3.5 °C,
109 whereas total precipitation vary between 1150 and 1280 mm (Supporting Information, Figure
110 S1). Across the Spanish Pyrenees total precipitation amounts increase westwards (about 1500-
111 2500 mm), whereas the driest sites are located southwards either in the Pre-Pyrenees or in the
112 Iberian System (1100-1200 mm). During the past century, the whole study area has
113 experienced a significant warming trend (on average +0.015 °C yr⁻¹; see Galván *et al.*, 2014)
114 but no evident changes in the amount of precipitation have been observed (Supporting
115 Information, Fig. S2).

116

117 *Tree dataset*

118 We reconstructed growth trends for 544 living *P. uncinata* individuals. In each sampled site
119 10 to 65 dominant trees representative of the population size and age distributions were
120 sampled. Trees that were at least 10 m apart from each other were randomly selected.
121 Topographic (elevation, slope, and aspect) and biometric (dbh, diameter at breast height
122 measured at 1.3 m, and tree height) variables were recorded for each tree. From each sampled
123 tree, two or three cores were taken at 1.3 m height using increment borers. The diameter,
124 excluding bark, was converted to basal area assuming a circular shape of the stem. Cores were
125 visually cross-dated and measured to a precision of 0.01 mm using a LINTAB measuring

126 device (Rinntech, Heidelberg, Germany). We evaluated the cross-dating and measurement
127 accuracy with the program COFECHA, which calculates cross correlations between
128 individual series of each core and a master chronology, obtained by averaging all measured
129 series in each site except the one being checked (Holmes, 1983).

130 In the cases of cores without pith, the distance to the pith was estimated by fitting a
131 template of concentric circles with known radii to the curve of the innermost rings (Norton *et*
132 *al.*, 1987). This allowed the estimation of the missing radius length to transform it into the
133 number of missing rings. In those trees in which the central core section could not be
134 estimated because the innermost rings did not curve, we used the dbh of each tree to estimate
135 the tree radius without bark. The conversion of the radius length into missing rings was
136 carried out using a subset of cores with pith ($n = 41$), and considering the innermost 40 rings,
137 by using a regression calculating the mean number of rings (y) for the estimated distance to
138 the pith (x): $y = 0.0109 x$ ($R^2 = 0.99$, $P < 0.001$). After calculating the missing rings to the
139 pith, we estimate the cambial age (at 1.3 m) adding the number of calculated rings to the total
140 number of measured rings. We estimated tree age at 1.3 m following three criteria depending
141 on the method used and the suitability of each core in assessing the tree age: (a) when the
142 innermost part of the core lacks a tree-ring curvature and hence the pith locator method cannot
143 be used, we estimated age as a function of the dbh; (b) when both methods (dbh-age
144 regression and pith locator) have been applied to different cores of the same tree we
145 considered the age estimated by using the pith locator method; and (c) when the pith locator
146 method was used, we chose the age assessed from the core with a smaller estimated distance
147 to the pith. At the same time, we followed three criteria to establish a scale of uncertainty in
148 age estimation: (i) low uncertainty, when the core includes the pith or when the core has an
149 estimated distance to the theoretical pith smaller than 1.5 cm; (ii) medium uncertainty, when
150 cores with estimated distance to the pith was longer than 1.5 cm, and (iii) high uncertainty,

151 when the innermost tree rings of the core did not curve and tree age was estimated as a
152 function of dbh. On average, *P. uncinata* trees take 20 years to reach a height of 1.3 m
153 (Camarero, 1999). Therefore we added 20 years to the estimated age at 1.3 m to estimate the
154 age in the base of the trunk.

155

156 *Climate and atmospheric CO₂ data*

157 We used homogeneous and interpolated monthly climate data corresponding to the CRU TS
158 3.1 database produced by the Climate Research Unit for the period 1901-2009 at a 0.5° spatial
159 resolution (Harris *et al.*, 2014). We selected 0.5° grids including the study sites and the
160 monthly climatic variables which most growth variability of *P. uncinata* explain, namely
161 previous mean maximum November temperature (hereafter abbreviated as *pTMx11*), current
162 mean minimum May temperature (hereafter abbreviated as *TMi5*) and June precipitation
163 (hereafter abbreviated as *P6*) (see Tardif *et al.* 2003; Galván *et al.*, 2014). Annual *c_a* values
164 were computed from monthly values taken from the Mauna Loa (Hawaii) observatory from
165 1958 onwards (see <http://www.esrl.noaa.gov/gmd/ccgg/trends/>).

166

167 *Growth models*

168 The use of measurements such as basal area increment (BAI) partially avoids the problem of
169 removing long-term growth trends since BAI captures the sigmoid trajectory of tree growth
170 (Biondi & Qaedan, 2008). The dynamics of BAI usually display a young phase of exponential
171 growth and a stable phase when trees age and reach height and BAI plateaus (Fritts, 2001). To
172 model tree growth accurately, individual tree-ring width series were converted into BAI,
173 which allows removing the geometrical constraint of adding a volume of wood to a stem of
174 increasing radius (Biondi & Qaedan, 2008) as:

$$175 \quad \text{BAI} = \pi (r_t^2 - r_{t-1}^2) \quad (1)$$

176 where r_t^2 and r_{t-1}^2 are the squared stem radial increments corresponding to rings formed in
177 years t and $t-1$, respectively.

178 Since we expect that BAI trends and response to c_a are age dependent, trees were
179 classified in four groups according to their age: young trees (individuals with age ≤ 150
180 years), mature trees (151–300 years old trees), old mature trees (301–450 years old trees) and
181 old trees (individuals with age ≥ 451 years). Age classes were defined to represent different
182 life stages and environmentally contrasting periods (e.g., pre- vs. post-industrial periods) but
183 keeping a robust enough sample size for each class. Given that BAI trajectories vary strongly
184 among individuals and within populations flexible statistical methods can be used to represent
185 growth such as Generalized Additive Mixed Models (GAMM; Wood, 2006). This approach
186 allows describing how BAI varies with the additive increase of cambial age or calendar year.
187 BAI depends on site conditions as well as on the particular growth conditions to which each
188 individual tree is subjected along its ontogeny (e.g., Pokharel & Froese, 2009). In order to
189 avoid underrepresentation of some age- (4 classes) and site (28 levels) replications, sites were
190 grouped into regions with similar growth characteristics based on a previous study by Galván
191 *et al.* (2012). They considered five regions showing coherent geographical, topographical and
192 growth conditions (similar growth trends and responses to climate) shared by trees inhabiting
193 each region (see Table 1).

194 The GAMM we fitted was of the form:

$$195 \quad \text{BAI}_i = s(\text{dbh}_i) + s(\text{tree age}_i) + s(\text{cambial age}) + Z_i B_i + \nu_i \quad (2)$$

196 where the BAI of a tree i is modelled as smooth functions (s) of three predictors (dbh,
197 tree age, cambial age of tree-ring formation) and tree identity ($Z_i B_i$) considered a random
198 effect since multiple measurements were performed for each individual tree along its life.

199 Since BAI of year t depends on the previous-year ($t-1$) BAI we also included in the model an
200 error term (ν_i) with an AR1 ($p=1, q=0$) correlation structure. The smooth terms were

201 represented using thin plane regression splines (Wood, 2006). The degree of smoothness is
202 determined through an iterative fitting process (see Wood, 2003). Cambial age refers here to a
203 variable which represents tree ageing from its establishment (*age 0*) to the date in which the
204 annual ring was formed (*age n*), whereas tree age is a fixed value representing the age of the
205 tree. Therefore, cambial age varies within each tree along time, whereas tree age is a fixed
206 value which changes between trees. Since BAI has a skewed distribution, we first log (BAI
207 +1) - transformed this variable. To test if BAI depends on the particular time period in which
208 each individual tree was established separated models were performed for the trees grouped in
209 different age classes. In addition, BAI trends were characterized for each study region and age
210 class, and also since the 1950s when c_a started steeply rising.

211 To reveal whether recent trends in *P. uncinata* growth are only due to biological
212 features (e.g., tree ageing) or, alternatively, they are mainly influenced by climate and c_a , we
213 correlated age- and site-specific growth trends over the period 1958-1994 with selected
214 climatic variables (*pTMx11*, *TMi5*, *P6*) and annual values of c_a . Since we expect age-
215 dependent growth responses to climate, separate analyses were performed for each age class.
216 In addition, we also considered site-mediated growth responses to c_a . For each age class, the
217 following model was proposed to study the influence of year-to-year variability in climate
218 variables on BAI after removing mid-term fluctuations not related to climate:

$$219 \quad \text{BAI}_{res} = pTMx11s + TMi5 + P6 + c_a + Z_i B_i + \varepsilon_i \quad (3)$$

220 where BAI_{res} represent BAI residuals after extracting biological trends (i.e. after
221 removing the influence of dbh and tree age), and *pTMx11*, *TMi5* and *P6* are climatic
222 variables.

223 Separate analyses were carried out for each site by following a multi-model inference
224 approach based on information theory (Burnham & Anderson, 2002). This approach
225 calculates the probability that a given model is more appropriate than other competing models

226 in explaining the response variable. Multi-model inference is recommended for analysing
227 large-scale datasets across broad geographical ranges (Zuur *et al.*, 2009). We ranked all the
228 potential models that could be generated with the different explanatory variables according to
229 the second-order Akaike information criterion (AICc). For each model, we considered its
230 ΔAICc (i.e. the difference between AICc of each model and the minimum AICc found for all
231 models). After selecting the set of best candidate models (those having a $\Delta\text{AIC} < 2$) we
232 selected the coefficients for the model with the lowest ΔAIC . We evaluated the fit of the
233 model by graphical examination of the residual and fitted values (Zuur *et al.*, 2009). All
234 statistical analyses were performed using the R statistical software (R Development Core
235 Team, 2014). The *mgcv* package was used to calculate the GAMMs (Wood, 2006) and the
236 *MuMIn* package to perform multi model selection (Barton, 2013).

237

238 **Results**

239 The most abundant age classes were formed by trees with 251 up to 300 years old (Fig. 2).
240 During the first years of the tree life BAI values showed a marked increase with cambial age,
241 being larger for young trees, followed by mature, old mature and old trees (Fig. 3a; see also
242 Supporting Information, Table S2). In general, BAI decreased as trees aged, but the slope of
243 the decrease was lower for the old mature and old trees. For instance, at the age of 40 and 80
244 years, trees in the youngest age class (< 150 years) display significantly larger values of BAI
245 than trees in the rest of age classes (Fig. 3a).

246 We observed both accelerating and decelerating BAI trends in the first and second
247 halves of the past century, respectively, which mainly corresponded to improved growth of
248 young trees in response to the warm 1940s and 1950s (Fig. 3b). Such growth enhancement
249 seems to be exceptional when compared with other age classes in the context of the past seven

250 centuries. A slight growth deceleration was observed in all age classes during the second half
251 of the 20th century but it was more noticeable in young trees.

252 The models proposed to study the long-term BAI dynamics showed different patterns
253 depending on the age class, site and time periods considered (Figs. 4 and 5). For example,
254 BAI of young trees is best represented by an exponential function that reaches an asymptote
255 and decreases at age varying from 80 (e.g., Central Pyrenees) to 60 years (e.g., Iberian System
256 and Pre-Pyrenees). Trees in the remaining three classes also show a constant exponential BAI
257 trend that reaches an asymptote, although in several cases (e.g., Central Western Pyrenees) the
258 trend was represented by a straight line. An important part of the BAI variance was accounted
259 for by tree size (dbh) and age (Supporting Information, Table S2). However, the relevance of
260 tree size on determining growth decreased with tree age.

261 Significant BAI increases were only observed since 1950 in old-mature and mature
262 trees from the Western and Central-Western Pyrenees, and also in old-mature trees from the
263 Iberian System and Pre-Pyrenees (Fig. 5). Negative or low BAI trends were common among
264 the oldest trees and also in all age classes of the Central and Eastern Pyrenees. We found a
265 positive influence of temperature on BAI in the different analysed age classes, particularly in
266 the Central and Eastern Pyrenees (Table 2). Precipitation also enhanced BAI of young and
267 mature trees from the driest sites in the Iberian System and Pre-Pyrenees region.
268 Contrastingly, we only found a significant and positive influence of rising c_a on BAI in old
269 mature trees from the wet Western Pyrenees (Table 2), where the highest BAI enhancement
270 since 1950 was also observed (Fig. 5).

271

272 **Discussion**

273 We found that tree growth responds more to other factors (ontogeny, temperature, water
274 availability) than to rising c_a . We detected little evidence of widespread growth enhancement

275 in subalpine *Pinus uncinata* forests in response to increasing c_a and a related fertilization
276 effect. The much higher growth rates of post-industrial young trees than pre-industrial old
277 trees for the same age confirm our first hypothesis, namely that pre-industrial trees present
278 lower juvenile growth rates than post-industrial trees subjected to higher c_a . This must be
279 interpreted with caution since higher post-industrial growth rates could be also the result of
280 age-related selection against fast growing individuals irrespective of c_a trends (Voelker,
281 2011). The resurgence in radial growth was observed in old mature trees from the wettest
282 study region (Western Pyrenees) and not in young trees from the driest areas (Iberian System
283 and Pre-Pyrenees), where iWUE should be the most benefitted because of rising c_a , thus
284 contradicting our second hypothesis. Thus, the rapid growth increase of young or post-
285 industrial trees, mostly established in the 19th and 20th centuries, seems to be a response to
286 rising air temperatures across the study area. These findings have several implications for
287 studies of forest growth as related to global-change drivers such as climatic warming and
288 increasing c_a .

289 Firstly, long-term growth stimulation in response to rising c_a is unlikely in the field
290 because tree growth is more constrained by low temperatures or by low water availability than
291 by accessible carbon (Körner *et al.*, 2005; Körner, 2013). Along these lines, reviews of free-
292 air CO₂ enrichment experiments also reveal that the initial CO₂ stimulation of tree growth
293 under optimal nutrient conditions disappears after one or two decades suggesting ontogenetic
294 limitations (Kimball *et al.*, 2007; Norby & Zak, 2011). Secondly, trees showing higher iWUE
295 values or increments do not necessarily have to present growth enhancement resulting from
296 rising c_a as has been evidenced at local (Silva *et al.*, 2010; Nock *et al.*, 2011; Linares &
297 Camarero, 2012; Gómez-Guerrero *et al.*, 2013; Lévesque *et al.*, 2014) and global scales
298 (Peñuelas *et al.*, 2011; Silva & Anand, 2013). In the eastern Pyrenees the iWUE reconstructed
299 from carbon isotopic ratios of *P. uncinata* wood doubled during the 20th century whereas

300 radial growth declined at a mean rate of 0.002 mm yr^{-1} (Andreu-Hayles *et al.*, 2011). These
301 authors interpreted such iWUE rise as a response to significant increases in leaf intercellular
302 CO_2 concentration (c_i), but it did not suffice to enhance tree growth. Overall, our results do
303 not support any c_a -enrichment effect even if we studied trees growing at high elevations
304 where low partial pressures of CO_2 could make it more limiting than at lower elevations
305 (Körner *et al.*, 1991). Our findings suggest long-term anatomical and physiological
306 adaptations for adjusting c_i to increasing c_a such as changing stomatal density or
307 photosynthetic rates (Ward *et al.*, 2005). Such adjustments could explain why rising c_a might
308 modify climate sensitivity of trees, but not overall growth rates (Gerhart *et al.*, 2012).

309 The interactions between temperature and water availability can determine the tree
310 growth responses to rising c_a (Norby *et al.*, 2010). Rising c_a should enhance growth as long as
311 water is not limiting; but we found negative correlations between c_a and basal area increment
312 among all assessed age classes, particularly in old trees. Our findings agree with observations
313 in boreal black spruce (*Picea mariana*) forests where old trees also responded negatively to
314 rising c_a (Girardin *et al.*, 2014). Elevated CO_2 conditions increased the maximal
315 photosynthetic rate and iWUE of *Pinus mugo* at the alpine treeline where soil water
316 availability was high (Streit *et al.*, 2014). Consequently, the amount of carbon available to
317 sinks (growth, storage, root exudation, metabolic respiration) increased under those
318 conditions but again this did not translate into enhanced basal area growth (Handa *et al.*,
319 2006; Dawes *et al.*, 2011, 2013). In fact warming could also induce drought stress and
320 override any potential effect of rising c_a and improved iWUE on carbon supply and growth if
321 water supply is not adequate to sustain sink demand (Lévesque *et al.*, 2014). This could
322 explain the growth enhancement observed in the Western Pyrenean *P. uncinata* forests, where
323 climate conditions are wet. In addition, in that area warming was more pronounced in those
324 months most strongly related to growth (Supporting Information, Fig. S2).

325 The postulated CO₂ fertilization was observed in old mature trees but this effect could
326 be mediated by other features than tree ontogeny *per se* such as tree height, leaf or sapwood
327 area. In old trees the efficiency of water transport is maintained because xylem elements grow
328 progressively larger with tree age and only in very tall trees the hydrostatic gradient induces
329 limits on xylem functionality towards the top of the tree (Ryan & Yoder, 1997). Since *P.*
330 *uncinata* is a shade-intolerant species, tree height and competition for light play minor roles as
331 drivers of growth in these open forests (Supporting Information, Fig. S3). Accordingly, tree
332 size was not a significant factor controlling growth in older age classes confirming that once
333 those old trees reach a senescent phase their BAI rates do not depend on tree size. Regarding
334 ontogenic processes, young or small trees could also preferentially assimilate respired CO₂
335 when growing in closed canopies altering the isotopic composition of their wood and biasing
336 inferred iWUE trends (Bert *et al.*, 1997), but this effect seems to be unlikely since most of the
337 study sites are open stands. Thus, other size-related constraints related to leaf and sapwood
338 production could explain recent BAI trends (Galván *et al.*, 2012). Nevertheless, future growth
339 and iWUE assessments should consider the whole range of tree sizes and ages (Nehrbass-
340 Ahles *et al.*, 2014).

341 Regarding the roles played by c_a , temperature and water availability as drivers of long-
342 term growth trends, a survey of studies reporting positive growth responses to rising CO₂
343 suggests either a potential fertilization effect in fast-growing hardwood species growing in
344 moist sites such as *Populus* trees (Cole *et al.*, 2010; Battipaglia *et al.*, 2013) or improved
345 growth due to improved iWUE, particularly in dry sites (Soulé & Knapp, 2006). In the first
346 case the presumed stimulation of growth has been poorly discussed and could represent initial
347 stimulatory (ontogenetic) effects of growth in rapidly-growing sprouting *Populus* species. In
348 the second case, recent results dismiss the generality of this pattern since declining growth
349 trends have been described in the same conifer species coexisting either in xeric or in mesic

350 sites (Lévesque *et al.*, 2014). Despite a reduction in stomatal conductance in response to higher
351 c_a has been observed in broadleaf species drought-induced stomatal closure diminishes
352 growth in the long term (Lévesque *et al.*, 2014). Still, in these discussed cases the effects of
353 low temperatures on growth are minor compared with those described in this and other cold-
354 limited forests (Salzer *et al.*, 2009; Silva & Anand, 2013). Our findings also imply
355 considering warming-related drought stress as a major driver of growth in old trees from
356 mountain forests (Bellassen *et al.*, 2011). In the Pyrenees a warming trend has characterized
357 the past 700 years (Büngten *et al.*, 2008). Due to the rise in air temperature, young trees
358 experience longer seasons nowadays than older trees did when they were in their juvenile
359 phase, resulting in large growth rates nowadays (Way & Oren, 2010). Finally, we only
360 considered one tree species so future studies should investigate several coexisting tree species.
361 Those species could grow differently in response to rising c_a as a function of different
362 photosynthetic and phenological adjustments affecting carbon uptake and wood production.

363 To conclude, we show that forest growth responses to rising c_a and climate warming
364 depend on site conditions and tree ontogeny and are nonlinear. Our results illustrate how
365 growth of post-industrial *P. uncinata* trees has improved during the past 150 years. Such
366 growth improvement was linked to climate warming, while a positive response of tree growth
367 to rising c_a was only detected in relatively old trees from wet sites. We argue that growth,
368 stemwood production and productivity will increase as c_a rises in those wet sites, whereas
369 climate warming can directly enhance growth in other sites or even lead to growth decline if
370 rising temperatures amplify water shortage in the most xeric sites. Our findings emphasize the
371 need of using broader perspectives in temporal (ontogeny), biogeographic (site conditions)
372 and also functional (e.g., comparing conifers and broadleaf species) terms to comprehensively
373 evaluate long-term c_a effects on forest growth.

374

375 **Acknowledgments**

376 This study was supported by projects 012/2008 and 387/2011 (OAPN, Spain) and by ARAID
377 (JJC) and a JAE-CSIC grant (JDG). We also acknowledge projects which contributed to build
378 this dataset (FoRmat EU ENV4-CT97-0641, AMB95-0160 and CGL2011-26654). We are
379 indebted to all people who helped us in the field. We thank the ESRL-NOAA for providing
380 CO₂ data to the public and the scientific community.

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Tables

Table 1. Number of trees per age class studied in each region and site. See additional site information in Supporting Information, Table S1.

Region (code)	Site	No. trees				
		Total	Age classes (age)			
			Young trees (≤ 150 years)	Mature trees (151–300 years)	Old mature trees (301– 450 years)	Old trees (≥ 451 years)
Western Pyrenees (WP)	Contienda-Larra	20	0	5	13	2
	Atxerito	12	0	5	2	5
Central-Western Pyrenees (CWP)	Respomuso	14	1	8	4	1
	Pic d'Arnousse	6	1	3	2	0
Central Pyrenees (CP)	Mirador del Rey	17	1	16	0	0
	Las Cutas	10	10	0	0	0
	Bielsa	10	1	7	1	1
	Senda de Cazadores	32	2	14	9	7
	Sobrestivo	38	1	9	19	9
Eastern Pyrenees (EP)	Airoto	14	0	9	3	2
	Amitges	24	0	7	13	4
	Conangles	20	1	7	10	2
	Corticelles	23	0	2	7	14
	Estanys de la Pera	19	0	10	5	4
	Estany Gerber	28	1	6	11	10
	Barranc de Llacs	31	1	12	6	12
	Lladres	7	0	2	3	2
	Mata de València	8	0	6	2	0
	Mirador	31	1	7	14	9
	Monestero	25	0	9	12	4
	Estany Negre	40	0	14	10	16
	Ratera	2	1	1	0	0
	Sant Maurici	20	0	20	0	0
	Tessó del Son	9	0	5	1	3
Mulleres	10	0	3	2	5	
Iberian System and Pre-Pyrenees (IS-PP)	Vinuesa	22	1	7	7	7
	Teruel	30	14	8	7	1
	Guara	13	4	9	0	0

Table 2. Influence of climatic variables and atmospheric CO₂ concentrations on basal area increment from different regions and considering five age classes (period 1958-1994). For each region, the influence of the annual increment in CO₂ is shown by the *t* statistic and its associated probability (*P*). Coefficients were only considered for regions with more than 5 trees per age class. Abbreviations of climatic variables: *pTMx11*, previous mean maximum November temperature; *TMi5*, current mean minimum May temperature; *P6*, current June precipitation. Significant levels: **P* ≤ 0.05; ** *P* ≤ 0.01. Grey cells show significant positive effects of CO₂ on basal area increment.

Age class (age)	Region	<i>pTMx11</i>	<i>TMi5</i>	<i>P6</i>	CO ₂	No. models	Relative weight
Young trees (≤ 150 years)	Western Pyrenees	–	–	–	–	–	–
	Central-Western Pyrenees	–	–	–	–	–	–
	Central Pyrenees	0.056**	0.019**	–0.018**	–	1	1
	Eastern Pyrenees	–	–	–	–	–	–
	Iberian System and Pre-Pyrenees	0.057**	–	0.037**	–0.006*	1	1
Mature trees (151–300 years)	Western Pyrenees	0.036**	–0.006	0.013*	0.006	6	0.98
	Central-Western Pyrenees	0.031**	0.042**	–0.014	0.003	3	0.99
	Central Pyrenees	0.058**	0.015*	0.012*	–0.008**	1	1
	Eastern Pyrenees	0.056**	0.044**	0.018*	–0.005**	1	1
	Iberian System and Pre-Pyrenees	0.044**	0.022*	0.020**	–0.007**	1	1
Old mature trees (301– 450 years)	Western Pyrenees	0.009	0.018*	0.009	0.013**	6	0.99
	Central-Western Pyrenees	0.021*	0.027*	–0.005	–	6	0.99
	Central Pyrenees	0.049**	0.029**	–0.007	–0.008**	2	0.99
	Eastern Pyrenees	0.044**	0.043**	0.012*	–0.003**	1	1
	Iberian System and Pre-Pyrenees	0.030**	0.036**	0.003	0.003	3	0.99
Old trees (≥ 451 years)	Western Pyrenees	0.011	0.018	0.011*	–	5	1
	Central-Western Pyrenees	–	–	–	–	–	–
	Central Pyrenees	0.041**	0.007	–0.018*	–0.012*	2	0.99
	Eastern Pyrenees	0.034**	0.042**	–0.002	–0.002*	2	0.99
	Iberian System and Pre-Pyrenees	0.037**	0.034**	–0.007	–	2	0.99

Figure legends

Figure 1. Expected responses of photosynthetic rates (a) and growth or basal area increment (b, c, d) to rising atmospheric CO₂ concentrations (c_a) and temperatures as a function of either tree ontogeny (cambial age) or time. (c) Postulated ontogenetic trajectories of growth as a function of temperature for three levels of tree performance (low –clear grey–, mid –dark grey– and high performance –black line). Symbols indicate the trajectories of warming-induced growth increase for different performance levels. (d) We expect a departure of the observed basal area increment (BAI) (red continuous lines, circles) as compared with ontogenetically expected BAI (dashed blue line, triangles) in response to rising c_a (grey area). Panels a, b and c are adapted and modified from Sage & Kubien (2007), Phillips *et al.* (2008), and Way & Oren (2010).

Figure 2. Age structure of *Pinus uncinata* trees sampled in the Iberian Peninsula. The age classification was based on 25-year age classes considering three levels of uncertainty in age estimation (see *Material and Methods*).

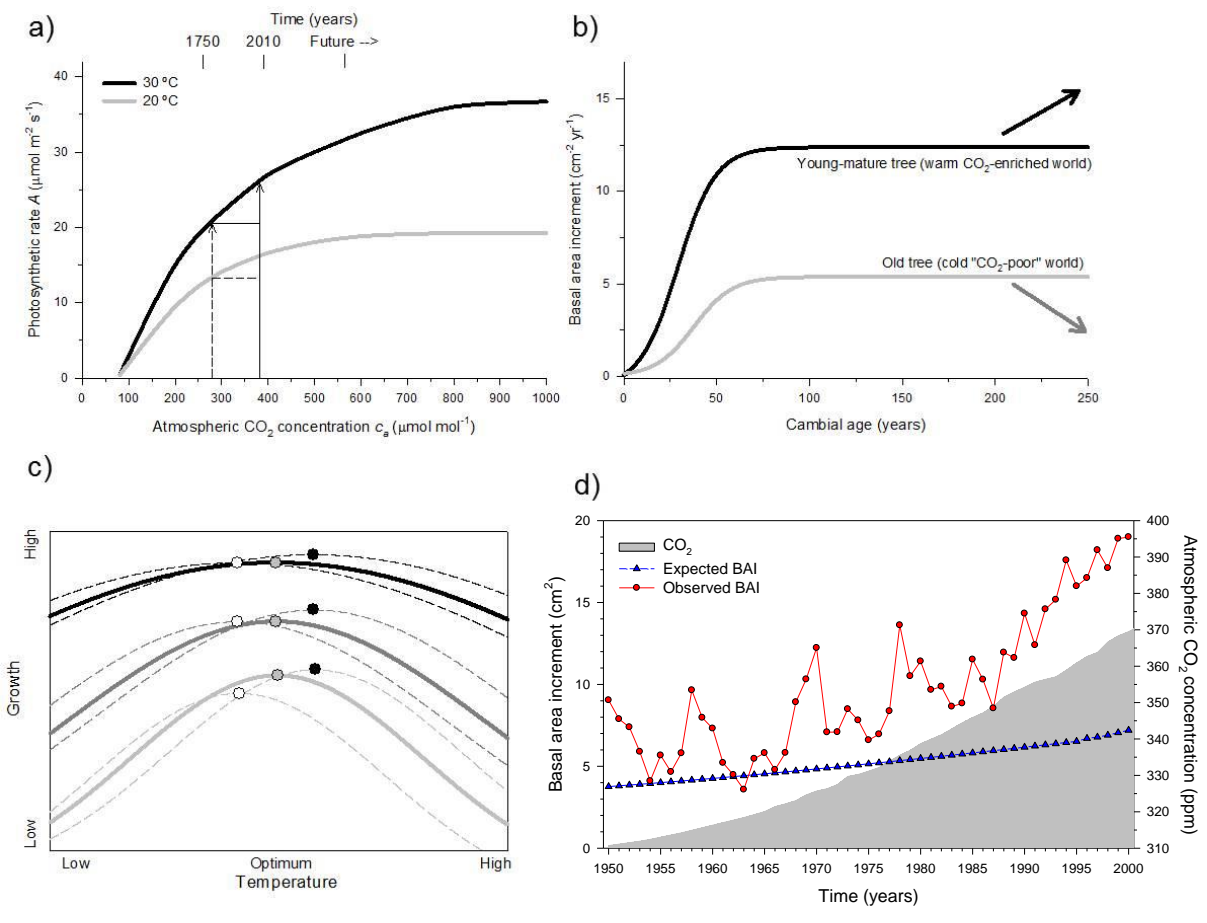
Figure 3. Basal area increment (mean \pm SE) as a function of cambial age (a) and calendar year (b) for the trees in the four age classes considered. The upper and lower insets show basal area increment trends from 20 up to 100 years and for the 20th century, respectively. Different colours of lines indicate different age classes: red lines, young trees (individuals with age \leq 150 years); green lines, mature trees (151–300 years old trees); blue lines, old mature trees (301–450 years old trees); and black lines, old trees (individuals with age \geq 451 years).

Figure 4. Long-term trends in basal area increment (BAI, y axes) displayed as a function of cambial age (x axes) for trees grouped in four age classes (rows) and five study regions (columns; see regions' abbreviations in Table 1). The lines show the fitted GAMMs used to model age-dependent trends in BAI while dots show raw values (the darker the point fills the larger the tree diameter).

Figure 5. Recent trends in basal area increment (BAI, y axis) of *Pinus uncinata* as a function of year grouped in four age classes (rows) and considering the five study regions (columns; see Table 1). The continuous and dotted lines indicate the observed and fitted BAI trends, while the vertical line shows the first year with data of atmospheric CO₂ concentration used in BAI models. In each graph the correlations show the associations between mean BAI values (black lines) and year (significant trends are written in bold characters). Dots show raw BAI values (the darker the point fills the larger the tree diameter). Note that the fact that the observed BAI exceeds that modelled by GAMMs is an artefact since GAMMs were fitted to a longer period than the most recent 50 years presented in the figure.

Figures

Figure 1



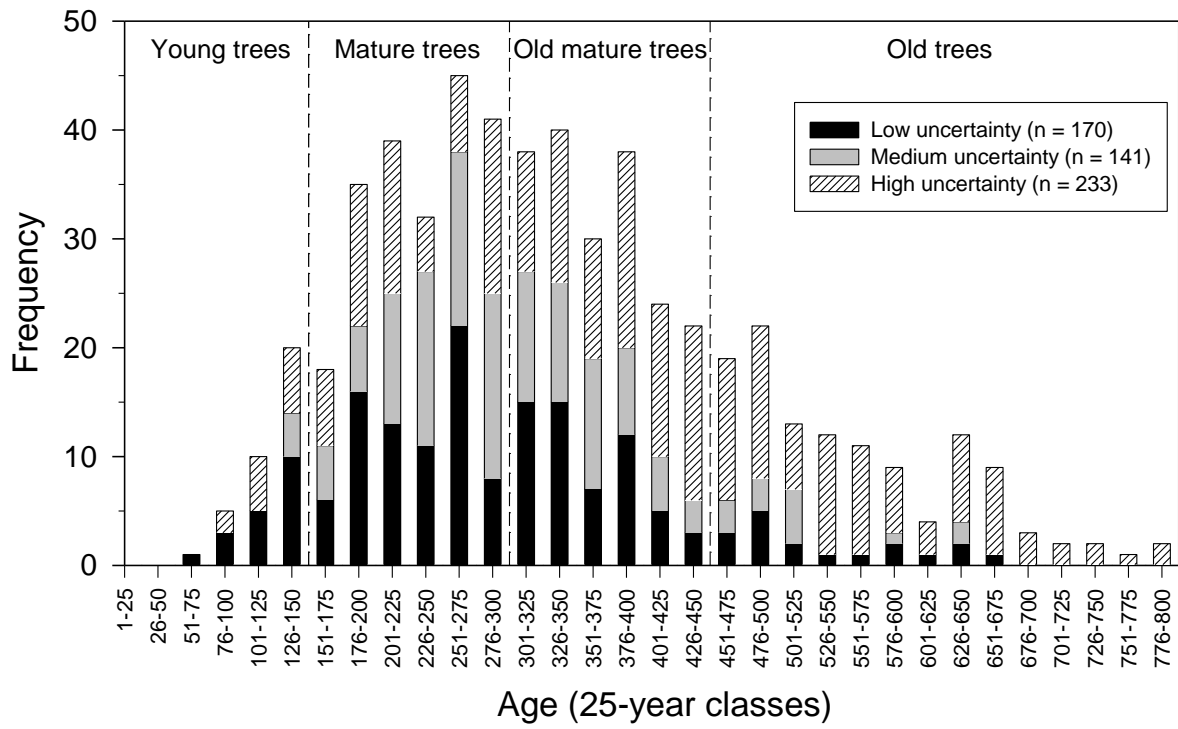


Figure 2

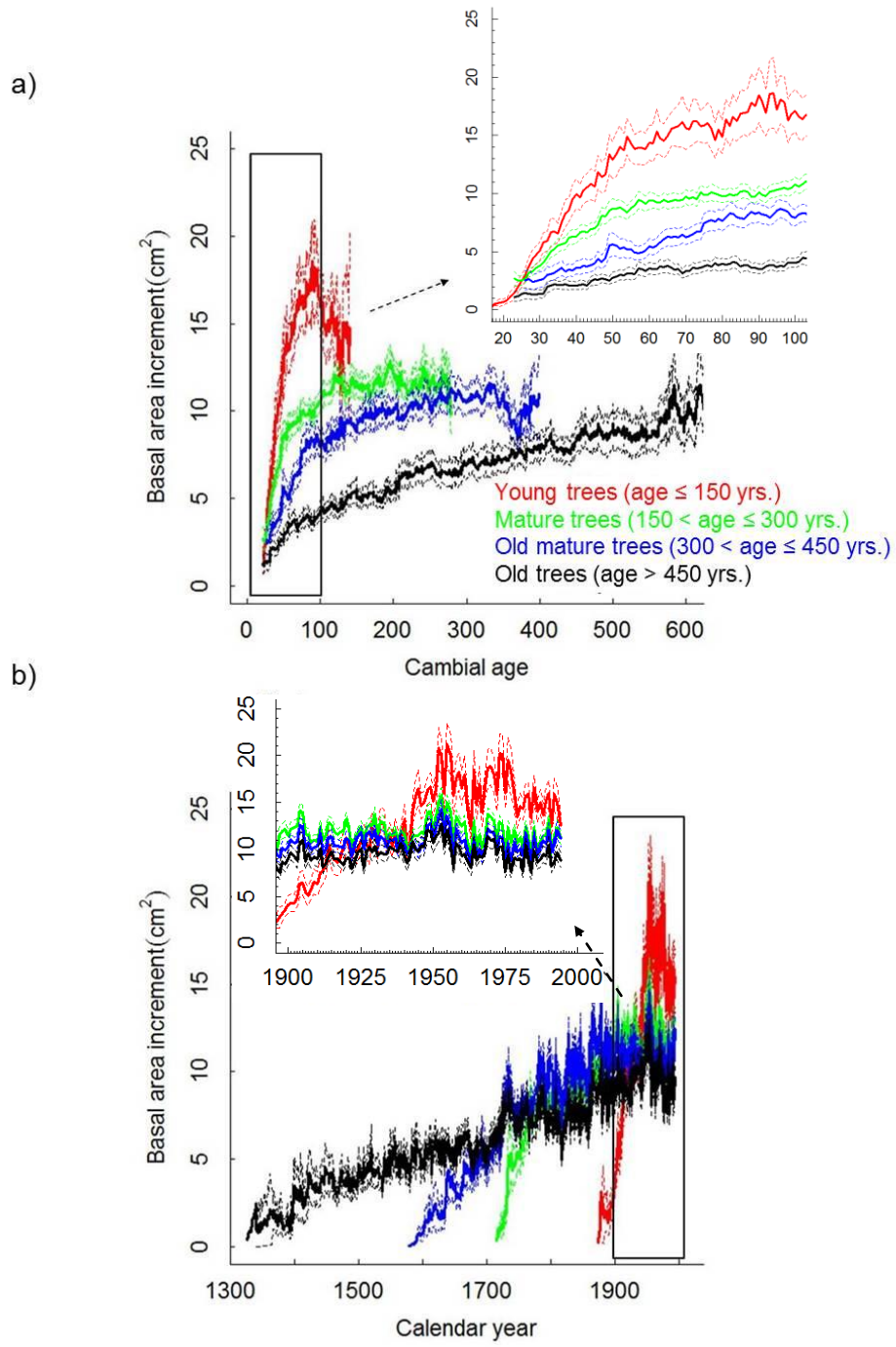


Figure 3

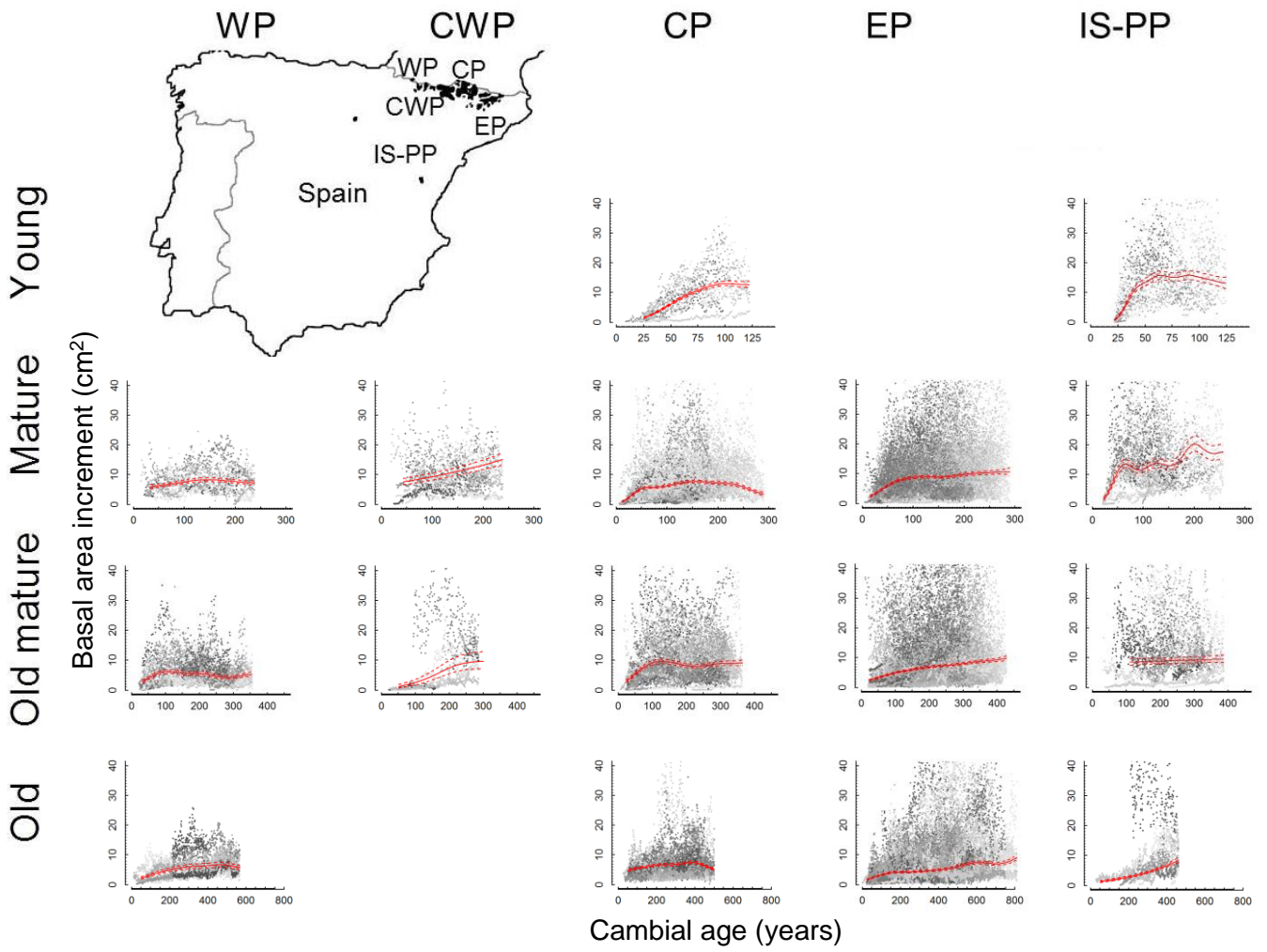


Figure 4

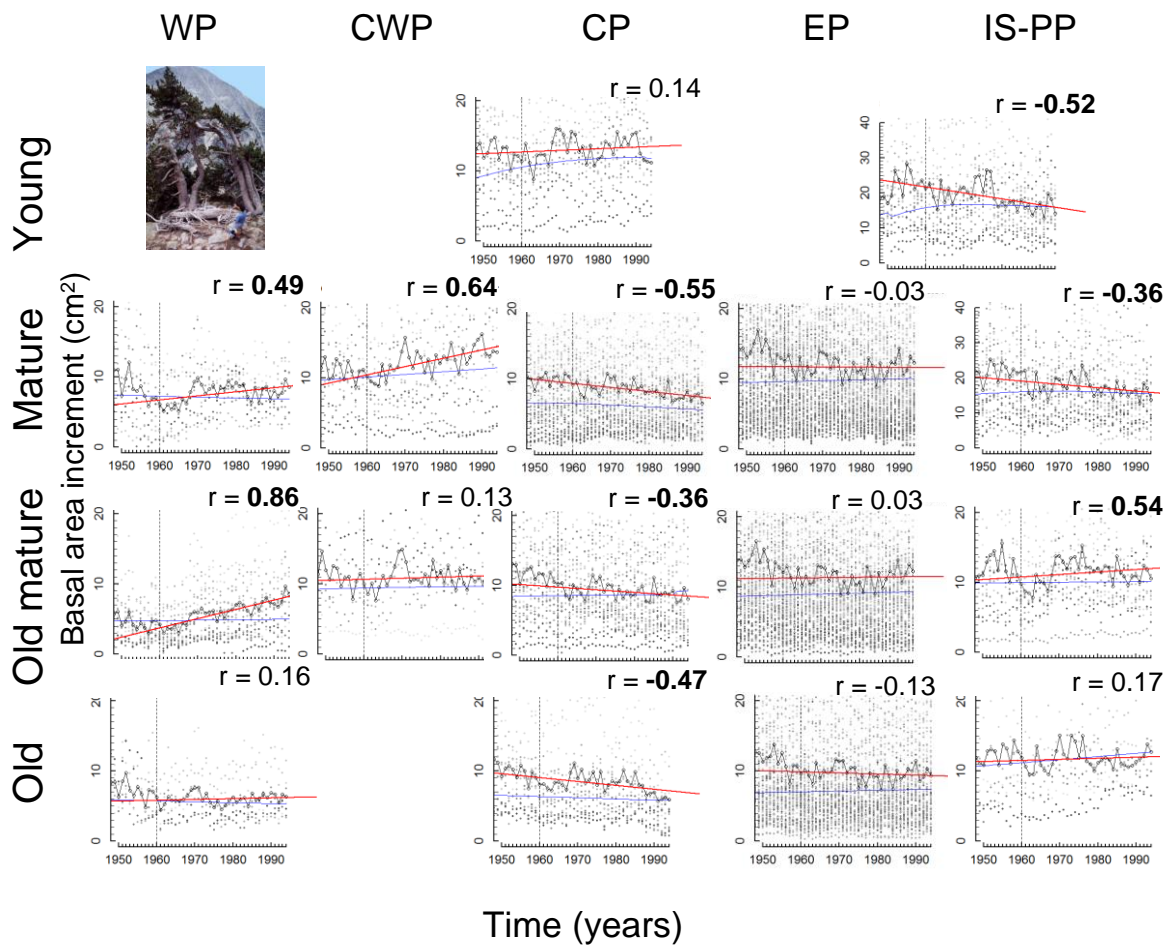


Figure 5