

Accepted Manuscript in Agricultural and Forest Meteorology, v. 264, pp. 309-321.

Calama, R., Conde, M., De-Dios-García, J., Madrigal, G., Vázquez-Piqué, J., Gordo, J., Pardos, M., 2019. Linking climate, annual growth and competition in a Mediterranean forest: *Pinus pinea* in the Spanish Northern Plateau. *Agric. For. Meteorol.* vol. 264: 309-321. Doi: 10.1016/j.agrformet.2018.10.017

This is a PDF file of an unedited manuscript (post-print version) that has been accepted for publication.

1 **Linking climate, annual growth and competition in a Mediterranean forest: *Pinus pinea* in**
2 **the Spanish Northern Plateau**

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12 **Abstract**

13 Climate, competition and site conditions are the main drivers controlling annual secondary
14 growth in tree species. These factors do not act independently on tree growth, but by means of
15 interactions, resulting in mediated interactive effects. For example, the stress gradient
16 hypothesis postulates alleviated interspecific competition under limiting spatial (site) or
17 temporal (climate) resources. According to this, models predicting annual growth and yield for
18 a given forest should consider these issues in their formulation. In this study, we present a
19 modelling approach based on using data from permanent plots and dendrochronological
20 analysis in order to describe annual tree growth in pure, even-aged stands of *Pinus pinea* L. in
21 the Spanish Northern Plateau, a highly limiting environment due to its Mediterranean
22 continental climate. Our method is based on identifying the different sources of variability by
23 means of a multilevel linear mixed model, and thereby identifying the potential covariates
24 explaining observed variability at the different spatiotemporal scales. Our results indicate that
25 site related factors such as site index or dominant height exert a greater influence on annual
26 secondary growth than size-symmetric competition. In addition, we found that the controlling
27 influence of water stress is greater than that of temperatures on tree growth. Furthermore, our
28 results allow evidence to be identified for the stress gradient hypothesis in temporal
29 intraspecific interactions, since trees exposed to a higher degree of competition tend to grow
30 more than expected in dry periods. In contrast, the effect of competition on growth, on average,
31 tends to be aggravated at very poor sites. Finally, our modelling approach allows us to conduct
32 growth and yield simulations under different climate scenarios at different spatial scales,
33 providing results which point to significant decreases in timber and cone production under the
34 more severe scenarios, which can be alleviated through more intensive silviculture.

35 **Highlights**

- 36
 - *Site conditions exert larger influence over growth than competition*
 - 37 - *Secondary growth in *Pinus pinea* is mainly controlled by water stress*
 - 38 - *Effect of competition on growth is alleviated on extreme dry years*
 - 39 - *Under future climate scenarios a significant decrease of production is expected*

40 **Keywords**

41 *Multilevel mixed model, climate sensitive model, size-symmetric competition, stress gradient*
42 *hypothesis, adaptive silviculture*

43 **Introduction**

44 Climate, competition and site conditions are among the main drivers defining spatiotemporal
45 patterns of variability in annual secondary growth of tree species (Madrigal-González and Zavala,
46 2014). Site conditions – fertility, soil water holding capacity, soil depth, aspect and slope, as well
47 as mean values for rainfall, temperature or irradiance - determine the potential maximum
48 growth for a given tree, and characterize the pattern of spatial variability between stands, blocks
49 or forests. Furthermore, current annual climatic conditions determine aspects such as annual
50 net carbon assimilation and evapotranspiration, which in turn can lead to greater resource
51 availability for processes such as respiration, reproduction, leaf production, primary and
52 secondary growth. Competition plays a double role: (i) competition determines the limitation or
53 regulation of the access of a subject tree to limited resources – light, water or nutrients - due to
54 neighbouring effects (Linares et al. 2010, Contreras et al. 2011), thus defining the patterns of
55 resource availability and spatial differences in growth between individuals from the same stand;
56 and (ii) competition mediates the effect of site and/or climate on growth and other forest
57 dynamics processes as recruitment (Wang et al. 2016). As regards the latter, the general theory
58 postulates that negative plant-plant interactions – including competition – increase in resource-
59 limiting environments (Tilman 1988, Gómez-Aparicio et al. 2011; Sánchez-Salguero et al. 2015).
60 On the other hand, the commonly cited stress gradient hypothesis (Bertness and Callaway, 1994;
61 Callaway and Walker, 1997) postulates that association with neighbours can provide benefits
62 under more unfavourable conditions, resulting in a shift from negative to positive interactions
63 across a benign to harsh environmental gradient. Although the two theories seem
64 contradictory, this apparent contradiction can be understood if we assume that competition is
65 responsible for long-term growth trends along resource availability gradients (Canham et al.
66 1994), while in the short-term, annual variation in growth can be controlled by a shift from
67 competition to facilitation in very restrictive annual conditions (Armas and Pugnaire, 2005). It
68 should be noted that while general theories of competition among plants have considered
69 intraspecific as well as interspecific factors, much of the evidence supporting the stress gradient
70 hypothesis has centred on interspecific interactions. However, recent studies have focused on
71 the importance of positive intraspecific plant-plant interactions in driving population dynamics
72 (Eränen and Kozlov, 2008; Gimeno et al., 2015), some evidence even pointing to the existence
73 of intraspecific facilitation between conspecific individuals of the same cohort (Fajardo and
74 McIntire, 2011; McIntire and Fajardo, 2011).

75 Regulation of intraspecific and interspecific competition through thinning is one of the main
76 elements of forest management. Forest management planning requires models that accurately
77 predict the growth of a given stand under different management schedules. In this context, the
78 functions, routines or submodels describing secondary growth (diameter or basal area
79 increment) provide the main “engine” in forest growth and yield models. However, while forest
80 models commonly assess the impact of competition and site characteristics on growth and yield,
81 the potential impact of climate has been largely ignored. Two basic assumptions underlie this
82 lack of attention to climatic impacts: (i) interannual variability in environmental drivers such as
83 rainfall or temperature is compensated over the set of years commonly used as a step in growth
84 projections (5-10 years); and (ii) despite short-term variability in these drivers, there are no
85 trends for long term change, thus, past environmental conditions will remain constant in the
86 future.

87 The abovementioned assumptions may not hold true under current scenarios of climate change
88 uncertainty. Evidence of recent changes in forest dynamics and productivity associated with
89 climate change has been reported in various studies (Sarris et al. 2007, Macias et al. 2006). In
90 addition, it has been shown that the occurrence of a single extreme-climatic event – such as a
91 severe summer drought or a heat wave - can have a long-lasting negative impact on forest
92 growth and dynamics (Peñuelas et al. 2001), not necessarily compensated by subsequent
93 favourable years (de-Dios-García et al. 2015). Negative effects of climate change on forest
94 growth and productivity are expected to be especially dramatic in Mediterranean ecosystems,
95 where Global Climate Models predict increments in air temperature, more frequent heat-waves,
96 severe and more recurrent drought episodes, and a general decrease in precipitation (IPCC,
97 2013). In this context, negative impacts on forest growth dynamics and productivity are likely to
98 be aggravated.

99 Adaptation of forests to these changing scenarios requires predictive models that assess and
100 compare different management alternatives under different climate scenarios, as well as the
101 potential impacts on the provision of ecosystems services. Therefore, models to support forest
102 management should be sensitive to both climate and management practices (Ameztegui et al.,
103 2017). In addition, forest management under scenarios of climatic uncertainty require flexible
104 tools that can integrate and evaluate the impact of a single climatic event over the subsequent
105 years. Hence, the temporal scale of the models should be downscaled, at least to an annual
106 scale. Finally, forest models should be able to assess the effect of spatial variability on site
107 conditions at the spatial scale (block, stand, forest) required by the managers.

108 The inclusion of climate in forest models can be approached from different perspectives. Process
109 based models describe physiological-based processes such as photosynthesis, respiration or
110 evapotranspiration as a response to climate drivers (Makela et al. 2010). The sound physiological
111 basis of these models permits their generalization to changing scenarios, having been widely
112 used to identify the potential response of forests to climate change on forest productivity at
113 very detailed temporal scales (ranging from minutes to days). However, they require detailed
114 ecological and physiological data for accurate calibration, which limits their range of
115 applicability. In addition, while widely valid for large-scale global assessment of forest
116 productivity, their predictive capacity at typical management scales (forest unit, blocks) is lower
117 in comparison to traditional empirical approaches, since between-site differences, tree-level
118 interactions and management practices are not considered in such detail (Ashraf et al. 2015).
119 Finally, the main output from process-based models is net primary production, which should
120 therefore be translated into above and belowground biomass production. In this regard,
121 detailed outputs of other ecosystem services are lacking in process-based models or are
122 computed through empirical functions.

123 A second approach for constructing climate-sensitive models is based on using climate attributes
124 as predictors of site index, which is the site productivity indicator of typical empirical growth and
125 yield models (e.g. Bravo-Oviedo et al. 2008, Crookston et al. 2010, Sharma et al. 2015). While
126 this approach can be valid for matching long-term changes in productivity, it has important
127 limitations for predicting the growth response to interannual climate variations and contributes
128 to propagating the error through the different models involved (Trasobares et al. 2016).

129 A final approach – presented in this study – is to integrate climate drivers as explanatory
130 covariates into empirical growth and yield models (Linares et al. 2010, Manso et al. 2015,
131 Trasobares et al. 2016). These models – sometimes known as semi-empirical models – will retain
132 the beneficial characteristics of empirical models in terms of accuracy of predictions at different

133 forest scales, easy integration of site and competition effects, inputs commonly measured in
134 forest inventories, sensitivity to management options and detailed outputs matching managers'
135 requirements. In addition, given the climate sensitivity of the model, this approach allows us to
136 predict forest evolution within the range of climate conditions for which the model was
137 constructed. In this regard, while traditional growth and yield empirical models rely on the
138 assumption that "past environmental drivers remain constant" the proposed approach assumes
139 that "past responses to environmental drivers remain constant". The construction of this type
140 of model requires repeated measurements of growth at the temporal scale, which can be
141 obtained from permanent plots (Manso et al. 2015, González-García et al. 2015), stem analysis
142 (Sharma et al. 2015), dendrochronological data (Martín-Benito et al. 2008, Linares et al. 2010)
143 or a combination of different methods (Fernández de Uña et al., 2015), as well as detailed
144 climate data at the same or lower temporal scales.

145 The aim of this study was to construct a climate sensitive empirical tree level model for
146 predicting annual basal area increment in pure stands of *Pinus pinea* L. in the Spanish Northern
147 Plateau. Due to its aridity, the region conforms one of the ecological limits for the species, thus
148 the effect of drought and increasing temperature on growth is expected to be more severe in
149 this area (Macias et al. 2006). Significant declines in timber (Pardos et al. 2015) and cone
150 production (Mutke et al. 2005, Calama et al. 2016), as well as phenomena of local extinction are
151 expected under more severe climate scenarios. Much effort has been devoted to modelling
152 growth, yield and dynamics for the species (Calama et al. 2017), including the construction of a
153 management oriented integrated tree-level model and simulator (PINEA2, Calama et al. 2007),
154 which is climate insensitive (except for the cone production submodule). In addition, although
155 the process-based model PICUS was calibrated to the characteristics of the species in the region
156 (Pardos et al. 2015), its use in practical management at forest scale is limited and it lacks a
157 specific cone production submodule.

158 Data for constructing the model were obtained by combining repeated measurements from
159 permanent plots and dendrochronological data. The new model is constructed as a multilevel
160 linear mixed model, in order to account for different levels of spatiotemporal correlation among
161 the observations. The process of model construction allows us to identify the main drivers
162 affecting growth and to describe the relationships linking climate, competition and growth. The
163 annual basal area increment model was therefore integrated within the general model for the
164 species (PINEA2) and used to simulate the expected changes in volume, biomass stock and cone
165 production under different climate scenarios and management alternatives. Our main
166 hypotheses were (i) tree level competition and stand stocking are the key drivers influencing
167 basal area increment; (ii) annual basal area increment is more influenced by rainfall regime and
168 water stress than by extremely cold / hot temperatures; (iii) positive interactions can
169 overwhelm competition between conspecifics in very dry years as well as in limiting
170 environments, in line with the stress gradient hypothesis extended to intraspecific interactions;
171 (iv) we expect a severe decline in timber, biomass and cone production under more severe
172 climate scenarios, which can be alleviated by the application of a more intense thinning regime
173 and extending the rotation length.

174 **Material**

175 • **Study region**

176 The Northern Plateau of Spain is a plain defined by the Basin of the Duero River, and which has
177 two main differentiated units: sandy areas, at an average altitude of 700 – 750 m and limestone

178 plains, at an altitude over 800-850 m. Within the region, *Pinus pinea* covers more than 60,000
179 ha, mainly in the province of Valladolid. Lithological differences have resulted in different soil
180 types. Sandy soils present a very high sand content (> 90%) and very low water holding capacity
181 (WHC<100 mm), while soils in the limestone area, with a percentage of clay and lime over 40-
182 50% , reach WHC values of > 250 mm. With respect to the climate conditions, the Northern
183 Plateau is a relatively homogeneous territory, characterized by a Mediterranean continental
184 climate, with very low precipitation (average annual rainfall: 440 mm, ranging from 220 - 620
185 mm), summer drought (average rain of 54 mm between July-September) and cold winter
186 temperatures (average annual temperature 11.7-13.7 °C, minimum absolute temperature
187 below -10 °C). These forests have been managed since the end of 19th century, the objectives of
188 this management being to guarantee soil protection and optimize cone and timber production,
189 resulting in pure, even-aged stands.

190 • ***Network of permanent plots***

191 In 1996, INIA-CIFOR, in cooperation with the forest services of Valladolid installed a network of
192 permanent plots in pure even-aged stands of *Pinus pinea* within the studied region. The network
193 included 141 circular plots, with variable radius, including a fixed number of 20 trees. Plots were
194 selected so as to cover the whole range of site conditions, stand stocking and ages identified
195 within the region, attempting to achieve a uniform spatial distribution. Plots were located in
196 public forests, and were selected in forests blocks that had not been altered over at least the
197 previous ten years.

198 At plot installation, diameter at breast height, total height, crown diameter, height to crown
199 base and tree coordinates were measured for all the trees within the plot. In a subsample of two
200 trees per plot, total age was determined by extracting cores at stump height with a Pressler
201 increment borer. These cores were used to backdate information and predict the state of trees
202 and plots in 1991, five years prior to installation (see Calama and Montero, 2005, for further
203 details). Plots were reinventoried in 2001, 2008 and 2016.

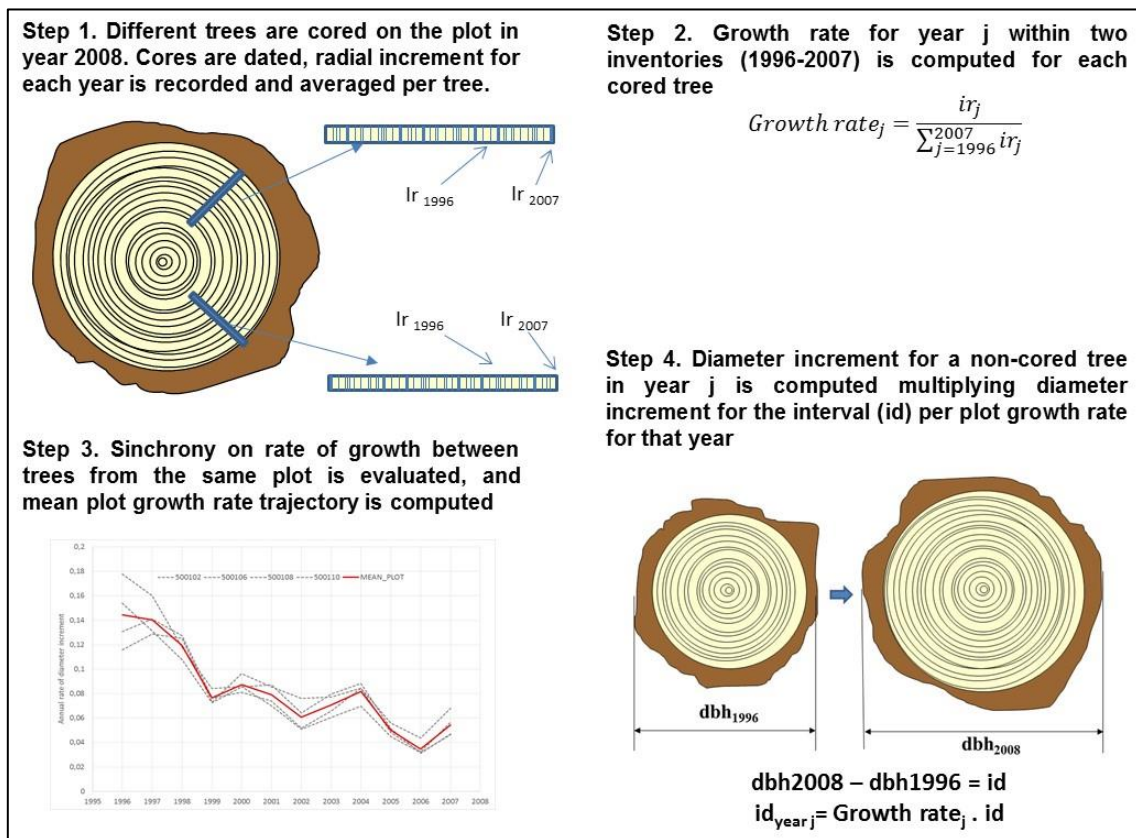
204 Throughout the 20 year- monitoring period, the silviculture applied in the plots has been similar
205 to that applied in the adjacent forest, consisting mainly of low thinnings, as those described for
206 the Business as Usual (BAU) alternative in the *Case study* section. When a thinning treatment
207 was applied in a plot, the date and trees extracted were recorded. During this period several
208 plots (22) were removed from the experiment, due to illegal harvesting, excessive thinning,
209 forest fires, land use change and budget restrictions.

210 • ***Reconstructing annual increment data***

211 During the 2008 and 2016 inventories, two radial increment cores per tree were extracted
212 perpendicularly at breast height (1.30 m) from a subset of two to four trees per plot. Cores were
213 oven dried at 35°C for one week, mounted on wooden slides and polished using sand paper of
214 different grain sizes. After being processed, samples were scanned and ring width was measured
215 with a resolution of 0.01 mm using Lignovision 1.37 software (Rinntech, Heidelberg, Germany).
216 The two series from the same tree were averaged and cross dating was then performed visually
217 using standard methods, comparing tree ring series with the master series proposed for the
218 species in the region (Natallini et al. 2016). The total number of sampled trees was 234 in 2008

219 and 300 in 2016. Trees cored in 2008 were not resampled in 2016, thus, on average; two to six
 220 individual tree-ring series were available per plot.

221 Annual series of tree ring growth were then transformed into annual series of tree growth rate
 222 by dividing the observed radial increment in year i among total radial increment for a given
 223 period. We considered the four inter-inventory periods: 1991-1995; 1996-2001; 2002-2008 and
 224 2009-2015. In a second step, we checked for synchrony in the tree growth rates among cored
 225 trees from the same plot, by means of Pearson's correlation coefficient. If significant synchrony
 226 was detected, we constructed an annual series of plot growth rate by averaging individual tree
 227 growth rate series from the plot. Finally, this average plot growth rate series was used to
 228 calculate annual individual tree diameter increment from all the non-cored trees, by multiplying
 229 the expected annual growth rate by the diameter increment observed in the trees during the
 230 analyzed period (difference in dbh measured between two consecutive inventories). See figure
 231 1 for more details of the process.



232 **Figure 1. Reconstruction of annual increment data for all the trees in a plot inventoried in 1996 and 2008**

233 This approach is based on two assumptions, (i) the rate of annual diameter increment over bark
 234 is equivalent to the rate of annual radial increment under bark, and (ii) the existence of
 235 synchrony in annual growth rate series among the sampled trees in the plot implies synchrony
 236 among all the trees within the plot. After discarding the data from the six plots showing no
 237 pattern of between-tree synchrony, evident measurement errors and deficiencies in increment
 238 cores (broken samples), the final number of valid annual diameter increment records was 28622,
 239 obtained from 1634 trees in 113 plots, covering 25 years (from 1991 to 2015). ANOVA test
 240 showed no significant differences between discarded and remaining plots in terms of site index

241 (p-value: 0.2305), basal area (p-value 0.1994), Reineke's stand density index (p-value 0.0669) or
242 age (p-value: 0.1248).

243 **Methods**

244

245 • **Response variable**

246 Annual diameter increment for tree i within plot j in year k (DI_{ijk} , cm) was transformed into
247 annual basal area increment (BAI_{ijk} , cm^2):

$$248 \quad BAI_{ijk} = \frac{\pi}{4} [DI_{ijk}^2 + 2DI_{ijk}dbh_{ijk-1}]$$

249 Where dbh_{ijk-1} represents diameter at breast height for the i^{th} tree within the j^{th} plot at the end
250 of the $k-1^{\text{th}}$ year. Annual basal area increment was then log transformed in order to attain
251 normality and reduce heterocedasticity in the variance. The logarithmic transformation of
252 annual BAI – $\log(BAI)_{ijk}$ – was therefore used as response variable in the analysis.

253 • **Explanatory covariates**

254 Spatiotemporal variation in the response variable is explained by means of different covariates
255 acting at different levels:

256 *Plot level attributes*

- 257 - Maturation: plot dominant height, mean squared diameter per plot (dg), crown
258 cover (projected surface of the crowns divided per plot area), stand age
259 - Stocking: number of stems/ha (N), basal area (BA), Reineke's stand density index
260 (SDI), defined as
- $$261 \quad - \quad SDI = N \left(\frac{dg}{25} \right)^{1,605}$$
- 262 - Productivity: site index, defined as the expected plot dominant height at a stand age
263 of 100 years, computed according to the model by Calama et al. (2003)

264 *Tree level attributes*

- 265 - Tree size: diameter at breast height (dbh) and section at breast height (g), referred
266 to the beginning of the growth period
267 - Distance independent competition indices: ratio dbh/dg , ratio $g/\text{mean tree section}$
268 per plot, basal area of the trees larger than the subject tree (BAL). As we aimed to
269 construct a new module for PINEA2 model, which is a distance-independent one, we
270 didn't evaluate distance-dependent competition indices.

271 Logarithmic, root and inverse transformation of these variables were also evaluated as potential
272 predictors.

273 *Climate attributes*

- 274 - Rainfall: monthly, seasonal and annual precipitation, computed from the 1st October
275 of the year before increment. Selection for this date aims to cover the whole
276 hydrological year, when rainfall starts to fill up water soil reserves after summer
277 drought. Apart from monthly precipitation, we evaluated the cumulative sum of
278 precipitation fallen in periods covering different months (e.g. from February to May)

279 - Temperature: monthly, seasonal, mean annual temperature, and mean values of
280 maximum and minimum temperatures, covering the whole hydrological year. As in
281 the previous paragraph, the average values of temperature computed for periods
282 covering different months were also evaluated.

283 Monthly series for rainfall and temperature were obtained from the most complete
284 meteorological data for the region, from the meteorological station at Valladolid (41° 39' 8" N -
285 4° 43' 24" W, 690 m a.s.l.), located at an average distance of 25 km from the plots (range 8.6 –
286 52.9 km). To ensure compatibility among annual and periodic predictions, climatic variable
287 response was standardized by subtracting the mean value for the 1991-2015 series from the
288 observed annual value and dividing by the standard deviation. In this way, periodic predictions
289 over an average year can be performed by fixing a value of zero for all the temporal attributes.
290 Additionally, the standardization allows us to gain an insight into the relative importance of each
291 temporal predictor on the response variable.

292

293 • **Modelling approach**

294 The basal area increment dataset includes observations recorded in repeated trees within plots
295 in different years. Due to this spatiotemporal structure of the data, the observations coming
296 from the same tree, plot and year tend to be more similar among them than the average. To
297 account for this severe departure from the basic assumption of independence, we utilized a
298 multilevel linear mixed model (MLMM), including random effects acting at tree, plot, year and
299 plot x year scales. The basic structure for the MLMM is:

$$300 \quad y_{ijk} = \mathbf{X}_{ijk}\boldsymbol{\beta} + u_i + v_j + w_k + z_{jk} + e_{ijk}$$

301 Where y_{ijk} is the observation for the response variable (log BAI) recorded in the i^{th} tree within
302 the j^{th} plot in the k^{th} year; \mathbf{X}_{ijk} represents a (1 x n) vector containing the observed values for the
303 explanatory covariates in the ijk^{th} observation; $\boldsymbol{\beta}$ is the vector of Best Linear Unbiased estimator
304 for the fixed parameters; u_i, v_j, w_k and z_{jk} represents the realization of the random effects
305 acting at tree, plot, year and plot x year scales of variability, distributed following a normal
306 distribution with mean zero and variance $\sigma_u^2, \sigma_v^2, \sigma_w^2$, and σ_z^2 respectively; e_{ijk} represents a
307 residual term, independent realization of a normal distribution with mean zero and variance σ_e^2 .
308 However, in subsequent steps of the model construction we evaluated alternative structures of
309 covariance among the repeated observations recorded for the same tree, such as the
310 autoregressive structure, in order to account for possible dependency among the residuals e_{ijk} .

311 The first step in the process of model construction is to fit the basic model, entering only
312 intercept as a fixed effect, as well as the complete set of random effects. In subsequent steps
313 we evaluated the inclusion of covariates explaining observed variability in the following order:
314 tree size attributes, distance-independent competition indices, plot level attributes, site index
315 and climate variables. Preselection of the covariates was carried out by checking correlation
316 among the empirical best linear unbiased predictors (EBLUPs) for a given level of random
317 variability (e.g. plot) predicted in a previous step along with different explanatory covariates
318 acting at that level (e.g. stand density, dominant height...). Since all these preliminary models
319 show different mean structure, comparison and selection among them should be based on
320 information criteria derived after maximum likelihood (ML) fitting. Once the final set of fixed

321 covariates had been selected, we then tested alternative structures of variance-covariance for
322 the within tree dependence among observations, which are then compared in terms of
323 Restricted Maximum Likelihood inference, which results in unbiased estimates for the variance
324 components of the model (see Verbeke and Molenberghs, 2000, section 6.2.5 for more details).
325 As comparisons involved nested and non-nested models we prioritized both BIC (for non-nested
326 models) and -2LL (for nested) criteria for selecting among different models. BIC was preferred
327 over AIC to compare non-nested models since it takes into account sample size and its
328 application lead to more parsimonious models under large sample sizes (Dziak et al., 2010), as
329 is our case (n = 28622).

330 Accuracy of the model for predicting over the fitting data set was evaluated by means of
331 goodness-of-fit statistics as Mean Error, Root Mean Squared Error and Modelling Efficiency.
332 These statistics were computed for the conditional (including fixed effects and the predicted
333 EBLUPs for the random effects) and the marginal (only including fixed effects), in both raw
334 (following antilogarithmic transformation) and logarithmic scales. All the statistical analyses
335 were carried out using SAS® 9.4.

336 • ***Validation process***

337 Since no additional validation data set was available, we decided to carry out a cross-validation
338 process. In our case, we performed 100 fittings of the model, each time randomly omitting 1%
339 of the observations. The fitted models at each realization were then used to predict the response
340 variable in the omitted observations. Predicted values were used to estimate prediction
341 residuals, defined as the difference between the observed value and the predicted value using
342 the model fitted without considering that observation (Vanclay and Skovsgaard, 1997). These
343 residuals were then used to compute *press* statistics such as mean error (E), Root Mean Squared
344 Error (RMSE) and modelling efficiency (EF).

345 • ***Competition hypothesis***

346 After fitting the definitive model for BAI the remaining sources of non-explained variability were
347 used to analyse and contrast different hypotheses concerning competition. The remaining
348 variability at plot x year level indicates a specific pattern of annual increment response acting at
349 plot level. The values for the EBLUPs associated with this plot x year effect can be used to test
350 whether this specific annual pattern varies with certain plot attributes such as age, site quality
351 or stocking, depending on the conditions of the year. In our case, based on extending of the
352 stress gradient hypothesis to intraspecific interactions, we would expect an attenuation of
353 competitive effects in a dry year. Thus, in a dry year, we should observe a positive relationship
354 between the EBLUPs for the plots in that year and stocking attributes (such as basal area or
355 stand density index), while in a moist year this relationship should be either negative or
356 nonsignificant. This would indicate that in a dry year, basal area increment in high density stands
357 would be greater than predicted by the fixed parameters of the model.

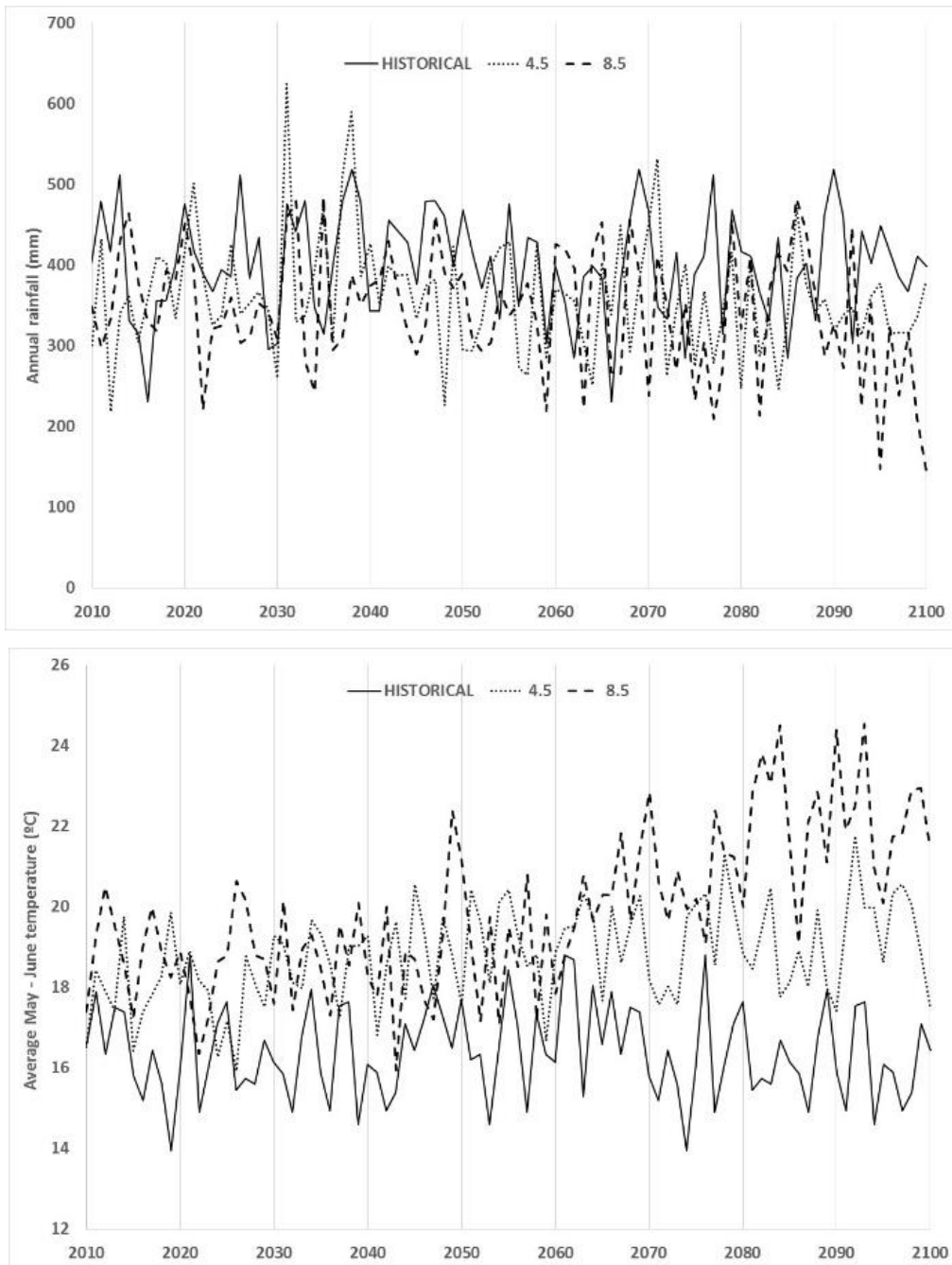
358 In addition, we used the EBLUPs for the random plot effects to test whether the effect of
359 competition is aggravated or alleviated in low productivity environments. For this purpose, we
360 splitted plots in the data base into low quality (site index \leq 12 m) and high quality (site index $>$
361 12 m) and checked for the existence of relationships among stocking and EBLUPs for the plot
362 effect.

363 • ***Case study***

364 The constructed model for annual basal area increment was incorporated into the integrated
365 model for the species, PINEA2, in order to simulate the effect of the expected climate change
366 scenarios on growth and yield. PINEA2 is a distance-independent single tree level model
367 constructed for pure even-aged stands of *Pinus pinea*, which permitted to obtain projections on
368 timber, biomass and cone production under different management scenarios on 5-year steps.
369 While originally climate insensitive, by substituting the initial 5 year-diameter increment
370 function with the BAI model constructed in this study it is possible to make annual simulations
371 of the growth and yield of the stands under different climate scenarios. More details on the
372 model can be found in Calama et al. (2007).

373 We simulated the evolution of a pure even-aged stand of medium-high quality (site index = 17
374 m), from an initial stand age of 20 years, and initial stocking density 500 stems/ha. We simulated
375 the current *business as usual* (BAU) silviculture oriented towards cone and timber production,
376 with a rotation length of 100 years, two thinnings from below at 30 and 45 years, leaving 250
377 and 150 stems/ha respectively. Regeneration is carried out using the shelterwood system, which
378 in this case consists of a seeding felling at 80 years, reducing stand density to 75 stems/ha; a
379 single secondary felling at 90 years, leaving 25 stems/ha, and a final cutting at 100 years. As an
380 alternative we tested the cone-oriented schedule with an extended rotation length of 110 years,
381 a single thinning reducing initial stocking to 150 stems/ha at 30 years, a seeding felling at 100
382 years (leaving 75 stems/ha), a secondary felling at 105 years (leaving 25 stems/ha) and a final
383 cutting at 110 years.

384 These silvicultural alternatives were simulated under three different climate scenarios: a current
385 climate scenario, based on the historical records for the 1960 – 2010 period, as well as two
386 climate change scenarios based on IPCC R.C.P's 4.5 and 8.5 (figure 2). Climate scenarios were
387 obtained from the Spanish National Agency for Meteorology (AEMET,
388 http://www.aemet.es/es/serviciosclimaticos/cambio_climat). Simulations were carried out for
389 the 2010 – 2100 period. Outputs from the different climate scenarios were compared in terms
390 of mean annual volume increment, average annual stocking biomass, and mean annual cone
391 production evaluated over the whole cycle.



393

394 *Figure 2. 2010-2100 series for annual rainfall (above) and mean temperature for May – June (below) based on*
 395 *current climate (historical) and RCP scenarios 4.5 and 8.5.*

396 **Results**

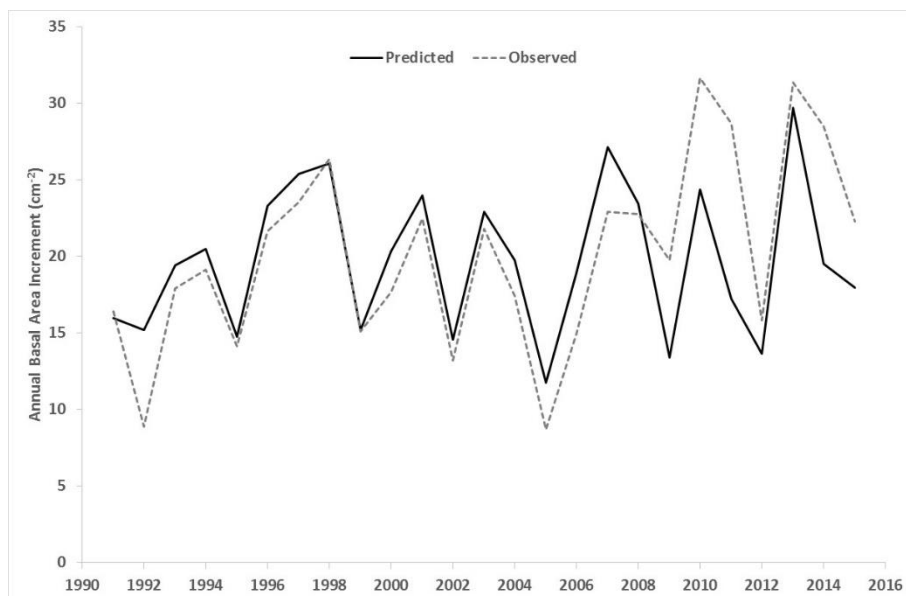
397 • **Model fitting**

398 After the sequential procedure of model construction (table 1), the final structure of the model
 399 included the following explanatory covariates (table 2) acting at tree or plot level: breast height
 400 diameter and its quadratic form, dominant height, the logarithm of plot basal area and site
 401 index. In addition, standardized climate related variables were entered in the model, such as the
 402 rainfall occurring during the period between 1st October-30th September of the current growth

403 year, and the average temperature of May and June of the year). Fixed effects included in the
404 model explained 59%, 38% and 58% of the initial observed variability between plots, between
405 trees within the same plot and between years, respectively.

406 After the selection of the explanatory covariates, different structures for the variance-
407 covariance matrix of the within-tree residuals were tested, with AR(1) structure leading to the
408 best results. By considering this covariance structure, the random tree effect was no longer
409 significant and therefore was removed from the model. The high value for the AR(1) parameter
410 (0.9422) indicates large temporal dependence among lagged observations from the same tree.

411 Goodness-of-fit statistics (table 3) point to unbiased estimates for the conditional model in both
412 raw and logarithmic scales, as well as for the raw scale in the marginal model. The observed bias
413 in marginal response for the logarithmic scale could be related with the severe unbalance in the
414 number of observations among year and plots. Conditional models explain 65% – 71% of the
415 observed variability in annual BAI at tree level, while marginal models explain 31%-36% of the
416 annual BAI. However, marginal models in raw untransformed scale accurately match the
417 observed interannual pattern of variability in basal area increment (figure 3) and are able to
418 mimic the growth decay in dry years (e.g. 2005 and 2012) as well as growth enhancement in
419 moist periods (e.g. 1996-1998). Less accurate agreement among predicted-observed values
420 identified in the last years of the series can be related with the inherent propagation of error in
421 long term projections as well as with the effect of the intense thinning campaign carried out in
422 the territory by the period starting in 2007-2008, which in some occasions resulted in a much
423 more intense thinning in the surrounding environment of the plot than that applied within the
424 plot.



425 *Figure 3. Average value of the observed and predicted values of annual BAI using marginal model in raw scale –*
426 *antilogarithmic transformed - for the studied period*

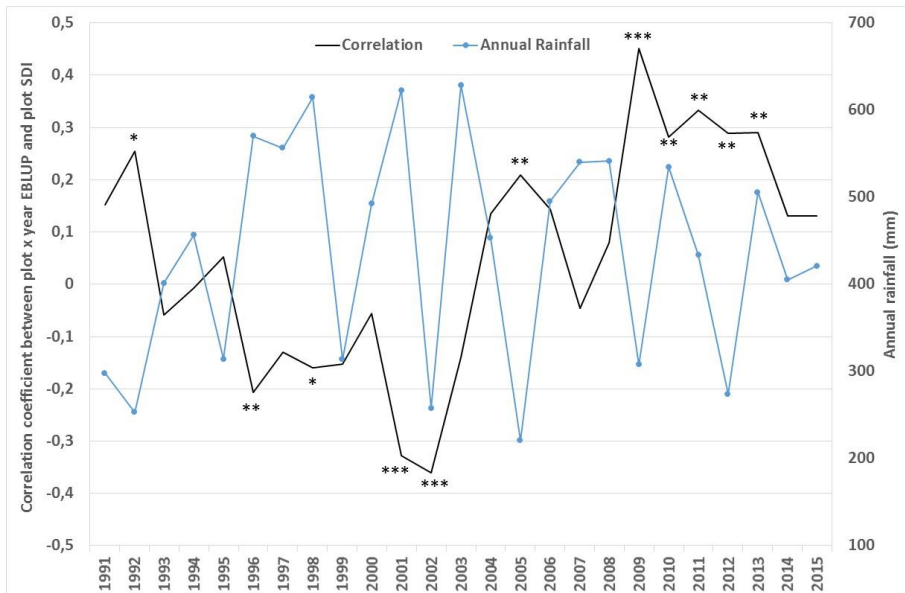
427 • **Validation**

428 Given the large amount of computational resources required to fit the definite model (step 17
429 in table 1, with more than 4 hours and 45 minutes for a single run), validation of the model was
430 carried out using model for the step 15 (table 1), with the complete structure of fixed and
431 random effects, but without considering AR(1) residual covariance structure or REML fit. *Press*
432 statistics showed slight variation if compared with the results from the fit of the definite model

433 (table 4), except in the case of the modelling efficiency for conditional responses. In this case it
 434 should be noted that the conditional response for the model used in validation (step 15 in table
 435 1) includes the EBLUP for a tree random effect, which was skipped in the fit of the definite model
 436 (after including an autoregressive parameter, AR1).

437 • **Evidence for competition hypothesis**

438 Throughout the whole sequential process of the model fitting, the observed random variability
 439 acting at plot x year level remains almost unchanged (table 1), indicating that the explanatory
 440 covariate does not explain the observed variability at this scale. Plot x year variability indicates
 441 the specific response in BAI of the trees in a plot for a given year, once fixed covariates, as well
 442 as random plot, tree and year effects are accounted for. This random variability can be
 443 associated with certain phenomena, the observation of which and consideration in the model
 444 are not easily achieved (e.g. local climatic vents). Correlation tests among the EBLUPs from
 445 random plot x year effects and different stocking attributes, such as Stand Density Index,
 446 revealed a pattern of shift from high competition in moister years to an attenuated effect of
 447 competition in drier years (figure 4). In particular, while in moister periods (e.g. 1996-1998,
 448 2000-2001, 2006-2008), the relationship between plot x year EBLUPs and stocking tends to be
 449 nonsignificant or significantly negative, in drier periods (1992, 2005, 2009-2013) this correlation
 450 tends to be significant and positive. This means that in drier years we observe positive values
 451 for the plot x year EBLUPs in denser plots, and negative values in low density plots, while the
 452 opposite trend is observed under moister conditions. Hence, in drier years, trees in denser plots
 453 tend to grow more than predicted by the model. A detailed analysis permits to identify a
 454 significant negative relation between the correlation coefficient plot x year EBLUP – stocking
 455 and annual rainfall (Spearman’s rank coefficient of correlation = - 0.4223, p-value 0.0355), as
 456 well as significant difference (p-value: 0.0290) between the mean value of the correlation
 457 coefficient plot x year EBLUP – stocking between moist ($r = 0.1191$) and dry ($r = -0.0111$) years).

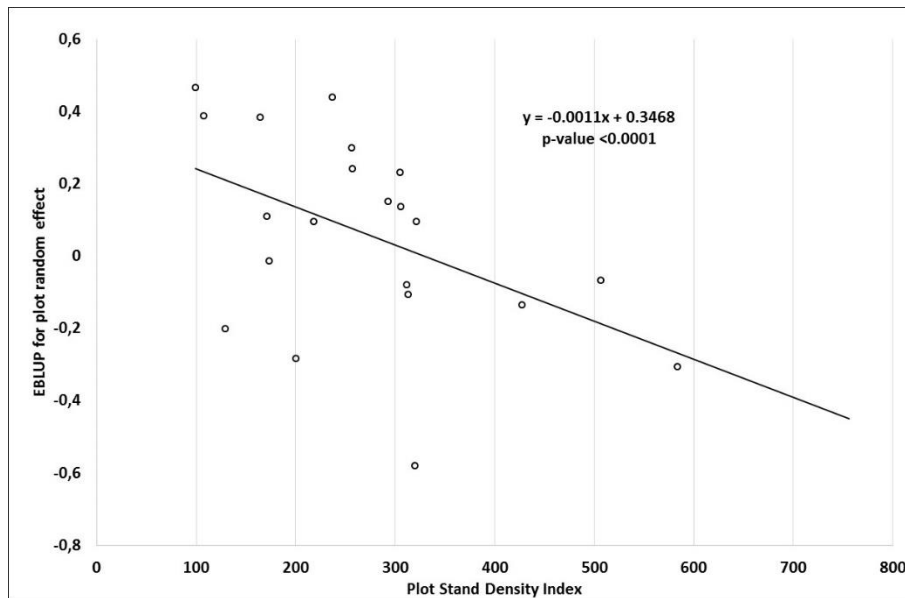


458 **Figure 4. Interannual variation in the correlation coefficient between annual plot x year EBLUP and plot Stand**
 459 **Density Index, and relation with annual rainfall (* p-value <0.05, ** p-value < 0.01, *** p-value < 0.0001)**

460 Focusing on the interactive effect between competition and site once the common effect of
 461 competition in the model is discounted, we observed that in low quality plots (site index =< 12
 462 m) there remains a pattern of significant negative correlation between the EBLUP for plot

463 random effect and Reineke's Stand Density Index. Thus, in very dense, low quality plots, trees
464 tend to grow less than predicted by the model (figure 5), while in medium and high quality plots,
465 no remnant relationships with stocking density are found.

466



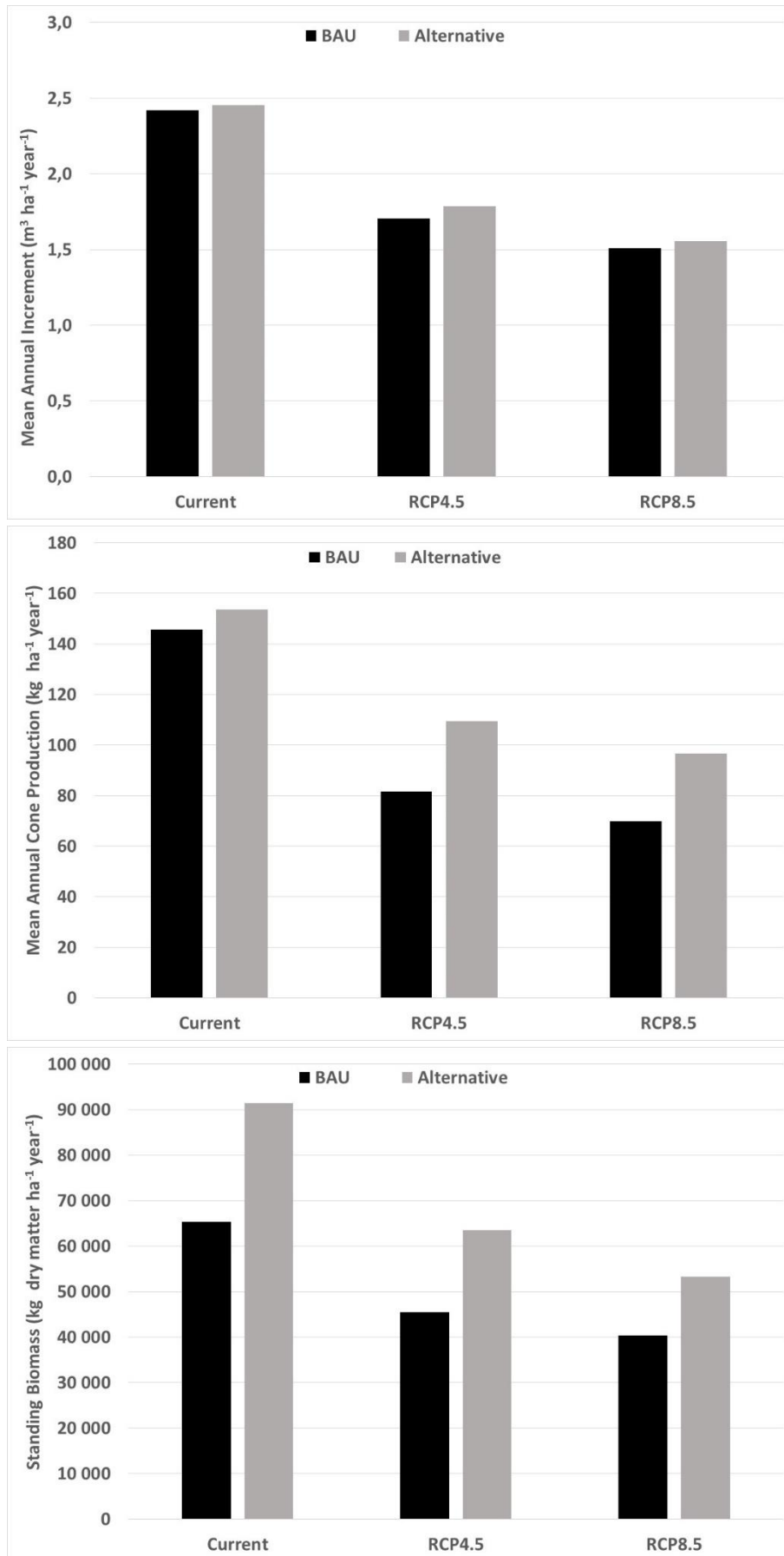
467 *Figure 5. Relation between EBLUP for plot random effect and plot Stand Density Index in low quality plots (Site*
468 *Index ≤ 12 m)*

469 • **Case study: impact of climate change**

470 Simulations reveal a severe impact of climate change on mean annual increment, average stock
471 of standing biomass and mean cone production, although somewhat alleviated in the case of
472 the cone-oriented silviculture alternative (figure 6). Climate scenario RCP 4.5. results in a
473 decrease of 27% - 30% in mean annual increment ($\text{m}^3 \text{ha}^{-1} \text{year}^{-1}$), while the decrease in RCP 8.5
474 reaches 37% - 38% in comparison to current climate conditions. As regards the average stock of
475 standing biomass, expected decreases under RCP 4.5. are about 30% for both silvicultural
476 alternatives, while the decrease is 38%-41% under RCP 8.5. In all cases, smaller decreases are
477 associated with the cone oriented alternative schedule. In the case of cone production, even
478 greater decreases due to climate change, as well as the mitigating effect of cone oriented
479 silviculture, are predicted. Under RCP 4.5. and RCP 8.5., BAU schedule results in decreases of
480 44% and 52% in mean cone production in comparison to the current climate, while alternative
481 silviculture results in decreases of 29% and 37%. In addition, it should be noted that for the
482 period 2010 – 2100, under current climate conditions, alternative silviculture was always better
483 than BAU in terms of mean annual increment, stocking biomass and cone production.

484

485



486 **Figure 6.** Effect of business as usual and alternative silvicultures and climate scenarios (current, RCP 4.5 and 8.5) on
 487 mean annual increment (a), annual cone production (b) and average standing biomass (c). Mean values for 2010 –

488 **2100 simulation period.**

489 **Discussion and Conclusions**

490 • **Factors driving secondary annual growth in *Pinus pinea***

491 Our results provide evidence that the secondary growth in *Pinus pinea* forests is a process which
492 displays large variability at different spatial and temporal scales (Natalini et al. 2016). The initial
493 decomposition of the observed variability (model 1 in table 1) reveals that pure spatial effects
494 (plot and tree) account for 53.7% of the variability, with temporal effects (year, plot x year and
495 tree x year residual) accounting for the remaining 46.3%. This fact highlights the importance of
496 considering patterns of temporal variation in the studies focusing on tree growth and dynamics
497 (del Río et al. 2014). In addition, the balance among the different temporal scales at which
498 variability is shown reflects the fact that a common temporal response at regional scale (e.g. to
499 a climate event) does not exist alone, but that there is a need to consider the effect of climate
500 and other abiotic events, such as shifts in site productivity, on plant-plant interactions at
501 different spatial scales (Coomes and Allen, 2007; Looney et al. 2016).

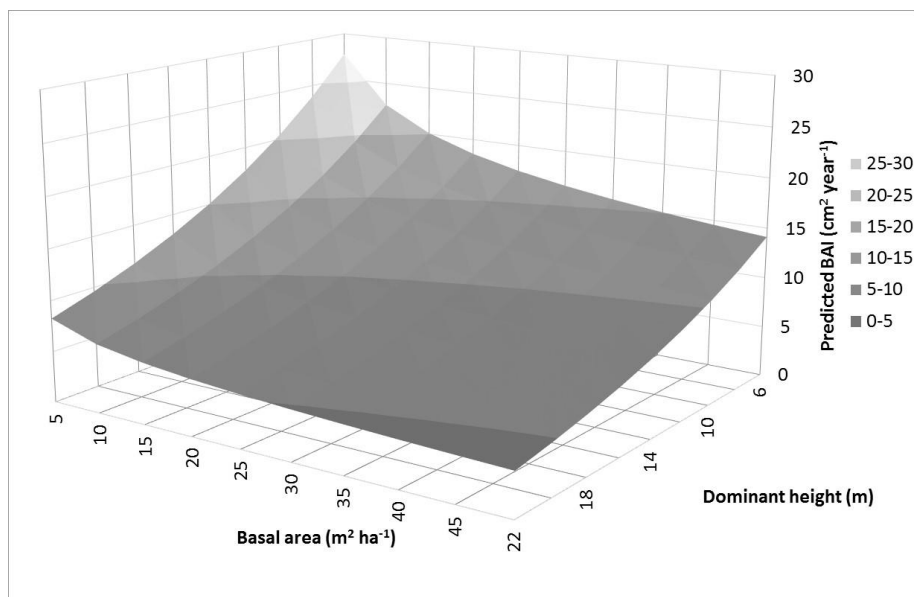
502 Throughout the sequential procedure of model construction we aimed to identify the different
503 factors explaining observed variability at the different scales. Focusing on between-tree
504 variability, tree size – defined by tree diameter at breast height – influences basal area
505 increment, showing a positive relationship up to a maximum basal area increment for very large
506 dbh (trees over 90 cm), a common pattern in forest tree species (Gómez-Aparicio et al. 2011).
507 However, this positive effect of increasing tree size is attenuated at stand level by the negative
508 effect of dominant height – a proxy of the joint effect of tree maturity and average tree size in
509 pure even-aged stands – over basal area increment. This result reflects that target tree size and
510 stand ageing exert a strong influence over individual tree growth (Madrigal-González and Zavala,
511 2014), and this influence may change during stand development, from positive during younger
512 stages to neutral at maturity (Foster et al. 2014, Ruiz-Benito et al. 2015).

513 Competition is directly represented in the model through stand basal area, which outperformed
514 other stand-level parameters– such as Stand Density Index or number of stems/ha – and
515 distance independent tree-level competition indices – such as BAL or the ratio between target
516 tree dbh and mean squared diameter. Structural uniformity of pure even-aged stands, low
517 stocking density and homogeneity in the applied silviculture can explain the superiority of stand-
518 level competition indices over tree-level ones (Gea-Izquierdo and Cañellas, 2009). Our findings
519 also support the existence of size-symmetric competition (Schwinning and Weinwe, 1998) in this
520 type of forests where water (belowground competition) is the main limiting resource and, given
521 the homogeneity of tree sizes in these even-aged stands, tree size acts as a proxy of competition
522 and the outcome of long-term tree-tree interactions (Looney et al. 2016). This correlated effect
523 between individual competition and target tree size may underlie our finding in this study that
524 competition exerts a smaller influence on individual tree growth than other factors such as size
525 or dominant height (figure 7, Looney et al. 2016), therefore, our first hypothesis that tree-level
526 competition is the main driver of annual tree growth is not supported.

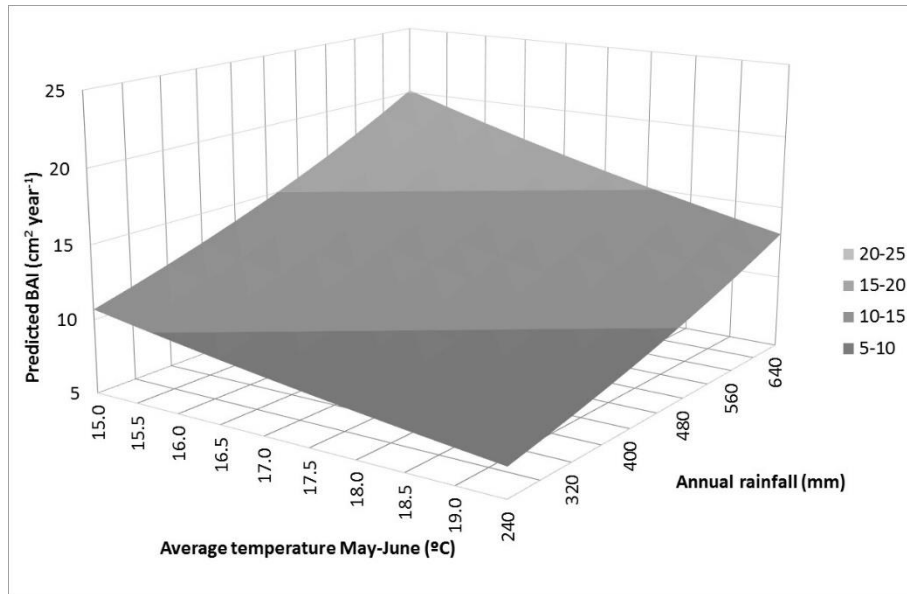
527 Our results point to a significant growth response to climate, as expected in this type of
528 Mediterranean continental ecosystem (Madrigal-González and Zavala, 2014). Total rainfall
529 occurring during the period between October of the previous year to September of the current
530 growth year, as well as mean temperature in May and June are the main climatic factors driving
531 secondary growth in *Pinus pinea*. As expected, we detected a positive relationship between
532 rainfall and growth, extending over time as far back as the precipitation occurring during the

533 previous autumn and winter seasons. Similar findings have been reported in previous studies on
 534 dendroecological growth-climate relationships for the species (Mazza et al. 2014, Natalini et al.
 535 2015, 2016). These findings reveal the importance of winter recharge of deeper layers in these
 536 sandy soils, which will act as the main water input for tree growth during the next spring season
 537 (Campelo et al. 2006). Moreover, in evergreen conifers the positive response to autumn and
 538 winter rainfall points to a dependency on the photosynthetic reserves produced during this
 539 period (Baldocchi et al. 2010), in which, despite freezing temperatures, there is no winter
 540 dormancy (Pardos et al 2010). On the other hand, the observed negative relationship between
 541 May-June temperatures and secondary growth has previously been observed in the species
 542 (Natalini et al. 2016), as well as in other Mediterranean pines (Martin-Benito et al. 2013). These
 543 result must be interpreted not only as a pure thermal effect preventing net assimilation and increasing
 544 respiration at elevated temperatures (Calama et al. 2013) but also as an indirect drought effect due to
 545 increased evapotranspiration in critical months for higher net photosynthetic rates, which in the species
 546 occurs in late May and June. . Taking into account this interdependence among increasing
 547 temperatures and decreasing water availability, the observed higher sensitivity of growth to
 548 drought than to temperatures (figure 8), as previously reported for other Mediterranean species
 549 (Gómez-Aparicio et al. 2011, Sánchez-Salguero et al. 2015), points to a clear dependence of
 550 growth in water stress, what is in accordance with our second hypothesis.

551



552 **Figure 7. Dependence of BAI on Dominant Height and Basal Area, for an average tree with dbh = 25 cm, growing**
 553 **on a stand with site index=18 m, under average conditions of annual rainfall (442 mm) and May-June temperature**
 554 **(17.4 °C). Grey scales represent values of BAI.**



556 *Figure 8. Dependence of BAI on May-June temperatures and Annual rainfall for an average tree with dbh = 25 cm,*
 557 *growing on a 50 years old stand with Basal Area = 20 m² ha⁻¹, Site index = 16 m. Grey scales represent values of BAI.*

558 **• Effects of environmental gradients on tree competition**

559 Our results indicate that once we discount the effect of the main factors driving tree growth,
 560 there is still a pattern of remnant unexplained response of the species to competition, varying
 561 along spatial and temporal gradients. We observed (figure 5) a more negative response to
 562 competition in low site quality stands. This finding is in accordance with general theories
 563 postulating that competition increases when resources are more limiting (Tilman, 1988).
 564 However, this differential effect is only evident in very low quality stands, generally located in
 565 more arid areas with shallow and very poor sandy soils, resulting in severe, permanent scarcity
 566 of nutrients and available soil for root development.

567 We detected a shift in the climate – competition relationships from moist (1996-2001) to dry
 568 (2009 – 2014) periods (figure 4), resulting in a significantly attenuated effect of competition in
 569 the drier period, indicating that in those conditions BAI tend to be larger than that predicted by
 570 the model. Again, this result is in accordance with the proposed stress gradient hypothesis
 571 postulating more frequent positive interactions under harsher conditions (Bertness and
 572 Callaway, 1994). The validity of this hypothesis has been evidenced when evaluating
 573 interspecific interactions, as in the case of the increased biomass production on different species
 574 growing in mixed forests (del Río et al. 2014), or the attenuated effect of warmer-induced shift
 575 of tree-lines in mixed stands (Liang et al. 2016). Our results suggest that this theory may be valid
 576 for intraspecific interactions (Eränen and Kzlov, 2008; García-Cervigón et al. 2013, Svanfeldt et
 577 al. 2017), and that positive interactions can even exist among conspecific individuals of the same
 578 cohort (McIntire and Fajardo, 2011).

579 Our findings give partial support to our third hypothesis, since we observe a shift to positive
 580 interactions between conspecifics in very dry years but not under very limiting environments,
 581 where competition dominates. These apparently contradictory results can be interpreted by
 582 assuming a long-term baseline response of an aggravated effect of competition in those
 583 environments where resource availability is highly limiting (as evidenced in multiannual studies,
 584 e.g. Gómez-Aparicio et al. 2011). Meanwhile, in the short term (annual), the balance of plant
 585 interactions may shift to positive as a response to temporal changes in resources such as water

586 availability, resulting in more stressful conditions (Armas and Pugnaire, 2005). In this regard,
587 water influences interactions not only because of its scarcity but also because of its variability
588 over time and the unpredictability of rainfall events. Under these conditions of non-permanent
589 resource limitation, it is assumed that for positive interactions to occur, the presence of
590 neighbours must directly increase the availability of the limiting resource (Maestre et al. 2009,
591 Svanfeldt et al. 2017). In the case of monospecific *Pinus pinea* forests, where we detected that
592 water shortage is the main limiting factor for growth, certain density dependent mechanisms
593 favouring water availability in very dry years could be related to the ability for root fusion by
594 spontaneous graftage (*anastomosis*, Mutke et al. 2012), permitting deeper ground layers to be
595 explored and favouring mycorrhizal activity. In addition, close neighbours in *Pinus pinea* forests
596 tend to maximize light interception by forming a single, umbrella like deep crown. This effect
597 would also result in a reduction of the irradiance reaching the forest soil, and a reduction in
598 water losses due to evapotranspiration (Fajardo and McIntire, 2011).

599 • ***Expected impacts of climate change***

600 Simulations carried out after including the constructed annual BAI model in the integrated
601 model and simulator PINEA2 reveal severe decreases in mean annual increment, total stocking
602 biomass and cone production under more extreme climate scenarios. As previously stated
603 (Calama et al. 2016, Pardos et al. 2015), cone production is much more sensitive to changing
604 climatic conditions than biomass production, indicating a preferential allocation to vegetative
605 growth rather than to reproduction structures under harsher conditions. The results of the
606 simulations mainly agree with those obtained after applying the process-based model PICUS to
607 the same species and environmental conditions (Pardos et al. 2015), hence supporting the utility
608 of the proposed empirically based modelling approach. In addition, these results are in
609 accordance with the expected impacts simulated for other Mediterranean forests, pointing to
610 severe reductions in biomass increment, timber production, wild forest products and/or other
611 ecosystem services associated with the more severe climate scenarios. In the case of *Pinus pinea*
612 forests, our results indicate that this negative effect of climate can be partially alleviated through
613 more intensive silviculture consisting of heavier as well as earlier thinnings along with extended
614 rotation length (García-Güemes and Calama, 2015).

615 • ***Validity of the approach***

616 Our modelling approach, based on incorporating both climate and spatially explicit drivers as
617 explanatory covariates into an empirical growth and yield model permits us to recognise the
618 main factors explaining annual secondary growth in *Pinus pinea*. In addition, our approach relies
619 on splitting and identifying the different sources of unexplained variability by means of a
620 multilevel linear mixed model, allowing us to evaluate potential shifts in competition patterns
621 depending on the availability of spatially and temporally varying resources. Finally, given the
622 empirical formulation of our model, it allows simulations to be carried out under different
623 climate and management scenarios. Our results support the growing body of evidence that shifts
624 in plant–plant interactions are correlated not only with changes in stress across spatial scales
625 but also with changes in stress conditions (such as temperature and moisture) across temporal
626 scales (Sthultz et al. 2007, García-Cervigón et al. 2013). In this regard, our results reveal the
627 importance of considering different spatial and temporal scales when analysing the intensity
628 and sign of the response to competition under specific environmental conditions (Soliveres et
629 al. 2010) and when constructing predictive models to provide support for forest management.

630 ***Acknowledgements***

631 This work has been carried out under the financial and functional framework of the National
632 Projects RTA-2013-00011.C2.1, PCIN-2014-138 INFORMED, AGL-2017-83828-C2.1 and the
633 PROPINEA agreement between INIA, ITACYL and Deputation of Valladolid. Authors wish to thank
634 Forest Service of Valladolid for their permanent support with the inventory and maintenance of
635 the experimental trials.

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Table 1. Sequential procedure for model selection

	Step	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	
Random Effects	Plot	0.1725	0.2528	0.2623	0.2557	0.1857	0.2013	0.2740	0.1299	0.1109	0.1101	0.1171	0.1183	0.0705	0.0704	0.0706	0.0724	0.0699	
	Tree	0.1490	0.0953	0.0930	0.0942	0.0928	0.0927	0.0931	0.0926	0.0923	0.0923	0.0923	0.0923	0.0922	0.0922	0.0923	0.0923	0.0923	ns
	Year	0.0961	0.0959	0.0973	0.0967	0.0987	0.0976	0.0986	0.1000	0.1019	0.1038	0.1011	0.1004	0.1070	0.0549	0.0409	0.0462	0.0474	
	Plot X Year	0.0878	0.0940	0.0959	0.0949	0.0933	0.0927	0.0954	0.0942	0.0904	0.0893	0.0897	0.0896	0.0895	0.0895	0.0895	0.0895	0.0895	0.0756
	AR(1)																		0.9433
	Residual	0.0932	0.0914	0.0913	0.0913	0.0912	0.0912	0.0913	0.0912	0.0912	0.0912	0.0912	0.0912	0.0912	0.0912	0.0912	0.0912	0.0911	0.1995
Fixed effects	Intercept	μ	μ	μ	M	μ	μ	μ	μ	μ	μ	μ	μ	μ	μ	μ	M	μ	
	Tree		dbh	dbh	dbh	dbh	dbh	dbh	dbh	dbh	dbh	dbh	dbh	dbh	dbh	dbh	dbh	Dbh	dbh
				dbh ²	1 / dbh	dbh ²	dbh ²	dbh ²	dbh ²	dbh ²	dbh ²	dbh ²	dbh ²	dbh ²	dbh ²	dbh ²	dbh ²	dbh ²	dbh ²
	Stand					BA	SDI	log(N)	Hdom	Hdom	Hdom	Hdom	Hdom	Hdom	Hdom	Hdom	Hdom	Hdom	Hdom
										1/BA	log(BA)	1/SDI	log(SDI)	log(BA)	log(BA)	log(BA)	log(BA)	log(BA)	log(BA)
														SI	SI	SI	SI	SI	SI
Climate															pp_STD	pp_STD	pp_STD	pp_STD	
																Tmed_5_6STD	Tmed_5_6STD	Tmed_5_6STD	
Fitting Method		ML	ML	ML	ML	ML	ML	ML	ML	ML	ML	ML	ML	ML	ML	ML	REML	REML	
Information Criteria	BIC	24501	23555	23530	23548	23437	23434	23531	23399	23297	23273	23290	23289	23237	23225	23223	23248	-15711	
	-2LL	24472	23522	23492	23510	23394	23391	23489	23356	23250	23225	23243	23242	23184	23169	23162	23224	-15734	

Where dbh: diameter at breast height; BA: basal area; N : number stems per ha; SDI: Reineke's stand density index; Hdom: dominant height; SI: Site index; pp_STD: standardized annual rainfall; Tmed_5_6STD: standardized mean temperature for May and June; ML: maximum likelihood; REML: restricted maximum likelihood; AR(1): order one autoregressive parameter

Table 2. Parameter estimates for the definitive model (step 17 in table 1)

	Estimate	Std error	t-statistic	p-value
Intercept	1.6319	0.1622	9.82	<0.0001
dbh	0.07028	0.00527	13.6	<0.0001
dbh ²	-0.0004	0.00006	-6.21	<0.0001
Hdom	-0.07577	0.00901	-8.41	<0.0001
Log(BA)	-0.2937	0.03123	-9.41	<0.0001
SI	0.06172	0.00965	6.4	<0.0001
pp_STD	0.2009	0.04619	4.35	<0.0001
Tmed_5_6STD	-0.1186	0.04539	2.61	0.009

Where dbh: diameter at breast height; BA: basal area; Hdom: dominant height; SI: Site index; pp_STD: standardized annual rainfall; Tmed_5_6ST: standardized mean temperature for May and June; STD error: Standard error of the parameter estimate; t-statistic: t statistic for the parameter estimate; p-value: level of significance for the parameter estimate

Table 3. Goodness of fit statistics for definitive model (step 17 in table 1)

		E	p-value	Obs	Pred	EF(%)	RMSE
Log scale	Conditional	0.0010	0.6726	2.7487	2.7476	70.92	0.4147
	Marginal	-0.0615	<0.0001	2.7487	2.8102	36.11	0.6148
Raw scale	Conditional	0.0225	0.6807	20.4419	20.4193	64.95	9.2831
	Marginal	0.0010	0.9891	20.4419	20.4408	30.63	13.0610

Where E: mean error value; p-value: level of significance for E; Obs and pred refer to observed and predicted values for the response variable; ED: modelling efficiency; RMSE: root mean square error; Conditional refers to predictions achieved including EBLUPs for the random parameters; Marginal refers to predictions achieved not including EBLUPs for the random parameters

Table 4. Press evaluation statistics (computed over model for step 15 in table 1, not considering AR1 autoregressive parameter and fitted using Maximum Likelihood method)

		E	p-value	Obs	Pred	EF(%)	RMSE
Log scale	Conditional	0.0005	0.8059	2.7493	2.7488	82.13	0.3252
	Marginal	-0.0623	<0.0001	2.7493	2.8116	36.32	0.6141
Raw scale	Conditional	0.0034	0.9422	20.4486	20.4453	75.11	7.7832
	Marginal	-0.0426	0.5858	20.4486	20.4912	28.54	13.1888

Where E: mean error value; p-value: level of significance for E; Obs and pred refer to observed and predicted values for the response variable; ED: modelling efficiency; RMSE: root mean square error; Conditional refers to predictions achieved including EBLUPs for the random parameters; Marginal refers to predictions achieved not including EBLUPs for the random parameters