

1 *Agricultural and Forest Meteorology*

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3 What drives growth of Scots pine in continental Mediterranean climates:
4 drought, low temperatures or both?

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46 **Abstract**

47 Scots pine forests subjected to continental Mediterranean climates undergo cold winter
48 temperatures and drought stress. Recent climatic trends towards warmer and drier
49 conditions across the Mediterranean Basin might render some of these pine populations
50 more vulnerable to drought-induced growth decline at the southernmost limit of the
51 species distribution. We investigated how cold winters and dry growing seasons drive
52 the radial growth of Scots pine subject to continental Mediterranean climates by relating
53 growth to climate variables at local (elevational gradient) and regional (latitudinal
54 gradient) scales. Local climate-growth relationships were quantified on different time
55 scales (5-, 10- and 15-days) to evaluate the relative role of elevation and specific site
56 characteristics. A negative water balance driven by high maximum temperatures in June
57 (low-elevation sites) and July (high-elevation sites) was the major constraint on growth,
58 particularly on a 5- to 10-day time scale. Warm nocturnal conditions in January were
59 associated with wider rings at the high-elevation sites. At the regional scale, Scots pine
60 growth mainly responded positively to July precipitation, with a stronger association at
61 lower elevations and higher latitudes. January minimum temperatures showed similar
62 patterns but played a secondary role as a driver of tree growth. The balance between
63 positive and negative effects of summer precipitation and winter temperature on radial
64 growth depends on elevation and latitude, with low-elevation populations being more
65 prone to suffer drought and heat stress, whereas high-elevation populations may be
66 favoured by warmer winter conditions. This negative impact of summer heat and
67 drought has increased during the past decades. This interaction between climate and site
68 conditions and local adaptations is therefore decisive for the future performance and
69 persistence of Scots pine populations in continental Mediterranean climates. Forecasting
70 changes in the Scots pine range due to climate change should include this site-related

71 information to obtain more realistic predictions, particularly in Mediterranean rear-edge
72 areas.

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74 **Keywords:** *Pinus sylvestris*; drought stress; elevational gradient; latitudinal gradient;
75 minimum temperature; dendroecology.

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79 **Highlights**

80 - High variability in space and time of tree-growth response to climate in Spain

81 - Negative impact of low summer rainfall is higher at low elevations and high latitudes

82 - Growth at low elevations is more dependent on spring climate than at high elevations

83 - Negative impact of summer heat and drought has increased during the past decades

84 - Local adaptation to climate change is a key factor for future Mediterranean forests

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92 **1. Introduction**

93 Plant growth seasonality is characterized by favorable and adverse climatic conditions
94 for tree growth, such as those faced by forests subjected to continental Mediterranean
95 climates, where trees endure the double climatic stress of cold winters and summer
96 droughts (Mitrakos, 1980). As a result, optimal growth conditions occur during the two
97 milder periods with increased rainfall (i.e., spring and autumn) which usually produce a
98 bimodal pattern of cambial activity (Camarero et al., 2010), so the question arises:
99 which climatic factor limits tree growth to a greater extent, the winter cold constraints
100 or drought during the main growing season (spring to summer)? The roles of the two
101 stressors on growth processes such as wood formation are clearly different. For
102 instance, the winter cold affects prior carbohydrate use by reducing photosynthesis and
103 respiration rates (Gimeno et al., 2012), and may determine how well dry soils are
104 recharged with water before spring cambial resumption takes place in spring (Pasho et
105 al., 2011); whereas drought directly constrains growth rates during the growing season
106 (Camarero et al., 2014; Gutiérrez et al., 2011).

107 Understanding the effects of climate on tree growth is particularly relevant in
108 continental areas of the Mediterranean Basin, which are considered major climate-
109 change hot-spots where both warming and aridification trends have been observed
110 (Giorgi, 2006). The Mediterranean region is exposed to transitional climatic conditions
111 between the temperate and continental climate in the North and the subtropical climates
112 further South (Köppen, 1936). Recent trends toward a warmer and drier climate have
113 had negative effects on tree growth (Sánchez-Salguero et al., 2012) and forest
114 productivity (Madrigal-González and Zavala, 2014). Thus, it would be of interest to
115 assess how cold and droughts are related to tree growth in such area, particularly over
116 the western Mediterranean Basin (Xoplaki et al., 2012).

117 In connection to recent climate trends, in cold-limited Circum-Mediterranean
118 areas such as the high-elevation ranges (e.g., Pyrenees, Iberian mountains, Balkans,
119 Apennines, etc.) or plateaus (e.g., Iberian and Anatolian peninsulas) warmer winter
120 temperatures could facilitate subsequent tree growth by extending the length of the
121 growing season (Vaganov et al., 2006). In contrast, more frequent summer heat waves
122 (Pichler and Oberhuber, 2007) and/or related droughts could limit tree growth by
123 shortening the growing season (Eilmann et al., 2011; Galván et al., 2014). Lastly, the
124 responsiveness of trees to climate is, however, highly dependent on topographical
125 features such as elevation or aspect (Büntgen et al., 2012; Rigling et al., 2002), which
126 moderate the water availability in Mediterranean mountain sites (Camarero et al., 2013;
127 Candel-Pérez et al., 2012).

128 A comparison of long-term climate and tree growth data usually reveals that the
129 climatic conditions prior to the growing season play a prominent role in wood formation
130 (Fritts, 2001), and Circum-Mediterranean forests are no exception (e.g., Büntgen et al.,
131 2010; Camarero et al., 2013). The dendrochronological approach allows a tree's growth
132 responses to climate to be inferred on a monthly scale, albeit such inferences should be
133 complemented with short-term data (e.g., by using climate data compiled on a weekly
134 or biweekly basis) and would be validated through xylogenesis studies (Camarero et al.,
135 2010; Vaganov et al., 2006).

136 We used this multi-scalar approach to investigate how low winter temperatures
137 and drought during the growing season in a continental Mediterranean climate drive the
138 seasonal radial growth of Scots pine (*Pinus sylvestris* L.). This is the most widespread
139 conifer species in the world, but it reaches its southern and dry limit in the Iberian
140 Peninsula (Mirov, 1967). First, we relate growth to changing climate conditions since
141 1900 at local scales by sampling three sites in the Spanish Central System at different
142 elevations, and therefore varying climatic conditions. We expected lower winter

143 temperatures would be the main climatic constraint on tree growth at high-elevation
144 sites and spring-to-summer water deficits at low-elevation sites. Second, we
145 extrapolated this local analysis to a regional scale along a latitudinal gradient using
146 existing Scots pine tree-ring growth series from continental Mediterranean sites in
147 Spain. We hypothesize that at the global limit to Scots pine distribution, the lowest sites
148 and southernmost sites will be responsive to drought, whereas the highest and
149 northernmost sites will be most sensitive to winter temperature conditions.

150

151 **2. Material and methods**

152 ***2.1. Local study area***

153 The local study area is located in the Valsaín forests in “Sierra de Guadarrama”
154 National Park, a mountainous area situated on the north-facing slopes of the Spanish
155 Central System near Madrid (40° 49’ N, 4° 1’ W, elevation range 1100-2125 m a.s.l.).
156 The forests studied are dominated by managed Scots pine stands and mixed with other
157 less abundant tree species such as *Quercus pyrenaica* Willd. The geological substrates
158 are granite and gneiss. Soils are usually acid, with humic cambisols or leptosols on the
159 high-elevation sites.

160 The study area has a Mediterranean climate with a continental influence,
161 characterized by dry summers and cool winter conditions. The total annual rainfall is
162 1266 mm and the mean annual temperature 6.5 °C, at 1890 m a.s.l., where the mean
163 December-January temperature is -0.4°C and that of July-August 16.5°C (the coldest
164 and warmest periods, respectively) for the period 1943-2011. We used local daily and
165 monthly climatic data (mean maximum and minimum temperatures and total
166 precipitation) to characterize the climatic conditions along the elevation gradient. For
167 that purpose we obtained climatic data for the abovementioned period from three
168 meteorological stations located in the study area at different elevations (Puerto de

169 Navacerrada, 40° 47' N, 4° 00' W, 1894 m a.s.l.; Granja de San Ildefonso, 40° 46' N 4°
170 00' W, 1191 m a.s.l. and Observatorio de Segovia, 40° 56' N, 4° 10' W, 1005 m a.s.l.; see
171 Appendix A1). The temperature at the study site were estimated using data from these
172 three stations and additional forest climatic data provided by Martínez-Alonso et al.
173 (2007). To define a biologically realistic surrogate for the water availability for tree
174 growth, we also estimated the monthly water balance (abbreviated as P-PET) as the
175 difference between precipitation (P) and potential evapotranspiration (PET), according
176 to Hargreaves and Samani (1982). Temporal trends in the monthly temperature and
177 seasonal precipitation were calculated to characterize the climate of each site taking into
178 consideration the reconstructed meteorological data for each elevation (Appendix A1).

179

180 ***2.2. Field sampling and dendrochronological methods***

181 We sampled three Scots pine stands located at different elevations in Valsaín forest (see
182 Table 1; additional information on the study area is also available in Touchan et al.
183 2013). At each site, at least 25 dominant trees with diameters at 1.3 m (dbh) greater than
184 20 cm were sampled and their size (dbh, tree height) measured (Table 1). All the trees
185 measured were cored at 1.3 m with a Pressler increment borer and two cores were taken
186 per tree perpendicular to the maximum slope.

187 The cores were air dried, sanded with sand paper of progressively finer grain
188 until tree-rings became clearly visible and then visually cross-dated. Individual tree-ring
189 width series were measured to the nearest 0.01 mm using a LINTAB semi-automatic
190 measuring device (Rinntech, Heidelberg, Germany). Cross-dating quality was checked
191 using the program COFECHA (Holmes, 1983). To assess the quality of tree-ring width
192 series several dendrochronological statistics (Fritts, 2001) were calculated considering
193 the period 1950-2011 (Table 1): first-order autocorrelation of raw width data (AC),
194 mean sensitivity (MS) of indexed growth values, mean correlation between trees (*rbt*),

195 signal to noise ratio (SNR), variance accounted for by the first principal component
196 (PC1) and the expressed population signal (EPS), which measures the statistical quality
197 of the mean site chronology compared with a perfect infinitely replicated chronology
198 (Wigley et al., 1984). The segments of the site chronologies that reached EPS values
199 equal to or higher than 0.85 were regarded as reliable enough to use for the climate-
200 growth analyses.

201 To quantify climate-growth relationships, tree-ring widths were converted into
202 residual indices after removing the age-related trend using the program ARSTAN
203 (version 44h3) (Cook and Krusic, 2005). Tree-ring indices were obtained by dividing
204 the observed by the expected values, which were calculated by fitting either negative
205 linear or exponential functions. Autoregressive modelling was then performed on these
206 series to remove the majority of the first-order temporal autocorrelation. Finally, a
207 biweight robust mean was computed to average the individual series and to produce
208 mean residual chronologies of residual tree-ring width indices for each tree and site.

209

210 ***2.3. Regional scale study area***

211 To analyze the climate-growth relationships at a regional scale, we collected 23 Scots
212 pine chronologies along a Spanish latitudinal gradient, including the species rear-edge
213 from sites subjected to continental Mediterranean conditions (Table 2). Of these
214 chronologies, 17 reach back at least to the early 1980s and were provided by the
215 International Tree-Ring Data Bank (<http://www.ncdc.noaa.gov/paleo/treering.html>), and
216 6 were built explicitly for this study. The development of the tree-ring chronologies
217 involved the same approach as described for the local scale analyses. The climatic
218 variables are also similar to those used on the local scale but they were obtained from
219 the homogenized and quality-checked E-OBS v.10.0 dataset gridded with a 0.25° spatial
220 resolution (Haylock et al., 2008). Temporal trends in annual temperature and

221 precipitation were calculated to characterize the climate of each site (Appendix A1), and
222 only those variables highly correlated with growth indices were considered in the
223 analyses of the climate-growth associations.

224

225 ***2.4. Climate-growth relationships***

226 To quantify climate-growth relationships between residual tree-ring width indices and
227 monthly climate data (mean maximum and minimum temperatures, P-PET), we
228 calculated Pearson correlation coefficients for the common period 1950-2011. To assess
229 whether these relationships were stable over time, we calculated 20-year long moving
230 correlations overlapping by one year, taking into consideration only those variables
231 strongly correlated with growth indices. Differences in trees climate-growth correlations
232 between sites were computed using one-way ANOVAs.

233 To analyse the daily constraints of coldness and drought stress on tree growth
234 along the elevational gradient at the local scale, we calculated Pearson correlation
235 coefficients between residual chronologies and mean daily temperatures or water
236 balance data (P-PET). We made calculations for different intervals (5-, 10- and 15-days)
237 to capture time-dependent growth responses to climate (Gutiérrez et al., 2011). These
238 correlations were performed for the period January to October, which encompasses the
239 growing season of the study species and also the previous late winter (Camarero et al.,
240 2010). To account for the effects of temporal autocorrelation, we estimated the 95%
241 confidence intervals for the correlation coefficients by bootstrapping with an average
242 block length proportional to the estimated data autocorrelation (Mudelsee, 2003).

243

244 **3. Results**

245 ***3.1. Climate-growth associations along the local elevational gradient***

246 Trees from the high-elevation site were older and larger than those from the other sites,
247 which may explain why they formed wider tree-rings (Table 1). Trees from the middle-
248 and low-elevation sites were shorter than those from the high-elevation, respectively.
249 The year-to-year persistence (AC) and inter-annual variability (MS) of growth were also
250 greater at higher elevation which suggests that climatic constraints on growth are more
251 important for high-elevation site (Table 1). The remaining dendrochronological
252 statistics confirm a general and coherent growth response of trees to climatic variability
253 across the elevational gradient.

254 Temperatures have negative effects during the months of June and July, when
255 the most tree-ring growth occurs if water does not limit cell production, and also in
256 October, when trees still have high photosynthetic rates and even produce new cells
257 (Fig. 1). A negative effect means that the tree's growth is limited by high temperatures.
258 This is also the case for the months of August-September to December the year prior to
259 tree ring formation, when bud formation takes place and trees accumulate reserves for
260 the next growing period. From January to May, the effect of temperature on tree-ring
261 formation is positive, so the growth is limited by low temperatures. The effect of a
262 water deficit is opposite to that of high temperatures.

263 The main climatic factor stimulating growth in the high-elevation site was the
264 mean maximum temperature in January and in the low-elevation site a positive water
265 balance in June (Fig. 1). Warm February and dry March conditions also enhanced
266 growth in the low-elevation site, whereas warm January temperatures and cool and wet
267 conditions from June to July favored growth in the middle-elevation site. Warm and dry
268 conditions in the previous late summer were related to lower growth indices in all sites,
269 while warm October conditions at the end of the growing season produced a similar
270 effect but only in the high-elevation site. At the individual tree level, June water balance
271 and January mean minimum temperature were both significantly positively related to

272 growth, when were compared the three sites along the elevational gradient (Table 3).
273 The growth indices correlate with low water availability at low-elevation site and with
274 temperature at high-elevation site, with correlations of similar magnitude.

275 At shorter time scales, a negative water balance driven by the high mean
276 maximum temperatures in June (low-elevation site) and July (high-elevation site)
277 appear to be the major constraints on growth particularly at 5- to 10-day scales (Fig. 2).
278 Regarding the mean minimum temperatures, warm minimum (means nocturnal)
279 conditions in January were associated with high growth indices at the high-elevation
280 site for the same time periods. Warm and short (5-days long) daytime conditions in late
281 winter or early spring were linked to enhanced growth in the low- and middle-elevation
282 sites.

283 The negative correlations between June-July maximum temperatures and growth
284 indices increased from the late 1970s onwards, as did the positive effect of the summer
285 water balance, particularly in the low-elevation site, but also July conditions in the other
286 two sites (Fig. 3). These shifts reflect the significant ($P < 0.05$) increases in mean
287 maximum temperatures that have been observed in all elevation plots from 1970 (Fig.
288 A2, Appendix A1). In contrast, seasonal precipitation did not show any significant
289 trend. From the mid 1980s onwards, warm nocturnal conditions in January were
290 strongly related to more growth in the high- and middle-elevation sites.

291

292 **3.2. Regional scale climate–growth associations**

293 At the regional scale, a significant ($P < 0.05$) increase in mean temperature and
294 decrease in precipitation increased with latitude (Table A1, Appendix A1). The trends in
295 temperature (positive) and precipitation (negative) during the growing season decreased
296 when latitude increase ($p=0.015$ and $p<0.0001$, respectively). The exception was the
297 mean minimum temperature that increased with latitude ($p<0.0001$). On the other hand,

298 the trends in precipitation ($p=0.003$) and temperature ($p=0.023$) significantly increased
299 with elevation at the regional scale (Table A1, Appendix A1).

300 Considering the whole set of chronologies, no clear correlation between latitude
301 and elevation was apparent ($p=0.30$), as the chronologies are located at similar
302 elevations across the sampled area, representing the wide gradient. In fact, the mean
303 values of tree-ring width and MS significantly decreased with latitude ($p=0.0005$ and
304 $p=0.024$, respectively) but no significant relationship was found with elevation (Table
305 2). Similarly, AC significantly increased with latitude ($p=0.021$), but did not correlate
306 with elevation (Table 2). Furthermore, the inter-annual variability in growth (quantified
307 as MS) decreased significantly with growing-season precipitation ($p<0.0001$). In
308 contrast, AC significantly ($p<0.0001$) increased with precipitation and temperature of
309 the growing season.

310 On the regional scale, Scots pine growth indices mainly responded to June-July
311 precipitation, especially at lower elevations but also at higher latitudes (Spearman $r=$
312 0.44 , $p<0.01$) (Fig. 4). The significant limiting effect of the minimum January
313 temperature on tree growth was secondary in comparison with June-July precipitation,
314 but presented similar patterns with respect to elevation and latitude (Spearman $r= 0.22$,
315 $p<0.10$).

316 The positive correlations between January temperatures and growth indices
317 increased from the late 1970s onwards as did the positive effect of summer water
318 balance, particularly at high-elevations and low latitudes (*results not shown*). These
319 shifts agree with the significant ($P < 0.05$) increases in temperatures and decreases in
320 precipitation observed in the latitudinal and elevational gradient studied from 1970
321 (Table A2, Fig. A2, Appendix A1).

322

323 **4. Discussion**

324 Dry conditions during the growing season constitute the main constraint on Scots pine
325 growth under continental Mediterranean climates, although previous low winter
326 temperatures also play an important role as a growth limiting factor. Furthermore, recent
327 climate warming is exacerbating the negative impact of summer drought on radial
328 growth of southern European Scots pine populations, presumably due to increased
329 evapotranspiration and reduced soil water availability (Gea-Izquierdo et al., 2014;
330 Herrero et al., 2013). If drought becomes the main stressor of Scots pine growth in a
331 continental Mediterranean climate also cone production and the recruitment rates of the
332 species will also be negatively affected under future warmer scenarios, particularly the
333 Circum-Mediterranean populations (Vilà-Cabrera et al., 2011).

334 In trees and other perennial plants, the adjustment of anatomical and functional
335 traits to environmental variability (phenotypic plasticity and genetic variability) is
336 strong at the margins of the plants range, but the overall performance of a tree species
337 may decline as the southernmost distributional limits are reached and vulnerability to
338 climatic stressors increases (Valladares et al., 2014; Vergee and Kunin, 2013). This
339 could be the case for the Iberian Scots pine populations at the lowest elevations, which
340 were most dependent on summer precipitation. The strong positive effects of summer
341 precipitation on growth are in line with the results of previous studies of dry areas in
342 central Europe, which indicate that drought constrains the physiological activity of
343 Scots pine during summer (Eilmann et al., 2010, 2011; Lebourgeois, 2000; Lévesque et
344 al., 2014). As others have also found (e.g., Génova, 2012), summer precipitation is the
345 main limiting factor on Scots pine growth in the Spanish Central System (Figs. 1 and 2),
346 but its importance has significantly increased since the 1970s (Fig. 3) as the climate has
347 become warmer and water availability has decreased due to increasing
348 evapotranspiration. Our analyses show a late 20th century warming trend in the study
349 area (+1.2 °C from 1943 to 2011; see Fig. A1), as well as a higher frequency of extreme

350 drought events towards the end of the 20th century, such as those that affected most of
351 the Iberian Peninsula in the 1980s and 1990s (Vicente-Serrano, 2006). The negative
352 correlation found between growth and summer drought suggests that cumulative
353 negative drought effects have a relatively higher impact on tree performance than the
354 amount of rainfall received throughout one year or the average dryness (Madrigal-
355 González and Zavala, 2014). Moreover, recurrent droughts reduce the carbon uptake by
356 trees and increase their respiration rates, thus reducing their capacity to grow (Galiano
357 et al., 2011; McDowell et al., 2008). Recurrent and extended droughts might therefore
358 lead to accumulated carbon deficits, which could result in long-term limitation on
359 growth and eventually tree death (McDowell et al., 2008).

360 The elevational gradient at the regional scale revealed remarkable differences in
361 the growth responses of Scots pine to changes in climate. The low-elevation sites
362 located at low latitudes appear to be most sensitive to warming and drought stress, (Fig.
363 4) as has been suggested for other pine species (Candel-Pérez et al., 2012). These low-
364 elevation Scots pine populations are therefore likely to be the most vulnerable to future
365 climate warming and the related increasing aridification, with resulting retractions of the
366 distribution of the species. These effects have already been observed to some extent in
367 the form of growth decline, forest dieback and intense mortality events (Peñuelas et al.,
368 2007).

369 Regarding the latitudinal gradient, significant relationships between the growth
370 of the majority of Scots pine sites and summer drought (negative) and winter minimum
371 temperatures (positive) are consistent with previous results for the Mediterranean
372 (Andreu et al., 2007). In high-elevation and high latitude sites, there were positive
373 growth trends driven by warmer winters similar to the response of other Mediterranean
374 forests. This probably is caused by increased winter photosynthesis and accumulation of
375 carbohydrates that leads to wider earlywood in the following year (Lebourgeois, 2000).

376 Despite the general long-term trend for less annual precipitation and higher
377 temperatures (Table A1, Appendix A1), the climate-growth analysis at country scale
378 revealed a south-north latitudinal advance of this effect contrary to that found for the
379 influence of seasonal climate variables in the elevational gradient (Fig. 4). At country
380 scale, the latitudinal gradient has more effect on growth response than elevation (Fig. 4),
381 but the climate and growth trends at the local elevation gradient strongly support the
382 rapid northward advance of the Mediterranean climate caused by climatic change.

383 On the other hand, our findings confirm that the southernmost Scots pine
384 populations have adapted to the dry conditions characteristic of their locations
385 (Appendix A1, Fig. A3) (Herrero et al., 2013). Support for this claim comes from, first,
386 the fact that wood anatomy and cambial phenology differ depending on tree provenance
387 (Martín et al., 2010), with reduced secondary growth when exposed to different stress
388 conditions such as drought (Eilmann et al., 2011) or frost (Hantemirov et al., 2004). For
389 instance, the Scots pine provenances in the driest Iberian regions are characterized by
390 having tracheids with large lumens and thick cell walls, which increase hydraulic
391 conductivity and reduce the risk of drought-induced cavitation (Martín et al., 2010).
392 Furthermore, the trees forming the xeric limit of the species distribution also have a
393 high ray tracheid frequency, which could imply they can store more water in the
394 sapwood so they can modify the growth response to drought stress (Camarero et al.,
395 2013).

396 At a continental scale, Scots pine appear to have made little structural hydraulic
397 adjustment in response to local climatic conditions across Europe, apart from
398 modifications in the leaf-to-sapwood area ratio of branches (Martínez-Vilalta et al.,
399 2009). This suggests that water storage in the sapwood is important as a buffer
400 mechanism against drought stress (Barnard et al., 2011). Another factor that indicates
401 that pines adapt to climate is that, the climate-growth associations observed at a local

402 (Figs. 1 and 2) and regional scale (Fig. 4) indicate that the timing of the response of
403 cambial activity to climate. This confirms phenological differences found even at local
404 scales along the elevational gradient (Figs. 1 and 3). Differences can also be observed
405 after just a short time (5- to 10-days; Fig. 2), which is further support for the claim that
406 short-term variations in growth and wood anatomy are related to climate fluctuations
407 and rapid changes in soil water reserves (Bouriaud et al., 2005).

408 As expected, the importance of June-July precipitation for Scots pine growth
409 increased with decreasing latitude. At lower latitudes trees are subjected to intensified
410 drought stress, whereas further North January minimum temperatures have more effect
411 on growth as minimum temperatures are lower (Fig. 4). Some of the Scots pine stands
412 located in eastern Spain, however, are very responsive to summer rainfall (e.g.,
413 Corbalán), and are currently showing drought-induced dieback and increased mortality
414 rates (JJ Camarero, *pers. observ.*). These biogeographical patterns coincide with the
415 existence of the adaptation, described above, and are probably an expression of the
416 genetic differences observed among Spanish Scots pine provenances (Catalán et al.,
417 1991; Valladares et al., 2014). However, we also detected unexpected biogeographical
418 patterns, such as cold temperatures becoming more important over time also at low
419 elevations, and less growth dependence on summer rainfall near the southernmost
420 distribution limit of the species (Fig. 4). Why do such unforeseen patterns appear?

421 The divergent growth responses to climate may have to do with other
422 confounding factors, such as: i) changing competition between trees or between trees
423 and undergrowth due to changes in land use and past management, ii) phenotypic
424 variability, including anatomical or phenological adjustments or iii) genetic variation
425 and site characteristics (such as soil depth, nutrient availability, geomorphological
426 features, etc) which can act as buffers against the expected response to climate
427 (Camarero et al., 2013; Prus-Glowacki and Stephan, 1994). For instance, the wide

428 genetic differentiation found in southern Scots pine populations in Spain might be the
429 results of a variety of local adaptations to seasonally dry conditions, and could alter the
430 responses to precipitation observed (Fig. 4) (Catalán et al., 1991). Our results support
431 that of other studies in Iberian Scots pine stands that found they are less vulnerable to
432 embolism than their northern counterparts (Martinez-Vilalta et al., 2009).

433 Water deficit does seem, as we hypothesized, to be the main constraint on Scots
434 pine radial growth in continental Mediterranean climates. Nonetheless, low temperature
435 effects on radial growth became predominant at higher elevations indicating extremely
436 steep moisture gradients populations at these elevation may not be regarded *sensu*
437 *stricto* as Mediterranean sites. The balance between positive and negative effects of
438 seasonal water availability and temperatures on radial growth, and factors such as site-
439 specific conditions or local adaptations, may determine the future performance and
440 persistence of the southernmost populations of Scots pine. The low-elevation
441 populations will be prone to suffer from drought and heat stress, but this effect varies
442 according to the position in the latitudinal range considered in this study. High-elevation
443 populations situated nearby, however, will be favored by warmer winter conditions in
444 the Circum-Mediterranean region. Hence it is crucial to include site conditions as well
445 as data related to local adaptations in order to improve the forecasts of distributional
446 shifts in response to climate change and potential local extinctions of species. More
447 information on local adaptations to site conditions will help us to assess the
448 vulnerability of Scots pine to drought and cold stress over a large latitudinal range. This
449 information could also be used to improve management and conservation practices in
450 order to mitigate and prevent the likely impact of climate change on Mediterranean pine
451 forests.

452

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468

469

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618

619 **Tables**

620

621 **Table 1.** Main topographic, structural and dendrochronological features of the study
 622 sites along the gradient in Valsaín. The dendrochronological statistics are based on tree-
 623 ring index series. Values are means \pm SE. Different letters indicate significant ($P <$
 624 0.05) differences between plots (Mann-Whitney U test). The dendrochronological
 625 statistics were calculated for the period 1950-2011.

626

	Low-elevation site	Middle-elevation site	High-elevation site
Elevation (m a.s.l.)	~1400	~1650	~1900
Aspect	North-West	North-East	North-East
Slope (%)	18 \pm 1	25 \pm 3	35 \pm 2
Mean age at 1.3 m (years)	83 \pm 16b	70 \pm 34a	124 \pm 29c
dbh (cm)	34.4 \pm 8.9b	31.3 \pm 1.2a	40.9 \pm 2.4 c
Tree height (m)	16.8 \pm 2.6b	13.6 \pm 0.3a	20.3 \pm 4.7c
Time span of tree-ring series	1882-2011	1807-2011	1822-2011
No. trees (No. radii)	31 (62)	49 (98)	27 (54)
Tree-ring width (mm)	1.76 \pm 0.13a	1.60 \pm 0.14a	2.02 \pm 0.13b
AC	0.77 \pm 0.09 a	0.82 \pm 0.4 0b	0.86 \pm 0.01b
MS	0.26 \pm 0.05a	0.28 \pm 0.01b	0.33 \pm 0.01b
<i>rbt</i>	0.56 \pm 0.03	0.59 \pm 0.01	0.60 \pm 0.01
SNR	11.71	12.09	14.26
PC1 (%)	58.98	58.36	60.99
Period with EPS > 0.85	1900-2011	1850-2011	1882-2011

627

628 Abbreviations: AC, first-order autocorrelation; MS, mean sensitivity; *rbt*, mean between-trees
 629 correlation of ring-width indices; EPS, Expressed Population Signal; SNR, signal to noise ratio;
 630 PC1, variance accounted for by the first principal component.

631

632 **Table 2.** Scots pine sites used in the analyses of climate-growth relationships at the regional scale. Dendrochronology variables (AC = first-order
633 autocorrelation, MS = mean sensitivity, PC1= variance accounted for by the first principal component. EPS = expressed population signal) are as in
634 Table 1.

Site name or ITRDB code	Latitude (N)	Longitude (-W, +E)	Elevation (m a.s.l.)	Ring-width \pm SD (mm)	N° series	AC	MS	PC1 (%)	Time span (years)	Period EPS > 0.85
spai024	42.83	-0.78	1275	0.92 \pm 0.21	8	0.784	0.245	47.93	1696-1985	1800-1985
Corbalán *	40.43	-0.97	1390	0.70 \pm 0.34	16	0.612	0.481	69.03	1838-2012	1850-2012
spai030	40.33	-1.98	1400	1.28 \pm 0.42	5	0.743	0.240	52.98	1809-1983	1900-1983
spai033	40.33	-5.17	1465	0.83 \pm 0.19	25	0.833	0.292	52.32	1813-1985	1825-1985
spai034	40.33	-5.13	1470	1.21 \pm 0.29	26	0.785	0.282	50.53	1769-1985	1775-1985
spai062	40.25	-0.68	1500	1.49 \pm 0.43	31	0.697	0.303	48.67	1900-2008	1925-2008
spai061	40.38	-0.70	1520	1.93 \pm 0.99	52	0.712	0.354	53.26	1937-2008	1950-2008
spai060	40.38	-0.68	1580	1.42 \pm 0.62	23	0.647	0.405	62.15	1931-2008	1950-2008
Guara *	42.28	-0.25	1620	0.77 \pm 0.25	12	0.642	0.306	40.37	1900-2012	1900-2012
spai014	41.02	-0.12	1630	0.81 \pm 0.28	28	0.847	0.241	54.00	1791-1992	1800-1992
spai044	42.80	-0.70	1646	0.72 \pm 0.13	30	0.812	0.230	44.44	1605-1985	1700-1985
spai020	40.67	-0.33	1648	1.23 \pm 0.29	18	0.893	0.271	40.83	1763-1991	1800-1991
spai021	40.87	-4.20	1650	0.78 \pm 0.16	14	0.808	0.275	44.07	1715-1988	1824-1988
spai063	40.35	-0.70	1660	2.42 \pm 1.13	29	0.837	0.259	54.98	1956-2008	1956-2008
spai047	41.98	-2.87	1751	0.98 \pm 0.20	31	0.864	0.206	41.11	1567-1983	1600-1983
Sarradé *	42.55	0.88	1800	1.35 \pm 0.46	27	0.836	0.240	37.61	1825-2010	1850-2010
spai048	42.02	-2.90	1839	0.85 \pm 0.19	17	0.803	0.219	48.41	1671-1983	1750-1983
spai049	42.03	-3.03	1839	0.90 \pm 0.14	27	0.859	0.208	38.27	1593-1985	1775-1985
spai038	40.80	-3.95	1850	0.75 \pm 0.15	23	0.852	0.241	41.51	1599-1984	1700-1984
spai037	40.78	-3.80	1950	0.90 \pm 0.26	26	0.839	0.234	45.93	1661-1985	1725-1985
Baza *	37.20	-3.16	1970	2.01 \pm 0.40	20	0.726	0.271	40.53	1828-2007	1875-2007
Vinuesa *	42.00	-2.73	1980	0.89 \pm 0.13	15	0.821	0.192	41.88	1648-1995	1675-1995
Sierra Nevada *	37.07	-3.46	2000	2.32 \pm 0.65	30	0.570	0.382	58.04	1875-1999	1875-1999

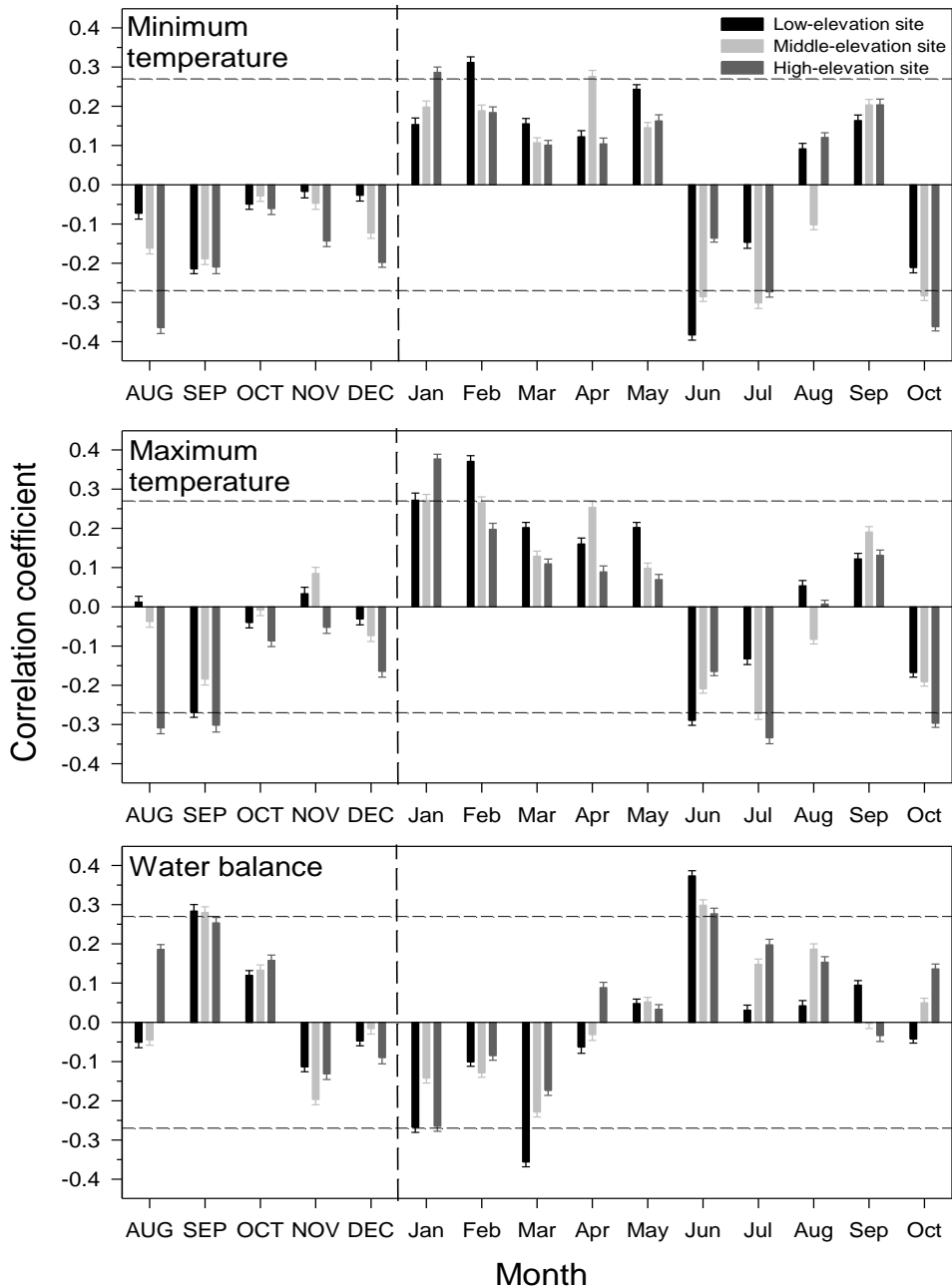
*Chronologies built for this study.

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638 **Table 3.** Comparisons of climate-growth relationships (r , Pearson correlation
639 coefficients) between study plots located at different elevations. Correlations (means \pm
640 SE) were calculated between individual tree ring-width indices and monthly climatic
641 variables (water balance is the difference between precipitation and potential
642 evapotranspiration). The individual correlations were then compared between sites
643 using one-way ANOVAs (F and P statistics are reported in the last column). Different
644 letters indicate significant ($P < 0.05$) differences between sites based on Tukey HSD
645 post-hoc tests.
646

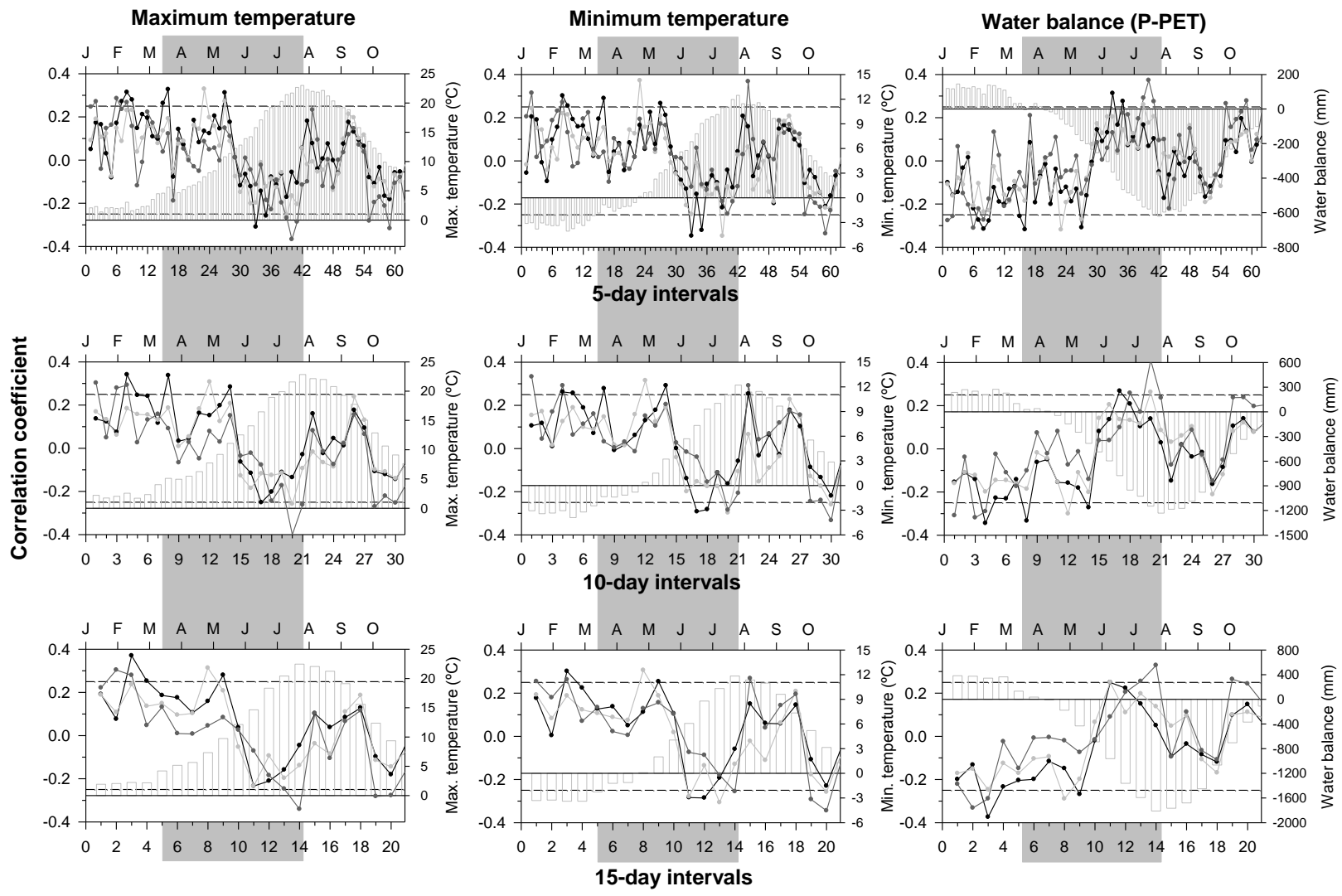
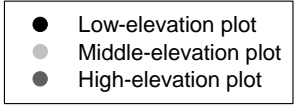
Climatic variable	Site	r	F (P)
June water balance (P-PET)	Low-elevation site	0.42 ± 0.10 c	112.8 (0.001)
	Middle-elevation site	0.30 ± 0.01 b	
	High-elevation site	0.24 ± 0.09 a	
January mean minimum temperature	Low-elevation site	0.27 ± 0.01 a	56.5 (0.001)
	Middle-elevation site	0.35 ± 0.01 b	
	High-elevation site	0.45 ± 0.06 c	

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650

651 **Figure 1.** Correlation coefficients obtained by relating individual tree-ring width indices and
 652 monthly climatic data (mean, maximum and minimum temperature and water balance (P-
 653 PET)) for low- (black bars), middle- (grey bars) and high-elevation (dark grey bars) Scots
 654 pine sites. Growth is related to monthly climatic data from the previous year (months
 655 abbreviated by uppercase letters) up to the year of tree-ring formation (months abbreviated by
 656 lowercase letters). The bars surpassing dashed lines indicate significant ($P < 0.05$) correlation
 657 coefficients.



659 **Figure 2.** Pearson correlations calculated for the period 1950-2011 between tree-ring width indices and daily climatic data (mean maximum and
660 minimum temperatures and total precipitation) for low- (lines with black dots), middle- (lines with grey dots) and high-elevation plots (lines with
661 dark grey dots) at different time intervals (5-, 10- and 10-day long intervals). The vertical grey bands indicate the months of maximum cambial
662 activity for *P. sylvestris* in central Spain based on Camarero et al. (2010). The grey bar diagram shows each pentad's mean temperature and
663 precipitation (right y axes), and the continuous horizontal lines correspond to values of temperature equal to 0° C or precipitation equal to 0 mm
664 (see right y axes). The dashed horizontal lines indicate significance thresholds ($P < 0.05$) after accounting for the presence of temporal
665 autocorrelation in the compared series.

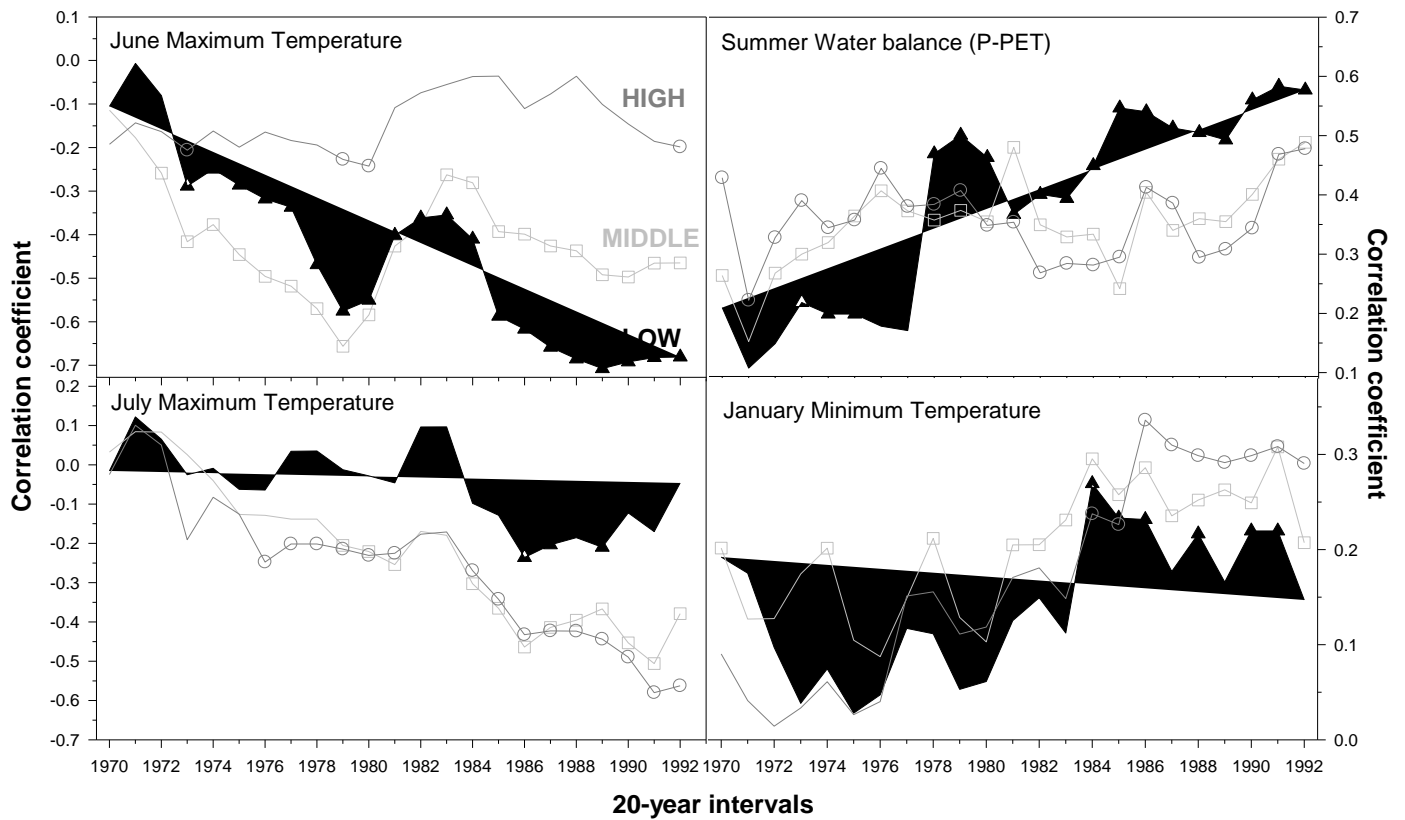


Figure 3. Moving correlations (Pearson coefficients) calculated between residual tree-ring width indices for each of the three plots located at different elevations and selected monthly climate variables. The coefficients were calculated for 20-year periods lagged by 1 year for the period 1950–2011. The ticks in the x axes show the last value of the corresponding 20-year interval (e.g., 1990 stands for the period 1971–1990, etc.). Filled symbols correspond to significant ($P < 0.05$) correlation coefficients.

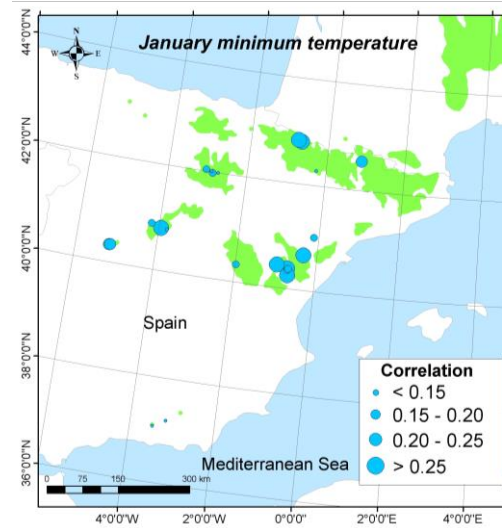
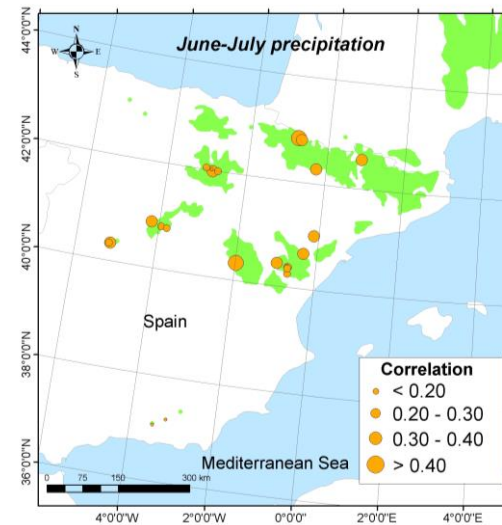
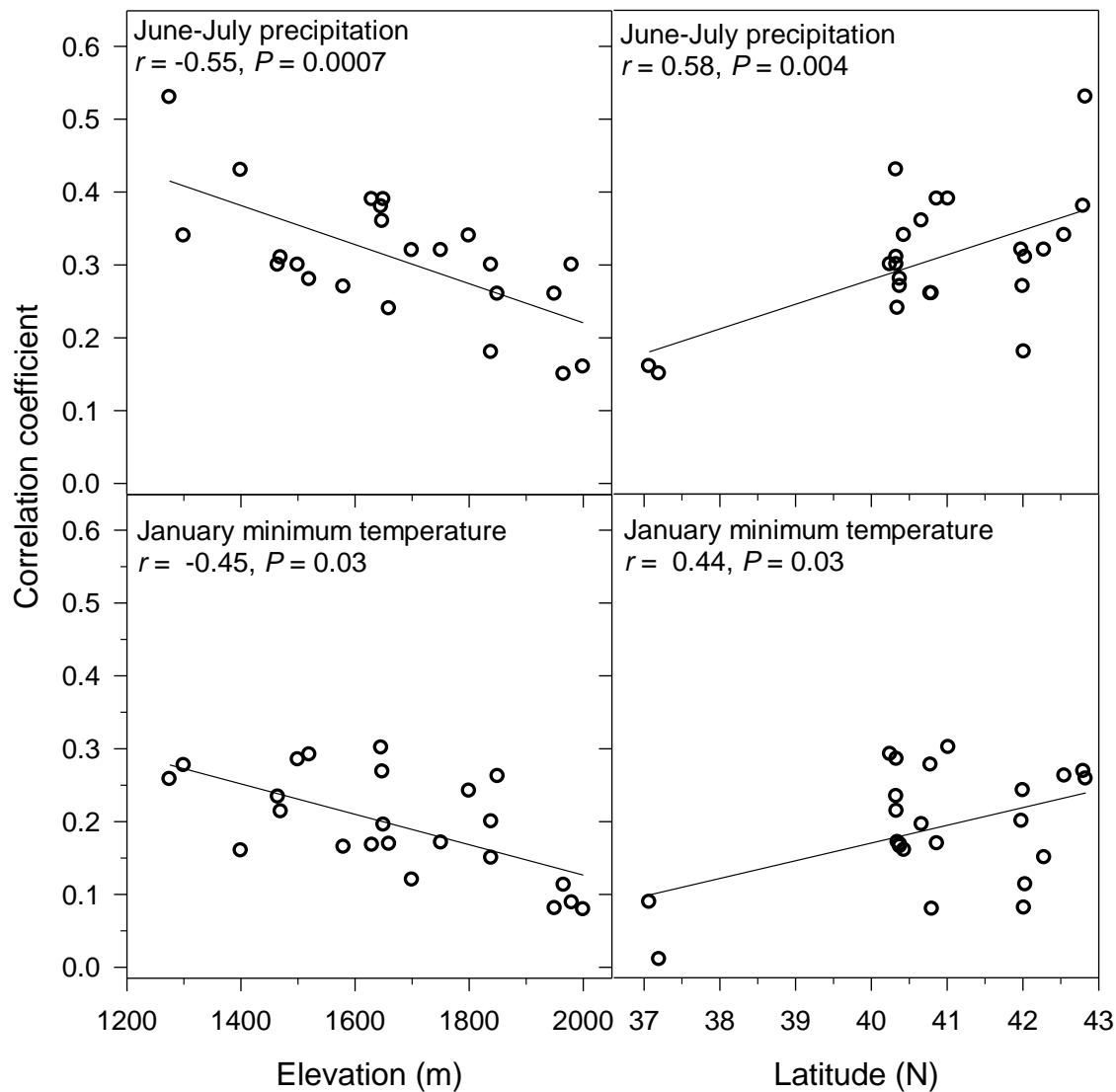


Figure 4. Main associations with elevation and latitude of the Scots pine growth indices responses to major climatic constraints, i.e. summer drought (represented by correlations with July precipitation) and winter coldness (represented by correlations with January mean minimum temperature). The statistics shown (Pearson correlation coefficient, r , and associated probability level, P) refer to the reported associations (see on the right the maps produced for this paper to showing the geographical patterns of correlations found in Spain).

Appendix

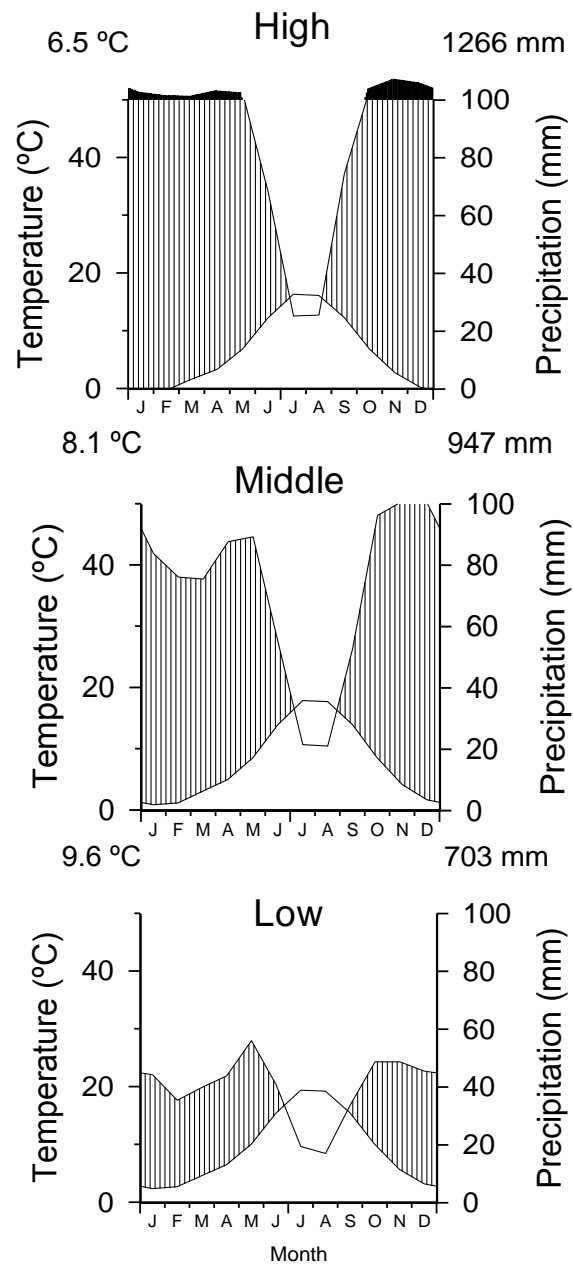


Figure A1. Climatic diagrams of the three study plots with Scots pine (data for the period 1943-2011) located at low-, middle- and high-elevation sites in the Spanish Central System. The mean annual temperature and total precipitation are indicated for each site.

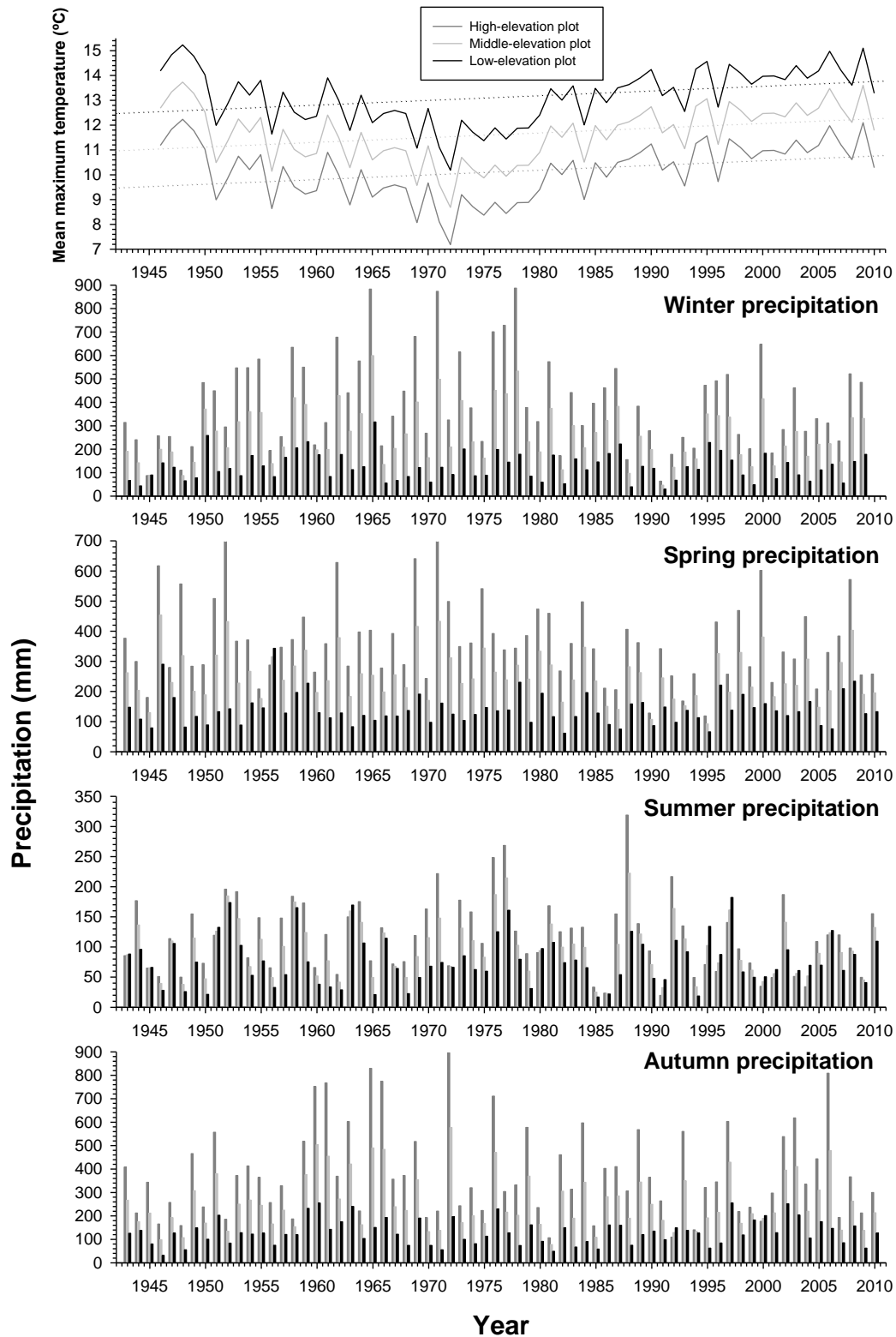


Figure A2. Mean annual maximum temperature and seasonal precipitation patterns and trends for the three Scots pine plots located at low-, middle- and high-elevation sites (period 1943-2011).

Table A1. Climatic characteristics (means \pm SD) and trends (τ , Pearson correlation coefficient) obtained for the study sites considering mean temperatures (T) and total precipitation (P) for different periods (year, June-July, January-February). Data were obtained using the meteorological homogenized and quality-checked E-OBS v.10.0 dataset gridded at a 0.25° spatial resolution (Haylock et al., 2008) for the period 1950-2011. Significant ($p < 0.05$) trends are shown in bold.

Code	Latitude (N)	Longitude (-W, +E)	Elevation (m a.s.l.)	Mean Annual				Mean JJ				Mean JF	
				T (°C)	<i>Trend</i> T (τ)	P (mm)	<i>Trend</i> P (τ)	T (°C)	<i>Trend</i> T (τ)	P (mm)	<i>Trend</i> P (τ)	Mean JF T (°C)	<i>Trend</i> T (τ)
spai024	42.83	-0.78	1275	8.5 \pm 0.8	0.58	1014 \pm 143	-0.24	15.4 \pm 1.3	0.40	120 \pm 46	-0.20	1.7 \pm 1.4	0.41
Corbalán	40.43	-0.97	1390	9.8 \pm 0.7	0.48	521 \pm 117	-0.21	17.7 \pm 1.3	0.48	65 \pm 32	-0.18	2.6 \pm 1.2	0.20
spai030	40.33	-1.98	1400	8.6 \pm 0.7	0.54	656 \pm 147	-0.20	16.7 \pm 1.3	0.48	73 \pm 35	-0.22	1.3 \pm 1.1	0.35
spai033	40.33	-5.17	1465	11.5 \pm 1.1	0.79	720 \pm 153	-0.14	18.1 \pm 2.1	0.82	54 \pm 31	-0.17	5.6 \pm 1.1	0.19
spai034	40.33	-5.13	1470	9.0 \pm 0.7	0.44	721 \pm 157	-0.14	17.1 \pm 1.3	0.32	55 \pm 33	-0.17	1.8 \pm 1.1	0.30
spai062	40.25	-0.68	1500	8.5 \pm 0.7	0.50	627 \pm 125	-0.15	16.7 \pm 1.4	0.48	67 \pm 28	-0.18	1.7 \pm 1.1	0.27
spai061	40.38	-0.70	1520	8.4 \pm 0.8	0.50	630 \pm 126	-0.15	16.5 \pm 1.5	0.48	68 \pm 30	-0.18	1.6 \pm 1.2	0.27
spai060	40.38	-0.68	1580	8.3 \pm 0.7	0.50	634 \pm 132	-0.14	16.2 \pm 1.4	0.48	71 \pm 34	-0.18	1.3 \pm 1.1	0.27
Guara	42.28	-0.25	1620	10.4 \pm 0.8	0.59	732 \pm 134	-0.25	18.2 \pm 1.4	0.42	92 \pm 44	-0.20	2.9 \pm 1.4	0.44
spai014	41.02	-0.12	1630	15.5 \pm 0.6	0.57	359 \pm 99	-0.30	23.2 \pm 1.2	0.55	40 \pm 30	-0.22	7.9 \pm 1.1	0.23
spai044	42.80	-0.70	1646	7.2 \pm 0.8	0.57	1098 \pm 155	-0.23	14.2 \pm 1.3	0.41	130 \pm 49	-0.18	0.5 \pm 1.5	0.42
spai020	40.67	-0.33	1648	11.4 \pm 0.7	0.50	484 \pm 110	-0.22	18.9 \pm 1.3	0.50	58 \pm 32	-0.25	4.2 \pm 1.2	0.26
spai021	40.87	-4.20	1650	10.5 \pm 0.7	0.58	620 \pm 135	-0.18	18.5 \pm 1.3	0.36	59 \pm 34	-0.18	3.2 \pm 1.3	0.41
spai063	40.35	-0.70	1660	8.4 \pm 0.7	0.51	634 \pm 132	-0.14	16.2 \pm 1.3	0.49	71 \pm 34	-0.18	1.3 \pm 1.1	0.26
spai047	41.98	-2.87	1751	8.9 \pm 0.7	0.56	631 \pm 115	-0.18	16.4 \pm 1.3	0.40	72 \pm 34	-0.22	1.8 \pm 1.2	0.38
Sarradé	42.55	0.88	1800	4.4 \pm 0.8	0.54	1249 \pm 218	-0.14	11.4 \pm 1.4	0.39	141 \pm 61	-0.17	-2.1 \pm 1.4	0.37
spai048	42.02	-2.90	1839	8.1 \pm 0.6	0.58	702 \pm 122	-0.20	15.4 \pm 1.2	0.41	78 \pm 36	-0.20	1.2 \pm 1.1	0.40
spai049	42.03	-3.03	1839	8.2 \pm 0.7	0.59	701 \pm 125	-0.20	15.5 \pm 1.3	0.42	77 \pm 35	-0.20	1.3 \pm 1.2	0.40
spai038	40.80	-3.95	1850	8.9 \pm 0.8	0.62	839 \pm 189	-0.14	16.9 \pm 1.3	0.45	65 \pm 39	-0.17	1.7 \pm 1.2	0.41
spai037	40.78	-3.80	1950	9.0 \pm 0.8	0.62	840 \pm 192	-0.14	17.0 \pm 1.4	0.45	66 \pm 38	-0.17	1.8 \pm 1.3	0.41
Baza	37.20	-3.16	1970	7.7 \pm 0.8	0.70	414 \pm 110	-0.14	14.6 \pm 1.3	0.64	18 \pm 16	-0.18	1.2 \pm 1.1	0.35
Vinuesa	42.00	-2.73	1980	8.5 \pm 0.7	0.58	680 \pm 117	-0.22	15.8 \pm 1.3	0.40	79 \pm 36	-0.20	1.5 \pm 1.3	0.40
S. Nevada	37.07	-3.46	2000	8.7 \pm 0.8	0.69	725 \pm 162	-0.14	16.9 \pm 1.4	0.65	37 \pm 26	-0.20	1.6 \pm 1.2	0.41

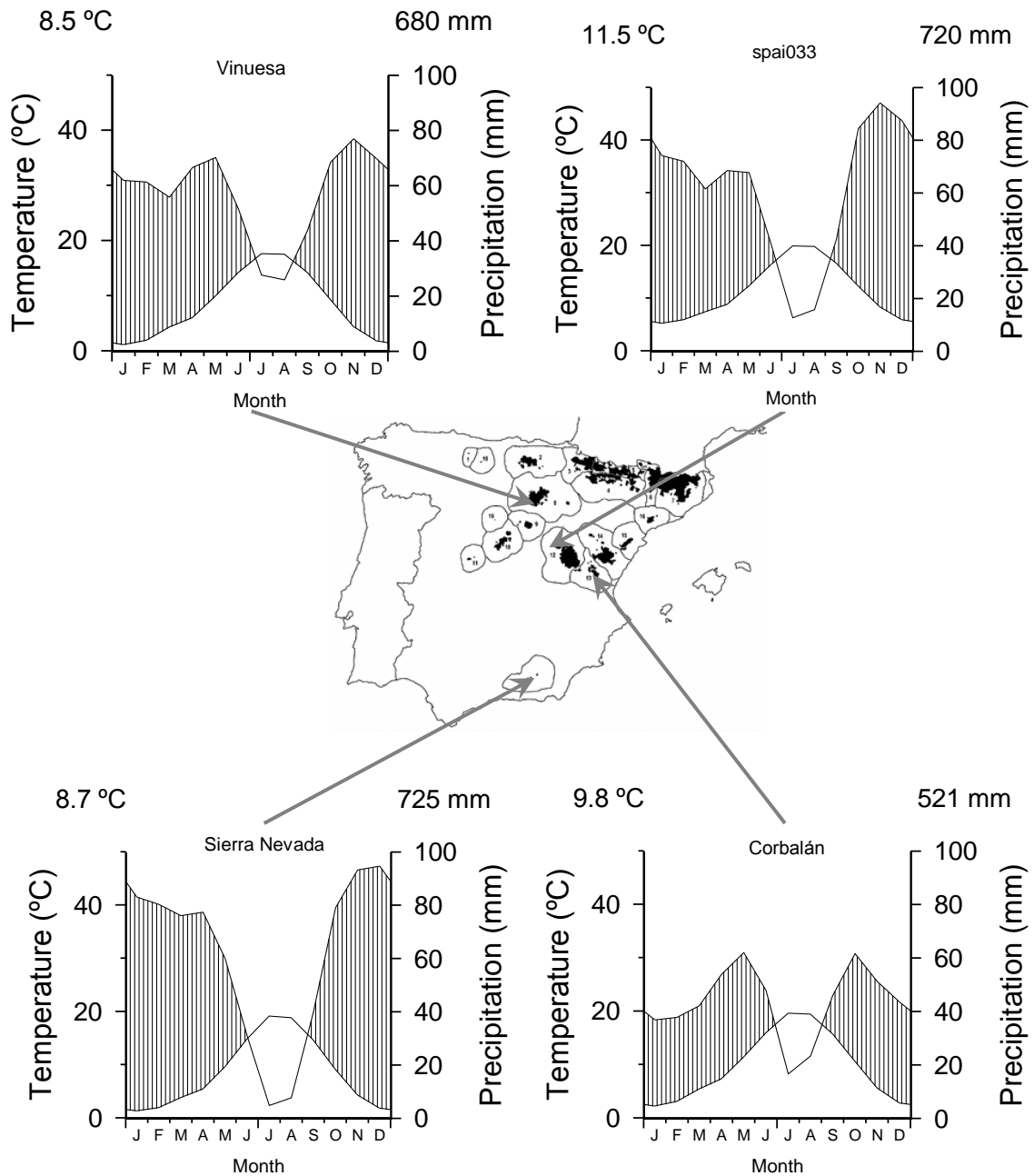


Figure A3. Climatic diagrams for 0.25° grids containing selected Iberian Scots pine sites and their approximate locations in Spain. Climate data correspond to the E-OBS v.10.0 dataset gridded at a 0.25° spatial resolution (Haylock et al., 2008) calculated for the period 1950-2011. The estimated mean annual temperature and total precipitation are indicated for each site. The numbers on the map refer to the Iberian Scots pine provenances and the black areas show the species distribution area (Catalán et al., 1991).