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

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## Abstract

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

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

## Highlights

- High variability in space and time of tree-growth response to climate in Spain
- Negative impact of low summer rainfall is higher at low elevations and high latitudes
- Growth at low elevations is more dependent on spring climate than at high elevations
- Negative impact of summer heat and drought has increased during the past decades
- Local adaptation to climate change is a key factor for future Mediterranean forests

## 1. Introduction

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

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

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

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

We used this multi-scalar approach to investigate how low winter temperatures and drought during the growing season in a continental Mediterranean climate drive the seasonal radial growth of Scots pine (*Pinus sylvestris* L.). This is the most widespread conifer species in the world, but it reaches its southern and dry limit in the Iberian Peninsula (Mirov, 1967). First, we relate growth to changing climate conditions since 1900 at local scales by sampling three sites in the Spanish Central System at different elevations, and therefore varying climatic conditions. We expected lower winter temperatures would be the main climatic constraint on tree growth at high-elevation sites and spring-to-summer water deficits at low-elevation sites. Second, we extrapolated this local analysis to a regional scale along a latitudinal gradient using existing Scots pine tree-ring growth series form continental Mediterranean sites in Spain. We hypothesize that at the global limit to Scots pine distribution, the lowest sites and southernmost sites will be responsive to drought, whereas the highest and northernmost sites will be most sensitive to winter temperature conditions.

## 2. Material and methods

### *2.1. Local study area*

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

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

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

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

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

The cores were air dried, sanded with sand paper of progressively finer grain until tree-rings became clearly visible and then visually cross-dated. Individual tree-ring width series were measured to the nearest 0.01 mm using a LINTAB semi-automatic measuring device (Rinntech, Heidelberg, Germany). Cross-dating quality was checked using the program COFECHA (Holmes, 1983). To assess the quality of tree-ring width series several dendrochronological statistics (Fritts, 2001) were calculated considering the period 1950-2011 (Table 1): first-order autocorrelation of raw width data (AC), mean sensitivity (MS) of indexed growth values, mean correlation between trees (*rbt*), signal to noise ratio (SNR), variance accounted for by the first principal component (PC1) and the expressed population signal (EPS), which measures the statistical quality of the mean site chronology compared with a perfect infinitely replicated chronology (Wigley et al., 1984). The segments of the site chronologies that reached EPS values equal to or higher than 0.85 were regarded as reliable enough to use for the climate-growth analyses.

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

### ***2.3. Regional scale study area***

To analyze the climate-growth relationships at a regional scale, we collected 23 Scots pine chronologies along a Spanish latitudinal gradient, including the species rear-edge from sites subjected to continental Mediterranean conditions (Table 2). Of these chronologies, 17 reach back at least to the early 1980s and were provided by the International Tree-Ring Data Bank (http://www.ncdc.noaa.gov/paleo/treering.html), and 6 were built explicitly for this study. The development of the tree-ring chronologies involved the same approach as described for the local scale analyses. The climatic variables are also similar to those used on the local scale but they were obtained from the homogenized and quality-checked E-OBS v.10.0 dataset gridded with a 0.25º spatial resolution (Haylock et al., 2008). Temporal trends in annual temperature and precipitation were calculated to characterize the climate of each site (Appendix A1), and only those variables highly correlated with growth indices were considered in the analyses of the climate-growth associations.

### *2.4. Climate-growth relationships*

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

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

## 3. Results

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

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

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

The main climatic factor stimulating growth in the high-elevation site was the mean maximum temperature in January and in the low-elevation site a positive water balance in June (Fig. 1). Warm February and dry March conditions also enhanced growth in the low-elevation site, whereas warm January temperatures and cool and wet conditions from June to July favored growth in the middle-elevation site. Warm and dry conditions in the previous late summer were related to lower growth indices in all sites, while warm October conditions at the end of the growing season produced a similar effect but only in the high-elevation site. At the individual tree level, June water balance and January mean minimum temperature were both significantly positively related to growth, when were compared the three sites along the elevational gradient (Table 3). The growth indices correlate with low water availability at low-elevation site and with temperature at high-elevation site, with correlations of similar magnitude.

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

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

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

At the regional scale, a significant ($P < 0.05$) increase in mean temperature and decrease in precipitation increased with latitude (Table A1, Appendix A1). The trends in temperature (positive) and precipitation (negative) during the growing season decreased when latitude increase ($p=0.015$ and $p<0.0001$, respectively). The exception was the mean minimum temperature that increased with latitude ($p<0.0001$). On the other hand, the trends in precipitation (p=0.003) and temperature (p=0.023) significantly increased with elevation at the regional scale (Table A1, Appendix A1).

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

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

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

## 4. Discussion

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

In trees and other perennial plants, the adjustment of anatomical and functional traits to environmental variability (phenotypic plasticity and genetic variability) is strong at the margins of the plants range, but the overall performance of a tree species may decline as the southernmost distributional limits are reached and vulnerability to climatic stressors increases (Valladares et al., 2014; Vergee and Kunin, 2013). This could be the case for the Iberian Scots pine populations at the lowest elevations, which were most dependent on summer precipitation. The strong positive effects of summer precipitation on growth are in line with the results of previous studies of dry areas in central Europe, which indicate that drought constrains the physiological activity of Scots pine during summer (Eilmann et al., 2010, 2011; Lebourgeois, 2000; Lévesque et al., 2014). As others have also found (e.g., Génova, 2012), summer precipitation is the main limiting factor on Scots pine growth in the Spanish Central System (Figs. 1 and 2), but its importance has significantly increased since the 1970s (Fig. 3) as the climate has become warmer and water availability has decreased due to increasing evapotranspiration. Our analyses show a late 20th century warming trend in the study area (+1.2 ºC from 1943 to 2011; see Fig. A1), as well as a higher frequency of extreme drought events towards the end of the 20th century, such as those that affected most of the Iberian Peninsula in the 1980s and 1990s (Vicente-Serrano, 2006). The negative correlation found between growth and summer drought suggests that cumulative negative drought effects have a relatively higher impact on tree performance than the amount of rainfall received throughout one year or the average dryness (Madrigal-González and Zavala, 2014). Moreover, recurrent droughts reduce the carbon uptake by trees and increase their respiration rates, thus reducing their capacity to grow (Galiano et al., 2011; McDowell et al., 2008). Recurrent and extended droughts might therefore lead to accumulated carbon deficits, which could result in long-term limitation on growth and eventually tree death (McDowell et al., 2008).

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

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

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

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

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

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

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

The divergent growth responses to climate may have to do with other confounding factors, such as: i) changing competition between trees or between trees and undergrowth due to changes in land use and past management, ii) phenotypic variability, including anatomical or phenological adjustments or iii) genetic variation and site characteristics (such as soil depth, nutrient availability, geomorphological features, etc) which can act as buffers against the expected response to climate (Camarero et al., 2013; Prus-Glowacki and Stephan, 1994). For instance, the wide genetic differentiation found in southern Scots pine populations in Spain might be the results of a variety of local adaptations to seasonally dry conditions, and could alter the responses to precipitation observed (Fig. 4) (Catalán et al., 1991). Our results support that of other studies in Iberian Scots pine stands that found they are less vulnerable to embolism than their northern counterparts (Martinez-Vilalta et al., 2009).

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

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## Tables

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

| | **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 ± 1 | 25 ± 3 | 35 ± 2 |
| Mean age at 1.3 m (years) | 83 ± 16b | 70 ± 34a | 124 ± 29c |
| dbh (cm) | 34.4 ± 8.9b | 31.3 ± 1.2a | 40.9 ± 2.4 c |
| Tree height (m) | 16.8 ± 2.6b | 13.6 ± 0.3a | 20.3 ± 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 ± 0.13a | 1.60 ± 0.14a | 2.02 ± 0.13b |
| AC | 0.77 ± 0.09 a | 0.82 ± 0.4 0b | 0.86 ± 0.01b |
| MS | 0.26 ± 0.05a | 0.28 ± 0.01b | 0.33 ± 0.01b |
| *rbt* | 0.56 ± 0.03 | 0.59 ± 0.01 | 0.60 ± 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 |

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

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

| Site name or ITRDB code | Latitude (N) | Longitude (-W, +E) | Elevation (m a.s.l.) | Ring-width ± SD (mm) | Nº series | AC | MS | PC1 (%) | Time span (years) | Period EPS > 0.85 |
|---|---|---|---|---|---|---|---|---|---|---|
| spai024 | 42.83 | -0.78 | 1275 | 0.92 ± 0.21 | 8 | 0.784 | 0.245 | 47.93 | 1696-1985 | 1800-1985 |
| Corbalán* | 40.43 | -0.97 | 1390 | 0.70 ± 0.34 | 16 | 0.612 | 0.481 | 69.03 | 1838-2012 | 1850-2012 |
| spai030 | 40.33 | -1.98 | 1400 | 1.28 ± 0.42 | 5 | 0.743 | 0.240 | 52.98 | 1809-1983 | 1900-1983 |
| spai033 | 40.33 | -5.17 | 1465 | 0.83 ± 0.19 | 25 | 0.833 | 0.292 | 52.32 | 1813-1985 | 1825-1985 |
| spai034 | 40.33 | -5.13 | 1470 | 1.21 ± 0.29 | 26 | 0.785 | 0.282 | 50.53 | 1769-1985 | 1775-1985 |
| spai062 | 40.25 | -0.68 | 1500 | 1.49 ± 0.43 | 31 | 0.697 | 0.303 | 48.67 | 1900-2008 | 1925-2008 |
| spai061 | 40.38 | -0.70 | 1520 | 1.93 ± 0.99 | 52 | 0.712 | 0.354 | 53.26 | 1937-2008 | 1950-2008 |
| spai060 | 40.38 | -0.68 | 1580 | 1.42 ± 0.62 | 23 | 0.647 | 0.405 | 62.15 | 1931-2008 | 1950-2008 |
| Guara* | 42.28 | -0.25 | 1620 | 0.77 ± 0.25 | 12 | 0.642 | 0.306 | 40.37 | 1900-2012 | 1900-2012 |
| spai014 | 41.02 | -0.12 | 1630 | 0.81 ± 0.28 | 28 | 0.847 | 0.241 | 54.00 | 1791-1992 | 1800-1992 |
| spai044 | 42.80 | -0.70 | 1646 | 0.72 ± 0.13 | 30 | 0.812 | 0.230 | 44.44 | 1605-1985 | 1700-1985 |
| spai020 | 40.67 | -0.33 | 1648 | 1.23 ± 0.29 | 18 | 0.893 | 0.271 | 40.83 | 1763-1991 | 1800-1991 |
| spai021 | 40.87 | -4.20 | 1650 | 0.78 ± 0.16 | 14 | 0.808 | 0.275 | 44.07 | 1715-1988 | 1824-1988 |
| spai063 | 40.35 | -0.70 | 1660 | 2.42 ± 1.13 | 29 | 0.837 | 0.259 | 54.98 | 1956-2008 | 1956-2008 |
| spai047 | 41.98 | -2.87 | 1751 | 0.98 ± 0.20 | 31 | 0.864 | 0.206 | 41.11 | 1567-1983 | 1600-1983 |
| Sarradé* | 42.55 | 0.88 | 1800 | 1.35 ± 0.46 | 27 | 0.836 | 0.240 | 37.61 | 1825-2010 | 1850-2010 |
| spai048 | 42.02 | -2.90 | 1839 | 0.85 ± 0.19 | 17 | 0.803 | 0.219 | 48.41 | 1671-1983 | 1750-1983 |
| spai049 | 42.03 | -3.03 | 1839 | 0.90 ± 0.14 | 27 | 0.859 | 0.208 | 38.27 | 1593-1985 | 1775-1985 |
| spai038 | 40.80 | -3.95 | 1850 | 0.75 ±0.15 | 23 | 0.852 | 0.241 | 41.51 | 1599-1984 | 1700-1984 |
| spai037 | 40.78 | -3.80 | 1950 | 0.90 ± 0.26 | 26 | 0.839 | 0.234 | 45.93 | 1661-1985 | 1725-1985 |
| Baza* | 37.20 | -3.16 | 1970 | 2.01 ± 0.40 | 20 | 0.726 | 0.271 | 40.53 | 1828-2007 | 1875-2007 |
| Vinuesa* | 42.00 | -2.73 | 1980 | 0.89 ± 0.13 | 15 | 0.821 | 0.192 | 41.88 | 1648-1995 | 1675-1995 |
| Sierra Nevada* | 37.07 | -3.46 | 2000 | 2.32 ± 0.65 | 30 | 0.570 | 0.382 | 58.04 | 1875-1999 | 1875-1999 |

*Chronologies built for this study.

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

| **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 | |

## Figures

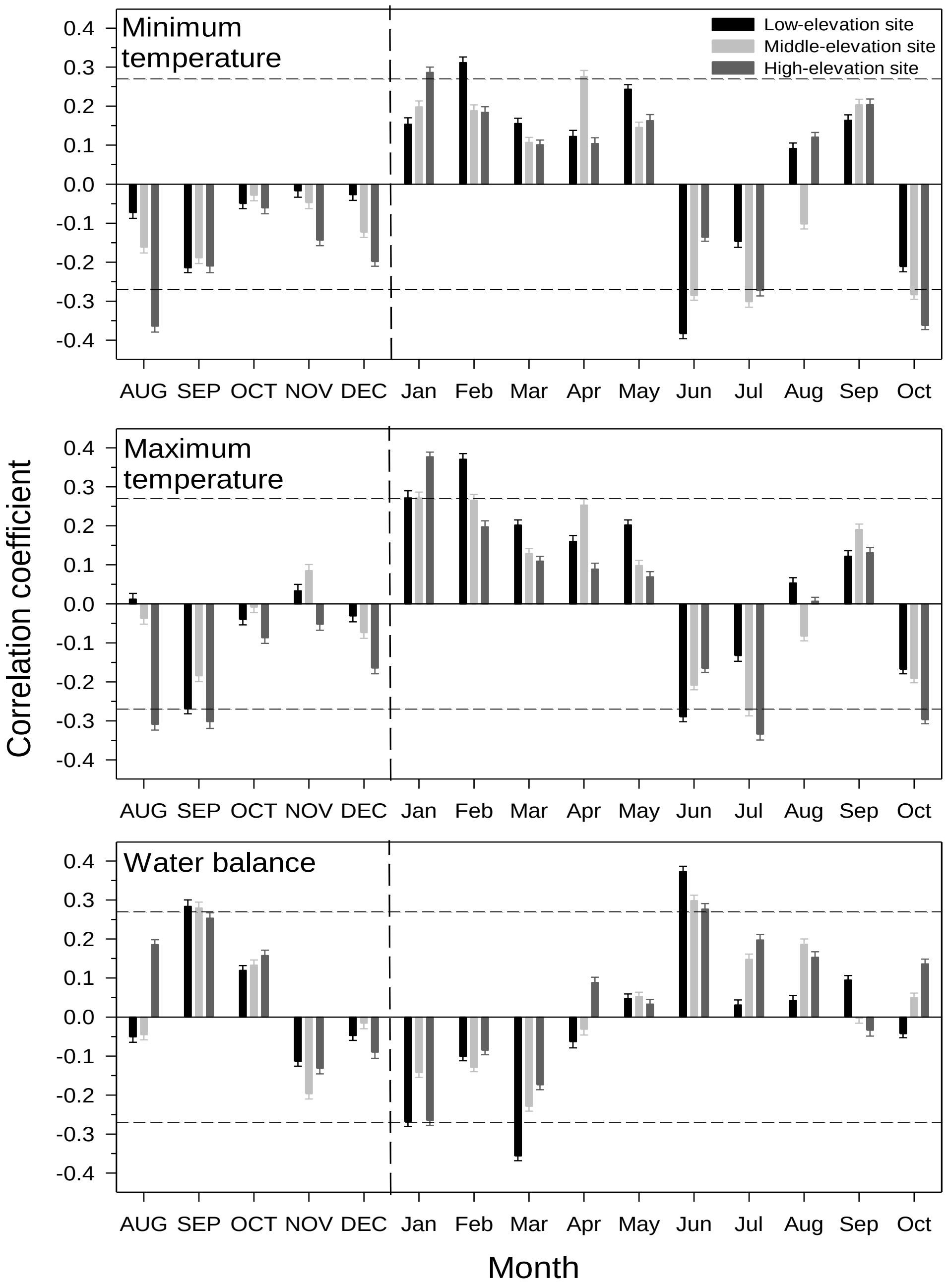
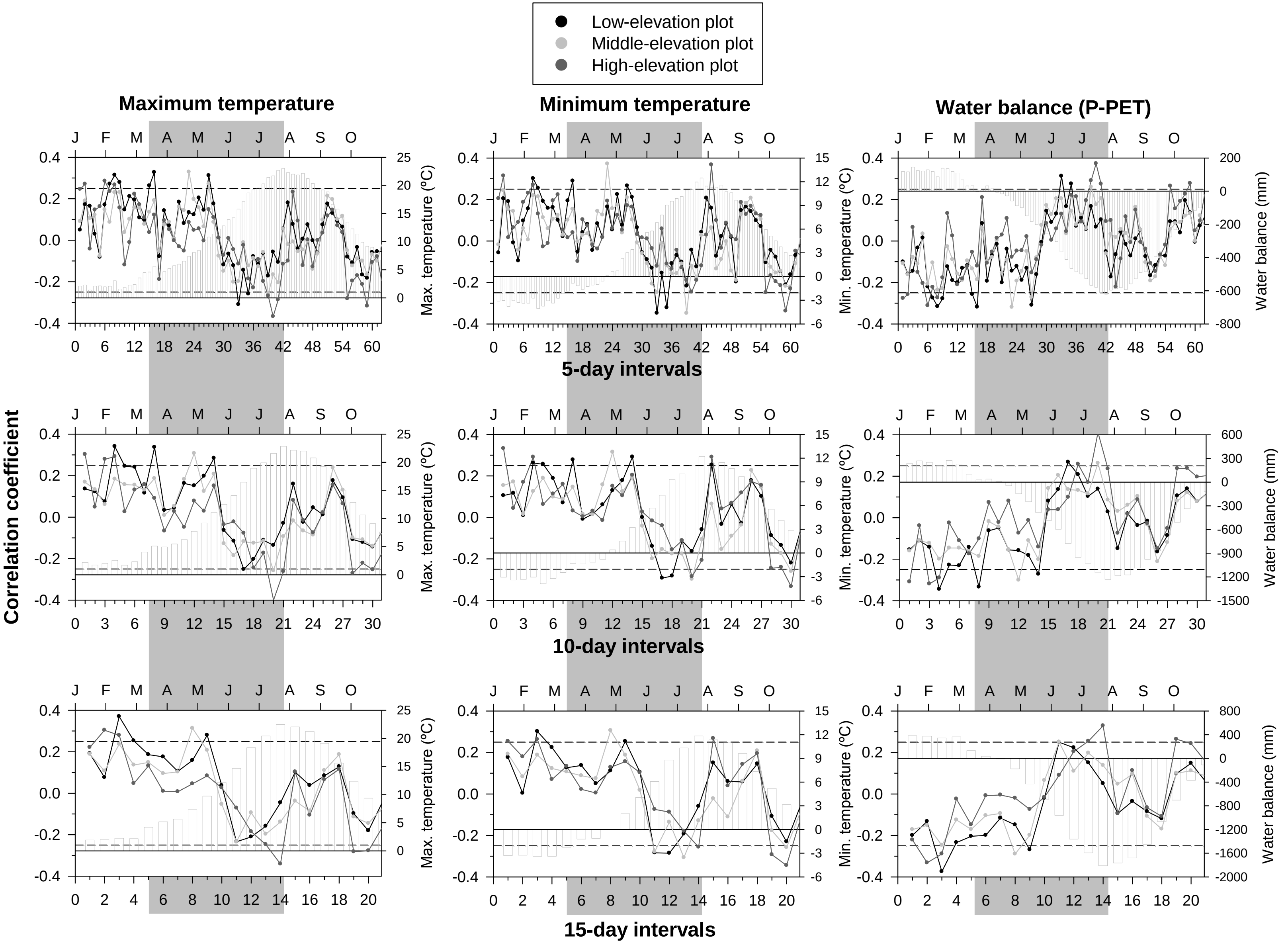


**Figure 1.** Correlation coefficients obtained by relating individual tree-ring width indices and monthly climatic data (mean, maximum and minimum temperature and water balance (P-PET)) for low- (black bars), middle- (grey bars) and high-elevation (dark grey bars) Scots pine sites. Growth is related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



● Low-elevation plot
● Middle-elevation plot
● High-elevation plot
Maximum temperature
Minimum temperature
Water balance (P-PET)
J F M A M J J A S O
Correlation coefficient
0.4
0.2
0.0
-0.2
-0.4
Max. temperature (ºC)
25 20 15 10 5 0
Min. temperature (ºC)
15 12 9 6 3 0 -3 -6
Water balance (mm)
200 0 -200 -400 -600 -800
600 300 0 -300 -600 -900 -1200 -1500
800 400 0 -400 -800 -1200 -1600 -2000
0 6 12 18 24 30 36 42 48 54 60
5-day intervals
0 3 6 9 12 15 18 21 24 27 30
10-day intervals
0 2 4 6 8 10 12 14 16 18 20
15-day intervals

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

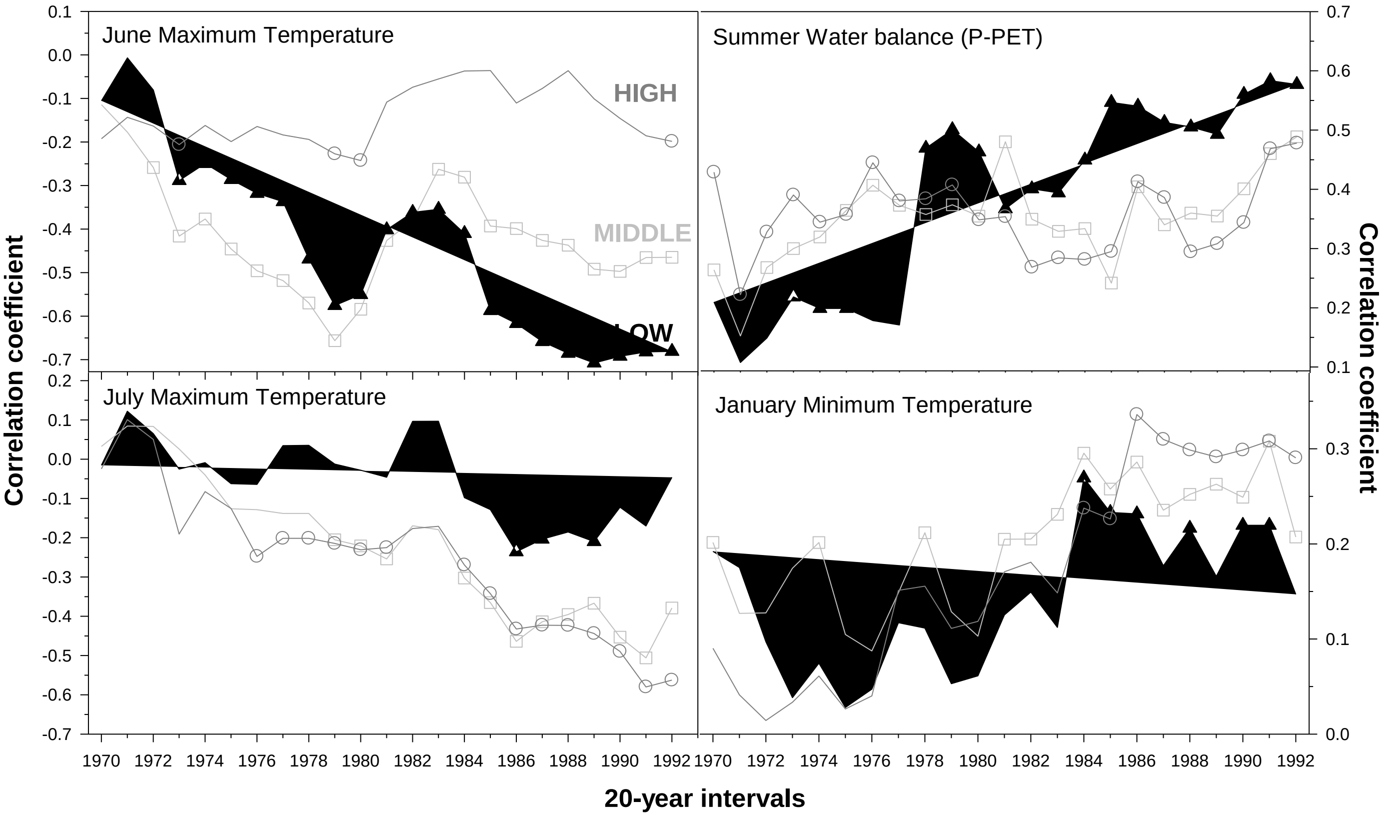


**Figure 3.** Moving correlations (Pearson coefficients) calculated between residual tree-ring width indices for each of the three plots located at different elevations and selected monthly climate variables. The coefficients were calculated for 20-year periods lagged by 1 year for the period 1950-2011. 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.

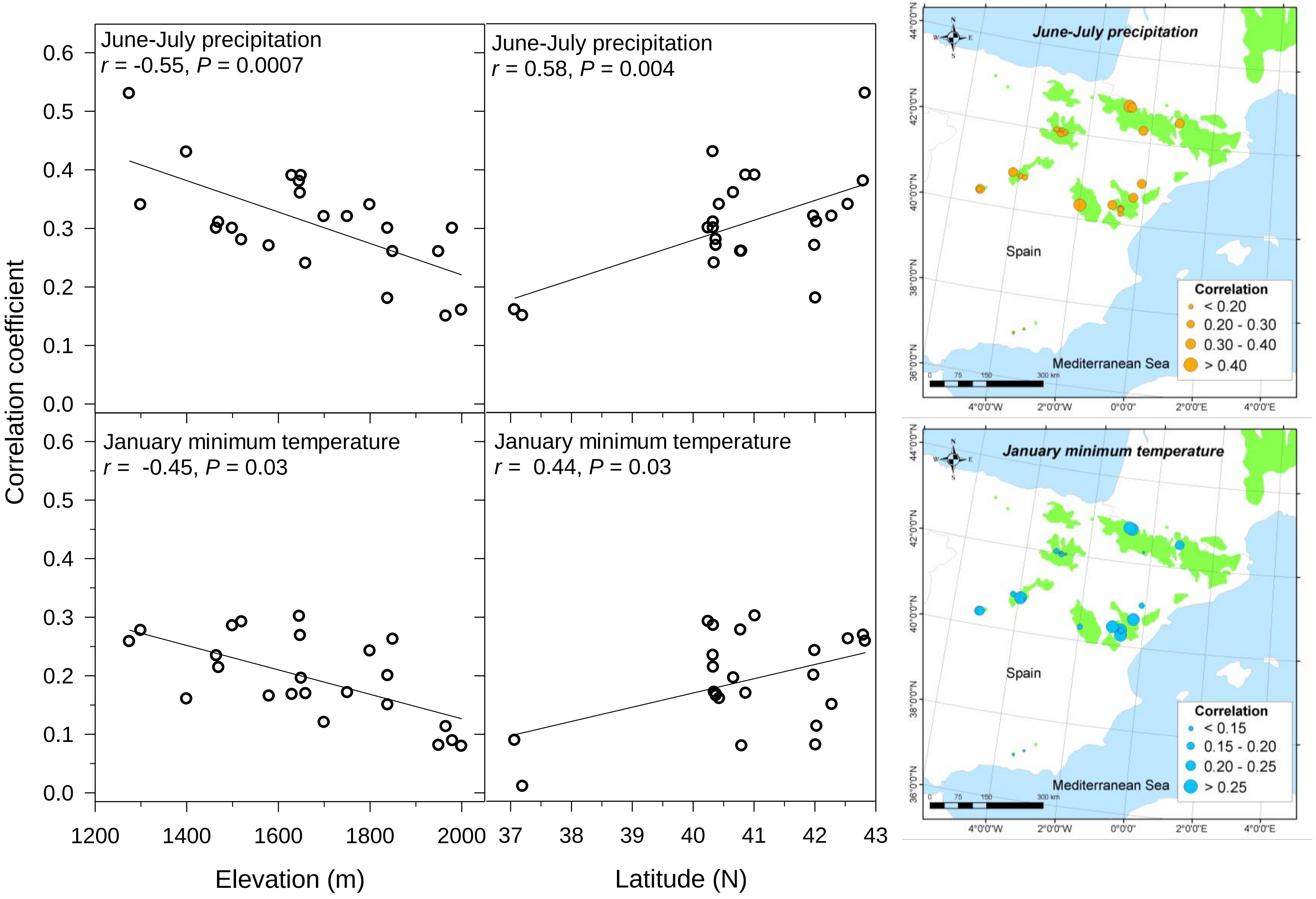

June-July precipitation
r = -0.55, P = 0.0007
June-July precipitation
r = 0.58, P = 0.004
January minimum temperature
r = -0.45, P = 0.03
January minimum temperature
r = 0.44, P = 0.03
Correlation coefficient
0.0
0.1
0.2
0.3
0.4
0.5
0.6
1200
1400
1600
1800
2000
Elevation (m)
37
38
39
40
41
42
43
Latitude (N)
June-July precipitation
January minimum temperature
Spain
Mediterranean Sea
Correlation
< 0.20
0.20 - 0.30
0.30 - 0.40
> 0.40
< 0.15
0.15 - 0.20
0.20 - 0.25
> 0.25
44°0'0"N
42°0'0"N
40°0'0"N
38°0'0"N
36°0'0"N
4°0'0"W
2°0'0"W
0°0'0"
2°0'0"E
4°0'0"E
0
75
150
300 km
N
S
E
W

**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

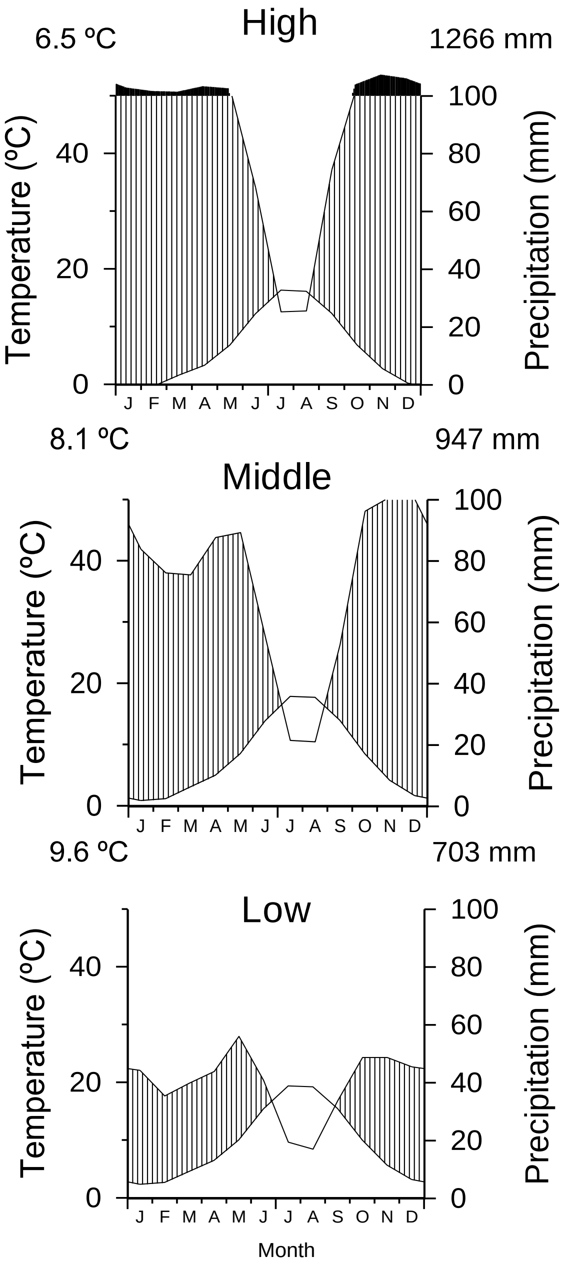


**Figure A1.** Climatic diagrams of the three study plots with Scots pine (data for the period 1943-2011) located at low-, middle- and high-elevation sites in the Spanish Central System. The mean annual temperature and total precipitation are indicated for each site.

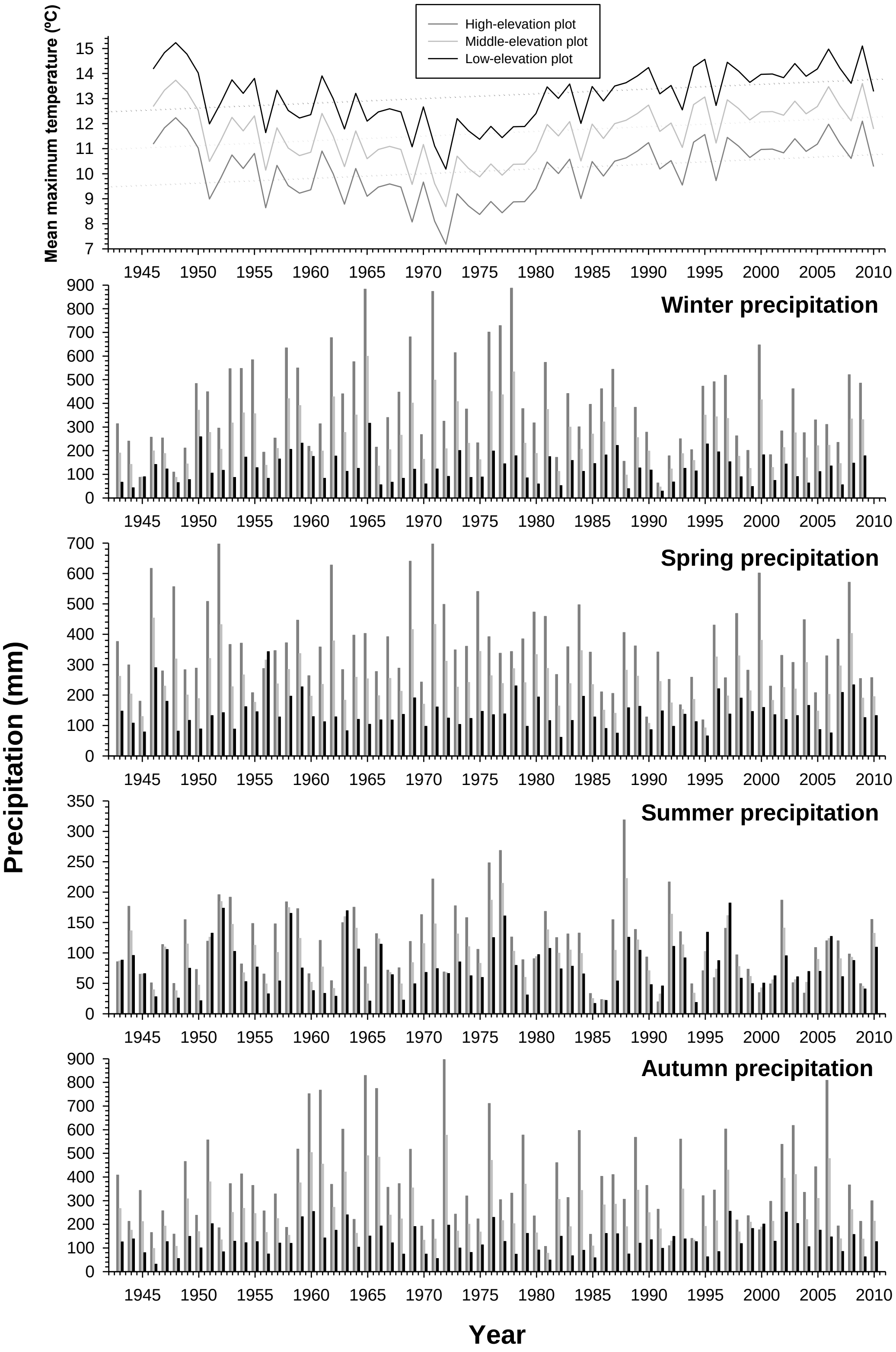


**Figure A2.** Mean annual maximum temperature and seasonal precipitation patterns and trends for the three Scots pine plots located at low-, middle- and high-elevation sites (period 1943-2011).

**Table A1.** Climatic characteristics (means ± SD) and trends ($\tau$, 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 0.25º spatial resolution (Haylock et al., 2008) for the period 1950-2011. Significant ($p < 0.05$) trends are shown in bold.

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

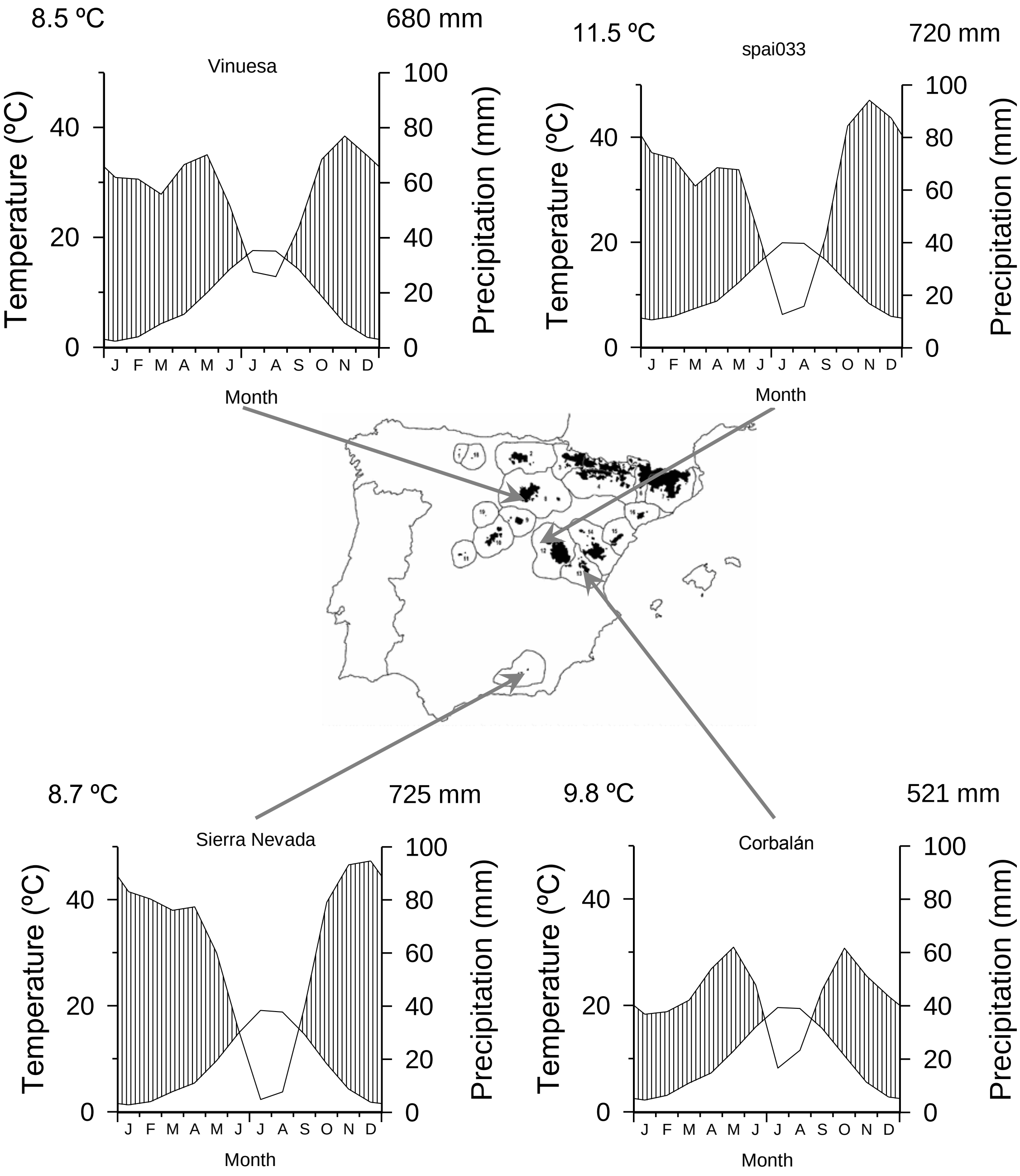


**Figure A3.** Climatic diagrams for 0.25º grids containing selected Iberian Scots pine sites and their approximate locations in Spain. Climate data correspond to the E-OBS v.10.0 dataset gridded at a 0.25º spatial resolution (Haylock et al., 2008) calculated for the period 1950-2011. The estimated mean 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).