Universidad de Huelva

Departamento de Ciencias Agroforestales

A dendroecological approach to growth dynamics of Mediterranean forests in Southwestern Spain: climate change impacts, vulnerability and adaptive capacity

Aproximación dendroecológica a la dinámica del crecimiento de especies forestales mediterráneas en el suroeste de España: impactos, vulnerabilidad y respuesta adaptativa al cambio climático

Memoria para optar al grado de doctor
presentada por:

Fabio Natalini

Fecha de lectura: 19 de enero de 2017

Bajo la dirección de los doctores:

Reyes Alejano Monge

Francisco Javier Vázquez Piqué

Huelva, 2017

UNIVERSIDAD DE HUELVA
ESCUELA TÉCNICA SUPERIOR DE INGENIERÍA
Departamento de Ciencias Agroforestales

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Directores:
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Agradecimientos / Acknowledgements / Ringraziamenti

A muchas personas dirijo mis agradecimientos en este momento, cuando la redacción de esta tesis llega finalmente a su última fase. A algunas de ellas por su contribución técnica, científica o profesional; a otras, por su papel que tienen en mi vida o que han tenido en los últimos cuatro años. Algunas de ellas en España, otras en Italia, y en otros lugares de Europa y del mundo: a todos os agradezco vuestro apoyo, colaboración y confianza, a cada uno de vosotros en el idioma que más conviene para expresar mi gratitud.

Now, when this manuscript is about to be printed, I think about many people I met and cooperated with during the last four years. I sincerely acknowledge your support, collaboration and trust. Some of you, for your technical, scientific of professional contribution. Some others simply, but not less importantly, for your significant role in my life. Some of you in Spain, others in Italy, in Europe and the world: to everyone, here I am writing in the most convenient language to express my acknowledgement.

Alla conclusione di questa tesi, il mio ringraziamento va a molte persone. Alcuni di voi hanno contribuito direttamente, apportando conoscenza, valore scientifico, professionalità e tecnica. Ad altri il mio pensiero va per l'importante ruolo che avete nella mia vita o per essere stati protagonisti in alcuni momenti significativi durante questi ultimi quattro anni. Alcuni di voi in Spagna, altri in Italia, altri in Europa e nel mondo: il mio rigraziamento va ad agnuno di voi, nella lingua che meglio si adatta per esprimere questo pensiero.

A mis directores de tesis, Reyes y Javier, que supieron transmitir con eficacia su conocimiento, que aportaron su profesionalidad, su valiosa dirección científica, sus preciosos consejos, y que pusieron en mi su confianza para la elaboración de una tesis doctoral, un trabajo duro y largo, incluso cuando las circunstancias no fueron de las mejores. Un trabajo que sin embargo se entrega hoy, con sus índices de impacto y todo. Gracias por vuestra maestría.

A Guillermo Gea-Izquierdo, importantísima guía en mis primeros pasos en la ciencia dendroecológica, e Isabel Cañellas, que dirigió un sostén imprescindible en esa fase. Ambos son coautores de uno de los artículos que componen esta tesis. Sí que costó sacar este artículo, fue un reto. Y sin embargo, ahí va y me enorgullece. Gracias por vuestro apoyo y confianza.

A Rafael Calama y Marta Pardos, coautores de uno de los artículos que componen esta tesis. Mi participación en estas investigaciones ha sido un momento fundamental en mi trayectoria científica y profesional. Agradezco mucho esta oportunidad tan valiosa.

I sincerely thank Ulf Büntgen, who was supervisor during my scientific stay at the WSL in Switzerland. That was an exciting and lively experience, I really enjoyed our interaction. You used to say that you were learning a lot in those days from our conversations about climate, ecology and tree growth in Spain; but I assure you that I was actually learning much more. This was extremely valuable for me. Finally we also get a paper, recently published and included in this thesis, a really nice one. Thank you for your kindness and for being such a good guide.

I sincerely thank Alexandra Correia, coauthor of one of the papers included in this thesis. When we met at the MedPine conference in Solsona and you told me you were interested in sharing data for writing a paper together, I immediately realized that was a fantastic suggestion. That paper is now part of this thesis and I am really happy to have your tree-ring data from Portugal included here. Thank you so much for your kindness and willingness to cooperate.

Mi agradecimiento a Mariano Morales, que fue tutor durante mi estancia en Mendoza, Argentina, y también revisor de esta tesis doctoral. Te aseguro que durante aquellos dos meses aprendí muchísimo: con eficacia me enseñaste técnicas, herramientas y una aproximación al problema dendroclimatológico que ahora son parte importante de mis habilidades. Con tu revisión y consejos, además, mi tesis ha mejorado. Muchas gracias por tu amabilidad y tus enseñanzas.

Un sentito ringraziamento a Alfredo Di Filippo, referee di questa tesi di dottorato. La tua revisione è stata importante, ed ho apprezzato molto l'attenzione con cui hai letto il testo e di cui erano prova le tue note e correzioni, accurate laddove mancava una virgola o sbagliavo una lettera. Questa tesi è un po' il coronamento di un cammino nella dendrocronologia iniziato ormai diversi anni fa a Viterbo, con la tesi di laurea. Grazie per essere tornato a contribuire in questo cammino.

Gracias a Daniel Martín, compañero de trabajo en diversos momentos desde que en 2009 pisé por primera vez el suelo de Huelva, siendo alumno Erasmus lejos aún de su trabajo fin de Máster. Volviste a enseñarme cosas cuando volví por aquí para empezar la tesis. Me trasmitiste tu conocimiento sobre el crecimiento de la encina y también tus experiencias con la dendrocronología. Gracias por haber tenido siempre una palabra útil en mi camino.

Gracias a Enrique Garriga, que me enseñó lo que hay que hacer para que una rodaja de encina quede bien, para que esos anillos tan inciertos se dejen ver. Aquellas horas pasadas entre lijadoras y serrín dieron la base imprescindible para que este trabajo viera luz. Gracias por haber sido buen guía en esos momentos.

Mi agradecimiento va a muchas otras personas cuya acciones, en distintos momentos y maneras, han sido significativas para la elaboración de esta tesis en particular, así como en mi actividad investigadora en general. A los miembros del grupo de investigación Análisis y Planificación del Medio Natural y otros profesores del Departamento de Ciencias Agroforestales de la Universidad de Huelva, por sus útiles consejos y cooperación. Al personal técnico y a los agentes de la Consejería de Medio Ambiente de la Junta de Andalucía, por su preciosa colaboración en la recopilación de información medioambiental y en las inspecciones de campo. Gracias a todos.

Gracias a Noemí. Tú también estás aquí, en estas páginas. Aquí no hay solamente de ciencias y matemáticas, sino también sudor, esperanza, ilusión, excitación, preocupación, agobio, expectativa, reflexión; todos mis desvelos que bien conoces. Gracias por estar ahí en cada momento; la dicha que esto me procura es el mejor ingrediente de mi vida.

Gracias a la familia Raposo Gutiérrez. Mi sostén importante en muchos momentos, especialmente en mis primeros pasos en la vida onubense, con mis problemas y necesidades de joven foráneo recién llegado. Gracias por vuestro cariño.

A mia madre. E il motivo per cui si ringraziano le madri non è mai ovvio né mai sufficientemente spiegato. Ti voglio bene.

Las entidades financiadoras de los trabajos incluidos en esta tesis doctoral fueron el Ministerio de Economía y Competitividad, la Unión Europea (fondos FEDER), el Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria, el Campus de Excelencia Internacional de Medio Ambiente, Biodiversidad y Cambio Global (programa de ayudas para estancias predoctorales en Europa, y programa de incentivos para publicaciones científicas), el banco Santander (programa de Becas Iberoamérica Jóvenes Profesores e Investigadores), la "Association for Tree-ring Research" (ayudas para la participación en congresos), y la "Tree-Ring Society" (ayudas para la participación en congresos).
Fabio Natalini ha sido investigador predoctoral contratado en la Universidad de Huelva en el marco del proyecto de investigación "Vulnerabilidad de las masas de Pinus pinea ante un escenario de cambio global" (Plan Nacional I+D+i RTA2013-00011-C02-02).

Dedico questo lavoro

a mia madre;

a Noemí;

a Isabella, cara sorella, lontana nell'età e nelle esperienze,
ma così vicina ora che anch'io vado crescendo;

ad Andrea, Lorenzo e Giulia, per i quali ho un pensiero almeno una volta al giorno;

ed anche un po' a mio padre, per il quale ho sentimenti diversi e contrastanti: uno di essi, la mancanza.

FE DE ERRATAS / *ERRATA*

En la última línea del índice (Contents): donde dice “16 APPENDIX 2. Conference presentation”, debe decir “16 APPENDIX 2. Conference presentation**s**”.
*The last point of Contents: “16 APPENDIX 2. Conference presentation”, is “16 APPENDIX 2. Conference presentation**s**”.*

Página 15: los tres espacios blancos en las gráficas “Drought intensity”, deben estar en verde (como el fondo).
Page 15: the white space in the graphs of “Drought intensity” is green as the background.

Página 34: al pie de la Figura 4 debe añadirse: “For the numeration of the study sites, see Tables 1 and 2”.
Page 34: the caption of Figure 4 is incomplete: “For the numeration of the study sites, see Tables 1 and 2”.

Páginas 39, 42, 58 (pie de la Figura 15) y 59: donde dice “section **5.4** Tree ring studies of P. pinea and Q. ilex in the Southern Iberian Peninsula”, debe decir “section **6.4** Tree ring studies of P. pinea and Q. ilex in the Southern Iberian Peninsula”.
Pages 39, 42, 58 (caption of figure 15) and 59: “secion 5.4 Tree ring studies of” is “section 6.4 Tree ring studies”.

Página 31: el párrafo que empieza con “With exception of the articles included in this thesis and the southernmost P. pinea study” no es un punto de viñeta, debía alinearse a la izquierda.
Page 31: The paragraph “With exception of the articles included in this thesis” is not a list term; should be left-aligned.

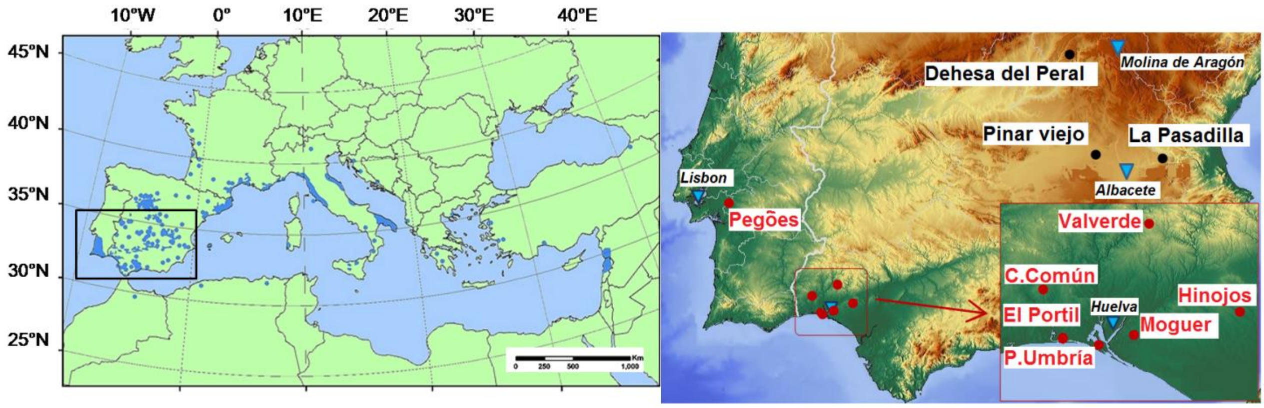
Página 36: las referencias (1), (2), (3) y (4) de la Tabla 1 deben ser las mismas para la Tabla 2.
Page 36: The references (1), (2), (3) y (4) of Table 1 are the same of the Table 2.

Página 37: la referencia de la tabla donde dice “**(9)** Mean Pearson correlation coefficient between the individual tree chronologies and the mean chronology of the stand”, debe decir “**(8)** Mean Pearson correlation coefficient between the individual tree chronologies and the mean chronology of the stand”.
*Page 37: the reference of the table “**(9)** Mean Pearson correlation coefficient between the individual tree chronologies and the mean chronology” is “**(8)** Mean Pearson correlation coefficient between the individual tree chronologies and the mean chronology”.*

Página 38: las referencias de (1) a (10) de la Tabla 4 son las mismas de la Tabla 3 en la página anterior.
Page 38: the references from (1) to (10) of Table 4 are the same of the Table 3 in the previous page.

Página 122: en la ecuación de Ms, el término 1/n-1 debía estar sin paréntesis y sin barras verticales.
Page 122: in the equation of Ms, the term 1/n-1 is without parenthesis and without vertical bars.

Página 135: en el panel derecho de la imagen Online resource 1, “Mazagón” no debe estar, y falta “El Portil”; la imagen correcta es la siguiente:
Page 135: in the right side of the figure Online resource 1, “Mazagon” is removed and “El Portil” is added; the correct figure is the following:



Página 147: el título de epígrafe “4.1 Influence of detrending methods on growth-climate relationships, uncertainties from climate data and choice of climate parameters”, debe estar sin “4.1”, en negrita y cursive.
Page 147: the first sentence starting with “4.1 Influence of detrending methods” is the title of a paragraph, should be in bold and italics, without “4.1”.

Página 198: donde dice “APPENDIX 2. CONFERENCE PRESENTATION”, debe decir: “APPENDIX 2. CONFERENCE PRESENTATION**S**”.
*Page 198: “APPENDIX 2. CONFERENCE PRESENTATION”, is “APPENDIX 2. CONFERENCE PRESENTATION**S**”.*

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15.2 Article 2. Natalini F., Correia A.C., Vázquez-Piqué J., Alejano R., 2015. Tree rings reflect growth adjustments and enhanced synchrony among sites in Iberian stone pine (Pinus pinea L.) under climate change. Annals of Forest Science, 72(8), pp.1023-1033, DOI: 10.1007/s13595-015-0521-6.......... 118

15.3 Article 3. Natalini F., Alejano R., Vázquez-Piqué J., Pardos M., Calama R., Büntgen U., 2016. Spatiotemporal variability of stone pine (Pinus pinea L.) growth response to climate across its geographical range in the Iberian Peninsula. Dendrochronologia, DOI: 10.1016/j.dendro.2016.07.001.......... 139

15.4 Article 4. Natalini F., Alejano R., Vázquez-Piqué J., Cañellas I., Gea-Izquierdo G., 2016. The role of climate change in the widespread mortality of holm oak in open woodlands of Southwestern Spain. Dendrochronologia, 38, pp.51-60.......... 174

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1 EXECUTIVE SUMMARY

Tree-ring chronologies were studied using samples of dead holm oaks (*Q. ilex* ssp. *ballota* [Desf.] Samp.) in declining open-woodlands in southwestern Spain and samples of stone pine (*Pinus pinea* L.) from forests along a latitudinal gradient in Spain, Portugal and Italy. Growth trends and climate change-related chronology signal in *Q. ilex* were analyzed to assess the role of climate change in the tree mortality process. Growth responses of *P. pinea* to spatiotemporal variability of climate were examined to gain knowledge about the species' adaptive capacity. Different techniques to extract the climatic signal from the tree-ring series were applied according to standard dendroclimatological approaches. A cubic spline with a period of 30 years was the best approach to remove the non-climatic variance related to silviculture-induced growth releases. The climate variability was obtained from meteorological station records and gridded climate datasets from international databases. There are common Mediterranean macroclimatic features, but the distribution of precipitation over the year and the duration and intensity of meteorological droughts vary among sites. Temperatures and aridity increased since the 1970s in all sites. The most significant growth-climate correlations were found with precipitation and drought indices in all sites, indicating that water availability is the main limiting factor for growth. Growth reductions in *Q. ilex* occurred during the intense and prolonged droughts of the recent decades, and temporal changes of growth-climate correlations indicates trees' sensitivity to the increasing aridity. Climate change played an important role as stress factor determining the inception of mortality processes, and probably aggravated the impacts of other mortality factors. This is the first evidence of the direct effects of climate change on the current widespread stand decline and increase of mortality in oak open-woodlands in the southwestern Iberian Peninsula. Growth-climate correlations patterns in *P. pinea* varied over time and space, indicating the species' growth adaptation to site-specific climatic conditions and suggesting physiological adjustments in response to climatic variations. The plasticity of this species suggests that different populations have different capacities for acclimation to climate change, and this will probably influence future vegetation dynamics. This is the first assessment of tree species' plasticity in Iberian Mediterranean forests from a dendrochronological perspective. The vulnerability to drought of southern Iberian forests should be considered when making decisions for adaptive management. This thesis presents the first tree-ring dataset in southwestern Spain and a novel dendroecological approach for studying climate-related forest growth dynamics in this region.

Key words: *Pinus pinea*, *Quercus ilex*, tree rings, climate change, Mediterranean, Iberian Peninsula

2 RESUMEN EJECUTIVO

En la presente tesis doctoral se han estudiado cronologías de anchura de anillos a partir de muestras de encinas muertas (*Q. ilex* ssp. *ballota* [Desf.] Samp.) en dehesas afectadas por decaimiento forestal en el suroeste de España, y muestras de pino piñonero (*Pinus pinea* L.) precedentes de bosques distribuidos a lo largo de un gradiente latitudinal en España, Portugal e Italia. Las tendencias de crecimiento y la señal climática contenida en las cronologías de *Q. ilex* se analizaron para evaluar el papel del cambio climático en el fenómeno de mortandad. La respuesta de *P. pinea* a la variabilidad espaciotemporal del clima se estudió para conocer la capacidad adaptativa de la especie. Se utilizaron diferentes técnicas para extraer la señal climática de las cronologías de anillos según los criterios dendroclimatológicos estándar. Una spline con una longitud de 30 años fue la mejor aproximación para eliminar la varianza no climática relacionada con las variaciones de crecimiento debidas a factores selvícolas. El clima se analizó a partir de registros de estaciones meteorológicas próximas, y de datos obtenidos de bases de datos internacionales que proporcionan datos climáticos de cuadricula. Se encontraron características macroclimáticas mediterráneas comunes, pero la distribución anual de las precipitaciones y la duración y la intensidad de la sequía estival varían entre los sitios de estudio. Las temperaturas y la aridez aumentaron en todos los sitios de estudio desde los años 70. Las correlaciones clima-crecimiento más significativas se encontraron con las precipitaciones y con los índices de sequía en todos los sitios, lo que indica que la disponibilidad hídrica es el principal factor climático limitante para el crecimiento. Reducciones de crecimiento en *Q. ilex* ocurrieron durante las sequías más intensas y prolongadas de las últimas décadas, y los cambios temporales de las relaciones clima-crecimiento indican la alta sensibilidad de estos árboles al aumento de la aridez. El cambio climático tuvo un papel importante como factor de estrés que determinó el comienzo de los procesos de mortalidad, y probablemente agravó los impactos de otros factores de estrés. Esta es la primera evidencia del efecto directo del cambio climático en la actual mortandad de especies del género *Quercus* en el suroeste de la Península Ibérica. Las correlaciones clima-crecimiento en *P. pinea* variaron en el espacio y en el tiempo con el clima, lo que indica la capacidad de la especie de adaptarse a condiciones climáticas especificas de cada zona y sugiere una respuesta fisiológica del crecimiento a las variaciones climáticas. La plasticidad de esta especie sugiere que rodales en distintas zonas tienen diversas capacidades de aclimatación al cambio climático, y esto tendrá probables implicaciones en la futura dinámica de la vegetación. Este es el primer estudio de la plasticidad de una especie arbórea en bosques Mediterráneos Ibéricos desde una perspectiva dendrocronológica. La vulnerabilidad al aumento de la sequía de los bosques Ibéricos meridionales debería tenerse en cuenta en las políticas y prácticas de gestión forestal adaptativa. Esta tesis presenta la primera colección de datos dendrocronológicos y una novedosa aproximación dendroecológica en el estudio de la dinámica forestal con relación al clima en en el suroeste de España.

Palabras claves: *Pinus pinea, Quercus ilex,* anillos de crecimiento de los árboles, cambio climático, Mediterráneo, Península Ibérica

3 EXTENDED ABSTRACT

The study of tree growth is important for understanding the ecological dynamics of forests and providing scientific foundations for sustainable forestry. Dendrochronology is the science of measuring and dating the growth rings of woody plants. The radial increment of woody plants is influenced by a number of environmental factors, thus growth rings store information about the natural environment. The terms “dendroecology” and “dendroclimatology” refer to applications of dendrochronological techniques to study ecological events and climate using dated tree-ring chronologies. Research methods of dendroecology are used to gain knowledge about processes in forest ecosystems, including wood production, health of trees, and stand dynamics. Tree-ring chronologies store information about climatic conditions over long-term periods, thus dendroclimatological methods can be applied to investigate climate change impacts on forests. However, there are some uncertainties in the methodological approach to assess the tree growth response to climate. In particular, uncertainties mainly arise from the climate data used to analyze the tree growth-climate relationships, and especially from the lack of homogeneity in meteorological station records. Moreover, the assessment of growth-climate relationships is influenced by the smoothing functions used to detrend tree-ring series, i.e. to retain the climate-related variability of tree-ring series (referred to as “climatic signal”) and to remove the variance unrelated to climate (referred to as “noise”). Furthermore, tree species present diverse growth response depending on site-specific and temporally changing conditions, thus patterns of species-specific climate-growth relationships can vary in space and time, making our understanding of forest dynamics more complex.

Stone pine (*Pinus pinea* L.) and holm oak (*Quercus ilex* ssp. *ballota* [Desf.] Samp.) are highly important species in the Mediterranean forests of the Iberian Peninsula. Iberian *P. pinea* stands normally present an even-aged structure, they are managed for production of timber and non-wood forest products, especially pine nuts, and they provide a wide range of environmental services. *Q. ilex* is the most widespread species of the Spanish open woodlands, which are managed as silvopastoral systems with important socio-economic and environmental benefits, but currently present widespread declining processes and increase of tree mortality in the southernmost areas. Dendrochronological studies of *P. pinea* and *Q. ilex* are scarce, because the high intra-annual variability of Mediterranean climate causes discontinuity in wood production during the growing season, which makes dating annual rings difficult, and forestry-related growth variance constitutes a noise for detrending procedures. However, studying the climate-related dynamics of these two species can provide valuable information for assessing the species’ vulnerability and adaptive capacity under climate change and implementing management options that may mitigate climate change impacts, improve the species’ response and enhance ecosystem sustainability.

In this thesis, dendroecological and dendroclimatological methods were applied to ring-width chronologies of *P. pinea* and *Quercus ilex* ssp. *ballota* with the following purposes: (1) to provide dated tree-ring chronologies of these two species, including managed forests at low Mediterranean latitudes; (2) to validate the procedures to extract

climatic signals from these chronologies; (3) to examine the variability of growth in relations to site-specific climatic conditions and temporal variations of climate.

P. pinea samples were from 242 trees in 10 sites along a latitudinal gradient in Spain, one site in Portugal and one site in Italy. *Q. ilex* samples were from 31 dead trees in two silvopastoral systems in southwestern Spain. Smoothing curves with different degrees of flexibility were tested to detrend the tree-ring series. The non-climatic variance removed with each detrending curve and the climatic signal retained were evaluated, and the most appropriate curve was applied to study the growth response to climate. Climate data from different sources, including meteorological station records and gridded climate datasets, were used to check for uncertainties. The climatic conditions of the study sites were compared, and climatic changes over time were examined. The growth-climate relationships were assessed using bootstrapped correlation and response function analysis. The diversity of growth response between sites was analyzed in relation to site-specific climatic conditions, and the variability of growth response over time was examined in relation to climatic changes.

Tree-ring series were successfully cross-dated and a master chronology was established for each study site. Climate and silviculture mainly influenced the growth trends. The inter-annual climate variability (e.g. annual precipitation amounts) and short-term climatic events (e.g. protracted droughts) had an effect on the high/middle-frequency growth variability, while long-term climate change (e.g. increasing temperature at the multi-decadal scale) was reflected in low-frequency growth variability. Forest thinning induced sustained growth releases. Stiff detrending curves retained the low-frequency climatic signal, but did not remove the forestry-related noise, while very flexible curves enhanced the climatic signal at the high-frequency but removed it at the middle/low-frequencies. Smoothing splines with a period of about 30 years was the best approach retaining as much climatic signal as possible and yet removing the noise.

All chronologies showed highly positive correlation with precipitation and minimum temperature of the winter previous to the ring formation, indicating the importance of soil recharge (which improves water availability favoring growth in subsequent months) and the positive effect of photosynthesis (which can occur in winter in evergreen species producing carbohydrates for subsequent growth). The response to precipitation during spring varied among sites and was related to drought regimes. In particular, *P. pinea* growth response to spring rainfall was high in the northernmost sites, where spring precipitation is more abundant and drought normally occurs in summer, while it was lower in the southernmost sites, where drought already starts in spring. The pattern of growth-climate relationships of the holm oaks was similar to that of the southern pines. No significant growth response was found in July-August, because these months are hot and dry in all sites. Significant correlations are found in the subsequent autumn, although not always and lower than in winter and spring, suggesting that tree growth is sensitive to climatic conditions after summer.

Temperature and aridity increased in all study sites since the 1970s, reflecting the large-scale climate trends in the Mediterranean Basin. Temporally unstable growth-climate relationships showed a connection with climate change. In fact, the overall changes in the correlation patterns indicate that tree sensitivity to water availability increased over time in all sites, indicating a common reaction to the drier climate, and a common increase in the response to winter minimum temperature suggested a positive effect of milder winters. The unstable growth-response patterns could suggest physiological adjustments of tree growth to the changing climatic conditions. However, changes in growth-climate relationships were also mediated by site-specific conditions. In particular, in the southernmost *P. pinea* stands, growth response to winter precipitation increased markedly and the negative effect of water deficit in spring was more significant. Climate is warmer and drier in the southern sites, and a further increase of temperature may have induced some shifts in the distribution of cambial activity over the year.

In the case of *Q. ilex*, climate change probably had an important role in the mortality process. In fact, the holm oaks were highly sensitive to water shortage and sustained growth suppressions occurred during droughts in recent decades before tree death. The increase in temperature and aridity may have been a significant stress factor for these trees. The climate change impact may have been added to other stress factors, including poor soils, intense management, and pathogens.

Some uncertainties arose from climate data, and were especially reflected by discrepancies among climate mean values and tree growth-climate correlation coefficients calculated using different climate data sources. They may be due to temporal changes in the quality and availability of meteorological station records. However, these uncertainties, although suggested the importance of careful screening of climate data in dendroecological studies, did not alter the assessment of the spatiotemporal variability of climate, and did not affected the interpretation of the growth-climate relationships in the study sites.

The tree-ring dataset presented in this thesis include the southernmost data of *P. pinea* and *Q. ilex* in the Iberian Peninsula, amplifying the geo-climatic range of the available tree-ring chronologies in this region. The climatic signal was extracted from all the studied chronologies, and the climate variables that mostly influence tree growth were assessed. Water availability is the main limiting factor in all sites. The spatial variability of *P. pinea* growth response to climate indicates the adaptation if this species to a gradient of climatic conditions, and the temporal shifts of growth-climate relationships suggest plastic physiological adjustments of tree growth as a reaction to the variations of climate. The capacity of *P. pinea* to grow in diverse and changeable conditions can be crucial for future forest dynamics and species distribution under climate change, especially at the lower latitudes, where forests will probably undergo further increases of aridity. In the open woodlands of southern Spain the recent warming had an important role in the widespread increase of holm oak mortality and probably amplified the impacts of additional stress factors, including intense management. These finding reflect that adaptive measures are a priority in drought-sensitive forests. This thesis validates dendroecological and dendroclimatological methods to study tree growth in managed Mediterranean forests. It provides a novel comprehensive assessment of climate-related growth dynamics of *P. pinea* in the Iberian Peninsula across a wide range of growing conditions. Moreover, *Q. ilex* sensitivity to climate in silvopastoral systems at a xeric ecotone was assessed, providing evidence of the vulnerability of these ecosystems under current climate change.

4 RESUMEN AMPLIADO

El estudio del crecimiento de los árboles es importante para comprender las dinámicas ecológicas de los bosques y proporcionar fundamento científico a la gestión forestal sostenible. La dendrocronología es la ciencia que se ocupa de la medición y la datación de los anillos de crecimiento de las especies leñosas. El crecimiento diametral de las plantas leñosas es influenciado por diversos factores ambientales, por tanto los anillos de crecimiento almacenan información acerca del entorno medioambiental. Los términos "dendroecología" y "dendroclimatología" se refieren a las aplicaciones de las técnicas de investigación dendrocronológicas para el estudio de los eventos ecológicos y del clima utilizando cronologías de anillos de árboles. Los métodos de dendroecología se aplican para obtener información acerca de distintos procesos en los ecosistemas forestales, incluyendo producción de madera, estado de salud de los individuos, o dinámicas estructurales. Los anillos de los árboles contienen información sobre las condiciones climáticas a lo largo de largos periodos, por lo que los métodos dendroclimatológicos se pueden aplicar para investigar los impactos del cambio climático en los bosques. Sin embargo, incertidumbres en la aproximación metodológica complican el estudio de las relaciones entre el crecimiento y el clima. Las incertidumbres derivan de los datos climáticos utilizados para investigar estas relaciones, y especialmente de la heterogeneidad de los registros meteorológicos. Además, la evaluación de la respuesta del crecimiento al clima es influenciada por las funciones utilizadas para efectuar el "detrending" de las series de anillos, es decir mantener la varianza debida al clima en los valores de anchura de anillo (que se define como "señal climática"), y eliminar la varianza que no está relacionada con el clima (el "ruido"). Finalmente, las especies forestales presentan diversas respuestas al clima dependiendo de las condiciones climáticas especificas del lugar de estudio, así como de las variaciones temporales del clima, y por tanto los patrones de las correlaciones clima-crecimiento en una especie pueden cambiar en el espacio y en el tiempo, complicando el entendimiento de las dinámicas de crecimiento forestal.

El pino piñonero (*Pinus pinea* L.) y la encina (*Quercus ilex* ssp. *ballota* [Desf.] Samp.) son especies muy importantes de los bosques mediterráneos de la Península Ibérica. Los bosques de pino piñonero en esta región presentan normalmente una estructura regular , se gestionan especialmente para la producción de madera y de productos no leñosos, principalmente el piñón, y proporcionan numerosos servicios medioambientales. La encina es la especie más abundante de los ecosistemas silvopastorales españoles, las dehesas. Las dehesas proporcionan importantes beneficios económicos y medioambientales, pero en la actualidad presentan graves y difusos procesos de decaimiento y muerte de los árboles, especialmente en el suroeste peninsular. Los estudios dendrocronológicos en pino piñonero y encina son escasos, debido a la alta variabilidad intra-anual del clima mediterráneo, que provoca discontinuidades en la formación del xilema que dificultan la distinción de anillo anuales, y a la selvicultura, que provoca oscilaciones en los patrones de crecimiento diametral que constituyen un ruido en las series dendrocronológicas. Sin embargo, estudiar la ecología del crecimiento en estas dos especies puede proporcionar información importante para evaluar su vulnerabilidad y su capacidad de adaptación al cambio climático, así cómo conocimientos útiles para desarrollar prácticas de gestión que puedan mitigar los impactos del cambio climático, mejorar la respuesta adaptativa del ecosistema y apoyar su conservación.

En esta Tesis se aplican métodos dendroecológicos y dendroclimatológicos en series de anchura de anillos de *P. pinea* y *Q. ilex* ssp. *ballota* con los siguientes objetivos: (1) producir cronologías datadas para estas dos especies, incluyendo bosques gestionados en latitudes bajas en España; (2) validar las técnicas de extracción de la señal climática de estas cronologías; (3) examinar la variabilidad del crecimiento en relación con las condiciones climáticas específicas de los sitios de estudio y con la variabilidad temporal del clima.

Las muestras de pino piñonero proceden de 242 árboles en 10 áreas a lo largo de un gradiente latitudinal en España, un sitio en Portugal, y un sitio en Italia. Las muestras de encina proceden de 31 árboles muertos en dos dehesas en la provincia de Huelva. Curvas de *detrending* con diferentes grados de flexibilidad fueron testadas para estandarizar las series dendrocronológicas. La varianza eliminada y la varianza retenida con cada curva fueron evaluadas, y se aplicaron las curvas más apropiadas para estudiar las relaciones entre crecimiento y clima. Para evaluar las incertitumbres en los datos climáticos, se utilizaron registros de estaciones meteorológicas próximas a los sitios de estudio así como datos climáticos de cuadrícula obtenidos en bases de datos internacionales. Se compararon las condiciones climáticas de los sitios de estudio, y se analizaron las variaciones temporales del clima. Las correlaciones clima-crecimiento se examinaron mediante análisis de correlación con el método bootstrapping y con funciones de respuesta. La diversidad de la respuesta del crecimiento al clima entre los sitios de estudio se analizó con relación a las condiciones climáticas específicas de cada sitio, y la variabilidad de la respuesta en el tiempo se analizó con relación al cambio climático.

Las series cronológicas se dataron con éxito y se estableció una cronología media para cada sitio de estudio. Los principales factores que influenciaron los patrones de crecimiento fueron el clima y la selvicultura. La variabilidad climática inter-anual (p. e. la precipitación anual) y los eventos climáticos puntuales (p. e. sequías prolongadas) tuvieron un efecto en la varianza del crecimiento en la alta/media frecuencia, mientras los cambios climáticos a largo plazo (p. e. el aumento de las temperaturas y el consiguiente aumento de la aridez en escala multi-decenal) se reflejaron en la varianza de baja frecuencia. Las claras se manifestaron en aumentos de crecimiento. Curvas de detrending rígidas retuvieron la señal climática en las bajas frecuencias, pero no removieron el ruido debido a las claras, mientras las curvas más flexibles resaltaron la señal climática en las altas frecuencias, pero eliminaron completamente la señal en las bajas frecuencias. Curvas ajustadas como la spline con longitud próxima a los 30 años fue la mejor opción para retener la mayor porción de señal climática y al mismo tiempo remover el ruido.

Todas las cronologías revelaron altas correlaciones positivas con las precipitaciones y las temperaturas mínimas del invierno anterior al año de producción del anillo, lo que indica la importancia de la recarga hídrica del suelo (que mejora la disponibilidad de agua para el crecimiento en los meses siguientes) y el efecto positivo de la fotosíntesis (que puede ser activa en invierno en las especies perennifolias produciendo hidratos de carbono para el crecimiento en los meses siguientes). La respuesta a las precipitaciones durante la primavera varía entre los sitios de estudio y está relacionada con los regímenes de sequía. La respuesta del pino piñonero a las precipitaciones de primavera fue alta en los sitios septentrionales, donde las precipitaciones en esta estación son más abundantes y la sequía ocurre en verano, y relativamente inferior en el sur, donde la sequía y las condiciones de estrés hídricos empiezan ya en mayo. Los valores de correlación clima-crecimiento en las encinas fueron parecidos a los observados en *P. pinea.* Ninguna correlación significativa se encontró en julio y agosto, meses secos y cálidos en todos los sitios de estudio. Correlaciones significativas se observaron también en el otoño del año de formación del anillo, aunque inferiores y con menos frecuencia que en invierno y primavera, lo que sugiere que el crecimiento de estos árboles responde a las condiciones climáticas después de la sequía estival.

Las temperaturas y la aridez aumentaron en todos los sitios de estudio desde los años 70, lo que refleja una tendencia climática común a escala regional. Las correlaciones clima-crecimiento inestables en el tiempo muestras una conexión con las variaciones climáticas. Los cambios en las correlaciones indican que en todos los sitios de estudio la sensibilidad del crecimiento a la disponibilidad hídrica aumentó en el tiempo, lo que sugiere una respuesta común a la intensificación de la aridez. Asimismo, el aumento común de la correlación con las temperaturas mínimas en invierno indica un efecto positivo de las temperaturas más templadas en los inviernos más recientes. La variabilidad de la señal climática en el tiempo sugiere un cambio en la fisiología del crecimiento como respuesta al cambio climático. Sin embargo, esta variabilidad fue también condicionada por las condiciones específicas de los sitios de estudio. En efecto, en los rodales más meridionales de pino piñonero, la respuesta del crecimiento a la precipitación del invierno aumentó de forma significativa, y el efecto del déficit hídrico en primavera fue más importante. El clima es más seco y cálido en el sur, y un ulterior incremento de las temperaturas podría haber causado algún cambio en la distribución anual de la actividad del cambium.

En el caso de las encinas, el cambio climático tuvo probablemente un papel muy importante en el proceso de mortandad. En efecto, el crecimiento en estos árboles fue muy sensible al déficit hídrico, y las reducciones de crecimiento prolongadas ocurrieron durante los periodos más secos de las últimas décadas. El aumento de las temperaturas y de la aridez podrían haber sido un importante factor de estrés para estos árboles. El impacto del cambio climático se pudo añadir a otros factores de estrés, especialmente las condiciones edáficas adversas, el manejo intensivo y agentes patógenos.

Se encontraron algunas incertidumbres en los datos climáticos. En particular, se encontraron discrepancias entre los registros de estaciones meteorológicas y los datos climáticos de cuadrícula. Estas discrepancias se reflejaron en diferencias entre los valores climáticos medios y entre los coeficientes de correlación clima-crecimiento. Una posible causa es la variabilidad temporal en la calidad y la disponibilidad de los registros meteorológicos. La existencia de este tipo de incertitumbre indíca la importancia de efectuar una evaluación preliminar de los datos climáticos para la aproximación dendroecológica a los efectos del clima en el crecimiento forestal. Sin embargo, en los sitios de estudio de esta tesis, las incertidumbres en los datos climáticos no alteraron el estudio de la variabilidad espaciotemporal del clima y no afectó la interpretación dendroecológica de las variaciones del crecimiento forestal en relación con la variabilidad climática.

Los datos dendrocronológicos presentados en esta tesis incluyen las cronologías más meridionales de las especies *P. pinea* y *Q. ilex* en la Península Ibérica, lo que amplía la extensión geográfica de las cronologías disponibles en esta región. La señal climática se pudo extraer de todas las cronologías y se definieron las variables climáticas que más influencian el crecimiento. La disponibilidad hídrica es el principal factor limitante en todos los sitios de estudio. La variabilidad espacial de la respuesta del pino piñonero al clima indica la adaptación de esta especie a un gradiente de condiciones climáticas, y las variaciones temporales de las correlaciones clima-crecimiento sugieren una respuesta fisiológica a los cambios climáticos. La capacidad del pino piñonero de crecer en diversas condiciones puede tener importantes implicaciones para las futuras dinámicas de vegetación y para la distribución geográfica de esta especie en escenarios de cambio climático, especialmente en las latitudes inferiores, donde los ecosistemas probablemente serán afectados por ulteriores aumentos de aridez. En las dehesas del suroeste peninsular, el calentamiento atmosférico reciente tuvo un papel importante en el aumento de mortalidad de los árboles y probablemente aumentó el impacto de factores de estrés adicionales. Estas observaciones indican que medidas de gestión adaptativa son una prioridad en los ecosistemas forestales sujetos a sequías intensas. Esta tesis valida los métodos dendroecológicos y dendroclimátológicos para estudiar el crecimiento forestal en los bosques mediterráneos y proporciona una novedosa y extensa caracterización de las dinámicas del crecimiento relacionadas con el clima de la especie *P. pinea* en diversas condiciones en la Península Ibérica. Además, se evaluó la sensibilidad al clima de la especie *Q. ilex* en dehesas ubicadas en ecosistemas meridionales, proporcionando envidencias de la vulnerabilidad de éstos a los actuales cambios climáticos.

5 GRAPHICAL ABSTRACT

Premises

Context

Climate change has impacts on forest ecosystem functions.

There is a need to implement adaptive management.

Requires to understand climate-related forest growth dynamics.

Iberian Peninsula

Climate change: increasing temperatures and aridity

Pinus pinea and *Quercus ilex* forests:

- Great socio-economic and environmental importance
- Massive decline and mortality processes in southern *Q. ilex* silvopastoral systems

Priority: assessing species' vulnerability and adaptive capacity in future climatic scenarios.

how?

Research methods of dendrochronology provide valuable information about tree growth trends in the past and growth response to climate

Can be accomplished with dendrochronological methods.

but

Problems in studying tree-ring response to climate:

- dendroclimatological approach: choosing proper tree-ring standardization methods and climate data;
- inherent complexity of tree growth response to climate: variability in time and space.

but

Problems in studying tree rings in managed Mediterranean forests:

- highly variable intra-annual climate;
- forestry → non-climatic noise in tree- ring series;
- difficulty to obtain and measure *Q. ilex* samples.

consequence

Scarcity of tree-ring studies of *P. pinea* and *Q. ilex* in the Iberian Peninsula.

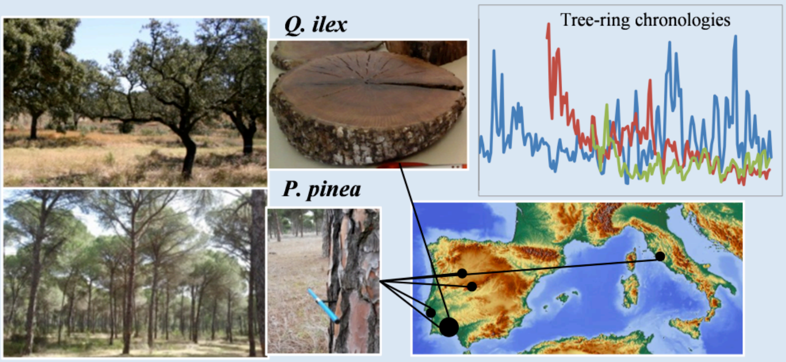
Questions:

- ➢What is the appropriate dendroclimatological approach in managed Iberian *Q. ilex* and *P. pinea* forests?
- ➢How does growth response to climate vary in Iberian *Q. ilex* and *P. pinea* forests, and what does this tell us about forest ecology?

Objectives:

1. To test tree-ring standardization procedures and climate data to analyze growth-climate relationships.
2. To assess species-specific response of growth to long-term climatic variations and to diverse site-specific climatic conditions.
3. To assess the role of climate change in the Iberian oak mortality.
4. Filling the gap in dendrochronological studies in the Iberian Peninsula

Materials



Climate data:

- •Precipitation
- •Max./min./mean temperatures
- •Palmer drought severity index (PDSI)
- •Diurnal temperature range (DTR)

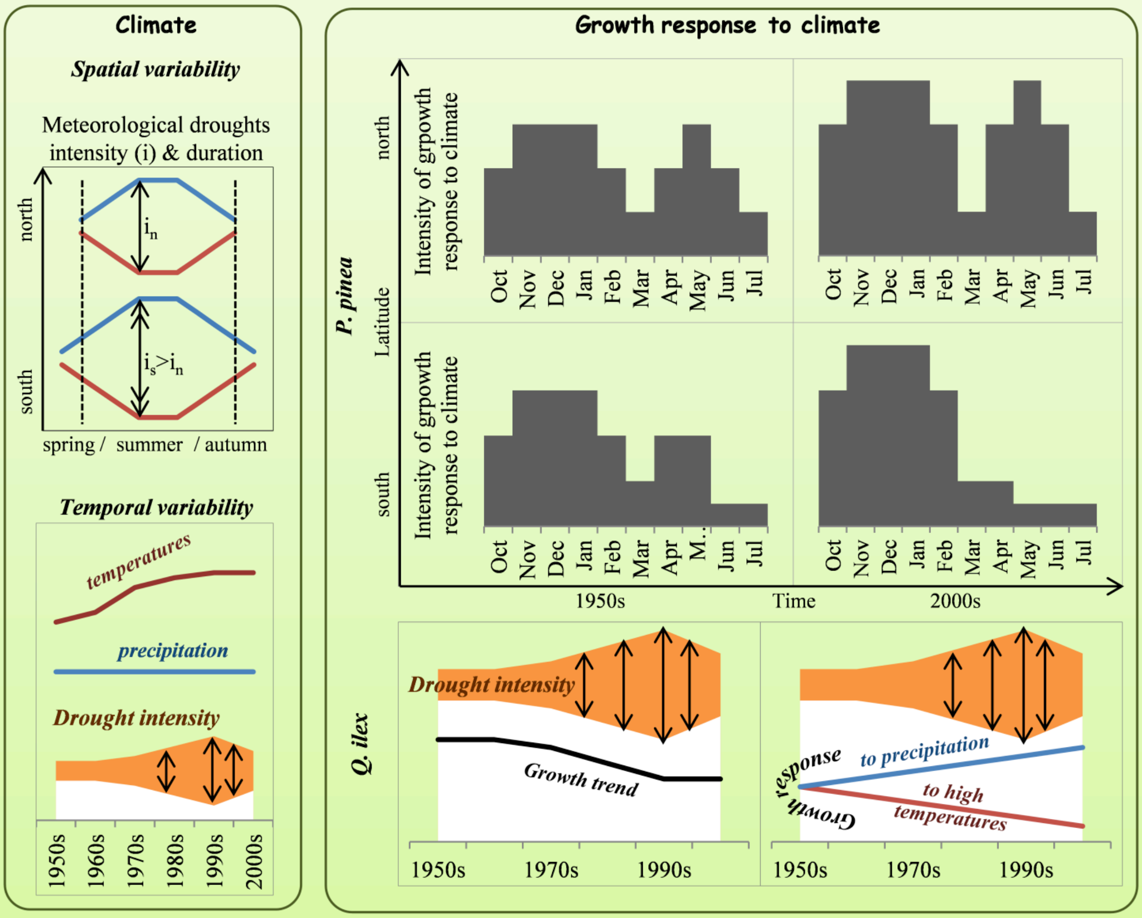
Climate data sources:

- •Meteorological station records
- •Gridded datasets

Species	*Number of sites*	*Location*	*Number of trees*	*Number of samples*	*Max. chronology length*
P. Pinea	7	Southwest Spain	133	266	1793-2014 (222 years)
	3	Centre/north Spain	67	134	
	1	South Portugal	24	24	
	1	Centre Italy	18	36	
Q. ilex	2	Southwest Spain	31	93	1862-2010 (149 years)

Main findings

- Standardization of tree-ring series: smoothing splines with a period of 30 years → good removal of non-climatic variance; good analysis of growth-climate correlations.
- Climate data: discrepancies between meteorological station records and gridded datasets; precipitation and temperature explained well high-frequency growth variability.
- Growth-climate relationships: strong positive response to precipitation; negative response to high temperatures → water availability was the main limiting factor for both species.



Conclusions

1. The best dendroclimatological approach in *P. pinea* and *Q. ilex* managed forests in the study regions includes:
   - ✓ smoothing flexible splines for standardizing tree-ring series;
   - ✓ precipitation and temperature data from gridded climate datasetes to assess growth-climate relationships.
2. *P. pinea* growth response to climate changed in space in association with site-specific climatic conditions.
3. Growth-climate relationships changed over time in association with the increase of aridity.
4. In died oaks, growth suppression and increasing sensitivity to water deficit coincided with recent droughts.

Final remarks	**Implications**
Spatiotemporal variability of *P. pinea* growth response to climate indicates species' plasticity, i.e. growth adaptation to site-specific climatic conditions and physiological adjustments in response to temporal variations of climate.	The plasticity of this species suggests that different populations have different capacities for acclimation to climate change, and this will probably influence future vegetation dynamics.
Climate change played an important role in inducing mortality processes in southern *Q. ilex* silvopastoral systems.	Increasing oak mortality in the Iberian Peninsula may occur in northern and colder sites if aridity further increases as it is projected by climate change scenarios.

6 INTRODUCTION

6.1 Basic concepts of dendrochronology and applications in the environmental science

Forests and woods have been very important for society and economy throughout human history. Since ancient times, people have exploited forests to establish cropland and pasture, and to fulfill their need for fuel wood and construction material, altering forests and natural environments for millennia (Williams, 2006; Kaplan et al., 2009). Since the industrial revolution, the increasing worldwide consumption of forest products and loss of forest cover have led to a growing concern for sustainable forest management (UNEP, 1992; UN, 2015). The need to establish measures for sustainable yield of timber and conservation of forest ecosystems is closely connected to the development of forestry. Forestry is the applied science "designed to create and maintain the kind of forest that will best fulfill the objectives of the owner and the governing society" (Smith et al., 1997), which include production of timber, non-wood products, and social and environmental benefits as water, wildlife, grazing, landscape, recreation or aesthetics. Forestry can be defined as an application of the science of ecology, because it relies on scientific knowledge about forest functioning (Smith et al., 1997). To fulfill the requirements of sustainability, natural sciences provides guidelines for integrating forest productivity, complexity and biodiversity (McCool and Stankey, 2004; Diaci, 2006; Ciancio and Nocentini, 2011) The foundation of forestry in the natural sciences includes different disciplines as dendrology, forest ecology and ecophysiology of trees.

The study of tree growth is very important in forest ecology. It has been mainly related to the interest in timber yield and effects of forestry measures (e.g. Schweingruber, 1996 pp. 342-363; Manetti and Cutini, 2006; Skovsgaard et al., 2008; Martín et al., 2015b), but it also provides knowledge about the health and vigor of forest ecosystems (e.g. Schweingruber, 1996 pp. 369-391; Hogg et al., 2008; Kols et al., 2009), the effects of climate on the species (Schweingruber, 1996 pp. 439-535; Martín et al., 2014; Beniston and Innes, 1998), the physiology of trees (e.g. Vaganov et al., 2006; Zweifel et al., 2010; Martín et al., 2015a), or the within-stand competition and structure dynamics (e.g. Gea-Izquierdo and Cañellas, 2009; Ziaco et al., 2012). Martín (2015) provides a review of the main techniques applied to study tree growth, which are: (*i*) dendrometry, which includes the measurements of various dimensions of the tree as diameter, height and crown size, and the collection of data for forest inventories (e.g. Biondi, 1996; Elfving and Tegnhammar, 1996; Charru et al., 2010) (*ii*) histological studies, aimed at determining the timing of cambial activity and xylogenesis (e.g. Rossi et al., 2006; Vieira et al., 2014); (*iii*) dendrometer measurements, aimed at quantifying the stem girth increment (Martín et al., 2014; Martín et al., 2015a, 2015b) and (*iv*) dendrochronology.

This thesis is concerned with research methods of dendrochronology with application to the study of tree growth and forest ecology. Among the sources of information about dendrochronology and its history and applications in environmental science, are books by Fritts (1976), Cook and Kairiukstis (1990), Schweingruber (1996), Speer (2010), Hughes et al. (2011). Dendrochronology is the science of measuring and dating the growth rings of woody plants (*sensu* Kaennel and Schweingruber, 1995). Growth rings are also referred to as "tree rings", due to the common use of trees in dendrochronological studies, although growth rings of shrubs can also be analyzed and used for ecological studies (Schweingruber and Poschlod, 2005). Reviews about wood structure, cell features and types, and physiological mechanisms involved in tree ring growth are provided by Fritts (1976), Vaganov et al. (2006), Schweingruber (2007) or Speer (2010). In temperate climates, cambial activity of woody species stops during the harsher seasons (normally, the cold season), thus annual rings are formed. In the humid tropics, where climate is only slightly seasonal, woody plants often fail to form distinct annual rings, although methods for identifying annual rings and exploring their relations with climate in some tropical species have recently improved (e.g. Chowdhury et al., 2016).

Research methods of dendrochronology are applied in different disciplines, including several fields of geoscience. Important developments of dendrochronological methods have been achieved in the field of archaeology. Archeologists recognize dendrochronology as an accurate tool for absolute dating, i.e. to estimate the age of artifacts. The Academic Press Dictionary of Science and Technology defines dendrochronology as a "method of dating wooden objects by analyzing the pattern of their annual rings and comparing this pattern to an established tree-ring sequence for the region". Thus, tree-ring sequences on wood samples of manufactures from archeological sites can be dated to infer the construction dates of those manufactures (see Speer, 2010, pp. 152-173). Correlation with established chronologies from other sites can also help to identify the provenance of historical wood objects (e.g. Domínguez-Delmás et al., 2013b). The procedure of dating tree rings was developed by Andrew Ellicott Douglass, at the Universtity of Arizona, USA, in the early 1900s (see Speer, 2010, pp. 28-41 and references therein), and has remained a basic principle of dendrochronology and related applications in environmental science.

Tree rings store information about the natural environment and can be used to study the processes and dynamics occurring in the surroundings where trees live. Tree rings are referred to as "proxy records" with reference to their suitability as biological substitute records for environmental conditions and ecological events (Kaennel and Schweingruber, 1995). Tree rings are proxy data because radial stem increment is influenced by a number of external factors, among which there are some that dominate the growth and are most likely to be recorded in a tree-ring chronology ("principle of limiting factor", see e.g. Speer, 2010, p. 15-17). Internal factors (e.g. growth regulators, enzymes, ageing) also have an impact in regulating growth (see Schweingruber, 1996, 21-39). A descriptive model of ring growth expresses the ring width in each year t as an aggregate of 5 components ("Conceptual linear aggregate model", see Cook and Briffa, 1990): (*i*) the age-related growth trend value in year t, (*ii*) the climatically explained ring-width variation in year *t*, (*iii*) the endogenous disturbance pulse originating from competition, canopy dynamics or other forces acting in year *t* on specific trees, (*iv*) the exogenous disturbance pulse caused by stand-wide events in year *t* or forces outside the forest community (e.g., fires, insect infestations, diseases, storms, air pollutants), and (*v*) the ring-width variation in year *t* which remains unexplained after taking into account the contribution of the previous components (e.g. micro-site differences within the stand or errors in measurements). Since a tree-ring chronology is the result of a combination of factors, extracting from tree-ring series the information related to one of those factors requires the retention of the variance linked to that single factor and the removal of the variance linked to the other factors. A detectable pattern in tree-ring series which is common in an ensemble of trees and can be attributed to a specific growth factor constitutes the chronology signal, while the variance of tree-ring series that cannot be attributed to a detectable common pattern is termed "noise" (Briffa and Jones, 1990; Kaennel and Schweingruber, 1995). In an ensemble of tree, the variance considered as "signal" depends on the growth factor of interest to the research.

The existence of a signal is what makes possible to cross-date, i.e. to find similarities in the growth patterns of different trees and thus to assign each ring to an exact calendar year (Hughes, 2011). In fact, cross-dating can be defined as an "emergence" in dendrochronology (Cook and Pederson, 2011). In natural sciences, emergence is a property of a system emerging from sub-systems or individuals which alone do not exhibit that property. Cross-dating is a property of tree growth that "emerges from the radial growth increments of trees being subjected to a highly variable set of microenvironmental conditions that contain within it a secondary set of common external growth-limiting factors" (Cook and Pederson, 2011).

Different subfields of dendrochronology deal with different growth factors by investigating different information stored in tree-ring series. Dendroecology, in the broadest sense, is the branch of dendrochronological science which encompasses all the subfields using dated tree rings to study ecological problems and the environment (Kaennel and Schweingruber, 1995). In the strictest sense, dendroecology uses dated tree rings to study ecological events in forests, such as fire, forest diseases or stand dynamics (Fritts and Swetnam, 1989). Subfields of dendroecology have reached high amount of research and refined methodologies, thus they can be considered as independent disciplines. The climatically explained variance in tree-ring series is the signal of interest to dendroclimatology. In dendroclimatology, the relationships between tree growth and climate are assessed and used to study climate (e.g. climate reconstructions, synoptic climatology, climate change) and climate-related forest dynamics (e.g. biogeography, bioclimatology) (Fritts, 1976; Hughes et al., 2011). Other established subfields of dendroecology are (see Wiles et al., 1996): dendrohydrology, which uses the chronology signal related to variations in water table height and flood events to reconstruct these phenomena; dendrogeomorphology, which uses tree rings to study and date geological processes that affect tree growth, such as landslides, rock movements, soil creeps etc.; dendroglaciology, which uses tree rings to study and date glacier movements. Additional definitions appear as further applications of dendrochronological methods develop (see Speer, 2010).

This thesis is focused on the study of forest tree growth in relation to climate. Dendroecological and dendroclimatological methods were used. Ring chronologies of two representative tree species of Mediterranean forests in the Iberian Peninsula were used and most of them were obtained in Southern Spain, a blank spot in Iberian dendrochronology. The thesis deals with challenging issues in dendroecology and dendroclimatology in Mediterranean Iberia, where climate variability and non-climatic disturbances influence the assessment of climate-growth relationships in a complex interplay, and it addresses some emerging questions about the vulnerability and adaptive capacity of Iberian Mediterranean forests to climate change processes.

6.2 Use of tree rings to study the effects of climate on forest tree growth.

The use of tree rings as archives of climate variability and ecological events presents strengths and weaknesses related to the dendrochronological approach, which includes consolidated techniques of tree-ring analysis, e.g. cross-dating, but also uncertainties in modeling growth-climate relationships. Moreover, some degree of unpredictability in growth-climate relationships derive from the inherent complexity of the tree growth-climate system. Hughes (2002) and Hughes et al. (2011) provided overviews of the strengths, the weaknesses, the open questions and prospects of dendroclimatology. In this section, the main aspects relevant to this thesis are outlined.

A strength of dendrochronological studies is the possibility to elaborate observations based on long-term data. The use of this strength is exemplified by dendroecological studies on stand dynamics. For instance, long tree-ring chronologies permit to reconstruct gap phases in forest canopies, stand disturbances and competition history (e.g. Gea-Izquierdo et al., 2011; Ziaco et al., 2012; Di Filippo et al., 2013). Anthropogenic changes in stand structure can be also studied with a dendrochronological approach. For instance, after forestry measures (e.g. thinning or pruning), tree ring series from standing trees can be used to verify whether the purposes of those measures (e.g. increasing wood production or quality) have been achieved (see e.g. Schweingruber, 1996, pp. 345-353).

A major strength of the use of dendrochronological methods in natural sciences is the capability to date tree rings to the calendar year with a very high degree of confidence. This is accomplished by cross-dating, i.e. the procedure of matching variations in ring width among several tree-ring series, allowing the identification of the exact year in which each ring was formed (Kaennel and Schweingruber, 1995). It permits to date climatic and ecological events as droughts, fires or insect outbreaks, to examine their frequency and to assess their impacts on tree growth (e.g. Stahle et al., 2000; Ryerson et al., 2003; Higuera et al., 2010).

The existence of strong, linear correlations between tree-ring chronologies and climate variables constitutes an important strength of dendroecology and dendroclimatology (Hughes, 2002). The statistical procedures typically used for modeling growth response to climate are based on the assumption of linear growth-climate relationships and involve regression between annual tree rings and annually, seasonally or monthly resolved climate data (Fritts, 1976, pp. 312-412; Guiot, 1990, 1991; Briffa and Cook, 1990). Actually, certain kinds of nonlinearity exist in tree-ring/climate relationships and models that do not assume linear relationships can be also applied (e.g. D'Arrigo et al., 2004; Anchukaitis, 2006; Vaganov et al., 2006, pp. 190-243; Gea-Izquierdo et al., 2011). The physiological response to environmental factors can be described by a sigmoid function with an asymptote or a bell-shaped curve with a maximum of the factor's influence (Figure 1). Physiological response functions denote that trees are sensitive to environmental factors within certain ranges. For instance, trees growing in drought-prone areas respond rapidly to water availability after precipitation; but variations within the optimum range of water conditions induce little variations in growth rates. Similarly, growth increases with temperature, but it reaches a maximum when temperature reaches some optimal value and it finally decreases with further increases of temperature. However, within the range of growth factor to which a tree is sensitive, the curve describing the relationship between growth factors and growth rates is almost linear (Figure 1). Vaganov et al. (2006, pp. 197-198) state that "although the overall form of the underlying physiological relationship is asymptotic, over the range of moisture availabilities to which the sensitive tree is almost always subject, the relationship is often effectively linear, as witnessed by the many highly significant correlations coefficients recorded between chronologies of trees from sensitive situations and dominant climatic factors". As suggested by Cook and Pederson (2011), the fact that linear models produce good climate reconstructions, even when compared with non-linear models (e.g. Mann and Bradley, 1999; Ni et al., 2002), indicates that nonlinearity is not large and linear models have not to be necessarily abandoned. Therefore, the study of the effects of climate on tree growth response to climate can be based on linear models with an acceptable degree of confidence, provided that caution is taken when biological and ecological interpretations of the statistical function are made.

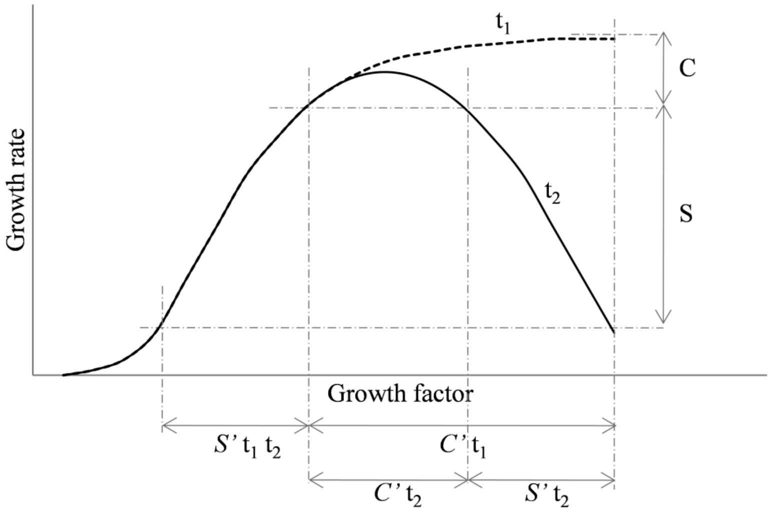


Figure 1. Diagram illustrating the curves of physiological response of two trees to environmental factors (form Vaganov et al., 2006, p. 197, modified). The trees are "t_1" and "t_2". The growth rates of t_1 follow a sigmoid function with an asymptote; the growth rates of t_2 follow a bell-shaped curve. "S" indicates the interval in which the tree is sensitive, i.e. each additional unit of the growth factor (e.g. soil moisture, temperature, solar radiation, etc.) has a strong effect on growth rates. "C" indicates the interval in which the tree is complacent, i.e. the change in growth for each additional unit of growth factor is very small or zero. "*S'*" and "C'" denote the ranges of growth factor to which the trees are sensitive and complacent.

The highlighted strengths of tree ring science are important for the study of forest ecology in the current context of climate change. Indeed, tree rings store information about climate change effects on ecosystem productivity, species' ecology, vegetation dynamics and other aspects of forest functioning. For instance, tree rings provide information about species-specific sensitivity to climate change (e.g. Linares et al., 2011; Candel-Pérez et al., 2012; Gimeno et al., 2012; Herrero et al., 2013; Granda et al., 2014). Tree ring studies have also indicated, for example, that fluctuations in altitudinal distribution of tree species can be dated and interpreted in relation to climate change (e.g. Camarero and Gutiérrez, 2004; Jump et al., 2007; Batllori and Gutiérrez, 2008). Other climate change-related processes in forest ecology have been also described using tree-ring chronologies, e.g. tree growth declines related to warmer and drier climate at the southern and lower limits of species' distribution (e.g. Macias et al., 2006; Peñuelas et al., 2008; Martín-Benito et al., 2010; Gea-Izquierdo et al., 2011, 2013, 2014; Linares and Tíscar, 2011; Linares and Camarero, 2012; Büntgen et al., 2013; Gazol et al., 2015), as weel as growth enhancement,. related to increased temperatures and atmospheric concentration of CO_2, in temperate forests close to the optimum conditions for growth (e.g. Martínez-Vilalta et al., 2008; Camarero et al., 2015).

Notwithstanding the strengths of tree ring science, research has noticed that the dendroecological and dendroclimatological methods can bear some uncertainties which can potentially bias the assessment of growth-climate relationships. Uncertainties arise from the procedures and data used for modeling tree growth trends and examining tree-ring growth response to climate. In dendroclimatology, the signal to be extracted from tree-ring series is the climatically-explained variance. To this end, the growth variability unrelated to climate from individual tree-ring series is removed. This is typically accomplished by a standardization procedure which involves fitting smoothing functions to the measured tree-ring series, a crucial step in dendroclimatological investigations (see Cook and Briffa, 1990, and the "Materials and methods" section in this thesis). Functions with different smoothness filter the tree-ring series and capture the climatic signal at different frequencies, emphasizing short-term or long-term climate variability. Therefore, the smoothing function must be carefully evaluated to avoid the influence of non-climatic noise in the assessment of the tree growth response. The selection of the appropriate function must be done on the basis of an evaluation of time-frequency domain of the resulting standardized chronology, and considering the purpose of the investigation, i.e. whether low-frequency or high-frequency climatic signal is searched (Cook and Peters, 1981; Briffa et al., 1996; Esper et al., 2002; Briffa and Melvin, 2011).

The suitability of climate data to assess growth-climate relationships also needs to be tested. Different climate parameters differ in their ability to explain growth depending on site-specific climatic conditions. For instance, at high elevations tree growth is particularly sensitive to temperature changes and a thermal boundary for vegetation is normally given (e.g.Körner and Paulsen, 2004; Frank and Esper, 2005; Büntgen et al., 2008). However, when temperatures are high, the importance of precipitation increases (e.g. Anfodillo et al., 1998; Carrer et al., 1998; Büntgen et al., 2006). Trees in Mediterranean forests, especially at low elevations, strongly respond to variations in precipitation and water conditions (e.g. Nicualt et al., 2008; Seim et al., 2014). Moreover, potential uncertainties are related to the choice of the time scale of the climatic variable, that can be annual, seasonal, monthly, or a combination of successive months or seasons. Uncertainties can also arise from the temporal instability of the quantity of available meteorological records, the uneven spatial representativeness of the meteorological records, and the non-climatic noise contained in the observational data and caused by changes in instruments and data processing (Esper et al., 2005, 2010; Frank et al., 2007; Büntgen et al., 2015).

Besides the uncertainties in the dendroclimatological approach, some degree of unpredictability in growth-climate relationships also arises from the inherent complexity of trees as organisms and the ways in which they interact with and are constrained by the external factors. Following Fritts (1976, pp. 46-51), the response of tree growth to climate is regulated at three levels, i.e. macroclimate and weather, operational environment (i.e. dynamics occurring at the micro-site level), and tree physiology. Processes occurring at each level are susceptible to changes in their spatial and temporal domains. For instance, climate (defined as the long-term statistics of weather revealing distinctive thermo-pluviometric patterns at a certain location) can change over extended periods of time. Likewise, sites can have common macro-climatic features but different micro/meso-climatic characteristics.

Research has reported temporal shifts in the correlations between tree-ring growth and climate variables for a variety of forest ecosystems (e.g. Tardif et al., 2003; Büntgen et al., 2006; Carrer and Urbinati, 2006; Macias et al., 2006; Gea-Izquierdo et al., 2009; Planells et al., 2009; Martín-Benito et al., 2010; De Soto et al., 2014; Galván et al., 2015). These shifts indicate a non-stationary nature of growth response to climate. This implies a possible deviation from the uniformitarianism principle applied for tree ring-based climate reconstructions (Carrer and Urbinati, 2006; Bradley, 2011; Hughes, 2011), which assumes that growth-climate relationships are stable over time so that we can infer past climate from a statistical calibration of these relationships (see Speer, 2010, pp. 10-11). Temporal shifts in growth-climate correlations might be partly explained by the climate data itself, whose quality and quantity, as explained above, can present temporal instability. On the other hand, the instability of growth-climate relationships can be related to changes in growing conditions. In fact, possible causes of the response shift include changes in temperature, precipitation, pollution, stratospheric ozone and solar radiation reaching the ground (see D'Arrigo et al., 2008). Trees may undergo some physiological adjustments in response to the changing growth conditions (Meyers and Bull, 2002). The stability of growth-climate relationships may also cease to exist at some threshold level beyond which environmental variations trigger physiological reaction (D'Arrigo et al., 2004; Wilmking et al., 2004; Rossi et al., 2007, 2008). Therefore, testing the stability of growth-climate relationship may give information about species' response to climate change.

Tree species also show a degree of spatial variability in their response to climate. Common climatic signal can be captured not only in trees derived from the same sites but also over distances of hundreds of kilometers (e.g. Hughes et al., 2001; Kelly et al., 2002; Cufar et al., 2014). This is significant for forest science: for instance, variations in the spatial synchrony of growth patterns among tree-ring chronologies across large areas may indicate temporal changes in the intensity of climatic constraints of tree growth (e.g. Andreu et al., 2007; Läänelaid et al., 2012; Latte et al., 2015). Common dendroclimatic signals are especially important for synoptic climatology and large-scale climate reconstructions (e.g. Meko et al., 1993; Girardin et al., 2006; Villalba et al., 2011). It ought to be noted that, in such large-scale climatological studies, tree-ring chronologies are built for multiple sites in a region to increase the chances of capturing regional-scale climatic signals, and to minimize "noises" deriving from the existing spatial variability of tree growth response to climate. In fact, variability in species-specific growth-climate relationships in tree rings have been associated with site-specific conditions (e.g. Neuwirth et al., 2004; Alla and Camarero, 2012; Mazza et al., 2014; De Luis et al., 2013; Düthorn et al., 2013). The spatial variability of growth response reflects the range of environmental conditions to which the species is adapted. The species' capacity to adapt and acclimate, and/or their plasticity under changing conditions, have important implications for their future persistence as well as for forest management (Alía et al., 2005; Matesanz et al., 2010; Nicotra et al., 2010; Alla and Camarero, 2012).

The spatiotemporal variability of growth-climate relationships, and the problems related to tree-ring standardization methods and climate data, describe a complex situation, in which a proper appraisal of forest dynamics under past, present and future climate is not straightforward. A better understanding of climate-related growth dynamics needs further investigation focused on the influence of the spatial and temporal variations of climate on species-specific growth responses, as well as a careful methodological approach seeking the most suitable climate data and tree-ring dtandardization methods to avoid the potential biases in the dendroclimatic signals.

6.3 The species

6.3.1 *Pinus pinea* L.

Common English names of *Pinus pinea* are "Stone pine", "Italian stone pine" and "umbrella pine" (Speer, 2010). Among the sources of information about morphology, phenology, ecology, distribution and silviculture in Spain of *P. pinea* are Agrimi and Ciancio (1994), Montero et al. (2004, 2008), Ruiz de la Torre (2006) and Bravo and Montero (2008a). It is a Mediterranean evergreen tree of the *Pinaceae* family. The crown is broad and flat in adult open-grown individuals. Although ≈15 m in height are more typical, it can exceed 25 meters and the diameter can reach 1.5-2 m. The bark is thick, red-brown and present deep longitudinal fissures. The foliage is composed of straight needles bundled in clusters of two, which can reach 20 cm in length and persist for 2-3 years. It is a monoecious species and flowering takes place between March and June, depending on the geographical location. The strobili take three years to mature;

they are broad, ovoid cones which can reach 20 cm in length, and release large, 2 cm long seeds (“pine nuts”). The species presents a masting behavior. The roots are expanded horizontally and can develop deep vertical branches. Rotation length in *P. pinea* managed forests is normally around 100 years, maximizing timber production, thus tree lifespan is limited; but isolated individuals older than 200 years can be found and some estimations suggest that this pine can live for more than 400 years (see Montero et al., 2004, pp. 12-13 and references therein).

P. pinea occurs throughout southern Europe and the eastern and southern Mediterranean coasts (Figure 2). It is an autochthonous species of the Iberian Peninsula (Martínez and Montero, 2004). It has been introduced in other regions, e.g. in southern Latin America it was introduced more than a century ago by European colonists and it is currently used for stabilizing dunes, cattle shading, ornamental purposes and production of pine nuts (Loewe et al., 2011, 2013, 2015). In Spain, the distribution range of this species has been heavily influenced by human activities and most of the *P. pinea* forests originated from reforestation and afforestation carried out during the 20th century (Torres, 2011; Montero et al., 2004 pp. 96-103). *P. pinea* pure forests are present in about 173 000 ha in Spain (data from 2nd Spanish national forests inventory, IFN2, 1986-1996, of the Ministry of Agriculture, Food and Environment, http://www.magrama.gob.es/es/biodiversidad/servicios/banco-datos-naturaleza/informacion-disponible/ifn2.aspx). If mixed forests (*P. pinea* with other pines and broad-leaf species) are taken into account, the total area reaches about 474000 ha, which is approximately the 3.5% of the total Spanish forest cover and more than the 70% of the total distribution area of the species in the Mediterranean region (Montero et al., 2004). The largest Spanish *P. pinea* forests are in southwestern Spain. In particular, in the province of Huelva, the species is present in almost 80 000 ha, which is approximately the 16.5% of its national area.

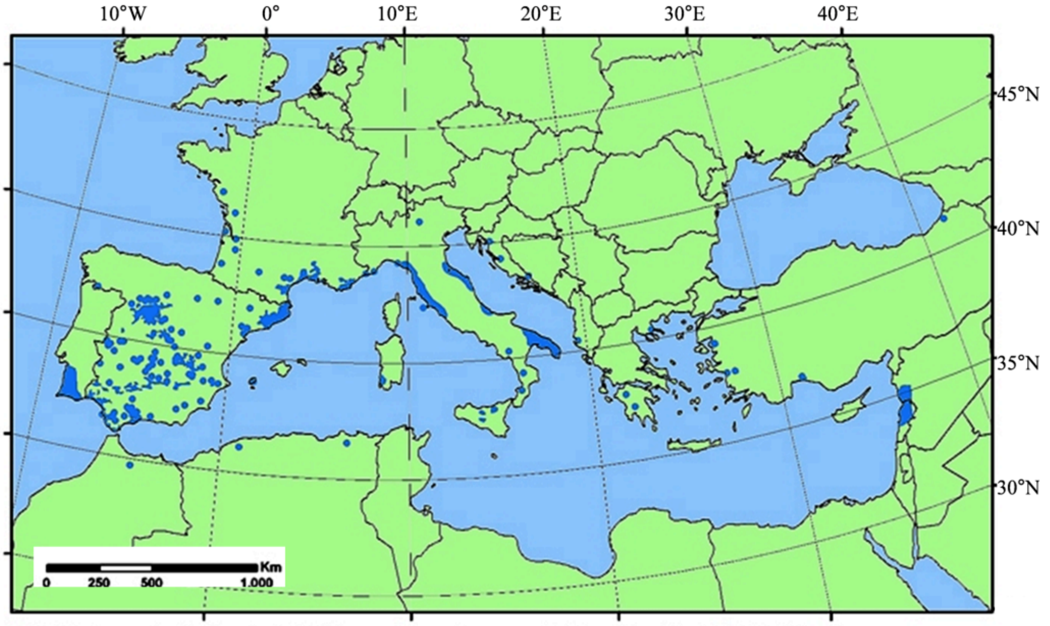


Figure 2. Distribution map showing the natural distribution area of Pinus pinea (source: European Forest Genetic Resources Programme, www.euforgen.org)

P. pinea in Spain grows within an altitudinal optimum range of 30-800 m a.s.l, on loam and sandy-loam soils in areas were annual precipitation ranges from 430 to 800 mm and mean annual temperatures is between 11 and 18 ºC (mean temperature of the warmest month 16-21 ºC, of the coldest month 3-11 ºC) (Bravo and Montero, 2008a). A typological classification of Spanish *P. pinea* forests is the following (Montero et al., 2008).

- In northern Spain, on the "Meseta Norte" plateau, *P. pinea* forests are located at elevations ranging from 650 to 900 m a.s.l., in nemoro-Mediterranean areas, i.e. transitional areas where evergreen sclerophyll broad-leaf and deciduous broad-leaf forests may occur (Allué, 1990). Thus, *P. pinea* stands in this area are pure or mixed (*Pinus pinaster, Quercus ilex, Quercus faginea* and *Juniperus thurifera*). Most of these forests are publicly owned and they are managed as protection forests (with an important function of fixing continental fossil dunes) and for production of timber and pine nuts.
- In Catalonia, northeastern Spain, *P. pinea* grows at lower elevations (0-600 m a.s.l.), in sub-nemoral/Mediterranean areas, where it forms mixed forests with *Quercus ilex, Quercus suber, Quercus faginea, Pinus halepensis, P. pinaster, Erica arborea* and *Arbutus unedo*. Private forest ownership is common in this area and silvicultural measures are sporadic.
- In central Spain, in the provinces of Madrid, Ávila and Toledo, *P. pinea* grows between 600 and 1000 m a.s.l. in Mediterranean and nemoro-Mediterranean areas, where it frequently forms mixed stands with *Quercus ilex, Juniperus oxycedrus* and *Pinus pinaster*. Intense livestock management has been traditionally carried out till recent times in these forests, which therefore have scarce importance for timber production and management is mainly aimed at protection and environmental conservation.
- In the provinces of Cuenca and Albacete, central-eastern Spain, *P. pinea* forests are fragmented due to the large presence of agricultural land use. Private forest ownership is prevailing and forest uses are secondary. *P. pinea* stands are pure or mixed with nemoro-Mediterranean vegetation including *Quercus ilex, Quercus coccifera, Pinus halepensis*, and they are located between 700 and 900 m a.s.l.
- On the "Sierra Morena" mountain range, southern Spain, *P. pinea* grows in Mediterranean conditions with *Quercus ilex* and *Quercus suber*, between 200 and 800 m a.s.l. Forest management in this area is mainly aimed at protection and environmental conservation.
- *P. pinea* forests in southwestern Spain grow at low elevations (0-200 m a.s.l.) under Mediterranean climate. These woodlands are publicly owned and have an important role as multifunctional forests. The stands located in the coastal zones of this area are mixed (*Juniperus oxycedrus, Juniperus phoenicea* and *Pistacia lentiscus*) and particularly important for the protection of dune ecosystems, while in the inland they are pure (with presence of *Quercus suber* in some locations) and primarily managed for timber production and biomass, and secondly for pine nuts.

The Iberian *P. pinea* forests are multifunctional forests providing edible pine nuts, which are highly valued in international markets, but also timber, biomass and important environmental services as soil protection, sand dune stabilization, biodiversity refuge, space for public and recreational activities, carbon sequestration and landscape amenities (see Pasalodos-Tato et al., 2016; Ovando et al., 2010; Montero et al., 2004)

6.3.2 *Q. ilex* ssp. *ballota* (Desf.) Samp

Common English names of *Quercus ilex* are "holm oak" and "holly oak" (Speer, 2010). Among the sources of information about morphology, phenology, ecology, distribution and silviculture in Spain of *Q. ilex* are Ruiz de la Torre (2006), Bravo et al. (2008), Bravo and Montero (2008b), Serrada and San Miguel (2008), Alejano et al. (2011) and Vericat et al. (2012). It is a Mediterranean evergreen tree of the *Fagaceace* family. The crown is ovoid and dense. It can exceed 25 m in height, although holm oaks of Spanish open-woodlands are smaller, and the diameter can reach 2 m. The bark is finely square-fissured and blackish. The leaves are simple, hard and oval and can persist for 3-4 years. *Q. ilex* is a monoecious species, flowering takes place in spring and acorns mature in October-November of the same year. The species presents a masting behavior. The roots have a deep, robust main branch and numerous, ramified, superficial secondary braches. Holm oaks can be long-living trees (400-500 years), but *Q. ilex* forests in Spain are managed, thus tree lifespan is limited. In coppice stands, the rotation length is normally between 20 and 30 years, while in open woodlands, managed as silvopastoral systems, tree ages can vary between 150 and 250 years, according to the adopted method of regeneration.

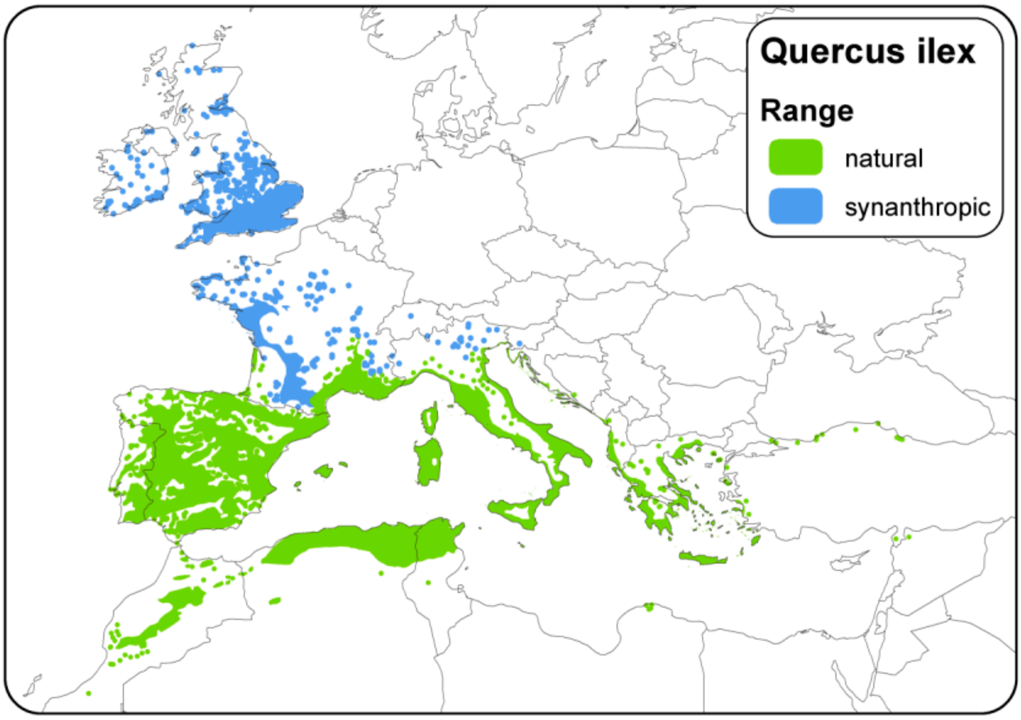


Figure 3. Distribution map showing the distribution area of *Quercus ilex* (courtesy of Erik Welk, Departement of Geobotany, Martin-Luther-University Halle-Wittenberg, Germany)

Q. ilex occurs throughout the Mediterranean region and it is prevalent in the Western Mediterranean (Figure 3). In Spain, pure *Q. ilex* populations are present in almost 824 000 ha. If mixed stands (*Q. ilex* with *Quercus pyrenaica, Quercus faginea, Quercus suber, Pinus halepensis* and *Juniperus thurifera*) are taken into account, the total distribution area is almost 1 867 000 ha, which is approximately the 13.5% of the national forest cover (data from the IFN2). In Spain, two subspecies are distinguished, i.e. *Q. ilex* ssp. *ilex* , which is present in NE Spain, and *Q. ilex* ssp. *ballota* (Desf.) Samp., which is the most widespread.

Q. ilex ssp. *ballota* is the most important tree species of the Spanish oak silvopastoral systems called "dehesas". The "dehesas" are open woodlands where stand density ranges from 20 to 100 trees/ha, and more frequently from 40 to 70 trees/ha (Navarro, 2011a). In addition to *Q. ilex*, the tree species constituting these woodlands are *Quercus suber* and *Quercus faginea*, while other species are present to a lesser extent, including other evergreen and deciduous *Quercus* species, *Pinus pinea, Castanea sativa, Olea sylvestris* and sclerophyllous shrubs (Alaejos, 2011b). These woodlands originated from deforestation carried out since the 13th century to establish cropland and pasture, and they have been exploited as silvo-pastoral systems until nowadays (Torres, 2011). The Spanish second national forest inventory (IFN2) does not include specific statistics about "dehesas", due to the variety in composition of these woodlands. It is estimated that the Iberian silvopastoral systems extend to approximately 3.5 million ha (including "dehesas" and "montados", i.e. woodlands in Portugal with similar structure and an important presence of *Quercus suber*), and the greatest areas are in southwestern Spain (about 1.25 million ha in Extremadura and 700000 ha in Andalusia) and in the region of Alentejo (southern Portugal, about 800000 ha) (Olea et al., 2005). These woodlands are characterized by a markedly Mediterranean climate, flat or hilly terrains, and a low fertility of soils which makes arable farming lowly sustainable and unprofitable (Olea and San Miguel-Ayanz, 2006). Most commonly, these systems are privately owned. They do not provide industrial timber and silvicultural measures (especially pruning, strimming and tillage) are aimed at enhancing the production of fuelwood, pasture and acorns. Acorns, especially in *Q. ilex* stands, are important for the feeding of the Iberian pig and related production of high-quality meat and especially ham. The production of cork in *Q. suber* stands, especially in Portugal, has also a great economic importance (see Pinto-Correia et al., 2011). In addition to their uses, these systems have an important role as an ecological niche for various fauna and flora species and provide environmental benefits, protection of water quality, conservation of landscape and cultural heritage (Diaz et al., 1997; Olea and San Miguel-Ayanz, 2006; Pinto-Correia et al., 2011). The "dehesa" is an ecosystem protected by the 92/43/EEC Habitats Directive, and included in the Natura 2000 network.

6.3.2.1 *Decline and tree mortality in the Spanish Q. ilex silvopastoral systems*

The spanish "dehesas" currently present an alarming health status. Most trees are old and present damages caused by silvicultural measures, especially pruning, which have affected trees for many decades (Navarro, 2011b). There is a lack of young trees and a serious problem of regeneration failure (Pulido et al., 2001; Plieninger et al., 2004). Moreover, in recent decades oak open woodlands in the southwestern Iberian Peninsula have undergone a weakening process characterized by nonspecific symptoms, including wilting of leaves, twigs, and branches, bark necrosis, and production of epicormic shoots (Brasier, 1996). These symptoms mostly occur in *Q. ilex* and *Q. suber*, although they have been also observed in other *Quercus* species and associated shrubs. In Spain, the phenomenon is referred to as “seca” and leads to tree death (Carrasco, 2009; Navarro, 2011b). Comprehensive up-to-date statistics of dieback processes and tree die-off in the Spanish “dehesas” are lacking, because etiology and symptomatology are complex and highly variable, and the private forest ownership, which is common, makes monitoring difficult. Leco Berrocal (1994) reported 20 010 ha affected by the “seca” in 1991 in Spain (58.5% of them in Andalusia and 38.5% in Extremadura). In recent years, there has been an alarming increase of oak mortality, especially in southwestern Spain, which threatens the sustainability of these systems. In the territory of 8 municipalities of the province of Huelva (W Andalusia), about 93 600 trees were lost and the mean decrease of the “dehesa” forest cover was 7% between 1997 and 2002 (Romero de los Reyes et al., 2007).

The environmental and socio-economic importance of the Iberian silvopastoral systems demand some solution for the problem. The mitigation of the impact of the decline process is mainly based on management measures aimed at controlling the spread of pests, including sanitation cuttings and biodiversity conservation (García Vázquez and Tapias, 2011; Sánchez and López, 2011). However, eliminating pathogenic fungi in infested soils is improbable and mitigation measures should be undertaken to keep the damage below an economic threshold (Zamora Rojas et al., 2014). The severity of symptoms shown by different oaks involves a genetic component and therefore the heritability of tolerance to the pathogen could induce different degrees of vulnerability in the progenies and suggests the possibility to obtain resistant progenies (León Sánchez, 2013). These findings, however, do not have yet any practical operation.

The implementation of definitive solutions is complicated by the difficulty of identifying the factors of tree mortality. Research has demonstrated that pathogenic chromista, in particular *Phytophthora cinnamomi*, are the main agents of root diseases in southern Spain (Sánchez et al., 2002). However, blights caused by other organisms (e.g. *Botryosphaeria* spp., *Biscogniauxia* spp.) and insect infestations (e.g. *Cerambix* spp., *Prinobius* spp.) have been also reported in the affected stands (see Carrasco, 2009). The phenomenon can be interpreted as a forest decline process in which predisposing, inciting and contributing factors are involved (Manion, 1981; Manion and Lachance, 1992). Thus, abiotic factors and anthropogenic disturbances can predispose tree to the effect of pests. In particular, soils in most “dehesas” have low levels of nutrients, they are shallow and susceptible to erosion, and this can interfere with root development and debilitate trees (de Sampaio e Paiva Camilo-Alves et al., 2013). Soils can also undergo desiccation and waterlogging, which increase the activity of pathogenic fungi (Sánchez et al., 2002). Moreover, soil treatments and livestock charge are often inappropriate, leading to soil degradation and compaction (Domingo-Santos and Vázquez-Piqué, 2011), and damages caused by improper silvicultural operations predispose trees to the impact of other stress factors (Navarro, 2011b).

Climatic factors are also involved in tree mortality processes (McDowell et al., 2008; Allen et al., 2010; Choat et al., 2012; Anderegg et al., 2013). However, for oak decline in the Iberian Peninsula, research has mainly focused on the climatic conditions that influence pathogens' activity (Brasier and Scott, 1994; Sánchez et al., 2002; Caetano et al., 2009; Corcobado et al., 2014). Climate change, namely the increasing temperature and aridity, is considered an inciting factor of oak decline in a theoretical framework, in which climate change is expected to increase trees' susceptibility to diseases (Wargo, 1996; Trapero et al., 2006; Zamora Rojas et al., 2014), but there is a lack of specific research assessing the role of climate change in the current widespread increase of oak mortality in the "dehesas" of southwestern Spain. Nevertheless, it is difficult to distinguish the role of predisposing, inciting and contributing factors, because factors act in a complex interplay in which the role of each factor can change over time. In particular, in the context of climate change, there are multiple potential mechanisms of interdependence between increasing drought, plant hydraulics, carbohydrates and defense metabolisms, and population dynamics of biotic agents (Allen et al., 2010; McDowell et al., 2011).

6.4 Tree ring studies of *P. pinea* and *Q. ilex* in the Southern Iberian Peninsula

Tree ring studies in *P. pinea* and *Q. ilex* Iberian forests can provide valuable information about their growth dynamics in the current context of climate change. The Iberian Peninsula has become drier in recent decades, and research indicates this change will continue (Kovats et al., 2014; Sumner et al., 2003; Rodrigo and Trigo, 2007). There is evidence that climate change has already several impacts on forest ecosystems in this region, including shifts in species distributions and phenology, decreases of growth and wood production (at least in the southern provenances and at lower edges of species altitudinal ranges), reductions of non-wood forest products, stand decline and increased tree mortality (as in the case of the Spanish "dehesas"), and increased disturbances such as pests and fires (see Lindner et al. 2010; Lindner and Calama 2013; Resco de Dios et al. 2007). Studying the climate-related growth dynamics of *P. pinea* and *Q. ilex* forests using tree rings can support the assessment of the species' vulnerability and adaptive capacity in future climatic scenarios and will guide the implementation of management options that may mitigate climate change impacts, improve the species' response and enhance ecosystem sustainability. Specifically, in the case of the southern *Q. ilex* open woodlands, tree ring studies can give an insight into the role of climate change in the current mortality process. Indeed, tree rings have been used to investigate growth patterns in declining forests and dead trees (see Schweingruber, 1996, pp. 369-438), to model mortality risk (e.g. Bigler and Bugmann, 2004) and to find relationships between mortality processes and external factors (e.g. Pedersen, 1998; Camarero et al.,2003; Bigler et al., 2006).

Nothwidstanding the information about forest ecology derivable from *Q. ilex* and *P. pinea* tree rings, few dendroecological and dendroclimatological studies in these two species have been carried out in Spain, especially in the southern areas, where dendrochronological studies in general, also for other species, are scarce. The first tree ring study in the Iberian Peninsula was an investigation on growth-climate relationships of *Pinus uncinata* at 1800 m a. s. l. in the Pyrenees, Northeastern Spain, by Creus Novau and Puigdefábregas (1976). Since then, dendrochronology with application in environmental science have developed in this region and mainly involved tree rings of conifers in the northern areas, which present humid/sub-humid climates with oceanic influence, and especially at high elevations (see Perez Antelo, 1994). A more recent review of the existing dendrochronological data from living trees for the Iberian Peninsula is provided by Domínguez-Delmás et al. (2015), who searched in reference databases for all published literature about chronologies in Spain and Portugal, only including chronologies spanning back in time up to at least 1950 and for which coordinates were provided: the authors report 406 chronologies, most of them from conifers (79.1%), spread throughout the Iberian mountain ranges, with a markedly higher number of sampling sites in the northern latitudes.

To review the availability of tree ring studies of *P. pinea* and *Q. ilex* in southern Iberian Peninsula, published works in which tree rings were used in different fields of geosciences were searched. The research was performed within the Scopus bibliographic database on the 28th of October 2016. All types of documents (articles published in peer-reviewed journals, books, book chapters and conference papers) were included. The first query included all terms referring to dendrochronology and its applications in geosciences, and all terms referring to Iberia, Spain and Portugal. At this step, 260 documents were found. The second query included all the terms of the first query and all synonyms of the two species (synonyms were checked in the Dendrochronology Species Database compiled by Henri D. Grissino-Mayer and hosted by the Swiss Federal Institute for Forest, Snow and Landscape Research – WSL at http://www.wsl.ch/dienstleistungen/produkte/glossare/dendro_species/index_EN). At this step, 33 documents were found: this is around the 13% of the result of the first query, and indicates the comparatively low number of tree ring studies in this two species in the Iberian Peninsula. In particular, 11 documents were found for *P. pinea*, and 22 for *Q. ilex*. Subsequently, the location of the 33 *P. pinea* and *Q. ilex* study sites weas checked. As a result, 11 studies carried out at low latitudes were found, 6 of them for *P. pinea* and 5 of them for *Q. ilex*. Specifically, the references of the five works on *P. pinea* were Natalini et al. (2016), Natalini et al. (2015), Nabais et al. (2014), Novak et al. (2011), De Luis et al. (2009) and Campelo et al. (2006). The first two are the Articles 2 and 3 included in the Appendix 1 of this thesis. The information about sites of the other four is the following:

- The articles by Novak et al. and De Luis et al. present results from a same site, a mixed stand of *P. halepensis* and *P. pinea* on coastal sand dunes, located in the province of Alicante, Valencian Community, Southeastern Spain (38.1°N, 0.66°W).
- Campelo et al. collected samples in Portugal between ~37.6° N and ~38.2° N.
- Nabais et al. analyzed chronologies along a latitudinal gradient in Portugal, and the southernmost site was one of those already found in Campelo et al..

The references of the five works on *Q. ilex* were Natalini et al. (2016), Campelo et al. (2009), Gea-Izquierdo et al. (2009), Patón et al. (2009), and Plieninger et al. (2003). The first is the Article 4 in the Appendix 1 of this thesis. The information about sites of the other four is the following:

- The sites of the article by Patón et al. were in the provinces of Badajoz and Cáceres, in the Extremadura region, Southwestern Spain (39.1°N, 6.68°W, 248 m a. s. l.).
- The southernmost study site in the article by Gea-Izquierdo et al., as well as the study site in Plieninger et al., were located in the province of Cáceres (respectively: 39.42°N, 6.42°W, and 39.5°N, 6.0°W).
- the study site of Campelo et al. was in Portugal, at ~38.5º N.
- With exception of the articles included in this thesis and the southernmost *P. pinea* study site in Campelo et al. and Nabais et al., no studies using *P. pinea* and *Q. ilex* trees rings were available in the Iberian Peninsula below latitude 38ºN by the date of this research. In Andalusia, the southernmost region in Spain covering latitudes from 36°N to ~38.7°N, tree ring studies are very scarce and only available for other species at high elevations (e.g. *Pinus nigra* in Domínguez-Delmás et al., 2013a).

The limited development of dendrochronological studies in southern Spain is largely explained by the climatic conditions of this region. Climate in southern Spain is Mediterranean and presents highly variable termo-pluviometric regimes, which often induce more than one stop of wood formation over the year (Cherubini et al., 2003). As a result of the high variability of climate, so-called “false rings” (or “double rings”) and other anomalies in ring patterns (in literature all included under the term “intra-annual density fluctuations” - IADFs) are widely found in Mediterranean tree species (see e.g. Cherubini et al., 2003; Campelo et al., 2007a, b; De Micco et al., 2016). IADFs make cross-dating difficult and constitute a source of “noise” in dendroclimatological studies. These problems are minimized in humid/sub-humid ecosystems in northern Spain, where IADFs are less frequent because the seasonality of climate permits wood formation to start and end regularly each year without intra-annual intermissions. Nonetheless, the practical application of dendrochronological methods in the Mediterranean regions has developed especially in recent times (Zhang and Romane, 1991; Cherubini et al., 2003) and IADFs can give potentially significant information about climate (Campelo et al., 2007a, b; Vieira et al., 2010; Battipaglia et al., 2013; De Micco et al., 2016).

The low number of tree ring studies in *P. pinea* and *Q. ilex* is further explicated by the characteristics of the stands where these species are present. In fact, the strengths of climatic signal is enhanced in lowly disturbed stands, which in Spain can be found at high elevations, where trees are less exposed to human disturbances due to the difficult access to the areas where they grow. Moreover, the strength of the climatic signal in tree-ring series is expected to be maximized at the altitudinal limits of the species distribution (Schweingruber, 1990). Therefore, dendroclimatological and dendroecological studies in Spain have been frequently carried out at high elevations. In contrast, the spanish *P. pinea* forests and *Q. ilex* open woodlands are mostly located at low elevations and they are systematically managed. Silvicultural measures (e.g. pruning, thinning) influence tree growth, therefore forestry-related variability in growth trends can be expected in these forests. When the climate-related variance of tree-ring series is the signal of interest, the forestry-related variance is considered as noise, and appropriate detrending methods must be applied to remove this noise and yet preserve climatic variance.

The low number of chronologies available for *Q. ilex* in southern Spain is also related to the difficulty of establishing tree ring chronologies of this species in this region. *Q. ilex* presents a complex xylem anatomy, i.e. narrow rings, missing rings and IADFs (Cherubini et al., 2003; Campelo et al., 2007, 2009; Gea-Izquierdo et al. 2009). Therefore, complete cross-sections are needed for dendrochronological analysis. Inspecting rings along the whole circumference on the stem sections is often necessary to correctly identify rings boundaries. However, in Spain obtaining holm oak stem section is difficult because the species is protected and holm oaks can be cut only in certain circumstances, e.g. when they are dead (see Article 4, Appendix 1) and during public works, e.g. for road or dump constructions (see Gea-Izquierdo et al., 2011). Furthermore, long *Q. ilex* tree-ring series in Spain can be only obtained in the "dehesa" systems, where it is more likely to find old holm oaks, but most "dehesas" are privately owned, and this makes difficult to acquire stem sections for scientific works. Finally, obtaining samples with an increment borer (as often done in dendrochronological studies) is unfeasible due to the hardness of holm oak wood.

7 OBJECTIVES

The general objectives of this thesis were (*i*) to enhance our understanding of the growth dynamics of *Pinus pinea* L. and *Quercus ilex* ssp. *ballota* (Desf.) Samp. in relation to climate variability, through a dendroecological and dendroclimatological approach, and (*ii*) to validate the application of dendroecological and dendroclimatological methods in managed Mediterranean forest ecosystems, with the specific case of this two species in southwestern Spain.

To accomplish the general objectives, 6 specific objectives were outlined. Works were designed to achieve the specific objectives, and the results are presented in 4 scientific articles enclosed in the Appendix 1 of this thesis. The specific objectives, and the articles in which they were included, were the following:

1. To provide dated chronologies of *Pinus pinea* L. and *Quercus ilex* ssp. *ballota* (Desf.) Samp, including sites at low latitudes in Spain, which will contribute to the ensemble of available chronologies for these two species. All results presented in the annexed articles are based on these chronologies, specifically: the *P. pinea* chronologies were analyzed in the Articles 1, 2, and 3, and the *Q. ilex* chronologies are included in the Article 4.
2. To test the procedures to extract the climatic signal from tree-ring series in managed stands presenting forestry-induced disturbances in growth trends. Results of these tests are presented in the Articles 1 and 3.
3. To evaluate how the climate data used in dendroclimatic analysis can influence the analysis of growth-climate relationships. Comparisons of growth-climate relationships using different climate parameters and climate data sources are presented in the Article 3.
4. To assess species-specific response of growth to long-term climatic variations. Climate change-related signals in tree-ring series were examined in both species, and results are presented in the Articles 2, 3 and 4.
5. To assess species-specific response of growth to diverse site-specific climatic conditions. Since the two *Q. ilex* sites were close between them and had very similar climatic conditions, this objective is focused on *P. pinea* and is included in the Articles 2 and 3.
6. To assess the role of climate change in the increasing oak mortality in the silvo-pastoral systems of southern Spain. This is an objective specifically related to *Q. ilex* and referred to the "seca" process existing in the "dehesas" woodlands in the province of Huelva. Results are presented in the Article 4.

8 MATERIALS AND METHODS

8.1 Sampling design

Tree-ring width chronologies of *Quercus ilex* subsp. *ballota* (Desf.) Samp. and *Pinus pinea* L. were used. The used tree-ring database was composed of Spanish sites for the most part. Specifically, the *Q. ilex* samples were from two sites in southwestern Spain and *P. pinea* samples were from 10 sites along a latitudinal gradient in Spain. Two additional *P. pinea* chronologies were form Portugal and Italy. The locations and main characteristics and pictures of the sites are in Figures 4, 5 and Tables 1 and 2. The number of trees, samples and the statistics of the chronologies are in Table 3 and 4. Additionally, three *P. pinea* tree-ring width chronologies from the International Tree Ring Data Base (ITRDB; Paleoclimatology Team of the National Center for Environmental Information, USA, and the World Data Center for Paleoclimatology, available at www.ncdc.noaa.gov/data-access/paleoclimatologydata/datasets/tree-ring; see Grissino-Mayer and Fritts, 1997) were used in the Article 2 (Appendix 1). They were from the area of La Mancha (central-eastern Spain), namely: Dehesa del Peral, Pinar viejo and La Pasadilla (ITRDB codes: spai057, spai056 and spai059, respectively; contributors: Briongos and Del Cerro-Barja).

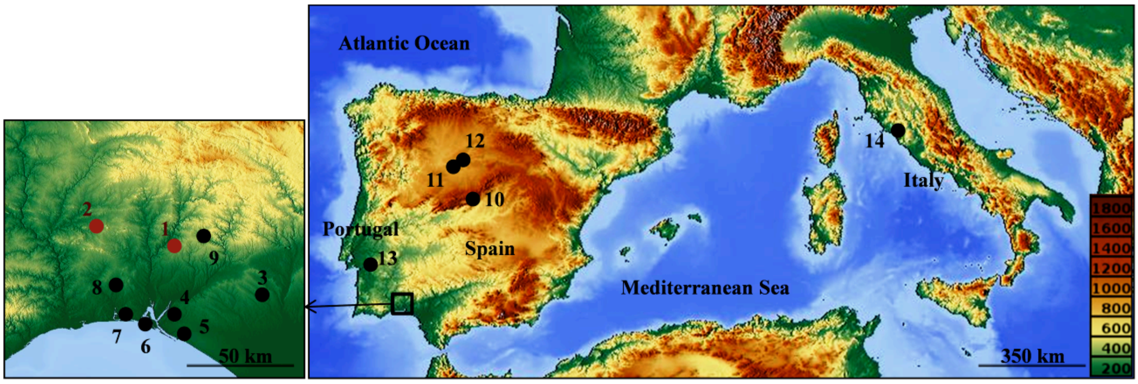


Figure 4. Locations of the study sites. *P. pinea* sites are indicated by the black dots; the *Q. ilex* sites are indicated by the red dots.

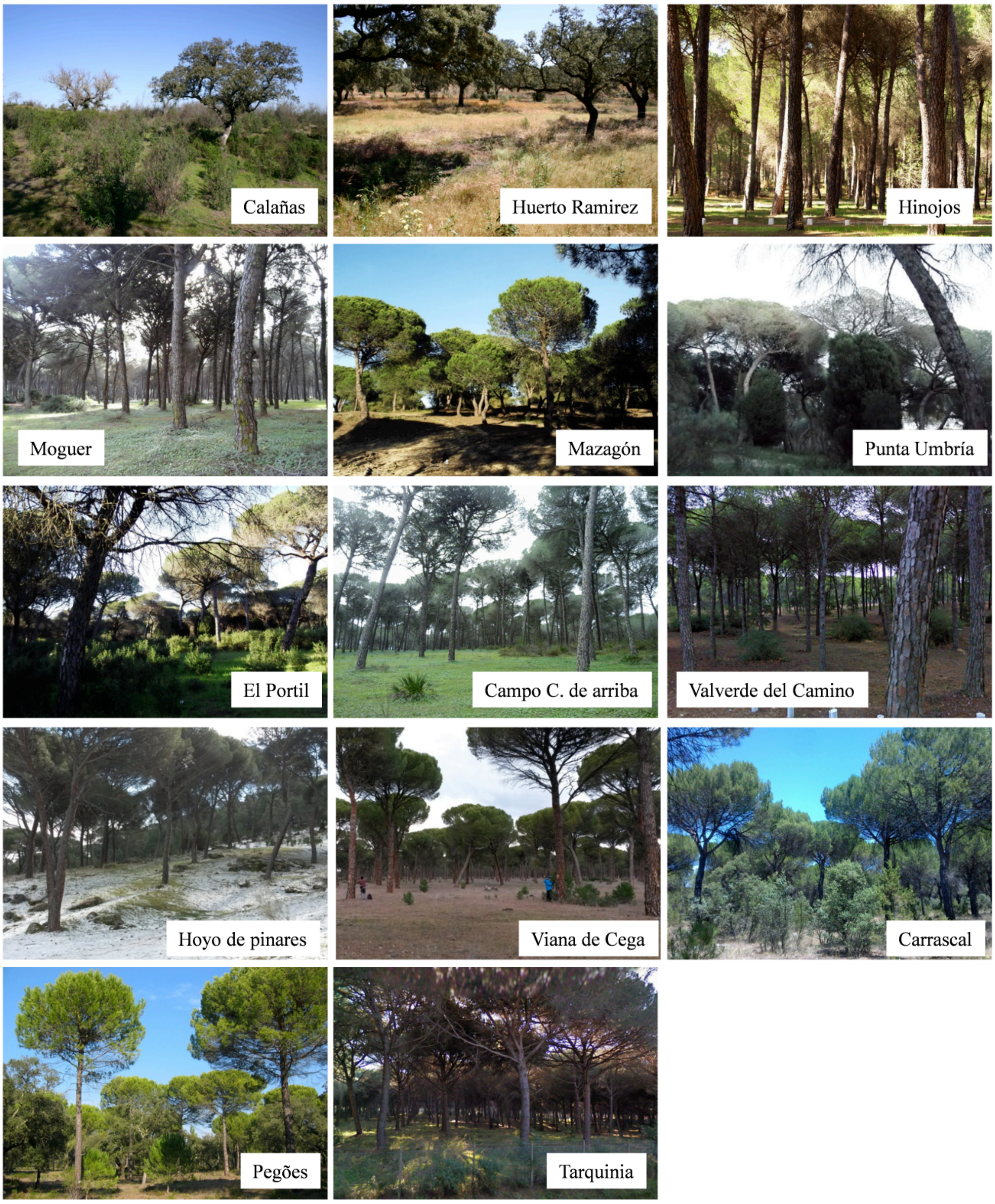


Figure 5. Pictures of the study sites (Pegões photo courtesy of Alexandra Correia)

Table 1. Characteristics of the study sites of *Q. ilex*

Site name	Calañas	Huerto Ramírez
Location on the map (1)	1	2
District (2)	Huelva	Huelva
Country	Spain	Spain
Latitude	37.52° N	37.57° N
Longitude	-6.92	-7.34
Elevation a. s. l. [m]	165	200
Slope [%]	0-25	0-50
Soil (3)	Cambisols, Regosols	Regosols, Luvisols
Mean tree diameter ± st.dev. [cm]	32±2	30±7
Mean tree height ± st.dev. [m]	6±0.5	7±1
Mean stand density [trees/ha] (4)	54	74
Forest canopy composition	Monospecific: *Q. ilex*	Monospecific: *Q. ilex*
Understory shrubs	*Cistus ladanifer*, *Cistus crispus*	*Cistus monspeliensis*

(1) See the map in Figure 4. (2) Local administrative division. (3) FAO soil classification.

(4) In the mixed stands, the value refers to the mean stand density including trees of all the present species.

Table 2. Characteristics of the study sites of *P. pinea*

Site name	Hinojos	Moguer	Mazagón	Punta Umbría	El Portil	Campo Común de arriba	Valverde del Camino	Hoyo de pinares	Viana de Cega	Carrascal	Pegões	Tarquinia
Location on the map (1)	3	4	5	6	7	8	9	10	11	12	13	14
District (2)	Huelva	Huelva	Huelva	Huelva	Huelva	Huelva	Huelva	Ávila	Valladolid	Valladolid	Lisbon	Viterbo
Country	Spain	Spain	Spain	Spain	Spain	Spain	Spain	Spain	Spain	Spain	Portugal	Italy
Latitude	37.29° N	37.21° N	37.12° N	37.20° N	37.21° N	37.39° N	37.53° N	40.51° N	41.47° N	41.59° N	38.63° N	42.29° N
Longitude	6.39° W	6.84° W	6.78° W	7.00° W	7.04° W	7.19° W	6.78° W	4.38° W	4.72° W	4.33° W	8.62° W	11.64° E
Elevation a. s. l. [m]	70	30	20	20	20	100	260	890	710	880	60	10
Slope [%]	0	25	0	0	0	0	0	50	0	0	0	0
Soil (3)	Cambisols, Regosols	Planosols	Regosols	Regosols	Regosols	Planosols	Luvisols	Leptosols	Arenosols	Cambisols	Podzols	Luvisols
Mean tree diameter ± st.dev. [cm]	72±8	55±9	27±10	28±7	22±8	67±7	62±6	75±8	60±9	45±4	19±4	28±2
Mean tree height ± st.dev. [m]	20±1	17±3	6±1	7±1	5±1	22±1	19±3	18±1	18±1	10±1	15±3	10±1
Mean stand density [trees/ha] (4)	155	160	230	235	260	190	145	100	100	200	90	100
Forest canopy composition	*P. pinea*	*P. pinea*	*P. pinea*	*P. pinea*	*P. pinea*, *P.pinaster*	*P. pinea*	*P. pinea*	*P. pinea*	*P. pinea*	*P. pinea*, *Q. ilex*	*P. pinea*, *P. pinaster*, *Q. suber*	*P. pinea*
Understory shrubs	absent	absent	*Juniperus phoenicea*	*J. phoenicea*, *Juniperus oxycedrus*	*J. phoenicea*	absent	absent	absent	absent	*Juniperus turiphera*	*Ulex* spp. *Cistus* spp.	absent

Table 3. Characteristics of the *Q.ilex* tree ring chronologies

	Calañas	Huerto Ramirez
No. of trees (1)	19	12
No. of samples (2)	57	36
Time-span > 1 tree (3)	1894-2006	1862-2010
Time span ≥ 5 trees (4)	1904-2006	1889-2010
Time span ≥ 10 trees (5)	1908-2006	1919-2008
Time span EPS > 0.85 (6)	1903-2006	1896-2010
Mean ring width [mm]	1.7	1.4
Mean ring width st.dev. [mm] (7)	0.95	1.16
Mean sensitivity	0.35	0.41
First-order autocorrelation	0.70	0.63
Mean correlation		
Trees vs. mean chronology (8)	0.69	0.70
Between trees (9)	0.68	0.59
Common interval (10):		
Time span	1934-2006	1972-2008
Between trees	0.70	0.68

(1) Number of tree sampled with the increment borer in *P. pinea* sites in Spain, and number of cross stem sections of *P. pinea* trees in Portugal and *Q. ilex* trees in Spain. (2) For *P. pinea* in Spain, the number of samples refers to the samples collected with the increment borer; for *P. pinea* samples in Portugal and *Q. ilex* in Spain, it refers to the number of cross-dated radii on the stem cross sections. (3) Years with at least two cross-dated individual tree chronologies. (4) Years with at least 5 cross-dated individual tree chronologies. (5) Years with at least 10 cross-dated individual tree chronologies. (6) Chronology time span in which the expressed population signal (EPS) was higher than 0.85. (7) Standard deviation of the ring widths along the chronology. (9) Mean Pearson correlation coefficient between the individual tree chronologies and the mean chronology of the stand. (9) Mean Pearson correlation coefficient among the individual tree chronologies. (10) Pearson correlation coefficient among the individual tree chronologies, computed over the time interval common to all the individual tree chronologies in each stand (indicated by "Time span").

Table 4. Characteristics of the P. pinea tree ring chronologies

	Hinojos	Moguer	Mazagón	Punta Umbría	El Portil	Campo Común de arriba	Valverde del Camino	Hoyo de pinares	Viana de Cega	Carrascal	Pegões	Tarquinia
No. of trees (1)	19	17	23	17	20	17	20	19	26	22	24	18
No. of samples (2)	38	34	46	34	40	34	40	38	52	44	24	36
Time-span > 1 tree (3)	1864-2012	1924-2012	1922-2011	1901-2011	1912-2011	1936-2012	1876-2011	1793-2014	1871-2014	1923-2014	1953-2007	1960-2013
Time span ≥ 5 trees (4)	1866-2012	1947-2012	1927-2011	1901-2011	1952-2011	1945-2012	1881-2011	1803-2014	1873-2014	1925-2014	1958-2007	1960-2013
Time span ≥ 10 trees (5)	1874-2012	1954-2012	1938-2011	1938-2011	1968-2011	1951-2012	1888-2011	1844-2014	1877-2014	1931-2014	1965-2007	1962-2013
Time span EPS > 0.85 (6)	1865-2012	1935-2012	1922-2011	1901-2011	1953-2011	1947-2012	1876-2011	1827-2014	1871-2014	1923-2014	1958-2007	1960-2013
Mean ring width [mm]	2.1	2.7	1.6	1.4	2.4	3.7	1.8	1.7	1.5	2.3	3.2	3.9
Mean ring width st.dev. [mm] (7)	1.5	1.9	1.3	0.85	1.5	2.3	1.3	0.53	1.3	0.90	2.5	3.0
Mean sensitivity	0.40	0.40	0.40	0.34	0.37	0.26	0.28	0.26	0.40	0.36	0.32	0.27
First-order autocorrelation	0.68	0.54	0.63	0.67	0.68	0.73	0.79	0.61	0.86	0.62	0.77	0.82
Mean correlation												
Trees vs. mean chronology (8)	0.70	0.68	0.71	0.70	0.64	0.52	0.69	0.75	0.80	0.82	0.69	0.71
Between trees (9)	0.48	0.55	0.46	0.40	0.37	0.36	0.49	0.59	0.75	0.62	0.77	0.73
Common interval (10):												
Time span	1958-2011	1970-2012	1973-2005	1970-2007	1978-2008	1963-2008	1921-2009	1940-2014	1913-2014	1972-2014	1973-1996	1970-2013
Between trees	0.69	0.64	0.54	0.44	0.42	0.45	0.69	0.59	0.82	0.67	0.58	0.80

According to standard dendroclimatological procedures, the most appropriate sites for sampling are those where trees grow at their climatic limits, where the influence of climate on tree-ring variability is maximized, i.e. northern, southern, upper and lower distribution limits of the species (Schweingruber et al., 1990). Long chronologies from old trees in undisturbed stands should be selected to minimize the effects of competition and stand structure dynamics which could mask the climatic signal in the tree ring series (Schweingruber et al., 1990). Tree ring chronologies from such sites can be used as proxies for climate reconstructions or synoptic climatology. Since our purposes were focused on the ecology of the species, rather than climatological investigation, our experimental design did not fully follow these recommendations. Furthermore, *Q. ilex* and *P. pinea* forests in the study regions present characteristics (latitude, elevation, management systems) which deviate from strictly dendroclimatological standards (see the section 5.4 "Tree ring studies of P. pinea and Q. ilex in the Southern Iberian Peninsula").

For *P. pinea*, our sampling covered a wide range of environmental conditions, including sites at the altitudinal limits as well as in more favorable conditions. The selected stands also differed between them in structures, ages and degrees of stand disturbances. The diversity of site-specific conditions allowed to study the adapted growth response within the ecological range of the species. When selecting the stands for sampling, we searched for homogeneity in micro-site conditions, which enhances the common signal among individual tree chronologies (Schweingruber et al., 1990). For each stand, we searched for the longest mean chronology by sampling the largest dominant/co-dominant trees. At least 20 trees were sampled in each stand, which is considered an adequate number to assure quality of the mean chronologies (Pilcher, 1990; Speer, 2010).

For *Q. ilex*, difficulties in collecting samples and constructing tree ring chronologies determined the sampling process (see the section 5.4 "Tree ring studies of P. pinea and Q. ilex in the Southern Iberian Peninsula"), which therefore could not follow a defined strategy, and samples were collected when they were available.

8.1.1 *P. pinea* sites and samples

In Spain, the two northernmost *P. pinea* sites, namely "Carrascal" and "Viana de Cega" are located on the "Meseta norte", a plateau of Tertiary and Quaternary deposits ranging from ~600 to ~900 m a.s.l. and covering a large part of the northwestern Spain. One site in Central Spain, "Hoyo de pinares", is located on the Sistema Central mountain range, which runs in an ENE-WSW direction along the southern border of the Meseta Norte, presents higher elevations with several peaks higher than 2000 m a.s.l., and it is composed of Paleozoic and Mesozoic granitic rocks with patches of Cenozoic sediments. Seven sites are in the province of Huelva, southwestern Spain, namely: "Valverde del Camino" is located on the southernmost limit of the Sierra Morena mountain range presenting Tertiary deposits; "Hinojos", "Moguer" and "Campo Común de arriba" are included in a post-orogenic depression characterized by mio-pliocenic sediments; "Mazagón", "Punta Umbria" and "El Portil" are on coastal dunes.

In Pegões, Portugal, *P. pinea* forests grow in coastal zones where soil types range from sand, loamy sand and sandy loam textures, derived from sandstone sedimentary rocks (Correia et al. 2010). The Italian site, "Tarquinia", is located on stabilized old dunes and is representative of the *P. pinea* forests of the Italian Tyrrhenian coasts (see Mazza and Manetti, 2013; Piraino et al., 2013; Mazza et al., 2014).

All *P. pinea* sites are characterized by Mediterranean-type climates. Site-specific conditions vary in temperatures, rainfall amounts, distribution of rainfall over the year, duration and intensity of meteorological droughts (see Articles 2 and 3 in Appendix 1).

The extraction and preparation of samples followed basic procedural recommendations (Pilcher, 1990; Speer, 2010). The samples in Spain and Italy were extracted at breast height with increment borers (Figure 6), taking two cores per tree, and glued onto wooden mounts (Figure 7). For the *P. pinea* stand in Portugal, ring widths measured on stem cross sections from a previous study by Correia et al. (2010) were used. The samples were sanded along the transverse sections with senders and abrasive paper with progressively finer grit sizes (from 60 to 180) to make the rings visible (Figure 8).

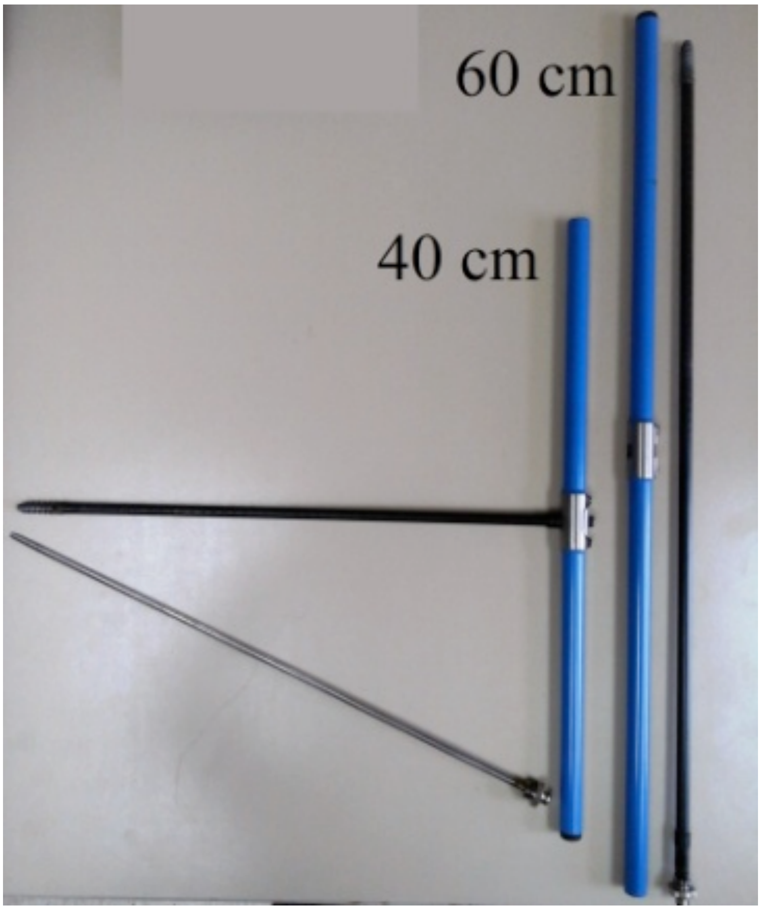


Figure 6. Increment borers

Figure 7. *P. pinea* samples glued onto wooden mounts and *Q. ilex* basal stem cross sections.

Figure 8. Sanders used to polish the samples. Hand-held sander (top), stationary belt sander (middle), and hand-held random orbital sander (bottom).

8.1.2 *Quercus ilex* sites and samples.

These *Q. ilex* chronologies were obtained using stem cross sections of dead holm oaks in two open woodlands managed as silvopastoral systems (“dehesas”) located in the province of Huelva, southwestern Spain. These woodlands are affected by widespread stand decline and massive tree die-off (see “Decline and tree mortality in the Spanish *Q. ilex* silvopastoral systems” in this thesis).

Stem cross sections were used in both sites (Figure 7). Only the use of stem sections makes cross-dating possible in this species (see the section 5.4 “Tree ring studies of P. pinea and Q. ilex in the Southern Iberian Peninsula”). Samples were collected as they were available without a pre-defined sampling strategy, due to restrictions to sample collections (*ibid.*), and the study was started when the number of samples was sufficient to obtain a reliable mean chronology for each stand. Cutting trees, and thus obtaining sections, was possible only when trees were dead. A tree was assumed to be dead when it was completely defoliated for at least two successive growing seasons. In Calañas, 30 basal stem sections were available but 11 were discarded because unclear ring borders and rots made cross-dating impossible. In Huerto Ramirez, 12 trees were logged and discarding sections could have leaded to a low replication of samples; thus basal stem disks as well as cross sections at breast height of the same trees were collected and used for cross-dating. Rings from different stem heights do not alter results because the rings at different heights are proportional and provide coherent climatic signals (Zhang and Romane, 1991; Chhin and Wang, 2005).

The two stands are representative of holm oak open woodlands in the Southwestern Iberian Peninsula that are primarily used for livestock management. They are located on the southernmost limit of the "Sierra Morena" mountain range presenting Tertiary deposits. In the two stands the understory layer is composed of *Cistus ladanifer, Cistus crispus, Cistus monspeliensis* and an herbaceous layer of grasses. Further details about stand characteristics and tree health status are included in the Article 4 (Appendix 1).

8.2 Measurement of ring widths and cross-dating

Tree-ring widths were measured with a stereomicroscope and a LINTAB™ table (Rinntech®) connected to a TSAP-Win™ tree-ring analysis system (Rinntech®) (Figures 9, 10, 11). Ring width curves were plotted for visual inspection and cross-dated with determination of the Student's *t* value, coefficient of parallel variation (*Gleichlaeufigkeit*, Glk) and cross-date index (CDI). The Student's *t* tests the significance of the correlation between two tree-ring series on the overlap interval (Baillie and Pilcher, 1973). The Glk tests if two chronologies are simultaneously increasing or decreasing in each year-to-year interval and is calculated as the percentage of intervals showing matching inter-annual growth variations (see Speer, 2010, p. 108). The CDI is calculated in the TSAP-Win™ software as a combination of the *t*-value and the Glk (Rinn, 2011). The cross-dating was finally verified using the program COFECHA, one of the most used programs in dendrochronology for quality-control of ring width measurements (Holmes, 1983; Holmes et al., 1986; Grissino-Mayer, 2001; Speer, 2010, pp.115-133). COFECHA provides a statistical match between segments of each individual series and the master chronology that is made of the measurements entered into the program. COFECHA takes the tree-ring series and, by default, fits a 32-year smoothing spline to them for standardization. Subsequently, it averages all the indexed series to create a master chronology. Next, it removes the individual series that is to be analyzed, cuts it into segments of 50 years with 25 years of overlap (by default) and statistically correlates each segment against the master chronology. Finally, the correlations which are below a confidence level (set at 99% by default) are flagged. In this thesis, default options of COFECHA were applied as a standard procedure, but additional tests were also done entering other values (e.g. different spline periods for tree-ring standardization, different time window lengths and overlaps for correlations) depending on the characteristics of the chronologies to be analyzed (e.g. chronology length and time-frequency domain).

The samples and all tree ring data are stored at the Department of Agroforestry Sciences of the University of Huelva, Spain.

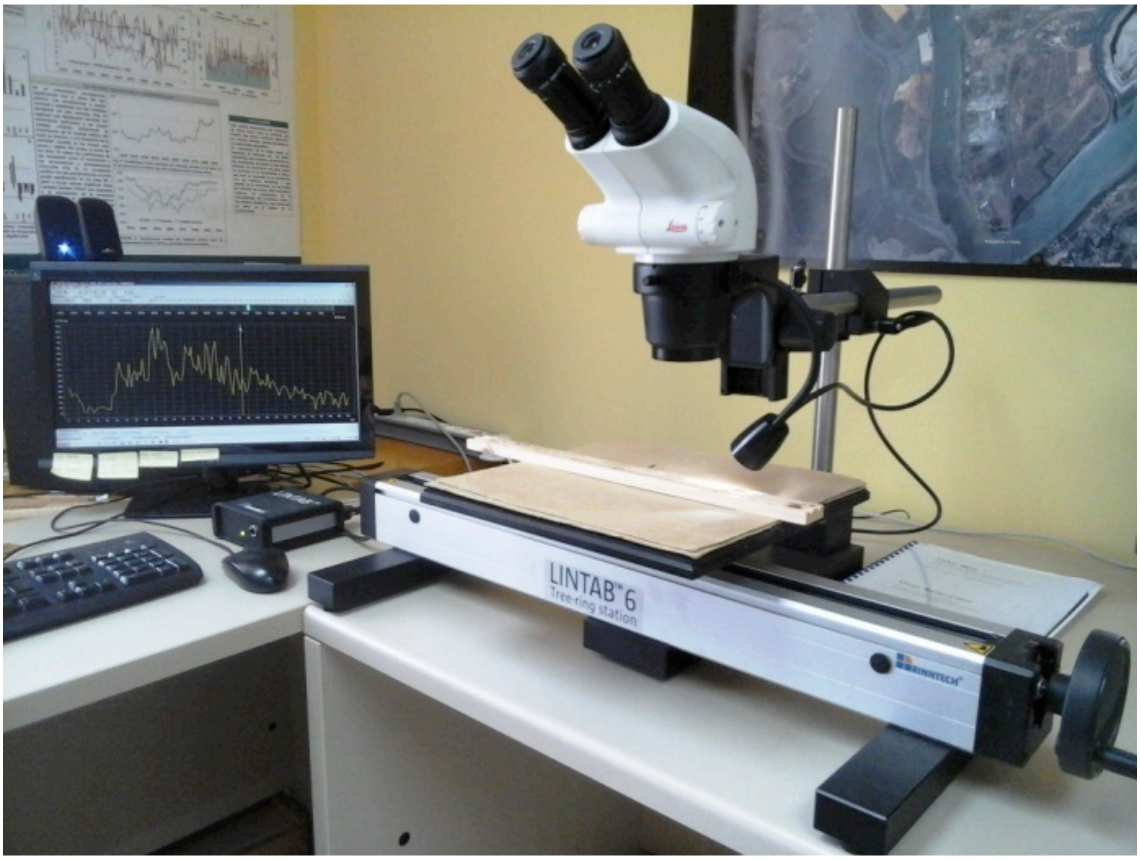


Figure 9. Stereomicroscope and LINTAB™ table, connected to a computer running the program TSAP-Win™.

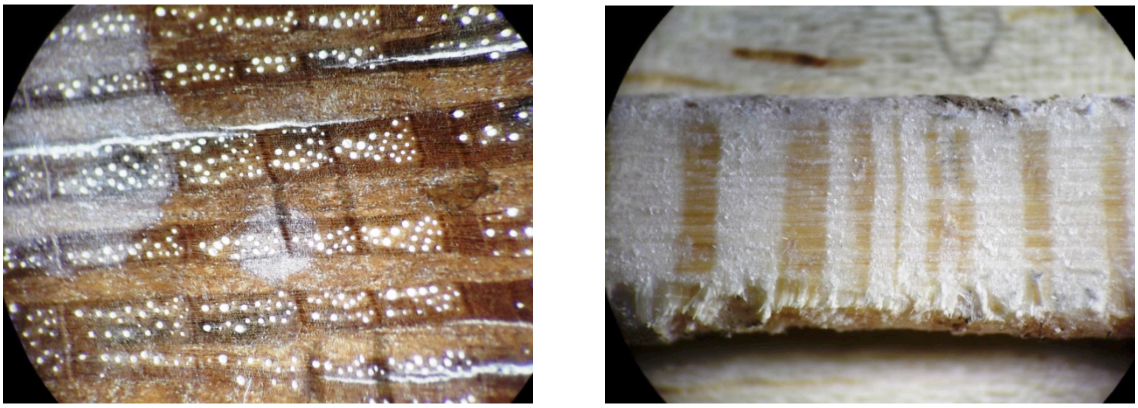
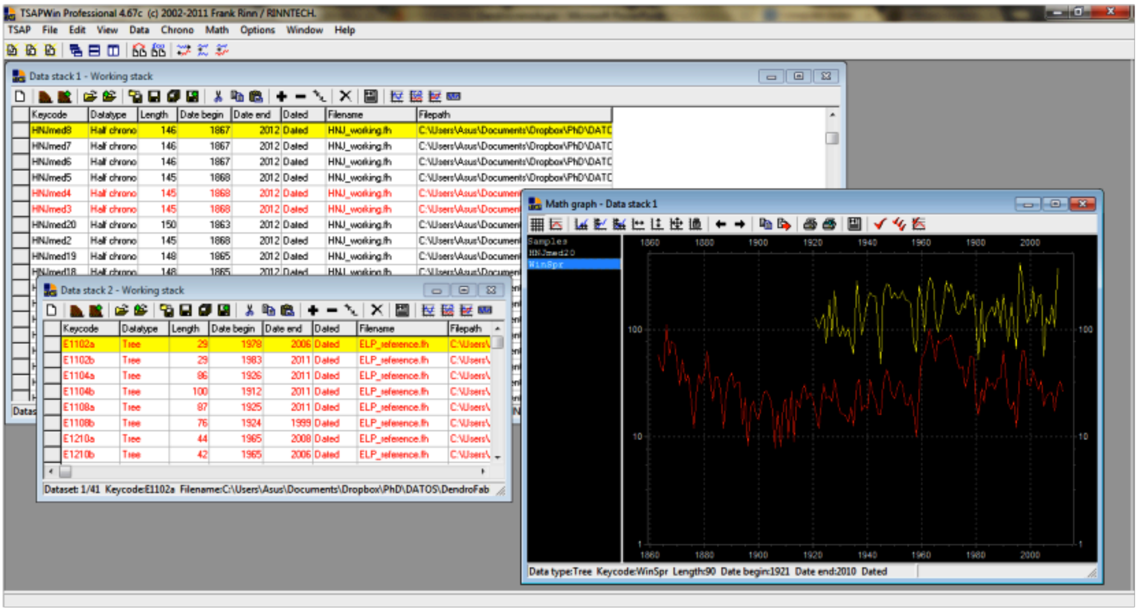


Figure 10. Pictures of the rings of *Q. ilex* (left) and *P. pinea* (right) taken on the eyepiece of the stereomicroscope.



Keycode	Datatype	Length	Date begin	Date end	Dated	Filename	Filepath
HNJmed8	Half chrono	146	1867	2012	Dated	HNJ_working.fh	C:\Users\Asus\Documents\Dropbox\PhD\DATC
HNJmed7	Half chrono	146	1867	2012	Dated	HNJ_working.fh	C:\Users\Asus\Documents\Dropbox\PhD\DATC
HNJmed6	Half chrono	146	1867	2012	Dated	HNJ_working.fh	C:\Users\Asus\Documents\Dropbox\PhD\DATC
HNJmed5	Half chrono	145	1868	2012	Dated	HNJ_working.fh	C:\Users\Asus\Documents\Dropbox\PhD\DATC
HNJmed4	Half chrono	145	1868	2012	Dated	HNJ_working.fh	C:\Users\Asus\Documen
HNJmed3	Half chrono	145	1868	2012	Dated	HNJ_working.fh	C:\Users\Asus\Documen
HNJmed20	Half chrono	150	1863	2012	Dated	HNJ_working.fh	C:\Users\Asus\Documen
HNJmed2	Half chrono	145	1868	2012	Dated	HNJ_working.fh	C:\Users\Asus\Documen
HNJmed19	Half chrono	148	1865	2012	Dated	HNJ_working.fh	C:\Users\Asus\Documen
HNJmed18	Half chrono	148	1865	2012	Dated	HNJ_working.fh	C:\Users\Asus\Documen

Keycode	Datatype	Length	Date begin	Date end	Dated	Filename	Filepath
E1102a	Tree	29	1978	2006	Dated	ELP_reference.fh	C:\Users\
E1102b	Tree	29	1983	2011	Dated	ELP_reference.fh	C:\Users\
E1104a	Tree	86	1926	2011	Dated	ELP_reference.fh	C:\Users\
E1104b	Tree	100	1912	2011	Dated	ELP_reference.fh	C:\Users\
E1108a	Tree	87	1925	2011	Dated	ELP_reference.fh	C:\Users\
E1108b	Tree	76	1924	1999	Dated	ELP_reference.fh	C:\Users\
E1210a	Tree	44	1965	2008	Dated	ELP_reference.fh	C:\Users\
E1210b	Tree	42	1965	2006	Dated	ELP_reference.fh	C:\Users\

Dataset: 1/41 Keycode:E1102a Filename:C:\Users\Asus\Documents\Dropbox\PhD\DATOS\DendroFab

Data type:Tree Keycode:WinSpr Length:90 Date begin:1921 Date end:2010 Dated

Figure 11. Snapshot of a TSAP-Win^{TM} working session. Tree-ring widths are measured using a stereomicroscope and the LINTAB^{TM} table (see Figure 9). The ring-width measurements of each sample are individually stored and then assembled into a chronology, which is subsequently plotted for visual check ("Math graph" on the right). The chronologies are compiled into a database, and "Working stacks" displaying a list of chronologies (on the left) are used to analyze (e.g. cross-dating, computing mean chronologies), edit (e.g. adding missing rings, removing false rings) and save them (as Tucson, Heidelberg, Excel or ASCII formats).

8.3 Statistics of tree ring chronologies

Statistical parameters are used in dendrochonology and related applications in environmental science to assess the quality of the tree ring chronologies and the variability in growth trends (Briffa and Jones, 1990; Cook and Pederson, 2011). In this thesis, the expressed population signal (EPS), the mean inter-series correlation (r) and the signal-to-noise ratio (SNR) were used to evaluate the quality of the chronology signal. The standard deviation (SD) and the mean sensitivity (MS) were used as measures of the variability of tree growth and its responsiveness to environmental factors. The 1st–order autocorrelation (AC) was used to measure the cross-correlation of the chronologies at 1-year lag.

The EPS is a measure of the confidence of the mean chronology of a site in expressing the signal attributable to climate or other population-level limiting factors (Briffa and Jones, 1990). A chronology is dominated by the individual tree-level signal rather than a common population-level signal when EPS is lower than a predetermined value. A value of 0.85 is suggested as a critical threshold for the EPS to be considered high enough to represent an acceptable level of chronology confidence (Briffa and Jones, 1990; and e.g. Andreu et al. 2007; Piovesan et al. 2008). The EPS was computed using the equation:

$$\mathrm{EPS} = \frac{\mathrm{N\,r}}{\mathrm{N\,r} + (1 - \mathrm{r})}$$

where *r* is the mean inter-series correlation and N is the number of trees in the ensemble of detrended series (Briffa and Jones, 1990).

The *r*, used as a measure of the strength of the common signal among trees, was computed as average of all the pairwise correlations between individual tree detrended series using the maximum overlap period between each pair of series (Briffa and Jones, 1990).

The SNR is an expression of the strength of the chronology signal (Briffa and Jones, 1990) and is defined as the proportion of explainable variation (due to a causal factor, e. g. climate) divided by the unexplainable variation (not accounted for by the causal factor) (Kaennel and Schweingruber, 1995). Using flexible curves to detrend tree-ring series leads to an increase of the signal-to-noise ratio and emphasizes the high-frequency response to climate (see e. g. Macías et al., 2006; Domínguez-Delmás et al. 2013a; Piermattei et al. 2014; Latte et al. 2015). The SNR is calculated as:

$$\mathrm{SNR} = \frac{\mathrm{N\ r}}{1 - \mathrm{r}}$$

where *r* is the mean inter-series correlation and N is the number of trees in the ensemble of detrended series (Cook et al.1990a; Briffa and Jones, 1990).

The SD is typically generated from a ring-width time series as a measure of the scatter of values about the mean (Fritts, 1976, p. 255). It is computed as follows (Cook and Pederson, 2011):

$$SD = \sqrt{\frac{\sum_{i=1}^{n}(x_i - \bar{x})^2}{n-1}}$$

where *x* is the ring width and *n* is the number of rings along the chronology.

The AC describes the variance of the current year's growth which is explained by the previous year's growth. It is a type of persistence in growth due to the unidirectionality and continuity in time of the development of biological organisms, e. g. in plants current year's growth and photosynthetic potential are partly influenced by the carbohydrate reserves and leaves produced in the previous year (Fritts and Swetnam, 1989; Speer, 2010, pp.18-20). It is computed as follows (Cook and Pederson, 2011):

$$AC = \frac{\sum_{i=2}^{n}(x_i - \bar{x}) \times (x_{i-1} - \bar{x})}{(n-1) \times SD_x^2}$$

where *x* is the ring width and *n* is the number of rings along the chronology.

The degree to which a tree-ring series reflects growth factors is conceptually defined as "sensitivity": a tree-ring series exhibiting high-frequency variance is termed "sensitive", while a tree with low variability in the ring sequence, indicating that growth is relatively unaffected by inter-annual variations of ecological factors, is referred to as "complacent" tree (Kaennel and Schweingruber, 1995; Speer, 2010, p. 22, 107). The

MS is calculated as average of the relative differences in width from one ring to the next and can be used as an indicator of the intensity of tree growth response to climate (Fritts, 1976). It is calculated with the formula (from Fritts, 1976):

$$MS = \left(\frac{1}{n-1}\right) \times \sum_{t=1}^{t=n-1} \left|\frac{2 \times (x_{t+1} - x_t)}{x_{t+1} + x_t}\right|$$

where x is the growth index and n is the number of annual rings in the tree-ring sequence. The MS ranges from 0 (in which adjacent rings have the same value) to 2 (in which a zero, i.e. “missing ring”, occurs next to a non-zero value). Although MS is a widely used statistic in dendroecology, it is a function of the time series properties of tree rings (i.e. variance and autocorrelations structure), thus its suitability for deducing the nature of growth-limiting factors is limited (Bunn et al., 2013). Therefore, the MS was used in association with a set of parameters, including SD and AC, to assess the degree of growth sensitivity (see Article 1 in Appendix 1).

The statistics were computed using the R software (Venables and Smith, 2015) with the dplR package (Bunn, 2008). The dplR package for R includes functionalities of the Dendrochronology Program Library (DPL) developed by Richard Holmes at the Laboratory of Tree-Ring Research, University of Arizona, Tucson, USA, http://ltrr.arizona.edu/research/software (Holmes, 1992).

8.4 Extraction of climatic signal from the tree ring chronologies and computation of the master chronologies

The extraction of the climatic signal from tree-ring series is done through the standardization procedure, which involves three steps: (1) “detrending”, i.e. removing the growth variability unrelated to climate from individual series of measured tree-ring series, (2) “indexing”, i.e. computing dimensionless tree-ring data from the detrended series, (3) estimating a master chronology containing the common climatic signal of the ensemble of trees by averaging the indexed series (see Cook and Briffa, 1990).

Detrending is a crucial step in the standardization procedure. The term, “detrending”, at first referred specifically to the removal of the age-related long-term decreasing trend of ring widths in open-grown trees (Fritts, 1976; Biondi and Qeadan, 2008), is relevant to all non-climatic ring-width variance which is considered as noise and removed, whatever the origin of this variance (e.g. ageing, increasing size and various disturbance pulses). The methods of trend removal typically involve fitting a smoothing function to the ring-width series and can be distinguished as parametric (or “deterministic”, following Cook et al., 1990a), when the fitted function is an *a priori* defined mathematical model (e. g. straight lines, exponential or polynomial functions), and non-parametric (or “stochastic”, *ibid.*) methods, which imply fitting a data-adaptive running function to the series, e.g. weighed moving average, Gaussian filters or splines. Since parametric models involve *a priori* assumptions regarding the form of the raw ring-width data and are functions of time only, the goodness-of-fit can vary with time because of the low/middle-frequency stochastic perturbations commonly found in ring-width series of trees growing within stands owing to competitions and stand dynamics. For that, data-dependent detrending methods can be more appropriate to find the best fitting to the data (Cook et al., 1990a). However, care must be taken when using a non-parametric model because, the more it closely follows the fluctuations of the ring width series (i.e. the more the smoothing function is flexible), the more the variance is removed at the low-frequencies (e.g. very flexible splines, see Speer, 2010, p. 23-27). Long-term climatic changes are recorded in low-frequency growth variability (e.g. Piovesan and Schirone, 2000; Jump et al, 2006; Piovesan et al. 2008; Gea-Izquierdo and Cañellas 2014), which hence should be also retained as climatic signal (Briffa et al. 1996; Esper et al. 2002; Hughes et al. 2002). Low-frequency signals can be detected by "conservative" detrending methods, which include deterministic models or derived approaches (see e.g. Bunn et al., 2004; Biondi and Qeadan, 2008; Linderholm et al. 2010), and stiff digital filters (see e.g. Helama et al. 2004). Moreover, smoothing functions fitted to ring-width series cannot detect fluctuations in climate lasting longer than the lifetime of the trees from which the ring-width series come (Cook et al. 1995), and other techniques can be considered to improve the capture of century-scale variability (see Briffa and Melvin, 2011).

The choice of the detrending method must be done on the basis of an evaluation of the time-frequency domain of the resulting standardized chronology. As suggested by Cook and Peters (1981), "we want to preserve as much low-frequency climatic variance as possible and yet remove divergent non-climatic anomalies that, in the time domain, could be wrongly interpreted as exceptional climatic events". The selection of a proper detrending method takes into account the purpose of the investigation, e.g. whether low-frequency or high-frequency response to climate is desired (Briffa et al., 1996; Esper et al., 2002), and those attributes of the primary data that can influence the applicability and performance of the detrending procedures, e.g. chronology length, age structure of the sampled stand, sample depth, amplitude and frequency of growth oscillations (Blasing et al., 1983; Esper et al., 2003; Bunn et al., 2004; Melvin and Briffa, 2008; Linderholm et al., 2010).

In the Article 1 (Appendix 1) detrending criteria based on smoothing functions were tested in two stands in Huelva. Ring-width measurements were smoothed by fitting functions with different degree of flexibility. Flexible splines with periods of 32 years were appropriate to extract the climatic signal. Similarly, in the Article 3 (Appendix 1), which also included stands from Northern and Central Spain, the best assessment of growth-climate relationships were obtained using splines with periods of 30 years. The appropriateness of flexible splines in the study sites is mainly related to the capability of these methods to remove the non-climatic silviculture-related growth variability (see discussion sections in the Articles 1 and 3). Therefore, splines with periods around 30 years were used to detrend all the tree-ring chronologies.

The indexing procedure involves computing dimensionless tree-ring indices. The non-stationary ring widths are transformed into a new series of stationary tree-ring indices that have a defined mean of 1 and an almost constant variance (Matalas, 1962). This is accomplished by dividing each measured ring width by its expected values, as estimated by the fitted detrending curve (Cook et al. 1990a). The indices are produced by division because ring-width series are heteroscedastic, i.e. the local variance of a time series is directly proportional to the local mean, where "local" refers to some subinterval of time within the whole time span covered by the time series (Matalas, 1962). Thus, local ring-width means are highly correlated with local ring-width variance. After calculating tree-ring indices as ratios, the linear dependence between the local mean and the local variance is for the most part removed.

Cook and Peters (1997) demonstrated that tree-ring indices calculated as ratios can be biased. The potential of bias is related to the negative slope of the detrending curve and to the lack of fit between the detrending curve and the ring width measurements. Thus they suggest that residuals from the curve, rather than ratios, can be computed in conjunction with appropriate transformation of primary data to stabilize the variance. However, this bias is not always serious and ratios can be used safely in many situations (see Cook and Peters, 1997). In particular, the 30-year splines used in the standardization process reduced the risk of bias deriving from the lack of fit between the detrending curve and the measurements. To tests the influence of indexing procedures on the study of growth-climate relationships, ring-width indices were computed as ratios and residuals after power transformation (following Cook and Peters, 1997) in the *P. pinea* study sites Carrascal, Viana de Cega, Hoyo de Pinares, Valverde del Camino and Hinojos. The chronologies calculated in the two manners were very similar (correlation coefficients: 0.93 to 0.99), and there were no significant differences in the growth-climate correlation patterns calculated using the two types of indexed chronologies. Therefore, it was assumed that the used indexing procedure had little impact in the purposes of this thesis, and the tree-ring series indexed as ratios were used in all sites.

To estimate the master chronology, a classical approach is averaging the detrended tree-ring data across series for each year through an arithmetic mean (Matalas, 1962; Fritts 1976, pp. 261-268). Since the arithmetic mean can be biased by outliers in the tree-ring indices caused by endogenous disturbances or other sources of noise, the estimation of the master chronology can be accomplished by the use of a robust mean, which reduces the influence of outliers (Cook et al. 1990b). In this thesis, the master chronology of each site was computed as a bi-weighed robust mean of the indexed chronologies. Finally, to assure the quality of the master chronologies used in the analyses of growth-climate relationships, the EPS was computed over successive time windows and only the intervals in which the EPS was higher than 0.85 were used.

Prewhitening techniques can be applied to remove the autocorrelation structure of the tree-ring series. In dendroclimatic studies, autocorrelation can represent a problem because the usual statistical analyses (e. g. regression models for climate-growth relationship calibration) assume that data are not autocorrelated since this can alter the correlation statistics, and growth variability deriving from autocorrelation is considered as noise (i.e. not linked to current year's climate) leading to a degradation of the common signal strength (Cook et al.1990b; Fritts and Guiot, 1990). Some amount of autocorrelation persists after detrending and is better removed by autoregressive models (see e.g. Meko et al. 1993). For statistical analysis in the Articles 1, 2 and 4, an autoregressive model was fitted to the indexed series to remove the autocorrelation before computing the master chronology, following Cook et al. (1990b). However, some amount of climate-related low frequency variability might be removed from chronologies along with autocorrelation, thus non-prewhitened series are also suitable when the purpose of the investigation is to examine the growth response to climate and not to use growth-climate relationships to reconstruct climate variables (see Martín-Benito et al., 2010). In the Article 3 (Appendix 1), no autoregressive model was used, but the index series were tested for autocorrelation.

All the standardization procedures were carried out using the dplR package within the R software (Bunn, 2008) and the program ARSTAN (version 41d and version 44h3, programmed by Edward R. Cook and Paul J. Krusic at the Tree-Ring Laboratory of the Lamont-Doherty Earth Observatory, Columbia University Earth Institute, New York, USA, http://www.ldeo.columbia.edu/tree-ring-laboratory/resources/software).

8.5 Climate data

Different climate parameter and climate data were used to examine the relationships between tree growth and climate (Table 5).

The used climate parameters were: precipitation, mean temperature, maximum temperature, minimum temperature, self-calibrating Palmer drought severity index (scPDSI) and diurnal temperature range (DTR). The scPDSI (Wells et al., 2004) improves upon the Palmer Drought Severity Index (PDSI; Palmer, 1965), which integrates seasonal values of temperature and precipitation as a balance between supply and demand of water over successive months. Specifically, the scPDSI enhances the PDSI by maintaining a consistent behavior of the index over diverse climatological regions, thus making spatial comparisons of the drought index values on large scales more meaningful. The DTR is the difference between the daily maximum and minimum temperature, is a measurement of climate change study and is linked to cloud cover (Karl et al., 1987, 1993; also see Qu et al., 2014).

The climate data were obtained from two sources: meteorological stations and gridded datasets. The meteorological stations provide actual records of weather, specifically precipitation and temperatures. The availability of records varies in time and space depending on the location of the station, the density of meteorological stations, and the year in which the station was placed and records started. The gridded datasets use station records to provide climate data with a consistent pattern over large areas. Moreover, the gridded datasets provide derived variables such as climate indices. The quality of the gridded datasets depends on the homogeneity of the station records and the resolution of the grid.

Table 5. Climate data sources and climate parameters.

Climate data sources		Grid resolution	Coordinates and elevation	Climate parameters	Time span
Gridded datasets	CRU TS3.23	0.5° x 0.5°		Precipitation; Temperatures; DTR (a)	1901-2013
	CRU 3.21	0.5° x 0.5°		scPDSI (b)	1901-2012
	E-OBS v11.0	0.25° x 0.25°		Precipitation; Temperatures	1950-2014
	Berkeley Earth	1° x 1°		Temperatures	1750-2014
Meteorological stations (c)	Valladolid-Villanubla		41.70° N, 4.85° W; 846 m	Precipitation; Temperatures	1936-2014
	Ávila		40.66° N, 4.68° W; 1130 m	Precipitation; Temperatures	1957-2014
	Huelva		37.26° N, 6.95° W; 17 m	Precipitation; Temperatures	1920-2014
	Lisbon		38.72° N, 9.15° W; 77 m	Precipitation; Temperatures	1901-2012
	Tarquinia		42.25º N, 11.74º E; 11 m	Precipitation; Temperatures	1952-2013
	Albacete		38.95° N, 1.86° W; 704 m	Precipitation; Temperatures	precipitation data: 1940-2010 temperature data: 1919-2010
	Molina de Aragón		40.84° N, 1.89° W; 1056 m	Precipitation; Temperatures	precipitation data: 1950-2010 temperature data: 1960-2010

(a) Diurnal temperature range; (b) self-calibrating Palmer drought severity index.

(c) The meteorological stations were used for different study sites, as follows:

Valladolid-Villanubla: Carrascal and Viana de Cega;

Ávila: Hoyo de Pinares;

Huelva: Calañas, Huerto Ramirez, Hinojos, Moguer, Mazagon, Punta Umbría, El Portil, Campo Común de arriba, Valverde del Camino

Lisbon: Pegões

Tarquinia: Tarquinia

Albacete: Pinar Viejo, La Pasadilla (ITRDB)

Molina de Aragón: Dehesa del Peral (ITRDB)

The meteorological station records (precipitation, mean/max./min. temperature) were obtained from the European Climate Assessment Dataset project (ECA&D, see Klok and Klein Tank, 2008; http://www.ecad.eu). The ECA&D includes "non-blended" (raw observations from meteorological stations) and "blended" (homogenized by infilling gaps with observations from nearby stations) series of daily meteorological station records provided by national weather services (see http://www.ecad.eu/FAQ). With regard to the meteorological station records used in this thesis, the national weather services are the Spanish State Meteorological Agency ("Agencia Estatal de Meteorología", AEMET) and the Portuguese Institute of the Sea and the Atmosphere ("Instituto Português do Mar e da Amosfera", IPMA). The closest station to each study site was chosen and the blended series were used (blended and non-blended series present very few differences in the case of Spanish stations; see the supplementary material of the Article 3, Appendix 1). The ECA&D do not include any station close to the study site in Tarquinia: in this case, meteorological records were obtained from the "Ufficio Idrografico e Mareografico" (hydrographic and mareographic service) of the administrative region of Lazio, available at http://www.idrografico.roma.it.

The sources of the gridded data were:

- the E-OBS v11.0 dataset by the EU-FP6 project ENSEMBLES (Haylock et al., 2008), including precipitation and temperature data since the 1950 with a grid resolution of 0.25ºx0.25º;
- the CRU TS3.23 (Harris and Jones, 2014) by the Climatic Research Unit, University of East Anglia, UK (hereinafter "CRU"), including DTR, precipitation and temperature data since the 1901 with a grid resolution of 0.5ºx0.5º;
- the CRU 3.21 (van der Schrier et al., 2006), including scPDSI values since the 1901 with a grid resolution of 0.5ºx0.5º.

For each gridded dataset, the closest grid point to the study site was selected through the Climate Explorer developed by the Royal Netherlands Meteorological Institute (KNMI). The KNMI Climate Explorer is a web application to search and analyze climate data, available at http://climexp.knmi.nl/. It compiles a large number of periodically updated climate databases, including station records and gridded datasets of weather variables and climate indices from different sources worldwide (Global Historical Climatology Network, www.ncdc.noaa.gov; Climatic Research Unit, www.cru.uea.ac.uk; National Climatic Data Center, www.ncdc.noaa.gov; National Centers for Environmental Prediction, www.ncep.noaa.gov; National Center for Atmospheric Research, https://ncar.ucar.edu; European Climate Assessment & Dataset, www.ecad.eu).

In the Articles 1, 2 and 4, scPDSI from gridded datasets and values of precipitation and mean/max./min. temperature from meteorological stations were used. In the Article 3, the full ensemble of climate parameters and climate data sources was used.

8.6 Analysis of growth-climate relationships

The relationships between tree growth and climate were examined computing correlation and response functions with bootstrapped confidence intervals. Correlation and response functions give a sequence of coefficients computed between a tree-ring chronology and monthly resolved climate data. In the case of correlations, the coefficients are univariate estimates of Pearson's product moment correlation. In the case of response functions, the coefficients are multivariate estimates from a principal component regression model. The response function was introduced by Fritts et al. (1971) and further developments of the method are illustrated by Briffa and Cook (1990). The response function addresses the problem of multicollinearity between climate series. Multiple regression analysis assumes that predictors (i.e. climatic covariates) are independent, thus multicollinearity contravenes this assumption. In the response function, the original set of predictors is converted to a set of new, uncorrelated predictors using principal component analysis.

The bootstrap method permits to assign measures of accuracy (e.g. confidence intervals, prediction errors) to sample estimates. In the case of regression and correlation, this technique is useful when no assumption about the probability distribution of the original observations can be made (Guiot, 1991). The idea is to replace the lack of information on the statistical properties of the data with a great number of estimates, each based on different subsamples of the data. The original *n* observations are randomly sampled with replacement to construct an arbitrary number of new data sets of size *n*. The mean of regression/correlation coefficients and their standard deviation are then calculated from these new data sets. Bootstrapped confidence intervals were used to estimate the significance of correlation and response functions, following Guiot (1990, 1991) and Till and Guiot (1990).

Correlation and response functions were computed using the program DENDROCLIM2002 (Biondi & Waikul, 2004) and the packages bootRes and treeclim of the program R (Zang & Biondi, 2012, 2015). Computations were carried out over full time series, i.e. the overlapping intervals of tree-ring series and climate data series, as well as successive time windows to test the stability of growth-climate relationships. Further details about computations of growth-climate relationships are provided in the annexed article (Appendix 1).

9 GENERAL DISCUSSION

9.1 Tree ring chronologies

The tree-ring chronologies are displayed in Figure 12 and their statistical characteristics are in Tables 3 and 4. The International Tree Ring Data Bank (ITRDB) includes 73 tree-ring chronologies from the Iberian Peninsula, mostly obtained from conifers and distributed across the central and north-eastern areas (Figure 13). More than half of these chronologies (48, i.e. 66%) have been dated before the 1990, 9 of them in the 1990s, and 16 of them between the 2000 and the 2008 (Figure 13). The tree-ring chronologies compiled in the ITRDB are provided by dendrochronologists worldwide, but the number of tree-ring data globally produced is higher than that included in the ITRDB. Indeed, the recent review by Dominguez-Delmás et al. (2015), including published scientific works using tree-ring chronologies from living trees, highlights the increase of tree-ring studies in the 2000s (Figure 14). However, this review still shows the higher number of tree-ring data in the northern areas of the peninsula. This thesis contributes to the development of the tree-ring database in the Iberian Peninsula, especially in the south of this region (Figure 15).

The new network of tree-ring chronologies developed in this thesis permitted to study tree growth dynamics in relation to climate change, including trees from different environments. This was possible thanks to the quality of the chronologies. Tree-ring width series from 553 samples (273 trees) were successfully cross-dated, 359 (164 trees) of which from southern Spain, collected in 14 sites, 9 of them in southern Spain (Tables 3 and 4). The inter-series correlation coefficients and the the EPS indicate good chronology signals in all the study sites (Tables 3 and 4). Principal component analyses of the chronologies in the province of Huelva indicated the existence of common dendroclimatic signal (see Article 2 in Appendix 1, and Conference presentation 6 in Appendix 2). Moreover, the comparison between the *Q. ilex* chronologies of Huerto Ramirez and Calañas, the *P. pinea* chronology of Valverde del Camino, and a *Q. ilex* chronology from Cáceres (a neighboring area in West-Central Spain, published by Gea-Izquierdo et al., 2011), validated the tree-ring chronologies (see Article 4 in Appendix 1).

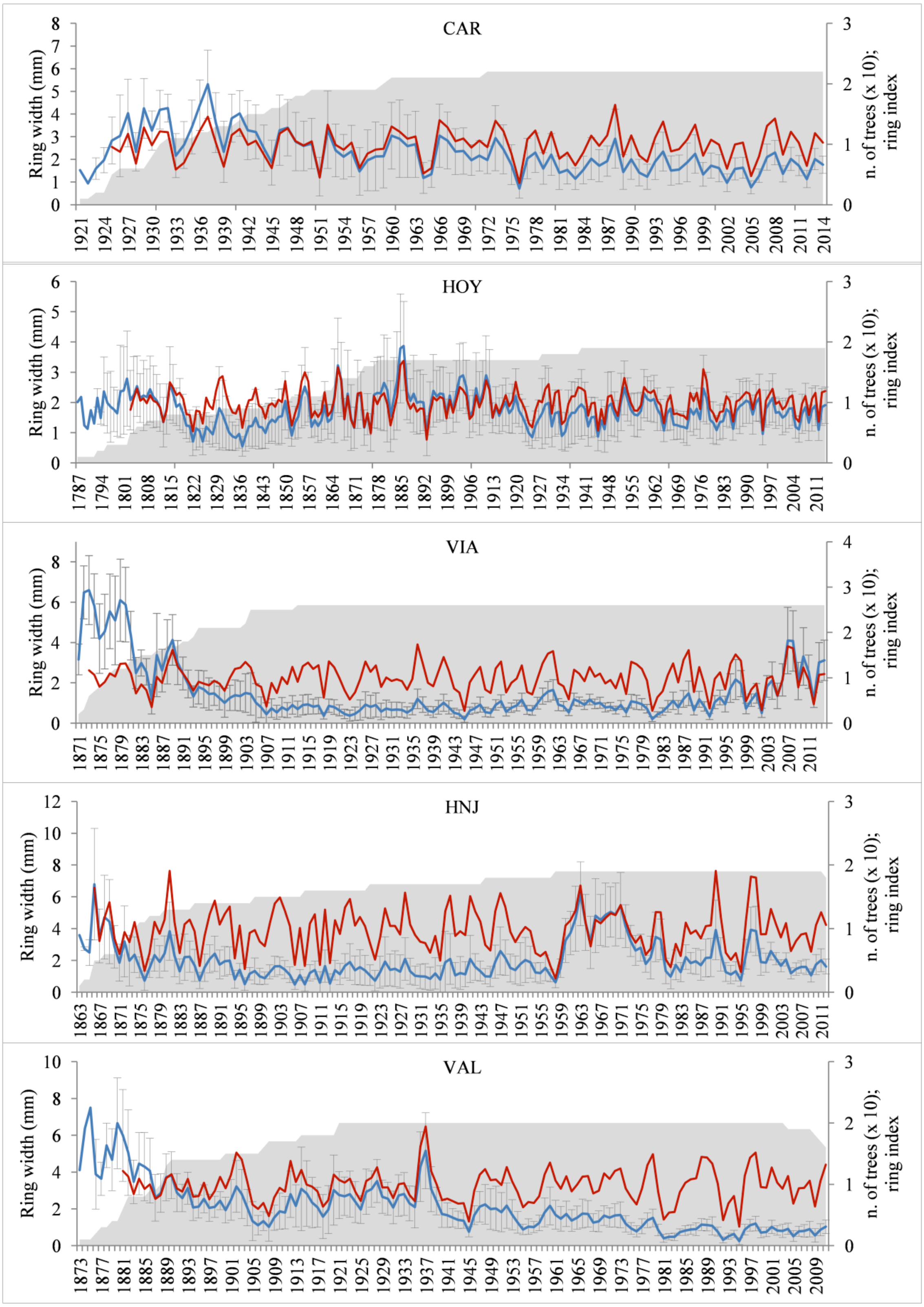


Figure 12. Mean tree ring width chronologies (blue curve) and standardized chronologies (red curves). The verticals bars are the standard deviation of the ring widths. The shadings indicate the sample depth (number of trees). The standardized chronologies are given for the period with at least 5 trees. Note the different scales of the *x* and *y* axes. The abbreviations of the study sites are: CAR (Carrascal), HOY (Hoyo de Pinares), VIA (Viana de Cega), HNJ (Hinojos), VAL (Valverde del Camino), CCA (Campo Común de Arriba), MOG (Moguer), MAZ (Mazagón), ELP (El Portil), PUM (Punta Umbría), QHR (Huerto Ramirez), QCA (Calañas).

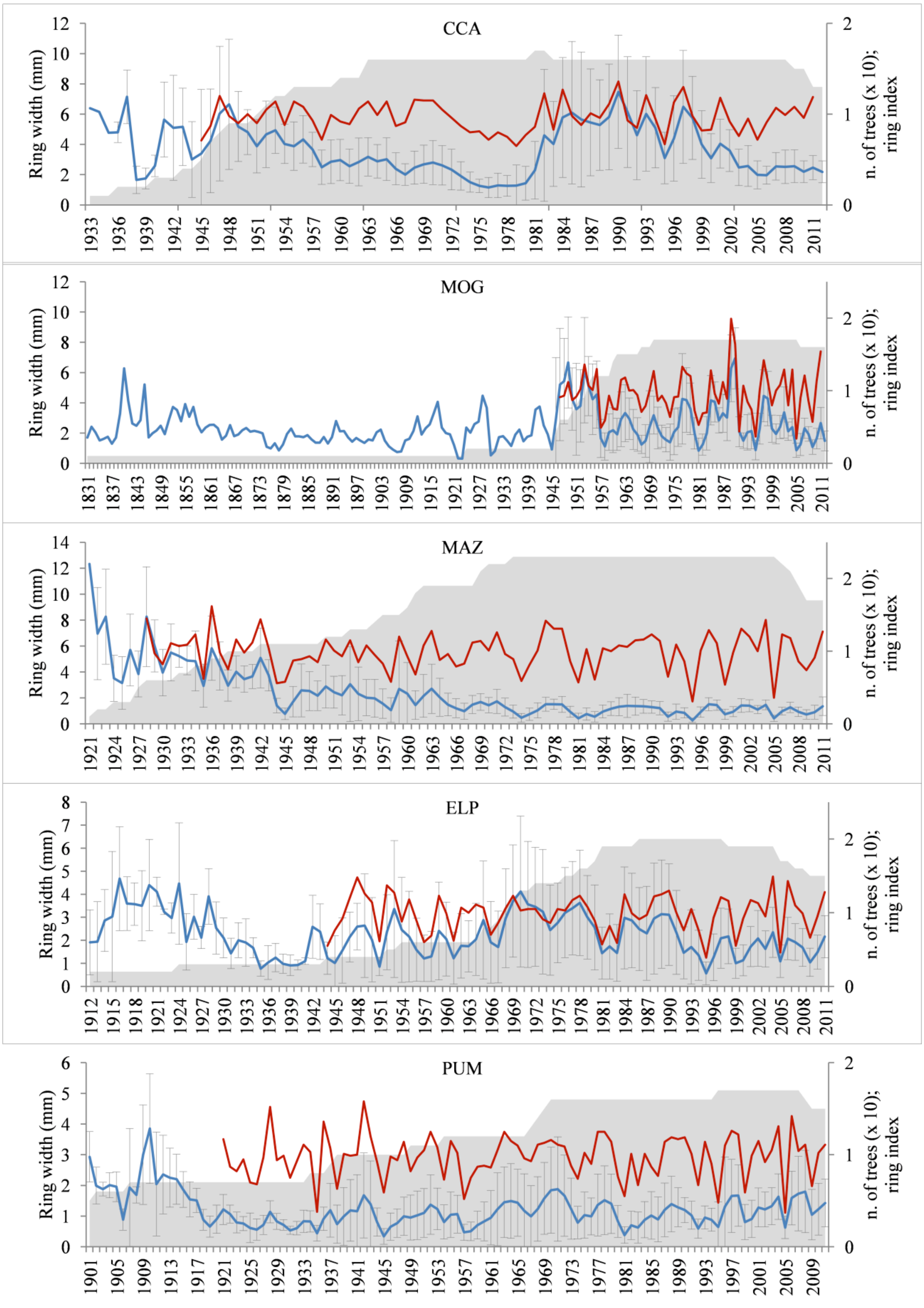
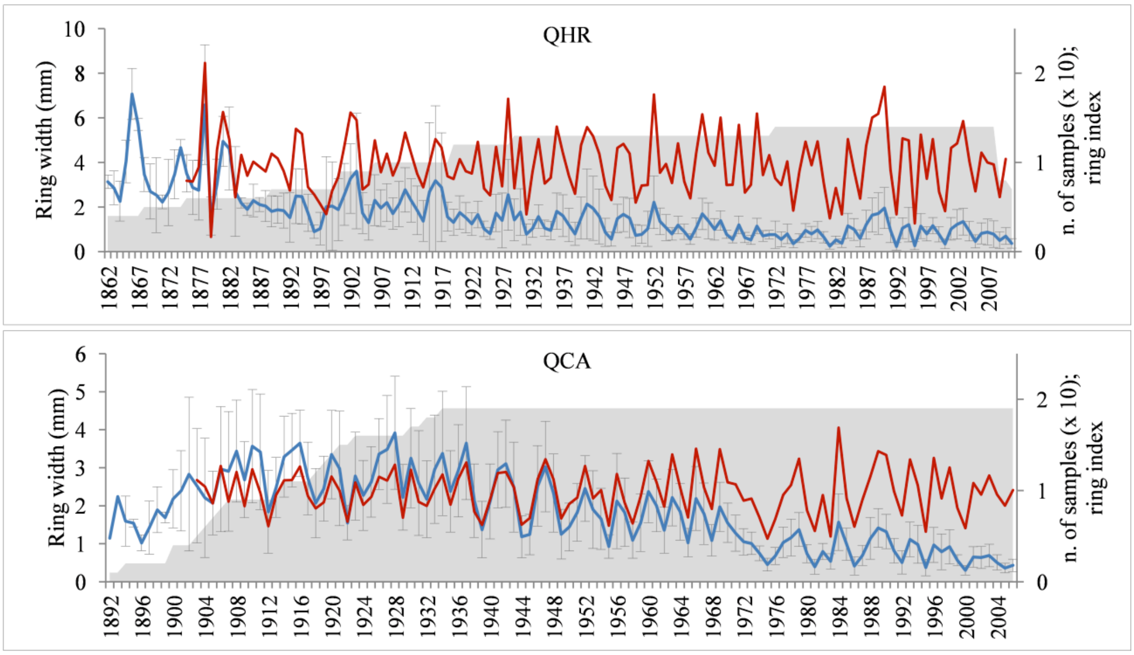


Figure 12 (continued)



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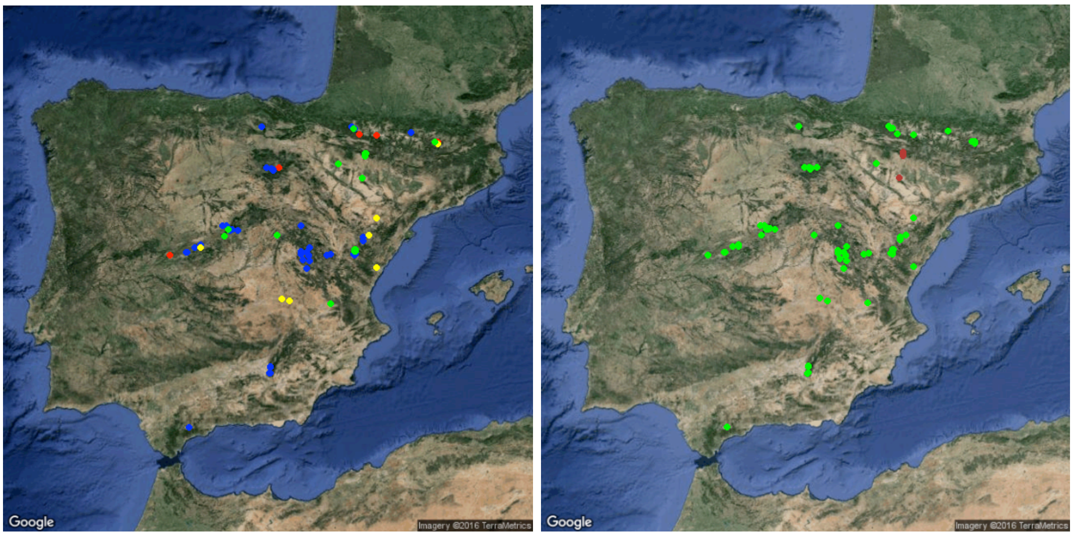


Figure 13. The tree ring chronologies available in the ITRDB by 6th May 2016 for the Iberian Peninsula (Spain and Portugal). Left: the red, blue, yellow and green dots indicate that the last year of the chronology is in the 1970s, 1980s, 1990s and 2000s, respectively (the earliest is 1977 and the most recent is 2008). Right: the brown and green dots indicate broadleaves and conifers, respectively. No chronology was available for Portugal.

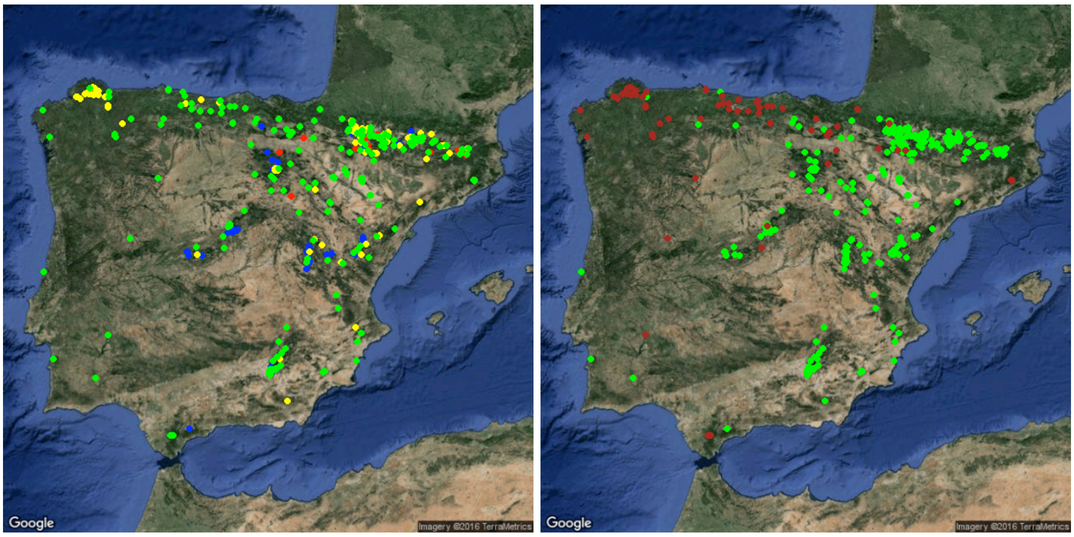


Figure 14. Tree-ring chronologies from living trees published in scientific works in the Iberian Peninsula. Left: the red, blue, yellow and green dots indicate that the last year of the chronology is in the 1970s, 1980s, 1990s and 2000s, respectively (the earliest is 1947 and the most recent is 2012). Right: the brown and green dots indicate broadleaves and conifers, respectively (from Domínguez-Delmás et al. 2015, modified).

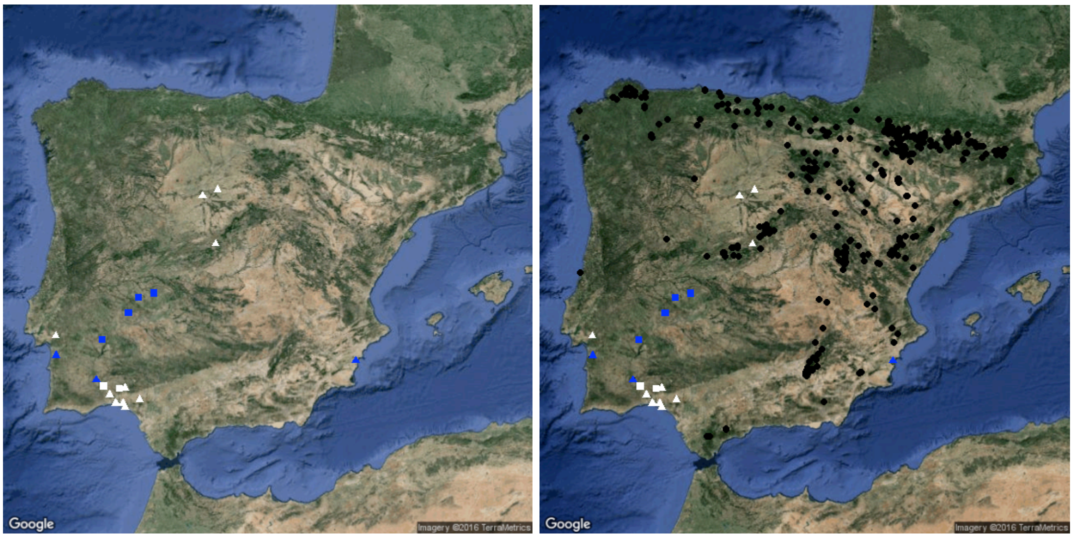


Figure 15. Left: the blue squares and triangles indicate the study sites of peer-reviewed scientific works on *Q. ilex* and *P. pinea*, respectively, in the southern Iberian Peninsula (see the section 5.4 “Tree ring studies of P. pinea and Q. ilex in the Southern Iberian Peninsula"). The white squares and triangles indicate the study sites of *Q. ilex* and *P. pinea*, respectively, of this thesis. Right: the same as left, with the black dots indicating the locations of all the chronologies of the ITRDB (see Figure 13) and all the study sites compiled by Domínguez-Delmás et al. 2015 (see Figure 13).

As described earlier (see the section 5.4 "Tree ring studies of P. pinea and Q. ilex in the Southern Iberian Peninsula"), the low number of tree-ring chronologies in the southern Iberian Peninsula is partly explained by the high intra-annual variability of climate in this region, which induces the formation of frequent intra-annual density fluctuations (IADFs) in tree-ring growth, and can make difficult to distinguish annual rings. In the samples used for this thesis, IADFs were detected through a careful inspection of the ring borders and visual cross-dating along several radii on the stem cross sections (in the case of *Q. ilex*) and by multiple comparisons of several increment cores (in the case of *P. pinea*). Same examples of IADFs are in Figure 16. The position of false rings was firstly detected by cross-dating several tree-ring series. However, recognizing false rings in Huelva was sometimes very difficult and could be done through the comparison between the observed patterns of wood formation and the climate diagrams. In particular, observing the distribution of rainfalls during the year was useful to detect some inclusion of latewood within the earlywood (see Figure 16). This kind of verification can be done only when several tree-ring series have been analyzed and cross-dated, and preliminary growth-climate correlation analyses have been done. Moreover, a previous study of the climate of the study area is necessary to know the normal climatic regimes and to identify those years in which the intra-annual climatic patterns did not follow the norm or presented higher variability, probably inducing the formation of IADFs. For instance, a decrease of precipitation in spring or early summer reduces water availability and can induce the formation of latewood-like cells (narrower xylem cell lumen and thicker xylem cell walls). A subsequent recovery of growth, following the return of precipitation in late summer or autumn, can induce the formation of earlywood-like cells (wider xylem cell lumen and thinner xylem cell walls). Some studies have addressed this "bi-modal" pattern of Mediterranean tree growth (e.g. Cherubini et al., 2003; Camarero et al., 2010; Gutiérrez et al., 2011; Martín et al., 2014). As a result of this intra-annual variability of precipitation amounts, two rings (even three rings, although rarely, in some *P. pinea* samples of this thesis) are formed within a growing season. The climatic interpretation of false rings in this thesis was also supported by published dendrochronological studies concerning IADFs. Campelo et al. (2007b), in *P. pinea* in Mediterranean areas in Portugal, found that the formation of earlywood-like cells within the latewood of a certain year was strongly correlated with precipitation in September and October of the same year. Campelo et al. (2007a) reported that double rings (i.e. "extra growth bands" within the latewood, see Figure 2 in Campelo et al., 2007a) in *Q. ilex* in Spain were positively correlated with precipitation in August and negatively correlated with temperatures in September of the year of formation of the ring. Vieira et al. (2010) described IADFs in the latewood of *Pinus pinaster* in Mediterranean areas in Portugal, which were also correlated with precipitation and temperature of the autumn (Sep-Nov) of the year of ring formation.

In the samples used for this thesis, missing rings were also found, i.e. locally absent rings, which are not uniformly formed along the whole circumference of the stem. An example of missing ring in *Q. ilex* is in Figure 17. In this case, different radii did not cross-date because some of them presented a higher number of rings. The examination of the ring borders along the circumference permitted to find out that some rings were formed only over a part of the stem. The analysis of missing rings was not included as a purpose of this thesis, but in both species most of the missing rings occurred during dry periods, especially in the mid 1990s (dry periods were identified using meteorological variables and drought indices: see the Articles in Appedix 1). This is in line with previous studies in Mediterranean pines, where high frequencies of missing rings are associated with decreases in precipitation and increases in temperatures, which cause water deficit and thus induce a reduction in wood formation (Novak et al., 2011, 2016).

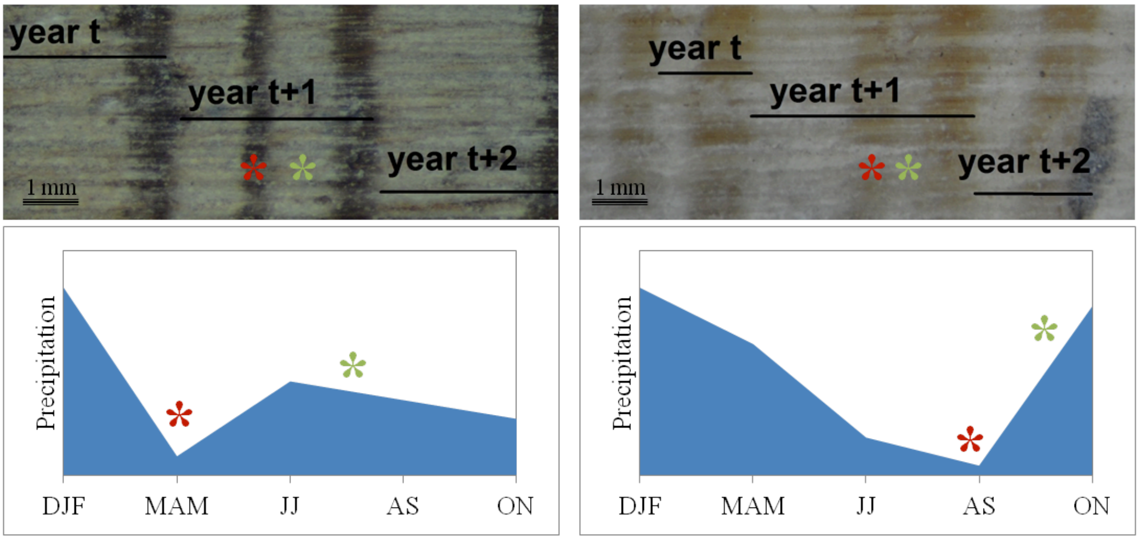


Figure 16. Intra-annual density fluctuations in *P. pinea* tree rings in samples from Huelva. There are false rings in the years t+1. The diagrams describe the distribution of precipitation during the year t+1. Left: the red asterisks indicate latewood-like cells within the earlywood and the associated descrease of precipitation during the spring (March-April-May, MAM in the diagram below). The subsequent recovery of growth is associated to the precipitation in June-July, JJ, and August-September, AS (green asterisks). Right: the red asterisks indicate the formation of latewood associated with the decrease of precipitation in summer (JJ and AS in the diagram below), while the green asterisks indicate earlywood-like cells within the latewood and the associated return of precipitation in October-November.

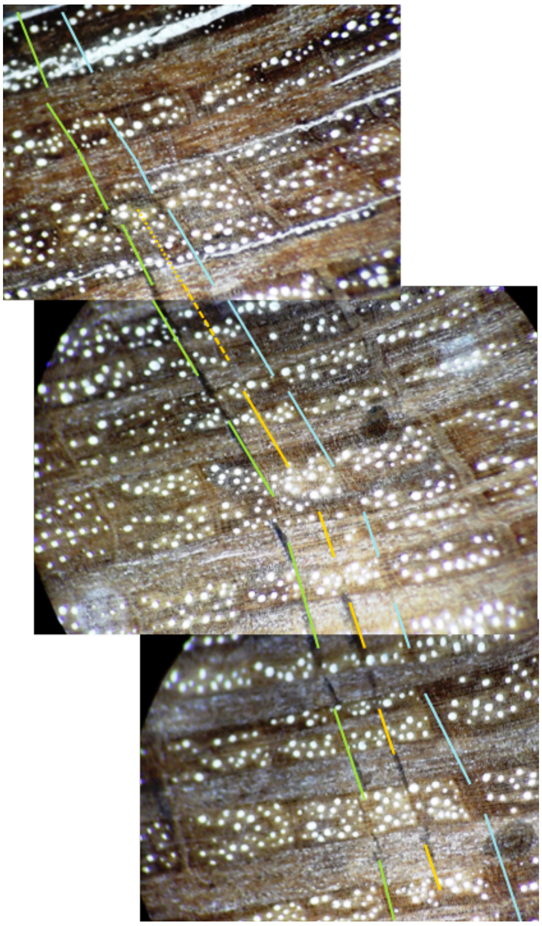


Figure 17. Photographs taken over three adjacent parts of a stem cross section of *Q. ilex* using a camera mounted on the eyepiece of the stereomicroscope. The green line indicates the beginning of an annual ring (year t), and the blue line indicates the end of the subsequent annual ring (year t+1). The yellow line in the middle shows how the boundary between t and t+1 is clearly visible at the bottom and disappears at the top.

9.2 Climatic signals from tree-ring chronologies: standardization techniques and climate data.

The standardization techniques in dendroclimatology are aimed at removing the non-climatic variance from the tree-ring series. This permits to extract a noise-free signal which can be used to examine climate-related growth patterns. However, climate acts on growth patterns at different time-scales, from the intra and inter-annual to the inter/multi-decadal. A number of studies have addressed the search for appropriate standardization techniques and, although mixed models have been experimented to account for the effect of stand competition (see Piutti and Cescatti, 1999; Pukkala et al., 2002), curve-fitting methods are largely used, providing robust climatic signals for climatological and ecological investigations (e.g. Fritts, 1976, pp. 261-281; Warren, 1980; Warren and MacMilliam, 1981; Cook and Peters, 1981; Blasing et al., 1983; Holmes et al., 1986; Shiyatov et al., 1989; Cook et al., 1995; Briffa et al., 1996; Cook and Peters, 1997; Esper et al., 2003; Bunn et al., 2004; Helama et al., 2004; Melvin et al., 2007; Biondi and Qeadan, 2008; Melvin and Briffa, 2008; Linderholm et al., 2010; Bontemps and Esper, 2011; Briffa and Melvin 2011; Yuan et al., 2013). The choice of the degree of flexibility of the detrending curve is a crucial step in the standardization procedure, as explained earlier (see sections 2.3, "Use of tree rings to study the effects of climate on forest tree growth", and 4.4, "Extraction of climatic signal from the tree ring chronologies and computation of the master chronologies"). There is agreement in stating that a "universally valid" or "best" method does not exist. Rather, the choice of the detrending method must be done on the basis of an evaluation of the time-frequency domain of the chronology, and it takes into account the purpose of the investigation, e.g. whether low-frequency rather than high-frequency response to climate is desired, and those attributes of the primary data that can influence the applicability and performance of detrending procedures.

In this thesis, the problem of selecting the detrending techniques was specifically addressed in the Article 1 and was further developed in the Article 3 (see Appendix 1). In both cases, a smoothing spline with a rigidity equal or close to 30 years was found to be the most suitable for our chronologies and study purposes. This is a rather flexible curve which has demonstrated to provide the highest inter-series correlations, i.e. strength of chronology signal (see Grissino-Mayer, 2001; Helama et al., 2004), and to be especially useful to study the climate-related growth patterns when noise at middle-frequencies potentially masks the climatic signal (Gea-Izquierdo et al. 2009, 2011, 2014a, 2014b). It retains less low-frequency variance than conservative curve-fitting methods as negative exponential curves, polynomial functions (see Fritts, 1976, pp. 261-268), or Hugershoff curves (see Fang et al., 2010). Conservative methods are generally more apt to capture low-frequency growth variations which can indicate a response of tree growth to long-term climatic changes. However, growth releases and suppressions are reflected in tree-ring chronologies of trees grown within stands, even in low-density stands, where a degree of between-tree competition exists and influences the growth patterns (Gea-Izquierdo and Cañellas, 2009; Gea-Izquierdo et al., 2011, Martín et al., 2014). In such situations, the goodness-of-fit decreases with conservative methods, and middle-frequency growth variability could be wrongly interpreted as climatic. Biondi and Qeadan (2008) explain that the conservative detrending method "was developed at the Laboratory of Tree-Ring Research in Tucson, Arizona, where a large portion of wood specimens being analyzed was from open-grown and/or shade-intolerant species". Citing the Edward Cook's PhD dissertation (University of Arizona, 1985), these authors add: "after a common short-lived increase in radial growth following germination, the growth increment curve of such open-grown trees reaches a maximum and then declines monotonically with increasing age to a relatively constant growth rate, so that the age trend is composed of two fairly distinct periods: an early youthful period where growth rate declines linearly with age, and a later mature period of equilibrium with the environment where the level of growth is constant over time. In other words, the conservative detrending option assumes that annual growth rate of mature trees fluctuates around a specific level, which is expressed by a constant ring width". This confirms the importance of considering site-specific characteristics when selecting the detrending criteria.

The tree-ring chronologies in this thesis are from managed stands, where disturbances due to silviculture are expected. Specifically, in the Spanish Mediterranean oak forests, thinning has been progressively carried out over the centuries and has led to the current low tree densities of the Spanish “dehesas” (see Gea-Izquierdo et al., 2011). All the *P. pinea* forests in Spain originated from plantations or have been subjected to forestry measures, and most of them produce timber and pine nuts, thus silvicultural treatments typically involve thinning for improving wood production and crown development. As a result, growth releases were frequently found in the tree-ring chronologies. These growth releases were properly filtered by the smoothing spline with a 50 % frequency cutoff at 30 and 32 years, which provided a better climatic signal than the more conservative methods and stiffer filters (see Article 1, Appendix 1). In the Article 3 (Appendix 1), the growth patterns of trees growing in climatically distinct regions in the north and south of Spain were examined. When the spatial distinction between chronologies was searched through correlations between sites, flexible splines clearly distinguished two patterns, one in the north and one in the south, while stiffer curves did not. Moreover, flexible splines led to meaningful results in growth-climate correlation analyses, while stiffer curves led to some contradiction (i.e. the correlation coefficients in a same month often changed largely when they were computed using chronologies detrended with different curves; see the supplementary material of the Article 3). More flexible splines did not improve the study of growth-climate relationships, and removed too much variance at the low frequencies (see Figures 2 and 4 in Article 1, Appendix 1). Therefore, very flexible splines were not used in this thesis, although they have been applied by other authors seeking the maximum enhancement of the high-frequency response to climate (e.g. Macías et al., 2006; Domínguez-Delmás et al. 2013a; Piermattei et al. 2014; Latte et al. 2015).

After removing non-climatic variance from the tree-ring series, the relationship between growth and climate is examined through regression or correlation analyses using the extracted climatic signal and a set of climate data. The purpose is to discover how climate influences tree growth. In this phase, the choice of the climate data is important and should include a variety of climate variables. Indeed, within an ensemble of climatic variables, a few are the most suitable. Dendroclimatological studies with tree rings from high elevations normally deal with temperature, because tree growth at high altitudes is especially sensitive, and the chronology signal highly related, to temperature variations (see Büntgen et al., 2006). In the study sites of this thesis, the strongest growth-climate relationships were found with precipitation (see Articles 2, 3 and 4, Appendix 1). The correlations with temperature were not as strong as those found with precipitation. Temperature data provided information about tree growth response when they were used in association with precipitation. Thus, the combined use of temperature and precipitation data permitted a more accurate interpretation of site-specific ecology of tree growth (discussed in the subsequent section of the thesis). In fact, precipitation is a known limiting factor for vegetation and a target climatic variable for dendroclimatological studies in the Mediterranean Basin (Cherubini et al., 2003; Akkemik and Aras, 2005). The self-calibrating Palmer Drought Severity Index (scPDSI) was also highly correlated with growth (see Articles 1 and 4, Appendix 1). The Palmer drought index is a good indicator to evaluate water availability during the growing season, it has showed strong relationship with growth in tree-ring studies and has been successfully used to reconstruct drought variations over time and space (e.g.

Cook et al., 1999; Nicault et al., 2008; see the North American Drought Atlas by Cook and Krusic, 2003, here:
http://iridl.ldeo.columbia.edu/SOURCES/.LDEO/.TRL/.NADA2004/.pdsi-atlas.html; see the Old World Drought Atlas by Cook et al., 2015, here:
https://www.ncdc.noaa.gov/cdo/f?p=519:1:0::::P1_study_id:19419).

The Article 3 (Appendix 1) includes an evaluation of the sources of climate data before proceeding to the ecological interpretation of the growth-climate correlation patterns. It was found that the use of different sources can lead to uncertainties in the study of the growth response. In particular, growth-climate correlation patterns showed some discrepancies when temperature data were alternately obtained from meteorological stations and gridded datasets. These discrepancies were linked to low correlation values between temperature data from the two different type of climate data sources (see the results of the Article 3). It was observed that such discrepancies can partly derive from differences in location and elevation between the study sites (specifically, Hoyo de Pinares and Valverde del Camino in the Article 3) and the station (specifically Ávila and Huelva in the Article 3). However, previous studies reported that biases in dendroclimatic investigations are related to the uneven availability and discontinuous quality of instrumental records over time and space (Dessen and Bücher, 1995; Frank et al., 2007; Liñán et al., 2012). For instance, in the case of Huelva, the agreement between station records of precipitation and gridded precipitation data (CRU and E-OBS) was stable over time (Figure 18). In contrast, the station records of temperatures showed deviations from the gridded temperature data in the late 1930s, in the 1940s, and 1960s-1980s, whereas the agreement between all climate data sources was visible in the subsequent decades (Figure 18). This may be due to some change in the characteristics of meteorological station or in the techniques applied to record station data, that may have been enhanced in recent times. On the other hand, the recent increase of agreement between data sources may be due to some improvement in the estimation of gridded climate values. In fact, each grid box provides estimates of climate data based on instrumental measurements collected from the meteorological stations that are inside the grid box. However, the number of stations, and available climate records, can vary over time within a grid box. In southern Spain, the number and technology of meteorological stations changed over time. Indeed, the stations of the Spanish State Meteorological Agency (AEMET) increased in number over the decades, especially when automatic weather stations were installed, and further stations were installed during the last 20 years by the Regional Government of Andalusia (Vázquez-Piqué, 2011). Therefore, the increase of available climate data may have enhanced the grid box climate estimations.

Despite possible uncertainties related to meteorological measurements, the mean climate values, the patterns of the annual distribution of precipitation and temperature, and the long-term variations of climate presented in this thesis, reflect the currently known climate features and trends in Spain. In fact, the climate diagrams (see Articles 2, 3 and 4 in Appendix 1) properly distinguished different sub-types of the Mediterranean climate across the Iberian Peninsula (Capel Molina, 1981; Font Tullot, 2000; AEMET-IM, 2011). On the other hand, the long-term meteorological series (see

Articles 2, 3 and 4 in Appendix 1) matched the climate change processes occurring in the Iberian Peninsula, namely the increasing temperatures and aridity (Briffa et al., 1994; Sumner et al., 2003; Rodrigo and Trigo, 2007; Pérez and Boscolo, 2010). This indicates that the uncertainties in climate data did not affect the assessment of the spatiotemporal variability of climate in the study regions.

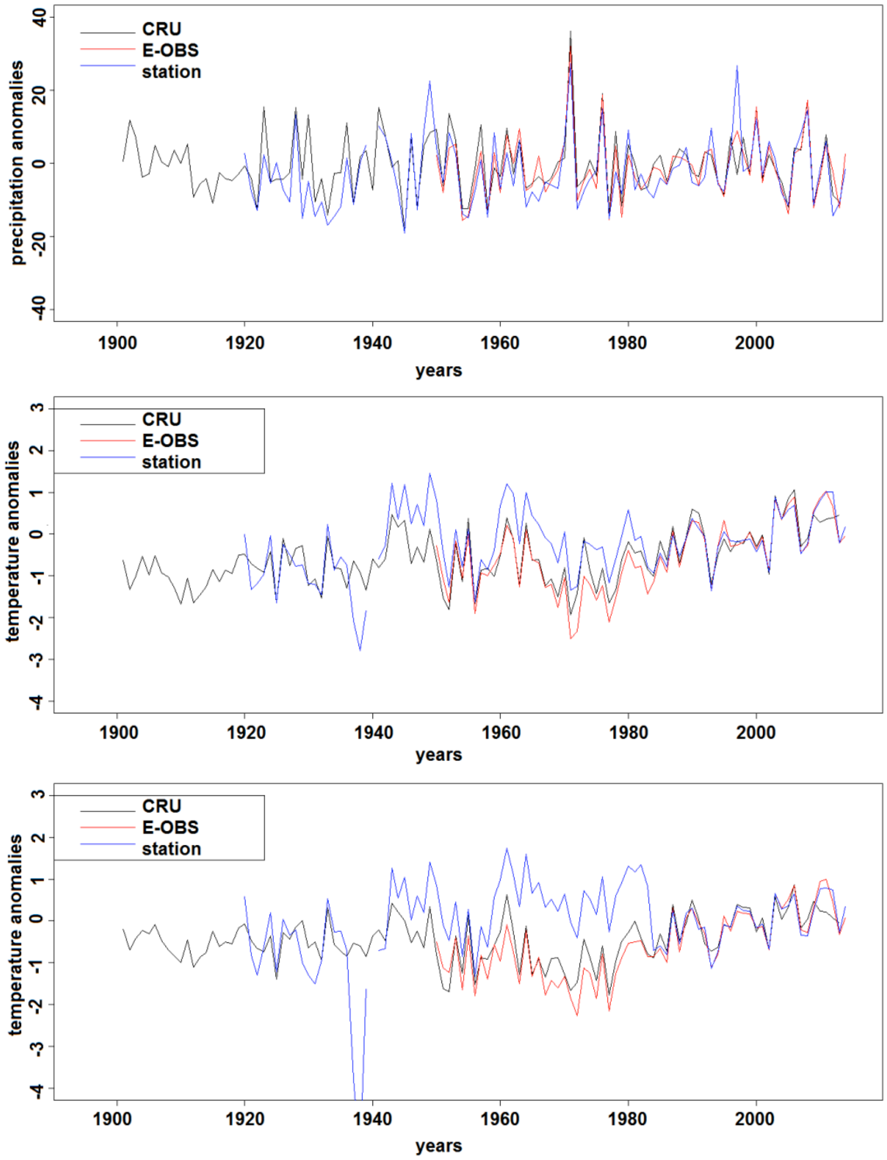


Figure 18. Precipitation, mean temperature and minimum temperature anomalies (from top to bottom) in Huelva. The blue line describes the trend of climate values recorded by the meteorological station. The other lines describe the trends of climate data retrieved from gridded datasets (CRU and E-OBS).

9.3 Spatial variability of growth-climate relationships

Previous tree-ring studies on *P. pinea* and *Q. ilex*, as well as on other species of the Mediterranean region (e.g. Corcuera et al., 2004b; De Luis et al., 2009, 2013; Vieira et al. 2010; Novak et al. 2013; Seim et al., 2014), have showed that radial growth is especially favored by precipitation during the autumn or winter of the year prior to that of ring formation, and during spring and beginning of summer in the year of ring formation (Zhang and Romane, 1991; Raventós et al., 2001; Corcuera et al., 2004a; Campelo et al., 2007b, 2009; Gea-Izquierdo et al., 2009, 2011; De Luis et al., 2009; Mazza and Manetti, 2013; Piraino et al. 2013; Mazza et al., 2014). These studies also report that correlation with temperature is generally lower than correlation with precipitation, but correlations with drought indexes are strong, suggesting that water conditions are a limiting factor for tree radial growth. Positive correlations with minimum temperatures during winter have been also observed in Mediterranean evergreen species and can be explained by photosynthetical activity, which takes place in this season in these species (Baldocchi et al., 2010; Carevic, 2010; Gratani et al., 2013; Catoni and Gratani 2014; Gea-Izquierdo et al., 2015). Mild temperatures during the winter can also alter phenological patterns, inducing an early dormancy interruption and consequently the formation of wider rings (Myking and Heide, 1995; Oribe and Kubo 1997; Begum et al. 2010). The analysis of growth-climate relationships in this thesis agrees with these findings.

The holm oaks from Calañas and Huerto Ramirez showed a positive response to precipitation from the previous October to the current March/April, but no significant relationship was found in May. In May, however, there was a negative relationship with high temperatures. For Mediterranean trees, water availability is important during spring when growth is maximal (Pereira et al., 2007; Vaz et al., 2010). However, in the area of Huelva meteorological droughts already occur during May (see climate diagrams in the Articles 2, 3 and 4). Therefore, heat and low rainfall amounts in this month, which can induce water deficit and limit the photosynthetic capacity of trees (Baquedano and Castillo, 2007), can explain the sensitivity of trees to high temperatures and the absence of significant relationships with precipitation in these two sites.

For *P. pinea*, the comparison between different sites permits to describe an ecologically significant degree of variability in the growth response patterns. All the *P. pinea* chronologies from the province of Huelva showed similar climatic signals (Articles 2 and 3, Appendix 1). The strongest correlations were found with precipitation from October/November to winter of the previous year (December of the previous year and January of the current year). A similar response to precipitation was observed in the study site in Pegões, Portugal (Article 2). The correlation values with precipitation in spring were low in both areas (Huelva and Pegões). With regard to Huelva, the chronologies of Valverde del Camino and Hinojos were significantly correlated with precipitation in April and May in the Article 1, but not in the Article 3: this may be due to the different climate data source used (meteorological station in the Article 1, and gridded datasets in the Article 3). Nonetheless, the response in winter was stronger in any case, and the pattern of growth-climate relationship, centered in winter, was evident when the whole set of tree-ring chronologies from Huelva was examined (see Figure 2 in the Article 2). The *P. pinea* chronologies from the northern Spanish study sites (Viana de Cega, Carrascal and Hoyo de Pinares; Article 3, Appendix 1), as well as the three chronologies of the ITRDB in La Mancha (used in the Article 2), showed positive correlations with precipitation from the previous October/November to the current January, as in Huelva and Pegões, but also a strong response to precipitation during spring, especially in May.

Therefore, two distinct patterns of growth-climate correlations can be distinguished across the study sites: a uni-modal pattern (with correlations centered in the previous winter) at the lowest latitudes, and a bi-modal pattern (with correlations in the previous winter and in the current spring) at the higher latitudes. This variability in the growth response is linked to the site-specific climatic conditions. Indeed, in the area of Huelva, maximum rainfall occurs from November to January (see the climate diagrams in Article 2 and 3, Appendix 1), thus annual growth largely depends on this rainfall. On the other hand, climate data for Viana de Cega, Carrascal, Hoyo de Pinares (see Article 2) and La Mancha (see Figure 19) indicate peaks of rainfall in April/May, thus the important influence of water availability from precipitation in these months is reflected in the dendroclimatic signal.

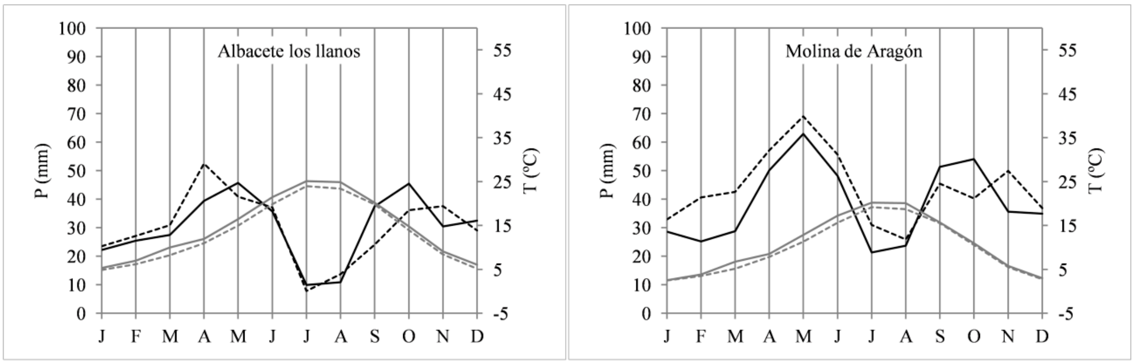


Figure 19. Climate diagrams with precipitation data (in black) and mean temperature data (grey) of successive periods (1957-1983, dotted lines, and 1984-2010, solid lines) of the meteorological stations "Albacete los llanos" and "Molina de Aragón". Data from these stations were used for the tree-ring chronologies "Pinar Viejo", "La Pasadilla" and "Dehesa del Peral" of the ITRDB (see Article 2, Appendix 1).

Variability in the duration and intensity of summer meteorological droughts was also noticed among sites. In Viana de Cega, Carrascal, Hoyo de Pinares and La Mancha, meteorological drought is normally extended from June/July to August/September (see climate diagrams in Article 3 and Figure 19), and the tree-ring chronologies correlated significantly with climate in late spring and summer. In particular, growth did not only responded positively to precipitation in May, but also negatively to high temperatures from May to July. In contrast, in the area of Huelva drought is normally extended from May to September (see the climate diagram in Article 3). Therefore, water conditions in the south are limiting since May, and this further explains the weak growth response in late spring and explains the absence of correlations during summer. Indeed, hot and dry Mediterranean summers can induce a reduction or stop of the cambial activity (Cherubini et al., 2003; Camarero et al., 2010; Gutiérrez et al., 2011; Martín et al., 2014).

The variability of growth-climate relationship related to the drought regimes was further examined by comparing the tree growth response in Tarquinia, Italy, with that observed in Huelva (see Conference presentation 3, Appendix 2, and Figure 20). The climate diagram in Tarquinia (Figure 20) indicates shorter and less intense meteorological droughts than in Huelva. In Tarquinia, growth-climate correlations increased from April to June, while in Huelva correlations where high only in April. Latewood-width chronologies were analyzed separately to check for distinct signal related to the climatic conditions during the late summer and autumn of the year of ring formation. Latewood formation correlated with precipitation during August and September in Tarquinia, and during September and October in Huelva. This diversity can be associated to the different duration of meteorological drought, which is normally extended up to September Huelva end up to August in Tarquinia.

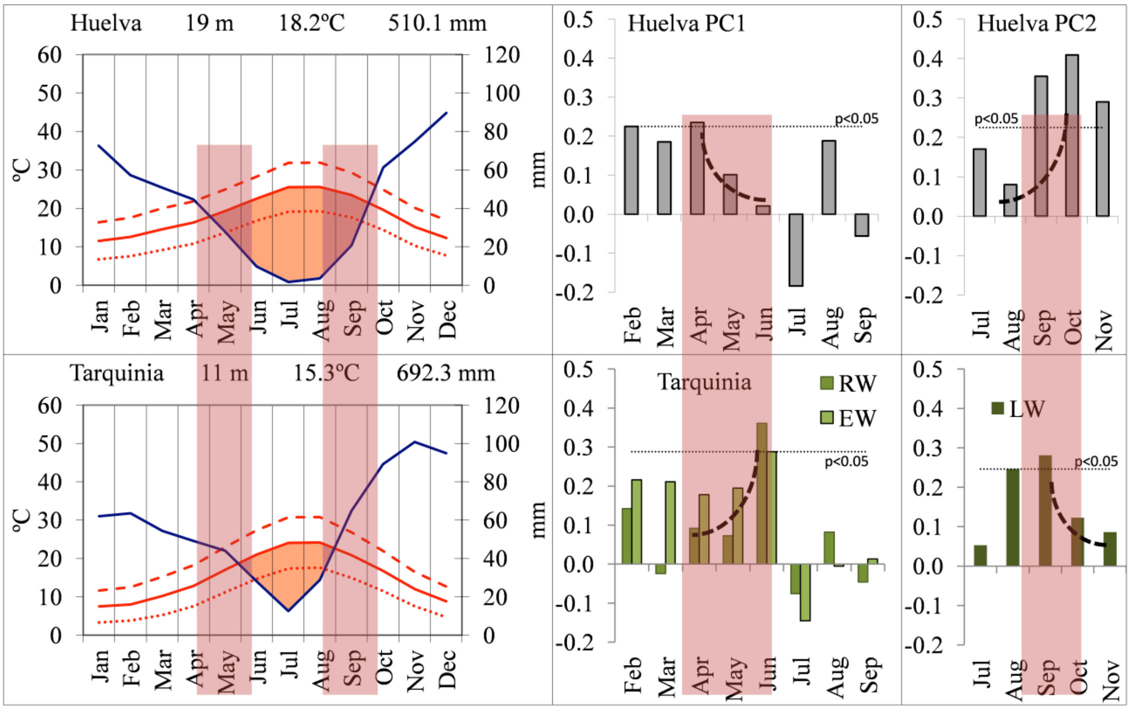


Figure 20. Left: climate diagrams obtained from the meteorological station of Huelva and Tarquinia. The blue line is precipitation, the red lines are maximum (upper dotted lines), mean (solid line) and minimum (lower dotted lines) temperatures. The shadings highlight the different extent of meteorological droughts between Huelva and Tarquinia. Right: correlations between growth and precipitation in Huelva and Tarquinia. In Huelva, 2 principal components (PC1 and PC2) were extracted from a dataset of ring-width, earlywood-width and latewood-width chronologies from six sites: the PC1 explains the variance of ring-width and earlywood-width chronologies, the PC2 explains the variance of the latewood-width chronologies. In Tarquinia, ring-width, earlywood-width and latewood-width chronologies were established in one site. The shadings indicate the corresponding months in the climate diagrams. The dotted black curves highlight the different patterns of growth-climate correlations between Huelva and Tarquinia. (From Conference presentation n. 3, Appendix 2)

The capacity of *P. pinea* trees to establish site-specific relationships with the local climate indicates a degree of plasticity of this species. Plastic dendroclimatic signals in different tree species have been observed in relation to spatial climate variability and provide information about the range of conditions to which the species are adapted (Tardif et al., 2003; Martín-Benito et al., 2010; De Luis et al., 2013; Mazza et al., 2014). The genetic variability of *P. pinea* is low (Fallour et al., 1997; Vendramin et al., 2008; Pinzauti et al., 2012). However, this is a widespread species occurring in different environmental conditions throughout the southern Europe and eastern and southern Mediterranean coasts, indicating that genetic variability is not the only factor influencing the adaptability (Vendramin et al., 2008; Soto et al., 2010). In fact, the successful adaptation of *P. pinea* seems to depend largely on epigenetic mechanisms and related variability at phenotypic traits, which is high in this species (Mutke et al., 2010, 2013; Sánchez-Gómez et al., 2011; Sáez-Laguna et al., 2014). Phenotypic plasticity is defined as the capacity of a genotype to generate a range of phenotypes depending on environmental pulses, and it influences the capacity of species to adjust to different conditions (see Nicotra et al., 2010). Phenotypic plasticity may be the mechanism underlying the observed variability in space of the growth response to climate, which, specifically, suggests the capacity of *P. pinea* to adapt the distribution of cambial activity over the year depending on local-level climatic conditions. Tree-ring analysis and xylogenesis indicate plastic cambial activity in *Pinus halepensis* (de Luis et al., 2011, 2013), a species ecologically close to *P. pinea* that also has little genetic variability (Soto et al., 2010). However, experimental data on xylogenesis of *P. pinea* to verify plastic cambial activity are still very scarce (Luz et al., 2014).

9.4 Temporal variability of growth-climate relationships

The stability of growth-climate relationships was checked by calculating correlations and response functions over successive time windows. Some changes in growth-climate relationships were observed in all the study sites. In *Q. ilex*, since the 1970s, the correlation between growth and precipitation during November and winter of the previous year became increasingly positive, while the correlation of growth with precipitation during the spring of the year of ring formation declined (see Article 4). Similar changes were observed in *P. pinea* in Huelva and Pegões. Indeed, in these sites correlations between growth and precipitation during spring and June were observed during the early periods of analysis, but were no longer observed in the late periods of analysis (see Articles 2 and 3). On the other hand, the correlation values with winter climate (i.e. minimum temperatures and precipitation) increased from the early to the late periods of analysis. In Carrascal, Viana de Cega and Hoyo de Pinares, the bimodal patterns of the growth-climate correlations were more marked during the late period of analysis than the early period. Specifically, in the late period the correlation with precipitation in spring was greater and the correlation with temperatures in May was more negative.

The uncertainties from climate data discussed above, in particular the possible unevenness of data quality and availability over time, could partly explain the instability of growth-climate correlations. However, in the study areas of this thesis, these uncertainties arose from the temperature data, but were not evident for precipitation, which could be assessed with an almost equal degree of confidence using either meteorological station records or gridded datasets (see Figure 18 and Article 3). Moreover, shifts in growth-climate relationships were reported in the Article 3, where meteorological records were discarded after an analytical evaluation of uncertainties, and growth response patterns were finally interpreted using gridded climate data only. In fact, shifting growth-climate relationships can result from changes in the tree growth response itself. The non-stationary nature of growth responses to climate (Carrer and Urbinati 2006) can be interpreted as physiological plasticity that enables an individual to acclimate to changing conditions (Meyers and Bull, 2002). Wood anatomy and physiological studies indicate that individual trees can alter their physiology in response to environmental changes (Walther et al., 2002; Fonti et al., 2010; Rossi et al., 2011). For example, alterations in plant phenology, including seasonal xylem growth patterns, have been observed with atmospheric warming (Peñuelas et al. 2002; Deslauriers et al. 2008; Morin et al., 2010; Rossi et al. 2011). Shifts in the correlation between growth and climate have been related to climate change in previous tree-ring studies (Gea-Izquierdo et al., 2009; Di Filippo et al., 2010; Martín-Benito et al., 2010; Latte et al., 2015). In the study sites of this thesis, the temporal variations in climate-growth relationships can be the result of physiological plasticity, probably a phenological adjustment of the cambial activity in relation to the increasing temperatures and the changing distribution of water availability over the year (Camarero et al. 2010; De Luis et al. 2011). In the southwestern Iberian Peninsula, climate data series did not describe any long-term increase in winter precipitation, which thus does not explain the increase in the growth response to precipitation in this season. On the other hand, springs became warmer and the intensity of meteorological droughts increased. Therefore, under more xeric conditions in recent decades, ring growth of *Q. ilex* and *P. pinea* became less sensitive to climate during the spring and June, when higher temperatures and less precipitation increased the water deficit, and enhanced its dependence on the water availability from precipitation of the previous autumn-winter.

Growth response shifts are also mediated by site-specific climate change. This was observed in the case of *P. pinea*, whose response to climate change varied in space (Article 3, Appendix 1). Indeed, in the northern sites (Carrascal, Viana de Cega and Hoyo de Pinares) growth response to climate change differed from that observed in Huelva. Specifically, the amounts of rainfalls during spring in the north were higher during the late period of analysis. This may explain the increased growth response to spring precipitation, while the more negative correlations with temperatures in May suggests an increased susceptibility of the active cambium to the negative effects of high temperatures. Finally, in the region of La Mancha (see Article 2) the response of tree growth to precipitation in April-May did not increase over time because precipitation of these months did not increase (except for a slight increase in the precipitation data of Albacete in May, which was not reflected in the dendroclimatic signal; Figure 19). Therefore, the plasticity of *P. pinea* and the spatio-temporal variability of climate are in a complex interplay determining variety in the species-specific growth-climate relationship.

9.5 Insight into forest ecology and dynamics from dendroclimatic signals

9.5.1 *Pinus pinea*

The biological fitness of forest tree species depends on the genetic variability to adapt to the new conditions, but also on the extent to which individuals are able to change their phenotypic traits in relation to environmental changes. The variable *P. pinea* growth response, observed in the study sites of this thesis, can be interpreted in terms of phenotypic plasticity as a mechanism of adaptation to site-specific conditions and acclimation to temporal changes of climate. Indeed, different types of phenotypic plasticity are observed in plants (see Chambel et al., 2005). Plasticity in physiological traits of an individual can be mediated by short-term, non-permanent environmental changes. Such process is in most cases reversible and constitutes the basis of homeostasis at the individual level. Developmental plasticity occurs when individuals with a same phenotype develop morphological and anatomical differences under sustained environmental pulses. This is in most cases irreversible and is considered particularly important for plants in case of adverse environmental conditions, because plants are not able to avoid adverse environmental conditions by moving (at least in one generation time), thus they need to adjust physiological or physical traits to endure adversity. Finally, a source of plasticity is the parental effect, i.e. plants modify their offspring in response to their own environmental conditions through adaptive cross-generational effects (a form of phenotypic plasticity) as a strategy to reduce the risks that environmental variations might pose to their offspring (Lundgren and Sultan, 2005; Wolf and Wade, 2009). Through these different mechanisms, phenotypic plasticity is of great importance for forest management and plays a non-secondary role in adaptation and evolution (Chambel et al., 2005). Indeed, the reaction of trees to forestry treatments, e.g. thinning or pruning, depends of their ability to cope with sharp changes in the forest micro-environments, and a better knowledge of this kind of plasticity is useful for evaluating adequate intensity and frequency of treatments. Plasticity of forest reproductive materials is also important to evaluate the areas in which a given material can be used successfully or with an acceptable degree of confidence. Finally, phenotypic plasticity, besides genetic variability, is very important to define the ability of a genotype to respond to climate change. In particular, the plasticity of plant species may play an important role in future vegetation dynamics, and a better understanding of plasticity in plant functional traits can contribute to predicting species distribution changes and shifts in vegetation types (Nicotra et al., 2010).

The methods to assess phenotypic plasticity typically involve experiments in which phenotypic traits, considered as key functional traits of adaptive plasticity, are observed across a gradient of controlled environmental conditions, and reactions norms (i.e. functions linking changes in the environment and changes in the phenotypic traits) are built (see Chambel et al., 2005; Nicotra et al., 2010). However, tree rings also give information about plasticity of trees. For instance, the adaptability of different provenances to the ecological conditions of a given site can be assessed through dendrochronologically assessed indicators of trees' adaptation as growth rates and frequency of missing rings (Leland et al., 2016). By analyzing ring widths and anatomy, Alla and Camarero (2012) assessed the growth plasticity of *Quercus faginea* across a climatic gradient in Spain spanning from a high-elevation, cold, humide site to a low-elevation, xeric site. Dendroclimatic signal can also give an insight into the plasticity of plants, as indicated by De Luis et al. (2013), who also state that plastic responses of trees to climate variability has been poorly explored from a dendrochronological perspective and it has been more often considered as due to environmental noise in the tree-ring chronology signals rather than a consequence of the plastic character of the species.

The results presented in this thesis suggest that *P. pinea* trees in northern sites have some capacity to resist future increases of temperatures and drought by adjusting cambial activity and thus becoming physiologically similar to trees in southern sites (which are currently adapted to warmer and drier conditions). On the other hand, the southern populations may already be approaching or exceeding their ecological limit, and their persistence under future conditions may be threatened (Figures 21, 22). This could be in agreement with existing dynamics in vegetation ecology. In fact, global warming induces spatial shifts in the ecological ranges of plant species (Walther et al., 2002), and in Spain this will likely lead to a northward shift of the distribution of tree species (Benito-Garzón et al. 2008; Pardos et al., 2015). Alternatively, the southern *P. pinea* populations could acclimate by activating the cambium during winter, if winter temperatures continue to increase (Prieto et al., 2004). In fact, maintaining cambial activity during winter is an adaptive trait already present in some Mediterranean trees which is manifested in certain precipitation and temperature conditions (Cherubini et al., 2003). For instance, previous research in Portuguese stands of *Pinus pinaster*, a species ecologically close to *P. pinea*, indicates some cambial activity during winter, although evidences are restricted to coastal (oceanic) zones during mild winters (Vieira et al., 2014). The tree-ring growth response of *P. pinea* during winter, also previously reported in Spain and Italy (de Luis et al., 2009; Mazza et al., 2014; Natalini et al., 2015), may reflect that this species can be physiologically active during winter (Pardos et al., 2010). In fact, cells in differentiation during winter have been observed in *P. pinea* in coastal areas of central Portugal, although this needs further investigation (Luz et al., 2014). There is no basis for making further speculations about future changes in cambial activity for trees in the southern study sites of this thesis, because there is no species-specific experimental evidence in drier locations which could be used for such predictions. However, the results presented here for *P. pinea* suggest that the species' capacity for acclimation to warmer and drier climate can vary among populations, and some measure of such variability should be considered in long-terms forecasts of vegetation dynamics (Alla and Camarero, 2012).

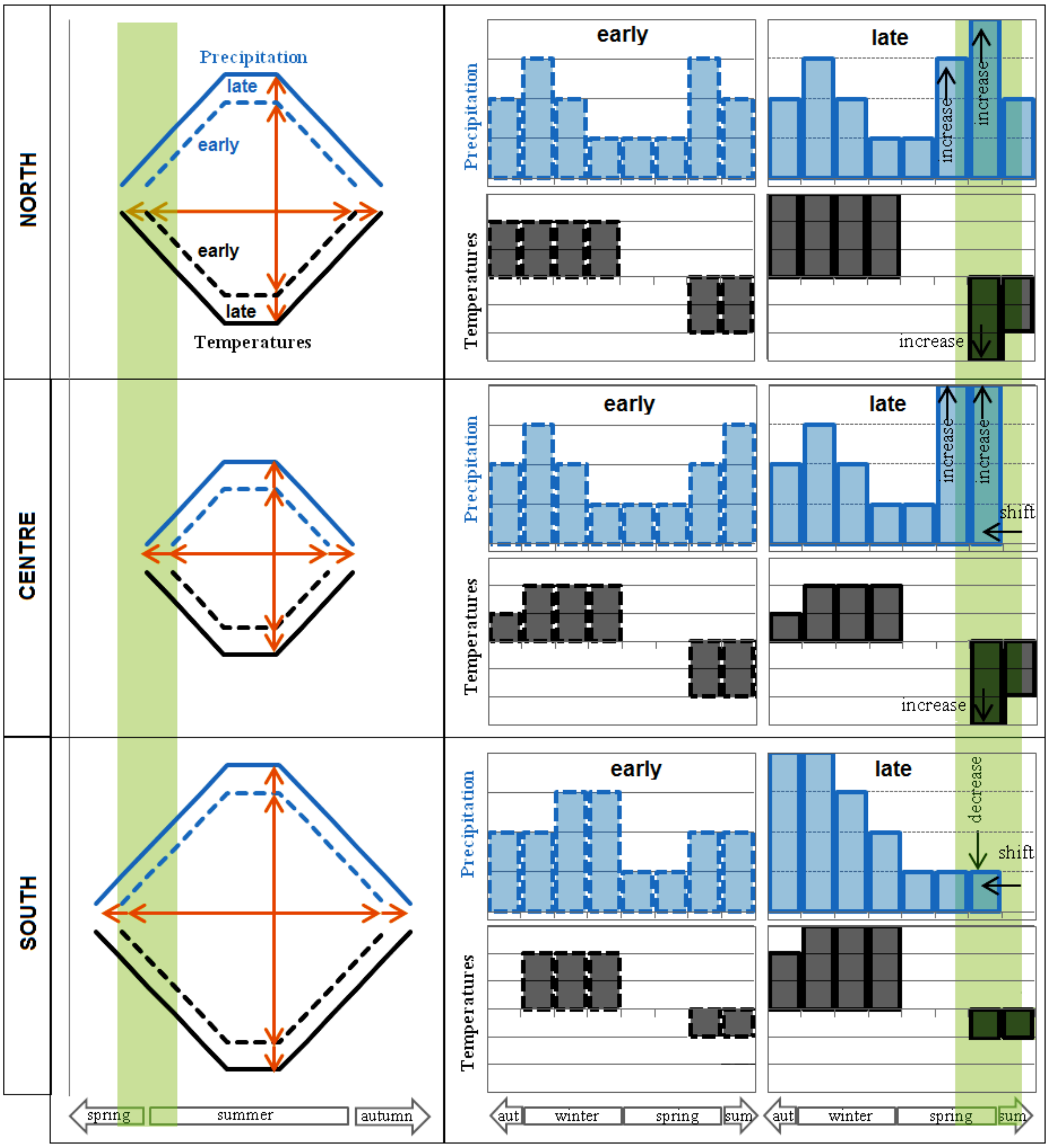


Figure 21. Diagram illustrating the most important results of the Article 3 (Appendix 1 of this thesis) about *P. pinea* growth-climate relationships along the latitudinal gradient (North, Centre and South). The left column shows the patterns of temperature (black lines) and precipitation (blue lines) from late spring to early autumn during the "early" period (1950-1980, dotted lines) and the "late" period (1981-2011, solid lines). The brown arrows indicate the duration and intensity of the meteorological drought (the tips of the arrows highlight the increase of aridity from the "early" to the "late" period). The right column shows how the growth-climate correlations (blue bars for precipitation, black bars for temperature) changed from the "early" period (bars with dotted contour) to the "late" period (bars with solid contour). The important temporal changes of growth-climate correlations in spring/summer are indicated by black arrows and labels ("increase" and "shift"; note: "increase" is used for both negative and positive correlations). The shaded green bands highlight the changing climatic conditions during spring/summer (on the left column) and the related tree growth responses (on the right column).

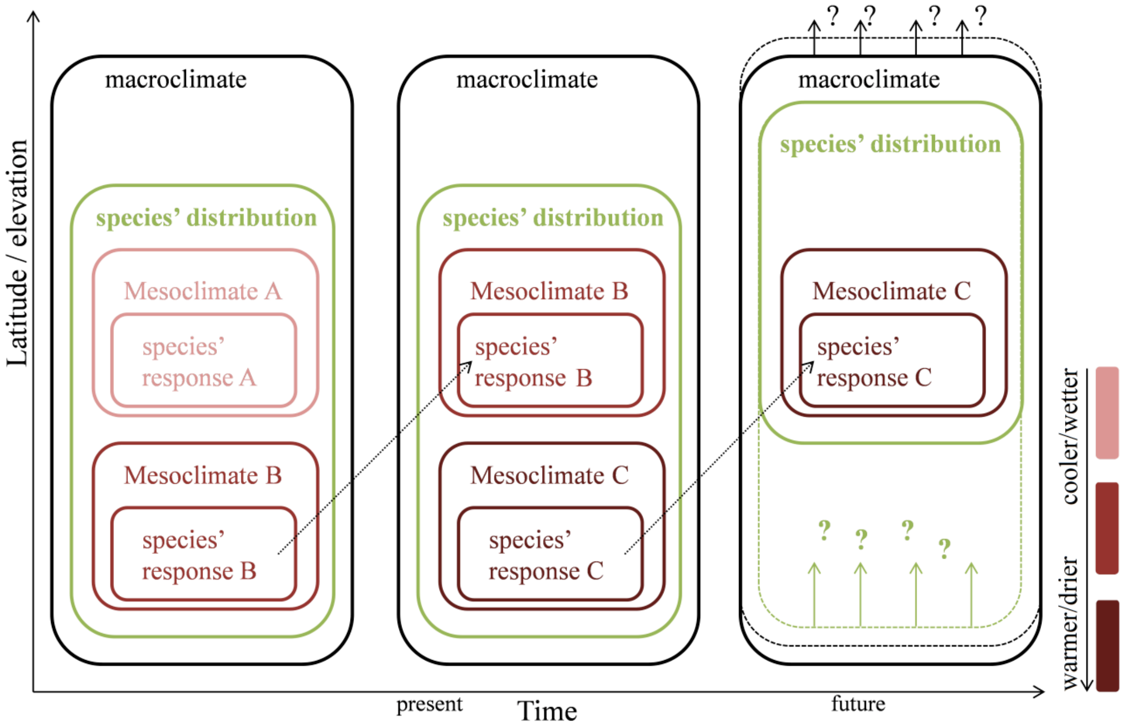


Figure 22. Hypothetical vegetation dynamics in Iberian *P. pinea* forests under climate change, based on spatiotemporal variability of tree-ring climatic signal. The *y* axis represents the geographical (latitude/altitude) gradient. The black boxes represents the same bioclimatic region (i.e. a region with a given macro-climate and vegetation) in three successive times. The geographical distribution range of the species within the bioclimatic region is represented by the green box. The variability of the local-level climatic conditions within the geographical distribution range of the species is referred to as "mesoclimates", represented by the brown boxes. The color scale from light brown to dark brown represents the climatic gradient (from milder/wetter mesoclimate to warmer/drier mesoclimate). There is a distinct species' tree-ring growth response for each mesoclimate. In the earlier period (left), the species has a response named "A" to the mesoclimate "A" (e.g. northern location with wetter conditions), and a response "B" to the mesoclimate "B" (southern and drier). In the subsequent period, the northern location becomes climatologically similar to the southern one, while the mesoclimate in the south becomes "C" (warmer and drier than before): as a consequence, the species' response to climate passes from "A" to "B" in the north, and becomes "C" (a new adapted response) in the south (these changes are indicated by the arrow). In the latest period (right), warming continues and the northern location becomes even drier, inducing a further change in the species' response, but in the south climatic conditions are no longer suitable for the species. Therefore, the species' distribution range undergoes a change, here hypothesized as a northward shift (green arrows). This is possibly matched by a northward shift of the bioclimatic region as well (black arrows). (From Conference presentation 7, Appendix 2).

9.5.2 *Quercus ilex*

Tree ring analysis gave also a dendroecological insight into the oak mortality process in Huelva. Tree mortality is a key bio-ecological process involved in the life cycle of natural forests characterized by a mosaic of patches belonging to different phases of stand structural development (see Piovesan et al., 2005). However, increases in tree mortality have been recently observed in forest ecosystems worldwide (Allen et al., 2010; Choat et al., 2012). Tree mortality is a complex phenomenon in which a number of factors are involved (Allen et al., 2010; McDowell et al., 2011). Tree rings have been used to investigate growth patterns in declining forests and dead trees (see

Schweingruber, 1996, p. 369-391), to model mortality risk (e.g. Bigler and Bugmann, 2004) and to find relationships between mortality processes and external factors, including climate-change related increases of stress (e.g. Pedersen, 1998; Camarero et al., 2003; Bigler et al., 2006). The climatic signal of the *Q. ilex* chronologies used in this thesis permitted to assess the role of climate change in the current massive oak die-off in the southwestern Iberian Peninsula. The findings indicating the implication of climate change (namely the increase of aridity) in this phenomenon are the following:

- The relationship between tree-ring growth and climate changed over time, in a way that indicates the sensitivity of trees to the increase in drought. This aspect has been discussed in the section 5.4 "Temporal variability of growth-climate relationships";
- Growth reductions (analyzed as trends of basal area increments and percentage growth changes; see Article 4, Appendix 1) occurred during the driest periods, suggesting drought-induced stress;
- Resilience of trees was indicated by growth recovery following the return of wetter climate after a protracted drought in the 1970s-80s, but it was not observed in the last years prior to death, when wetter climate returned again following a new drought in the mid 1990s, suggesting that trees entered a declining phase in which they were no longer able to respond to favorable conditions.

The physiological mechanisms underlying the occurrence of water stress cannot be described using tree-ring width chronologies. Likewise, tree-ring chronologies cannot directly prove the existence of physiological thresholds beyond which trees can be forced by warmer and drier climate, probably increasing their susceptibility to mortality (D'Arrigo et al., 2004; Wilmking et al., 2004; Allen et al., 2010; McDowell et al., 2011). However, previous physiological studies reported that other *Q. ilex* trees in the province of Huelva underwent water stress during 2005, a dry year (Alejano et al., 2008; Carevic et al., 2010). Carevic et al. (2010) also indicated stomatal closure as a reaction to water shortage. Dendrometer measurements on *Q. ilex*, also carried out in Huelva, indicated growth reductions in 2005 and 2009, when sharp decreases in precipitation occurred (Martín et al., 2014). These findings indicate a link between water stress and the loss of carbon gain, and therefore the reduction of growth (Tognetti et al., 1998; Ogaya and Peñuelas, 2003; Ogaya et al., 2003). Moreover, the loss of carbon gain, caused by stomatal closure to avoid hydraulic failure during protracted and intense drought, is involved in mortality processes, e.g. it affects defense metabolism (McDowell et al., 2008, 2011; McDowell, 2011). All this supports the dendroecological interpretation of *Q. ilex* growth dynamics, namely the growth suppressions and the inception of tree mortality process as induced by drought.

The trees may have been exposed to the effect of additional factors, other than climatic ones. These factors include pathogenic fungi, soil conditions, intense management and competitive advantage of co-existing shrubs (for further details and references see the section 2.4.2.1 "Decline and tree mortality in the Spanish *Q.* ilex silvopastoral systems", and the Article 4, Appendix 1). The negative impacts of all these factors may have been aggravated in the last years before tree death, because trees were more vulnerable after suffering water stress, and likely contributed to the mortality process.

10 CONCLUSIONS

1. The practicability of dendroecological and dendroclimatological methods in managed forests of *P. pinea* and *Q. ilex* in southwestern Spain was validated in this thesis. The tree-ring standardization method involving flexible splines with a period around 30 years was appropriate to filter the growth releases due to thinning. Stiffer functions, which retain more variance at low frequencies, do not satisfactorily removed this source of noise, potentially leading to an incorrect consideration of silviculture-induced growth releases as climate-related growth increases, and to their inclusion in growth-climate correlation analyses.

2. Climate data had an influence in the assessment of the tree growth response. Indeed, climate parameters explained tree growth with different degrees of completeness. Tree-ring chronologies were strongly correlated with precipitation, therefore tree growth sensitivity was best assessed using precipitation data. Evapotranspiration due to high temperatures during the warm months of the year has a negative effect on tree growth, but temperature data alone did not satisfactorily explain growth. Trees were also highly correlated with the self-calibrating Palmer Drought Severity Index. These findings showed that water availability is the main climatic factor controlling the radial growth of trees in the study regions, coherently with dendroecological and dendroclimatological studies in Mediterranean species.

3. The use of different climate data sources, including meteorological station records and gridded datasets, did not distort the assessment of climate mean values and variability in the study sites of this thesis, and had little effect on the appraisal of the spatiotemporal variability of tree growth response. However, there were some discrepancies between gridded data and meteorological station records, suggesting that preliminary screening of the available climate data is advisable to reduce potential biases in the analysis of growth-climate relationships.

4. In the case of *P. pinea*, the growth response to climate changed in space, reflecting different site-specific climatic conditions. The growth response to spring precipitation was strong in the northern sites, where the spring is normally more rainy and meteorological drought is in summer, but it was weak in the southern sites, where the meteorological drought already occurs in May. Therefore, in the southern populations water deficit in spring is greater and more limiting for tree growth, and this likely accounts for the lower growth sensitivity in this season. The climate-related spatiotemporal variability of *P. pinea* growth response can be interpreted as an expression of the phenotypic plasticity of this species. The plasticity of tree species is crucial for their persistence under future environmental conditions, but it has been poorly investigated from a dendroecological perspective. Therefore this thesis provides a valuable insight into the practicability of dendrochronological methods for assessing the plasticity of forest tree species in relation to the variability of climate over time and space.

5. Climate change-related signals were found in the tree-ring chronologies of both species. The relationship between tree growth and water availability became stronger over time in all the study sites, indicating a common reaction to the warmer and drier climate. In all the study sites the correlation between tree growth and winter precipitation increased and was always significant. A common increase in the response to winter minimum temperatures also suggested a positive effect of milder winters. In the southern sites, the correlations between tree-ring chronologies of both species and spring precipitation decreased in the recent decades, suggesting the negative effects of greater water deficit due to increasing temperatures. In the northern areas, where climate data did not indicate any increase of drought in spring, the correlation with precipitation in this season increased. These changes in growth-climate relationships suggest reactions of the growth physiology to the changing climatic conditions. Physiological reactions may include phonological adjustments of the cambial activity in relation to changes in the distribution of water availability and mean temperatures over the year.

6. The dendrochronological analysis permitted to assess the role of climate change in the current increase of oak mortality in southwestern Spain. The holm oaks were highly sensitive to water deficit. Growth decline was caused by droughts in recent decades, but climate was wetter in the last years before death, suggesting that trees were unable to recover despite the return of wetter conditions. Droughts probably caused water stress beyond a critical level, hampering tree resilience. The results presented for *Q. ilex* in this thesis cannot conclude about the physiological mechanisms underlying the mortality process. Moreover, other factors in addition to the increased aridity (including pathogens, porr soils and intense management) probably contributed synergistically to the mortality process. However, the relationships between tree-ring growth and climate made evident the important impacts that climate change had on the growth of the holm oaks, and suggest that climate change directly debilitated these trees, determining the inception of the mortality process. The holm oak stands studied here are among the southernmost and most xeric of the Iberian Peninsula, and it could be hypothesized that increasing oak mortality in the Iberian Peninsula may occur in northern and colder sites if aridity further increases.

11 FUTURE PERSPECTIVES AND FINAL REMARKS

The instability of growth-climate relationships were interpreted as a climate change-induced reaction of tree growth, but some uncertainties were also observed in the climate data itself, probably deriving from temporal changes in the quality and availability of meteorological station records. These uncertainties did not affect the dendroclimatological assessment of growth-climate relationships in this thesis, and unstable growth-climate relationships actually reflect trees' physiological plasticity, but the temporal unevenness of climate data quality could potentially influence the growth-climate correlation analysis. The effects of the unevenness of climate data quality might include, for instance, changes over time of the magnitude of the growth-climate correlation values. Such effects were not addressed in this thesis. Disentangling genuine physiological reactions and possible spurious effects of climate data may improve our understading of climate-realted forest dynamics, and it could be accomplished through further research.

The knowledge of trees' plasticity has important implications in forest management, because plasticity considerably determines the adaptability of trees to climate change. Trees' plasticity also determines their response to management measures, and further research could explore the practical utility of dendrochronology for measuring the effects on *P. pinea* growth of sharp changes in forest micro-environments and therefore to predict the results of specific silvicultural treatments on this species.

The extent of holm oak die-off differed between the two study sites, reflecting the unevenness of mortality rates in the Iberian oak woodlands. This indicates that other factors (e.g. degree of soil development, intensity of management, micro-climate, biotic agents) interact with climate. Further dendrochronological research of oak mortality in relation to climate change, including samples from other sites and other environmental variables (e.g. edaphic conditions), could assess the different degree of mortality risk according to site-specific conditions. Moreover, the existence of tolerance thresholds beyod which trees cannot recover from drought-induced physiological damages merits further investigations.

Some considerations can be done about the suitability of tree ring data from the study sites as proxy data for climate reconstruction or to calibrate models for forecasting tree growth in future climate change scenarios. The instability of growth-climate relationships may imply a deviation from uniformitarianism, a basic principle in dendroclimatology. In this thesis, the correlation with precipitation and temperature in spring changed significantly over time. However, the correlations with precipitation in winter were always positive and significant, although increased. This was evident when the climate variables were taken as mean values over several months, rather than monthly, that is to say: even if the correlation with precipitation during a single month of the winter changed, the overall correlation with cumulative precipitation of the season remained high. Climate reconstructions were not a purpose of this thesis, but a calibration-verification test involving two *P. pinea* chronologies (Article 1 in Appendix 1) suggested rather stable growth-climate relationship and therefore possible reconstruction, at least when the target climate variable was averaged over several months. This is in accordance with previous dencroclimatological studies underlining the importance of the choice of the proper target season for climate reconstructions.

The suitability of tree ring data from the study sites as proxy data for climate reconstruction can be hindered by the length of the chronologies that can be obtained. Gridded datasets provide climate data over long periods, and even some meteorological stations provide one-century-long climate data series, as in the case of Huelva. Since *P. pinea* forests in Spain are plantations and have been systematically managed, most trees are younger than 100 years old, and it is difficult to obtain very long chronologies. The oldest trees were found in Hoyo de Pinares, the highest location among the study sites, thus it can be hypothesized that long chronologies can be obtained from that area. The potential for climate reconstruction could increase if these chronologies were integrated with other tree ring data involving other species at a larger geographical scale.

The samples collected in this thesis can be re-used for future investigation, for example to analyze more in depth the intra-annual density fluctuations (IADFs). IADFs are induced by the intra-annual variability of climate and have been observed in the samples used in this thesis, especially in the province of Huelva. Dendroecology and dendroclimatology normally deal with growth data at the annual scale, thus examining IADFs means working at a finer scale. The analysis of IADFs in these samples would provide information about the climatic events that trigger their formation and the frequency of such events. Moreover, if it could be possible to establish a robust relationship between a specific growth anomaly and an anomalous climatic event (e.g. between latewood-like cells within the earlywood and rainy summer following dry spring), chronologies of that growth anomaly could be used to reconstruct the frequency of the related climatic event. Climate change effects could be also studied using IADFs. For instance, changes in the intra-annual climate could be reflected in the occurrence of different types of IADFs.

12 CONCLUSIONES

1. La aplicabilidad de los métodos dendroecológicos y dendroclimatológicos ha sido validada en esta tesis, que contribuye a la comprensión de las dinámicas del crecimiento de las especies *P. pinea* y *Q. ilex* en relación con la variabilidad climática. El método de estandarización de las series dendrocronológicas con curvas "splines" flexibles, con una longitud de onda próxima a los 30 años, fue el más apropiado para eliminar el ruido debido a oscilaciones del crecimiento, causadas por las cortas. Curvas más rígidas, que conservan más varianza en las bajas frecuencias, no eliminaron satisfactoriamente el ruido. Por tanto, curvas de detrending rígidas pueden llevar a interpretar erróneamente como climática la variabilidad del crecimiento debida a la selvicultura, por lo que no se pudieron utilizar en los sitios de estudio.

2. Los árboles fueron especialmente sensibles a la precipitación. La evapotranspiración debida a las temperaturas altas durante los meses cálidos del año tiene un efecto negativo en el crecimiento, pero los datos de temperaturas no explicaron satisfactoriamente la variabilidad del crecimiento cuando se utilizaron como única variable independiente en el análisis de las relaciones clima-crecimiento. Por eso, los resultados más concluyentes se obtuvieron cuando el análisis incluyó ambas variables. La correlación entre las series dendrocronológicas y el índice de sequía de Palmer (self-calibrating Palmer Drought Severity Index) también fue alta. Estos resultados indican que la disponibilidad de recursos hídricos es el factor limitante más importante para el crecimiento de los árboles en las áreas de estudio, coherentemente con estudios dendroecológicos y dendroclimatológicos previos en especies mediterráneas.

3. El uso de diferentes fuentes de datos climáticos (estaciones meteorológicas y datos de cuadrícula) no alteró la caracterización climática ni el cálculo de los valores climáticos medios en los sitios de estudio de esta tesis, y no afectó significativamente el estudio de la variabilidad espaciotemporal de la respuesta del crecimiento, que se pudo interpretar razonadamente en relación a la variabilidad del clima. Sin embargo, se encontraron discrepancias entre los datos de cuadrícula y los registros de estaciones meteorológicas, y esto sugiere que una revisión preliminar de las fuentes de datos climáticos disponibles es recomendable para reducir potenciales sesgos en el análisis de las relacione clima-crecimiento.

4. En el caso de *P. pinea*, la respuesta del crecimiento al clima cambió en el espacio, reflejando diferencias en las condiciones climáticas específica de cada sitio. La respuesta a las precipitaciones de primavera fue fuerte en los sitios de estudios más septentrionales, donde la primavera es normalmente más lluviosa y las condiciones de sequía ocurren en verano, mientras fue débil en el sur, donde la sequía es más intensa y prolongada, pudiendo ocurrir en primavera. Por tanto, en el sur el déficit hídrico en primavera es más intenso y mas limitante para el crecimiento de los árboles, lo que puede explicar la baja señal dendroclimática relacionada con la precipitación en esta estación. La variabilidad espaciotemporal de la respuesta de *P. pinea* al clima se puede interpretar como una expresión de la plasticidad fenotípica de esta especie. La plasticidad de las especies

arbóreas es muy importante para su persistencia bajo futuras condiciones medioambientales, pero ha sido poco estudiada mediante la aproximación dendrocronológica. Por tanto, los resultados de esta tesis proporcionan conocimientos sobre la aplicabilidad de los métodos de investigación dendrocronológica para evaluar la plasticidad de las especies arbóreas forestales en relación con la variabilidad del clima en el espacio y en el tiempo.

5. Las cronologías de ambas especies contenían señales relacionadas con las variaciones temporales del clima. La relación entre el crecimiento de los árboles y la disponibilidad de recursos hídricos aumentó en el tiempo en todos los sitios de estudio, lo que indica una reacción común al aumento de las temperaturas y de la sequía. En todos los sitios de estudio, la correlación entre crecimiento y precipitaciones en invierno aumentó en el tiempo, manteniéndose significativa. El aumento común de la correlación con las temperaturas mínimas de invierno también indica un positivo efecto de inviernos más templados. En los sitios más meridionales, la correlación entre el crecimiento de ambas especies y las precipitaciones en primavera disminuyó en décadas recientes, lo que indica un efecto negativo del incremento de déficit hídrico debido al aumento de las temperaturas. En los sitios del norte, donde los datos climáticos no indicaron aumentos de sequía en primavera, las correlaciones con las precipitaciones en esta estación creció. Estos cambios en las relaciones entre clima y crecimiento sugieren reacciones fisiológicas de los árboles frente a las variaciones climáticas. Estas reacciones pueden incluir ajustes de la actividad del cambium en relación con cambios en la distribución de la disponibilidad de recursos hídricos y de las temperaturas medias en el año.

6. El análisis dendrocronológico permitió determinar el papel del cambio climático en los procesos de mortandad de encinas en el suroeste de España. Las encinas estudiadas fueron muy sensibles al déficit hídrico. El declive de crecimiento fue causado por sequías intensas y prolongadas en décadas recientes, pero el clima fue más húmedo en los últimos años antes de la muerte de las encinas, lo que sugiere que estos árboles no fueron capaces de recuperarse a pesar del retorno de condiciones favorables. El estrés causado por las sequías probablemente superó un umbral de tolerancia fisiológica. Los resultados presentados en esta tesis no pueden aportar conclusiones sobre los mecanismos fisiológicos que determinan el proceso de mortalidad ya que otros factores, incluyendo plagas, enfermedades, manejo intensivo y características del suelo (someros y pobres en nutrientes en muchas zonas de Andalucía occidental), probablemente contribuyeron de forma sinérgica con el clima al proceso de mortalidad. Sin embargo, las relaciones observadas entre crecimiento y clima mediante series de anillos de encinas muertas evidencian los impactos importantes que el cambio climático ha tenido en el crecimiento de estos árboles, y sugieren que el cambio climático debilitó directamente los árboles, determinando el inicio de los procesos de mortalidad. La dehesas de las que proceden las encinas estudiadas en esta tesis están entre las más meridionales y xéricas de la Península Ibérica, por tanto se podría hipotetizar que un aumento de mortalidad de árboles del genero Quercus podría producirse en zonas más septentrionales y templadas frente a ulteriores aumentos de temperaturas y sequías.

13 PERSPECTIVAS FUTURAS Y COMENTARIOS FINALES

La inestabilidad de las relaciones clima-crecimiento fue interpretada como una reacción del crecimiento de los árboles al cambio climático, pero algunas incertidumbres se observaron también en los datos climáticos utilizados, probablemente debidas a cambios temporales en la disponibilidad y calidad de los registros de las estaciones meteorológicas. Estas incertidumbres no afectaron la interpretación de las relaciones clima-crecimiento y la inestabilidad de estas relaciones efectivamente refleja la plasticidad fisiológica de los árboles, pero la inestabilidad temporal en la calidad de los datos climáticos podrían tener una potencial influencia en el análisis de correlación. Los efectos de la calidad inestable de los datos climáticos puede incluir, por ejemplo, cambios en los valores de correlación. Estos efectos no fueron examinados en esta tesis. Una distinción entre las reacciones fisiológicas y los posibles efectos espurios de los datos climáticos podría mejorar el estudio de las dinámicas forestales en relación a la variabilidad climática, y se podría realizar en futuras investigaciones.

El conocimiento de la plasticidad de las especies arbóreas tiene importantes implicaciones en la gestión forestal, porque determina considerablemente la adaptabilidad de las especies al cambio climático. La plasticidad de los árboles determina también su respuesta a los tratamientos selvícolas, y nuevas investigaciones podrían explorar la utilidad práctica de la dendrocronología para medir los efectos en el crecimiento del pino piñonero de cambios súbitos en las condiciones micro-ambientales (debidos p. ej. a las cortas), y para predecir asimismo los resultados de tratamientos selvícolas específicos en esta especie.

La mortandad de encina fue diferente en los dos sitios de estudio, reflejando la variabilidad de las tasas de mortalidad de árboles de las dehesas. Esto indica que otros factores (p. ej. en nivel de desarrollo del suelo, la intensidad de los aprovechamientos silvo-pastorales, las condiciones micro-climáticas, los factores bióticos) interactúan con el clima. Nuevas investigaciones dendrocronológicas de la mortandad de especies de Quercus en relación al cambio climático, incluyendo muestras procedentes de otras áreas, con distintas condiciones, y otras variables (p. ej. las características edáficas), podrían proporcionar conocimiento sobre el riesgo de mortandad en función de específicas condiciones meso/micro-ambientales. Además, la existencia y definición de umbrales de tolerancia fisiológica bajo condiciones de sequía merecen más investigación.

Se pueden hacer algunas consideraciones acerca de la idoneidad de los datos dendrocronológicos de los sitios de estudio de esta tesis como datos “proxy” para realizar reconstrucciones del clima pasado o para calibrar modelos de proyección del crecimiento bajo futuros escenarios de cambio climático. La inestabilidad temporal de las relaciones clima-crecimiento puede contravenir el principio del uniformismo, que constituye una suposición básica en las reconstrucciones paleoclimáticas realizadas con métodos dendroclimatológicos. En esta tesis se observó que las correlaciones con precipitaciones y temperaturas en primavera manifestaron cambios importantes en el tiempo, incluyendo cambios de signo y pérdidas de significación estadística. Sin embargo, las correlaciones con precipitación en invierno fueron siempre positivas y significativas, aunque aumentaron. Esto resulta más evidente con los valores climáticos estacionales que con los valores mensuales, es decir: aunque la correlación con la precipitación de un mes especifico del invierno pueda tener variaciones importantes, la correlación con la precipitación acumulada en los meses de invierno se mantiene en valores altos. Las reconstrucciones climáticas no estaban entre los objetivos de esta tesis, pero se efectuó un test de calibración-verificación con dos cronologías de *P. pinea* (véase "Article" 1 en "Appendix 1"). Este test indicó relaciones clima-crecimiento estables, por lo que sugiere una posible reconstrucción del clima, al menos cuando la variable climática objeto de la reconstrucción es un valor medio estacional. Esto coincide con los estudios dendroclimatológicos, que recalcan la importancia de evaluar la variable climática estacional más adecuada como objeto de la reconstrucción.

La aplicabilidad de los datos dendrocronológicos procedentes de los sitios de estudio de esta tesis como datos "proxy" para una reconstrucción climática puede ser limitada por la escasa longitud de las cronologías. Los datos climáticos de cuadrícula proporcionan información climática para periodos largos (p. ej. desde el 1900 en el caso de las cuadrícula del Climatic Research Unit de la Universidad de East Anglia, http://www.cru.uea.ac.uk/, e incluso desde los siglos XVIII y XIX en el caso de otras variables y fuentes de datos, como las estimaciones de las anomalías de temperaturas elaboradas por el Berkeley Earth, http://berkeleyearth.org). Además, algunas estaciones meteorológicas proporcionan datos registrados a lo largo de muchas décadas, como en el caso de la estación de Huelva, con datos desde el 1920. Muchos bosques de pino piñonero en España proceden de plantaciones realizadas entre finales del siglo XIX y principio del XX, y además se han llevado a cabo aprovechamientos de manera constante. Por tanto, los árboles de *P. pinea* tienen, en su mayoría, menos de 100 años, y es difícil encontrar árboles viejos para obtener cronologías largas. Entre los pinos estudiados en esta tesis, los más viejos fueron encontrados en Hoyo de Pinares (Ávila), la localización más alta entre los sitios de estudio (890 m s. n. m.), por lo que se podrían obtener más cronologías largas en esta área con una potencial aplicación para reconstrucciones climáticas. Este potencial se podría incrementar si estas cronologías se integrasen con otras obtenidas en otros bosques de la zona o en una escala geográfica más amplia.

Las muestras recogidas en esta tesis podrán ser reutilizadas en futuras investigaciones. Se podrían estudiar más en profundidad las fluctuaciones del crecimiento intra-anual ("intra-annual density fluctuations", IADFs). Las IADFs se deben a la variabilidad intra-anual del clima y se han observado en muestras analizadas en esta tesis, especialmente en la provincia de Huelva. La dendroecología y la dendroclimatología normalmente tratan datos en escala anual, por tanto estudiar las IADFs significa trabajar a una escala temporal más fina. El estudio de las IADFs en estas muestras podría proporcionar información más detallada acerca de los eventos climáticos que causaron su formación, así como la frecuencia de estos eventos en el tiempo. Además, sería posible establecer una relación robusta entre una específica anomalía del crecimiento y un determinado evento climático o ecológico (p. ej. entre la formación, en la madera temprana de anillo, de xilema con características de madera tardía y un verano lluvioso después de una primavera seca): se podrían así desarrollar cronologías de esta anomalía de crecimiento especifica y reconstruir la frecuencia con la que el evento climático asociado ocurrió en el pasado. Los efectos del cambio climático en el crecimiento de los árboles de podrían también estudiar con el análisis de las IADFs: por ejemplo, cambios en los patrones climáticos intra-anuales podrían ser reflejados en diferentes tipos de IADFs.

14 REFERENCES

AEMET-IM, 2011. Iberian Climate Atlas. Agencia Estatal de Meteorología - Instituto de Meteorologia de Portugal, http://www.aemet.es/documentos/es/conocermas/publicaciones/Atlas-climatologico/Atlas.pdf

Akkemik, Ü., Aras, A., 2005. Reconstruction (1689–1994 AD) of April–August precipitation in the southern part of central Turkey. International Journal of Climatology 25(4): 537-548.

Alaejos, J., 2011a. Distribución de las dehesas en Andalucía occidental. In: Alejano, R., Domingo, J., Fernández, M. (Ed.) Manual para la gestión sostenible de las dehesas andaluzas. Foro para la Defensa y Conservación de la Dehesa – Universidad de Huelva. Huelva, Spain, pp. 24-35

Alaejos, J., 2011b. Tipología de formaciones adehesadas. In: Alejano, R., Domingo, J., Fernández, M. (Ed.) Manual para la gestión sostenible de las dehesas andaluzas. Foro para la Defensa y Conservación de la Dehesa – Universidad de Huelva. Huelva, Spain, pp. 50-51

Alejano, R., Domingo, J., Fernández, M. (Eds.), 2011. Manual para la gestión sostenible de las dehesas andaluzas. Foro para la Defensa y Conservación de la Dehesa – Universidad de Huelva. Huelva, Spain, http://hdl.handle.net/10272/6641

Alejano, R., Tapias, R., Fernández, M., Torres, E., Alaejos, J., Domingo, J., 2008. Influence of pruning and the climatic conditions on acorn production in holmoak (Quercus ilex L.) dehesas in SW Spain. Annals of Forest Science 65 (2):20–684.

Alía, R., Chambel, M.R., Valladares, F., Climent, J., 2005. Phenotypic plasticity: a useful framework for understanding adaptation in forest species. Investigación agraria. Sistemas y recursos forestales 14(3), pp.334-344.

Alla, A.Q. , Camarero, J.J., 2012. Contrasting responses of radial growth and wood anatomy to climate in a Mediterranean ring-porous oak: implications for its future persistence or why the variance matters more than the mean. European Journal of Forest Research 131(5):1537-1550.

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.T. , Gonzalez, P., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. Forest Ecology and Management 259(4): 660-684.

Allué, J.L., 1990. Atlas fitoclimático de España. Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria, Madrid, Spain.

Anchukaitis, K.J., Evans, M.N., Kaplan, A., Vaganov, E.A., Hughes, M.K., Grissino-Mayer, H.D. , Cane, M.A., 2006. Forward modeling of regional scale tree-ring patterns in the southeastern United States and the recent influence of summer drought. Geophysical Research Letters 33(4), DOI:10.1029/2005GL025050.

Anderegg, W.R., Kane, J.M. , Anderegg, L.D., 2013. Consequences of widespread tree mortality triggered by drought and temperature stress. Nature Climate Change 3(1): 30-36.

Andreu, L., Gutiérrez, E., Macias, M., Ribas, M., Bosch, O. , Camarero, J.J., 2007. Climate increases regional tree-growth variability in Iberian pine forests. Global Change Biology 13(4): 804-815.

Anfodillo, T., Rento, S., Carraro, V., Furlanetto, L., Urbinati, C. , Carrer, M., 1998. Tree water relations and climatic variations at the alpine timberline: seasonal changes of sap flux and xylem water potential in Larix decidua Miller, Picea abies (L.) Karst. and Pinus cembra L. Annales des Sciences Forestières 55(1-2): 159-172

Baillie MGL, Pilcher JR, 1973. A simple crossdating program for tree-ring research. Tree-Ring Bulletin 33: 7-14

Baldocchi, D.D., Ma, S., Rambal, S., Misson, L., Ourcival, J.M., Limousin, J.M., Pereira,J., Papale, D., 2010. On the differential advantages of evergreenness and deciduousness in mediterranean oak woodlands: a flux perspective. Ecological Applications 20 (6): 1583–1597.

Baquedano, F.J., Castillo, F.J., 2007. Drought tolerance in the Mediterranean species Quercus coccifera, Quercus ilex, Pinus halepensis, and Juniperus phoenicea. Photosynthetica 45 (2): 229–238.

Batllori, E. , Gutiérrez, E., 2008. Regional tree line dynamics in response to global change in the Pyrenees. Journal of Ecology 96(6): 1275-1288.

Battipaglia, G., De Micco, V., Brand, W.A., Saurer, M., Aronne, G., Linke, P. , Cherubini, P., 2014. Drought impact on water use efficiency and intra-annual density fluctuations in Erica arborea on Elba (Italy). Plant, Cell & Environment 37(2): 382-391.

Begum, S., Nakaba, S., Oribe, Y., Kubo, T. , Funada, R., 2010. Cambial sensitivity to rising temperatures by natural condition and artificial heating from late winter to early spring in the evergreen conifer Cryptomeria japonica. Trees-Structure and Functions 24(1): 43-52.

Beniston, M., Innes, J.L. (eds.) The impacts of climate variability on Forests. Springer Berlin Heidelberg

Benito Garzón, M., Sánchez de Dios, R., Sainz Ollero, H., 2008. Effects of climate change on the distribution of Iberian tree species. Applied Vegetation Science 11(2): 169-178.

Bigler, C., Bräker, O.U., Bugmann, H., Dobbertin, M., Rigling, A., 2006. Drought as aninciting mortality factor in Scots pine stands of the Valais, Switzerland. Ecosystems 9 (3): 330–343.

Bigler, C., Bugmann, H., 2004. Predicting the time of tree death using dendrochronological data. Ecological Applications 14 (3): 902–914

Biondi F., Qeadan F., 2008. A theory-driven approach to tree-ring standardization: defining the biological trend from expected basal area increment. Tree Ring Research 64(2): 81-96

Biondi F., Waikul K., 2004. DENDROCLIM2002: A C++ program for statistical calibration of climate signals in tree-ring chronologies. Computers & Geosciences 30: 303–311

Biondi, F., 1996. Decadal-scale dynamics at the Gus Pearson Natural Areas: evidence for inverse (a) symmetric competition?. Canadian Journal of Forest Research, 26(8): 1397-1406.

Blasing, T.J., Duvick, D.N. , Cook, E.R., 1983. Filtering the effects of competition from ring-width series. Tree-Ring Bulletin 43: 19-30

Blasing T.J., Duvick D.N., West D.C., 1981. Dendroclimatic calibration and verification using regionally averaged and single staion precipitation data. Tree-Ring Bulletin 41:37-43

Bontemps, J.D. , Esper, J., 2011. Statistical modelling and RCS detrending methods provide similar estimates of long-term trend in radial growth of common beech in north-eastern France. Dendrochronologia 29(2): 99-107.

Bradley, R.S., 2011. High-resolution paleoclimatology. In: Hughes, M.K., Swetnam, T.W. , Diaz, H.F. (Eds.), 2011. Dendroclimatology: progress and prospects. Springer Science & Business Media, pp. 3-16

Brasier, C. M., 1996. Phytophthora cinnamomi and oak decline in southern Europe. Environmental constraints including climate change. Annales des Sciences Forestieres 53(2-3): 347-358

Brasier, C. M., Scott, J. K. ,1994. European oak declines and global warming: a theoretical assessment with special reference to the activity of Phytophthora cinnamomi. EPPO Bulletin 24(1): 221-232

Bravo, A., Montero, G., 2008a. Descripción de los caracteres culturales de las principales especies forestales de España. Pinus pinea L. In: Serrada, R., Montero, G., Reque, J.A. Compendio de selvicultura aplicada en España. Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria, Madrid, Spain, pp. 1081-1082

Bravo, A., Montero, G., 2008b. Descripción de los caracteres culturales de las principales especies forestales de España. Quercus ilex L. In: Serrada, R., Montero, G., Reque, J.A. Compendio de selvicultura aplicada en España. Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria, Madrid, Spain, pp. 1103-1104

Bravo, J. A., Roig, S., Serrada, R., 2008. Selvicultura en montes bajos y medios de Quercus ilex L., Q. pirenaica Willd. Y Q. faginea Lam. In: In: Serrada, R., Montero, G., Reque, J.A. Compendio de selvicultura aplicada en España. Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria, Madrid, Spain, pp. 657-743

Briffa K.R., Melvin T.M., 2011. A closer look at Regional Curve Standardization of tree-ring records. In: Hughes, M.K., Swetnam, T.W. , Diaz, H.F. (Eds.), 2011. Dendroclimatology: progress and prospects (Vol. 11). Springer Science & Business Media

Briffa, K. R., Jones, P. D., Schweingruber, F. H., Karlén, W., Shiyatov, S. G.,. 1996. Tree-ring variables as proxy-climate indicators: problems with low-frequency signals. In: Jones PD, Bradley RS, Jouzel J (Eds.) Climatic Variations and Forcing Mechanisms of the Last 2000 Years. Springer Berlin Heidelberg, pp. 9-41

Briffa, K. R., Jones, P. D., Hulme, M., 1994. Summer moisture variability across Europe, 1892–1991: an analysis based on the Palmer drought severity index. Int J Climatol 14(5): 475-506.

Briffa K., Jones, P.D., 1990. Basic chronology statistics and assessment. In: Cook ER, Kairiukstis LA (Eds.) Methods of dendrochronology: applications in the environmental sciences. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp 137-152

Briffa K., Cook, E.R. ,1990. Methods of Response Function Analysis. In: Cook ER, Kairiukstis LA (ed). Methods of dendrochronology: applications in the environmental sciences. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 240-247

Bunn, A.G., Jansma, E., Korpela, M., Westfall, R.D. , Baldwin, J., 2013. Using simulations and data to evaluate mean sensitivity (ζ) as a useful statistic in dendrochronology. Dendrochronologia 31(3):250-254.

Bunn, A.G., 2008. A dendrochronology program library in R (dplR). Dendrochronologia 26(2): 115-124.

Bunn A.G., Sharac T.J., Graumlich L.J., 2004. Using a simulation model to compare methods of tree-ring detrending and to investigate the detectability of low-frequency signals. Tree Ring Research 60(2):77-90

Büntgen, U., Trnka, M., Krusic, P. J., Kyncl, T., Kyncl, J., Luterbacher, J. et al., 2015. Tree-Ring Amplification of the Early Nineteenth-Century Summer Cooling in Central Europe. Journal of Climate 28(13): 5272-5288

Büntgen, U., Martínez-Peña, F., Aldea, J., Rigling, A., Fischer, E.M., Camarero, J.J., Hayes, M.J., Fatton, V. , Egli, S., 2013. Declining pine growth in Central Spain coincides with increasing diurnal temperature range since the 1970s. Global and Planetary Change 107: 177-185.

Büntgen, U., Frank, D., Grudd, H. , Esper, J., 2008. Long-term summer temperature variations in the Pyrenees. Climate Dynamics 31(6):615-631.

Büntgen, U., Frank, D.C., Schmidhalter, M., Neuwirth, B., Seifert, M. , Esper, J., 2006. Growth/climate response shift in a long subalpine spruce chronology. Trees-Structure and Functions, 20(1): 99-110.

Caetano, P., Ávila, A., Sánchez, M.E., Trapero, A. , Coelho, A.C., 2009. Phytophthora cinnamomi populations on Quercus forests from Spain and Portugal. In: Goheen, E., Frankel, S. (Ed.) Phytophthoras in Forests and Natural Ecosystems. Proceedings of the Fourth Meeting of the International Union of Forest Research Organizations (IUFRO) Working Party S07.02.09, August 26–31, 2007, Monterey, California. U.S. Department of Agriculture, Forest Service - Pacific Southwest Research Station - Albany, CA. General Technical Report PSW-GTR-221. pp.261-269.

Camarero, J.J., Gazol, A., Galván, J.D., Sangüesa-Barreda, G. , Gutiérrez, E., 2015. Disparate effects of global-change drivers on mountain conifer forests: warming-induced growth enhancement in young trees vs. CO2 fertilization in old trees from wet sites. Global Change Biology 21(2): 738-749.

Camarero, J.J., Olano, J.M. , Parras, A., 2010. Plastic bimodal xylogenesis in conifers from continental Mediterranean climates. New Phytologist 185(2): 471-480.

Camarero, J.J. , Gutiérrez, E., 2004. Pace and pattern of recent treeline dynamics: response of ecotones to climatic variability in the Spanish Pyrenees. Climatic Change 63(1-2):181-200.

Camarero, J.J., Martín, E., Gil-Pelegrín, E., 2003. The impact of a needleminer (Epinotia subsequana) outbreak on radial growth of silver fir (Abies alba) in the Aragón Pyrenees: a dendrochronological assessment. Dendrochronologia 21 (1): 3-12.

Campelo, F., Nabais, C., García-González, I., Cherubini, P., Gutiérrez, E., Freitas, H., 2009. Dendrochronology of Quercus ilex L. and its potential use for climate reconstruction in the Mediterranean region. Canadian Journal of Forest Research: 39(12): 2486-2493.

Campelo, F., Gutierrez, E., Ribas, M., Nabais, C., Freitas, H., 2007a. Relationships between climate and double rings in Quercus ilex from northeast Spain. Canadian Journal of Forest Research 37(10): 1915-1923.

Campelo, F., Nabais, C., Freitas, H., Gutiérrez, E., 2007b. Climatic significance of tree-ring width and intra-annual density fluctuations in Pinus pinea from a dry Mediterranean area in Portugal. Annals of Forest Science 64(2): 229-238.

Candel-Pérez, D., Linares, J.C., Viñegla, B. , Lucas-Borja, M.E., 2012. Assessing climate–growth relationships under contrasting stands of co-occurring Iberian pines along an altitudinal gradient. Forest Ecology and Management 274: 48-57.

Capel Molina, J.J., 1981. Los Climas de España. Oikos-Tau, Barcelona, 429 pp.

Carevic, F., 2010. Evaluación de la producción de bellota de Quercus ilex ssp. ballota(Desf) Samp., y de factores ecofisiológicos influyentes, en dehesas de laprovincia de Huelva. Dissertation, Universidad de Huelva

Carevic, F., Fernández, M., Alejano, R., Vázquez-Piqué, J., Tapias, R., Corral, E., Domingo, J., 2010. Plant water relations and edaphoclimatic conditions affecting acorn production in a holm oak (Quercus ilex L. ssp. ballota) open woodland. Agroforestry Systems 78 (3): 299–308.

Carrasco, A. (Ed.), 2009. Procesos de Decaimiento Forestal (la Seca), Situación del Conocimiento. Consejería de Medio Ambiente, Junta de Andalucía, Córdoba, http://www.juntadeandalucia.es/medioambiente/site/portalweb/menuitem.7e1cf46ddf59bb227a9ebe205510e1ca/?vgnextoid=fc0ccd83981a5210VgnVCM1000001325e50aRCRD&vgnextchannel=e2a89950905f4310VgnVCM1000001325e50aRCRD

Carrer, M., Urbinati, C., 2006. Long□term change in the sensitivity of tree□ring growth to climate forcing in Larix deciduas. New Phytologist 170(4): 861-872.

Carrer M., Urbinati C., 2006. Long-term change in the sensitivity of tree ring growth to climate forcing in Larix decidua. New Phytologist 170: 861–872

Carrer, M., Anfodillo, T., Urbinati, C. , Carraro, V., 1998. High-altitude forest sensitivity to global warming: results from long-term and short-term analyses in the Eastern Italian Alps. In: Beniston, M., Innes, J.L. (eds.) The impacts of climate variability on Forests. Springer Berlin Heidelberg, pp. 171-189

Catoni, R., Gratani, L., 2014. Variations in leaf respiration and photosynthesis ratioin response to air temperature and water availability among Mediterraneanevergreen species. Journal of Arid Environments 102: 82–88.

Chambel, M.R., Climent, J., Alía, R., Valladares, F., 2005. Phenotypic plasticity: a useful framework for understanding adaptation in forest species.Investigación agraria. Sistemas y recursos forestales, 14(3), pp. 334-344. http://www.inia.es/gcontrec/pub/CHAMBEL-CLIMENT-ALIA-VALLADARES_(SRF14-3)_1162282729312.pdf

Charru, M., Seynave, I., Morneau, F. , Bontemps, J.D., 2010. Recent changes in forest productivity: an analysis of national forest inventory data for common beech (Fagus sylvatica L.) in north-eastern France. Forest Ecology and Management 260(5): 864-874.

Cherubini, P., Gartner, B. L., Tognetti, R., Braker, O. U., Schoch, W., Innes, J. L., 2003. Identification, measurement and interpretation of tree rings in woody species from Mediterranean climates. Biological Reviews 78(01): 119-148.

Chhin, S. , Wang, G.G., 2005. The effect of sampling height on dendroclimatic analysis. Dendrochronologia 23(1): 47-55.

Choat, B., Jansen, S., Brodribb, T.J., Cochard, H., Delzon, S., Bhaskar, R., Bucci, S.J., Feild, T.S., Gleason, S.M., Hacke, U.G. , Jacobsen, A.L., 2012. Global convergence in the vulnerability of forests to drought. Nature 491(7426): 752-755.

Chowdhury, M.Q., Kitin, P., De Ridder, M., Delvaux, C. , Beeckman, H., 2016. Cambial dormancy induced growth rings in Heritiera fomes Buch.-Ham.: a proxy for exploring the dynamics of Sundarbans, Bangladesh. Trees-Structure and Functions 30(1): 1-13.

Ciancio, O. , Nocentini, S., 2011. Biodiversity conservation and systemic silviculture: Concepts and applications. Plant Biosystems 145(2): 411-418, http://www.tandfonline.com/doi/abs/10.1080/11263504.2011.558705

Cook, E.R., Seager, R., Kushnir, Y., Briffa, K.R., Büntgen, U., Frank, D., Krusic, P.J., Tegel, W., van der Schrier, G., Andreu-Hayles, L., Baillie, M., et al., 2015. Old World megadroughts and pluvials during the Common Era. Science Advances 1(10), p.e1500561.

Cook, E.R., Pederson, N., 2011. Uncertainty, emergence and statistics in dendrochronology. In: Hughes, M.K., Swetnam, T.W. , Diaz, H.F. (Eds.), 2011. Dendroclimatology: progress and prospects. Springer Science & Business Media, pp. 77-112

Cook, E.R. , Krusic, P.J., 2003. The North American Drought Atlas. In American Geophysical Union, Fall Meeting 2003, http://adsabs.harvard.edu/abs/2003AGUFMGC52A..01C

Cook, E.R., Meko, D.M., Stahle, D.W. , Cleaveland, M.K., 1999. Drought reconstructions for the continental United States. Journal of Climate 12(4): 1145-1162.

Cook, E. R., Peters, K., 1997. Calculating unbiased tree-ring indices for the study of climatic and environmental change. The Holocene 7(3): 361-370

Cook E.R., Briffa K.R., Meko D.M., Graybill D.A., Funkhouser G., 1995. The segment length curse in long tree-ring chronology development for palaeoclimatic studies. Holocene 5: 229-235

Cook E.R., Kairiukstis L.A., 1990. Methods of dendrochronology: applications in the environmental sciences. Kluwer Academic Publishers, Boston

Cook, E.R., 1990. A conceptual linear aggregate model for tree rings. In: Cook ER, Kairiukstis LA (ed). Methods of dendrochronology: applications in the environmental sciences. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 98-104

Cook E.R., Briffa K.R., Shiyatov S., Mazepa V., 1990a. Tree-ring standardization and growth-trend estimation. In: Cook ER, Kairiukstis LA (ed). Methods of dendrochronology: applications in the environmental sciences. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp 104-123

Cook E.R., Shiyatov S., Mazepa V., 1990b. Estimation of the Mean Chronology. In: Cook ER, Kairiukstis LA (ed). Methods of dendrochronology: applications in the environmental sciences. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp 123-132

Cook, E.R., Briffa, K., 1990. Data analysis. In: Cook, E.R., Kairiukstis, L.A. (Ed). Methods of dendrochronology: applications in the environmental sciences. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 97-162

Cook E.R. , Peters K., 1981. The smoothing spline: a new approach to standardizing forest interior tree-ring width series for dendroclimatic studies. Tree Ring Bulletin 41:45-5

Corcobado, T., Cubera, E., Juárez, E., Moreno, G. , Solla, A., 2014. Drought events determine performance of Quercus ilex seedlings and increase their susceptibility to Phytophthora cinnamomi. Agricultural and Forest Meteorology 192: 1-8.

Corcuera, L., Camarero, J. J., Gil-Pelegrín, E., 2004a. Effects of a severe drought on Quercus ilex radial growth and xylem anatomy. Trees-Structure and Functions 18(1): 83-92.

Corcuera, L., Camarero, J. J., Gil-Pelegrín, E., 2004b. Effects of a severe drought on growth and wood anatomical properties of Quercus faginea. IAWA Journal 25(2): 185-204.

Correia A.C., Tomé M., Pacheco C.A., Faias S., Dias A.C., Freire J., Carvalho P.O., Pereira J.S., 2010. Biomass allometry and carbon factors for a Mediterranean pine (Pinuspinea L.) in Portugal. Forest Systems 19(3):418-433

Creus Novau L., Puigdefábregas T.J., 1976. Climatología histórica y dendocronología de Pinus Uncinata Ramond. Cuadernos de investigación: Geografía e Historia 2(2): 17-30.

D'Arrigo, R., Wilson, R., Liepert, B. , Cherubini, P., 2008. On the ‘divergence problem’in northern forests: a review of the tree-ring evidence and possible causes. Global and Planetary Change 60(3): 289-305.

D'Arrigo, R.D., Kaufmann, R.K., Davi, N., Jacoby, G.C., Laskowski, C., Myneni, R.B. , Cherubini, P., 2004. Thresholds for warming-induced growth decline at elevational tree line in the Yukon Territory, Canada. Global Biogeochemical Cycles, 18(3), DOI:10.1029/2004GB002249

De Luis, M., Cufar, K., Di Filippo, A., Novak, K., Papadopoulos, A., Piovesan, G., Rathgeber C.B.K., Raventos, J., Saz, M.A., Smith K.Y., 2013. Plasticity in dendroclimatic response across the distribution range of Aleppo pine (Pinus halepensis). Plos One, 8(12), e83550, DOI:10.1371/journal.pone.0083550

De Luis, M., Novak, K., Raventós, J., Gričar, J., Prislan, P., Čufar, K., 2011. Cambial activity, wood formation and sapling survival of Pinus halepensis exposed to different irrigation regimes. Forest Ecolofy and Management 262(8): 1630-1638

De Luis M., Novak K., Čufar K., Raventós J., 2009. Size mediated climate–growth relationships in Pinus halepensis and Pinus pinea. Trees-Structure and Functions 23:1065–1073

De Micco, V., Campelo, F., De Luis, M., Bräuning, A., Grabner, M., Battipaglia, G. and Cherubini, P., 2016. Intra-annual density fluctuations in tree rings: how, when, where, why. IAWA Journal 37(2): 232-259.

De Sampaio e Paiva Camilo-Alves, Maria Ivone Esteves da Clara, Nuno Manuel Cabral de Almeida Ribeiro, 2013. Decline of Mediterranean oak trees and its association with Phytophthora cinnamomi: a review. European Journal of Forest Research 132(3): 411-432

De Soto, L., Varino, F., Andrade, J.P., Gouveia, C.M., Campelo, F., Trigo, R.M. , Nabais, C., 2014. Different growth sensitivity to climate of the conifer Juniperus thurifera on both sides of the Mediterranean Sea. International Journal of Biometeorology 58(10): 2095-2109.

Deslauriers A., Rossi S., Anfodillo T., Saracino A., 2008. Cambial phenology, wood formation and temperature thresholds in two contrasting years at high altitude in southern Italy. Tree Physiology 28:863–871

Dessens, J., Bücher, A., 1997. A critical examination of the precipitation records at the Pic du Midi observatory, Pyrenees, France. In: Diaz, H.F., Beniston, M., Bradley, R.S. (ed.) Climatic Change at High Elevation Sites. Springer, pp. 113-121

Di Filippo, A., Biondi, F., Ziaco, E., Piovesan, G., 2013. Dendroecological networks to investigate forest dynamics: The case of European beech in Italy. In: Helle, G., Gärtner, H., Beck, W., Heinrich, I., Heußner, K.-U., Müller, A., Sanders, T. (Eds.) Proceedings of the DENDROSYMPOSIUM 2012: May 8th - 12th, 2012 in Potsdam and Eberswalde, Germany, (Scientific Technical Report ; 13/05), 11th TRACE conference (Tree Rings in Archaeology, Climatology and Ecology) (Potsdam and Eberswalde 2012), Potsdam : Deutsches GeoForschungsZentrum GFZ, 178 S. p. DOI: http://doi.org/10.2312/GFZ.b103-13058

Di Filippo, A., Alessandrini, A., Biondi, F., Blasi, S., Portoghesi, L., Piovesan, G., 2010. Climate change and oak growth decline: dendroecology and stand productivityof a Turkey oak (Quercus cerris L.) old stored coppice in Central Italy. Annals of Forest Science 67 (7) 706, http://dx.doi.org/10.1051/forest/2010031.

Diaci, J., 2006. Nature-based forestry in Central Europe: alternatives to industrial forestry and strict preservation. Biotechnical Faculty, University of Ljubljana, Slovenia

Diaz, M., Campos, P. , Pulido, F.J., 1997. The Spanish dehesas: a diversity in land-use and wildlife. In: Pain, D.J. , Pienkowski, M.W. (Eds.) Farming and birds in Europe: the Common Agricultural Policy and its implications for bird conservation. Academic Press, London, pp. 178-209

Domingo-Santos, J.M., Vázquez-Piqué, J., 2011. Manejo del suelo en la dehesa. In: Alejano, R., Domingo, J., Fernández, M. (Eds.) Manual para la gestión sostenible de las dehesas andaluzas. Foro para la Defensa y Conservación de la Dehesa – Universidad de Huelva. Huelva, Spain, pp. 329-331

Domínguez-Delmás, M., Alejano-Monge, R., Van Daalen, S., Rodríguez-Trobajo, E., García-González, I., Susperregi, J., Wazny, T. , Jansma, E., 2015. Tree-rings, forest history and cultural heritage: current state and future prospects of dendroarchaeology in the Iberian Peninsula. Journal of Archaeological Science 57: 180-196.

Domínguez-Delmás, M., Alejano-Monge, R., Wazny, T., González, I. G., 2013a. Radial growth variations of black pine along an elevation gradient in the Cazorla Mountains (South of Spain) and their relevance for historical and environmental studies. European Journal of Forest Research 132(4): 635-652

Domínguez-Delmás, M., Nayling, N., Ważny, T., Loureiro, V. , Lavier, C., 2013b. Dendrochronological dating and provenancing of timbers from the Arade 1 Shipwreck, Portugal. International Journal of Nautical Archaeology 42(1): 118-136.

Düthorn E., Holzkämper S., Timonen M., Esper J., 2013. Influence of micro-site conditions on tree-ring climate signals and trends in central and northern Sweden. Trees-Structure and Functions 27:1395–1404

Elfving, B. , Tegnhammar, L., 1996. Trends of tree growth in Swedish forests 1953–1992: an analysis based on sample trees from the National Forest Inventory. Scandinavian Journal of Forest Research 11(1-4): 26-37.

Esper, J., Frank, D., Büntgen, U., Verstege, A., Hantemirov, R.M. , Kirdyanov, A.V., 2010. Trends and uncertainties in Siberian indicators of 20th century warming. Global Change Biology 16(1): 386-398.

Esper, J., Frank, D.C., Wilson, R.J. , Briffa, K.R., 2005. Effect of scaling and regression on reconstructed temperature amplitude for the past millennium. Geophysical Research Letters 32(7), DOI:10.1029/2004GL021236

Esper, J., Cook, E. R., Krusic, P. J., Peters, K., Schweingruber, F. H., 2003. Tests of the RCS method for preserving low-frequency variability in long tree-ring chronologies. Tree-Ring Research 59(2):81 -98

Esper, J., Cook, E. R., Schweingruber, F. H., 2002. Low-frequency signals in long tree-ring chronologies for reconstructing past temperature variability. Science 295(5563): 2250-2253

Fallour, D., Fady, B. , Lefevre, F., 1997. Study on isozyme variation in Pinus pinea L.: evidence for low polymorphism. Silvae Genetica 46(4): 201-206.

Fang, K., Gou, X., Peters, K., Li, J. , Zhang, F., 2010. Removing biological trends from tree-ring series: testing modified Hugershoff curves.Tree-Ring Research 66(1):51-59.

Font Tullot, I., 2000. Climatología de España y Portugal. Universidad de Salamanca, Salamanca, 422 pp.

Fonti P., von Arx G., García González I., Eilmann B., Sass.Klaassen U., Gärtner H., Eckstein D., 2010. Studying global change through investigation of the plastic responses of xylem anatomy in tree rings. New Phytologist 185:42–53

Frank, D., Büntgen, U., Böhm, R., Maugeri, M. , Esper, J., 2007. Warmer early instrumental measurements versus colder reconstructed temperatures: shooting at a moving target. Quaternary Science Reviews 26(25): 3298-3310.

Frank, D. , Esper, J., 2005. Characterization and climate response patterns of a high-elevation, multi-species tree-ring network in the European Alps. Dendrochronologia 22(2): 107-121.

Fritts H.C., Guiot J., 1990. Methods of calibration, verification and reconstruction. In: Cook ER, Kairiukstis LA (ed). Methods of dendrochronology: applications in the environmental sciences. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp 163-217

Fritts, H.C. , Swetnam, T.W., 1989. Dendroecology: a tool for evaluating variations in past and present forest environments. Advances in ecological research, 19. Academic Press

Fritts, H.C., 1976. Tree rings and climate. Academic Press, London

Fritts, H.C., Blasing, T.J., Hayden, B.P. , Kutzbach, J.E., 1970. Multivariate techniques for specifying tree-growth and climate relationships and for reconstructing anomalies in paleoclimate. Journal of Applied Meteorology 10(5):845-864

Galván, J.D., Büntgen, U., Ginzler, C., Grudd, H., Gutiérrez, E., Labuhn, I. , Camarero, J.J., 2015. Drought-induced weakening of growth–temperature associations in high-elevation Iberian pines. Global and Planetary Change 124: 95-106.

García Vázquez, F.J., Tapias R., 2011. Medidas para la conservación y el fomento de la diversidad biológica. In: Alejano, R., Domingo, J., Fernández, M. (Ed.) Manual para la gestión sostenible de las dehesas andaluzas. Foro para la Defensa y Conservación de la Dehesa – Universidad de Huelva. Huelva, Spain, pp. 339-346

Gazol, A., Camarero, J.J., Gutiérrez, E., Popa, I., Andreu-Hayles, L., Motta, R., Nola, P., Ribas, M., Sangüesa-Barreda, G., Urbinati, C. , Carrer, M., 2015. Distinct effects of climate warming on populations of silver fir (Abies alba) across Europe. Journal of Biogeography 42(6): 1150-1162.

Gea-Izquierdo, G., Guibal, F., Joffre, R., Ourcival, J.M., Simioni, G., Guiot, J., 2015. Modelling the climatic drivers determining photosynthesis and carbonallocation in evergreen Mediterranean forests using multiproxy long timeseries. Biogeosciences 12: 3695–3712.

Gea-Izquierdo G., Cañellas I., 2014. Local Climate Forces Instability in Long-Term Productivity of a Mediterranean Oak Along Climatic Gradients. Ecosystems 17(2): 228-241

Gea-Izquierdo, G., Viguera, B., Cabrera, M. , Cañellas, I., 2014. Drought induced decline could portend widespread pine mortality at the xeric ecotone in managed mediterranean pine-oak woodlands. Forest Ecology and Management, 320: 70-82.

Gea-Izquierdo, G., Battipaglia, G., Gärtner, H. , Cherubini, P., 2013. Xylem adjustment in Erica arborea to temperature and moisture availability in contrasting climates. IAWA Journal 34(2): 109-126.

Gea-Izquierdo, G., Cherubini, P., Cañellas, I., 2011. Tree-rings reflect the impact of climate change on Quercus ilex L. along a temperature gradient in Spain over the last 100years. Forest Ecology and Management 262(9): 1807-1816.

Gea-Izquierdo G., Martín-Benito D., Cherubini P., Cañellas I., 2009. Climate growth variability in Quercus ilex L West Iberian open woodlands of different stand density. Annals of Forest Science 66 (8) 802, http://dx.doi.org/10.1051/forest/2009080

Gea-Izquierdo, G. , Canellas, I., 2009. Analysis of holm oak intraspecific competition using Gamma regression. Forest Science 55(4): 310-322.

Gimeno, T. E., Camarero, J. J., Granda, E., Pías, B., Valladares, F., 2012. Enhanced growth of Juniperus thurifera under a warmer climate is explained by a positive carbon gain under cold and drought. Tree Physiology 32(3): 326-336.

Girardin, M.P., Tardif, J.C., Flannigan, M.D. , Bergeron, Y., 2006. Synoptic-scale atmospheric circulation and boreal Canada summer drought variability of the past three centuries. Journal of Climate 19(10): 1922-1947.

Granda, E., Rossatto, D.R., Camarero, J.J., Voltas, J. , Valladares, F., 2014. Growth and carbon isotopes of Mediterranean trees reveal contrasting responses to increased carbon dioxide and drought. Oecologia 174(1):.307-317.

Gratani, L., Catoni, R., Varone, L., 2013. Morphological, anatomical and physiological leaf traits of Q. ilex, P. latifolia, P. lentiscus, and M. communis and their response to Mediterranean climate stress factors. Botanical Studies 54 (1): 1–12.

Grissino-Mayer H.D., 2001. Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. Tree-Ring Bulletin 57:205–221

Grissino-Mayer, H.D., Fritts, H.C., 1997. The International Tree-Ring Data Bank: an enhanced global database serving the global scientific community. The Holocene 7(2): 235-238

Guiot, J., 1991. The bootstrapped response function. Tree-Ring Bulletin 51, 39–41.

Guiot, J., 1990. Methods of calibration. In: Cook, E.R., Kairiukstis, L. (Eds.), Methods of Dendrochronology. Kluwer, Dordrecht, The Netherlands, pp. 165–178.

Gutiérrez, E., Campelo, F., Camarero, J.J., Ribas, M., Muntán, E., Nabais, C. , Freitas, H., 2011. Climate controls act at different scales on the seasonal pattern of Quercus ilex L. stem radial increments in NE Spain.Trees-Sctructure and Functions 25(4): 637-646.

Helama S., Lindholm M., Timonen M., Eronen M., 2004. Detection of climate signal in dendrochronological data analysis: a comparison of tree-ring standardization methods. Theoretical and Applied Climatology 79: 239–254

Herrero, A., Rigling, A. , Zamora, R., 2013. Varying climate sensitivity at the dry distribution edge of Pinus sylvestris and P. nigra. Forest Ecology and Management 308:50-61.

Higuera, P.E., Whitlock, C. , Gage, J.A., 2010. Linking tree-ring and sediment-charcoal records to reconstruct fire occurrence and area burned in subalpine forests of Yellowstone National Park, USA. The Holocene 21 (2): 327-341

Hogg, E.H., Brandt, J.P. , Michaelian, M., 2008. Impacts of a regional drought on the productivity, dieback, and biomass of western Canadian aspen forests. Canadian Journal of Forest Research 38(6):1373-1384

Holmes, R.L., 1992. Dendrochronology Program Library, Instruction and Program Manual (January 1992 update). Laboratory of Tree-Ring Research, University of Arizona, Tucson, USA

Holmes, R.L., Adams, R.K., Fritts, H.C., 1986. Tree-ring chronologies of Western North America, California, Eastern Oregon and Northern Great Basin, with procedures used in the chronology development work, including users manuals for computer programs COFECHA and ARSTAN. Chronology series VI. Laboratory of Tree-Ring Research, University of Arizona (Tucson, AZ)

Holmes, R.L., 1983. Computer-assisted quality control in tree-ring dating and measurement. Tree-ring Bulletin 43(1): 69-78.

Hughes, M.K., 2011. Dendroclimatology in high-resolution paleoclimatology. In: Hughes, M.K., Swetnam, T.W. , Diaz, H.F. (Eds.), 2011. Dendroclimatology: progress and prospects (Vol. 11). Springer Science & Business Media, 17-34

Hughes, M.K., Swetnam, T.W. , Diaz, H.F. (Eds.), 2011. Dendroclimatology: progress and prospects (Vol. 11). Springer Science & Business Media

Hughes, M.K., 2002. Dendrochronology in climatology–the state of the art. Dendrochronologia 20(1): 95-116.

Jump, A.S., Hunt, J.M. , Penuelas, J., 2007. Climate relationships of growth and establishment across the altitudinal range of Fagus sylvatica in the Montseny Mountains, northeast Spain. Ecoscience 14(4): 507-518.

Jump A.R., Hunt J.M., Peñuelas J., 2006. Rapid climate change-related growth decline at the southern range edge of Fagus sylvatica. Global Change Biology 12:2163–2174

Kaennel, M., Schweingruber, F.H., 1995. Multilingual Glossary of Dendrochronology. Swiss Federal Institute for Forest, Snow and Landscape Research, Birmensdorf / Paul Haupt Publishers, Berne http://www.wsl.ch/dienstleistungen/produkte/glossare/dendro_glossary/index_EN

Kaplan, J.O., Krumhardt, K.M. , Zimmermann, N., 2009. The prehistoric and preindustrial deforestation of Europe. Quaternary Science Reviews 28(27): 3016-3034.

Karl, T.R., Knight, R.W., Gallo, K.P., Peterson, T.C., Jones, P.D., Kukla, G., Plummer, N., Razuvayev, V., Lindseay, J. , Charlson, R.J., 1993. A new perspective on recent global warming: asymmetric trends of daily maximum and minimum temperature. Bulletin of the American Meteorological Society 74(6): 1007-1023.

Karl, T.R., Kukla, G. , Gavin, J., 1987. Recent temperature changes during overcast and clear skies in the United States. Journal of Climate and Applied Meteorology 26(6): 698-711.

Klok, E.J. , Klein Tank, A.M.G., 2009. Updated and extended European dataset of daily climate observations. International Journal of Climatology 29(8): 1182-1191.

Klos, R.J., Wang, G.G., Bauerle, W.L. , Rieck, J.R., 2009. Drought impact on forest growth and mortality in the southeast USA: an analysis using Forest Health and Monitoring data. Ecological Applications 19(3): 699-708.

Körner, C. , Paulsen, J., 2004. A world-wide study of high altitude treeline temperatures. Journal of Biogeography 31(5): 713-732.

Kovats R.S., Valentini R., Bouwer L.M., Georgopoulou E., Jacob D., Martin E., Rounsevell M., Soussana J.F., 2014. Europe. In: Barros V.R., Field C.B., Dokken D.J., Mastrandrea M.D., Mach K.J., Bilir T.E., Chatterjee M.E., Ebi K.L., Estrada Y.O, Genova R.C., Girma G., Kissel E.S., Levy A.N., MacCracken S., Mastrandrea P.R., White L.L. (Eds.) Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, pp 1267–1326

Läänelaid, A., Helama, S., Kull, A., Timonen, M. , Jaagus, J., 2012. Common growth signal and spatial synchrony of the chronologies of tree-rings from pines in the Baltic Sea region over the last nine centuries. Dendrochronologia 30(2): 147-155.

Latte, N., Lebourgeois, F. , Claessens, H., 2015. Increased tree-growth synchronization of beech (Fagus sylvatica L.) in response to climate change in northwestern Europe. Dendrochronologia 33: 69-77.

Leco Berrocal, F., 1994. La seca de encinares y alcornocales en España: aproximación del origen del fenómeno. Perfiles actuales de la geografía cuantitativa en España, pp. 129-142

Leland C, Hom J, Skowronski N, Ledig FT, Krusic PJ, et al., 2016. Missing Rings, Synchronous Growth, and Ecological Disturbance in a 36-Year Pitch Pine (Pinus rigida) Provenance Study. PLoS ONE 11(5): e0154730. DOI: 10.1371/journal.pone.0154730

León Sánchez, I., M., 2013. Selección de progenies de encina (Quercus ilex L. spp ballota) y alcornoque (Quercus suber L) tolerantes al patógeno Phytophthora cinnamomi. PhD dissertation, University of Huelva, Spain

Liñán, I. D., Büntgen, U., González-Rouco, F., Zorita, E., Montávez, J. P., Gómez-Navarro, J. J., Brunet, M., Heinrich, I., Helle, G., Gutiérrez, E., 2012. Estimating 750 years of temperature variations and uncertainties in the Pyrenees by tree ring reconstructions and climate simulations. Climate of the Past 8(3): 919-933

Linares, J.C. , Camarero, J.J., 2012. Growth patterns and sensitivity to climate predict silver fir decline in the Spanish Pyrenees. European Journal of Forest Research 131(4): 1001-1012.

Linares, J.C. , Tíscar, P.A., 2011. Buffered climate change effects in a Mediterranean pine species: range limit implications from a tree-ring study. Oecologia 167(3): 847-859.

Linares, J.C., Delgado-Huertas, A. , Carreira, J.A., 2011. Climatic trends and different drought adaptive capacity and vulnerability in a mixed Abies pinsapo–Pinus halepensis forest. Climatic Change 105(1-2): 67-90.

Linderholm H.W., Gunnarson B.E., Liu Y., 2010. Comparing Scots pine tree-ring proxies and detrending methods among sites in Jämtland, west-central Scandinavia. Dendrochronologia 28: 239-249

Lindner M., Calama R., 2013. Climate Change and the Need for Adaptation in Mediterranean Forests. In: Lucas-Borja ME (Ed.) Forest management of Mediterranean forests under the new context of climate change: building alternatives for the coming future. Nova Science Publishers, New York, pp 13–30

Lindner M., Maroschek M., Netherer S., Kremer A., Barbati A., Garcia- Gonzalo J., Seidl R., Delzon S., Corona P., Kolstro M., Lexer M.J., Marchetti M., 2010. Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. Forest Ecology Management 259: 698–709

Loewe, V., Rodríguez, C.D., Balzarini, M., Contreras, A.Á. , Navarro-Cerrillo, R.M., 2015. Impact of climate and management variables on stone pine (Pinus pinea L.) growing in Chile. Agricultural and Forest Meteorology 214: 106-116.

Loewe V., Venegas A., Delard C., González M., 2013. Thinning effect in two young stone pine plantations (Pinus pinea L.) in central southern Chile. In : Mutke, S., Piqué, M., Calama R. (ed.) Mediterranean stone pine for agroforestry. Zaragoza : CIHEAM / FAO / INIA / IRTA / CESEFOR / CTFC, pp. 49-55 (Options Méditerranéennes : Série A. Séminaires Méditerranéens; n. 105) http://om.ciheam.org/om/pdf/a105/00006781.pdf

Loewe V., Venegas A., 2011. Pine nut (Pinus pinea L.) production, an alternative for temperate areas. Asia Pacific Agroforestry Newsletter 39: 4-7, http://www.fao.org/3/a-am992e.pdf

Lundgren, M.R. , Sultan, S.E., 2005. Seedling expression of cross-generational plasticity depends on reproductive architecture. American Journal of Botany 92(2): 377-381.

Luz, A.L., Pereira, H., Lauw, A. and Leal, S., 2014. Monitoring intra-annual cambial activity based on the periodic collection of twigs–A feasibility study. Dendrochronologia 32(2): 162-170.

Macias, M., Andreu, L., Bosch, O., Camarero, J.J. , Gutiérrez, E., 2006. Increasing aridity is enhancing silver fir Abies alba mill.) water stress in its south-western distribution limit. Climatic Change 79(3-4): 289-313.

Manetti, M.C. , Cutini, A., 2006. Tree-ring growth of silver fir (Abies alba Mill.) in two stands under different silvicultural systems in central Italy. Dendrochronologia 23(3): 145-150.

Manion, P.D. , Lachance, D., 1992. Forest decline concepts. American Phytopathological Society Press, St. Paul, MN, USA

Manion, P.D., 1981. Tree disease concepts. Prentice-Hall, Inc., Englewood, New Jersey, USA

Mann, M.E., Bradley, R.S. , Hughes, M.K., 1999. Northern hemisphere temperatures during the past millennium: inferences, uncertainties, and limitations. Geophysical Research Letters 26(6): 759-762.

Martín D., 2015. Influencia de factores ecológicos y selvícolas en el crecimiento diametral de la encina (Quercus ilex ssp. ballota (Desf.) Samp.) en el suroeste de España. PhD dissertation, University of Huelva, Spain

Martín, D., Vázquez-Piqué, J., Carevic, F.S., Fernández, M. , Alejano, R., 2015a. Trade-off between stem growth and acorn production in holm oak. Trees-Structure and Functions 29(3): 825-834.

Martín, D., Vázquez-Piqué, J. , Alejano, R., 2015b. Effect of pruning and soil treatments on stem growth of holm oak in open woodland forests. Agroforestry Systems: 89(4): 599-609.

Martín, D., Vázquez-Piqué, J., Fernández, M. , Alejano, R., 2014. Effect of ecological factors on intra-annual stem girth increment of holm oak. Trees-Structure and Functions 28(5): 1367-1381.

Martín-Benito D., Del Río M., Cañellas I., 2010. Black pine (Pinus nigra Arn.) growth divergence along a latitudinal gradient in Western Mediterranean mountains. Annals of Forest Science 67 (4) 401, http://dx.doi.org/10.1051/forest/2009121

Martínez, F., Montero, G., 2004. The Pinus pinea L. woodlands along the coast of South-western Spain: data for a new geobotanical interpretation. Plant Ecology 175(1): 1-18

Martínez-Vilalta, J., López, B.C., Adell, N., Badiella, L. , Ninyerola, M., 2008. Twentieth century increase of Scots pine radial growth in NE Spain shows strong climate interactions. Global Change Biology 14(12): 2868-2881.

Matalas, N.C., 1962. Statistical properties of tree ring data. International Association of Scientific Hydrology Bulletin 7(2): 39-47.

Matesanz, S., Gianoli, E. , Valladares, F., 2010. Global change and the evolution of phenotypic plasticity in plants. Annals of the New York Academy of Sciences 1206(1): 35-55.

Mazza, G., Cutini, A., Manetti, M. C., 2014. Site-specific growth responses to climate drivers of Pinus pinea L. tree rings in Italian coastal stands. Annals of Forest Science 71(8): 927-936.

Mazza, G., Manetti, M. C., 2013. Growth rate and climate responses of Pinus pinea L. in Italian coastal stands over the last century. Climatic Change 121(4): 713-725.

McCool, S.F. , Stankey, G.H., 2004. Indicators of sustainability: challenges and opportunities at the interface of science and policy. Environmental Management 33(3): 294-305.

McDowell, N.G., 2011. Mechanisms linking drought, hydraulics, carbonmetabolism, and vegetation mortality. Plant Physiology 155 (3): 1051–1059.

McDowell, N.G., Beerling, D.J., Breshears, D.D., Fisher, R.A., Raffa, K.F. , Stitt, M., 2011. The interdependence of mechanisms underlying climate-driven vegetation mortality. Trends in Ecology & Evolution 26(10): 523-532.

McDowell, N., Pockman, W.T., Allen, C.D., Breshears, D.D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A., Williams, D.G. , Yepez, E.A., 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought?. New Phytologist 178(4) 719-739.

Meko, D. M., E. R. Cook, D. W. Stahle, C. W. Stockton, , M. K. Hughes, 1993. Spatial Patterns of Tree -Growth Anomalies in the United States and Southeastern Canada. Journal of Climate 6(9): 1773 -1786

Melvin, T. M., Briffa, K. R., 2008. A “signal-free” approach to dendroclimatic standardisation. Dendrochronologia 26(2): 71-86.

Melvin, T.M., Briffa, K.R., Nicolussi, K. , Grabner, M., 2007. Time-varying-response smoothing. Dendrochronologia 25(1): 65-69.

Meyers, L.A. , Bull, J.J., 2002. Fighting change with change: adaptive variation in an uncertain world. Trends in Ecology & Evolution 17(12): 551-557.

Montero, G., Calama R., Ruiz-Peinado, R., 2008. Selvicultura de Pinus pinea L. In: Serrada, R., Montero, G., Reque, J.A. Compendio de selvicultura aplicada en España. Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria, Madrid, Spain, pp. 431-470

Montero, G., Candela, J.A., Rodríguez, A., 2004 (Eds.). El pino piñonero en Andalucía: ecología distribución y selvicultura. Dirección General de Gestión del Medio Natural, Consejería de 508 Medio Ambiente, Junta de Andalucía, Sevilla, http://www.juntadeandalucia.es/medioambiente/consolidado/publicacionesdigitales/80-409_EL_PINO_PINHONERO_EN_ANDALUCIA/80-409.htm?lr=lang_es

Morin, X., Roy, J., Sonié, L., Chuine, I., 2010. Changes in leaf phenology of threeEuropean oak species in response to experimental climate change. New Phytologist 186 (4): 900–910.

Mutke, S., Gordo, J., Khouja, M.L., Fady, B., 2013. Low genetic and high environmental diversity at adaptive traits in Pinus pinea from provenance tests in France and Spain. In : Mutke S., Piqué M. , Calama R. (ed.) Mediterranean stone pine for agroforestry. Zaragoza : CIHEAM / FAO / INIA / IRTA / CESEFOR / CTFC, p. 73-79. (Options Méditerranéennes: Série A. Séminaires Méditerranéens; n. 105). AGROPINE 2011, International Meeting on Mediterranean Stone Pine for Agroforestery, 2011/11/17-19, Valladolid (Spain), http://om.ciheam.org/om/pdf/a105/00006784.pdf

Mutke, S., Gordo, J., Chambel, M. R., Prada, M. A., Álvarez, D., Iglesias, S., Gil, 523 L., 2010. Phenotypic plasticity is stronger than adaptative differentiation among Mediterranean stone pine provenances. Forest Systems 19(3): 354-366.

Myking, T. , Heide, O.M., 1995. Dormancy release and chilling requirement of buds of latitudinal ecotypes of Betula pendula and B. pubescens. Tree Physiology 15(11): 697-704.

Navarro, R., 2011a. ¿Qué es una dehesa?. In: Alejano, R., Domingo, J., Fernández, M. (Ed.) Manual para la gestión sostenible de las dehesas andaluzas. Foro para la Defensa y Conservación de la Dehesa – Universidad de Huelva. Huelva, Spain, pp. 19-24

Navarro, R., 2011b. Situación actual. In: Alejano, R., Domingo, J., Fernández, M. (Ed.) Manual para la gestión sostenible de las dehesas andaluzas. Foro para la Defensa y Conservación de la Dehesa – Universidad de Huelva. Huelva, Spain, pp. 62-68

Neuwirth, B., Esper, J., Schweingruber, F. H., Winiger, M., 2004. Site ecological differences to the climatic forcing of spruce pointer years from the Lötschental, Switzerland. Dendrochronologia: 21(2): 69-78.

Ni, F., Cavazos, T., Hughes, M.K., Comrie, A.C. , Funkhouser, G., 2002. Cool-season precipitation in the southwestern USA since AD 1000: comparison of linear and nonlinear techniques for reconstruction.International Journal of Climatology 22(13): 1645-1662.

Nicault, A., Alleaume, S., Brewer, S., Carrer, M., Nola, P. , Guiot, J., 2008. Mediterranean drought fluctuation during the last 500 years based on tree-ring data. Climate Dynamics 31(2-3): 227-245.

Nicotra, A. B., Atkin, O. K., Bonser, S. P., Davidson, A. M., Finnegan, E. J., Mathesius, U., Poot , P., Purugganan, M.D., Richards, C.L., Valladares, F., , van Kleunen, M., 2010. Plant phenotypic plasticity in a changing climate. Trends in Plant Sciences 15(12): 684-692.

Novak, K., De Luis, M., Gričar, J., Prislan, P., Merela, M., Smith, K.T. and Čufar, K., 2016. Missing and dark rings associated with drought in Pinus halepensis. IAWA Journal 37(2): 260-274.

Novak K., de Luís M., Raventós J., Čufar K., 2013. Climatic signals in tree ring widths and wood structure of Pinus halepensis in contrasted environmental conditions. Trees-Structure and Functions 27: 927–936

Novak, K., De Luis, M., Čufar, K., Raventós, J., 2011. Frequency and variability of missing tree rings along the stems of Pinus halepensis and Pinus pinea from a semiarid site in SE Spain. Journal of Arid Environments 75(5): 494-498.

Ogaya, R., Peñuelas, J., 2003. Comparative field study of Quercus ilex and Phillyrealatifolia: photosynthetic response to experimental drought conditions. Environmental and Experimental Botany 50 (2): 137–148.

Ogaya, R., Peñuelas, J., Martínez-Vilalta, J., Mangirón, M., 2003. Effect of droughton diameter increment of Quercus ilex, Phillyrea latifolia, and Arbutus unedo in aholm oak forest of NE Spain. Forest Ecology and Management 180 (1): 175–184.

Olea, L., San Miguel-Ayanz, A., 2006. The Spanish dehesa. A traditional Mediterranean silvopastoral system linking production and nature conservation. In: (Lloveras, J., González-Rodríguez, A., Vázquez-Yáñez, O., Piñeiro, J., Santamaría, O., Olea L., Poblaciones, M.J. (Ed.) "Sustainable Grasland Productivity" - Proceedings of the 21st General Meeting of the European Grassland Federation, Badajoz, Spain, 3-6 April 2006. Sociedad Española para el Estudio de los Pastos, Madrid, Spain, pp.3-13, http://www.europeangrassland.org/printed-matter/proceedings.html

Olea, L., López-Bellido, R.J. , Poblaciones, M.J., 2005. European types of silvopastoral systems in the Mediterranean area: dehesa. In: Mosquera-Losada, M.R., McAdam, J., Rigueriro-Rodríguez, A. (Ed.) Proceedings of the International Congress on Silvopastoralism and Sustainable Management (Lugo, Spain, April 2004). CABI Publishing, Oxfordshire, UK, pp. 30-33.

Oribe, Y., Kubo, T., 1997. Effect of heat on cambial reactivation during winter dormancy in evergreen and deciduous conifers. Tree Physiology 17(2): 81-87.

Ovando, P., Campos, P., Calama, R., Montero, G., 2010. Landowner net benefit from Stone pine (Pinus pinea L.) afforestation of dry-land cereal fields in Valladolid, Spain. Journal of Forest Economics, 16(2): 83-100.

Palmer, W. C, 1965: Meteorological Drought. Res. Paper No.45, 58pp., Dept. of Commerce, Washington, D.

Pardos, M., Calama, R., Maroschek, M., Rammer, W., Lexer, M. J., 2015. A model-based analysis of climate change vulnerability of Pinus pinea stands under multiobjective management in the Northern Plateau of Spain. Annals of Forest Science 72(8): 1009-1021.

Pasalodos-Tato, M., Pukkala, T., Calama, R., Cañellas, I., Sánchez-González, M., 2016. Optimal management of Pinus pinea stands when cone and timber production are considered. European Journal of Forest Research 135 (4): 607-619.

Pedersen, B.S., 1998. The role of stress in the mortality of midwestern oaks asindicated by growth prior to death. Ecology 79 (1): 79–93.

Peñuelas, J., Hunt, J.M., Ogaya, R. , Jump, A.S., 2008. Twentieth century changes of tree-ring δ13C at the southern range-edge of Fagus sylvatica: increasing water-use efficiency does not avoid the growth decline induced by warming at low altitudes. Global Change Biology 14(5): 1076-1088.

Peñuelas J., Filella I., Comas P., 2002. Changed plant and animal life cycles from 1952 to 2000 in the Mediterranean region. Global Change Biology 8: 531–544

Pereira, J.S., Mateus, J.A., Aires, L.M., Pita, G., Pio, C., David, J.S., Rodrigues, A., 2007.Net ecosystem carbon exchange in three contrasting Mediterranean ecosystems—the effect of drought. Biogeosciences 4 (5): 791–802.

Perez Antelo, A., 1994. Nota de revisión de la investigación dendrocronológica en España. Investigación agraria. Sistemas y recursos forestales 3(2): 221-235

Piermattei A., Garbarino M., Urbinati C., 2014. Structural attributes, tree-ring growth and climate sensitivity of Pinusnigra Arn. at high altitude: common patterns of a possible treeline shift in the central Apennines (Italy). Dendrochronologia 32: 210–219

Pilcher, J.R., 1990. Primary data. In: Cook ER, Kairiukstis LA (ed.): Methods of dendrochronology: applications in the environmental sciences. KluwerAcademicPublishers, Dordrecht, The Netherlands, p.40-50

Pinto-Correia, T., Ribeiro, N. , Sá-Sousa, P., 2011. Introducing the montado, the cork and holm oak agroforestry system of Southern Portugal. Agroforestry Systems 82(2): 99-104.

Pinzauti, F., Sebastiani, F., Budde, K.B., Fady, B., González-Martínez, S.C. , Vendramin, G.G., 2012. Nuclear microsatellites for Pinus pinea (Pinaceae), a genetically depauperate tree, and their transferability to P. halepensis. American Journal of Botany, DOI: 10.3732/ajb.1200064

Piovesan G., Biondi F., Di Filippo A., Alessandrini A., Maugeri M., 2008, Drought-driven growth reduction in old beech (Fagus sylvatica L.) forests of the central Apennines, Italy. Global Change Biology 14: 1265–1281

Piovesan, G., Di Filippo, A., Alessandrini, A., Biondi, F. , Schirone, B., 2005. Structure, dynamics and dendroecology of an old-growth Fagus forest in the Apennines. Journal of Vegetation Science 16(1): 13-28.

Piovesan G., Schirone B., 2000. Winter North Atlantic oscillation effects on the tree rings of the Italian beech (Fagus sylvatica L.). International Journal of Biometeorology 44: 121–127

Piraino S., Camiz S., Di Filippo A., Piovesan G., Spada F., 2013. A dendrochronological analysis of Pinus pinea L. on the Italian mid-Tyrrhenian coast. Geochronometria 40: 77–89

Piutti, E. , Cescatti, A., 1999. A new detrending method for the analysis of the climate-competition relations in tree-ring sequences. In: Wimmer, R., Vetter, R.E. (Eds.) Tree-ring Analysis: biological, methodological, and environmental aspects. CABI Publishing, Wallingford, pp.249-264.

Planells, O., Gutiérrez, E., Helle, G. , Schleser, G.H., 2009. A forced response to twentieth century climate conditions of two Spanish forests inferred from widths and stable isotopes of tree rings. Climatic Change 97(1-2): 229-252.

Plieninger, T., Pulido, F. J., Schaich, H., 2004. Effects of land-use and landscape structure on holm oak recruitment and regeneration at farm level in Quercus ilex L. dehesas. Journal of Arid Environments 57(3): 345-364.

Prieto, L., Herrera, R. G., Díaz, J., Hernández, E., del Teso, T., 2004. Minimum extreme temperatures over Peninsular Spain. Global and Planetary Change 44(1): 59-71.

Pukkala, T., Miina, J. Palahí, M. 2002. Thinning response and thinning bias in a young Scots pine stand. Silva Fennica 36(4): 827–840.

Pulido, F. J., Díaz, M., de Trucios, S. J. H., 2001. Size structure and regeneration of Spanish holm oak Quercus ilex forests and dehesas: effects of agroforestry use on their long-term sustainability. Forest Ecology and Management 146(1): 1-13

Qu, M., Wan, J., Hao, X., 2014. Analysis of diurnal air temperature range change in the continental United States. Weather and Climate Extremes 4: 86-95.

Raventós J., De Luís M., Gras M.J., Čufar K., González-Hidalgo J.C., Bonet A., Sánchez J.R., 2001. Growth of Pinus pinea and Pinus halepensis as affected by dryness, marine spray and land use changes in a Mediterranean semiarid ecosystem. Dendrochronologia 19: 211-220

Resco de Dios V., Fischer C., Colinas C., 2007. Climate change effects on Mediterranean forests and preventive measures. New Forests 33: 29-40

Rinn F., 2011. TSAP-WinTM: time series analysis and presentation for dendrochronology and related applications. Rinntech®, Heidelberg, Germany

Rodrigo, F. S., Trigo, R. M., 2007. Trends in daily rainfall in the Iberian Peninsula from 1951 to 2002. International Journal of Climatology 27(4), 513-529

Romero de los Reyes, E., Navarro, R., , García-Ferrer, A., 2007. Aplicación de ortofotos para la estimación de pérdida de individuos en dehesas de encina (Quercus ilex L. subsp. ballota (Desf.) Samp.) afectadas por procesos de decaimiento. Boletín de Sanidad Vegetal. Plagas 33: 121-134 http://www.magrama.gob.es/ministerio/pags/Biblioteca/Revistas/pdf_Plagas%2FBSVP_33_01_121_134.pdf

Rossi, S., Morin, H., Deslauriers, A., Plourde, P. Y., 2011. Predicting xylem phenology in black spruce under climate warming. Global Change Biology 17(1): 614-625

Rossi, S., Deslauriers, A., Griçar, J., Seo, J.W., Rathgeber, C.B., Anfodillo, T., Morin, H., Levanic, T., Oven, P. , Jalkanen, R., 2008. Critical temperatures for xylogenesis in conifers of cold climates. Global Ecology and Biogeography 17(6): 696-707.

Rossi, S., Deslauriers, A., Anfodillo, T. , Carraro, V., 2007. Evidence of threshold temperatures for xylogenesis in conifers at high altitudes. Oecologia: 152(1):1-12.

Rossi, S., Deslauriers, A. , Anfodillo, T., 2006. Assessment of cambial activity and xylogenesis by microsampling tree species: an example at the Alpine timberline. IAWA Journal 27(4) : 383-394.

Ruiz de la Torre, J., 2006. Flora Mayor. Organismo Autónomo de Parques Nacionales, Madrid

Ryerson, D.E., Swetnam, T.W. , Lynch, A.M., 2003. A tree-ring reconstruction of western spruce budworm outbreaks in the San Juan Mountains, Colorado, USA. Canadian Journal of Forest Research 33(6): 1010-1028.

Sáez-Laguna, E., Guevara, M. Á., Díaz, L. M., Sánchez-Gómez, D., Collada, C., Aranda, I., Cervera, M. T., 2014. Epigenetic variability in the genetically uniform forest tree species Pinus pinea L. Plos One, DOI: 10.1371/journal.pone.0103145

Sánchez, I., López, G., 2011. Tratamientos sanitarios: actuaciones para el control de plagas y enfermedades en la dehesa. In: Alejano, R., Domingo, J., Fernández, M. (Ed.) Manual para la gestión sostenible de las dehesas andaluzas. Foro para la Defensa y Conservación de la Dehesa – Universidad de Huelva. Huelva, Spain, pp. 224-339

Sánchez, M. E., Caetano, P., Ferraz, J., Trapero, A., 2002. Phytophthora disease of Quercus ilex in south-western Spain. Forest Pathology 32(1): 5-18.

Sánchez-Gómez, D., Velasco-Conde, T., Cano-Martín, F. J., Guevara, M. Á., Cervera, M. T., Aranda, I. 2011. Inter-clonal variation in functional traits in response to drought for a genetically homogeneous Mediterranean conifer. Environmental and Experimental Botany 70(2): 104-109.

Schweingruber, F.H., 2007: Wood Structure and Environment. Springer Berlin, Heidelberg

Schweingruber, F.H., Poschlod, P., 2005. Growth Rings in Herbs and Shrubs: life span, age determination and stem anatomy. Swiss Federal Research Institute WSL, Birmensdorf-Haupt, Berne, Stuttgart, Vienna

Schweingruber, F.H., 1996. Tree rings and environment. Dendroecology. Birmensdorf, Swiss Federal Institute for Forest, Snow and Landscape Research. Haupt Publishers, Berne, Stuttgart, Vienna

Schweingruber, F.H., Kairiukstis, L., Shiyatov, S., 1990. Sample selection. In: Cook, E.R., Kairiukstis, L.A. (Ed.) Methods of dendrochronology: applications in the environmental sciences. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 23-35

Seim, A., Treydte, K., Trouet, V., Frank, D., Fonti, P., Tegel, W., Panayotov, M., Fernández-Donado, L., Krusic, P. and Büntgen, U., 2015. Climate sensitivity of Mediterranean pine growth reveals distinct east–west dipole. International Journal of Climatology 35(9): 2503-2513.

Serrada, R., San Miguel, A., 2008. Selvicultura en dehesas. In: Serrada, R., Montero, G., Reque, J.A. Compendio de selvicultura aplicada en España. Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria, Madrid, Spain, pp. 861-876

Shiyatov, S.G., Fritts, H.C. , Lofgren, R.G., 1989. Comparative Analysis of the Standardization Methods of Tree-Ring Chronologies. In: Noble, R.D., Martin, J.L., Jensen, K.F. (Eds.) Proceedings of the Second US-USSR Symposium on Air Pollution on Vegetation Including Forest Ecosystems. US Department of Agriculture-Forest Service and US Environmental Protection Agency (pp. 13-25).

Skovsgaard, J.P. , Vanclay, J.K., 2008. Forest site productivity: a review of the evolution of dendrometric concepts for even-aged stands. Forestry 81(1): 13-31.

Smith, D.M., Larson B.C., Kelty M.,J., Asthon P.M.S., 1997. The practice of silviculture: applied forest ecology. John Wiley & Sons, Inc., United States of America

Soto, A., Robledo-Arnuncio, J.J., González-Martínez, S.C., Smouse, P.E. , Alia, R., 2010. Climatic niche and neutral genetic diversity of the six Iberian pine species: a retrospective and prospective view. Molecular Ecology 19(7): 1396-1409

Speer J.H., 2010. Fundamentals of tree-ring research. University of Arizona Press, Tuscon, USA

Stahle, D.W., Cook, E.R., Cleaveland, M.K., Therrell, M.D., Meko, D.M., Grissino-Mayer, H.D., Watson, E. , Luckman, B.H., 2000. Tree-ring data document 16th century megadrought over North America. Eos, Transactions American Geophysical Union 81(12): 121-125.

Sumner, G. N., Romero, R., Homar, V., Ramis, C., Alonso, S., Zorita, E., 2003. An estimate of the effects of climate change on the rainfall of Mediterranean Spain by the late twenty first century. Climate Dynamics 20(7-8), 789-805.

Tardif, J., Camarero, J.J., Ribas, M. , Gutiérrez, E., 2003. Spatiotemporal variability in tree growth in the Central Pyrenees: climatic and site influences. Ecological Monographs 73(2): 241-257.

Till, C. , Guiot, J., 1990. Reconstruction of precipitation in Morocco since 1100 AD based on Cedrus atlantica tree-ring widths. Quaternary Research 33(3): 337-351.

Tognetti, R., Longobucco, A., Raschi, A., 1998. Vulnerability of xylem to embolism inrelation to plant hydraulic resistance in Quercus pubescens and Quercus ilexcooccurring in a Mediterranean coppice stand in central Italy. New Phytologist 139(3): 437–447.

Torres, E., 2011. Evolución histótica de las dehesas y su gestión. In: Alejano, R., Domingo, J., Fernández, M., 2011. Manual para la gestión sostenible de las dehesas andaluzas. Foro para la Defensa y Conservación de la Dehesa – Universidad de Huelva. Huelva, Spain, pp. 52-61

Trapero, A., Romero, M.A., Sánchez, J.E., 2006. La seca de encinas y alcornoques en Andalucía: decaimiento y enfermedad. Boletin informativo CIDEU N. 1, pp. 7-14

UN, 2015. Resolution adopted by the General Assembly on 25 September 2015. A/RES/70/1 - Transforming our world: the 2030 Agenda for Sustainable Development. United Nations, https://sustainabledevelopment.un.org/post2015/summit

UNEP, 1992. Report of the United Nations Conference on Environment and Development, Rio de Janeiro, 3-14 June 1992. Annex III – Non-legally binding authoritative statement of principles for a global consensus on the management, conservation and sustainable development of all types of forests. A/CONF.151/26 (Vol. III). United Nations General Assembly. http://www.un.org/documents/ga/conf151/aconf15126-3annex3.htm

Vaganov, E.A., Hughes, M.K., Shashkin, A.V., 2006.Growth Dynamics of Conifer Tree Rings: Images of Past and Future Environments. Springer.

Vaz, M., Pereira, J.S., Gazarini, L.C., David, T.S., David, J.S., Rodrigues, A., Maroco, J.,Chaves, M.M., 2010. Drought-induced photosynthetic inhibition and autumnrecovery in two Mediterranean oak species (Quercus ilex and Quercus suber).Tree Physiology 30: 946–956.

Vázquez-Piqué, J., 2011. Clima. In: Alejano, R., Domingo, J.M., Fernández, M. (Eds.). Manual para la gestión sostenible de las dehesas andaluzas. Foro para laDefensa y Conservación de la Dehesa Encinal y Universidad de Huelva, pp.85–107.

Venables W.N., Smith D.M., 2015 (Eds.). An introduction to R. R Core Team, http://cran.r-project.org/doc/manuals/r-release/R-intro.pdf

Vendramin, G.G., Fady, B., González-Martínez, S.C., Hu, F.S., Scotti, I., Sebastiani, F., Soto, Á. , Petit, R.J., 2008. Genetically depauperate but widespread: the case of an emblematic Mediterranean pine. Evolution 62(3): 680-688.

Vericat, P., Piqué, M., Serrada, R., 2012. Gestión adaptativa al cambio global en masas de Quercus mediterráneos. Centre Tecnològic Forestal de Catalunya. Solsona, Lleida

Vieira, J., Rossi, S., Campelo, F., Freitas, H., Nabais, C., 2014. Xylogenesis of Pinus pinaster under a Mediterranean climate. Annals of Forest Science 71(1): 71-80

Vieira, J., Campelo, F. , Nabais, C., 2010. Intra-annual density fluctuations of Pinus pinaster are a record of climatic changes in the western Mediterranean region. Canadian Journal of Forest Research 40(8): 1567-1575.

Villalba, R., Luckman, B.H., Boninsegna, J., D'Arrigo, R.D., Lara, A., Villanueva-Diaz, J., Masiokas, M., Argollo, J., Soliz, C., LeQuesne, C., Stahle, D.W., Roig., F., Aravena, J.C., Hughes, M.K., Wiles, G., Jacoby, G., Hartsough, P., Wilson, R.J.S., Watson, E., Cook, E.R., Cerano-Paredes, J., Therrel, M., Cleaveland, M., Morales, M.S., Graham, N.E., Moya, J., Pacajes, J., Massacchesi, G., Biondi, F., Urrutia, R., Martinez Pastur, G., 2011. Dendroclimatology from regional to continental scales: Understanding regional processes to reconstruct large-scale climatic variations across the Western Americas. In: Hughes, M.K., Swetnam, T.W. , Diaz, H.F. (Eds.) Dendroclimatology: progress and prospects. Springer Science & Business Media, pp. 175-230

Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J., Fromentin, J.M., Hoegh-Guldberg, O. , Bairlein, F., 2002. Ecological responses to recent climate change. Nature 416(6879): 389-395

Warren, M.G., MacWilliam, S.L. 1981. Test of a new method for removing the growth trend from dendrochronological data. Tree-Ring Bulletin 41: 55-66.

Warren, W.G. 1980. On removing the growth trend from dendrochronological data. Tree-Ring Bulletin 40: 35-44

Wells, N., Goddard, S. , Hayes, M. J., 2004. A Self-Calibrating Palmer Drought Severity Index, Journal of Climate 17: 2335-2351

Wiles, G.C., Calkin, P.E. , Jacoby, G.C., 1996. Tree-ring analysis and Quaternary geology: principles and recent applications. Geomorphology 16(3): 259-272.

Williams, M., 2006. Deforesting the earth: from prehistory to global crisis. University of Chicago Press.

Wilmking, M., Juday, G.P., Barber, V.A. , Zald, H.S., 2004. Recent climate warming forces contrasting growth responses of white spruce at treeline in Alaska through temperature thresholds. Global Change Biology 10(10): 1724-1736.

Wolf, J.B. , Wade, M.J., 2009. What are maternal effects (and what are they not)?. Philosophical Transactions of the Royal Society of London B: Biological Sciences 364(1520): 1107-1115.

Yuan, Y.J., Zhang, T.W., Wei, W.S., Nievergelt, D., Verstege, A., Yu, S.L., Zhang, R.B. , Esper, J., 2013. Development of tree-ring maximum latewood density chronologies for the western Tien Shan Mountains, China: Influence of detrending method and climate response. Dendrochronologia 31(3): 192-197.

Zamora Rojas, E., Andicoberry de los Reyes, S., Sánchez Hernández., M. E., 2014. El decaimiento y la podedumbre radical en las dehesas andaluzas. In: Diputación Provincial de Huelva (Ed.) El Andévalo. Historia y Paisaje. Actas de las IV jornadas del Patrimonio de El Andévalo, El Cerro del Andévalo, Huelva, 15-17 de noviembre 2013. Servicio de publicaciones de la Diputación de Huelva, Huelva, Spain, pp.49-78

Zang C., Biondi F., 2015. treeclim: an R package for the numerical calibration of proxy-climate relationships. Ecography 38(4): 431-436.

Zang C., Biondi F., 2012. Dendroclimatic calibration in R: The bootRes package for response and correlation function analysis. Dendrochronologia 31(1): 68-74

Zhang, S.H. , Romane, F., 1991. Variations de la croissance radiale de Quercus ilex L en fonction du climat. Annales des Sciences Forestières 48 (2) :225-234

Ziaco, E., Biondi, F., Di Filippo, A. , Piovesan, G., 2012. Biogeoclimatic influences on tree growth releases identified by the boundary line method in beech (Fagus sylvatica L.) populations of southern Europe. Forest Ecology and Management 286: 28-37.

Zweifel, R., Eugster, W., Etzold, S., Dobbertin, M., Buchmann, N. , Häsler, R., 2010. Link between continuous stem radius changes and net ecosystem productivity of a subalpine Norway spruce forest in the Swiss Alps. New Phytologist 187(3): 819-830.

15 APPENDIX 1. SCIENTIFIC ARTICLES DERIVED FROM THIS THESIS

15.1 **Article 1.** Natalini F., Vázquez-Piqué J., Alejano R., 2016. Dendroclimatic signal in managed Mediterranean forests.: a case study in SW Spain. In: Hevia, A., Sánchez-Salguero, R., Linares, J. C., Olano, J. M., Camarero, J. J., Gutiérrez, E., Helle, G., Gärtner, H. (2016), TRACE - Tree Rings in Archaeology, Climatology and Ecology, Volume 14 (pp.102-110). Scientific Technical Report 16/04, GFZ German Research Centre for Geosciences. DOI: 10.2312/GFZ.b103-16042.

Natalini F., Vázquez-Piqué J., Alejano R.: Departamento de Ciencias Agroforestales, Escuela Técnica Superior de Ingeniería, Universidad de Huelva, Campus de La Rábida, 21819 Palos de la Frontera, Huelva, Spain

Introduction

Processes and dynamics of the natural environment can be studied through the information stored in tree rings. Since radial stem increment is influenced by a number of external factors (Cook & Briffa, 1990), extracting from a tree-ring chronology the information related to one of those factors requires the retention of the chronology variance linked to that single factor and the removal of the variance linked to the others. The climatically explained ring-width variance common to an ensemble of trees is the "signal" of interest in dendroclimatology. The extraction of the climatic signal is done through the standardization procedure, which involves three steps: (1) "detrending", i.e. removing the growth variability which is not related to climate from individual series of measured tree-ring parameters, (2) "indexing", i.e. computing a-dimensional tree-ring data from the detrended series, (3) estimating a master chronology containing the common climatic signal of the ensemble of trees by averaging the indexed series (see Cook and Briffa, 1990). Detrending methods are crucial in dendroclimatology and typically involve fitting a smoothing function to the tree ring series. They are defined "deterministic", when the fitted function is an a priori defined mathematical model (e. g. straight lines, exponential functions), or "stochastic", when a data-adaptive running function is fitted to the series (e.g. splines) (Cook et al., 1990a). When deterministic models are used, the goodness-of-fit can vary with time because of the middle-frequency perturbations commonly found in ring-width series of trees growing within stands owing to stand dynamics. For that, data-adaptive models can be more appropriate to find the best fitting (Cook et al., 1990a). However, care must be taken when using a stochastic model because, the more it closely follows the fluctuations of the ring width series (i.e. more the smoothing function is flexible), the more the variance is removed at the low-frequencies. Long-term climatic changes are recorded in low-frequency growth variability which hence should be also retained as climatic signal (Briffa et al. 1996).

In the Mediterranean forests of the Iberian Peninsula, dendroclimatological studies can provide valuable information about forests dynamics in relation to climate change (e.g.

Gea-Izquierdo et al., 2011, 2014). However, the Iberian Mediterranean forests are systematically managed, thus anthropogenic disturbances influence tree growth.

Pinus pinea L. is an important tree species of Iberian Mediterranean forests. In Spain, it forms monospecific or mixed woodlands which occupy more than 500˙000 ha. Most of these woodlands originated from plantations during the 20th century and present even aged stand structure. In *P. pinea* forests of Southwestern Spain, the production of timber and pine nuts are among the main purposes of silvicultural measures, which typically involve thinning for improving wood production and crown development. Therefore, forestry-related variability in growth patterns can be expected in these forests.

We tested detrending criteria based on smoothing functions in managed *P. pinea* woodlands in SW Spain. Ring-width series were smoothed by fitting functions with different degree of flexibility. We hypothesized that flexible curves would provide a better climatic signal at the high frequencies by smoothing the stochastic growth oscillations related to silvicultural measures, while more conservative criteria would retain higher amounts of climate change-related low-frequency growth trends.

Materials and methods

Study site, samples and measurements

The samples were collected from two *Pinus pinea* monospecific stands with flat sandy terrains located in Valverde del Camino (37.53°N, 6.78°W; 200 m a.s.l.) and Hinojos (37.28°N, 6.39°W; 100 m a.s.l.), SW Spain. The stand in Valverde presents a mean tree height of 19 m, a mean DBH of 60 cm and a density of 150 trees/ha. The stand in Hinojos presents a mean tree height of 20 m, a mean DBH of 70 cm and a density of 200 trees/ha. The climate of the region is Mediterranean and summer drought normally lasts for 3 months (Jun-Aug). Hence, we expected to find a chronology signal related to water availability as a limiting growth factor. When selecting the study sites, we searched for the oldest stands, which could provide chronologies long enough for climate investigation, and site homogeneity, which enhanced the common chronology signal (Pilcher, 1990). The samples were extracted from 20 dominant trees in each site with an increment borer at breast height (two samples per tree). Individual ring-width series were measured and cross-dated (Pilcher, 1990; Grissino-Mayer, 2001). Since we found chronologies of different lengths, in the subsequent analyses we only included the trees older than 110 years to ensure the use of the oldest trees only and thus to buffer the possible differences in the response to climate between trees of different age (Carrer and Urbinati, 2004). The confidence of the chronology was verified through the Expressed Population Signal (EPS) (Briffa and Jones, 1990).

Detrending criteria and computation of the master chronologies

We used 4 criteria to detrend the tree-ring width series:

1) Spline with a period equal to the 67% of the series length expressed in years (SP67). This method enables the retention of some portion of growth variability at medium/low frequencies (Cook et al., 1990a).

2) Double detrending (DDET). This criterion follows the 2-step method introduced by Holmes et al. (1986). We computed tree-ring indices through a negative exponential curve, which fits well the descending juvenile portion of the ring-width series, and then we detrended a second time by applying to the indices a spline with a period equal to the 67% of the series length, which was meant to remove the growth trends that were not smoothed in the first step.

3) Spline with a period that maximized the signal-to-noise ratio (MSNR). This was proposed by Cook et al. (1990a) as an objective criterion to choose the proper flexibility of a digital filter. The signal-to-noise ratio (SNR) is an expression of the strength of the chronology signal (Briffa and Jones, 1990). This criterion produces short wavelengths that emphasize the high-frequency response to climate (see e.g. Piermattei et al. 2014).

4) Spline with a fixed period of 32 years ("SP32"). Periods approaching 30 years produce quite flexible splines which can properly filter tree-ring series from closed-canopy stands and managed woodlands, where medium/low-frequency growth oscillations are expected as a result of competition, stand dynamics and silviculture (e.g. Gea-Izquierdo et al. 2009). The period of 32 years is generally used as a default spline rigidity to accomplish the optimum job of discovering errors in cross-dating (Grissino-Mayer, 2001) and was chosen here as a reference against the other criteria.

Since we were mainly interested in testing detrending methods, we followed the same indexing procedure and master chronology estimation for all the four detrending criteria (Cook et al. 1990b): firstly, the indices were computed as ratios of the measured ring widths to the values estimated by the fitted detrending model; secondly, an autoregressive model was fitted to the indexed series to remove the autocorrelation; finally, two master chronologies were computed as biweight robust means for each site, i.e. a standard chronology (computed from the indexed series, without autoregressive model), and a residual chronology (calculated from the prewhitened series). The standard and the residual chronologies were used in the subsequent analyses.

Statistical comparison of the master chronologies

To evaluate the quality of the standard chronologies in terms of common signal among trees captured through detrending, we used the EPS, the SNR and the mean inter-series correlation (r) (Briffa and Jones, 1990).

The standard deviation (SD), the 1st–order autocorrelation (AC) and the mean sensitivity (MS) were used as measures of the retained growth variability in the standard chronologies. The SD was used as a measure of the dispersion of the dataand to evaluate the reduction of dispersion after detrending. We calculated the AC to examine the capacity of the detrending criteria to reduce the noise deriving from the one-year lag persistence in growth (Cook et al.1990b). The MS, defined as the average of the relative differences from one ring to the next (Fritts, 1976), was used to assess the amount of retained year-to-year growth variability after detrending.

The power spectra of the standard chronologies were studied to determine how the power of the chronology signal was distributed across the range of frequencies after each detrending criterion.

A growth-climate correlation analysis was performed to examine the dendroclimatic signal at the high frequencies. We used monthly cumulative precipitation and averages of minimum and maximum temperatures from a close meteorological station (Fig. 1) as independent variables and residual chronologies as dependent variables to compute bootstrapped correlations with a statistical critical value α = 0.05. Through the significance test we searched for the months in which climatic conditions had more influence on annual growth, and we expected to find out some differences in the pattern of significant months depending on the detrending method applied to obtain the chronology used in the analysis.

We compared the suitability of the residual chronologies for climate reconstruction through a calibration-verification procedure (Fritts and Guiot, 1990). We used mean annual values of self-calibrated Palmer Drought Severity Index (PDSI) (Dai et al., 2004).The overlap period between the chronologies and the PDSI series was divided into two intervals of equal length: the first interval was the dependent set for calibration, and the second was the independent set for verification. The independent set included the recent decades because we wanted to test the capacity of the chronologies to estimate the increase of aridity over recent decades previously documented for the region (Romero et al. 1998). In the calibration phase, the relationship between PDSI and chronologies was modeled through a simple linear regression (Fritts and Guiot, 1990). The regression coefficients obtained in the calibration phase were applied to the tree-ring data of the independent set to obtain PDSI estimates. In the verification phase, the actual PDSI values of the independent set were compared with the PDSI estimates through correlation coefficients and the reduction of error (RE) (see Blasing et al., 1981).

Results and discussion

The chronology lengths ranged from 90 to 139 years in Valverde and from 70 to 150 in Hinojos. The trees older than 110 years were 15 in Valverde and 16 in Hinojos. The raw ring width series and the master chronologies are plotted in figure 1. Residual fluctuations remained after standardization at the low frequencies, with higher amplitudes in the case of DDET and SP67. The statistics of the standard chronologies are reported in table 1. The EPS was above the minimum threshold of 0.85 (Briffa and Jones, 1990) and rather similar among the four standard chronologies, indicating that reliable chronologies were obtained with all four criteria. However, we found that the lowest values of r and SNR were brought by the stiffer smoothing functions, which in contrast produced the highest values of SD, AC and MS.

The power spectra (Fig. 2) show that the amounts of signal power at the lowest frequencies were higher for the SP67 and were almost eliminated by the MSNR criterion, in accordance with the different amplitudes observed in the oscillations retained in the master chronologies (Fig. 1). The higher amounts of variance at the low frequencies found with DDET and SP67 in Hinojos can be related to the growth release in the 1960s-70s, which was originated by thinning.

The correlation analysis between the master chronologies and meteorological covariates (Fig. 3) indicates that flexible splines accomplish a better job in analyzing the high-frequency growth response to climate. Correlation between radial growth and winter (Dec-Jan-Feb) rainfall was found with all four detrending criteria. It is probably explained by the winter maximum precipitation in the study area and may reflect the importance of soil recharge for improving water availability and subsequent growth in spring (Campelo et al. 2006). We also observed in all cases (except for MSNR in Hinojos) a positive response to mild temperatures in winter, suggesting that in evergreen trees the ring formation is linked to the photosynthesis and carbohydrates produced during this season (Baldocchi 2010). In Valverde, the contribution of spring rainfalls, an important factor for the formation of rings (Campelo et al. 2006; De Luis et al. 2013) were well indicated by the relationship between the MSNR chronology and precipitation from March to May, while significant correlations were found only in May with the other detrending criteria. The correlation with rainfall of the previous autumn, indicating the importance of soil water reserves for the formation of rings (Di Filippo et al. 2010), and with precipitation in the autumn of the current year, reflecting the activity of the cambium in Mediterranean species in this season (e.g. Camarero et al 2010), was found only in the case of MSNR chronology. Furthermore, the dendroclimatic signal related to the negative effect of high temperatures in May and June, which can be explained by the reduction of stomatal conductance and photosynthetic inhibition induced by water stress (Vaz et al. 2010), was better assessed with the SP32 master chronology. Negative responses to high temperatures in spring and summer were not detected in Hinojos, but the positive relationship with temperatures in April and June was found with the DDET and SP67 criteria, that was surprising because high temperatures in these seasons induce water stress and inverse (or not significant) responses by trees should be expected (e.g. Campelo et al. 2006; De Luis et al. 2013), and seems to indicate that stiff detrending models were not appropriate to study the relationships with climate in this site.

The RE and the correlation coefficients between the actual PDSI and the PDSI estimates are listed in table 2. Both statistics indicate that the MSNR method was the least effective in estimating climate. For Valverde, the correlation coefficient increased slightly when the detrending methods were applied in the order SP32-SP67-DDET, but the SP32 brought the highest RE. In Hinojos, the RE was higher with SP67, but the correlation coefficients obtained with SP67 and SP32 were equal. The actual PDSI and the PDSI estimates are plotted in figure 4: the actual values showed fluctuations in the mid/low frequencies, which were induced by an arid period in the 1980s and 1990s and were matched by the PDSI series estimated from the SP32, DDET and SP67 residual chronologies. Our results suggest that good climate reconstructions can be accomplished by the use of stiff detrending functions. The verification analysis involving the SP32 chronology suggested that good estimates can be provided by flexible splines as well, but very flexible splines are not appropriate for climate reconstructions. This is confirmed by the PDSI estimated by the MSNR chronology, which was positively correlated with the actual PDSI and produced positive RE, but showed no coherence at the low frequencies with the actual data.

Conclusions

Conservative detrending methods retain higher amounts of low-frequency growth variability, which can reflect the impacts on growth of long-term climatic changes, but can fail in removing non-climatic anomalies that could be wrongly interpreted as exceptional climatic events. In managed closed-canopy woodlands, detrending methods involving flexible smoothing functions properly filter the middle/low-frequency growth variance deriving from stand dynamics and provide meaningful results when climate-growth relationships are analyzed. However, very flexible functions can even entirely remove the low-frequency variance, so they could fail in conserving growth responses to long-term climatic changes. The choice of the detrending method should be done on the basis of a careful evaluation of the stand characteristics and frequency domain of the resulting standardized chronology. In our study case, the SP32 criterion was appropriate to preserve as much low frequency as possible and yet remove the noise deriving from stand dynamics, indicating that smoothing functions with period approaching 30 years are suitable for dendroclimatic studies in the managed woodlands in our region.

Table 1. Statistics of the standard chronologies (r: inter-series correlation, AC: 1st order autocorrelation; SNR: signal-to-noise ratio; EPS: expressed population signal; MS: mean sensitivity)

	Hinojos				Valverde			
	MSNR	SP32	DDET	SP67	MSNR	SP32	DDET	SP67
r	0.61	0.60	0.59	0.59	0.55	0.51	0.49	0.49
AC	0.10	0.32	0.53	0.53	0.29	0.44	0.57	0.57
SNR	22.96	22.28	21.17	21.43	16.63	14.27	13.06	13.37
EPS	0.96	0.96	0.95	0.95	0.94	0.93	0.93	0.93
SD	0.26	0.32	0.34	0.33	0.19	0.22	0.25	0.25
MS	0.30	0.37	0.39	0.39	0.22	0.25	0.27	0.27

Table 2. Statistic verification of the climate reconstruction: reduction of error (RE) and correlation coefficients between the actual climatic records of the indipendent period and the climate values estimated from the residual chronologies.

	Hinojos				Valverde			
	MSNR	SP32	DDET	SP67	MSNR	SP32	DDET	SP67
Correlation	0.38	0.70	0.66	0.70	0.56	0.66	0.68	0.67
RE	0.13	0.44	0.36	0.47	0.19	0.29	0.28	0.27

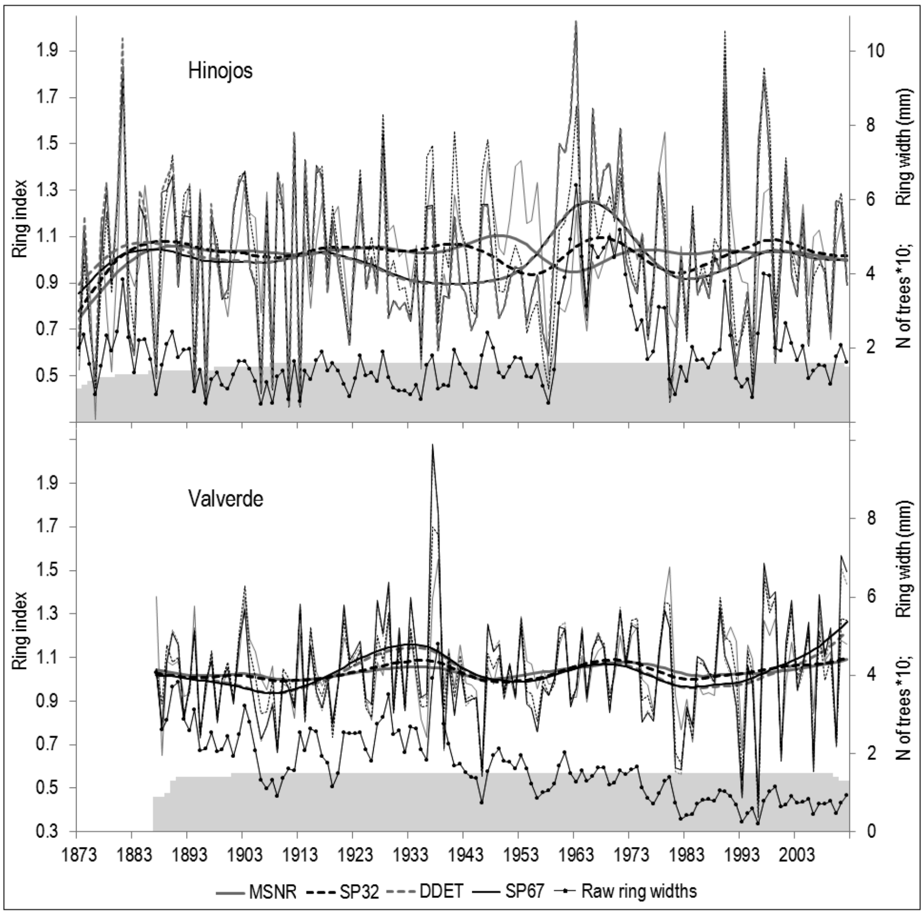


Figure 1. Residual chronologies, mean ring-width series and sample depth

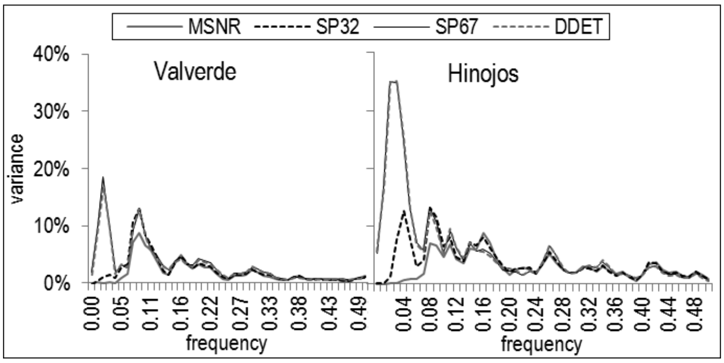


Figure 2. Power spectra of the standard chronologies

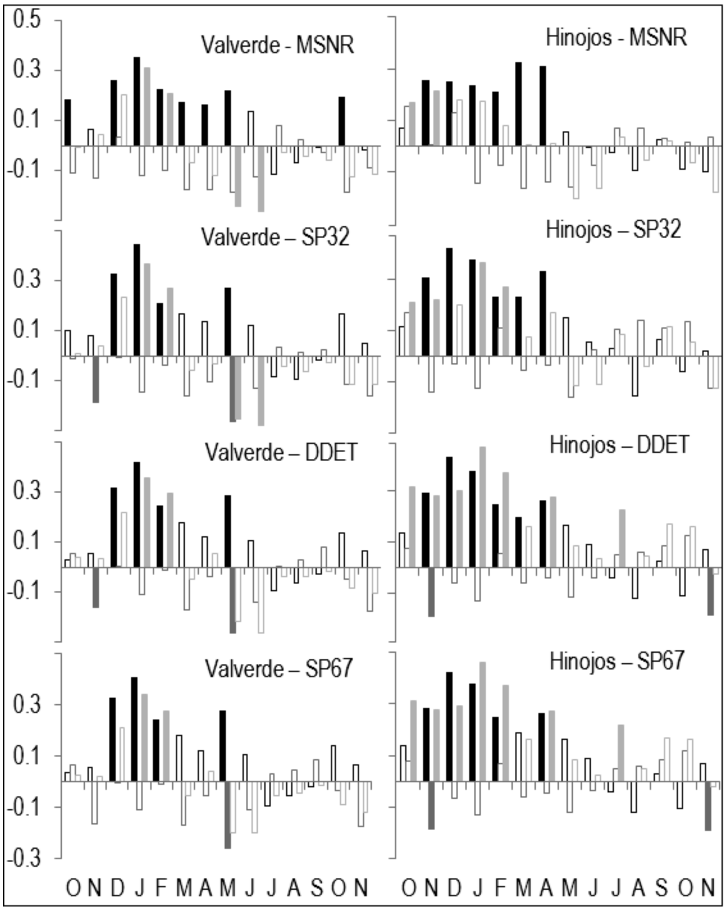


Figure 3. Bootstrapped correlations between residual chronologies and monthly values of climatic covariates from the previous October to the current November (precipitation, maximum temperature and minimum temperatures: first, second and third bar, respectively). Filled bars indicate statistically significant relationships ($p < 0.05$).

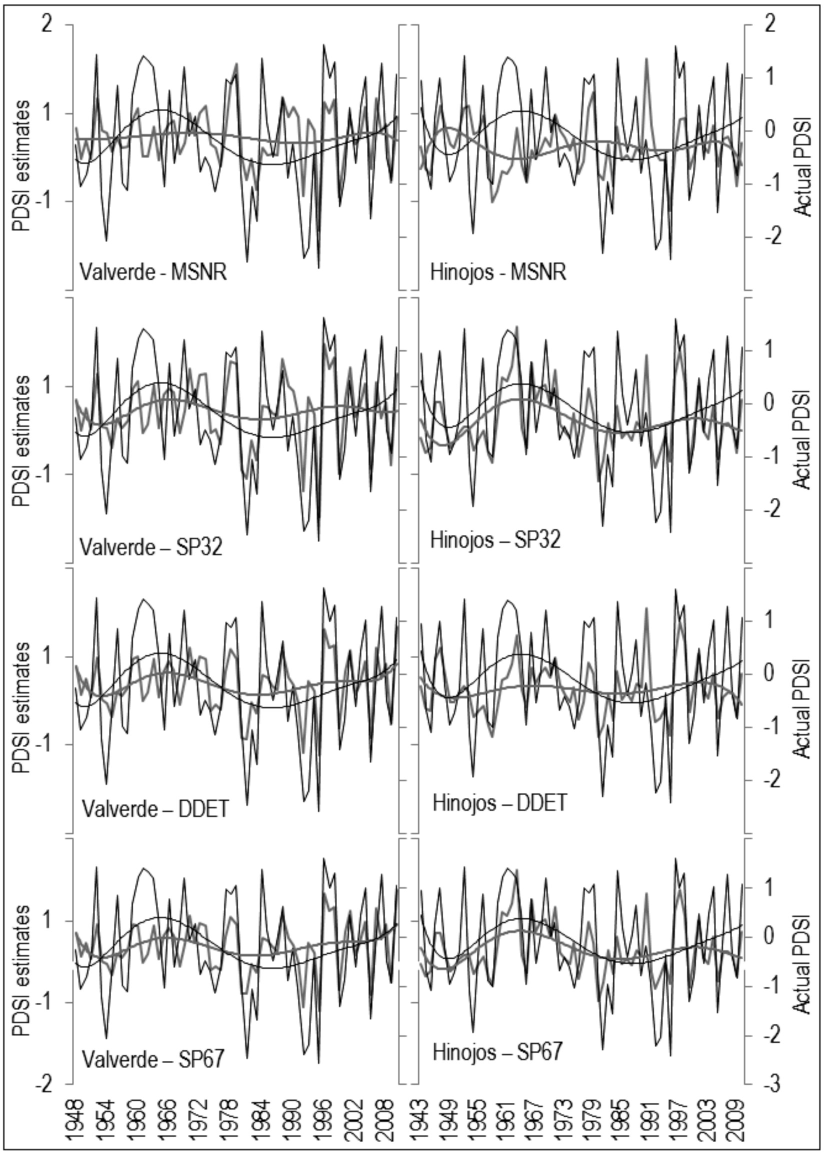


Figure 4. Climate reconstructions. Black lines are the actual PDSI values of the indipendent period; grey lines are the climate values estimated from the residual chronologies. The fitted curves are 6th-degree polynomials.

References

Baldocchi, D.D., Ma, S.Y., Rambal, S., Misson, L., Ourcival, J.M., Limousin, J.M., Pereira, J., Papale, D. (2010): On the differential advantages of evergreenness and deciduousness in mediterranean oak woodlands: a flux perspective. *Ecol Appl* 20(6):1583-1597

Blasing, T.J., Duvick, D.N., West, D.C. (1981): Dendroclimatic calibration and verification using regionally averaged and single staion precipitation data. *Tree-Ring Bull* 41:37-43

Briffa, K., Jones, P.D. (1990): Basic chronology statistics and assessment. In: Cook, E.R., Kairiukstis, L.A. (ed.) Methods of dendrochronology: applications in the environmental sciences. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp 137-152.

Briffa, K. R., Jones, P. D., Schweingruber, F. H., Karlén, W., & Shiyatov, S. G. (1996): Tree-ring variables as proxy-climate indicators: problems with low-frequency signals. In: Jones PD, Bradley, R.S., Jouzel, J. (ed.): Climatic Variations and Forcing Mechanisms of the Last 2000 Years. Springer Berlin Heidelberg, pp. 9-41

Camarero, J.J., Olano, J.M., Parras, A. (2010): Plastic bimodal xylogenesis in conifers from continental Mediterranean climates. *New Phytol* 185(2): 471-480

Campelo, F., Nabais, C., Freitas, H., Gutiérrez E. (2006): Climatic significance of tree ring width and intra-annual density fluctuations in *Pinus pinea* from a dry Mediterranean area in Portugal. *Ann For Sci* 64: 229–238

Cook, E.R., Briffa, K.R. (1990): Data Analysis. In: Cook, E.R., Kairiukstis, L.A. (ed.): Methods of dendrochronology: applications in the environmental sciences. Kluwer Academic Publishers, Dordrecht, The Netherlands, p. 97-162

Cook, E.R., Briffa, K.R., Shiyatov, S., Mazepa, V. (1990a): Tree-ring standardization and growth-trend estimation. In: Cook, E.R., Kairiukstis, L.A. (ed.). Methods of dendrochronology: applications in the environmental sciences. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp 104-123

Cook, E.R., Shiyatov, S., Mazepa, V. (1990b): Estimation of the Mean Chronology. In: Cook ER, Kairiukstis LA (ed). Methods of dendrochronology: applications in the environmental sciences. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp 123-132

Dai, A.K., Trenberth, K.E., Qian, T. (2004): A global data set of Palmer Drought Severity Index for 1870-2002: Relationship with soil moisture and effects of surface warming. *J Hydrometeorology*, 5, 1117-1130

De Luis, M., Čufar, K., Di Filippo, A., Novak, K., Papadopoulos, A., et al. (2013) Plasticity in dendroclimatic response across the distribution range of Aleppo pine (Pinus halepensis). *PLoS ONE* 8(12) e83550, doi: 10.1371/journal.pone.0083550

Di Filippo, A., Alessandrini, A., Biondi, F., Blasi, S., Portoghesi, L., Piovesan, G. (2010): Climate change and oak growth decline: Dendroecology and stand productivity of a Turkey oak (Quercuscerris L.) old stored coppice in Central Italy. *Ann For Sci*, *67*(7), 706.

Fritts, H.C. (1976): Tree Rings and Climate. Academic Press, London

Fritts, H.C., Guiot, J. (1990): Methods of calibration, verification and reconstruction. In: Cook ER, Kairiukstis LA (ed.). Methods of dendrochronology: applications in the environmental sciences. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp 163-217.

Gea-Izquierdo, G., Cherubini, P., Cañellas, I. (2011): Tree-rings reflect the impact of climate change on Quercus ilex L. along a temperature gradient in Spain over the last 100 years. *Forest Ecol Manag*, *262*(9), 1807-1816.

Gea-Izquierdo, G., Viguera, B., Cabrera, M., Cañellas, I. (2014): Drought induced decline could portend widespread pine mortality at the xeric ecotone in managed mediterranean pine-oak woodlands. *Forest Ecol Manag*, *320*, 70-82.

Grissino-Mayer, H.D. (2001): Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. *Tree-Ring Bull* 57:205–221

Holmes, R.L., Adams, R.K., Fritts, H.C. (1986): Tree-ring chronologies of western North America: California, eastern Oregon and Northern Great Basin, with procedures used in the chronology development work. University of Arizona, Tucson. Chronology Series VI

Piermattei, A., Garbarino, M., Urbinati, C. (2014): Structural attributes, tree-ring growth and climate sensitivity of PinusnigraArn. at high altitude: common patterns of a possible treeline shift in the central Apennines (Italy). *Dendrochronologia*, *32*(3), 210-219

Pilcher, J.R. (1990): Primary data. In: Cook ER, Kairiukstis LA (ed.): Methods of dendrochronology: applications in the environmental sciences. Kluwer Academic Publishers, Dordrecht, The Netherlands, p.40-50

Romero, R., Guijarro, J. A., Ramis, C., & Alonso, S. (1998): A 30-year (1964-1993) daily rainfall data base for the Spanish Mediterranean regions: First exploratory study. *Int J Climatol* 18(5), 541-560.

Vaz, M., Pereira, J.S., Gazarini, L.C., David, T.S., David, J.S., Rodrigues, A., Maroco, J., Chaves, M.M. (2010): Drought-induced photosynthetic inhibition and autumn recovery in two Mediterranean oak species (Quercus ilex and Quercus suber). *Tree Physiol* 30:946–956

15.2 **Article 2**. Natalini F., Correia A.C., Vázquez-Piqué J., Alejano R., 2015. Tree rings reflect growth adjustments and enhanced synchrony among sites in Iberian stone pine (Pinus pinea L.) under climate change. Annals of Forest Science, 72(8), pp.1023-1033, DOI: 10.1007/s13595-015-0521-6

Natalini F., Vázquez-Piqué J., Alejano R.: Departamento de Ciencias Agroforestales, Escuela Técnica Superior de Ingeniería, Universidad de Huelva, Campus de La Rábida, 21819 Palos de la Frontera, Huelva, Spain
Correia A.C.: Centro de Estudos Florestais, Instituto Superior de AgronomiaUniversidade de Lisboa

Abstract

Context. Understanding the response of Mediterranean forests to climate change is required to assess their vulnerability and to develop measures that may limit the impact of future climate change.
Aims. We analyzed the sensitivity of several populations of *Pinus pinea* (Stone pine) in Southern and Central Spain and Portugal to climate and identified some responses to climate change.
Methods. We constructed tree-ring chronologies and studied the dendroclimatic signal over the last century.
Results. There were similarities in tree ring growth and response to climate among sites. Growth was enhanced after precipitation during the previous autumn and the current spring, and was limited by water shortage. In recent decades, aridity increased in the study region and the sensitivity of tree-ring growth to water availability increased at all study sites. We also observed an enhanced growth synchrony among chronologies as well as an increase in ring-width variability during the last decades.
Conclusion. The radial growth of *Pinus pinea* indicated strong effects of climate change. The climatic signal in tree ring chronologies suggested a plastic growth response to climate of this species, although the enhanced growth synchrony and variability in recent years suggest the presence of conditions that are limiting for growth. This study provides the first assessment of the responses of Iberian populations of *Pinus pinea* to changes in climate.

Key-words: Mediterranean pines, tree-ring sensitivity, climate-growth relationships, regional growth synchrony

Executive summary. We used tree ring analysis to assess the response of Pinus pinea to climate change in South Iberia. Climate-growth relationships changed over time, with greater sensitivity in recent years due to increasing aridity. A common dendroclimatic signal among sites was found suggesting that climate change is the main responsible for the observed variation in tree growth.

Introduction

Climate change significantly affects the conservation, productivity and management of forest ecosystems worldwide (see *e.g.* Ciesla 1995). Climate models for the Mediterranean region forecast atmospheric warming, reduced rainfall, longer dry spells, and more frequent heat waves and heavy precipitation events (Kovats et al. 2014). These changes will alter plant phenology, decrease growth (especially in the southern provenances and at the edges of species ranges), reduce non-wood forest products, increase forest decline and die-back processes, change species distributions, and increase pests and fires (Lindner et al. 2010; Lindner and Calama 2013; Resco de Dios 2007). Thus, studying the driving factors and the extent of changes in Mediterranean forests will provide important information on their ecological behavior and vulnerability, and guide the implementation of management options that may improve their response to future climate change.

Dendrochronology and dendroecology provide valuable information on the response of forests to environmental factors (Fritts 1976; Schweingruber 1996; Cook and Kairiukstis 1990). Recent dendroecological studies in the Mediterranean basin demonstrated that tree-ring data can be used as climate proxies in this region (*e.g.* Bogino and Bravo 2008; Campelo et al. 2009; Gea-Izquierdo et al. 2009, 2011; Vieira et al. 2010).

Stone pine (*Pinus pinea* L.) is native to southern Europe, occurs around the northern and eastern Mediterranean (Online Resource 1), and is present in more than 500 000 ha in the Iberian Peninsula (Montero González et al. 2004). In southern and central Iberia, stone pine stands are considered multifunctional forests, because they provide wood and edible pine nuts that are highly valued in international markets (see Mutke et al. 2005). These trees also provide soil protection, sand dune stabilization, biodiversity refuge, space for public and recreational activities, and carbon sequestration (Montero González et al. 2004). Previous studies of *P. pinea* indicated a close relationship between radial growth and climatic factors, and highlighted that tree ring formation in this species is sensitive to drought (Campelo et al. 2006; De Luis et al. 2009; Mazza et al. 2011; Novak et al. 2011; Raventós et al. 2001). Thus, tree-ring analysis in this species can be potentially useful in climate change studies in the Mediterranean basin, which is considered particularly vulnerable to climate change (de Sherbinin 2014; Giorgi 2006). Nevertheless, no studies have yet thoroughly assessed climate change response in *P. pinea* populations, particularly those in Southern Iberia.

In this paper we investigated the growth response of *P. pinea* populations to climate change in South and Central Spain and Portugal by examining the climatic signal in tree ring chronologies. Our working hypothesis were the following: (1) variations in climate entail a response in wood growth that will be reflected in temporal changes of the high-frequency response to climate; (2) if climate in a given region becomes more limiting for growth, different population from the same region will intensify their response to climate and will increase the shared variance in growth trends. To test the first hypothesis, we related the annual tree-ring growth to the climate of the study areas and checked if climate-growth relationships varied over recent decades. To test the second hypothesis, we compared the high-frequency growth variability of the studied stands to detect similarities in the growth patterns and check whether these similarities were stable over time.

Materials and methods

Study sites, samples and tree-ring analysis

Samples were collected from six sites in the province of Huelva, in southwestern Spain (Campo común, El Portil, Moguer, Hinojos, Punta Umbría, and Valverde del Camino) and one site in Pegões, in central Portugal (Table 1, Online Resource 1). These woodlands are managed for production of pine nuts and timber, and for the protection of coastal ecosystems. We also used three chronologies from the International Tree Ring Data Base (ITRDB, www.ncdc.noaa.gov/data-access/paleoclimatology-data/datasets/tree-ring) in the area of La Mancha (central-eastern Spain; Table 1, Online Resource 1): Dehesa del Peral, Pinar viejo and La Pasadilla (ITRDB codes: spai057, spai056 and spai059, respectively; contributors: Briongos and Del Cerro-Barja). The woodlands in this area are mainly managed for forest ecosystem conservation and timber production.

The climate in all areas is Mediterranean (Online Resource 2), but presents gradients in drought and precipitation regimes. Based on data from the meteorological stations of Huelva, Lisbon, Albacete, and Molina de Aragón (Online Resource 1), total annual precipitation and mean temperature are 520 mm and 18.2°C in Huelva, 730 mm and 16.9°C in Pegões, 362 mm and 13.8°C in Pinar Viejo and La Pasadilla, and 496 mm and 10.2°C in Dehesa del Peral. The annual distribution of rainfalls reaches a peak between November and February in Huelva and Pegões, while in the areas of La Mancha rainfall maximums normally occur in April-May and October. The dry period is larger in Huelva and Pegões (three months, from June to August), normally lasts for two months in Pinar Viejo and La Pasadilla (July-August) and one month in Dehesa del Peral (August) (Online Resource 2).

For the construction of the chronologies (Table 2) we used stem cross sections at breast height from previous harvests in Pegões (Correia et al. 2010). For Huelva, samples were extracted with an increment borer at breast height (two cores per tree), glued onto wooden mounts, and sanded along the transverse sections to make the rings visible. Tree ring widths were measured with a stereomicroscope and a LINTAB^{TM} table (Rinntech®) connected to a TSAP-Win^{TM} tree-ring analysis system (Rinntech®). Ring width curves were plotted for visual inspection and cross-dated with determination of the coefficient of parallel variation (*Gleichlaeufigkeit*, *Glk*), *t*-value and cross-date index (CDI). The *Glk* tests if two chronologies are simultaneously increasing or decreasing in each year-to-year interval and is calculated as the percentage of intervals showing matching growth variations (see Speer 2010, p. 108). The CDI was calculated in the TSAP-Win^{TM} software as a combination of the *t*-value and the *Glk* (Rinn 2011). The cross-dating was verified using COFECHA (Grissino-Mayer 2001). For the stands from La Mancha the ITRDB provided individual cross-dated ring-width series.

Each cross-dated ring-width series was standardized by applying a smoothing spline with a 50% frequency cutoff at 32 years, the autocorrelation was removed, and growth indexes (Gi) were computed as the ratios between the observed ring widths and the values from the fitted spline (Cook et al. 1990). The 32-year period produces a rather flexible spline which is a good filter to smooth the medium-frequency variability in the growth trends due to management and enhance the high-frequency climatic signal (see *e.g.* Gea-Izquierdo et al. 2009, 2011; Helama et al. 2004). By averaging the Gi-series with a biweight robust mean, a residual chronology was obtained for each stand (Cook et al. 1990). The standardization and computation of residual series were performed using the R software package (Venables and Smith 2015) with the dplR library (Bunn 2008). The residual chronologies eventually used in the subsequent dendroecological analyses only included years with at least five cross-dated series (Gea-Izquierdo et al. 2011) and we checked that the included years had an Expressed Population Signal higher than 0.85, which is a measure of the confidence of the chronology in expressing the signal attributable to climate (Briffa and Jones 1990).

To identify the common dendroclimatic signal in the areas of Huelva and La Mancha, we performed principal component analyses (PCA). The use of PCA in dendroclimatic studies enables finding the common signal from a set of chronologies (*e.g.* Fritts 1990; D'Arrigo et al. 1999). For La Mancha, we computed the PCA of the correlation matrix of the residual series of Dehesa del Peral, Pinar Viejo and La Pasadilla. The first principal component (PC) was used in subsequent analyses. The PCA was also performed for successive windows of 30 years to determine the stability of the common dendroclimatic signal.

The selected stands in Huelva are included in even-aged plots originated from plantations, with similar tree ages within each plot, but different ages between plots. Since tree response to climate can be age-dependent (*e.g.* Carrer and Urbinati 2004), we grouped the stands in Huelva into age clusters to increase the resolution of dendroclimatic signals (see Vieira et al. 2008). The age of the trees was firstly estimated by counting rings on each individual cross-dated chronology, from the ring closest to the pith up to the ring beneath the bark. Subsequently, the oldest and youngest trees were determined for each stand. On the basis of the observed tree age structure, the stands were eventually grouped into two age clusters: young (≤70 years old) and old (≥100 years old). The tree ages in the "young" cluster are equal or lower than the shortest rotation age for timber production in *Pinus pinea* in Spain, which is between 60 and 80 years, while tree ages in the "old" cluster are equal or higher than the optimal rotation age for timber and nut production, which ranges from 80 to 120 years (Montero González et al. 2004). The PCA of the correlation matrix of the series of each age cluster was then performed. The PC that contained the common dendroclimatic signal of each age cluster was used in subsequent analyses. As above, the PCA was performed for successive windows of 30 years.

Climate and dendroecological analyses

For climate change analysis over time, we used the series of self-calibrating Palmer Drought Severity Index (PDSI), which is based on the high-resolution surface climate data set CRU TS 2.1 of the Climate Research Unit of University of East Anglia, UK, and available in the KMNI Climate Explorer (http://climexp.knmi.nl; van der Schrier et al. 2006). Drought is the main growth-limiting factor in Mediterranean forests (see *e.g.*

Cherubini et al. 2003), so we considered this index to be a good descriptor of the impact of climate in our study areas.

For the analysis of the high-frequency response of radial growth to climate, we computed bootstrapped correlations and response functions, using climatic covariates as independent variables and tree-ring data as dependent variables. The climatic covariates were the monthly cumulative precipitation and the monthly averages of minimum and maximum temperatures computed from daily observations at the closest meteorological stations of the national weather services (see Online Resource 1), which were available in the KMNI Climate Explorer (Klein Tank et al. 2002). For the area of Huelva, the dependent variables used in correlation and response function analysis were the PCs of each tree age class and the climatic covariates were from the meteorological station of Huelva (37.26ºN, 6.9ºW; 19 m a.s.l.; time-span of precipitation and temperature records: 1920-2011). For Portugal, the analysis included the residual chronology of Pegões and the climatic data from the station of Lisbon (38.72ºN, 9.15ºW; 77 m a.s.l.; time-span of precipitation and temperature data: 1901-2012). For the area of La Mancha, in which the sites were farther apart and had larger climatic gradients, no single meteorological station was suitable; thus correlation and response function analysis was performed separately for the residual chronologies of Dehesa del Peral, Pinar Viejo and La Pasadilla, using the closest available meteorological station for each site (see Online Resource 1). In particular, the station of Albacete (38.95ºN, 1.86ºW; 704 m a.s.l.; time-span of precipitation data: 1940-2010; time-span of temperature data 1919-2010) was used for Pinar Viejo and La Pasadilla, and the station of Molina de Aragón (40.84ºN, 1.89ºW; 1056 m a.s.l.; time-span of precipitation data: 1950-2010; time-span of temperature data: 1960-2010) was used for Dehesa del Peral. The bootstrapped correlations and response functions were computed with the bootRes library (Zang and Biondi 2012) in the R software package. Bootstrapped correlations were also performed for successive windows of 30 years to verify whether climate-growth relationships were stable over time.

We used mean sensitivity (Ms, average of the relative differences in width from one ring to the next [Fritts, 1976]) to determine the intensity of tree response to climate. Ms was calculated as:

$$Ms = \left(\frac{1}{n-1}\right) \cdot \sum_{t=1}^{t=n-1} \left| \frac{2 \cdot (x_{t+1} - x_t)}{x_{t+1} + x_t} \right|$$

where x is the growth index and n is the number of annual rings in the tree-ring sequence. Thus, sensitivity ranges annually from 0 (in which adjacent rings have the same value) to 2 (in which a zero [“missing ring”] occurs next to a non-zero value) (Fritts 1976). As above, the Ms was computed for successive windows of 30 years to check if the intensity of response to climate varied over time.

For examination of the common dendroclimatic signal at a large scale, we compared the growth patterns by checking the cross-dating through the Glk coefficient and computing Pearson correlations between the study sites, using the residual chronology from Pegões and the PCs from Huelva and La Mancha. Again, the correlations were computed for successive 30-year windows to test the stability of the common signal.

Results

Chronologies

In the area of Huelva, the youngest and oldest trees were 47 and 68 years old in El Portil, 53 and 70 in Campo Común, 52 and 69 in Moguer, 127 and 150 years old in Hinojos, 100 and 110 in Punta Umbría, and 120 and 139 in Valverde del Camino. Therefore, the chronologies from El Portil, Campo Común and Moguer were included in the "young" cluster, while the chronologies from Hinojos, Punta Umbría and Valverde del Camino were included in the "old" cluster. One PC, with eigenvalue > 1, explained 70% of the variance of the chronologies included of the "young" cluster, and one PC, with eigenvalue > 1, explained 72% of the variance of the chronologies in the "old" cluster. The variance accounted for by the first PC increased over recent decades for both old and young trees (Online Resource 3). The tree ages in Pegões ranged from 50 to 60 years. In the area of La Mancha, the youngest and oldest trees were 82 and 119 years old in Pinar Viejo, 65 and 113 in Dehesa del Peral, and 50 and 89 in La Pasadilla. One PC, with eigenvalue > 1, explained 67% of the variance of the chronologies from La Mancha and the amount of variance explained by this PC tended to increase over time (Online Resource 3).

Dendroecological analyses

Analysis of the PDSI series indicated increasing aridity during recent decades in Central Portugal, SW Spain, and CE Spain (Fig. 1). In particular, these regions had prolonged droughts, mainly in the 1970s, early 1980s, and mid-1990s. Furthermore, 30-year running inter-correlations between the PDSI series of the three areas showed an increase over time, with a mean value equal to 0.5 up to 1965 and a mean value of 0.75 in the subsequent decades, which suggests that the increase of aridity, with more frequent and severe droughts, is common at the large scale in our study region.

Radial growth of *P. pinea* trees in Huelva had a significant positive correlation with precipitation from the previous November to the current spring (up to May in old trees, March in young trees) (Fig. 2). Except for the young trees in Huelva (in which growth correlated with maximum temperature in the previous October), the relationship of growth and maximum temperature was not significant. However, there was a positive correlation of growth with minimum temperatures from December to February in old trees and from the previous October to the current January in young trees. In Pegões, radial growth correlated with precipitation from the previous October to February of the current year, had no significant relationship with maximum temperature, and had a positive correlation with minimum temperatures of December and January.

The chronologies in La Mancha indicated correlations of radial growth with precipitation in the previous November, winter, and the current May (Fig. 3). There was a negative correlation between maximum temperature and radial growth in La Pasadilla and Pinar Viejo in the previous October-November and the current May; in Dehesa del Peral the correlation was negative in May and in summer. The relationship between minimum temperature and growth in La Pasadilla and Pinar Viejo was positive in winter and negative in May and July; in Dehesa del Peral, the correlation was positive in the previous November, winter, and current April.

The relationship of climate and radial growth changed over time in all study areas (Figs. 4 and 5). In particular, growth of old trees in Huelva had an increasing correlation with precipitation and minimum temperature of the previous December, and a declining correlation with spring rainfall. Growth of young trees in Huelva had negative correlations with May maximum temperature in the most recent decades, did not have significant correlations with March rainfalls between the 1960s and the 2000s, and became insensitive to rainfall in June since the 1960s, but was more correlated with temperature in February and precipitation of the previous October and the current September. The trees in Pegões had increasing dependence on rainfall of the previous November (there was also decreasing correlation with rainfalls in April, although not statistically significant). In Huelva, Pegões and La Pasadilla we found significantly negative correlations with temperature in June from the 1970s to the mid-1990s (Fig. 4, 5), suggesting that radial growth was sensitive to high temperature during these years, characterized by extreme and prolonged droughts (Fig. 1). In La Mancha, analysis of all chronologies indicated increasing correlation with winter and current November precipitation, but decreasing correlation with rainfalls in March (and in June for Pinar Viejo), whereas the correlation with temperatures (Fig. 5) increased during winter and became negative in the current November.

The mean sensitivity of all tree-ring series increased over the last decades (Online Resource 4), indicating an increasing intensity of the response to climate. Up to the 1960s, Ms in Huelva ranged from 0.1 to 0.3, but increased in the subsequent decades and reached values between 0.3 and 0.5. In Pegões, Ms increased up to 0.3 from the 1970s and in La Mancha increased from 0.2-0.3 before the 1960s to 0.3-0.4 in subsequent decades.

The residual chronologies from Pegões and the PCs extracted from the chronologies in Huelva and La Mancha had good cross-dating and were significantly correlated (Table 3). Moreover, the correlations among these series increased over time, with a notable increase from the mid-1960s (Fig. 6). The mean correlations of the old trees in Huelva with Pegões, La Mancha and the young trees in Huelva were 0.60, 0.34 and 0.68, respectively, before the 1965; whereas after this year were 0.63, 0.58 and 0.81. The mean correlation of the young trees in Huelva with Pegões and La Mancha increased from 0.30 and 0.26 to 0.38 and 0.51 (the running correlation analysis between Pegões and La Mancha was not meaningful due to the short overlap).

Discussion

The *P. pinea* trees from the three study areas showed similarities in the high-frequency growth patterns and response to climate during the study period. These similarities indicate the presence of a common signal in the tree-ring chronologies, suggesting that climatic factors control tree growth variability at a large scale irrespective of population distribution and local environmental conditions (Andreu et al. 2007; Čufar et al. 2014).

The correlations of radial growth with previous autumn and winter rainfall reflect the importance of soil recharge for improving water availability and subsequent growth in the spring. These results agree with previous studies of *P. pinea* in Portugal (Campelo et al. 2006) and Spain (Raventós et al. 2001) and with studies of other Mediterranean species (*e.g.* Campelo et al. 2009; Corcuera et al. 2004; David et al. 2007). Moreover, for evergreen trees, the positive response to rainfall and mild temperature in winter suggests the dependency of ring formation on the photosynthesis and carbohydrates produced during this period (Baldocchi et al. 2010). Mild temperatures during the winter can also alter phenological patterns, inducing an early dormancy interruption and consequently the formation of wider rings (Begum et al. 2010; Oribe and Kubo 1997).

The dendroclimatic signal that we recorded also reflected the influence of local climatic factors. The stands in La Mancha had higher responses to precipitation in May; this can be partly explained by the rainfall maximum occurring in May in this area (Online Resource 2), which provides an important water supply for ring formation. We found no relationship between summer climate and radial growth in the drier sites, Huelva and Pegões (Fig. 2). This can be expected for trees growing under these conditions (Campelo et al. 2009; Gea-Izquierdo et al. 2011), in which scarce and irregular summer rainfall is insufficient to alleviate water stress due to the high temperature, and there may even be a contraction of the radial growth. In contrast, trees in La Mancha were sensitive to summer temperatures although did not correlate to precipitation in this season. This suggests that in La Mancha, even though summer rainfall is scarce, the growing season is extended throughout summer, so that the radial growth can be affected by high temperatures during this season (Gea-Izquierdo et al. 2009).

Age-mediated response to climate has been observed in different species and climates and the interpretation of forest dynamics can be improved if the age effect is accounted for (Carrer and Urbinati 2004). In Huelva, the growth of young trees correlated with temperature and was more sensitive to rainfall in the previous autumn than old trees (Fig. 2). This may indicate that, under the same climatic conditions, young trees respond more rapidly to climate than older trees, and xylogenesis in young trees is higher in the earlier phases of the growing season (Rossi et al. 2008). Vieira et al. (2008) reported similar observations for *P. pinaster* in the Mediterranean climate of central Portugal.

Previous studies reported that spring precipitation increased radial growth in Mediterranean pines (*e.g.* Vieira et al. 2010; Campelo et al. 2006; De Luis et al. 2009, 2013; Piraino et al. 2013; Novak et al. 2013) and other Mediterranean trees (*e.g.* Campelo et al. 2009; Gea-Izquierdo et al. 2011). Although we found similar results for the old trees in Huelva, showing a positive correlation with rainfall up to May (Fig 2), the young trees in Huelva and in Pegões (see Fig. 2 and 4) were less sensitive to spring precipitation. The time span covered by the tree-ring sequences of the young trees (El Portil, Campo Común and Moguer in Huelva and Pegões, see Table 2) largely overlapped with the downward slope of the PDSI curves (Fig. 1). This means that the young trees grew under more xeric conditions, which possibly limited the cambial activity in the warmer months and consequently led to a weak chronology signal related to spring rainfall. This also suggests that the different dendroclimatic signals observed in trees of different ages depends not only on endogenous growth factors (*i.e.* physiological changes related to aging, see *e.g.* Rossi et al. 2008, Szeicz and Macdonald 1994) but also on the climatic conditions in which the trees were established and developed.

The observed changes in the relationships between climate and growth reflect the non-stationary nature of the growth responses of trees to climate (Carrer and Urbinati 2006). Other Iberian Mediterranean tree stands exhibited changes in high-frequency responses to climate suggesting a reaction to warming and increased water stress (Gea-Izquierdo et al. 2009; Martín-Benito et al. 2010). Wood anatomy and physiological studies indicate that tree species present some degree of plasticity to changing environmental conditions, *i.e.* the ability of a genotype to adjust the phenotype as a result of the physiological responses to environmental variability (see Fonti et al. 2010). For example, alterations in plant phenology, including seasonal xylem growth patterns, have been observed with atmospheric warming (Peñuelas et al. 2002; Rossi et al. 2011; Deslauriers et al. 2008). We may speculate that the plastic variations in climate-growth relationships observed in our study can be the result of a phenological adjustment of the cambial activity in relation to the distribution of water availability over the year (de Luis et al. 2011; Camarero et al. 2010). This could explain that, under more xeric conditions observed in recent decades, *P. pinea* ring growth became less sensitive to climatic conditions in the spring, when higher temperatures increased the water stress, and enhanced its dependence on water availability in the previous autumn-winter and current autumn, when climate is milder. We made similar observations in our dendroecological studies for *Quercus ilex* in Huelva (data not published). Although in the young trees we observed that the chronology signal related to spring climate was weak (in Huelva) or absent (in Pegões), improved relationships with autumn/winter climate were found. Therefore, an alteration of climate-growth relationships was observed in all sites with a reduction of the growth sensitivity to climate in the warmer months and an enhanced dependence of growth on the milder months (also see Fig. 7 in Gea-Izquierdo et al. 2009; and Fig. 7 in Martín-Benito et al. 2010). This suggests that climate variability in the region induce similar responses in the cambial activity of trees from different populations.

The similarity in the high-frequency growth variability among sites can be interpreted as a common response to the regional climate (Andreu et al. 2007; Macias et al. 2006; Tardif et al. 2003). Trees with Ms values greater than 0.4 are considered extremely sensitive to climate, while trees with Ms values lower than 0.2 are less climate-sensitive (Speer 2010, p. 107). In our sites, the Ms values increased in recent years (Online Resource 4), indicating that trees were exposed to harsh environmental conditions that controlled growth to a wider extent. In agreement with our findings, previous research in Iberian forests also reported high year-to-year variability of growth at dry sites (Campelo et al. 2006; Nabais et al. 2014) and increases in Ms over time (Andreu et al. 2007; Martín-Benito et al. 2010; Tardif et al. 2003; Gea-Izquierdo et al. 2009). Furthermore, the good cross-dating and correlation among sites in our study region support the presence of a significant dendroclimatic signal at the large scale. In particular, the increased similarity in growth patterns (Online Resource 3 and Fig. 6) indicates increasing growth synchrony. This suggests that, despite the differences in the dendroclimatic signal related to local environmental conditions and tree age structure, the climate of the region becomes increasingly important as a factor driving the variability of ecosystem growth. The increase of aridity over the second half of the 20th century matching the increase of Ms and growth synchrony (Fig. 1, Online Resource 4 and Fig. 6), together with the clear dependence of growth on water availability (Figs. 2-5), suggests that the observed changes in the growth patterns were linked to the higher frequency, severity and duration of droughts (Andreu et al. 2007).

Conclusions

In this study we have found a robust dendroclimatic signal in newly established *P. pinea* tree-ring chronologies in Southwestern Spain and Central Portugal and archived chronologies from Central-Eastern Spain. We provide a valuable assessment of the sensitivity of Iberian sites of *P. pinea* to changing growing conditions. The growth of studied trees was sensitive to high temperatures and water shortage, as the most limiting factors in Mediterranean forests. Our findings suggest that cambial activity adjusted to the increased water stress. In recent decades, the inter-annual variability of growth increased, indicating an intensified response to climate, and there was enhancement of growth synchrony among forests, reflecting that climatic conditions became more limiting for growth. We also observed that climate change induced similar responses in the cambial activity over wide areas, including forests with different site characteristics and ages. Further research is needed to assess the degree to which climate change impacts can be mediated by the stand age structure and local site conditions. These issues can improve the knowledge regarding species vulnerability to climate change and should be taken into account for forest growth modeling and adaptive management.

References

Andreu L, Gutiérrez E, Macías M, Ribas M, Bosch O, Camarero JJ (2007) Climate increases regional tree-growth variability in Iberian pine forests. Global Change Biol 13:804–815

Baldocchi DD, Ma SY, Rambal S, Misson L, Ourcival JM, Limousin JM, Pereira J, Papale D (2010) On the differential advantages of evergreenness and deciduousness in Mediterranean oak woodlands: a flux perspective. Ecol Appl 20(6):1583–1597

Begum S, Nakaba S, Oribe Y, Kubo T, Funada R (2010) Cambial sensitivity to rising temperatures by natural condition and artificial heating from late winter to early spring in the evergreen conifer Cryptomeria japonica. Trees-Struct Funct 24(1):43-52

Bogino SM, Bravo F (2008) Growth response of Pinus pinaster Ait. to climatic variables in central Spanish forests. Ann For Sci 65(5):506-506

Briffa K, Jones PD (1990) Basic chronology statistics and assessment. In: Cook ER, Kairiukstis LA (Eds.) Methods of dendrochronology: applications in the environmental sciences. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp 137-152

Bunn AG (2008) A dendrochronology program library in R (dplR). Dendrochronologia 26(2):115-124

Camarero JJ, Olano JM, Parras A (2010). Plastic bimodal xylogenesis in conifers from continental Mediterranean climates. New Phytol 185(2): 471-480

Campelo F, Nabais C, Freitas H, Gutiérrez E (2006) Climatic significance of tree ring width and intra-annual density fluctuations in *Pinus pinea* from a dry Mediterranean area in Portugal. Ann For Sci 64: 229–238

Campelo F, Nabais C, García-González I, Cherubini P, Gutiérrez E, Freitas H (2009) Dendrochronology of Quercus ilex L. and its potential use for climate reconstruction in the Mediterranean region. Can J For Res 39(12):2486-2493

Carrer M, Urbinati C (2004). Age-dependent tree-ring growth responses to climate in Larix decidua and Pinus cembra. Ecology 85(3):730-740.

Carrer M, Urbinati C (2006) Long-term change in the sensitivity of tree-ring growth to climate forcing in *Larix decidua.* New Phytol 170:861–872

Cherubini P, Gartner BL, Tognetti R, Braker OU, Schoch W, Innes JL (2003) Identification, measurement and interpretation of tree rings in woody species from Mediterranean climates. Biol Rev Camb Philos Soc 78(1):119–148

Ciesla WM (1995) Climate change, forests and forest management: an overview. FAO, Rome

Cook ER, Briffa KR, Shiyatov S, Mazepa V (1990) Tree-ring standardization and growth-trend estimation. In: Cook ER, Kairiukstis LA (ed). Methods of dendrochronology: applications in the environmental sciences. Kluwer Academic Publishers, Boston, pp 104-123

Cook ER, Kairiukstis LA (1990). Methods of dendrochronology: applications in the environmental sciences. Kluwer Academic Publishers, Boston

Corcuera L, Camarero JJ, Gil-Pelegrin E (2004*)* Effects of a severe drought on growth and wood anatomical properties of *Quercus faginea.* IAWA J 25(2):185–204.

Correia AC, Tomé M, Pacheco CA, Faias S, Dias AC, Freire J, Carvalho PO, Pereira JS (2010) Biomass allometry and carbon factors for a Mediterranean pine (*Pinuspinea* L.) in Portugal. Forest Systems 19(3):418-433

Čufar K, Grabner M, Morgós A, Martínez del Castillo E, Merela M, de Luis M (2014) Common climatic signals affecting oak tree-ring growth in SE Central Europe. Trees-Struct Funct 28(5): 1267-1277

D'Arrigo R, Wiles G, Jacoby G, Villalba R (1999). North Pacific sea surface temperatures: past variations inferred from tree rings. Geophys Res Lett 26(17):2757-2760.

David TS, Henriques MO, Kurz-Besson C, Nunes J, Valente F, Vaz M, Pereira JS, Siegwolf R, Chaves MM, Gazarini LC, David JS (2007) Water-use strategies in two co-occurring Mediterranean evergreen oaks: surviving the summer drought. Tree Physiol 27(6):793-803

De Luis M, Čufar K, Di Filippo A, Novak K, Papadopoulos A, et al. (2013) Plasticity in Dendroclimatic Response across the Distribution Range of Aleppo Pine (Pinus halepensis). PLoS ONE 8(12): e83550. doi:10.1371/journal.pone.0083550

De Luis M, Novak K, Raventós J, Gričar J, Prislan P, Čufar K (2011). Cambial activity, wood formation and sapling survival of Pinus halepensis exposed to different irrigation regimes. Forest Ecol Manag 262(8):1630-1638

De Luis M, Novak K, Čufar K, Raventós J (2009) Size mediated climate–growth relationships in Pinus halepensis and Pinus pinea. Trees-Struct Funct (2009) 23:1065–1073

De Sherbinin A (2014) Climate change hotspots mapping: what have we learned? Climatic Change 123(1):23-37

Deslauriers A, Rossi S, Anfodillo T, Saracino A (2008). Cambial phenology, wood formation and temperature thresholds in two contrasting years at high altitude in southern Italy. Tree Physiol 28(6):863-871

Fonti P, von Arx G, García-González I, Eilmann B, Sass-Klaassen U, Gärtner H, Eckstein D (2010) Studying global change through investigation of the plastic responses of xylem anatomy in tree rings. New Phytol 185(1):42-53

Fritts H C (1976) Tree rings and climate. Academic Press, London

Fritts HC (1990) Statistical reconstruction of spatial variations in climate using 65 chronologies from semiarid sites. In: Cook ER, Kairiukstis LA (Eds.) Methods of dendrochronology: applications in the environmental sciences. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp 193-211

Gea-Izquierdo G, Martín-Benito D, Cherubini P, Cañellas I (2009) Climate growth variability in *Quercus ilex* L West Iberian open woodlands of different stand density. Ann Forest Sci 66:802

Gea-Izquierdo G, Cherubini P, Cañellas I (2011) Tree-rings reflect the impact of climate change along a temperature gradient in Spain over the last 100 years. Forest Ecol Manag 262:1807-1816

Giorgi F (2006) Climate change hot-spots. Geophys Res Lett 33(8)

Grissino-Mayer HD (2001) Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. Tree-Ring Bull 57:205–221

Helama S, Lindholm M, Timonen M, Eronen M (2004) Detection of climate signal in dendrochronological data analysis: a comparison of tree-ring standardization methods. Theor Appl Climatol 79:239–254

Klein Tank AMG and coauthors (2002) Daily dataset of 20th century surface air temperature and precipitation series for the European Climate Assessment. Int J Climatol 22:1441–1453

Kovats RS, Valentini R, Bouwer LM, Georgopoulou E, Jacob D, Martin E, Rounsevell M, Soussana JF (2014) Europe. In: Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Barros VR, Field CB, Dokken DJ, Mastrandrea MD, Mach KJ, Bilir TE, Chatterjee ME, Ebi KL, Estrada YO, Genova RC, Girma G, Kissel ES, Levy AN, MacCracken S, Mastrandrea PR, White LL (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, pp. 1267-1326

Lindner M, Maroschek M. Netherer S, Kremer A, Barbati A, Garcia-Gonzalo J, Seidl R, Delzon S, Corona P, Kolstro M, Lexer MJ, Marchetti M (2010) Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. Forest Ecol Manag 259:698–709

Lindner M, Calama R (2013) Climate Change and the Need for Adaptation in Mediterranean Forests. In: Lucas-Borja ME (ed.) Forest Management of Mediterranean Forests under the New Context of Climate Change: Building Alternatives for the Coming Future. New York, Nova Science Publishers, pp. 13-30

Macias M, Andreu L, Bosch O, Camarero JJ, Gutiérrez E (2006) Increasing Aridity is Enhancing Silver Fir Abies Alba Mill.) Water Stress in its South-Western Distribution Limit. Climatic Change 79(3-4):289-313

Martín-Benito D, Del Río M, Cañellas I (2010). Black pine (*Pinus nigra* Arn.) growth divergence along a latitudinal gradient in Western Mediterranean mountains. Ann For Sci 67(4):401

Mazza G, Cutini A, Manetti MC (2014) Site-specific growth responses to climate drivers of *Pinus pinea* L. tree rings in Italian coastal stands. Ann For Sci 71(8): 927-936

Montero González G, Candela Plaza JA, Rodríguez Navarro A (ed.) (2004) El pino piñonero en Andalucía: ecología distribución y selvicultura. Dirección General de Gestión del Medio Natural, *Consejería* de *Medio Ambiente*, Junta de *Andalucía, Sevilla*

Mutke S, Gordo J, Gil L (2005) Variability of Mediterranean Stone pine cone production: yield loss as response to climate change. Agr Forest Meteorol 132:263–272

Nabais C, Campelo F, Vieira J, Cherubini P (2014) Climatic signals of tree-ring width and intra-annual density fluctuations in *Pinus pinaster* and *Pinus pinea* along a latitudinal gradient in Portugal. Forestry DOI 10.1093/forestry/cpu021

Novak K, De Luis M, Čufar K, Raventós J (2011). Frequency and variability of missing tree rings along the stems of *Pinus halepensis* and *Pinus pinea* from a semiarid site in SE Spain. J Arid Environ 75:494-498

Novak K, de Luís M, Raventós J, Čufar K (2013). Climatic signals in tree-ring widths and wood structure of Pinus halepensis in contrasted environmental conditions. Trees-Struct Funct 27(4), 927-936.

Oribe Y, Kubo T (1997) Effect of heat on cambial reactivation during winter dormancy in evergreen and deciduous conifers. Tree Physiol 17(2):81-87

Peñuelas, J., Filella, I., & Comas, P. (2002). Changed plant and animal life cycles from 1952 to 2000 in the Mediterranean region. Glob Change Biol 8(6):531-544

Piraino S, Camiz S, Di Filippo A, Piovesan G, Spada F (2013) A dendrochronological analysis of *Pinus pinea* L. on the Italian mid-Tyrrhenian coast. Geochronometria 40(1):77-89

Raventós J, De Luís M, Gras MJ, Čufar K, González-Hidalgo JC, Bonet A, Sánchez JR (2001) Growth of *Pinus pinea* and *Pinus halepensis* as affected by dryness, marine spray and land use changes in a Mediterranean semiarid ecosystem. Dendrochronologia 19 (2): 211-220

Resco de Dios V, Fischer C, Colinas C (2007) Climate change effects on Mediterranean forests and preventive measures. New Forest 33:29-40

Rinn F (2011) TSAP-Win^{TM}: time series analysis and presentation for dendrochronology and related applications. Rinntech®, Heidelberg, Germany

Rossi S, Deslauriers A, Anfodillo T, Carrer M (2008) Age-dependent xylogenesis in timberline conifers. New Phytol 177:199–208

Rossi, S., Morin, H., Deslauriers, A., & PLOURDE, P. Y. (2011). Predicting xylem phenology in black spruce under climate warming. Glob Change Biol 17(1):614-625

Schweingruber F H (1996), Tree rings and Environment. Dendroecology. Paul Haupt Publishers, Vienna

Speer J (2010) Fundamentals of Tree-Ring Research. The University of Arizona Press, Tucson

Szeicz JM, Macdonald GM (1994) Age-dependent tree-ring growth responses of subarctic white spruce to climate. Can J For Res 24:120–132

Tardif J, Camarero JJ, Ribas M, Gutiérrez E (2003) Spatiotemporal variability in tree growth in the Central Pyrenees: climatic and site influences. Ecol Monogr 73(2):241–257

Van der Schrier G, Briffa KR, Jones PD, Osborn TJ (2006) Summer moisture variability across Europe. J Climate 19:2818-2834

Venables WN, Smith DM (ed.) (2015) An introduction to R. R Core Team, http://cran.r-project.org/doc/manuals/r-release/R-intro.pdf Accessed 7 July 2015

Vieira J, Campelo F, Nabais C (2008) Age-dependent responses of tree-ring growth and intra-annual density fluctuations of Pinus pinaster to Mediterranean climate. Trees-Struct Funct 23(2):257-265

Vieira J, Campelo F, Nabais C (2010) Intra-annual density fluctuations of *Pinus pinaster* are a record of climatic changes in the western Mediterranean region. Can J For Res 40:1567–1575

Zang C, Biondi F (2012) Dendroclimatic calibration in R: The bootRes package for response and correlation function analysis. Dendrochronologia. Dendrochronologia 31(1):68-74

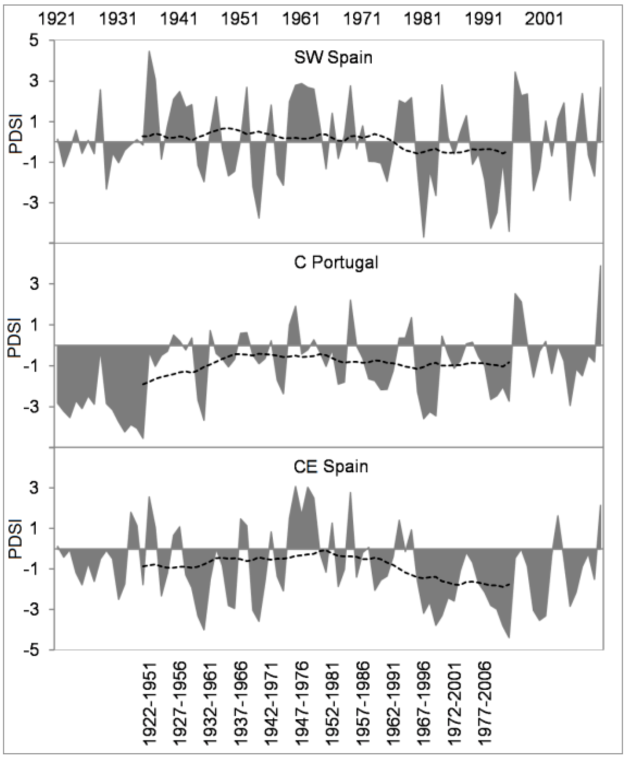


Figure 1. Annual mean Palmer Drought Severity Index in south-west Spain, Central Portugal, and central-eastern Spain (the upper x axis shows the years of the PDSI series). The dotted lines indicate 30-year moving averages, centered in the mid-year of the window (the lower x axis shows the 30-year windows of the moving averages).

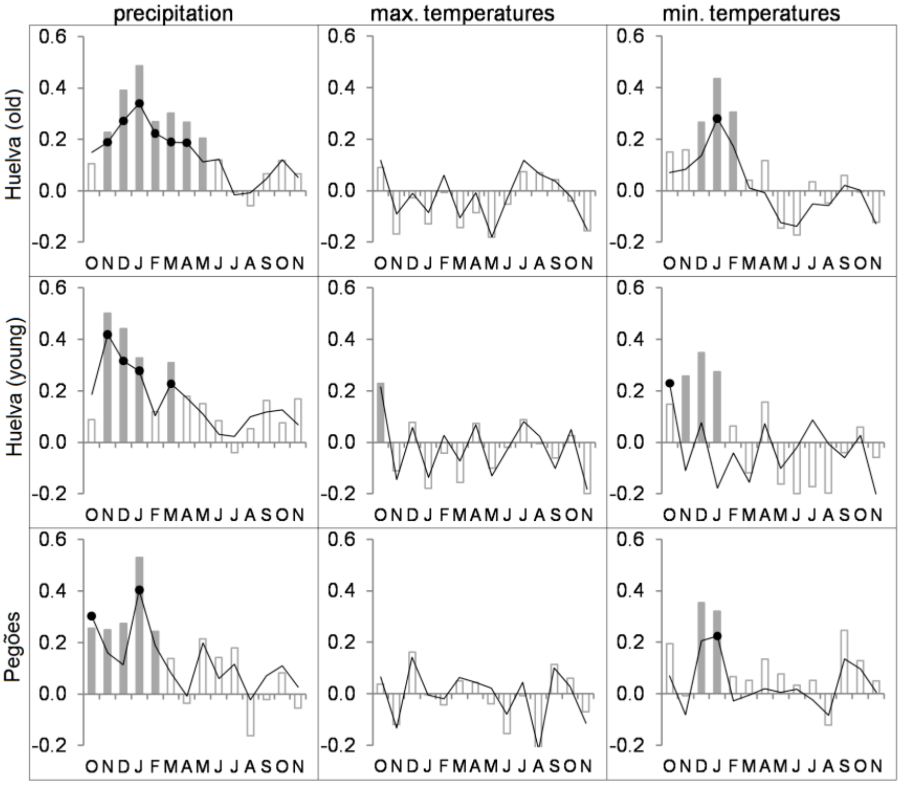


Figure 2. Bootstrapped correlations (bars) and response functions (lines with dots) for monthly values of climatic covariates (precipitation, maximum temperature, minimum temperature) with the first principal component of old trees and young trees from Huelva and residual series from Pegões. Grey bars and black dots indicate statistically significant relationships ($p < 0.05$).

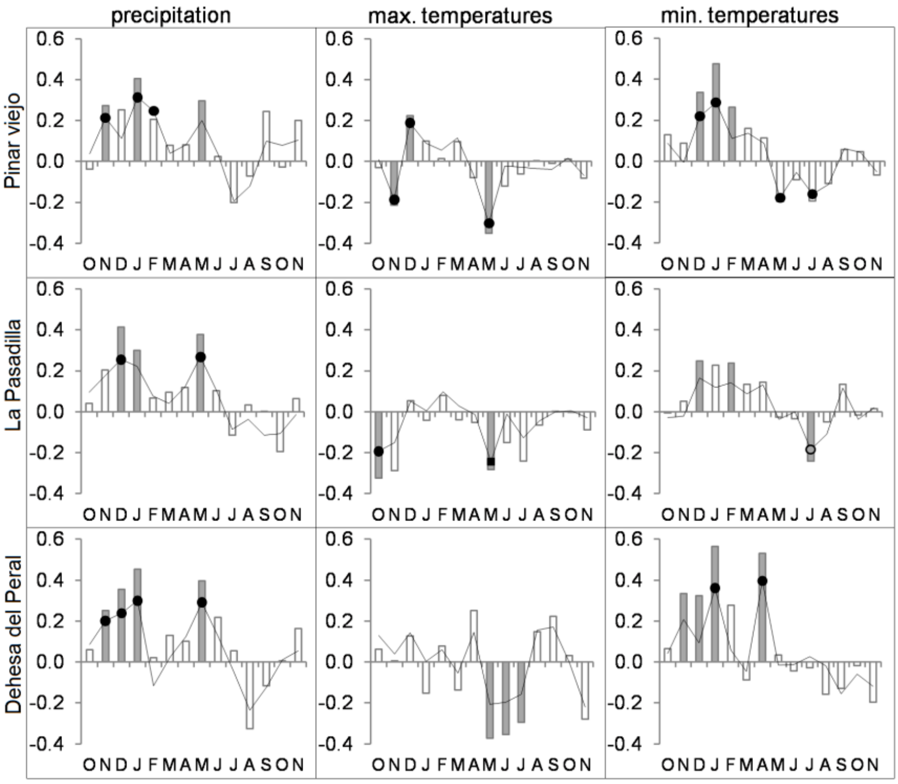


Figure 3. Bootstrapped correlations (bars) and response functions (lines with dots) between monthly values of climatic covariates (precipitation, maximum temperature, minimum temperature) and residual chronologies from La Mancha. Grey bars and black dots indicate statistically significant relationships (p< 0.05).

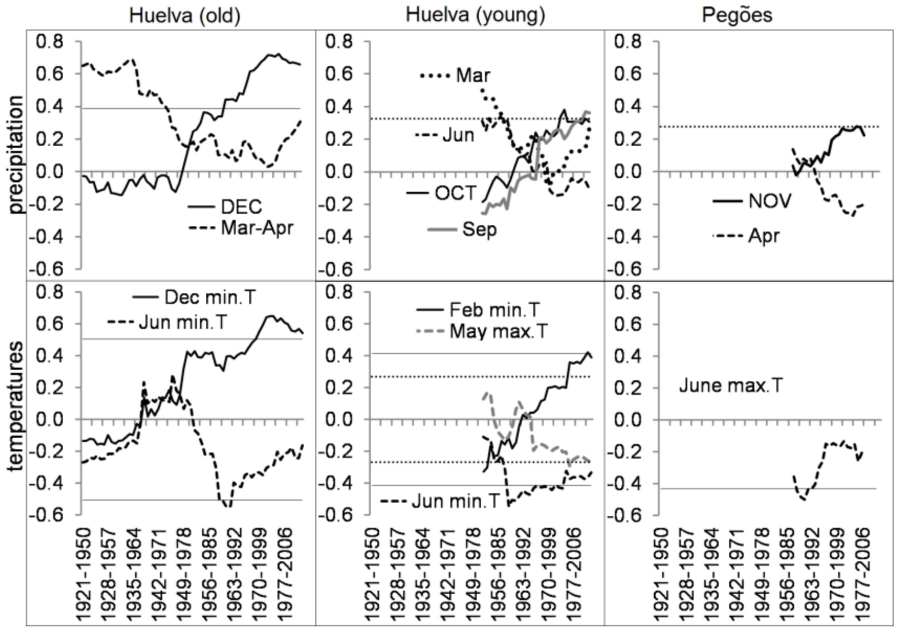


Figure 4. Thirty-year running-window bootstrapped correlations between monthly values of precipitation and temperature (months of previous year are in capital letters) with the first PC of old trees and young trees from Huelva and residual series from Pegões. Horizontal solid and dotted lines indicate thresholds for statistically critical values (α = 0.01 and α = 0.05, respectively).

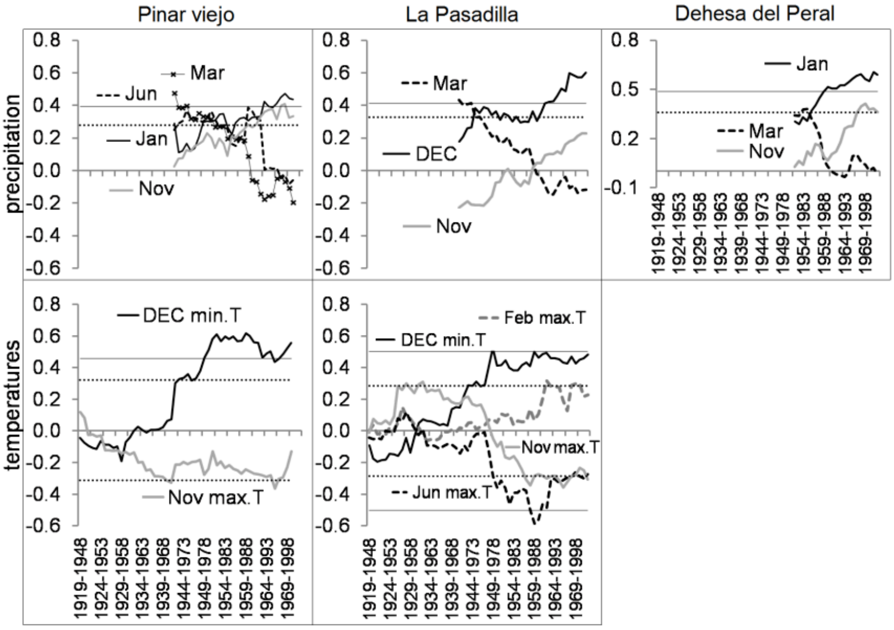


Figure 5. Thirty-year running-window bootstrapped correlations between monthly values of precipitation and temperature (months of previous year are in capital letters) and chronologies from La Mancha. Horizontal solid and dotted lines indicate thresholds for statistically critical values (α = 0.01 and α = 0.05, respectively). There were no significant results after the correlation analysis between Dehesa del Peral and temperatures due to the short time-span of the temperature records in the meteorological station of Molina de Aragón.

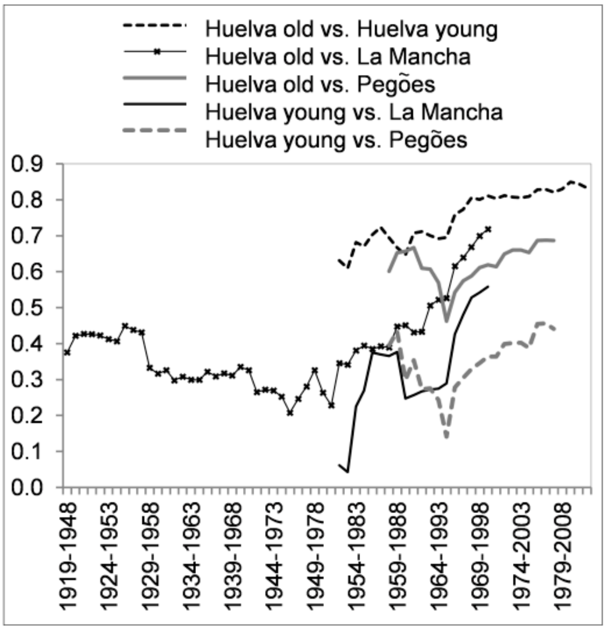
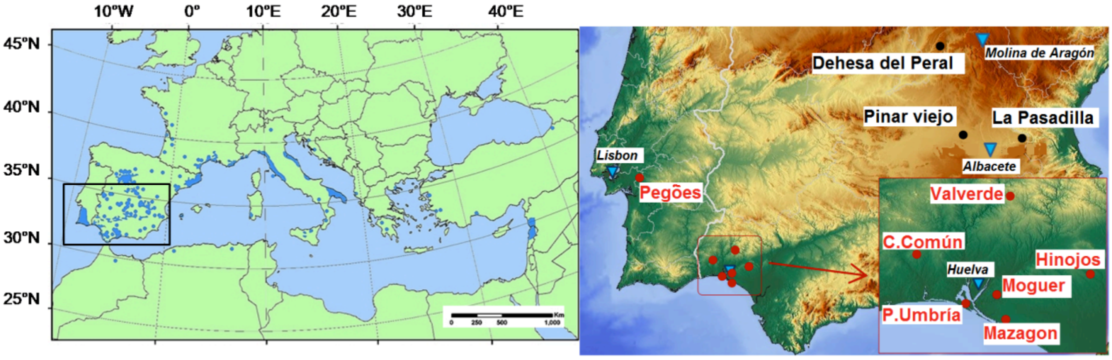
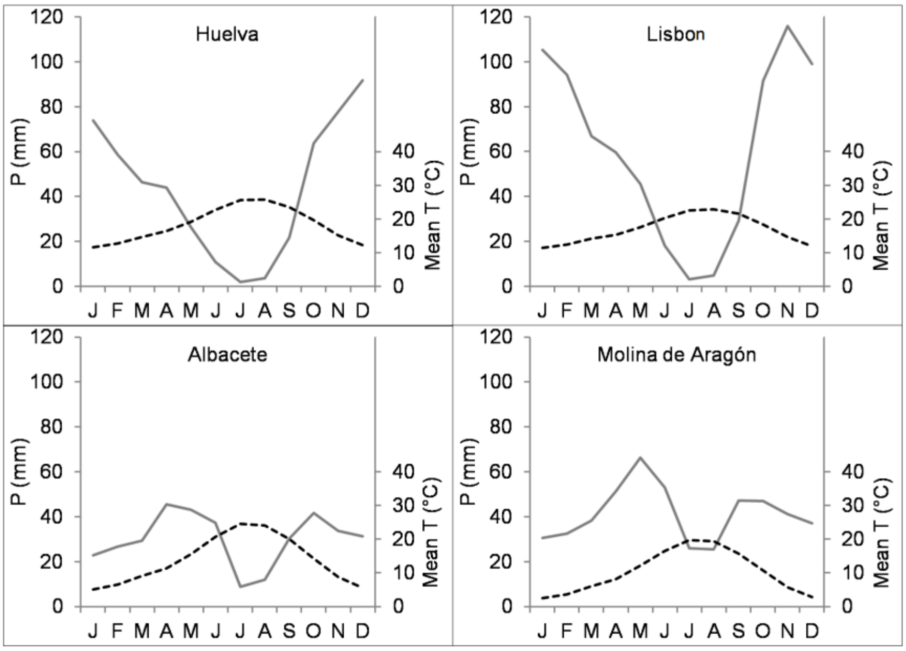


Figure 6. Pearson's correlations for 30-year moving windows, calculated as pair-wise comparisons between the residual chronologies from Pegões and the PCs from Huelva and La Mancha. The x axis shows the 30-yr intervals

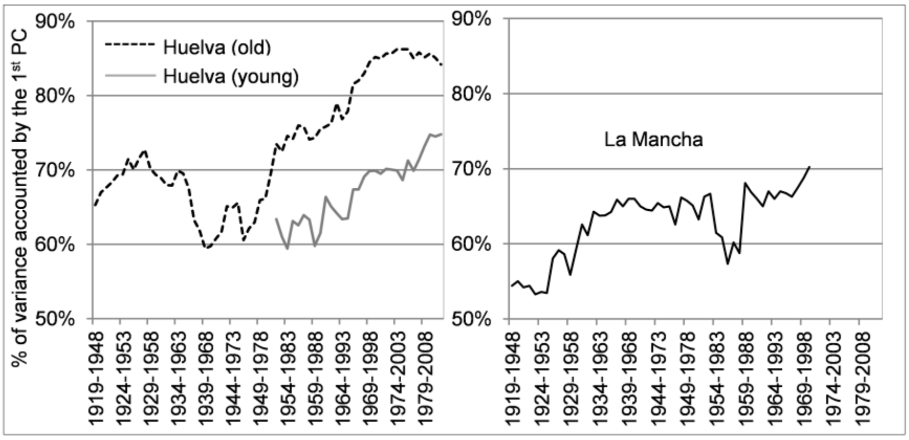
Supplementary material of Article 2



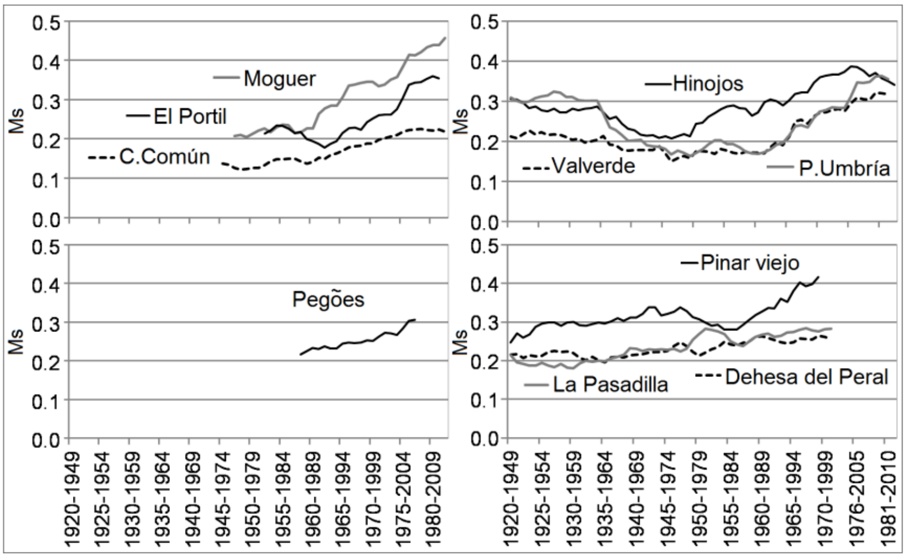
Online resource 1. Distribution of Pinus pinea (left, from EUFORGEN 2009 [www.euforgen.org]), and location of study sites (right). Blue triangles indicate meteorological stations, red dots indicate newly established chronologies, and black dots indicate chronologies from the International Tree Ring Data Base (see Table 1 and text for details).



Online resource 2. Climatic diagrams of the meteorological stations of Huelva (SW Spain), Lisbon (C Portugal), Albacete, and Molina de Aragón (CE Spain) (grey solid lines: precipitation; black dotted lines: mean temperature).



Online resource 3. Percentage of variance accounted by the first PC with 30-year running window PCA of the chronologies of young and old trees from Huelva (left) and chronologies from La Mancha (right). The x axis shows the 30-yr intervals.



Online resource 4. 30-year running mean sensitivity (Ms) of the chronologies of young trees from Huelva (top left), old trees from Huelva (top right), trees from Pegões (bottom left), and trees La Mancha (bottom right). The x axis shows the 30-yr intervals.

Table 1. Geographic coordinates, elevations and stand structural attributes of the study sites. (*) The chronologies in the area of La Mancha are from the International Tree Ring Data Base (ITRDB, see text for details).

Geographic area	Site name	Lat (º N)	Long (º W)	Elevation (ma.s.l.)	mean diameter ± st.dev. (cm)	main height ± st.dev. (m)	stand density (trees/ha)
Huelva (south-west Spain)	Campo Común	37.39	7.19	100	67±7	22±1	209
	El Portil	37.21	7.04	20	22±8	5±1	264
	Moguer	37.21	6.84	30	55±9	17±3	158
	Hinojos	37.29	6.39	70	72±8	20±1	197
	Punta Umbría	37.20	7.00	20	28±7	7±1	237
	Valverde del Camino	37.53	6.78	260	62±6	19±3	300
Central Portugal	Pegões	38.63	8.62	60	19±4	15±3	135
La Mancha (central-eastern Spain)	Dehesa del Peral (*)	40.67	2.77	1057	34±6	9±1	450
	Pinar Viejo (*)	39.55	2.77	750	26±5	8±1	350
	La Pasadilla (*)	39.28	1.35	705	27±7	9±1	250

Table 2.Statistics of tree ring chronologies from Huelva (El Portil, Campo Común, Moguer, Hinojos, Punta Umbría and Valverde del Camino), Pegões and La Mancha (Pinar Viejo, Dehesa del Peral and La Pasadilla). Time-spans include at least 5 cross-dated series with Expressed Population Signal>0.85 (see text for details). (*) 24 stem cross sections were used for Pegões. (**) Individual tree chronologies of the area of La Mancha (Pinar Viejo, Dehesa del Peral and La Pasadilla) were from the International Tree Ring Data Base (ITRDB, see text for details).

	El Portil	Campo Común	Moguer	Hinojos	Punta Umbría	Valverde del Camino	Pegões	Pinar Viejo	Dehesa del Peral	La Pasadilla
Time-span (years)	1952-2011 (60)	1945-2012 (68)	1946-2012 (67)	1866-2012 (147)	1902-2011 (110)	1881-2011 (131)	1958-2007 (50)	1906-1999 (94)	1899-2001 (103)	1919-2001 (83)
No. of trees (no. of cores)	20 (40)	17 (34)	17 (34)	19 (38)	17 (34)	20 (40)	24 (*)	13 (**)	21 (**)	26 (**)
Mean width (mm)	2.4	3.7	2.7	2.1	1.4	1.8	3.2	1.4	2.0	2.5
Median width (mm)	2	3	2.2	1.7	1.2	1.4	2.3	1.0	1.7	2.1
Standard deviation (mm)	1.5	2.3	1.9	1.5	0.8	1.3	2.5	1.2	1.1	1.6
Mean sensitivity	0.28	0.20	0.32	0.37	0.28	0.23	0.26	0.36	0.24	0.30
First-order autocorrelation • raw series • after standardization	 0.68 0.007	 0.73 0.013	 0.54 0.024	 0.68 0.034	 0.67 0.066	 0.79 0.052	 0.77 0.027	 0.77 0.036	 0.77 0.020	 0.72 0.040
Mean correlation: • series *vs.* master chronology • among series	 0.64 0.37	 0.52 0.36	 0.68 0.55	 0.70 0.48	 0.70 0.40	 0.69 0.49	 0.69 0.77	 0.65 0.54	 0.63 0.45	 0.65 0.41

Table 3. Glk and Pearson correlation coefficients (r) calculated from pair-wise comparisons between the residual chronologies from Pegões and the PCs from Huelva and La Mancha. Significance of Pearson correlation coefficients is indicated in brackets.

	Huelva (young)	La Mancha	Pegões
Huelva (old)	*Glk*:76% *r*: 0.76 (p<0.01)	*Glk*: 67% *r*: 0.54 (p<0.01)	*Glk*: 75% *r*: 0.64 (p<0.01)
Huelva (young)		*Glk*: 62% *r*: 0.36 (p<0.05)	*Glk*: 67% *r*: 0.41 (p<0.01)
La Mancha			*Glk*: 75% *r*: 0.55 (p<0.01)

15.3 **Article 3**. Natalini F., Alejano R., Vázquez-Piqué J., Pardos M., Calama R., Büntgen U., 2016. Spatiotemporal variability of stone pine (Pinus pinea L.) growth response to climate across its geographical range in the Iberian Peninsula. Dendrochronologia, DOI: 10.1016/j.dendro.2016.07.001

Natalini F., Alejano R., Vázquez-Piqué J.: Departamento de Ciencias Agroforestales, Escuela Técnica Superior de Ingeniería, Universidad de Huelva, Campus de La Rábida, 21819 Palos de la Frontera, Huelva, Spain
Pardos M., Calama R.: CIFOR-INIA, Ctra. de la Coruña km 7.5, Madrid 28040, Spain
Büntgen U.: Swiss Federal Research Institute WSL, Birmensdorf, Switzerland; Oeschger Centre for Climate Change Research, Bern, Switzerland; Global Change Research Centre AS CR, Brno, Czech Republic

Abstract

Climate warming and increasing aridity have impacted diverse ecosystems in the Mediterranean region since at least the 1970s. *Pinus pinea* L. has significant environmental and socio-economic importance for the Iberian Peninsula, so a detailed understanding of its response to climate change is necessary to predict its status under future climatic conditions. However, variability of climate and uncertainties in dendroclimatological approach complicate the understanding of forest growth dynamics. We use an ensemble approach to analyze growth-climate responses of *P. pinea* trees from five sites along a latitudinal gradient in Spain over time. The growth responses to April-June precipitation totals were stronger in the north than in the south. Since the 1950s, the sensitivity of growth to April-June precipitation increased in the north and decreased in the south. Meteorological drought usually started in May in the southern sites, but in June-July in the northern sites. The water deficit in the southern sites is thus greater and more limiting for tree growth, and this likely accounts for the lower growth sensitivity during these months. Our results indicate that *P. pinea* has a high degree of plasticity, suggesting the species will withstand changing climatic conditions. However, growth response to drought regimes varies among *P. pinea* populations, suggesting that different populations have different capacities for acclimation to warmer and drier climate, and this may influence future vegetation composition.

Keywords: climate change; dendroecology; growth plasticity; Mediterranean; tree rings; drought

Introduction

Climate forecasts for the Mediterranean region indicate there will be an increase of temperature, decrease of rainfall, longer dry spells, more frequent heat waves, and more heavy precipitation events, all of which will exacerbate the existing problems of soil loss and desertification (Kovats et al., 2014). Significant changes in climate and related social dynamics, such as land use and food production, migration, and social conflicts, make the Mediterranean region a major climate change “hotspot” (Giorgi, 2006; Scheffran and Battaglini, 2011). The Iberian Peninsula, located in the western sector of the Mediterranean basin, has diverse climatic conditions: the northern zones have a Eurosiberian climate, and large parts of the peninsula have a Mediterranean-type climate, with warm summers and cold winters in the center and hot summers and mild winters in the south. The Iberian Peninsula has become drier in recent decades, and research indicates this change will continue (Pérez and Boscolo, 2010). There is evidence that climate change has already impacted forest ecosystems in this region. These impacts include shifts in species distributions and phenology (Peñuelas et al. 2002), decreases of growth, at least in the southern provenances and at lower edges of species altitudinal ranges (Jump et al. 2006; Martín-Benito et al. 2010), reductions of non-wood forest products (Büntgen et al. 2015a), stand decline processes and increased mortality (Carnicer at al. 2011; Natalini et al., 2016), and increased disturbances such as pests and fires (Hódar et al., 2003; Pausas, 2004). Distribution shifts of tree species are also expected for the future (Benito-Garzón et al. 2008).

Pinus pinea L. is an important tree species of Iberian Mediterranean forests. This species occurs throughout southern Europe and the eastern and southern Mediterranean coasts, and is native to the Iberian Peninsula (Martínez and Montero, 2004). *P. pinea* forests in Spain have considerable socio-economic value and, because of the easy access to areas where it grows (for the most part flat terrains at low elevations), it is exposed to human disturbances. Most *P. pinea* forests in Spain originated from plantations during the 20th century. These forests occupy more than 500,000 ha and are managed as multifunctional forests that provide timber, biomass, non-wood forest products (especially pine “nuts”), soil protection, sand dune stabilization, biodiversity refuge, space for public and recreational activities, and carbon sequestration (Montero González et al. 2004). It is necessary to understand the effects of climate change on the ecology of *P. pinea* forests to assess the adaptive capacity of this species and to develop management programs that ensure the conservation of this environmentally and socio-economically important species.

P. pinea tree ring data can provide accurate information about the relationships between growth and climate (Campelo et al., 2006). Natalini et al. (2015) studied *P. pinea* tree ring growth in relation to climate change in southern Iberian Peninsula. In particular, they focused on temporal shifts of growth-climate relationships and increasing high-frequency variability and synchrony of growth in different populations as common responses to drier and warmer climate. However, trees also have diverse responses to climate depending on site-specific conditions (e.g. De Luis et al., 2013; Mazza et al., 2014). In fact, *P. pinea* grows under very different environmental conditions (Montero González et al. 2004), and variable growth responses to climate may be therefore expected across its geographical distribution range. The range of climatic conditions to which a species is adapted potentially determines its capacity to acclimate to future climatic conditions, and this should be considered when investigating the effects of climate change on forest dynamics (Tardif et al., 2003). For a proper assessment of growth-climate relationships, tree-ring detrending procedures also must be carefully considered. In particular, detrending curves with different degree of flexibility enhance the climatic signal and remove the non-climatic variance at different frequencies, and their suitability depends on the frequency domain of the tree-ring series (Helama et al., 2004). Moreover, uncertainties in growth-climate relationships can derive from the climate data, especially the choice of climate parameters and the lack of homogeneity of meteorological records (Frank et al., 2007; Büntgen et al., 2015b). Therefore, the spatiotemporal variability of species' response to climate, and the influence of different dendroclimatological approaches, make the assessment of climate-related forest growth dynamics more complex.

The purpose of this study is to provide a better understanding of climate-related *P. pinea* forest growth dynamics in Spain. We hypothesize that the species-specific growth response to climate varies over space and time in association with climatic spatial variability and temporal changes. To test our hypothesis, we examined growth-climate relationships and their variability over time in climatologically distinct sites along a latitudinal gradient in Spain. We tested the suitability of different tree-ring detrending methods and we used a comprehensive set of climatic parameters and climate data sources to check for uncertainties in climate data that could influence the assessment of growth-climate relationships. Finally, we discuss the observed variability of growth response to climate and its potential implications in Iberian *P. pinea* forest dynamics.

Materials and methods

Sampling sites

The sampling sites are along a latitudinal gradient in Spain and present different environmental conditions (Figure 1, Table 1). Two sites ("Carrascal" – hereinafter CAR -- and "Viana de Cega" – VIA) are in the province of Valladolid on the "Meseta Norte" (northern Spain), one site ("Hoyo de Pinares" -- HOY) is in the province of Ávila (Central Spain), on the "Sistema Central" mountain range, and two sites ("Hinojos" – HNJ -- and "Valverde" -- VAL) are in the province of Huelva, Southwestern Spain. The Meseta Norte is a vast plateau of Tertiary and Quaternary deposits with altitudes of ~600 to ~900 m a.s.l., where *P. pinea* grows within nemoro-Mediterranean vegetation, i.e. transitional areas where evergreen sclerophyll and deciduous broad-leaf forests occur (Allué et al., 1990). The Sistema Central is composed of Paleozoic and Mesozoic granitic rocks with patches of Cenozoic sediments, runs in an ENE-WSW direction (between the Meseta Norte to the north and the Meseta Sur to the south). Here, several peaks are higher than 2000 m a.s.l., and *P. pinea* grows at 600-1000 m a.s.l. within Mediterranean and nemoro-Mediterranean vegetation. VAL is on the southernmost limit of the "Sierra Morena" mountain range, HNJ is on the coastal zone of the Baetic depression (alluvial plain of the Guadalquivir river), and both have Tertiary and Quaternary deposits and low elevations (under 300 m). In this area, vegetation is Mediterranean including the most xeric *P. pinea* forests of Spain. In Carrascal and Viana de Cega, they are on flat terrains and are managed as protection forests (with an important function of fixing continental fossil dunes) and for production of timber and pine nuts. In Hinojos and Valverde del Camino, *P. pinea* forests are on flat terrains, they are primarily managed for timber production and nowadays biomass, and secondarily for pine nuts. Silvicultural measures for productive functions typically involve thinning and pruning for improving wood production and crown development. In Hoyo de Pinares, *P. pinea* trees grow on a south-facing slope within less disturbed protection forests, where productive functions are not important. The sampled stands in VIA, HOY, VAL and HNJ are pure, even-aged, single-canopied *P. pinea* stands, and the stand in CAR is a single-cohort stratified mixture, with a dominant storey of *P. pinea* trees and a lower storey of Quercus ilex L. subsp. ballota [Desf.] Samp. and Juniperus thurifera L. Climatic conditions are similar between the two northern sites (VIA and CAR) and between the two southern sites (VAL and HNJ), but differ along the latitudinal gradient. Annual precipitation and mean temperature are 404 mm and 12ºC in CAR, 357 mm and 12ºC in VIA, 548 mm and 11ºC in HOY, 525 mm and 17ºC in VAL, 527 mm and 18ºC in HNJ (climate values calculated over the period 1950-2013 using the E-OBS gridded climate dataset).

Tree-ring chronologies

All samples (2 cores per tree) were extracted with an increment borer at breast height from the largest dominant or co-dominant trees. The cores were glued onto wooden mounts and sanded along the transverse sections to make the rings visible. Tree ring widths were measured with a stereomicroscope and a LINTABTM table connected to a TSAP-WinTM tree ring analysis system (Rinntech®). Ring width curves were plotted for visual inspection and cross-dated by determination of the coefficient of parallel variation (Gleichlaeufigkeit, Glk; see Speer, 2010, p. 108), t-value, and cross-date index (CDI) using TSAP-WinTM software. The cross-dating was verified using COFECHA (Grissino-Mayer, 2001).

The stands in the study sites are subjected to forestry treatments that affect growth trends and may mask the climatic signals stored in the ring width measurements. To remove the non-climatic growth variance from the ring-width measurements, we applied 2 detrending techniques: a negative exponential curve (NEXP), and a cubic smoothing spline with 50% frequency-response cutoffs at 30 years (SP30). The NEXP removes the age-related trends and retain other low-frequency variability, allowing the detection of low-frequency climatic signals, while the SP30 removes the low-frequency variance and enhances the high-frequency climatic signal (Helama et al., 2004; Cook et al., 1990a). To obtain dimensionless tree ring series and to remove the heteroscedasticity, tree ring indexes were annually calculated for each individual series as ratios between the raw ring width measurement and the corresponding statistical fit (Cook et al., 1990a). The final mean chronology of each site was computed as a bi-weight robust mean of the indexed series, which removes the effects of outliers (Cook et al., 1990b). To assess the strength of the site chronologies we used the expressed population signal (EPS), which is a measure of the confidence of a mean chronology in expressing the population-level signal (Briffa and Jones, 1990). To verify the stability of the chronology signal strength over time, we computed the EPS for each site using 30-year windows lagged by 15 years along the mean ring-width chronology.

Climate data

A composite database of meteorological parameters from different climate data sources was created to check for uncertainties in climate data and to develop a robust assessment of climate variability. Specifically, we used 6 climate parameters (precipitation, self-calibrating Palmer Drought Severity Index [scPDSI], diurnal temperature range [DTR], and maximum, minimum, and mean temperature), from 6 climate data sources (3 meteorological stations and 3 gridded datasets) (Table S2). The scPDSI is suitable to assess growth sensitivity and has been widely used in dendroclimatological studies (e.g. Cook et al., 2015). The scPDSI improves upon the Palmer Drought Severity Index (PDSI) by maintaining a consistent behavior of the index over diverse climatological regions, thus making spatial comparisons of the drought index values on large scales more meaningful (van der Schrier et al., 2006). The DTR is a metric used in climate change studies and is linked to cloud cover (Karl et al., 1993). Since cloud cover controls solar radiation, that influences terrestrial temperatures and soil moisture, the DTR can be an appropriate hydroclimatic metric to study tree growth (Gimeno et al., 2012; Büntgen et al., 2013).

The meteorological station records were obtained from the European Climate Assessment Dataset project (ECAD, Klok and Klein Tank, 2008; http://eca.knmi.nl). We used homogenized meteorological records from three stations: "Valladolid-Villanubla", which was the closest station to CAR and VIA, "Ávila", the closest station to HOY, and "Huelva", the closest station to HNJ and VAL. The ECAD does not provide any other station to characterize separately the climate conditions of the two northernmost sites (VIA and CAR) nor of the two southernmost sites (HNJ and VAL) (see "Meteorological station data" in Supplementary Material).

The sources of the gridded data were: (i) the E-OBS v11.0 dataset by the EU-FP6 project ENSEMBLES (Haylock et al., 2008; hereinafter "E-OBS"); (ii) the CRU scPDSI 3.21 (van der Schrier et al., 2006) and (iii) the CRU TS3.23 (Harris and Jones, 2014) by the Climatic Research Unit, University of East Anglia, UK (hereinafter "CRU") (see Table S2). The E-OBS provides climate data with higher geographical resolution, but the CRU covers a longer period (see Table S2); therefore, we used the CRU to study the long-term climatic changes, and we included the E-OBS to have more detailed information about site-specific climate. For each gridded dataset, we selected the closest grid point to each study site through the KNMI Climate Explorer (http://climexp.knmi.nl). There was a distinct grid point for each study site.

We computed monthly sums of precipitation and monthly averages of scPDSI, DTR and maximum, minimum, and mean temperatures. Hence there was a total of 62 sets of monthly resolved climate data (Table S1).

The monthly climate values were very similar between CAR and VIA and between HNJ and VAL (compared using the gridded datasets), but varied with latitude. Therefore, we distinguished three climatic regions: the north (including CAR and VIA), the centre (HOY) and the south (VIA and HNJ). A climate diagram was produced for each climatic region by averaging per year the monthly values of precipitation and temperature within the common period of the climate datasets. To study the temporal variability of climate in each region, climate diagrams were also produced for two successive time windows by dividing the common period of the datasets into two sub-periods of equal length. In the climate diagrams, all months with P less than 2T (where P is mm of total precipitation and T is mean temperature in Celsius degrees) were classified as “dry”.

Moreover, we calculated the departures of the climate data from the average of the last 30 years of the climate datasets. The values so obtained for the months April, May, June, July, August, and September (AMJJAS) were averaged per year. AMJJAS were used following previous tree ring studies (e.g. Büntgen et al., 2007; Nicault et al., 2008; Galván et al., 2014) and taken as a general time window comprising months in which high temperatures and water deficit significantly influence Mediterranean tree growth (e.g. de Luis et al., 2013, Seim et al., 2014). Subsequently, the AMJJAS time series were plotted for each region to study the temporal trends. Moreover, correlations between the AMJJAS series of different climate data sources were computed to examine the discrepancies among the different climate data sources.

Analysis of growth-climate relationship

The relationships of growth with climate were analyzed with bootstrapped correlation and response functions, which remove the multicollinearity between climatic variables (Zang and Biondi, 2015), using the standardized tree ring chronologies and the climate datasets. We applied an ensemble approach (Büntgen et al., 2012) to assess how P. *pinea* growth response varies with climate in space and time, and to evaluate how the assessment of growth-climate relationships can be influenced by the choice of tree-ring detrending methods, climate data sources and climate parameters. This approach was accomplished in three successive steps:

Growth-climate correlations were computed for each site using all monthly resolved climate datasets and standardized tree ring chronologies. Unsuitable tree ring detrending methods, and climate data sources that generated uncertainties in the growth-climate relationships, were excluded from the analyses. Moreover, we identified the climate parameters which best explained tree growth.

We examined the spatial variability of growth-climate correlations and response functions in association with the spatial variability of climate.

Correlations and response functions were computed over two successive time periods – by dividing the common period between tree-ring and climate data into two sub-periods of equal length – to examine the temporal shifts of the growth response to climate and their connection with climate change.

A total of 240 correlation analyses were performed (Table S3).

Results

Tree-ring chronologies

The number of cross-dated ring width measurement series per site ranged from 38 (19 trees, in HOY and 5) to 52 (26 trees, in VIA). The oldest trees were in HOY and the youngest in CAR, and the ranges of the chronologies were: 43-94 years in CAR, 102-144 years in VIA, 75-228 years in HOY, 91-139 years in VAL, and 69-150 years in

HNJ (Table 2). These differences in chronology length within each stand were due to the uneven distances between the pith and the innermost cross-dated ring, rather than the age structure of the stands (which are even-aged). The EPS value for each site and consistently was above the minimum threshold of 0.85 back to ~1880 in CA, VIA, HNJ and VAL, and above 0.85 back to 1842 in HOY (Figure 3).

Influence of detrending methods on growth-climate relationships and uncertainties from climate data

There were discrepancies between the NEXP chronologies and the SP30 chronologies, especially in VIA and HNJ, while CAR and HOY the agreement between the detrending methods was greater (Figure 2B). The discrepancies were due to non-climatic growth releases (in the 2000s in VIA and in the 1960s in HNJ) that were not removed by the NEXP curve. The highest between-site correlations were found with the SP30 detrending method between CAR and VIA and between VAL and HNJ (Table 3). Therefore, the SP30 enhanced the climatic signal and confirmed the existence of three distinct dendroclimatic signals, one in the north (common to CAR and VIA), one in the center (HOY), and one in the south (common to VAL and HNJ).

The effects of different detrending methods were also visible in the growth-climate correlation patterns. In particular, the growth-climate correlations obtained with the NEXP chronologies differed from those obtained with the SP30 chronologies in VIA, VAL and HNJ (Figures S2, S4 and S5). On the other hand, the similarities between VIA and CAR and between VAL and HNJ were higher when we applied the SP30 (compare Figures S1 with S2, and S4 with S5), supporting the notion of similar growth response within each region.

Uncertainties in the assessment of growth-climate relationships occurred when we used different climate data sources. In particular, growth-climate correlation patterns differed within HOY, VAL and HNJ when we used temperature data from meteorological stations (Figures S3, S4, d, S5). Notably, the AMJJAS series computed using meteorological station records had disagreements with the other climate data sources (Table S4). In particular, the correlations were low (~0.50) for the mean temperature series in the south and even lower (≤0.3) for the minimum temperature series in the south and center (Table S4).

Consequently, because the NEXP detrending method was less appropriate to remove the non-climatic variance from the tree ring chronologies and the uncertainties mainly derived from the use of meteorological station data, we only considered the results obtained with the gridded climate data and the SP30 chronologies.

Climate variability

The climate diagrams of the three climatic regions show different patterns (Figure 4). In the south, the winters were mild and most precipitation was during winter; in the northern and central sites, the winters were cold and the maximum of precipitation was during spring and autumn. In the north, there was a more delayed onset of meteorological droughts than in the south. Moreover, meteorological droughts in the south lasted longer and were more intense due to higher temperatures and less precipitation.

The intensity and duration of meteorological droughts increased over time (Figure 4). Specifically, from the “early” (1950-1980) to the “late” (1981-2011) period, the number of dry months (i.e. $P < 2T$) increased from 3 (Jul-Sep) to 4 (Jun-Sep) in the north and from 2 (Jul-Aug) to 3 (Jul-Sep) in the central region. In the south, the number of dry months was 5 (May-Sep) during both periods, but drought intensity increased due to higher temperatures from May to August and less precipitation during June (Figure 4).

The AMJJAS scPDSI series showed different patterns of droughts before 1980 in the three regions, but the droughts in the early 1980s and mid 1990s were similar (Figure 5). The long-term trends of temperature were similar in all regions, with a warm period from the 1940s to 1960s and an increase of temperature during the last 40 years, although only the north and center had increases in DTR (Figure 5).

Growth response to climate variability

We can distinguish the patterns of growth-climate relationships by latitude. In particular, the growth-climate correlations in the northern sites had similar bimodal patterns (CAR and VIA in Figure 6). In particular, there were positive correlations with precipitation from the previous October/November to January and from April to June; the correlations with temperature were positive from December to February and negative from May to June/July. There were similar correlation patterns in HOY (Figure 6). A distinct growth-climate response pattern occurred in the south (VAL and HNJ in Figure 6). In particular, there were positive correlations with precipitation from November to January, but these correlations were not significant during spring and absent during summer. There were positive correlations with temperature in the south during winter, but only for mean and minimum temperatures, and these were absent during spring/summer.

The growth-climate relationships were unstable over time and had distinct temporal changes along the latitudinal gradient. In the northern sites, the bimodal patterns in the growth-climate correlations were more marked during the “late” (1981-2011) than the “early” (1950-1980) period. Specifically, in the “late” period the correlation with precipitation in spring was greater and the correlation with temperatures in May/June was more negative (Figures 7, 8). There were similar changes in the center (although there was a loss of positive correlation with precipitation during June, Figure 9). In the southern sites the correlation with precipitation in spring was low during both periods, and the growth response to precipitation in June was significant during the “early” period but absent during the “late” period (Figures 10, 11) Moreover, there was a marked increase of positive correlations with precipitation and mean/minimum temperatures in autumn/winter (Figures 10, 11).

The correlations with the scPDSI and DTR reflected the overall patterns observed with precipitation and temperature data (Figures S6, S7),The response function analysis led to a lower number of statistically significant coefficients, but confirmed the overall patterns and temporal changes of growth-climate relationships found with the bootstrapped correlation analysis (Figures 6-11, Figures S6, S7).

Discussion

4.1 Influence of detrending methods on growth-climate relationships, uncertainties from climate data and choice of climate parameters

The dendroclimatic signal was not properly assessed using the NEXP method in VIA, VAL and HNJ. The NEXP is a parametric method which retains low-frequency growth variance (other than the age-related one) which can be a proxy of long-term climatic changes (Esper et al., 2002). In this sense, it can be referred to as a "conservative" detrending method (Cook et al., 1990a; Biondi and Qeadan, 2008). Nevertheless, conservative methods are suitable for wood specimens from sites with minimal ecological and anthropogenic disturbances, which are preferred for climatic reconstructions (Schweingruber et al., 1990). In contrast, the goodness-of-fit is reduced in managed forests and shade-tolerant interior-forest trees, where stand dynamics produce stochastic perturbations in growth trends (Piovesan et al., 2005; Gea-Izquierdo et al., 2011). In such cases, non-climatic noise is better removed by data-adaptive detrending curves (Cook et al., 1990a). Growth releases due to thinning can be found in tree-ring samples from Iberian *P. pinea* productive forests, and in fact were evident in VIA and HNJ. In these two cases, growth pulses could be wrongly interpreted as climate-induced if conservative methods were used, thus the tree-ring series are better filtered by flexible curves that extract the middle/high-frequency climatic signal. Notably, the NEXP and SP30 chronologies were comparable in CAR and HOY, where the silviculture-induced noise is absent, although the NEXP estimated lower ring indexes in HOY during the 1920s and 1930s, that probably reflect droughts occurred in these decades (Figure 2) and may suggest the extraction of low-frequency climatic signals. However, we applied the SP30 method in all sites to obtain the same type of climatic information for a coherent spatial comparison of growth responses.

A possible explanation of the uncertainties arisen from the meteorological records can be the uneven quality of instrumental measurements over time, which actually causes biases in tree-ring based climate reconstructions (Dessen and Bücher, 1995; Frank et al., 2007; Dorado Liñán et al., 2012; Büntgen et al., 2015b). The uncertainties are also partly explained by the location of the stations. Indeed, differences in temperatures and humidity can be expected from the different elevation between the stations and the study sites, in particular between "Ávila" and HOY and between "Huelva" and VAL (a difference of around 240 m in both cases). However, there were no closer stations with long-term records, and our analysis indicated that the available meteorological station data are somewhat inappropriate for calibrating tree-ring proxy data in these sites. The grid boxes constituted the most suitable source of information about site-specific climate available for our study.

The relationships between tree ring chronologies and scPDSI reflect the suitability of this metric for dendroclimatological studies in the southern Europe (Cook et al., 2015). However, the combined use of precipitation and temperature data provided clearer seasonal patterns of statistically significant correlation values, permitting a better dendroecological comparison between sites. The DTR provided meaningful results, reinforcing its potential use to calibrate tree-ring proxy data. Negative growth response to DTR may refer to cloud-free sky, associated with high DTR, which generally boosts temperatures and reduces soil moisture, at least during the warm seasons, but the possible negative effects of atmospheric brightening on forest productivity needs further studies (Büntgen et al., 2013).

Spatiotemporal variability of climate

The three studied regions all have a Mediterranean macroclimate that is characterized by hot and dry summers. However, there were also climatic differences among the sites. The annual distribution of precipitation varied among regions, and the duration and intensity of meteorological droughts was greater at lower latitudes. The lower amount of rainfall during spring and summer in the southern sites is related to the dominant atmospheric circulation patterns in southern Spain (Romero et al., 1999). Furthermore, winter temperatures in the northern and central regions were lower, attributable to the "sub-continental" type of the Mediterranean climate which characterizes the supra-Mediterranean belt in central-northern Spain (Rivas-Martinez, 2007; Olano et al., 2012). In the central region, the annual precipitation is higher and the meteorological droughts are shorter than in the northern sites, due to humid winds from the Atlantic Ocean through the Tagus river valley, which lead to more frequent precipitation events (see Benito et al., 2003, and Figure 69 in AEMET-IM, 2011). The greater precipitation amount of this area is also associated with the higher elevation (Rodriguez-Puebla et al., 1998).

The dry periods during the 1980s and 1990s (scPDSI series in Figure 5) and the increase of temperature since the 1980s (Figure 5) occurred in all three regions. This confirms the existence of a large-scale climate change process characterized by increasing temperature and aridity, in line with previous findings in the Iberian Peninsula (Pérez and Boscolo, 2010). However, there were different dynamics in the drying process in the three study regions (Figure 4). In the northern and central regions, meteorological droughts increased in intensity and duration because of higher temperature and lower rainfall from June to September. In the south, meteorological droughts did not change in duration but increased in intensity due to higher temperature from May to August and decreased precipitation during June. Our observations indicate that our three study regions, although affected by a common macroclimate and by similar climate change processes, have different climate dynamics at the local level (Vicente-Serrano et al., 2004).

Spatiotemporal variability of growth-climate relationships

The differences in the duration and intensity of meteorological droughts among the study regions can explain the differences in tree growth sensitivity during the late spring and early summer. During this period, the moisture conditions were more limiting in the south, so the precipitation-related signal strength was lower in this region than in the other sites. This may indicate lower rates of wood formation under water deficit during spring/summer (Vieira et al., 2014). Moreover, the stronger growth response to spring precipitation in CAR, VIA and HOY may also be due to the spring maximum rainfall in these areas. In the northern and central sites, growth sensitivity to May/June temperature was also greater than in the southern sites. In fact, during late spring and early summer, an increase of temperature without an increase of precipitation can negatively affect cambial activity, and this underlies the sensitivity of ring formation to high temperature in this period of the year (de Luis et al., 2011; Martin-Benito et al., 2013).

Differences in additional factors other than climate, especially soils, probably influence growth rates and forest productivity in our study sites (Bravo-Oviedo and Montero, 2005). However, when stand dynamics were removed with appropriate tree ring detrending methods, the chronology signals were noticeably similar between sites of a same climatic region (north and south), despite the geological and edaphic differences. Therefore, non-climatic site-specific ecological characteristic barely influenced the assessment of dendroclimatic signals and did not affect our dendroecological comparison between regions.

The capacity of *P. pinea* trees to establish site-specific relationships with the local climate may be explained by the plasticity of this species. The genetic variability of *P. pinea* is low (Fallour et al., 1997; Vendramin et al., 2008; Pinzauti et al., 2012). However, this is a widespread species that grows under diverse environmental conditions, indicating that genetic variability does not entirely explain its adaptability (Vendramin et al., 2008; Soto et al., 2010). In fact, the successful adaptation of *P. pinea* seems to depend largely on the variability of phenotypic traits, which is high in this species (Mutke et al., 2010, 2013; Sánchez-Gómez et al., 2011; Sáez-Laguna et al., 2014). Thus, phenotypic plasticity may explain the observed variability of the growth response to climate in different regions, that could suggest the capacity of *P. pinea* to adapt the annual distribution of cambial activity depending on site-specific climatic conditions. Tree-ring analysis and xylogenesis indicate plastic cambial activity in Pinus halepensis (de Luis et al., 2011, 2013), an ecologically similar species that also has little genetic variability (Soto et al., 2010). However, experimental data on xylogenesis of *P. pinea* to verify plastic cambial activity are still very scarce (Luz et al., 2014)

The growth-climate correlations in our sites varied over the study period. This reflects the non-stationary nature of growth responses to climate (Carrer and Urbinati 2006) which can be interpreted as physiological plasticity that enables an individual to acclimate to changing conditions (Meyers and Bull, 2002). In fact, individual trees can alter their physiology in response to environmental changes (Walther et al., 2002; Rossi et al., 2011). In our study sites, climatic changes over time drove the shift of the growth-climate response patterns, as also reported in other tree-ring studies (Martín-Benito et al., 2010; Latte et al., 2015). This suggests an adjustment of growth physiology during the life of trees in response to a warmer and drier climate, as discussed in a previous study (Natalini et al., 2015). However, the response shifts observed in the present study also seem to be mediated by site-specific climate dynamics. In fact, the increased growth response to spring precipitation (and the increased sensitivity to temperature in May) in the northern and central sites appear linked to the higher spring rainfall during the "late" period in these regions. There were different changes in the south, where spring precipitation did not increase and growth response to climate was always low in this season. Hence, in this region, the climate change-related risk of water deficit during spring is higher and induces a distinct response in growth physiology. In the south there was also a significant decrease of the positive correlation with precipitation in June, which may be linked to the marked increase in drought intensity in this month in this region. These findings indicate that temporal changes and spatial variability in climate simultaneously influence tree growth and the acclimation response.

The plasticity of plant species may play an important role in future vegetation dynamics following climate change (Nicotra et al., 2010). Based on our results, we suggest that *P. pinea* in northern sites have some capacity to resist a future increase of drought by adjusting cambial activity and thus becoming more similar to trees in southern sites (which are currently adapted to drier conditions). On the other hand, the southern populations may already be approaching or exceeding their ecological limit, and their persistence under future conditions may be threatened. This could be in agreement with predicted vegetation dynamics. In fact, global warming induces spatial shifts in the ecological ranges of plant species (Walther et al., 2002), and in Spain this will likely lead to a northward shift of the distribution of tree species (Benito-Garzón et al. 2008; Pardos et al., 2015). Alternatively, the southern *P. pinea* populations could acclimate by activating the cambium during winter if winter temperatures continue increasing (Prieto et al., 2004). In fact, maintaining cambial activity during winter is an adaptive trait that some Mediterranean trees show in certain precipitation and temperature conditions (Cherubini et al., 2003). For instance, previous research in Portuguese stands of Pinus pinaster, a species ecologically close to *P. pinea*, indicates some cambial activity during winter, although evidences are restricted to coastal (oceanic) zones during mild winters (Vieira et al., 2014). The tree-ring growth response of *P. pinea* during winter, also previously reported in Spain and Italy (de Luis et al., 2009; Mazza et al., 2014; Natalini et al., 2015), may reflect that this species can be physiologically active during winter (Pardos et al., 2010). In fact, cells in differentiation during winter have been observed in *P. pinea* in coastal areas of central Portugal, although this needs further investigation (Luz et al., 2014). There is no basis for making further speculations about future changes in cambial activity for trees in our southern sites because there is no species-specific experimental evidence in drier locations which could be used for such predictions. However, our results suggests that the species' plastic response to warmer and drier climate can vary among populations, and some measure of such variable plasticity should be considered in long-terms forecasts of vegetation dynamics (Alla and Camarero, 2012).

Conclusions

The study regions had similar Mediterranean macro-climates and were all affected by the long-term increases of temperature and aridity. However, climatic patterns and climate change dynamics were not uniform among sites. The *P. pinea* growth response to climate changed over time in response to climate change, but this varied in space according to site-specific climatic conditions. The variable growth-climate relationships suggested that *P. pinea* can adapt to a range of climatic conditions, and will be able to acclimate to temporal variations in climate. Few studies have investigated the plasticity of plants from a dendrochronological perspective (de Luis et al., 2013). In this context, the present study provides a tree ring-based assessment of the plastic growth response of *P. pinea* to climate variability in Spain. Our results do not support or contradict the persistence of *P. pinea* near its xeric distribution limit under future warmer and drier climate, but they indicate that the species' plasticity can be crucial for prediction of vegetation dynamics under climate change scenarios.

The dendroecological approach to climate-related forest growth dynamics requires a careful evaluation of the most suitable tree-ring detrending methods and climate data. There are no universally valid detrending methods, because chronologies from different stands, especially from managed stands, show different non-climatic perturbations, which determine the appropriate method and the type of climate signal that can be extracted. Uncertainties in growth-climate correlations can be related to climate data, thus the type, quality, sources and geographical validity of climate data should also be screened. To study the variability of climate and tree growth response in managed stands of our study areas, the most appropriate approach involved flexible splines and gridded climate data. We suggest that an ensemble approach, involving the evaluation of dendroclimatological procedures, and comparing species' responses across diverse site-specific climatic conditions and time periods, can enhance our understanding of forest growth dynamics.

References

AEMET-IM, 2011. Iberian Climate Atlas. Agencia Estatal de Meteorología - Instituto de Meteorologia de Portugal, http://www.aemet.es/documentos/es/conocermas/publicaciones/Atlas-climatologico/Atlas.pdf

Alla, A.Q., Camarero, J.J., 2012. Contrasting responses of radial growth and wood anatomy to climate in a Mediterranean ring-porous oak: implications for its future persistence or why the variance matters more than the mean. Eur J For Res 131 (5), 1537-1550.

Allué, J.L., 1990. Atlas fitoclimático de España. Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria, Madrid, Spain.

Benito, G., Sopeña, A., Sánchez-Moya, Y., Machado, M. J., & Pérez-González, A.. 2003. Palaeoflood record of the Tagus River (central Spain) during the Late Pleistocene and Holocene. Quaternary Sci Rev 22 (15), 1737-1756.

Benito Garzón, M., Sánchez de Dios, R., Sainz Ollero, H., 2008. Effects of climate change on the distribution of Iberian tree species. Appl Veg Sci 11 (2), 169-178.

Biondi, F., Qeadan, F., 2008. A theory-driven approach to tree-ring standardization: defining the biological trend from expected basal area increment. Tree-Ring Res 64 (2), 81-96.

Bravo-Oviedo, A., & Montero, G., 2005. Site index in relation to edaphic variables in stone pine (Pinus pinea L.) stands in south west Spain. Ann For Sci 62 (1), 61-72.

Briffa, K., Jones, P.D., 1990. Basic chronology statistics and assessment. In: Cook, E.R., Kairiukstis, L.A. (Eds.), Methods of dendrochronology: applications in the environmental sciences. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 137-152.

Büntgen, U., Egli, S., Galván, J. D., Diez, J. M., Aldea, J., Latorre, J., Martínez-Peña, F., 2015a. Drought-induced changes in the phenology, productivity and diversity of Spanish fungi. Fungal Ecol 16, 6-18.

Büntgen, U., Trnka, M., Krusic, P. J., Kyncl, T., Kyncl, J., Luterbacher, J. et al., 2015b. Tree-Ring Amplification of the Early Nineteenth-Century Summer Cooling in Central Europe. J Climate 28 (13), 5272-5288.

Büntgen, U., Martínez-Peña, F., Aldea, J., Rigling, A., Fischer, E. M., Camarero, J. J., Hayes, M.J., Fatton, V., Egli, S., 2013. Declining pine growth in Central Spain coincides with increasing diurnal temperature range since the 1970s. Global Planet Change 107, 177-185.

Büntgen, U., Kaczka, R.J., Trnka, M., Rigling, A., 2012. Ensemble estimates reveal a complex hydroclimatic sensitivity of pine growth at Carpathian cliff sites. Agr Forest Meteorol 160, 100-109.

Büntgen, U., Frank, D. C., Kaczka, R. J., Verstege, A., Zwijacz-Kozica, T., Esper, J., 2007. Growth responses to climate in a multi-species tree-ring network in the Western Carpathian Tatra Mountains, Poland and Slovakia. Tree Physiol 27 (5), 689-702.

Campelo. F., Nabais, C., Freitas, H., Gutiérrez, E., 2006. Climatic significance of tree ring width and intra-annual density fluctuations in Pinus pinea from a dry Mediterranean area in Portugal. Ann For Sci 64, 229–238.

Carnicer, J., Coll, M., Ninyerola, M., Pons, X., Sánchez, G., Peñuelas, J., 2011. Widespread crown condition decline, food web disruption, and amplified tree mortality with increased climate change-type drought. P Natl Acad Sci USA 108(4), 1474-1478.

Carrer, M., Urbinati, C., 2006. Long-term change in the sensitivity of tree-ring growth to climate forcing in Larix deciduas. New Phytol 170(4), 861-872.

Cherubini, P., Gartner, B. L., Tognetti, R., Braker, O. U., Schoch, W., Innes, J. L., 2003. Identification, measurement and interpretation of tree rings in woody species from Mediterranean climates. Biol Rev 78 (01), 119-148.

Cook, E.R., Briffa, K.R., Shiyatov, S., Mazepa, V., 1990a. Tree-ring standardization and growth-trend estimation. In: Cook, E.R., Kairiukstis, L.A. (Eds.) Methods of dendrochronology: applications in the environmental sciences. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 104-123

Cook, E.R., Shiyatov, S., Mazepa, V., 1990b. Estimation of the Mean Chronology. In: Cook, E.R., Kairiukstis, L.A. (Eds.), Methods of dendrochronology: applications in the environmental sciences. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 123-132

Cook, E. R., Seager, R., Kushnir, Y., Briffa, K. R., Büntgen, U., Frank, D. et al., 2015. Old World megadroughts and pluvials during the Common Era. Science Advances 1(10), e1500561, DOI: 10.1126/sciadv.1500561

de Luis, M., Cufar, K., Di Filippo, A., Novak, K., Papadopoulos, A., Piovesan, G., Rathgeber C.B.K., Raventos, J., Saz, M.A., Smith K.Y., 2013. Plasticity in dendroclimatic response across the distribution range of Aleppo pine (Pinus halepensis). Plos One 8 (12), e83550, DOI:10.1371/journal.pone.0083550

de Luis, M., Novak, K., Čufar, K., Raventós, J., 2009. Size mediated climate–growth relationships in Pinus halepensis and Pinus pinea. Trees-Struct Funct 23 (5), 1065-1073.

de Luis, M., Novak, K., Raventós, J., Gričar, J., Prislan, P., Čufar, K., 2011. Cambial activity, wood formation and sapling survival of Pinus halepensis exposed to different irrigation regimes. Forest Ecol Manag 262 (8), 1630-1638.

Dessens, J., Bücher, A., 1997. A critical examination of the precipitation records at the Pic du Midi observatory, Pyrenees, France. In: Diaz, H.F., Beniston, M., Bradley, R.S. (Eds.) Climatic Change at High Elevation Sites. Springer, pp. 113-121

Dorado Liñán, I. D., Büntgen, U., González-Rouco, F., Zorita, E., Montávez, J. P., Gómez-Navarro, J. J., Brunet, M., Heinrich, I., Helle, G., Gutiérrez, E., 2012. Estimating 750 years of temperature variations and uncertainties in the Pyrenees by tree ring reconstructions and climate simulations. Clim Past 8 (3), 919-933.

Esper, J., Cook, E. R., Schweingruber, F. H., 2002. Low-frequency signals in long tree-ring chronologies or reconstructing past temperature variability. Science 295 (5563), 2250-2253

Fallour, D., Fady, B., Lefevre, F., 1997. Study on isozyme variation in Pinus pinea L.: evidence for low polymorphism. Silvae Genetica 46 (4), 201-206.

Frank, D., Büntgen, U., Böhm, R., Maugeri, M., Esper, J., 2007. Warmer early instrumental measurements versus colder reconstructed temperatures: shooting at a moving target. Quaternary Sci Rev 26 (25), 3298-3310.

Galván, J. D., Camarero, J. J., Ginzler, C., Büntgen, U., 2014. Spatial diversity of recent trends in Mediterranean tree growth. Environ Res Lett 9 (8), 084001

Gea-Izquierdo, G., Cherubini, P., Cañellas, I., 2011. Tree-rings reflect the impact of climate change on Quercus ilex L. along a temperature gradient in Spain over the last 100years. Forest Ecol Manag 262 (9), 1807-1816.

Gimeno, T. E., Camarero, J. J., Granda, E., Pías, B., Valladares, F., 2012. Enhanced growth of Juniperus thurifera under a warmer climate is explained by a positive carbon gain under cold and drought. Tree Physiol 32 (3), 326-336

Giorgi, F., 2006. Climate change hot-spots. Geophys Res Lett 33 (8).

Grissino-Mayer, H.D., 2001. Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. Tree-Ring Bull 57, 205–221

Harris, I., Jones, P.D., 2014. CRU TS3.22: Climatic Research Unit (CRU) Time-Series (TS) Version 3.22 of High Resolution Gridded Data of Month-by-month Variation in Climate (Jan. 1901- Dec. 2013). NCAS British Atmospheric Data Centre, 24 September 2014. DOI:10.5285/18BE23F8-D252-482D-8AF9-5D6A2D40990C

Haylock, M.R., Hofstra, H., Klein Tank, A.M.G., Klok, E.J., Jones, P.D., New, M., 2008. A European daily high-resolution gridded dataset of surface temperature and precipitation for 1950-2006. J Geophys Res - Atmos 113, D20119, DOI:10.1029/2008JD10201

Helama, S., Lindholm, M., Timonen, M., Eronen, M., 2004. Detection of climate signal in dendrochronological data analysis: a comparison of tree-ring standardization methods. Theor Appl Climatol 79 (3-4), 239-254.

Hódar, J. A., Castro, J., Zamora, R., 2003. Pine processionary caterpillar Thaumetopoea pityocampa as a new threat for relict Mediterranean Scots pine forests under climatic warming. Biol Conserv 110 (1), 123-129.

Jump, A. S., Hunt, J. M., Penuelas, J., 2006. Rapid climate change-related growth decline at the southern range edge of Fagus sylvatica. Glob Change Biol 12 (11), 2163-2174.

Karl, T. R., Knight, R. W., Gallo, K. P., Peterson, T. C., Jones, P. D., Kukla, G. et al., 1993. A new perspective on recent global warming: asymmetric trends of daily maximum and minimum temperature. B Am Meteorol Soc 74 (6), 1007-1023.

Klok, E.J., Klein Tank, A.M.G., 2008. Updated and extended European dataset of daily climate observations. Int J Climatol 29, 1182–1191

Kovats, R.S., Valentini, R., Bouwer, L.M., Georgopoulou, E., Jacob, D., Martin, E., Rounsevell, M., Soussana, J.F., 2014. Europe. In: Barros, V.R., Field, C.B., Dokken, D.J., Mastrandrea, M.D., Mach, K.J., Bilir, T.E., Chatterjee, M.E., Ebi K.L., Estrada, Y.O., Genova, R.C., Girma, G., Kissel, E.S., Levy, A.N., MacCracken, S., Mastrandrea, P.R., White, L.L. (Eds.) Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, pp 1267–1326

Latte, N., Lebourgeois, F., Claessens, H., 2015. Increased tree-growth synchronization of beech (Fagus sylvatica L.) in response to climate change in northwestern Europe. Dendrochronologia 33, 69-77.

Luz, A.L., Pereira, H., Lauw, A. and Leal, S., 2014. Monitoring intra-annual cambial activity based on the periodic collection of twigs–A feasibility study. Dendrochronologia 32 (2),162-170.

Martin-Benito, D., Beeckman, H., Canellas, I., 2013. Influence of drought on tree rings and tracheid features of Pinus nigra and Pinus sylvestris in a mesic Mediterranean forest. European J For Res 132 (1), 33-45.

Martín-Benito, D., Del Río, M., Cañellas, I., 2010. Black pine (Pinus nigra Arn.) growth divergence along a latitudinal gradient in Western Mediterranean mountains. Ann For Sci 67 (4), 401.

Martínez, F., Montero, G., 2004. The Pinus pinea L. woodlands along the coast of South-western Spain: data for a new geobotanical interpretation. Plant Ecology 175 (1), 1-18.

Mazza, G., Cutini, A., Manetti, M. C., 2014. Site-specific growth responses to climate drivers of Pinus pinea L. tree rings in Italian coastal stands. Ann For Sci 71 (8), 927-936.

Meyers, L. A., Bull, J. J., 2002. Fighting change with change: adaptive variation in an uncertain world. Trends Ecol Evol 17 (12), 551-557.

Montero González, G., Candela Plaza, J.A., Rodríguez Navarro, A. (Eds.), 2004. El pino piñonero en Andalucía: ecología distribución y selvicultura. Dirección General de Gestión del Medio Natural, Consejería de Medio Ambiente, Junta de Andalucía, Sevilla, http://www.juntadeandalucia.es/medioambiente/consolidado/publicacionesdigitales/80-409_EL_PINO_PINHONERO_EN_ANDALUCIA/80-409.htm?lr=lang_es

Mutke, S., Gordo, J., Khouja, M.L., Fady, B., 2013. Low genetic and high environmental diversity at adaptive traits in Pinus pinea from provenance tests in France and Spain. In : Mutke, S., Piqué, M. , Calama, R. (Eds.) Mediterranean stone pine for agroforestry. Zaragoza: CIHEAM / FAO / INIA / IRTA / CESEFOR / CTFC, pp. 73-79. (Options Méditerranéennes: Série A. Séminaires Méditerranéens; n. 105). AGROPINE 2011 International Meeting on Mediterranean Stone Pine for Agroforestery, 2011/11/17-19, Valladolid (Spain), http://om.ciheam.org/om/pdf/a105/00006784.pdf

Mutke, S., Gordo, J., Chambel, M. R., Prada, M. A., Álvarez, D., Iglesias, S., Gil, L., 2010. Phenotypic plasticity is stronger than adaptative differentiation among Mediterranean stone pine provenances. Forest Systems 19 (3), 354-366.

Natalini, F., Correia, A. C., Vázquez-Piqué, J., Alejano, R., 2015. Tree rings reflect growth adjustments and enhanced synchrony among sites in Iberian stone pine (Pinus pinea L.) under climate change. Ann For Sci 72 (8), 1023-1033, DOI: 10.1007/s13595-015-0521-6

Natalini, F., Alejano, R., Vázquez-Piqué, J., Cañellas, I., & Gea-Izquierdo, G., 2016. The role of climate change in the widespread mortality of holm oak in open woodlands of Southwestern Spain. Dendrochronologia 38, 51-60, DOI: 10.1016/j.dendro.2016.03.003.

Nicault, A., Alleaume, S., Brewer, S., Carrer, M., Nola, P., Guiot, J., 2008. Mediterranean drought fluctuation during the last 500 years based on tree-ring data. Clim Dynam 31 (2-3), 227-245.

Nicotra, A. B., Atkin, O. K., Bonser, S. P., Davidson, A. M., Finnegan, E. J., Mathesius, U., Poot , P., Purugganan, M.D., Richards, C.L., Valladares, F., and van Kleunen, M., 2010. Plant phenotypic plasticity in a changing climate. Trends Plant Sci 15 (12), 684-692.

Olano, J. M., Eugenio, M., García-Cervigón, A. I., Folch, M., & Rozas, V., 2012. Quantitative tracheid anatomy reveals a complex environmental control of wood structure in continental Mediterranean climate. Int J Plant Sci 173 (2), 137-149

Pardos, M., Calama, R., Maroschek, M., Rammer, W., Lexer, M. J., 2015. A model-based analysis of climate change vulnerability of Pinus pinea stands under multiobjective management in the Northern Plateau of Spain. Ann For Sci 72 (8), 1009-1021.

Pardos, M., Puértolas, J., Madrigal, G., Garriga, E., de Blas, S., Calama, R., 2010. Seasonal changes in the physiological activity of regeneration under a natural light gradient in a Pinus pinea regular stand. Forest Systems, 19 (3), 367-380.

Pausas, J. G., 2004. Changes in fire and climate in the eastern Iberian Peninsula (Mediterranean basin). Climatic Change 63 (3), 337-350.

Peñuelas, J., Filella, I., Comas, P., 2002. Changed plant and animal life cycles from 1952 to 2000 in the Mediterranean region. Glob Change Biol 8 (6), 531-544.

Pérez, F.F., Boscolo, R. (Eds.), 2010. Climate in Spain: past, present and future. Regional climate change assessment report. CLIVAR: Ministerio de Medio Ambiente y Medio Rural y Marino : Ministerio de Ciencia e Innovacion. 83 pp., http://digital.csic.es/handle/10261/33470

Pinzauti, F., Sebastiani, F., Budde, K. B., Fady, B., González-Martínez, S. C., Vendramin, G. G., 2012. Nuclear microsatellites for Pinus pinea (Pinaceae), a genetically depauperate tree, and their transferability to P. halepensis. Am J Bot e362–e365, DOI: 10.3732/ajb.1200064

Piovesan, G., Di Filippo, A., Alessandrini, A., Biondi, F., Schirone, B., 2005. Structure, dynamics and dendroecology of an old-growth Fagus forest in the Apennines. J Veg Sci 16 (1), 13-28.

Prieto, L., Herrera, R. G., Díaz, J., Hernández, E., del Teso, T., 2004. Minimum extreme temperatures over Peninsular Spain. Global Planet Change 44 (1), 59-71.

Rivas-Martínez, S., 2007. Mapa de series, geoseries y geopermaseries de vegetación de España. Itinera Geobotanica 17, 5-436

Rodriguez-Puebla, C., Encinas, A. H., Nieto, S., & Garmendia, J., 1998. Spatial and temporal patterns of annual precipitation variability over the Iberian Peninsula. Int J Climatol 18 (3), 299-316.

Romero, R., Sumner, G., Ramis, C., Genovés, A., 1999. A classification of the atmospheric circulation patterns producing significant daily rainfall in the Spanish Mediterranean area. Int J Climatol 19(7), 765-785.

Rossi, S., Morin, H., Deslauriers, A., Plourde, P. Y., 2011. Predicting xylem phenology in black spruce under climate warming. Glob Change Biol 17 (1), 614-625.

Sáez-Laguna, E., Guevara, M. Á., Díaz, L. M., Sánchez-Gómez, D., Collada, C., Aranda, I., Cervera, M. T., 2014. Epigenetic variability in the genetically uniform forest tree species Pinus pinea L. Plos One, DOI: 10.1371/journal.pone.0103145

Sánchez-Gómez, D., Velasco-Conde, T., Cano-Martín, F. J., Guevara, M. Á., Cervera, M. T., Aranda, I., 2011. Inter-clonal variation in functional traits in response to drought for a genetically homogeneous Mediterranean conifer. Environ Exp Bot 70 (2), 104-109.

Scheffran, J., Battaglini, A., 2011. Climate and conflicts: the security risks of global warming. Reg Environ Change 11 (1), 27-39.

Schweingruber FH, Kairiukstis L, Shiyatov S., 1990. Sample selection. In: Cook, E.R., Kairiukstis, L.A. (Eds.) Methods of dendrochronology: applications in the environmental sciences. Kluwer Academic Publishers Dordrecht, The Netherlands, pp. 23-35

Seim, A., Treydte, K., Trouet, V., Frank, D., Fonti, P., Tegel, W., Panayotov, M., Fernández-Donado, L., Krusic, P. and Büntgen, U., 2014. Climate sensitivity of Mediterranean pine growth reveals distinct east–west dipole. Int J Climatol 35 (9), 2503-2513, DOI: 10.1002/joc.4137

Soto, A., Robledo-Arnuncio J. J., Gpnzález-Martínez S. C.,, Smouse, P. E., Alia, R., 2010. Climatic niche and neutral genetic diversity of the six Iberian pine species: a retrospective and prospective view. Mol Ecol 19 (7), 1396-1409.

Speer, J., 2010. Fundamentals of tree-ring research. The University of Arizona Press, Tucson

Tardif, J., Camarero, J. J., Ribas, M., Gutiérrez, E., 2003. Spatiotemporal variability in tree growth in the Central Pyrenees: climatic and site influences. Ecol Monogr 73 (2), 241-257.

van der Schrier, G., Briffa, K.R., Jones, P.D., Osborn, T.J., 2006a. Summer moisture variability across Europe. J Climate 19, 2818-2834, DOI:10.1175/JCLI3734.1

Vendramin, G.G., Fady, B., González-Martínez, S.C., Hu, F.S., Scotti, I., Sebastiani, F., Soto, Á. Petit, R.J.,, 2008. Genetically depauperate but widespread: the case of an emblematic Mediterranean pine. Evolution 62 (3), pp.680-688.

Vicente Serrano, S. M., González-Hidalgo, J. C., Luis, M. D., Raventós, J., 2004. Drought patterns in the Mediterranean area: the Valencia region (eastern Spain). Clim Res 26 (1), 5-15.

Vieira, J., Rossi, S., Campelo, F., Freitas, H., Nabais, C., 2014. Xylogenesis of Pinus pinaster under a Mediterranean climate. Ann For Sci 71 (1), 71-80.

Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J., Fromentin, J.M., Hoegh-Guldberg, O. and Bairlein, F., 2002. Ecological responses to recent climate change. Nature 416 (6879), pp.389-395

Zang, C., Biondi, F., 2015. treeclim: an R package for the numerical calibration of proxy-climate relationships. Ecography 38 (4), 431-436.

Tables

Table 1. Site locations and stand characteristics.

	Carrascal	**Viana de Cega**	**Hoyo de Pinares**	**Valverde del Camino**	**Hinojos**
Latitude [°N]	41.59	41.47	40.51	37.53	37.28
Longitude [°W]	4.33	4.72	4.38	6.78	6.39
Elevation [m a.s.l.]	880	710	890	260	80
Soils (FAO classification)	Cambisols	Arenosols	Leptosols	Luvisols	Cambisols/Regosols
Slope [%]	0	0	50-60	0	0
Species composition	Mixed (*P. pinea-Quercus ilex-Juniperus thurifera*)	Pure (*P. pinea*)	Pure (*P. pinea*)	Pure (*P. pinea*)	Pure (*P. pinea*)
Mean tree height [m]	10	17	19	18	18
Mean tree diameter [cm]	45	50	75	65	70

Table 2. Characteristics of tree ring chronologies at the different sites. Chronology length refers to the longest cross-dated individual tree series in each site. A chronology length with "≥10 trees" refers to the interval with a minimum of 10 cross-dated individual tree series. The mean growth rate refers to the average ring width over each chronology. Standard chronology refers to the mean ring index chronology calculated as ratios and detrended with a negative exponential curve (NEXP), or cubic smoothing splines with 50% frequency-response cutoffs at 30 years (SP30). EPS>0.85 indicates the period covered by the chronologies with an Expressed Population Signal greater than 0.85.

			Carrascal	**Viana de Cega**	**Hoyo de Pinares**	**Valverde del Camino**	**Hinojos**
No. of trees			22	26	19	20	19
Chronology length (years)			1921-2014 (94)	1871-2014 (144)	1787-2014 (228)	1873-2011 (139)	1863-2012 (150)
Chronology length with ≥10 trees (years)			1931-2014 (84)	1877-2014 (138)	1844-2014 (171)	1888-2011 (124)	1874-2012 (139)
Mean series length (years)			77	130	172	120	127
Mean growth rate (mm)			2.28	1.52	1.74	2.08	2.04
1st order autocorrelation	Raw ring width series		0.616	0.867	0.609	0.844	0.765
	Standard chronologies	NEXP	0.203	0.638	0.541	0.600	0.673
		SP30	0.070	0.268	0.311	0.444	0.259
EPS>0.85			1925-2014	1873-2014	1842-2014	1881-2011	1866-2012

Table 3. Correlation coefficients between sites using the mean standard chronologies after detrending with a negative exponential curve (NEXP), or cubic smoothing splines with 50% frequency-response cutoffs at 30 years (SP30). Correlations were calculated over the common interval with at least 10 trees (1931-2011).

(NEXP)	Carrascal	Viana de Cega	Hoyo de Pinares	Valverde del Camino
Viana de Cega	0.45			
Hoyo de Pinares	0.24	0.35		
Valverde del Camino	0.48	0.29	0.13	
Hinojos	0.21	0.14	0.14	0.26

(SP30)	Carrascal	Viana de Cega	Hoyo de Pinares	Valverde del Camino
Viana de Cega	0.63			
Hoyo de Pinares	0.38	0.41		
Valverde del Camino	0.47	0.52	0.40	
Hinojos	0.38	0.47	0.23	0.66

Figures

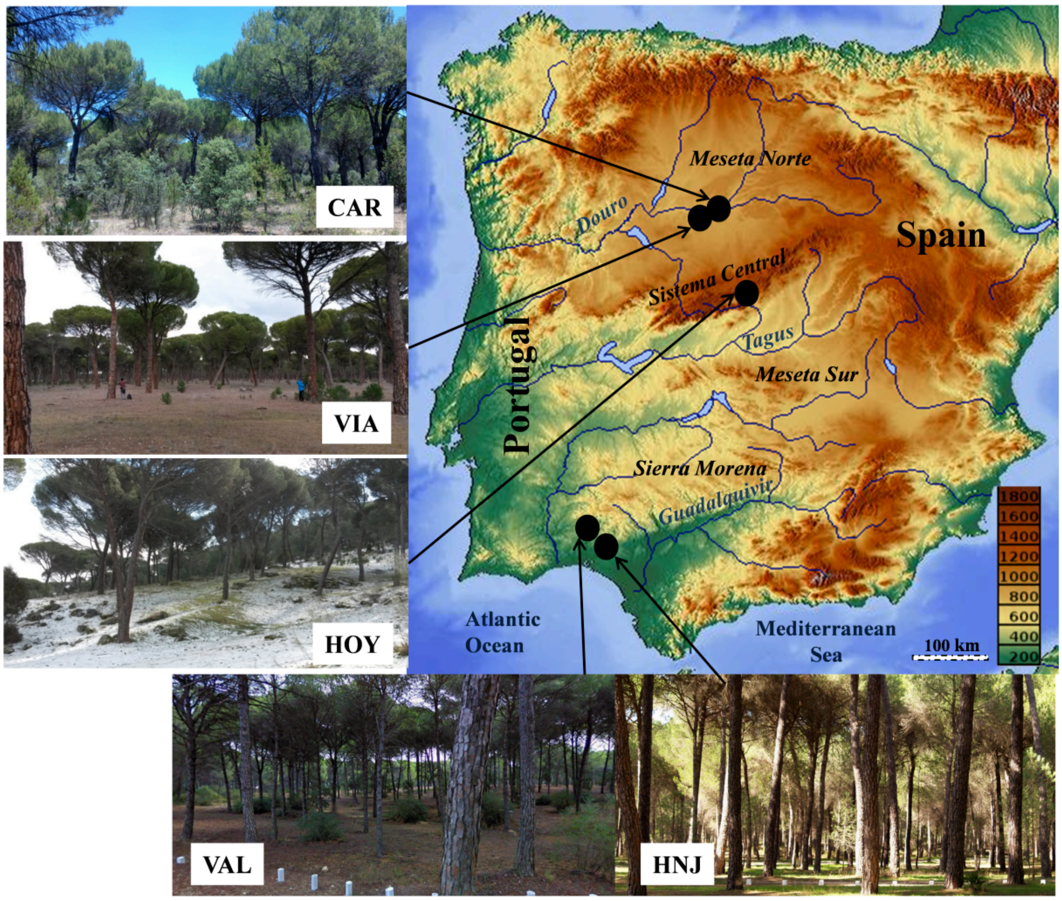


Figure 1. Locations of the study sites.

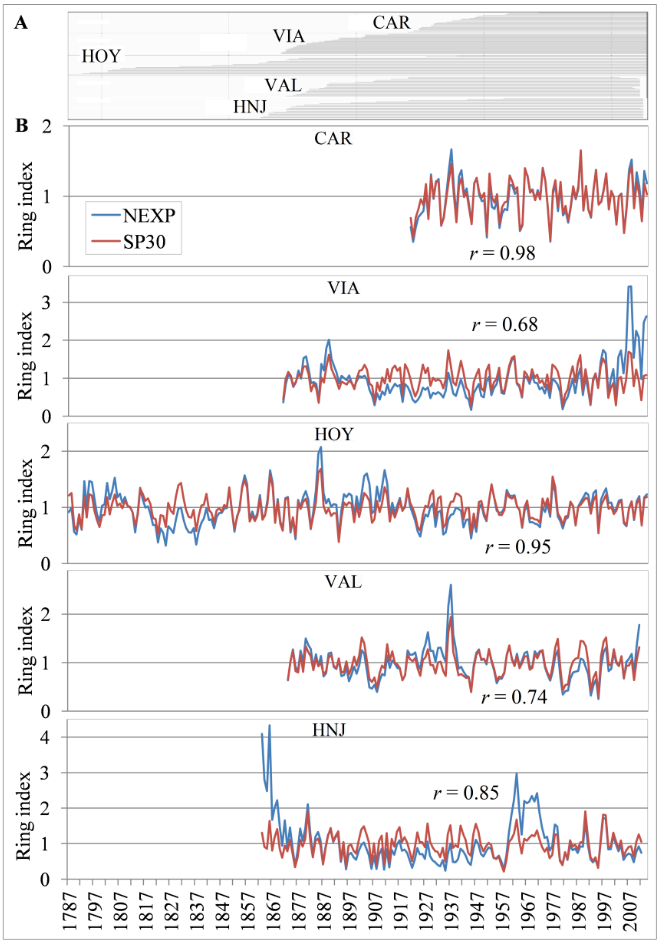


Figure 2. (A) Chronology replication in each site and (B) standard chronologies detrended with a negative exponential curve (NEXP), or with cubic smoothing splines with 50% frequency-response cutoffs at 30 years (SP30). Note the different scales of the abscissa in B. The r is the Pearson correlation coefficient between the NEXP and the SP30 chronologies in each site.

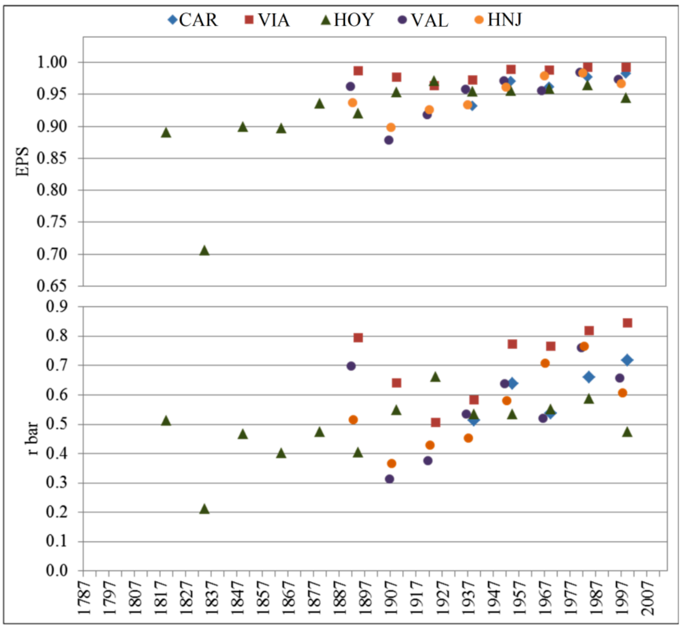


Figure 3. Expressed population signal (EPS) and inter-series correlations (r bar) computed for each site using 30-year windows lagged by 15 years along the mean ring-width chronologies.

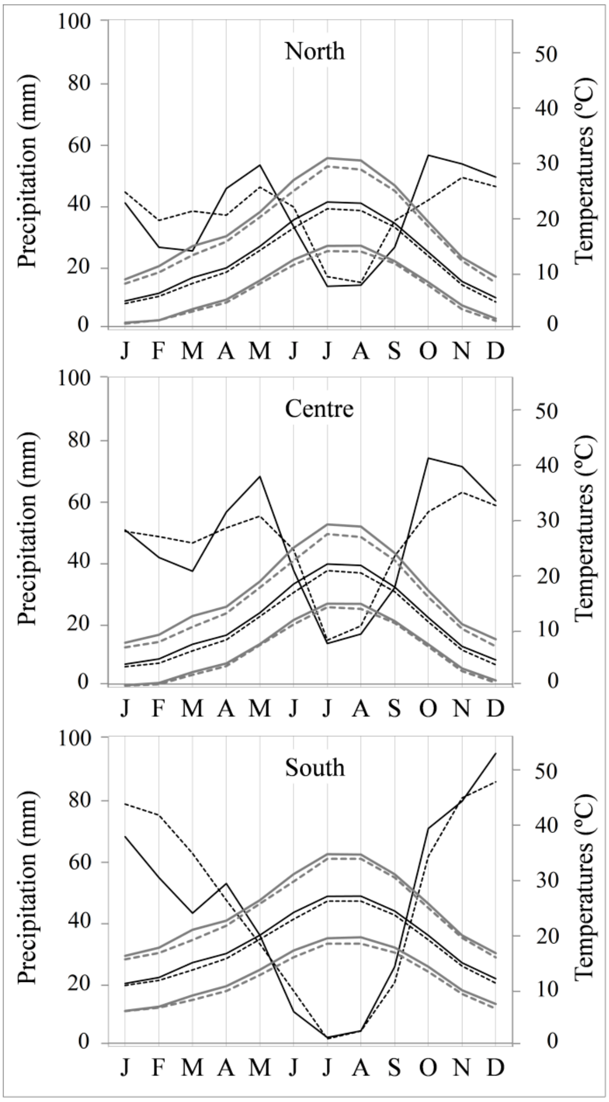


Figure 4. Climate diagrams of the north, center and south during the “early” period (1950-1980, dotted lines) and “late” period (1981-2011, solid lines). For temperature, the upper grey lines, the middle black lines, and the lower grey lines denote the average of the maximum, mean, and minimum, respectively. Temperature and precipitation values were calculated per year by averaging the climate data of two sites in the north (CAR and VIA), one site in the center (HOY), and two sites in the south (VAL and HNJ) using the gridded data (E-OBS and CRU).

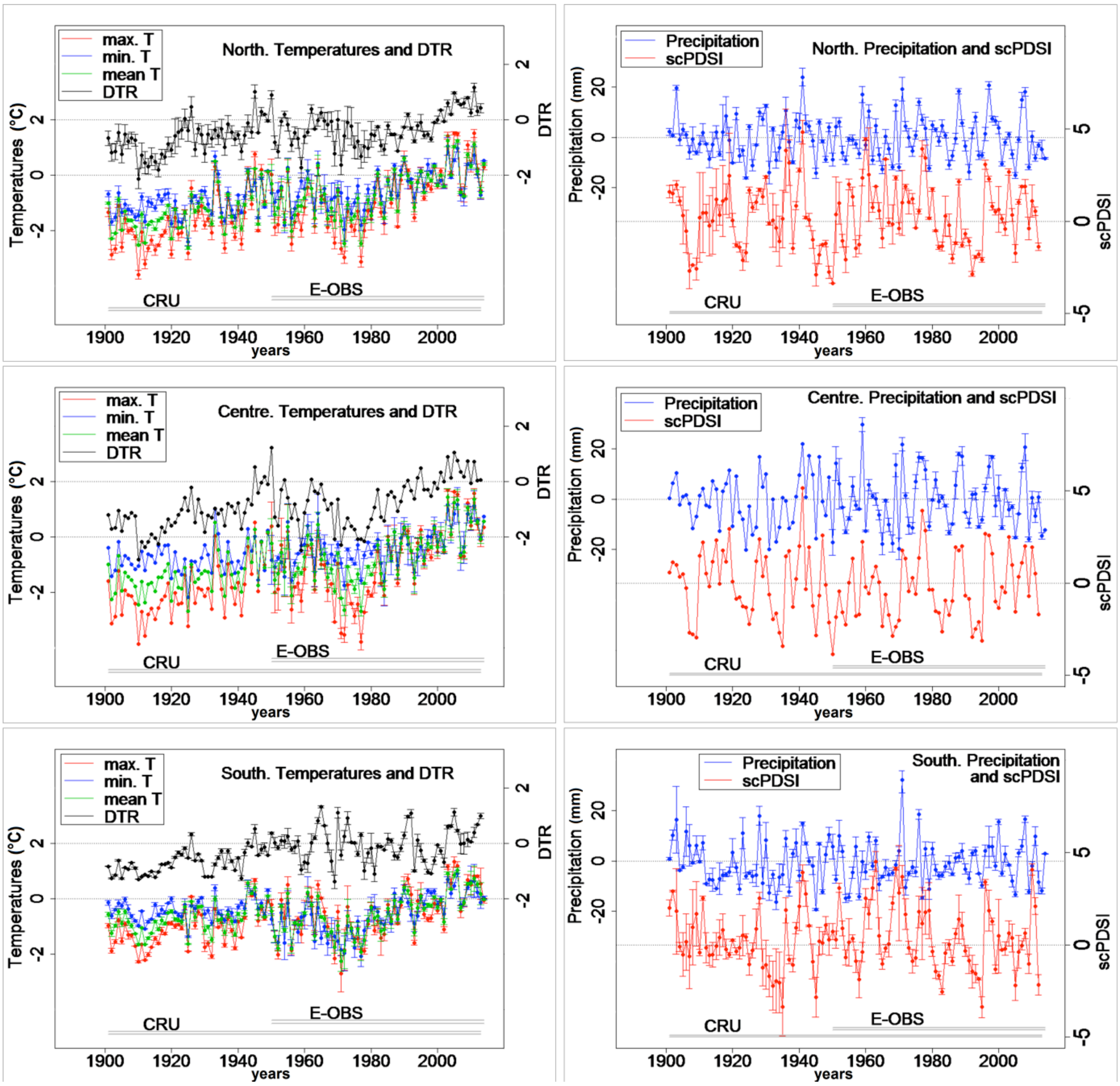


Figure 5. Departures from the 1982-2011 average of AMJJAS precipitation, maximum/minimum/mean temperature, scPDSI, and DTR in the north, center and south. AMJJAS values were calculated per year by averaging the climate data of two sites in the north (CAR and VIA), one site in the center (HOY), and two sites in the south (VAL and HNJ) using the gridded data (E-OBS and CRU for precipitation and temperatures; CRU for scPDSI and DTR). Error bars are standard deviations of the AMJJAS yearly means. Horizontal grey lines at the bottom of each figure indicate the time span covered by each AMJJAS series for each data source.

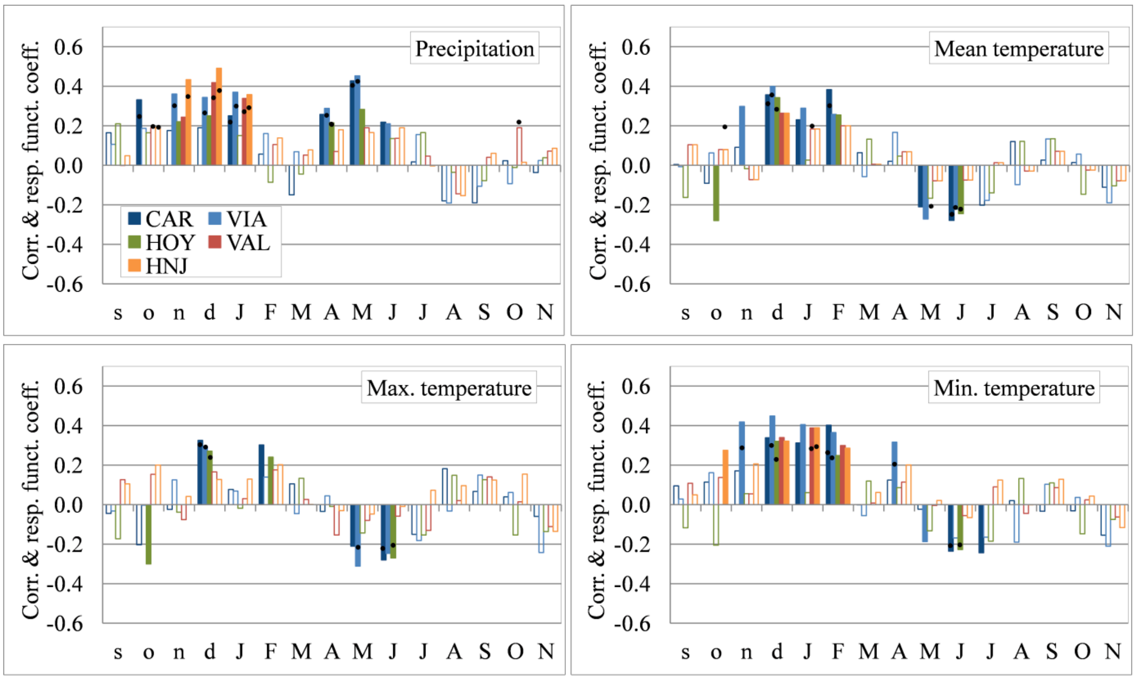


Figure 6. Bootstrapped correlations (bars) and response functions (dots) between the SP30-detrended standard chronologies of each site and monthly values (from previous September to current November) of climate variables (sums of precipitation, averages of maximum/minimum/mean temperatures) from 1950 to 2011. Precipitation and temperature data were calculated as averages of gridded climate data (E-OBS and CRU). Full bars indicate statistically significant correlations (α = 0.05). For response functions, only significant values (α = 0.05) are showed.

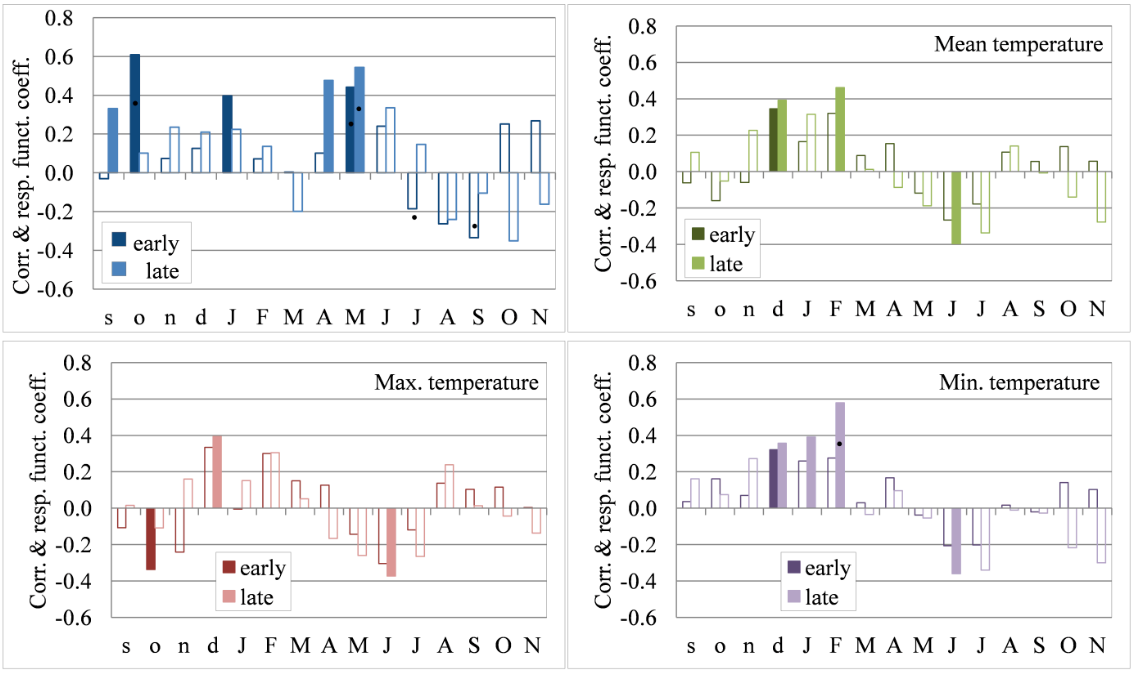


Figure 7. Bootstrapped correlations (bars) and response functions (dots) in CAR between SP30 chronology and climate variables (sums of precipitation, averages of maximum/minimum/mean temperatures) during the "early" (1950-1980) and "late" (1981-2011) periods. Precipitation and temperature data were calculated as averages of gridded climate data (E-OBS and CRU). Full bars indicate statistically significant correlations (α = 0.05). For response functions, only significant values (α = 0.05) are showed.

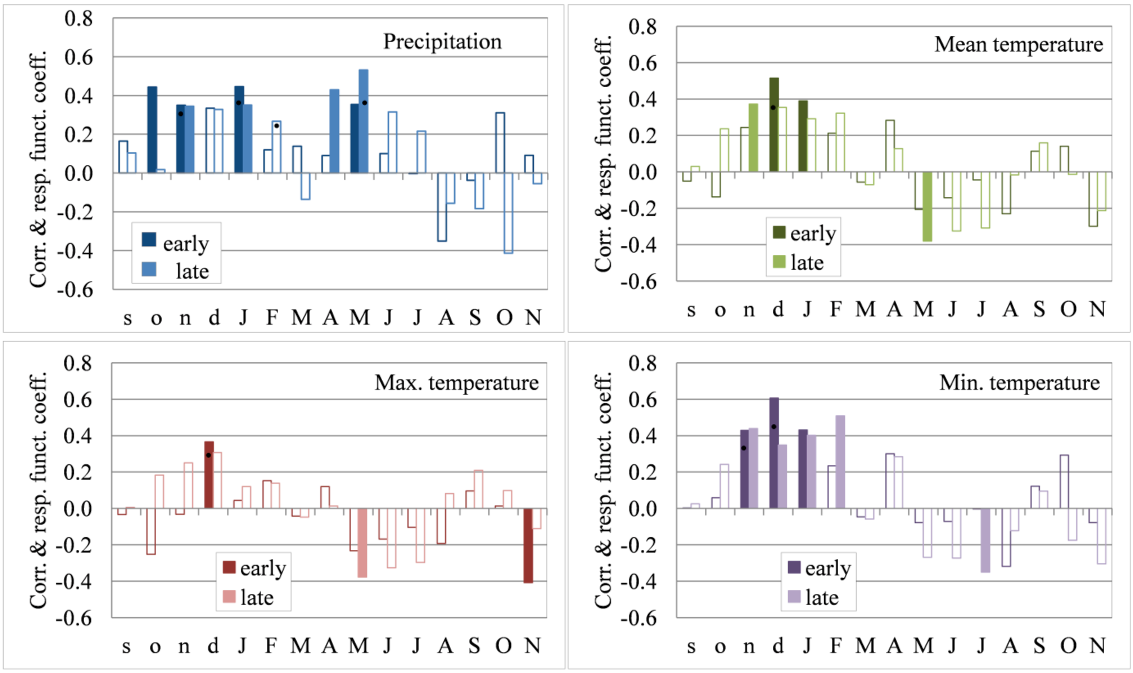


Figure 8. Bootstrapped correlations (bars) and response functions (dots) in VIA between SP30 chronology and climate variables (sums of precipitation, averages of maximum/minimum/mean temperatures) during the "early" (1950-1980) and "late" (1981-2011) periods. Precipitation and temperature data were calculated as averages of gridded climate data (E-OBS and CRU). Full bars indicate statistically significant correlations (α = 0.05). For response functions, only significant values (α = 0.05) are showed.

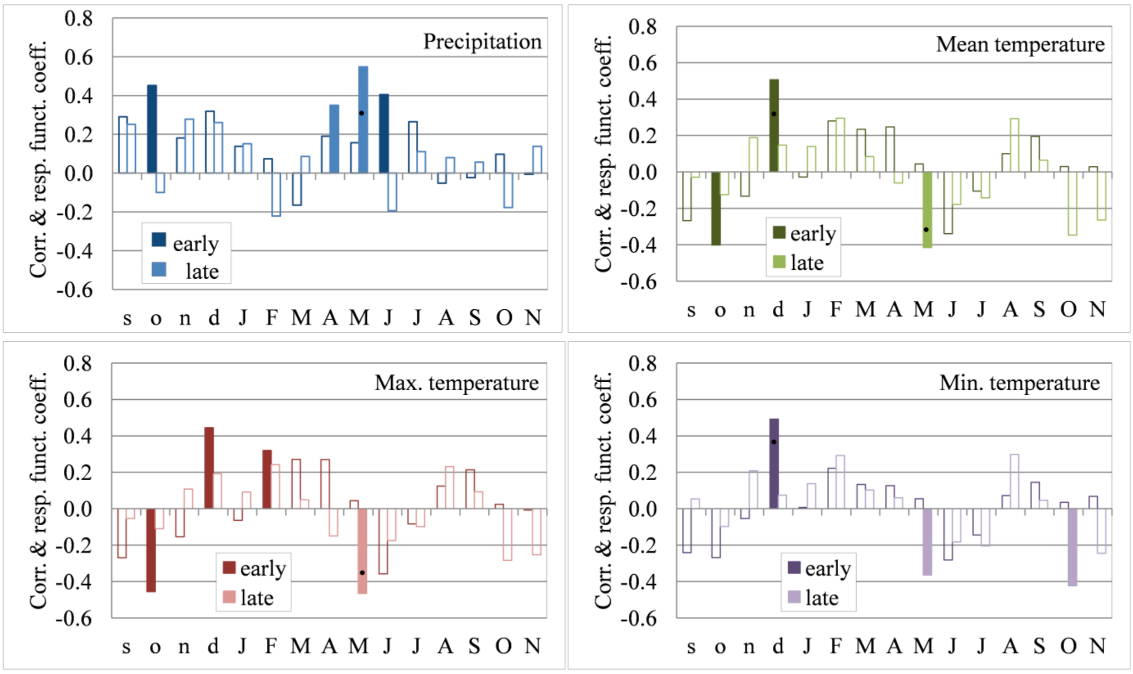


Figure 9. Bootstrapped correlations (bars) and response functions (dots) in HOY between SP30 chronology and climate variables (sums of precipitation, averages of maximum/minimum/mean temperatures) during the "early" (1950-1980) and "late" (1981-2011) periods. Precipitation and temperature data were calculated as averages of gridded climate data (E-OBS and CRU). Full bars indicate statistically significant correlations (α = 0.05). For response functions, only significant values (α = 0.05) are showed.

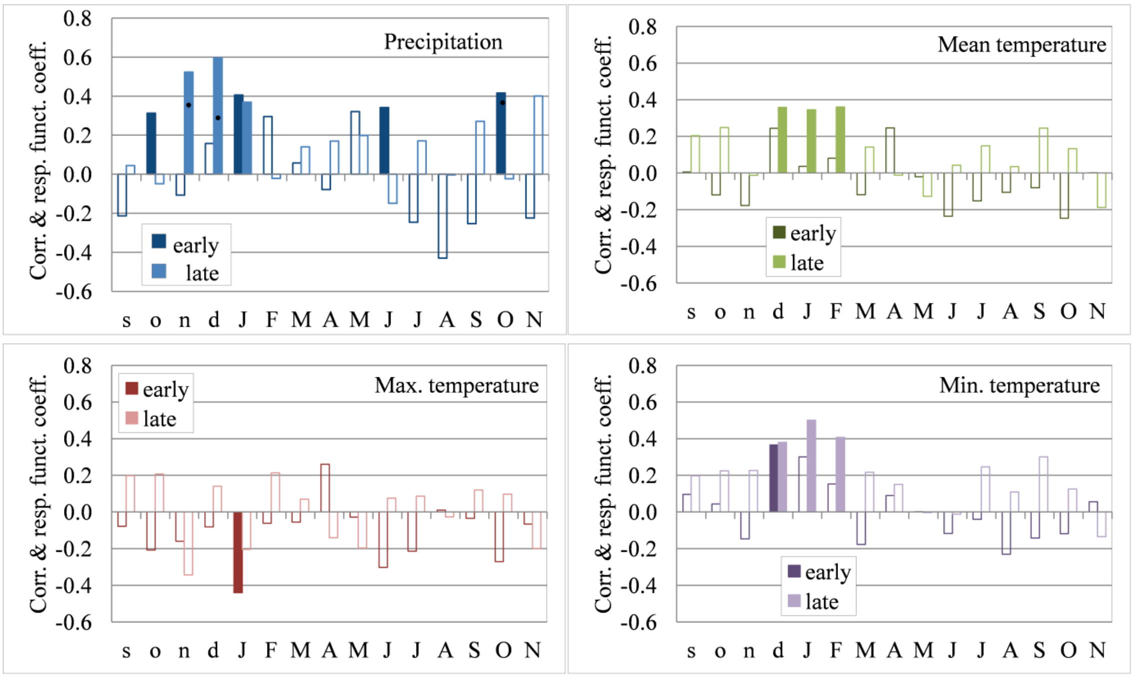


Figure 10. Bootstrapped correlations (bars) and response functions (dots) in VAL between SP30 chronology and climate variables (sums of precipitation, averages of maximum/minimum/mean temperatures) during the "early" (1950-1980) and "late" (1981-2011) periods. Precipitation and temperature data were calculated as averages of gridded climate data (E-OBS and CRU). Full bars indicate statistically significant correlations (α = 0.05). For response functions, only significant values (α = 0.05) are showed.

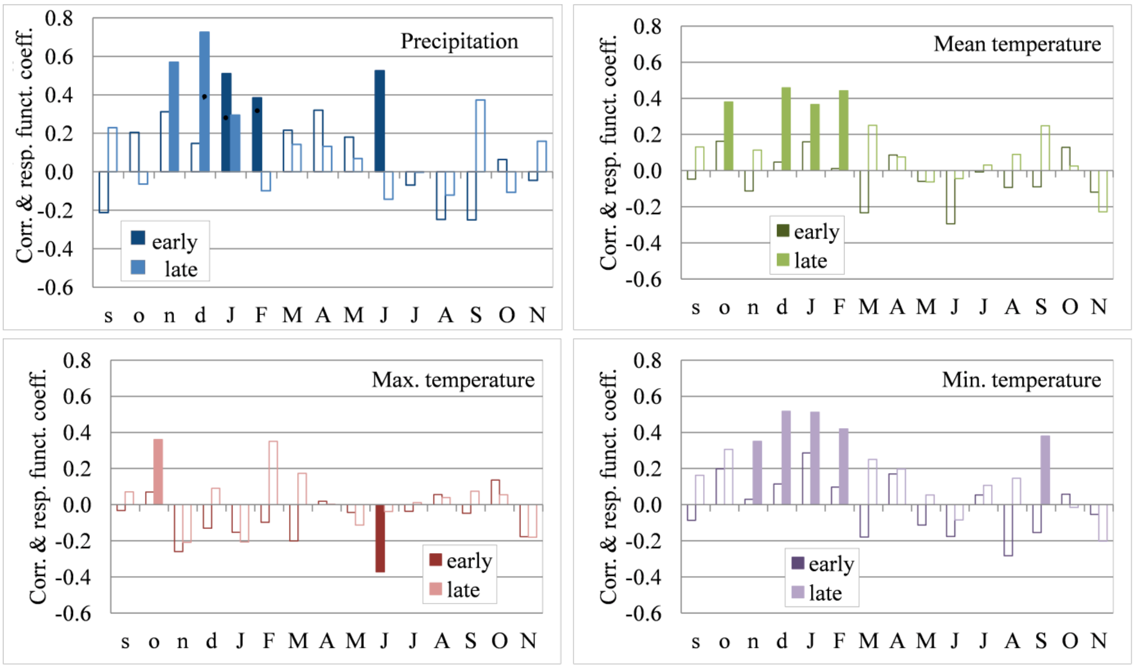


Figure 11. Bootstrapped correlations (bars) and response functions (dots) in HNJ between SP30 chronology and climate variables (sums of precipitation, averages of maximum/minimum/mean temperatures) during the "early" (1950-1980) and "late" (1981-2011) periods. Precipitation and temperature data were calculated as averages of gridded climate data (E-OBS and CRU). Full bars indicate statistically significant correlations (α = 0.05). For response functions, only significant values (α = 0.05) are showed.

Supplementary material of the Article 3

Meteorological station data

The ECA&D includes “non-blended” (raw observations from meteorological stations) and “blended” (homogenized by infilling gaps with observations from nearby stations) series of daily meteorological station records (see http://eca.knmi.nl/FAQ/) . We searched for the closest station to each site including “non-blended” and “blended” series. We found two stations for CAR and VIA (namely “Valladolid” and “Valladolid-Villanubla”), two stations for HOY (“Ávila” and “Ávila-ayuntamiento”) and two stations for VAL and HNJ (“Huelva” and “Huelva- Ronda-Este”). The stations of each pair in Huelva and Ávila were very close between them (distance < 5 km, difference in altitude ≤ 10 m), covered the same time span and presented no difference in the climate series (correlation coefficient = 0.99), so we only used the “Ávila” and “Huelva” stations. The two stations in Valladolid were 10 km apart, had a difference in altitude of 100 m and covered different time spans, but they showed no differences (correlations = 0.99) in the common period; therefore, we only used the “Valladolid-Villanubla” station, which covers the longest period. Temperature data in pure and blended “Ávila” series were missing in 1982 and were estimated through a simple linear regression analysis. The pure and the blended series in each site had no difference between them (correlation coefficient = 1.00), so we only used the blended series.

Table S1. Number of climate datasets used in the study. Columns indicate the climate data sources (grid datasets - CRU, E-OBS - and meteorological stations) and rows indicate the sites. For the grid datasets, grey squares contain the coordinates of the vertices of the grid boxes including the sites (longitudes range from -3 ° E to -7 ° E; latitudes from 37 ° N to 42 °N). Below, for each climate data source, are indicated the number of the grid boxes and stations, the number of the available climate parameters, and the resulting number (in bold) of climate datasets.

	Grid boxes				Meteorological stations
	CRU		E-OBS		
Carrascal	-4.5	-4	-4.5	-4.25	
	41.5	42	41.5	41.75	Valladolid-Villanubla
Viana de Cega	-4.5	-4	-4.5	-4.25	
	41	41.5	41.25	41.5	
Hoyo de Pinares	-4.5	-4	-4.5	-4.25	Ávila
	40.5	41	40.5	40.75	
Valverde del Camino	-7	-6.5	-7	-6.75	
	37.5	38	37.5	37.75	Huelva
Hinojos	-6.5	-6	-6.5	-6.25	
	37	37.5	37.25	37.5	
	5 gridboxes 6 parameters (1)		5 gridboxes 4 parameters (2)		3 stations 4 parameters (2)
	6 x 5 = 30		**5 x 4 = 20**		**3 x 4 = 12**

(1) : precipitation, max./min./mean temperatures, scPDSI and DTR; (2) : precipitations, max./min./mean temperatures

Table S2. Climate data sources and climate parameters used in the study. For the gridded datasets, the grid resolution is indicated. For the meteorological stations, the geographic coordinates and elevations (m a.s.l.) are indicated. The climate parameters from each data source are indicated. The time spans refer to periods covered by the time series of each climate parameter. CRU: Climatic Research Unit; E-OBS: EU ENSEMBLES project (see text for references); DTR: diurnal temperature range; scPDSI: self-calibrating Palmer Drought Severity Index.

Climate data sources		Grid resolution	Coordinates and elevation	Climate parameters	Time span
Gridded datasets	CRU TS3.23	0.5° x 0.5°		Precipitation Temperatures DTR	1901-2013
	CRU 3.21	0.5° x 0.5°		scPDSI	1901-2012
	E-OBS v11.0	0.25° x 0.25°		Precipitation Temperatures	1950-2014
Meteorological stations	Valladolid-Villanubla		41.70° N, 4.85° W; 846 m	Precipitation Temperatures	1936-2014
	Ávila		40.66° N, 4.68° W; 1130 m	Precipitation Temperatures	1957-2014
	Huelva		37.26° N, 6.95° W; 17 m	Precipitation Temperatures	1920-2014

Table S3. Number of growth-climate correlation analyses performed. Rows indicate the time periods over which correlations were computed and columns indicate the climate parameters. Each grey square indicates the detrending methods and climate data sources used in the analysis, the sites for which correlations were computed, and (in bold) the resulting number of correlation analyses.

	Precipitation	Maximum temperatures	Minimum temperatures	Mean temperatures	scPDSI	DTR
1957-2011	2 detrending (A) 3 sources (B) 5 sites **2 x 3 x 5 = 30**	2 detrending (A) 3 sources (B) 5 sites **2 x 3 x 5 = 30**	2 detrending (A) 3 sources (B) 5 sites **2 x 3 x 5 = 30**	2 detrending (A) 3 sources (B) 5 sites **2 x 3 x 5 = 30**	2 detrending (A) 1 source (C) 5 sites **2 x 1 x 5 = 10**	2 detrending (A) 1 source (C) 5 sites **2 x 1 x 5 = 10**
Early period (1950-1980)	1 detrending (D) 2 sources (E) 5 sites **1 x 2 x 5 = 10**	1 detrending (D) 2 sources (E) 5 sites **1 x 2 x 5 = 10**	1 detrending (D) 2 sources (E) 5 sites **1 x 2 x 5 = 10**	1 detrending (D) 2 sources (E) 5 sites **1 x 2 x 5 = 10**	1 detrending (D) 1 source (C) 5 sites **1 x 1 x 5 = 5**	1 detrending (D) 1 source (C) 5 sites **1 x 1 x 5 = 5**
Late period (1981-2011)	1 detrending (D) 2 sources (E) 5 sites **1 x 2 x 5 = 10**	1 detrending (D) 2 sources (E) 5 sites **1 x 2 x 5 = 10**	1 detrending (D) 2 sources (E) 5 sites **1 x 2 x 5 = 10**	1 detrending (D) 2 sources (E) 5 sites **1 x 2 x 5 = 10**	1 detrending (D) 1 source (C) 5 sites **1 x 1 x 5 = 5**	1 detrending (D) 1 source (C) 5 sites **1 x 1 x 5 = 5**

(A) NEXP and SP30; (B) CRU, E-OBS and meteorological stations; (C) CRU; (D) SP30; (E) CRU and E-OBS. Only the SP30 chronologies and the gridded climate data were used for the "early" and "late" periods (see paragraph 3.3). The common interval between the tree-ring chronologies and the gridded climate datasets is 1950-2011.

Table S4. Correlations between the AMJJAS series of each climate data sources (CRU, E-OBS and meteorological stations) for the climate variables P (precipitation), max. T (mean of maximum temperatures), min. T (mean of minimum temperatures) and mean T (mean temperatures), from 1957 to 2011. The correlation values are indicated from left to right for northern, central and southern study regions.

		E-OBS			station		
P	CRU	0.97	0.94	0.97	0.87	0.86	0.91
	E-OBS				0.86	0.82	0.94
Max. T	CRU	0.97	0.98	0.88	0.90	0.95	0.78
	E-OBS				0.95	0.99	0.94
Min. T	CRU	0.84	0.66	0.90	0.84	0.23	0.19
	E-OBS				0.92	0.80	0.03
Mean T	CRU	0.97	0.93	0.94	0.92	0.78	0.51
	E-OBS				0.97	0.94	0.55

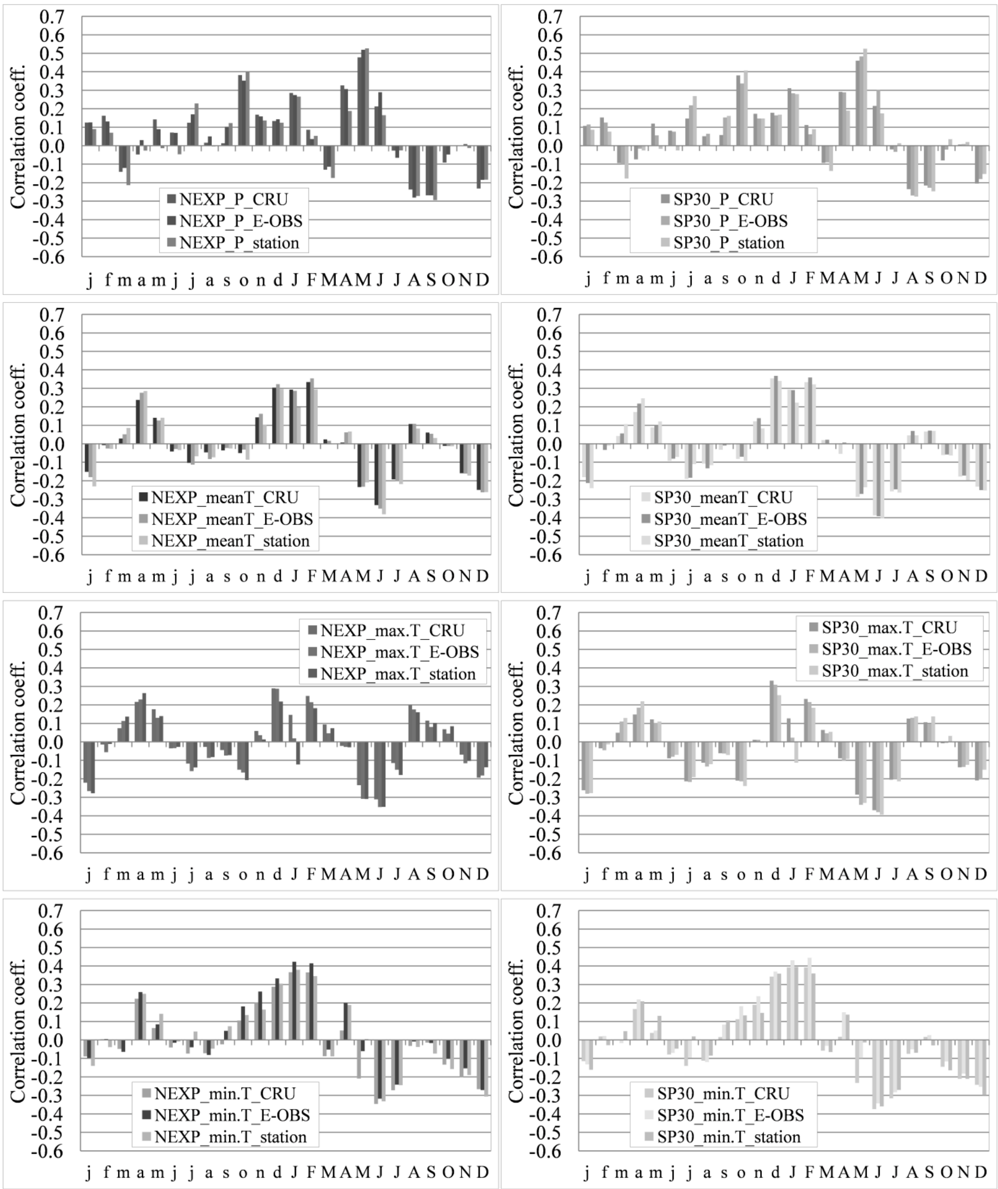


Figure S1. Bootstrapped correlations in Carrascal between standard chronologies (computed with negative exponential curve – NEXP - or cubic smoothing spline with 50% frequency-response cutoffs at 30 years - P30) and monthly values of precipitation data (P) and mean/maximum/minimum temperature data from meteorological stations, E-OBS and CRU. The correlations are computed from 1950 to 2011. Months of the year prior to the year of ring formation are in lower-case letters; months of the year of ring formation are in capital letters.

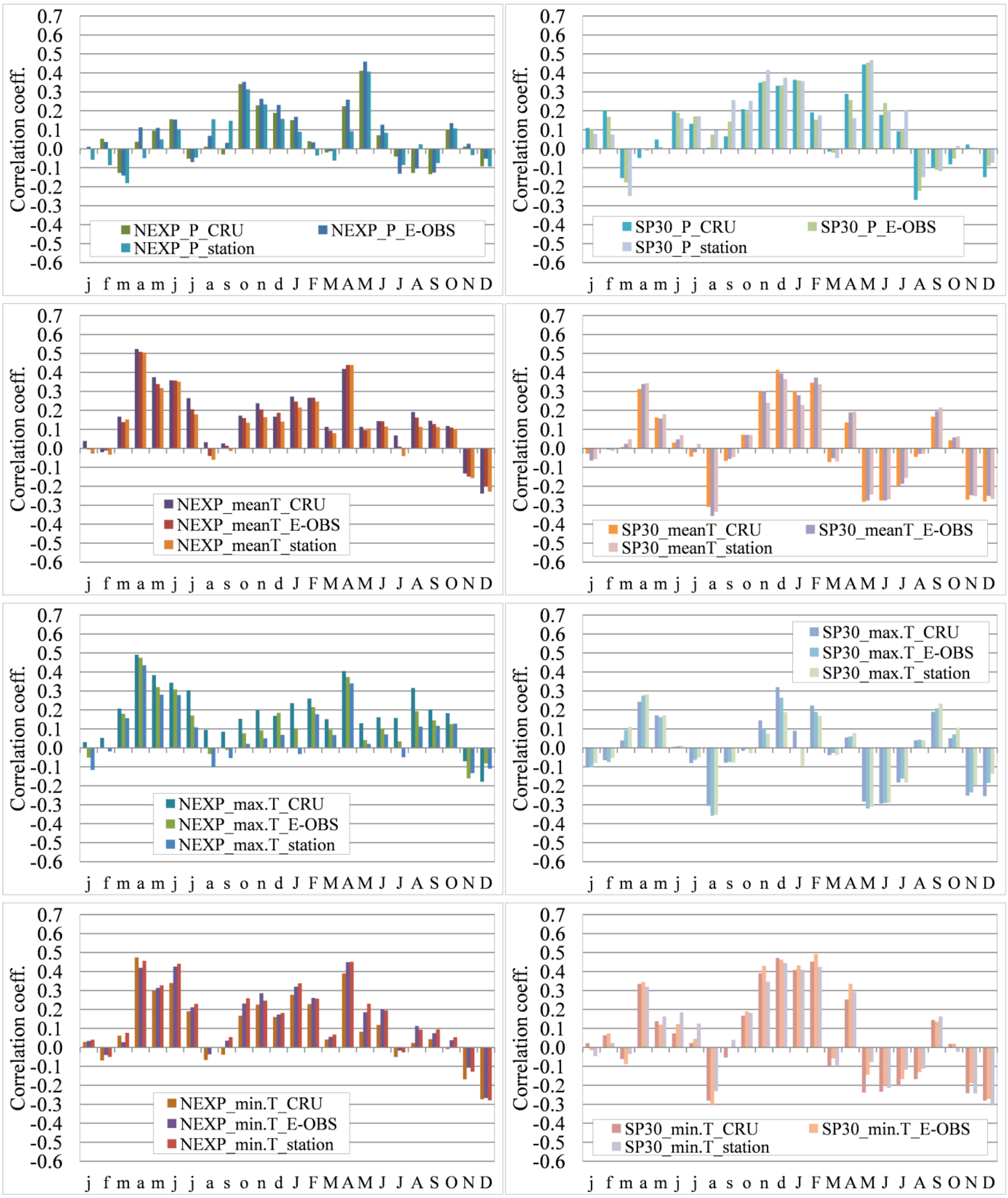


Figure S2. Bootstrapped correlations in Viana de Cega between standard chronologies (computed with negative exponential curve – NEXP - or cubic smoothing spline with 50% frequency-response cutoffs at 30 years - P30) and monthly values of precipitation data (P) and mean/maximum/minimum temperature data from meteorological stations, E-OBS and CRU. The correlations are computed from 1950 to 2011. Months of the year prior to the year of ring formation are in lower-case letters; months of the year of ring formation are in capital letters.

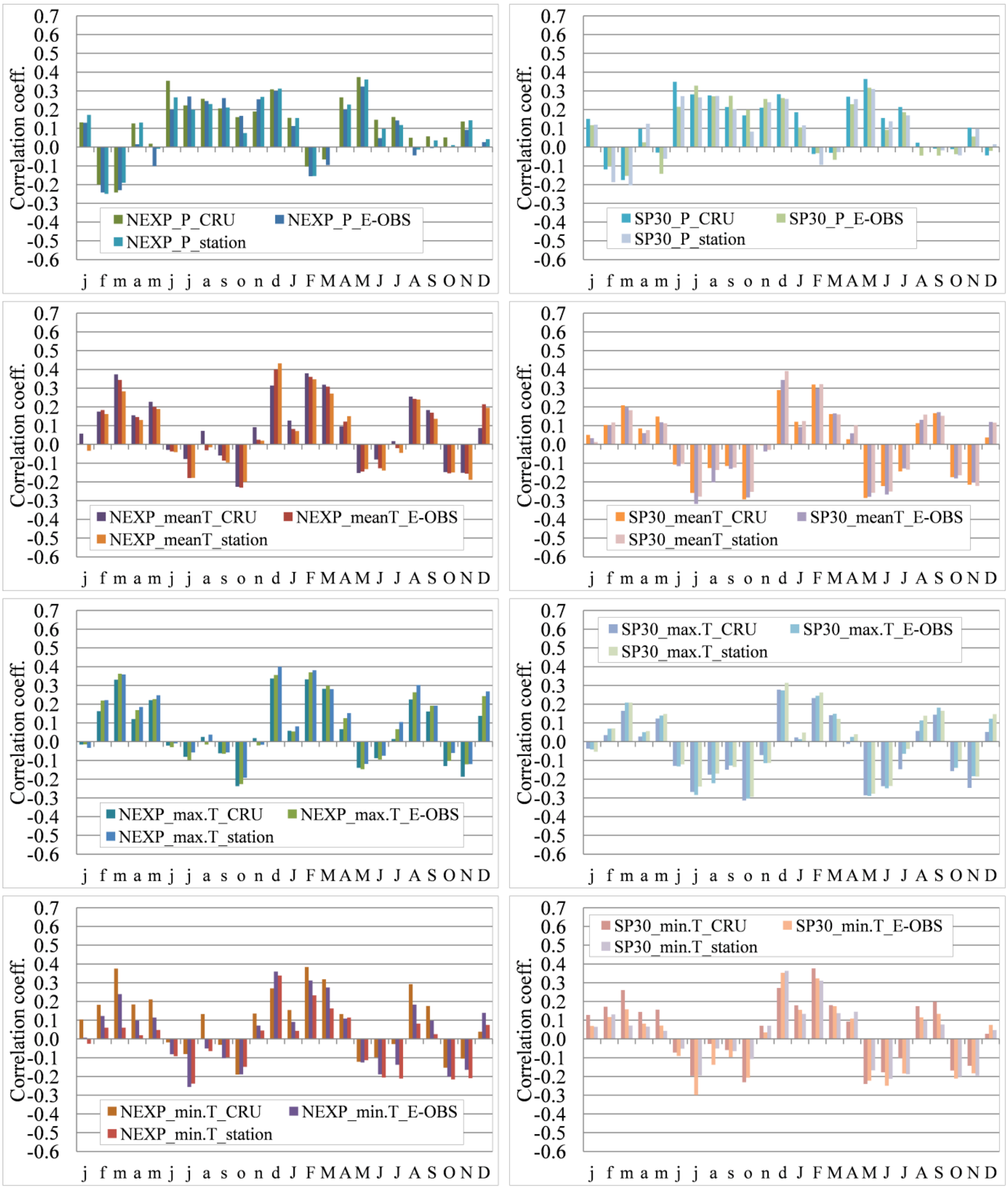


Figure S3. Bootstrapped correlations in Hoyo de Pinares between standard chronologies (computed with negative exponential curve – NEXP - or cubic smoothing spline with 50% frequency-response cutoffs at 30 years - P30) and monthly values of precipitation data (P) and mean/maximum/minimum temperature data from meteorological stations, E-OBS and CRU. The correlations are computed from 1950 to 2011. Months of the year prior to the year of ring formation are in lower-case letters; months of the year of ring formation are in capital letters.

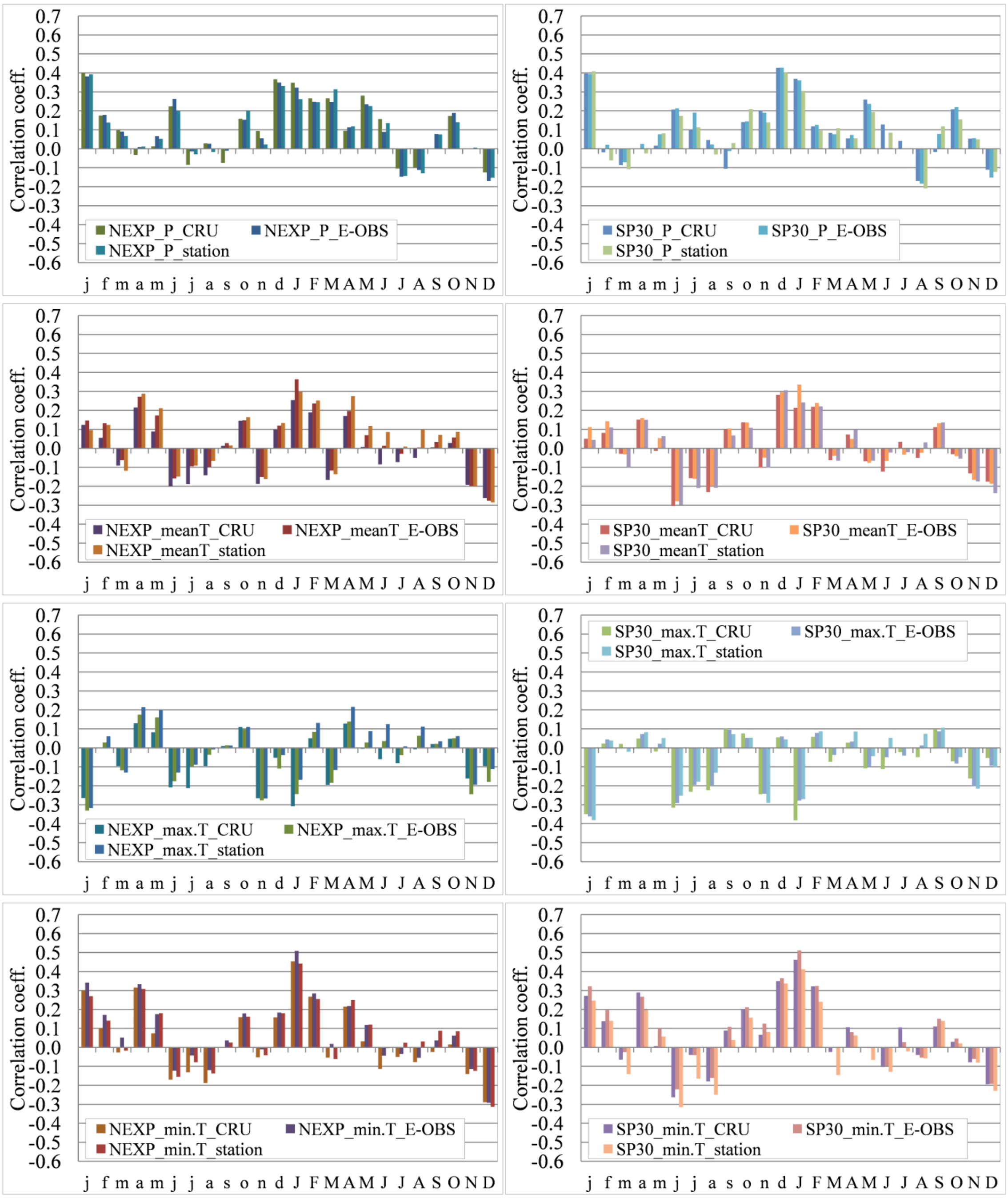


Figure S4. Bootstrapped correlations in Valverde del Camino between standard chronologies (computed with negative exponential curve – NEXP - or cubic smoothing spline with 50% frequency-response cutoffs at 30 years - P30) and monthly values of precipitation data (P) and mean/maximum/minimum temperature data from meteorological stations, E-OBS and CRU. The correlations are computed from 1950 to 2011. Months of the year prior to the year of ring formation are in lower-case letters; months of the year of ring formation are in capital letters.

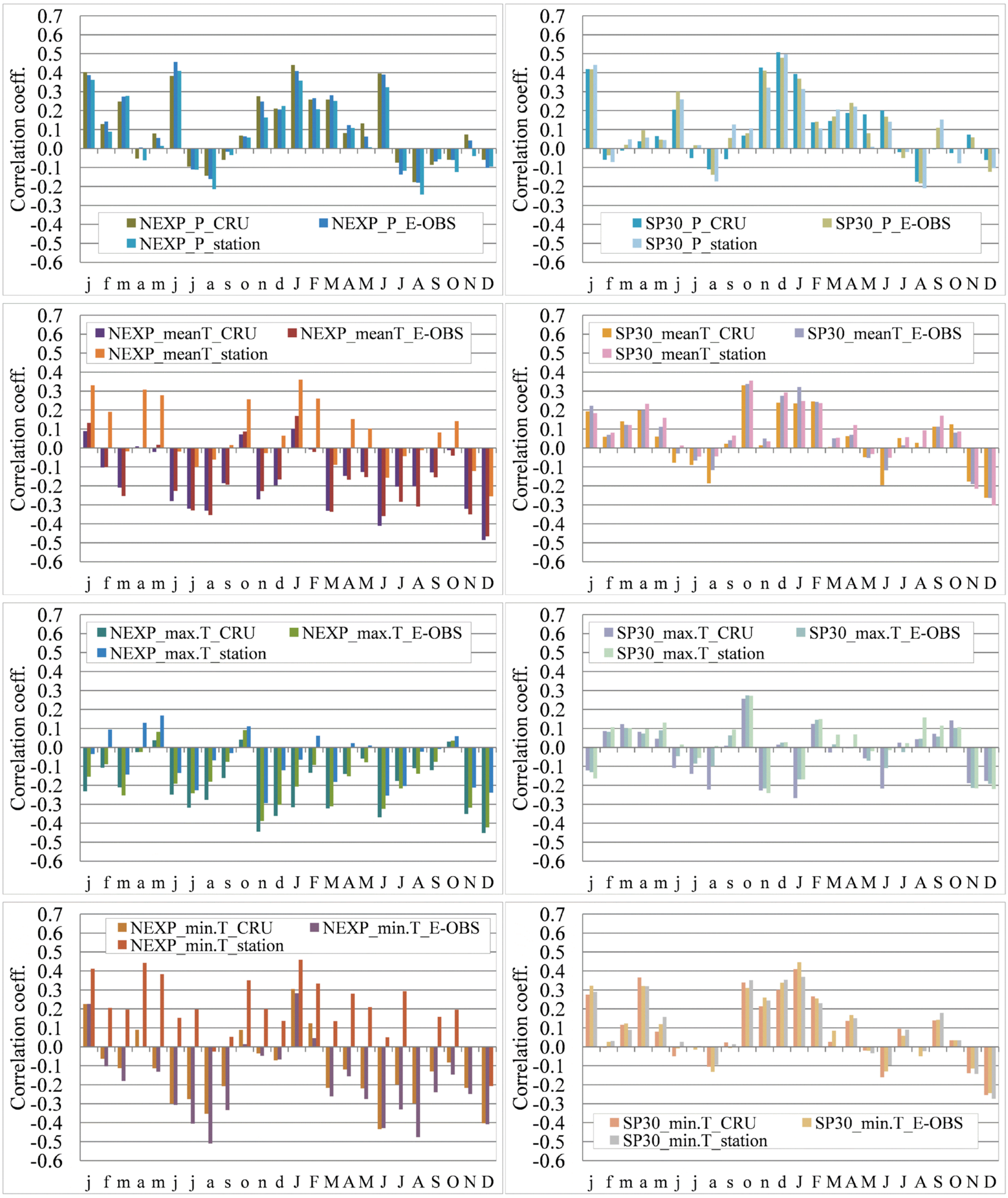


Figure S5. Bootstrapped correlations in Hinojos between standard chronologies (computed with negative exponential curve – NEXP - or cubic smoothing spline with 50% frequency-response cutoffs at 30 years - P30) and monthly values of precipitation data (P) and mean/maximum/minimum temperature data from meteorological stations, E-OBS and CRU. The correlations are computed from 1950 to 2011. Months of the year prior to the year of ring formation are in lower-case letters; months of the year of ring formation are in capital letters.

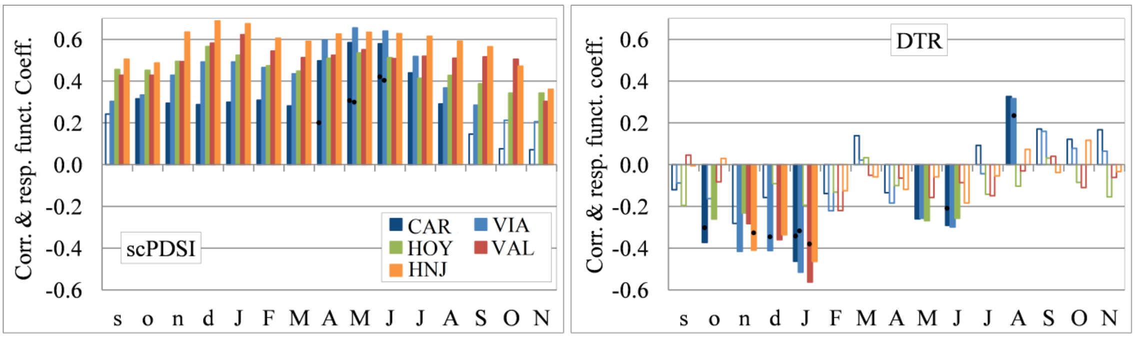


Figure S6. Bootstrapped correlations (bars) and response functions (dots) between the SP30-detrended standard chronologies of each site and monthly values (from previous September to current November) of self-calibrated Parlmer Drought Severity Index (scPDSI) and Diurnal Temperature Range (DTR) from 1950 to 2011. Full bars indicate statistically significant correlations (α = 0.05). For response functions, only significant values (α = 0.05) are showed.

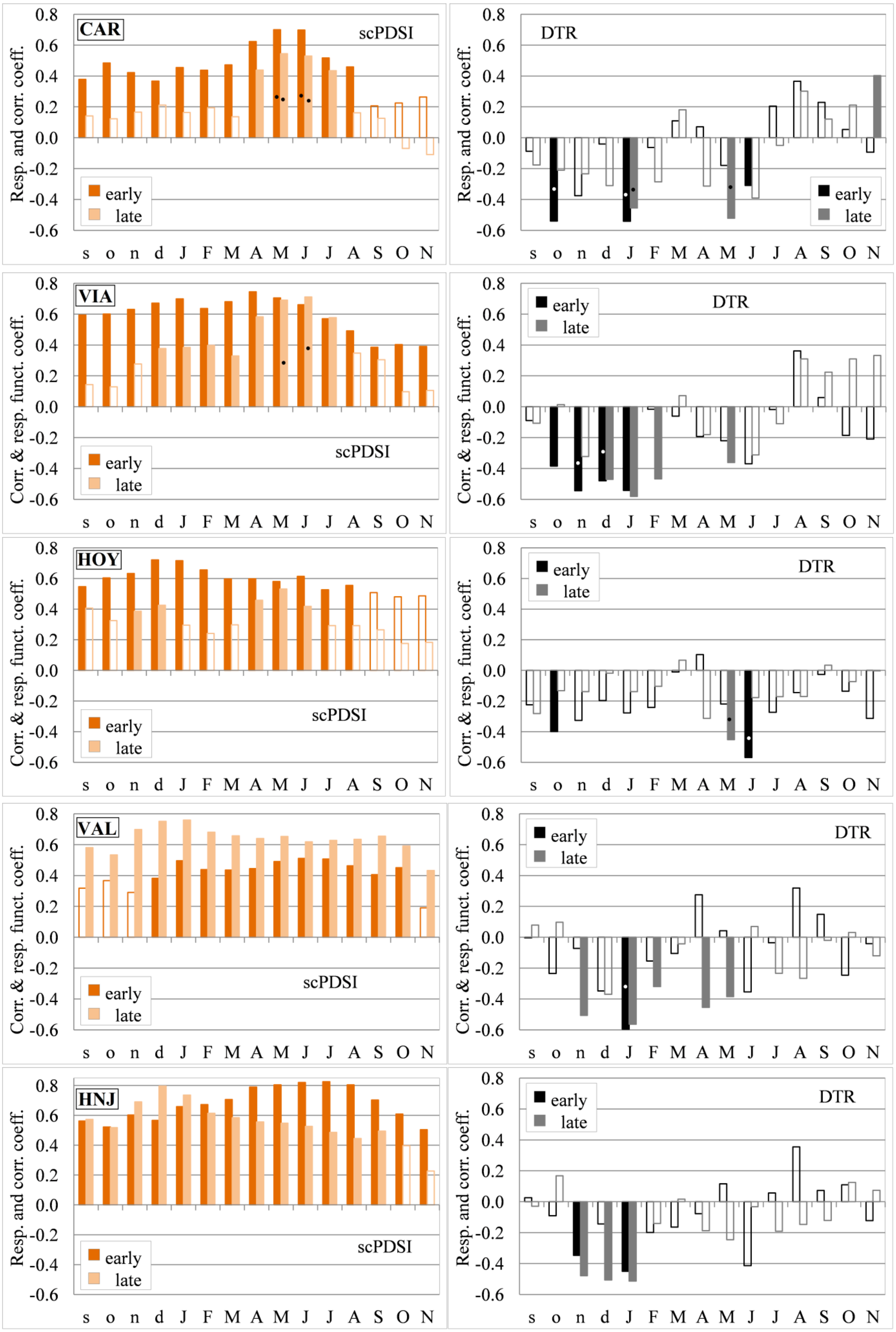


Figure S7. Bootstrapped correlations (bars) and response functions (dots) in each site between the SP30 chronology and monthly values (from previous September to current November) of self-calibrated Parlmer Drought Severity Index (scPDSI) and Diurnal Temperature Range (DTR) during the "early" (1950-1980) and "late" (1981-2011) periods. Full bars indicate statistically significant correlations (α = 0.05). For response functions, only significant values (α = 0.05) are showed.

15.4 Article 4. Natalini F., Alejano R., Vázquez-Piqué J., Cañellas I., Gea-Izquierdo G., 2016. The role of climate change in the widespread mortality of holm oak in open woodlands of Southwestern Spain. Dendrochronologia, 38, pp.51-60.

Natalini F., Alejano R., Vázquez-Piqué J.: Departamento de Ciencias Agroforestales, Escuela Técnica Superior de Ingeniería, Universidad de Huelva, Campus de La Rábida, 21819 Palos de la Frontera, Huelva, Spain
Cañellas I., Gea-Izquierdo G.: CIFOR-INIA, Ctra. de La Coruña km 7.5, Madrid 28040, Spain

Abstract

Forest decline and increasing tree mortality are of global concern and the identification of the causes is necessary to develop preventive measures. Global warming is an emerging factor responsible for the increasing tree mortality in drought-prone ecosystems. In the southwestern Iberian Peninsula, Mediterranean holm oak open woodlands currently undergo large-scale population-level tree die-off. In this region, temperature and aridity have increased during recent decades, but the possible role of climate change in the current oak mortality has not been investigated.

To assess the role of climate change in oak die-off in managed open woodlands in southwestern Spain, we analyzed climate change-related signals in century-long tree ring chronologies of dead holm oaks. We examined the high/low-frequency variability in growth and the relationship between growth and climate.

Similar to other Mediterranean forests, growth was favored by precipitation from autumn of the year prior to ring formation to spring of the year of ring formation, whereas high temperatures during spring limited growth. Since the 1970s, the intensity of the high-frequency response to water availability increased simultaneously with temperature and aridity. The growth trends matched those of climatic changes. Growth suppressions occurred during droughts in the 1970s, 1980s and 1990s. Widespread stand-level, age-independent mortality occurred since 2005 and affected trees that can not be considered old for the species standards.

The close relationship between growth and climate indicate that climate change strongly controlled the growth patterns. This suggests that harsher climatic conditions, especially increased aridity, affected the tree performance and could have played a significant role in the mortality process. Climate change may have exacerbated or predisposed trees to the impact of other factors (e.g. intense management and pathogens). These observations could suggest a similar future increase in oak mortality which may occur in more northern oak open woodlands if aridity further increases.

Keywords. Dendroecology; Quercus ilex; Tree mortality; Drought; Growth trends

Introduction

Increases in tree mortality have been recently observed in forest ecosystems worldwide (Allen et al.,2010; Choat et al., 2012). However, it is necessary to further understand the actual causes of tree mortality to assess the vulnerability of forest ecosystems and to evaluate potential preventive measures (McDowell et al., 2008; Allen et al., 2010). In the Western Mediterranean, different species show signs of decline, e.g. sustained growth reduction and defoliation (see Fig. 6 and Table 4 in Allen et al. 2010; Carnicer et al., 2011), which may indicate an increasing risk of tree mortality (Bigler and Bugmann, 2004; Gea-Izquierdo et al., 2014). In the southwest of the Iberian Peninsula, there is an alarming increase of oak mortality in managed oak open-woodlands over large areas (Carrasco, 2009). These ecosystems, dominated by evergreen holm oaks (*Quercus ilex* L.) and cork oaks (*Q. suber* L.), are among the most representative Iberian Mediterranean landscapes and have considerable socio-economic value (Carevic et al., 2010; Alejano et al. 2011). In recent decades, certain oak stands have undergone a decline characterized by nonspecific symptoms, including wilting of leaves, twigs, and branches, bark necrosis, and production of epicormic shoots (Brasier, 1996; Navarro, 2011). In Southwestern Spain, this decline has extended to the regional scale in recent years and oak die-off is currently widespread. This phenomenon is a major problem for forest owners and threatens sustainability of these woodlands (Carrasco, 2009). Pathogenic fungi are a factor of oak decline (Sánchez et al., 2002). Additionally, although there is a lack of experimental evidence of the effect of management on oak mortality, management is very intense in these ecosystems (thinning, livestock management, pruning, soil tillage) and may also be involved in this decline process.

The increase in drought an heat-induced tree die-off at the global scale indicates that climate change is an emerging factor of tree mortality processes (Allen et al., 2010; Choat et al., 2012; Anderegg et al., 2013). Increases in drought can predispose trees to mortality, or directly cause tree death, through different interrelated physiological mechanisms, including carbon starvation and hydraulic failure (McDowell et al., 2008, 2011). In the Iberian Peninsula, climate has become drier and warmer in recent decades (Sumner et al., 2003; Rodrigo and Trigo, 2007; Kovats et al., 2014). In Southern Spain, evergreen oaks grow under Mediterranean-type climates where meteorological drought (i.e. period in which P<2T, where “P” is mm of monthly precipitation and “T” is mean temperature in Celsius degrees) lasts for up to 5 months (Vázquez-Piqué, 2011) and is the most important limiting factor for vegetation. Moreover, narrow soils in many stands can amplify the impact of extreme climatic events like severe droughts (David et al., 2007; de Sampaio e Paiva Camilo-Alves et al., 2013). Atmospheric warming and climatic instability can increase pathogen activity and aggravate oak diseases (Brasier and Scott, 1994; Sanchez et al., 2002; Corcobado et al., 2013). Research indicates that climate change is a factor involved in forest mortality in some Spanish forests at higher latitudes (Martínez-Vilalta and Piñol, 2002; Linares et al., 2009; Hereş et al. 2012; Ruiz-Benito et al., 2013; Gea-Izquierdo et al., 2014), but a link between climate change and widespread increase of oak mortality in Southwestern Spain has not been established.

Dendrochronological data provide useful information to investigate forest dynamics in relationship with the environment (Fritts, 1976; Schweingruber, 1996). The xylem of Mediterranean evergreen species has anatomical features that make it difficult to establish chronologies (Cherubini et al., 2003), yet dendrochronological studies of *Q. ilex* has become well-established especially in recent times (Zhang and Romane, 1991;

Cherubini et al., 2003; Campelo et al., 2009; Gea-Izquierdo et al., 2009, 2011). These studies have demonstrated that *Q. ilex* ring formation is very sensitive to climate, indicating the suitability of this species for dendroecological investigations. On other species, tree rings have been used to investigate growth patterns in declining forests and dead trees (see Schweingruber, 1996, p.369-391), to model mortality risk (e.g. Bigler and Bugmann, 2004) and to find relationships between mortality processes and external factors (e.g. Pedersen, 1998; Camarero et al., 2003; Bigler et al., 2006). Moreover, annual tree-ring widths can be used to estimate the basal area increment (BAI), as an indicator of forest productivity (Piovesan et al., 2008; Di Filippo et al., 2010). The inverse relationship between ring width and age is eliminated when radial growth is calculated as BAI (Biondi and Qeadan, 2008). In the absence of major ecological constraints, changes in BAI should be positive or approach an asymptote in adult trees (Poage and Tappeiner, 2002; Biondi and Qeadan, 2008; Sillet et al., 2010). Thus, recent studies have interpreted negative BAI trends in adult trees as evidence that trees have entered a declining phase (Piovesan et al., 2008; Di Filippo et al., 2010; Gea-Izquierdo et al., 2014).

In this paper, our objective was to assess the role of climate change on the widespread mortality of holm oaks occurring in the SW Iberian Peninsula. We used century-long tree ring chronologies of dead holm oaks (*Quercus ilex* ssp. *Ballota* [Desf.] Samp.) from two managed open woodlands. We examined the climate change-related growth variability to verify whether negative impacts of climate change were reflected in the growth patterns before tree death. We analyzed (*i*) the relationship between climate and growth to determine the climatic variables that mostly influenced tree growth, (*ii*) the shifts in climate-growth relationships over time to evaluate the sensitivity of trees to the changing climate, and (*iii*) the low-frequency growth variability to identify its connections with climate trends.

Materials and methods

Study sites

The study sites are located in the province of Huelva, Spain (Fig. 1). Oak samples were collected from two monitoring experimental plots (2.9 ha per plot): Calañas (CA, 37º 31' N; 6º 55' W; 165 m a. s. l.) and Huerto Ramirez (HR, 3º 34' N; 7º 20' W; 200 m a. s. l.). The two stands are representative of oak open-woodlands in the SW Iberian Peninsula that are primarily used for livestock management. In the two stands the understory layer is composed of *Cistus ladanifer, C. crispus , C. monspeliensis* and an herbaceous layer of grasses. Soils in CA are shallower Regosols, Leptosols and Cambisols (25 to 50 cm depth) and deeper soils in HR range from Regosols and Cambisols (40-70 cm depth) to Acrisols, Alisols and Lixisols (60-100 cm depth). The stand density was 54 trees ha^{-1} (basal area: 4.5 m^2 ha^{-1}) till 2006 in CA and 74 trees ha^{-1} (basal area: 5.2 m^2 ha^{-1}) till 2010 in HR. Dead trees were logged since 2007 in CA and since 2011 in HR, and this led to decreases of stand density (Supplementary material 1). Similar to holm oak open woodlands in the province of Huelva, both stands present canopy dieback, widespread mortality and no regeneration.

Inventory of defoliation and mortality

Tree inventories were performed in the two plots to characterize canopy defoliation and tree mortality. Tree defoliation, defined as the loss (i.e. fall or complete dryness) of leaves, twigs, and side branches, was monitored between November and December in 2010 at HR and in 2001, 2005, and 2006 in CA; additional observations were performed in both plots in June 2013. All living trees were classified as "slightly affected" when defoliation was 10-20% of the crown, partially affected when defoliation was 30-60%, heavily affected when canopy defoliation was greater than 60% (López and Sanchez, 2011). A tree was classified as healthy when the crown was undamaged or defoliation was less than 10%. Furthermore, tree inventories reported the decrease in stand density due to the logging of dead trees. A tree was assumed to be dead when it was completely defoliated for at least two successive growing seasons.

Sampling and dendrochronological analyses

Complete cross-sections are needed for dendrochronological analysis of *Q. ilex* due to the complex xylem anatomy of this species (narrow rings, missing rings, and intra-annual density fluctuations [Cherubini et al*.,* 2003; Campelo et al., 2007, 2009; Gea-Izquierdo et al. 2009]). Previous dendroecological studies on tree mortality in Iberian forests included tree ring data from dead and healthy trees for comparative analyses (e.g. Hereş et al. 2012; Gea-Izquierdo et al., 2014). In both sites of this study, the whole stand had signs of decline, thus establishing a chronology from healthy trees was not possible. Furthermore, obtaining stem sections of living *Q. ilex* trees is difficult because this species is protected in the region. Therefore, only cross-sections from dead trees were used for this study. In particular, we used basal stem sections from 30 trees logged during 2007 in CA and 12 trees logged during 2011 in HR. The complex xylem anatomy also made difficult to measure and cross-date ring sequences along different radii on each section. Thus, 11 of the 30 disks were discarded in CA because cross-dating was impossible. In HR, discarding disks could have leaded to a low replication of samples, so cross sections at breast height of the same trees were also collected and used for cross-dating. Rings from different stem heights did not provide different results because the rings are proportional and provide coherent climatic signals (Zhang and Romane, 1991; Chhin and Wang, 2005).

The cross-sections were air-dried, sanded, and polished with progressively finer grits (60 to 1200) to make the rings visible. Ring widths were measured with a stereomicroscope connected to a LINTAB^{TM} table (Rinntech®). Ring width curves were plotted for visual checks and cross-dated using a coefficient of parallel variation (*Gleichlaeufigkeit* - Glk) (Speer, 2010: p. 107-109), *t*-value, and the cross-date index (CDI) as a combination of the *t*-value and Glk, which are executed in the software TSAP-Win^{TM} (Rinntech®). The cross-dating was then verified using COFECHA (Grissino-Mayer, 2001). Missing rings were detected by cross-dating chronologies from different trees and inspecting ring boundaries along the whole circumference on the stem sections. Tree ages were estimated by counting the number of annual rings on the cross-dated chronologies. To assure that annual rings were correctly identified and dated, we compared the chronologies from CA and HR with a previously established chronology of *Pinus pinea* from a close site

("Valverde del Camino", see Natalini et al., 2015) and a *Q. ilex* chronology from an open-woodland in a neighboring region of Spain (Cáceres, West-Central Spain; see Gea-Izquierdo et al*.,* 2011). Similar procedures to validate *Q. ilex* chronologies were used by Campelo et al. (2009) and Gea-Izquierdo et al. (2009).

The individual cross-dated ring-width series were detrended by applying a smoothing spline with a 50% frequency cutoff at 32 years. The growth index was computed using the ratio between the measured raw ring width and the value of the smoothing spline (Cook et al*.,* 1990a). An autoregressive model was used to remove the autocorrelation, and a mean chronology for each stand was obtained by averaging the pre-whitened indexed series with a biweight robust mean to reduce the influence of outliers (Cook et al., 1990b). The mean indexed series were used to analyze the high-frequency response to climate. The expressed population signal, with a minimum threshold of 0.85 (EPS; Wigley et al., 1984), and the inter-series correlation coefficients (*r*-bar) were used for additional quality control and computed over 30-year windows lagged by 15 years along the chronologies.

To study the long-term growth trends, we used the cross-dated ring-width series to compute basal area increments (BAI). Past BAI were estimated by subtracting twice the annual ring width from the annual diameter, starting from the measured diameter outside the bark (see Piovesan et al., 2008).

All computations were done using the dplR library within the software R (Bunn, 2008).

Climate-growth relationships

Climatic data were from the Huelva station (time span: 1920–2010; 37° 16' N; 6° 54' W; 19 m a.s.l.), and included daily precipitation, and minimum and maximum temperatures. To analyze the high-frequency responses of trees to climate, we computed bootstrapped correlations and response functions using DENDROCLIM2002 (Biondi and Waikul, 2004) between the mean indexed chronologies of CA and HR and monthly climate data (monthly cumulative precipitation and averages of minimum and maximum temperatures). To determine whether growth-climate relationships changed over time, we computed correlations for running windows of 30 years between the chronologies and seasonal climate data. In this analysis, the critical α value was modified using a Bonferroni correction to account for multiple comparisons.

Growth history and climatic changes

For analysis of the low-frequency climatic signal in growth trends, we used the average of the Palmer Drought Severity Index (PDSI) from November of the previous year to the current June, a period in which we expected to find the strongest growth response to climate (Gea-Izquierdo et al., 2011). Data of PDSI were obtained from the CRU 3.21 dataset (van der Schrier et al., 2006). The PDSI and BAI curves were compared to identify synchrony. We considered synchronous shifts of the BAI and PDSI curves to suggest that growth variations were induced by changes in drought. We used cross-wavelet analysis to compare the long-term (low frequency) changes in the PDSI and BAI series (Grinsted et al., 2004). This method identifies the common signal power of two time series in the time-frequency domain. The cross-wavelet analysis was performed between BAI series, pre-whitened with a 1st-order autoregressive model, and PDSI values standardized to a mean of 0 and a standard deviation of 1. This analysis was performed in R using the biwavelet package (Gouhier and Grinsted, 2013).

Additionally, we analyzed the percentage of growth changes (%GC; Nowacki and Abrams, 1997) in HR and CA to assess the effects of major disturbances or strong responses to periods of extreme climate (dry or wet periods). Yearly %GC was calculated between successive 10-year means of ring widths (Nowacki and Abrams, 1997):

$$\%GC = \frac{RW_2 - RW_1}{RW_1} \cdot 100$$

where RW_1 is the mean ring width of the preceding 10 years and RW_2 is the mean ring width of the subsequent 10 years. The yearly %GC was fixed to the last year of the preceding 10-year period. The threshold used to characterize a significant negative or positive peak in the %GC chronology depends on factors that influence the ability of a tree to respond to disturbances, including species, age, and diameter (Nowacki and Abrams, 1997; Black and Abrams, 2003; Gea-Izquierdo and Cañellas, 2014). In our analysis we considered a threshold of 50% as significant (Gea-Izquierdo and Cañellas, 2014). To adequately evaluate the relationship of climatic change with %GC, cumulative precipitation from the previous November to the current June was calculated for 10-year window differences:

$$P_{diff} = P_2 - P_1$$

where P_2 and P_1 are the amounts of precipitation of preceding and subsequent 10-year windows. Positive and negative peaks of differences indicated major shifts in precipitation that could impact growth.

Results

Inventory of defoliation and mortality

The tree inventories at both sites indicated increased defoliation and decreased stand density over time (Supplementary material 1). More specifically, the stand density in CA declined from 54 trees ha^{-1} in 2001 to 22 trees ha^{-1} in 2011. Large portions of this plot were treeless grasslands in 2011. Stand mortality in HR was less severe, but the measurements of defoliation indicated a deterioration of tree health. In fact, in this plot there was a marked increase in the number of heavily affected trees and a decrease in the number of healthy and slightly affected trees from 2010 to 2013. Remarkably, in 2013 only 5% of the trees in HR were healthy while there were no healthy trees in CA.

Tree-ring chronologies

Tree ages ranged from 73 to 113 in CA, and from 41 to 149 in HR. Thus, dying trees were not old relative to standards of this species (Gea-Izquierdo et al., 2011). The statistics of the *Q. ilex* tree ring chronologies are in Table 1. The indexed chronologies are shown in Figure 2. The last ring common to all *Q. ilex* series was in 2004 at CA and in 2008 at HR, so tree death occurred after 2005 and 2009, respectively. The HR and CA chronologies were highly correlated between them (Glk = 82, $p < 0.01$; CDI = 131; Pearson's $r = 0.79$, $p < 0.01$) and verified by the comparison with the reference chronologies (see Table 2). The *r*-bar and EPS confirmed the quality of the HR and CA chronologies (Supplementary material 2). The chronologies used for subsequent dendroecological analyses only included years replicated with at least five series (1903-2005 in CA and 1896-2010 in HR).

Climate-growth relationships

Holm oak growth correlated with cumulative precipitation from October of the year prior to ring formation (t-1) to March-April of the year of ring formation (t), but there was no significant correlation with precipitation in summer and autumn of the year t (Fig. 3). Holm oaks had significant responses to autumn/winter temperatures (positive to Oct/Nov$_{t-1}$-Dec$_{t-1}$/Jan$_t$ minimum temperatures, negative to Nov$_{t-1}$ and Jan$_t$ maximum temperatures), and negative response to high temperatures during May and November of the year t (Fig. 3).

The relationship between climate and tree growth changed over time (Fig. 4). In particular, since the 1970s, the correlation between growth and precipitation during November and winter of the year t-1 became increasingly positive, while the correlation of growth with precipitation during the spring of the year t declined.

Growth history and climatic changes

Overall, the changes in BAI and %GC were similar in trees from both sites (Fig. 5), suggesting the presence of a common low frequency climatic signal. In particular, trees from both stands had minor fluctuations from the 1930s to the 1960s, but a decline of BAI from the 1970s to the early 1980s. This growth decline corresponded to a downturn in PDSI (Fig. 5A), suggesting a connection between increasing drought and reduced growth. This interpretation is confirmed by the cross-wavelet analysis (Supplementary material 4), which indicates that both sites had similar growth responses to PDSI. In particular, the common power at lower frequencies in the 1970s and 1980s indicates a connection between shifts in the long-term trends of BAI and PDSI.

Analysis of the %GC in both stands indicates major declines of growth in the 1970s, corresponding to a negative peak of the 10-year differences in precipitation (Fig. 5B). Tree growth in both stands increased in the late 1980s, corresponding to an upturn in precipitations during these years (Fig. 5B), although the growth recovery was larger in the site with deeper soil HR (%GC > 50%) than in the shallower site CA (%GC ≈ 25%). At both sites, a second and final phase of growth decline started during a dry period in the mid-1990s (Fig. 5A, B). Trees died in the mid/late-2000s, when PDSI, nonetheless, was increasing (Fig. 5A).

The meteorological records showed an increasing trend of maximum temperature and a decreasing trend of spring precipitation since the 1970s (Supplementary material 3).

Discussion

Trees show sensitivity to increasing drought

Previous studies of *Q. ilex* stands in the Iberian Peninsula indicated that precipitation from autumn of the year t-1 to spring of the year t had a strong influence on growth (Campelo et al*.,* 2009; Gea Izquierdo et al*.,* 2011). In our study region, maximum rainfall occurs from November to January (Fig. 1), thus annual growth largely depends on this rainfall. There was also a relationship of growth with temperatures of autumn and winter of the year t-1 in other *Q. ilex* populations (Zhang and Romane, 1991; Gea Izquierdo et al*.,* 2009, 2011). The positive relationship with minimum temperatures may be explained by photosynthesis, which can take place in these seasons in evergreen species (Baldocchi et al*.,*2010; Gea-Izquierdo et al. 2015). In fact, photosynthesis rates in winter were measured in holm oaks in HR (Carevic, 2010), in line with other studies in Italy (Gratani et al., 2013; Catoni and Gratani 2014). Moreover, the positive response to temperatures in winter may indicate sensitivity to low temperatures leading to photoinibition (Oliveira and Peñuelas, 2000) and damage of the xylem (Lo Gullo and Salleo, 1993). On the other hand, the negative response to maximum temperatures in autumn/winter may indicate respiration-induced loss of carbohydrates. Gratani et al. (2013) reported positive respiration/photosynthesis ratio in winter. Ecosystem respiration and net carbon losses in autumn have been observed in evergreen oak open woodlands in Southern Portugal (Pereira et al., 2007). Moreover, in our study areas heat-induced evapotranspiration had a negative effect on radial growth of holm oaks in all seasons, including wet autumn and winter (Martín et al., under review). Therefore, the coupled positive response to minimum temperature and negative response to maximum temperatures from autumn to winter may reflect the contribution of carbon gain during these seasons to radial growth in subsequent months.

The trees responded positively to rainfall until March/April, but growth during May did not correlate with precipitation and correlated negatively with temperature. For Mediterranean trees (Campelo et al., 2009; Gea-Izquierdo et al*.,* 2011; De Luis et al., 2013), water availability is important during spring when growth is maximal (Pereira et al.,2007; Vaz et al,. 2010). However, in our study region drought can occur during May (Fig. 1). Heat and low rainfall amounts in this month, which can induce water deficit and limit the photosynthetic capacity of trees (Baquedano and Castillo, 2007), can explain the sensitivity of trees to high temperatures and the absence of significant relationships with precipitation in our sites. The absence of a growth response to summer climate, which was also reported for trees growing in other Iberian *Q. ilex* ecosystems (Campelo et al., 2009; Gea-Izquierdo et al*.,* 2011), can be explained by the duration and intensity of summer drought, which can suppress radial growth (Cherubini et al., 2003; Camarero et al*.,* 2010). The correlation of growth with temperature during November could suggest a re-activation of cambial activity at this time, as in other Mediterranean species (Campelo et al., 2007; Battipaglia et al., 2010; Camarero et al*.,* 2010).

The temporal changes in the relationship between growth and precipitation suggest that the holm oaks were sensitive to variations in the growing conditions. Shifts in the correlation between growth and climate can reflect climate change impacts on tree phenology (Morin et al., 2010) and have been related to warming and increasing aridity in previous studies on Iberian *Q. ilex* (Gea-Izquierdo et al., 2009) and other Mediterranean species (e.g. Di Filippo et al., 2010; Natalini et al., 2015). In our study region, meteorological records did not describe any long-term increase in winter precipitation (Supplementary material 3), which thus do not explain the increase in the growth response. On the other hand, rainfall amounts during spring decreased and maximum temperatures increased since the 1970s. The observed shifts in the growth-climate relationships may indicate the limitation of radial growth during the warmer and drier spring was increasingly dependent on water availability from the previous months.

Climate change could have determined the inception of the mortality process

The mortality process in HR and CA is representative of the current increase in oak die-off occurring in the province of Huelva (personal observation), which is one of the most affected areas in SW Spain (Carrasco, 2009). Research indicates an increase of forest decline in Iberian woodlands (Martínez-Vilalta and Piñol, 2002; Linares et al., 2009; ; Hereş et al. 2012; Carnicer et al., 2011; Gea-Izquierdo and Cañellas 2014). Nevertheless, the increase in oak mortality occurring in our study region is, to our knowledge, the first case in the Iberian Peninsula of massive population-level die-off threatening the sustainability of a forest ecosystem. Increasing oak mortality exacerbates existing problems of regeneration failure in the Spanish evergreen oak open woodlands (Pulido et al., 2001; Plieninger et al., 2004).

In recent decades, climatic changes have exerted a more intense synchronizing control on the growth trends of the studied holm oaks. Tree growth decreased during dry periods as expected in Mediterranean forests (Piovesan et al., 2008; Di Filippo et al., 2010; Gea-Izquierdo and Cañellas, 2014). On the other hand, growth changes (%GC) were positive and BAI did not decline in the late 1980s, when there was an upturn in precipitation and PDSI values were positive (Fig. 5). This suggests a recovery of growth favored by the attenuation of aridity. The response to wetter climate after drought-induced growth suppression also occurred in *Quercus* trees from other Mediterranean woodlands (Di Filippo et al., 2010; Gea-Izquierdo and Cañellas, 2014). The different extent of growth recovery between HR and CA in the late 1980s remains unexplained. It could be related to different soil depth and, hence, different soil water retention. Additionally, in HR some trees (e.g. dead or senescent trees) might have been logged in the 1980s, and growth release in neighboring trees could have been the result of reduced stand density and lower competition, which actually exists even with the low tree densities found today in the studied stands (Gea-Izquierdo et al., 2009, 2011; Martín et al., 2014). However, timber inventories are not available and we cannot verify this hypothesis based on our data.

The observed correlation of climate and growth, the increase of this correlation over time, and the synchronizing control of climatic variations on growth trends indicate that our trees were sensitive to warming and increasing aridity. In addition, they suggest that these changes in climate could have an important role in the mortality process in our study sites. Drought-induced decline processes preceding tree death simultaneous with drier and warmer climate have been recognized as an emerging factor involved in the increase of tree mortality (Pedersen, 1998; Bigler et al*.,* 2006; Hogg et al., 2008; Gea-Izquierdo et al*.,* 2014). The fundamental mechanisms underlying tree mortality during drought are still incompletely understood (Allen et al*.,* 2010). Theoretically, plants regulate their water status *via* stomatal closure and can undergo carbon starvation and/or hydraulic failure when drought is severe and protracted, and this could lead to metabolic problems and defense limitations (Martínez-Vilalta et al*.,* 2002; McDowell et al., 2008; McDowell, 2011). For instance, Breshears et al. (2008) reported water stress during a protracted period before death, suggesting carbon starvation and associated increases in susceptibility to other disturbances. The susceptibility of trees to mortality seems to be related to tolerance thresholds in tree physiology in a complex way that is not yet completely understood (Allen et al*.,* 2010; McDowell et al*.,* 2011). Warming and increasing aridity could force trees beyond certain thresholds from which they cannot recover (D'Arrigo et al., 2004; Wilmking et al*.,* 2004; McDowell et al*.,* 2011).

Based on our data, we cannot directly verify whether these mechanisms occurred in our trees. However, Alejano et al. (2008) and Carevic et al. (2010) demonstrated how holm oaks at the same studied sites underwent water stress when water potentials fell below critical levels during the driest periods. Carevic et al. (2010) also indicated stomatal closure as a reaction to water shortage. Following these findings, we may hypothesize that droughts during the last decades affected our trees by inducing water stress. Holm oaks can undergo loss of hydraulic conductivity and reduction of carbon gain in conditions of water stress (Tognetti et al., 1998; Ogaya and Peñuelas, 2003; Ogaya et al., 2003). These mechanisms could be associated to the growth decline observed during the dry periods in the 1970s-1980s and mid-1990s. In contrast to the recovery following the dry period of the 1970s-1980s, growth did not recover after the droughts of the mid-1990s, notwithstanding the return of wetter conditions (upturn of the PDSI trend and precipitation in the late 1990s). This may suggest that performance decreased below some critical level and trees were unable to regain vigor. Sharp decreases in precipitation occurred in 2005 and 2009, inducing to water stress and growth reduction in our study plots and neighboring sites (Alejano et al., 2008; Carevic et al., 2010; Martín et al., 2014). Thus, drought may have helped to trigger the inception of tree mortality events in these years.

Debilitated trees may have been exposed to the effect of additional factors, including biotic agents and disturbances related to site ecology and land use. The activity of pathogenic fungi, which have been recognized as agents of oak decline in SW Spain, is enhanced by climatic instability and stressed hosts (Sánchez et al., 2002). The effect of climate change on tree mortality is also mediated by site characteristics, including edaphic conditions, microclimate, stand structure and composition (Ruiz-Benito et al., 2013; Gea-Izquierdo et al., 2014). In our study sites, soils are shallow (particularly at CA); additionally, they have low levels of nutrients, and are susceptible to erosion, desiccation and waterlogging. These soil conditions, together with a negative impact of the intensive land use carried out during decades at the studied stands (e.g. livestock management, soil tillage), might have contributed to amplify the impact of drought on trees (Corcobado et al., 2013; de Sampaio e Paiva Camilo-Alves et al., 2013). Intense management is also considered a possible factor influencing the tree health in these ecosystems. However, experiment-based assessment of the implication of management in the increase of oak mortality in Iberian open woodlands is lacking (Sánchez and López, 2011). Finally, as an additional factor, shrubs (*Cistus* spp.) could have a competitive advantage under extreme droughts and could help synergistically to reduce resilience of oaks (Rivest et al., 2011; Caldeira et al., 2015). The negative impacts of all these factors may have been aggravated in the last years before tree death, due to the increased vulnerability of trees to enhanced water stress, and likely contributed to the mortality process (Pedersen 1998; Bigler et al., 2007; Breshears et al., 2009). The causal relationships between different factors actually triggering tree death merits further research for the development of urgent mitigation practices to prevent the widespread die-off observed in the studied ecosystem.

Conclusions

We investigated the role of climate change in the current widespread oak mortality in open woodlands in Southwestern Spain. Based on ring chronologies of dead holm oaks, we assessed the sensitivity to climate. Trees strongly responded to water availability. The increased temperature and aridity appeared to drive the temporal changes in tree growth response to climate. The trees had a common pattern in growth variability, suggesting they had a common response to climate change. Droughts in recent decades induced growth decline, but climate was wetter in the last years before death, suggesting that trees were unable to recover despite the return of wetter conditions. Droughts may have caused water stress beyond a critical level, hindering tree resilience. However, physiological mechanisms associated to water stress cannot be confirmed by our data, and the existence of tolerance thresholds also merits further investigation. Moreover, other factors in addition to the enhanced water stress (including pathogens, limiting site conditions and intense management) probably contributed synergistically to the mortality process. Including tree ring data from healthy and dead trees may permit a comparative analysis of the growth trends in relation to climate, but this could not be accomplished in our study sites. However, our results indicate that climate change may have a significant role in the tree die-off process. Finding a clear causal relationship between stress factors and tree death is difficult to achieve and understanding the mechanisms underlying tree mortality remains challenging. Thus, the current widespread oak mortality in SW Spain is most probably the result of different factors acting in a complex interplay. We assess climate change as a likely factor of this process. Our observations could suggest that increasing oak mortality in the Iberian Peninsula may occur in northern and colder sites if aridity further increases as it is projected by climate change scenarios (Kovats et al., 2014).

References

Allen, C. D., Macalady, A. K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.H., Allard, G., Running, S.W., Semerci. A, Cobb, N., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. Forest Ecol Manag 259(4), 660-684.

Alejano, R., Domingo, J. M., Fernández, M. (Ed.), 2011. Manual para la gestión sostenible de las dehesas andaluzas. Foro para la Defensa y Conservación de la Dehesa "Encinal" y Universidad de Huelva, 463 pp.

Anderegg, W. R., Kane, J. M., Anderegg, L. D., 2013. Consequences of widespread tree mortality triggered by drought and temperature stress. Nature Climate Change 3(1), 30-36.

Baldocchi, D. D., Ma, S., Rambal, S., Misson, L., Ourcival, J. M., Limousin, J. M., Pereira, J., Papale, D., 2010. On the differential advantages of evergreenness and deciduousness in mediterranean oak woodlands: a flux perspective. Ecol Appl 20(6), 1583-1597.

Baquedano, F. J., Castillo, F. J., 2007. Drought tolerance in the Mediterranean species Quercus coccifera, Quercus ilex, Pinus halepensis, and Juniperus phoenicea. Photosynthetica 45(2), 229-238.

Battipaglia, G., De Micco, V., Brand, W. A., Linke, P., Aronne, G., Saurer, M., Cherubini, P., 2010. Variations of vessel diameter and δ13C in false rings of Arbutus unedo L. reflect different environmental conditions. New Phytol188(4), 1099-1112.

Bigler, C., Bugmann, H., 2004. Predicting the time of tree death using dendrochronological data. Ecol Appl 14(3), 902-914.

Bigler, C., Bräker, O. U., Bugmann, H., Dobbertin, M., Rigling, A., 2006. Drought as an inciting mortality factor in Scots pine stands of the Valais, Switzerland. Ecosystems 9(3), 330-343.

Bigler, C., Gavin, D. G., Gunning, C., Veblen, T. T., 2007. Drought induces lagged tree mortality in a subalpine forest in the Rocky Mountains. Oikos116(12), 1983-1994.

Biondi, F., Qeadan, F., 2008. A theory-driven approach to tree-ring standardization: defining the biological trend from expected basal area increment. Tree-Ring Res 64(2), 81-96.

Biondi, F., Waikul, K., 2004. DENDROCLIM2002: a C++ program for statistical calibration of climate signals in tree-ring chronologies. Comput Geosci 30(3), 303-311.

Black, B. A., Abrams, M. D., 2003. Use of boundary-line growth patterns as a basis for dendroecological release criteria. Ecol Appl 13(6), 1733-1749.

Brasier, C. M., 1996. Phytophthora cinnamomi and oak decline in southern Europe. Environmental constraints including climate change. Ann For Sci 53 (2-3), 347-358.

Brasier, C. M., Scott, J. K., 1994. European oak declines and global warming: a theoretical assessment with special reference to the activity of Phytophthora cinnamomi. EPPO Bulletin 24(1), 221-232.

Breshears, D. D., Myers, O. B., Meyer, C. W., Barnes, F. J., Zou, C. B., Allen, C. D., McDowell, N.G., Pockman, W. T., 2008. Tree die-off in response to global change-type drought: mortality insights from a decade of plant water potential measurements. Front Ecol Environ 7(4), 185-189.

Bunn, A. G., 2008. A dendrochronology program library in R (dplR). Dendrochronologia 26(2), 115-124.

Caldeira, M. C., Lecomte, X., David, T. S., Pinto, J. G., Bugalho, M. N., Werner, C., 2015. Synergy of extreme drought and shrub invasion reduce ecosystem functioning and resilience in water-limited climates. Scientific reports 5:15110, DOI: 10.1038/srep15110

Camarero, J. J., Olano, J. M., Parras, A., 2010. Plastic bimodalxylogenesis in conifers from continental Mediterraneanclimates. New Phytol 185(2), 471-480.

Camarero, J. J., Martín, E., Gil-Pelegrín, E., 2003. The impact of a needleminer (Epinotia subsequana) outbreak on radial growth of silver fir (Abies alba) in the Aragón Pyrenees: a dendrochronological assessment. Dendrochronologia 21(1), 3-12.

Campelo, F., Gutierrez, E., Ribas, M., Nabais, C., Freitas, H., 2007. Relationships between climate and double rings in Quercus ilex from northeast Spain. Can J Forest Res 37(10), 1915-1923.

Campelo, F., Nabais, C., García-González, I., Cherubini, P., Gutiérrez, E., Freitas, H., 2009. Dendrochronology of Quercus ilex L. and its potential use for climate reconstruction in the Mediterranean region. Can J Forest Res 39(12), 2486-2493.

Carevic, F., 2010. Evaluación de la producción de bellota de Quercus ilex ssp. ballota (Desf) Samp., y de factores ecofisiológicos influyentes, en dehesas de la provincia de Huelva. Dissertation, Universidad de Huelva

Carevic, F. , Fernández, M., Alejano, R., Vázquez-Piqué, J., Tapias, R., Corral, E., Domingo, J., 2010. Plant water relations and edaphoclimatic conditions affecting acorn production in a holm oak (Quercus ilex L. ssp. ballota) open woodland. Agroforest Syst 78(3), 299-308.

Carnicer, J., Coll, M., Ninyerola, M., Pons, X., Sánchez, G., Peñuelas, J., 2011. Widespread crown condition decline, food web disruption, and amplified tree mortality with increased climate change-type drought. P Natl A Sci USA 108(4), 1474-1478.

Carrasco, A. (Ed.) 2009. Procesos de Decaimiento Forestal (la Seca), Situación del Conocimiento. Consejería de Medio Ambiente, Junta de Andalucía, Córdoba, 98 pp.

Catoni, R., Gratani, L., 2014. Variations in leaf respiration and photosynthesis ratio in response to air temperature and water availability among Mediterranean evergreen species. J Arid Environ 102, 82-88.

Cherubini, P., Gartner, B. L., Tognetti, R., Braker, O. U., Schoch, W., Innes, J. L., 2003. Identification, measurement and interpretation of tree rings in woody species from Mediterranean climates. Biol Rev 78(01), 119-148

Chhin, S., Wang, G. G., 2005. The effect of sampling height on dendroclimatic analysis. Dendrochronologia 23(1), 47-55.

Choat, B., Jansen, S., Brodribb, T.J., Cochard, H., Delzon, S., Bhaskar, R., Bucci, S.J., Feild, T.S., Gleason, S.M., Hacke, U.G. and Jacobsen, A.L., 2012. Global convergence in the vulnerability of forests to drought. Nature 491(7426), 752-755.

Cook, E.R., Briffa, K.R., Shiyatov, S., Mazepa, V.,1990a. Tree-ring standardization and growth-trend estimation. In: Cook, E.R., Kairiukstis, L.A. (Ed.) Methods of dendrochronology: applications in the environmental sciences. Kluwer Academic Publishers, Boston, pp. 104-123

Cook, E.R., Shiyatov, S., Mazepa, V., 1990b. Estimation of the mean chronology. In: Cook, E.R., Kairiukstis, L.A. (Ed.) Methods of dendrochronology: applications in the environmental sciences. Kluwer Academic Publishers, Boston, pp. 123-127

Corcobado, T., Cubera, E., Moreno, G., Solla, A., 2013. Quercus ilex forests are influenced by annual variations in water table, soil water deficit and fine root loss caused by Phytophthora cinnamomi. Agr Forest Meteorol169, 92-99.

D'Arrigo, R. D., Kaufmann, R. K., Davi, N., Jacoby, G. C., Laskowski, C., Myneni, R. B., Cherubini, P., 2004. Thresholds for warming-induced growth decline at elevational tree line in the Yukon Territory, Canada. Global Biogeochem Cy 18(3).

David, T.S., Henriques, M.O., Kurz-Besson, C., Nunes, J., Valente, F., Vaz, M., Pereira, J.S., Siegwolf, R., Chaves, M.M., Gazarini, L.C. and David, J.S., 2007. Water-use strategies in two co-occurring Mediterranean evergreen oaks: surviving the summer drought. Tree Physiol 27 (6), 793-803.

De Luis, M., Cufar, K., Di Filippo, A., Novak, K., Papadopoulos, A., Piovesan, G., Rathgeber, C.B.K., José Raventós, J., Saz, M.A., Smith, K. A., 2013. Plasticity in dendroclimatic response across the distribution range of Aleppo pine (Pinus halepensis). Plos One, 8(12), e83550.

de Sampaio e Paiva Camilo-Alves, Maria Ivone Esteves da Clara, Nuno Manuel Cabral de Almeida Ribeiro, 2013. Decline of Mediterranean oak trees and its association with Phytophthora cinnamomi: a review. Eur J For Res 132(3), 411-432

Di Filippo, A., Alessandrini, A., Biondi, F., Blasi, S., Portoghesi, L., Piovesan, G., 2010. Climate change and oak growth decline: Dendroecology and stand productivity of a Turkey oak (Quercus cerris L.) old stored coppice in Central Italy. Ann For Sci 67(7), 706

Fritts, H. C., 1976. Tree rings and climate. Academic Press, London

Gea-Izquierdo, G., Martín-Benito, D., Cherubini, P., Isabel, C., 2009. Climate-growth variability in *Quercus ilex* L. west Iberian open woodlands of different stand density. Ann For Sci 66(8), 802.

Gea-Izquierdo, G., Cherubini, P., Cañellas, I., 2011. Tree-rings reflect the impact of climate change on *Quercus ilex* L. along a temperature gradient in Spain over the last 100years. Forest Ecol Manag 262(9), 1807-1816.

Gea-Izquierdo, G., Cañellas, I., 2014. Local climate forces instability in long-term productivity of a Mediterranean oak along climatic gradients. Ecosystems17(2), 228-241.

Gea-Izquierdo, G., Viguera, B., Cabrera, M., Cañellas, I., 2014. Drought induced decline could portend widespread pine mortality at the xeric ecotone in managed mediterranean pine-oak woodlands. Forest Ecol Manag 320, 70-82.

Gea-Izquierdo, G., Guibal, F., Joffre, R., Ourcival, J. M., Simioni, G., Guiot, J., 2015. Modelling the climatic drivers determining photosynthesis and carbon allocation in evergreen Mediterranean forests using multiproxy long time series. Biogeosciences 12, 3695-3712.

Gouhier, T.C., Grinsted, A., 2013. Package “biwavelet”, http://biwavelet.r-forge.r-project.org (last access: 7th March 2016)

Gratani, L., Catoni, R., Varone, L., 2013. Morphological, anatomical and physiological leaf traits of Q. ilex, P. latifolia, P. lentiscus, and M. communis and their response to Mediterranean climate stress factors. Bot Stud, 54(1), 1-12.

Grinsted, A., Moore, J. C., Jevrejeva, S., 2004. Application of the cross wavelet transform and wavelet coherence to geophysical time series. Nonlinear Proc Geoph, 11(5/6), 561-566.

Grissino-Mayer, H. D., 2001. Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. Tree-Ring Res 57, 205–221

Hereş, A. M., Martínez-Vilalta, J., López, B. C., 2012. Growth patterns in relation to drought-induced mortality at two Scots pine (*Pinus sylvestris* L.) sites in NE Iberian Peninsula. Trees-Struct Funct 26(2), 621-630.

Hogg, E. H., Brandt, J. P., Michaelian, M., 2008. Impacts of a regional drought on the productivity, dieback, and biomass of western Canadian aspen forests. Can J Forest Res 38(6), 1373-1384.

Kovats, R.S., Valentini, R., Bouwer, L.M., Georgopoulou, E., Jacob, D., Martin, E., Rounsevell, M., Soussana, J.F., 2014. Europe. In: Barros, V.R., Field, C.B., Dokken, D.J., Mastrandrea, M.D., Mach, K.J., Bilir, T.E., Chatterjee M.E., Ebi, K.L., Estrada, Y.O., Genova, R.C., Girma ,G., Kissel, E.S., Levy, A.N., MacCracken, S., Mastrandrea, P.R., White, L.L. (Ed.) Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, pp. 1267–1326

Linares, J. C., Camarero, J. J., Carreira, J. A., 2009. Interacting effects of changes in climate and forest cover on mortality and growth of the southernmost European fir forests. Global Ecol Biogeogr 18(4), 485-497.

Lo Gullo, M. A., Salleo, S., 1993. Different vulnerabilities of Quercus ilex L. to freeze- and summer drought-induced xylem embolism: an ecological interpretation. Plant Cell Environ 16(5), 511-519.

López, G., Sánchez, I., 2011.Evaluación del estado fitosanitario. In: Alejano, R., Domingo, J.M., Fernandez, M. (Ed.) Manual para la Gestión Sostenible de las Dehesas Andaluzas. Foro Encinal-Universidad de Huelva, Huelva, p. 160

Martín, D., Vázquez-Piqué, J., Fernández, M., Alejano, R., 2014. Effect of ecological factors on intra-annual stem girth increment of holm oak. Tres-Struct Funct 28(5), 1367-1381.

Martínez-Vilalta, J., Piñol, J., 2002. Drought-induced mortality and hydraulic architecture in pine populations of the NE Iberian Peninsula. Forest Ecol Manag 161(1), 247-256.

McDowell, N., Pockman, W. T., Allen, C. D., Breshears, D. D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A., Williams, D.G., Yepez, E. A., 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought?. New Phytol 178(4), 719-739.

McDowell, N. G., Beerling, D. J., Breshears, D. D., Fisher, R. A., Raffa, K. F., Stitt, M., 2011. The interdependence of mechanisms underlying climate-driven vegetation mortality. Trends Ecol Evol 26(10), 523-532.

McDowell, N. G., 2011. Mechanisms linking drought, hydraulics, carbon metabolism, and vegetation mortality. Plant Physiol 155(3), 1051-1059.

Morin, X., Roy, J., Sonié, L., Chuine, I., 2010. Changes in leaf phenology of three European oak species in response to experimental climate change. New Phytol 186(4), 900-910.

Natalini, F., Correia, A. C., Vázquez-Piqué, J., Alejano, R., 2015. Tree rings reflect growth adjustments and enhanced synchrony among sites in Iberian stone pine (Pinus pinea L.) under climate change. Ann For Sci 72(8), 1023-1033.

Navarro, R.M., 2011. Situación actual de las dehesas andaluzas. In: Alejano, R., Domingo, J.M., Fernandez, M., (Ed). Manual para la Gestión Sostenible de las Dehesas Andaluzas. Foro Encinal-Universidad de Huelva. Huelva, pp. 62-68

Nowacki, G. J., Abrams, M. D., 1997. Radial-growth averaging criteria for reconstructing disturbance histories from presettlement-origin oaks. Ecol Monogr 67(2), 225-249.

Ogaya, R., Peñuelas, J., 2003. Comparative field study of Quercus ilex and Phillyrea latifolia: photosynthetic response to experimental drought conditions. Environ Exp Bot 50(2), 137-148.

Ogaya, R., Peñuelas, J., Martínez-Vilalta, J., Mangirón, M., 2003. Effect of drought on diameter increment of Quercus ilex, Phillyrea latifolia, and Arbutus unedo in a holm oak forest of NE Spain. Forest Ecol Manag 180(1), 175-184.

Oliveira, G., Peñuelas, J., 2000. Comparative photochemical and phenomorphological responses to winter stress of an evergreen (Quercus ilex L.) and a semi-deciduous (Cistus albidus L.) Mediterranean woody species. Acta Oecol 21(2), 97-107.

Pedersen, B. S., 1998. The role of stress in the mortality of midwestern oaks as indicated by growth prior to death. Ecology 79(1), 79-93.

Pereira, J. S., Mateus, J. A., Aires, L. M., Pita, G., Pio, C., David, J. S., Rodrigues, A., 2007. Net ecosystem carbon exchange in three contrasting Mediterranean ecosystems - the effect of drought. Biogeosciences 4(5), 791-802.

Piovesan, G., Biondi, F., Fillippo, A. D., Alessandrini, A., Maugeri, M., 2008. Drought-driven growth reduction in old beech (Fagus sylvatica L.) forests of the central Apennines, Italy. Glob Change Biol 14(6), 1265-1281.

Plieninger, T., Pulido, F. J., Schaich, H., 2004). Effects of land-use and landscape structure on holm oak recruitment and regeneration at farm level in Quercus ilex L. dehesas. J Arid Environ, 57(3), 345-364.

Poage, N. J., Tappeiner, II, J. C., 2002. Long-term patterns of diameter and basal area growth of old-growth Douglas-fir trees in western Oregon. Can J Forest Res 32(7), 1232-1243.

Pulido, F. J., Dı́az, M., de Trucios, S. J. H., 2001. Size structure and regeneration of Spanish holm oak Quercus ilex forests and dehesas: effects of agroforestry use on their long-term sustainability. Forest Ecol Manag 146(1), 1-13.

Rivest, D., Rolo, V., López-Díaz, L., Moreno, G., 2011. Shrub encroachment in Mediterranean silvopastoral systems: Retama sphaerocarpa and Cistus ladanifer induce contrasting effects on pasture and Quercus ilex production. Agr Ecosyst Environ 141(3), 447-454.

Rodrigo, F. S., Trigo, R. M., 2007. Trends in daily rainfall in the Iberian Peninsula from 1951 to 2002. Int J Climatol 27(4), 513-529

Ruiz-Benito, P., Lines, E. R., Gómez-Aparicio, L., Zavala, M. A., Coomes, D. A., 2013. Patterns and drivers of tree mortality in Iberian forests: climatic effects are modified by competition. PLos One, 8(2), e56843. DOI: 10.1371/journal.pone.0056843

Sánchez, M. E., Caetano, P., Ferraz, J., Trapero, A., 2002. Phytophthora disease of Quercus ilex in south-western Spain. Forest Pathol 32(1), 5-18.

Sánchez, I., López, G. 2011. Tratamientos sanitarios: actuaciones para el control de plagas y enfermedades en la dehesa. In: Alejano, R., Domingo, J.M., Fernández, M. (Ed.) Manual para la Gestión Sostenible de las Dehesas Andaluzas. Foro Encinal-Universidad de Huelva, Huelva, pp. 334-346

Schweingruber, F. H., 1996. Tree rings and Environment. Dendroecology. Paul Haupt Publishers, Vienna, 609 pp.

Sillett, S. C., Van Pelt, R., Koch, G. W., Ambrose, A. R., Carroll, A. L., Antoine, M. E., Mifsud, B. M., 2010. Increasing wood production through old age in tall trees. Forest Ecol Manag 259(5), 976-994.

Speer, J., 2010. Fundamentals of Tree-Ring Research. The University of Arizona Press, Tucson

Sumner, G. N., Romero, R., Homar, V., Ramis, C., Alonso, S., Zorita, E., 2003. An estimate of the effects of climate change on the rainfall of Mediterranean Spain by the late twenty first century. Clim Dynam 20(7-8), 789-805.

Tognetti, R., Longobucco, A., Raschi, A., 1998. Vulnerability of xylem to embolism in relation to plant hydraulic resistance in Quercus pubescens and Quercus ilex co-occurring in a Mediterranean coppice stand in central Italy. New Phytol 139(3), 437-447.

van der Schrier, G., Briffa, K.R., Jones, P.D., Osborn, T.J., 2006. Summer moisture variability across Europe. J Climate 19, 2818-2834, DOI:10.1175/JCLI3734.1,

Vaz M, Pereira JS, Gazarini LC, David TS, David JS, Rodrigues A, Maroco J, Chaves MM, 2010. Drought-induced photosynthetic inhibition and autumn recovery in two Mediterranean oak species (*Quercus ilex* and *Quercus suber*). Tree Physiol 30:946–956

Vázquez-Piqué, J., 2011. Clima. In: Alejano, R., Domingo, J. M., Fernández, M. (Ed.), 2011). Manual para la gestión sostenible de las dehesas andaluzas. Foro para la Defensa y Conservación de la Dehesa "Encinal" y Universidad de Huelva, pp. 85-107

Wigley, T. M., Briffa, K. R., Jones, P. D., 1984. On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. J Clim Appl Meteorol 23(2), 201-213.

Wilmking, M., Juday, G. P., Barber, V. A., Zald, H. S., 2004. Recent climate warming forces contrasting growth responses of white spruce at treeline in Alaska through temperature thresholds. Glob Change Biol 10(10), 1724-1736.

Zhang, S. H., Romane, F., 1991. Variations de la croissance radiale de Quercus ilex L en fonction du climat. Ann For Sci 48 (2), 225-234.

Figures

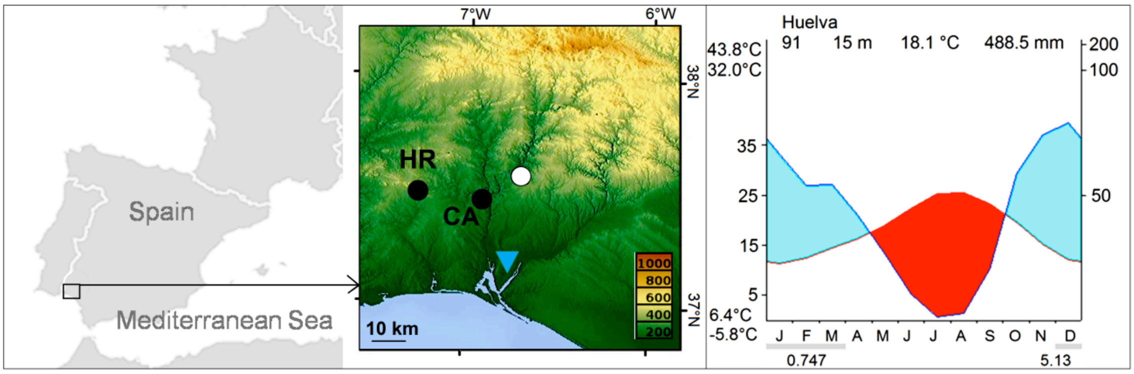


Figure 1. Locations of the study sites (CA and HR) and climate diagram based on data from the meteorological station of Huelva. In the map, the white circle indicates the location of the Pinus pinea chronology ("Valverde del Camino" in Natalini et al., 2015) used as reference for HR and CA chronologies, and the blue triangle indicates the location of the meteorological station of Huelva.

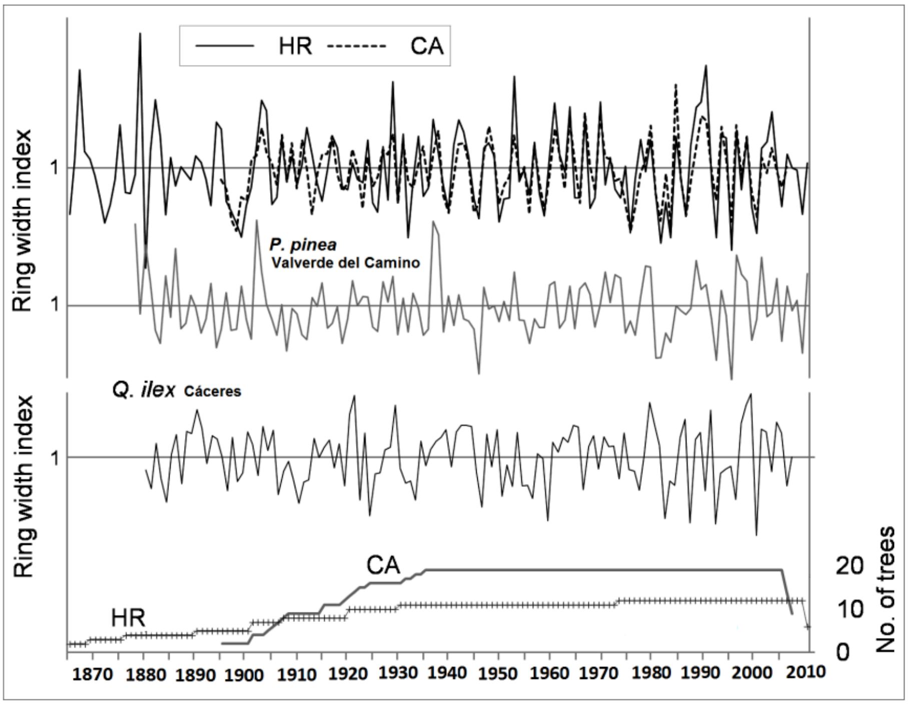


Figure 2. Indexed chronologies of the two study sites (CA and HR) and reference series (P. pinea from Valverde del Camino and Q. ilex from Cáceres). The bottom panel shows the number of measured trees in CA and HR.

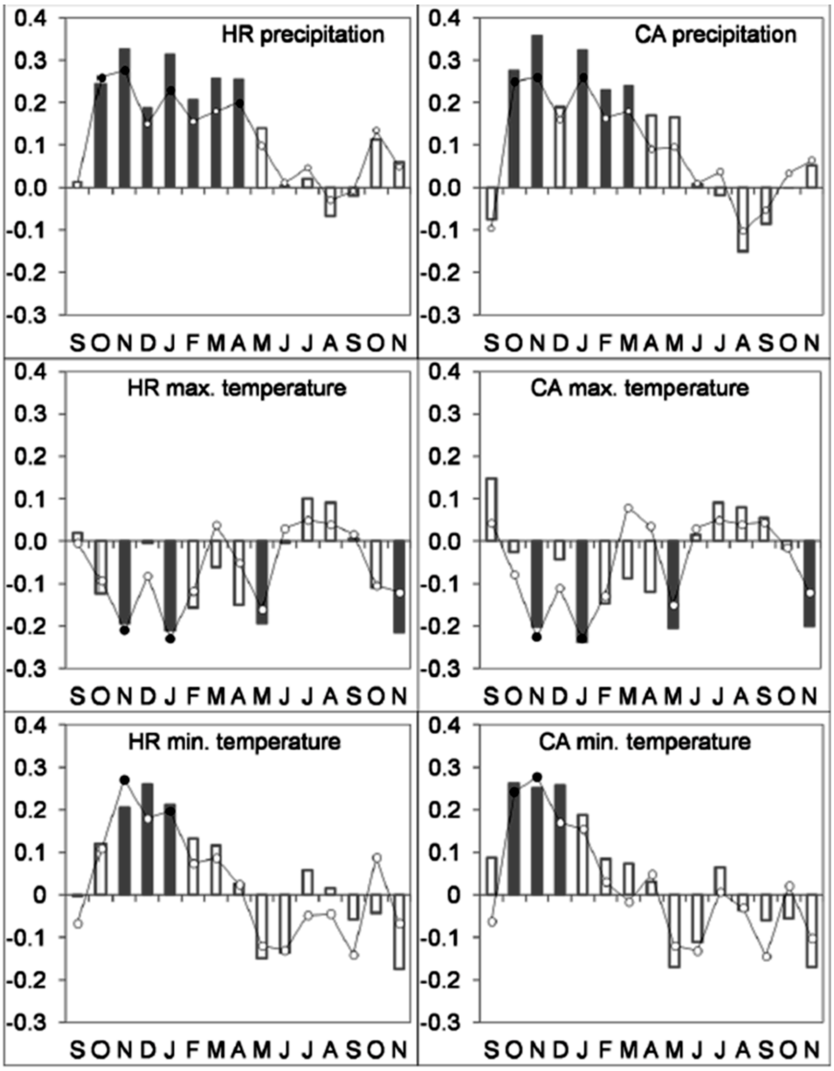


Figure 3. Bootstrapped correlations (bars) and response functions (circles) of tree-ring indexes with monthly precipitation (top), maximum temperature (middle), and minimum temperature (bottom) from September of the year prior to ring formation, to November of the year of ring formation. Grey bars and black circles indicate significant correlation and response function coefficients, respectively (α = 0.05).

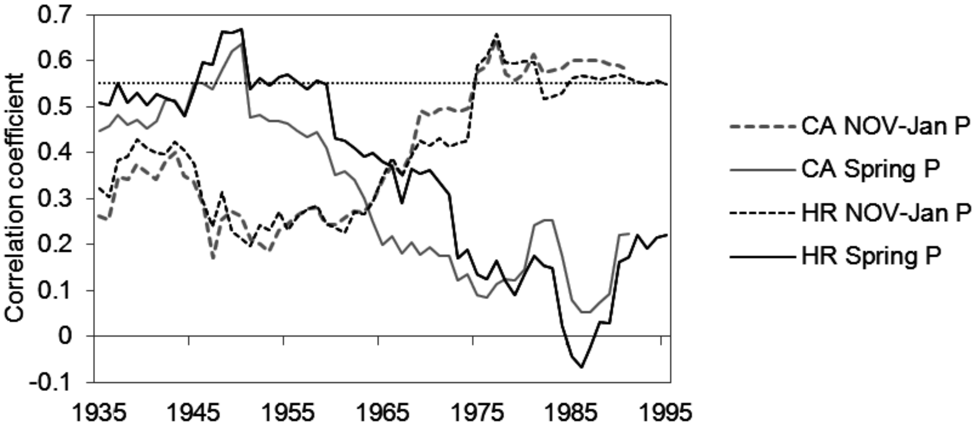


Figure 4. Thirty-year running-window correlation between growth indices and climate. Months of the year prior to the year of ring formation are in capital letters. The horizontal dotted line indicates the threshold for statistically critical value α = 0.05 modified using Bonferroni correction (α'CA = α/57 = 0.009; α'HR = α/61 = 0.008). The abscissa shows the mid-year of the 30-year running window.

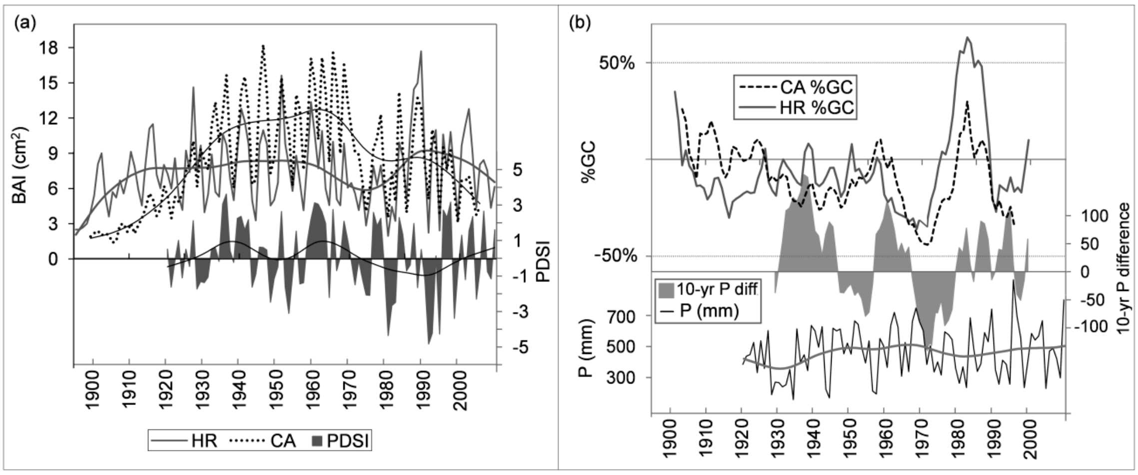
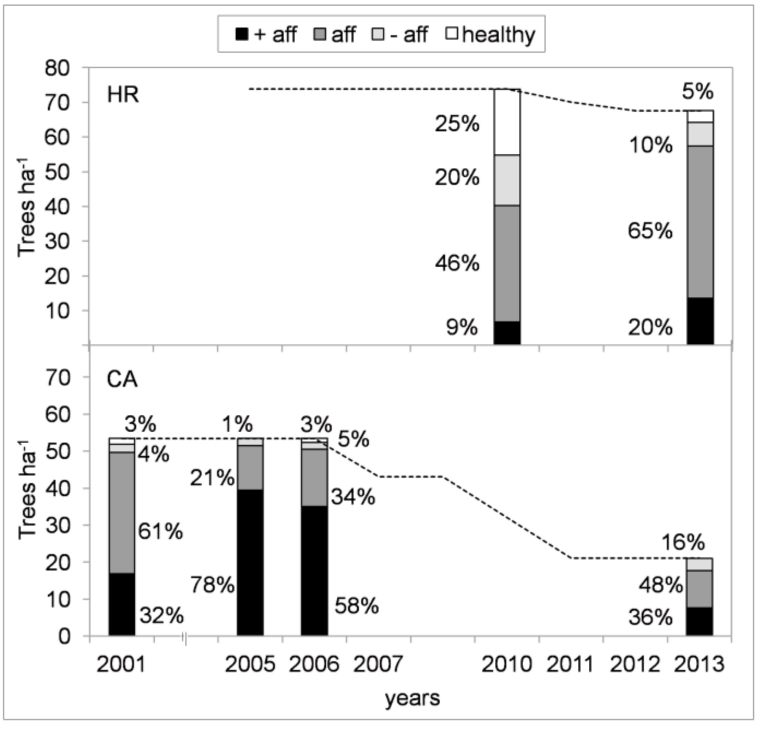
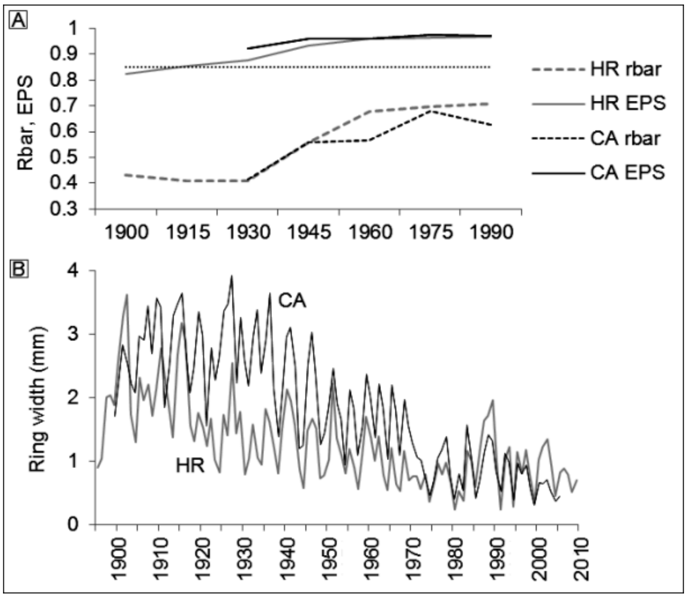


Figure 5. (a) Mean annual basal area increments (BAI) of trees in CA and HR and Palmer drought severity index (PDSI, calculated as mean of monthly values from the previous November to the current June). (b) Percent growth changes (%GC) of trees in HR and CA, precipitation (P), and 10-year differences of precipitation (10-yr P diff.). Precipitation is the cumulative precipitation from the previous November to the current June. Horizontal dotted lines in (b) correspond to the threshold (±50) of %GC. The fitted curves in BAI, PDSI and P are 30-year smoothing splines.

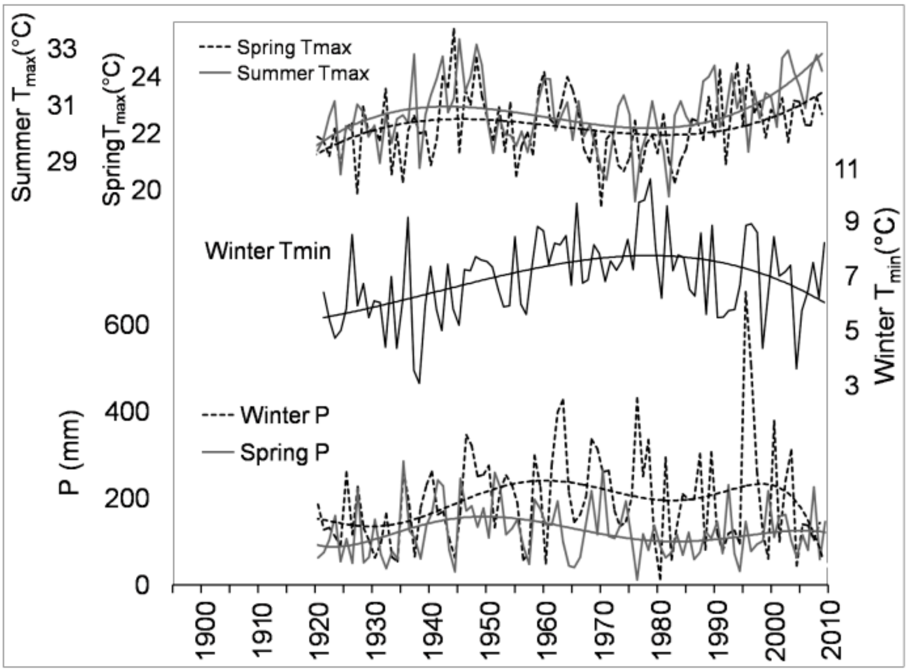
Supplementary material of Article 4



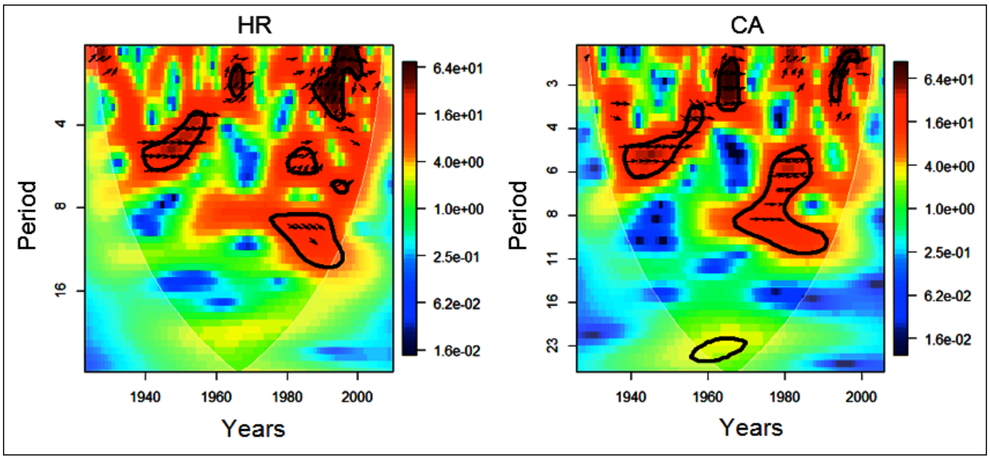
Supplementary material 1. Canopy defoliation (bars) and stand density (dotted lines) in HR and CA. Percentages in bars indicate the proportion of trees that were healthy, with crowns that were slightly affected (-aff), partially affected (aff), or heavily affected (+ aff).



Supplementary material 2. (A) Expressed population signal (EPS) and inter-series correlation coefficients (r-bar) over 30-year windows lagged by 15 years for the HR and CA chronologies. The horizontal dotted line is the critical threshold of the EPS (0.85). (B) Mean ring-width chronology in HR and CA.



Supplementary material 3. Average maximum temperatures (Tmax) in spring (March-April-May) and summer (Jun-Jul-Aug), average minimum temperaturas (Tmin) in winter (Dec-Jan-Feb), cumulative precipitation (P) in winter and spring. The smooth curves are 6th-degree polynomial functions.



Supplementary material 4. Cross-wavelet analysis of the PDSI series and HR chronology (left) and the PDSI series and CA chronology (right). The frequency domain is in the y axis (“Period”); the time domain is in the x axis (“Years”). The color bar on the right of each plot indicates the power levels. The thick black contours indicate the significant ($p<0.05$) common power between the signals of PDSI and tree-ring series. The arrows represent the relative phase relationship between signals, ranging from anti-phase (maximum phase-shift between signals, arrows pointing left) to in-phase (no differences in phase, arrows pointing right).

15.5 Information and quality index of the published scientific articles derived from this thesis

Article 1. Authors: Natalini Fabio, Vázquez-Piqué Javier, Alejano Reyes
Title: Dendroclimatic signal in managed Mediterranean forests.: a case study in SW Spain
Book : TRACE - Tree Rings in Archaeology, Climatology and Ecology, Volume 14, pp. 102-110,. DOI: 10.2312/GFZ.b103-16042
Year: 2016
ISSN: 2190-7110
Publisher: GFZ German Research Centre for Geosciences, Potsdam, Germany
Information: the publication is a result of the 14th TRACE conference (Tree Rings in Archaeology, Climatology and Ecology) organized by the Department Physical, Chemical and Natural Systems of the University Pablo de Olavide, and the Association for Tree-ring Research, and held on May 20-23, 2015, in Sevilla, Spain. The scientific articles included in the TRACE Volumes are subjected to peer review. The published manuscripts deal with different tree-ring research fields covered at the TRACE conferences, e.g. climatology, ecology, archaeology and wood anatomy.

Article 2. Authors: Natalini Fabio, Correia Alexandra, Vázquez-Piqué Javier, Alejano Reyes
Title: Tree rings reflect growth adjustments and enhanced synchrony among sites in Iberian stone pine (Pinus pinea L.) under climate change
Journal: Annals of Forest Science, Volume 72, Issue 8 (special issue "Mediterranean pines"), pp. 1023-1033, DOI: 10.1007/s00468-014-1041-y.
Year: 2015
Print ISSN: 1286-4560; Online ISSN: 1297-966X
Publisher: Springer France
Impact Factor 2015 (Thomson Reuters Journal Citation Reports® 2015): 2.086
Category: Forestry Position: 9/66. Quartile: Q1

Article 3. Authors: Natalini Fabio, Alejano Reyes, Vázquez-Piqué Javier, Marta Pardos, Rafael Calama, Ulf Büntgen
Title: Spatiotemporal variability of stone pine (Pinus pinea L.) growth response to climate across the Iberian Peninsula
Journal: Dendrochronologia, DOI: 10.1016/j.dendro.2016.07.001
Year: 2016
ISSN: 1125-7865
Publisher: Elsevier GmbH, Urban & Fischer Verlag
Journal Impact Factor 2015 (Thomson Reuters Journal Citation Reports®): 2.107
Category: Forestry Position 8/66. Quartile: Q1

Article 4. Authors: Natalini Fabio, Alejano Reyes, Vázquez-Piqué Javier, Cañellas Isabel, Gea-Izquierdo Guillermo
Title: The role of climate change in the widespread mortality of holm oak in open woodlands of Southwestern Spain
Journal: Dendrochronologia, 38, pp.51-60, DOI: 10.1016/j.dendro.2016.03.003
Year: 2016
ISSN: 1125-7865
Publisher: Elsevier GmbH, Urban & Fischer Verlag
Journal Impact Factor 2015 (Thomson Reuters Journal Citation Reports®): 2.107
Category: Forestry   Position 8/66. Quartile: Q1

16 APPENDIX 2. CONFERENCE PRESENTATION DERIVED FROM THIS THESIS

Conference presentation 1 (poster presentation). Natalini, F., Alejano, R., Vázquez-Piqué, J., Cañellas, I., Gea-Izquierdo, G., 2013. Dendroecología de Pinus pinea L. en el suroeste de España y su aplicación para el estudio de la vulnerabilidad de especies forestales ante el cambio global. 6º Congreso Forestal Español, 10-14 junio 2013, Vitoria-Gasteiz, País Vasco
Presentation **published as chapter of the proceedings**: Montero González, G., Guijarro Guzmán, M., et al. (Ed.), Actas 6º Congreso Forestal Español CD-Rom. 6CFE01-068: 12 pp. Sociedad Española de Ciencias Forestales, http://www.congresoforestal.es/index.php?men=434
Abstract. El patrimonio forestal del sur de España se encuentra amenazado por el cambio global. En ese contexto, destaca la importancia de evaluar la vulnerabilidad de las masas forestales y sus respuestas al clima. En este trabajo se estudió una cronología de Pinus pinea en Huelva, con el fin de estudiar cómo varía su productividad en relación con el clima. Las precipitaciones invernales y primaverales resultaron favorables para el crecimiento mientras las altas temperaturas en primavera fueron negativas. Los valores del incremento en área basimétrica revelaron una tendencia negativa a partir de los años 70 coincidiendo con un aumento en las condiciones de estrés hídrico. Los años de crecimiento mínimos coincidieron con los años de mínima disponibilidad hídrica. Este declive en el crecimiento puede indicar la vulnerabilidad de estas masas ante el cambio global. En las últimas décadas, se observó una correlación decreciente con las precipitaciones en junio y las temperaturas primaverales, y creciente con las temperaturas en invierno. La variabilidad de las relaciones clima-crecimiento puede indicar un proceso de adaptación a las nuevas condiciones climáticas en la fenología de la actividad cambial.

Conference presentation 2 (poster presentation). Natalini, F., Alejano, R., Vázquez-Piqué, J., Cañellas, I., Gea-Izquierdo, G., 2013. Growth trends and sensitivity to climate of declining Mediterranean open woodlands exhibiting widespread mortality in Southern Spain. Second American Dendrochronology Conference, 13-17 May 2013, Tucson, Arizona, USA. **Book of abstracts**: https://ameridendro.ltrr.arizona.edu/conferenceDisplay.py/abstractBook?confId=0 (p. 2)
Abstract. We present two chronologies of dead and weakened Quercus ilex trees from declining open woodlands of Southern Andalusia and discuss climate's implication in the current widespread mortality in these ecosystems. Basal area increments were used to find out periods of growth decline preceding death. Absent rings became frequent since the 1970s, coinciding with increasing drought. Negative pointer years matched dry years and became more pronounced in the last decades. Growth was correlated with the annual Palmer Drought Severity Index and precipitations from previous October to May. Mean sensitivity increased recently, ranging between high values (0.35-0.5). Correlations with spring temperatures turned from positive to negative, positive correlations with current autumn precipitation arose whereas significant positive

correlations with summer precipitations were no longer observed. These changes could suggest modifications on tree phenology. Intensively-used Mediterranean open woodlands of Southern Andalusia are vulnerable and the current dying process suggests that they are unlikely to overcome increasing stress climatic conditions.

Conference presentation 3 (oral presentation). Natalini, F., Vázquez-Piqué, J., Alejano, R., 2014. Plasticity in the dendroclimatic signal of *Pinus pinea* in connection to climate variability within its distribution range. EuroDendro, 8-12 September 2014, Lugo, Spain. **Book of abstracts**: García-González I., Souto-Herrero M. (Eds.), http://www.usc.es/export/sites/default/en/congresos/eurodendro/descargas/BookOfAbstracts.pdf (p. 53)

Abstract. The heterogeneous response of species to climate variability across their geographical distribution range is the result of phenotypic plasticity, which can be defined as the range of phenotypes that a single genotype can express as a function of local environmental conditions. In the actual climate change context, phenotypic plasticity of plant species is crucial for their acclimation or adaptation to new climatic conditions.

This study was aimed at contrasting the climate-growth relationships of stone pine (*Pinus pinea* L.) in coastal stands in Southwestern Spain and Central Italy to explore the heterogeneous response of this species to local climatic regimes. To this end, we established tree-ring (TR) earlywood (EW) and latewood (LW) chronologies for 7 sites in the province of Huelva (SW Spain) and for one site in Tarquinia (C Italy). Both studied regions feature Mediterranean climate. We used data from the closest meteorological stations (monthly sums of precipitations and monthly average temperatures) to characterize local climate and compute climate-growth correlations. Cross-dated TR, EW and LW width series of individual trees were standardized and averaged to attain mean site chronologies of TR, EW and LW indexes. A principal component analysis of the correlation matrix of the index chronologies from Huelva was performed. The two principal components (PC1 and PC2) were examined to identify the pattern of association of TR, EW and LW with each component. The eigenvectors were used as dependent variables and meteorological data as independent variables in correlation functions. For Tarquinia, the index chronologies were used in climate-growth correlation analysis.

The PC1 in all sites from Huelva was positively related to the TR and EW indexes, while the PC2 was positively related with the LW indexes. The first component eigenvector was positively correlated with precipitation of the previous November and current February, March and April, and negatively correlated with temperatures of the current spring (Mar-May). The second component eigenvector was positively correlated with precipitation in winter (Dec, Jan) and current autumn (Sep-Nov) and negatively correlated with temperatures in the current July. In Tarquinia, the TR and EW index chronologies were positively related to precipitation in the previous November and current June, while the LW index chronology was related to the June, August and September precipitations. No significant correlation with temperatures was found in Tarquinia.

The dendroclimatic signal in Huelva suggests that *P. pinea* in this region mostly depends on water availability in the months preceding summer and is significantly sensitive to the water stress induced by high temperatures in spring. The dendroclimatic signal in LW indicates a later phase of cambial activity in autumn. In contrast, *P. pinea* in Tarquinia is strongly influenced by precipitation in the beginning of summer, did not present any significant relationships with spring climate and LW is sensitive to precipitation also in late summer in this region. In Huelva the arid period generally lasts from May to September and drought events can also occur in April, while in Tarquinia aridity is normally limited between June and August. This study provides an insight into the plasticity of *P. pinea* in connection to climatic gradients, that could be decisive for the response of this species to climate change impacts across its geographical distribution range.

Conference presentation 4 (poster presentation). Natalini, F., Alejano, R., Vázquez-Piqué, J., 2014. Climate change-controlled dendroecological signal in Pinus pinea in Southern Spain. 5 th International Conference on Mediterranean Pines (medpine5), Solsona, Spain, September 22-26, 2014. **Book of abstracts**: Coll L., Climent J., Ximenis L., Bravo-Oviedo A., Mutke S. (Eds.), http://medpine5.ctfc.es/docs/BoA%20medPINE5_def.pdf (75).

Abstract. Researching the dynamic response to climatic variability of Mediterranean pine forests is a basic issue when evaluating the vulnerability of these ecosystems to climate change-induced abiotic stress. Tree-rings can provide valuable information to approach this purpose. We established five Pinus pinea ring-width chronologies in SW Spain. Tree-growth variability was analyzed using principal component analysis (PCA) for the period 1935-2011. A common climatic signal expressed by the first principal component (PC1) was found. Considering the PC1 scores as a regional chronology, significant correlations with meteorological data were found: correlation was positive for winter-spring precipitation and winter minimum temperatures, and negative for spring maximum temperatures. The PCA, the PC1-climate correlations and the inter-annual ringwidth variability (sensitivity) were computed for successive intervals to check whether the variance explained by the PC1, the climate-growth relationships and the intensity of growth response to climate varied over time. Both sensitivity and shared variance increased over the last decades. The correlation with winter precipitation and temperatures became stronger, spring precipitations lost significance and negative correlation with spring temperatures was enhanced. This indicates that climate became more limiting and a major force controlling growth in the recent decades. In agreement with our findings, meteorological series showed an increase of maximum temperatures in the warmer months, a decrease of minimum temperatures in winter and a marked increase of precipitation variability. Finally, running-interval correlations were performed between PC1 and three P. pinea reference chronologies from Central Spain: correlation increased significantly since the 1970s, indicating an enhanced common macroclimatic signal. Our study highlights the sensitivity of P. pinea to more restrictive climatic conditions and the synchronizing effect of climate change on P. pinea forest growth patterns at regional scale.

Conference presentation 5 (poster presentation). Natalini, F., Vázquez-Piqué, J., Alejano, R., 2015. Testing tree-ring climate proxies and detrending methods in Southwestern Iberian *Pinus pinea* L. ecosystems. Tree Rings in Archaeology, Climatology and Ecology – TRACE. 20-23 May 2015, Seville, Spain. **Book of abstracts**: http://www.dendrospain.es/?page_id=52

Abstract. The adaptive response of forests to climate change can be accessed through the study of dendroclimatic signal. Primary data and standardization methods influence the information content of dendroclimatic signals. We measured earlywood (EW), latewood (LW) and tree-ring (TR) widths in two 140-year-old even-aged *Pinus pinea* stands in SW Spain and tested three criteria for detrending tree-ring data: (1) double-detrending, *i.e.* tree-ring indices were computed from a negative exponential curve and then detrended a second time using a smoothing spline with a rigidity equal to 67% of series length (Cook, 1985; Holmes et al., 1986), (2) Regional Curve Standardization (RCS) (Esper et al., 2003), and (3) smoothing spline with a rigidity that maximized the signal-to-noise ratio (Cook et al., 1990). Tree-ring indices were computed as ratios of ring widths to the expected growth values, the 1st-order autocorrelation was removed with an autoregressive model, and mean chronologies were obtained with biweight robust means of the prewhitened indices. Residual low-frequency trends in the mean chronologies were examined by fitting polynomial curves. The high-frequency growth response to climate was studied through bootstrapped correlations between the mean chronologies and meteorological covariates. When EW and LW were examined and tree-ring data were detrended with the criterion 3, growth was highly related to rainfalls from winter to spring, negatively related to spring/early-summer high temperatures and positively related to autumn rainfalls. When TR width was examined as single variable and the detrending criteria 1 and 2 were used, the resolution of dendroclimatic signal was lower: correlations with spring rainfalls, spring/early-summer temperatures and autumn rainfalls were lower or not significant. The loss of low-frequency variability was higher with the detrending criterion 3. When dentrending criteria 1 and 2 were used, the residual low-frequency oscillations in the mean chronologies displayed effects of exogenous disturbaces (logging), and synchrony with long-term climatic changes (increasing temperatures and drought). Although maximizing the high-frequency signal can be useful to better interpret climate-growth relationships, more conservative dentrending methods may be of interest in the study of low-frequency response to climatic changes. Using multiple variables of tree-ring growth and comparing signals from different detrending methods can be advisable.

Conference presentation 6 (poster presentation). Natalini, F., Vázquez-Piqué, J., Alejano, R., 2015. Growth dynamics of Mediterranean woodlands under climate change: a dendroecological approach in southwest Iberian Peninsula. 10º Congresso Nazionale SISEF, 15-18 September 2015, Florence, Italy. **Book of abstracts**: http://www.sisef.it/sisef/x-congresso/?id=stuff

Abstract. Recently, vegetation in the Iberian Peninsula has exhibited global-change-type processes including species distribution shifts, altered plant phenology and enhanced forest decline and tree mortality. Studies based on long-term data sets, like tree rings, are providing evidences about the implication of climate change in these mechanisms. Dendrochronology is the science of dating tree rings. The term “dendroecology” refers to applications of dendrochronological techniques to obtain the information content of dated rings for studying dynamics in forest ecology and environment. Based on tree rings from 2 *Quercus ilex* L. and 7 *Pinus pinea* L. stands, we examined stand dynamics and sensitivity to climate in southwest Iberian Peninsula through dendroecological methods. In this presentation we summarize the results of these investigations and highlight common patterns in growth response to climate change.

The climate in the study region is Mediterranean. Meteorological register and climate indices describe increasing temperatures and more frequent extreme events, *i.e.* heavy rainfalls and heat waves, since the mid-1970s. The studied ecosystems differ in stand structure and silviculture (oak open-woodlands with silvo-pastoral use, closed-canopy pine stands for dune ecosystem conservation, timber and nut production), age (oaks are older than 100 years, pines vary from 70 to 150 year-old), soils (Arenosols, Cambisols, Regosols, Planosols and Luvisols in the pine stands; Regosols, Leptosols, Cambisols, Acrisols, Alisols and Lixisols in the oak stands), altitude and distance from the coast (oaks are at 170-200 m a.s.l. inland and pine stands are distributed from the coastline, 0-10 m a.s.l., to the inland, 250 m a.s.l.). The oak ecosystems were affected by massive tree mortality while pines showed no evident sign of weakening. Tree-ring width chronologies revealed growth suppressions coinciding with increasing drought. To extract the climatic signal, prewithened residual chronologies were calculated from biweight means of ratios between tree-ring widths and individual cubic splines. A common dendroclimatic signal was found in the 1st principal component of the residual chronologies. Moreover, a common response to changing climate over the last decades was indicated by increasing growth synchrony (*i.e.* intercorrelation among residual chronologies), enhanced sensitivity to climate (*i.e.* year-to-year growth variability) and similar temporal changes in climate-growth correlations (*i.e.* enhanced response to winter precipitation, lower correlation with late-spring/early summer precipitation, increasing sensitivity to high temperatures). These studies constitute the first application of dendroecology to growth dynamics in Southwest Iberian Mediterranean forests and provide an assessment of the adaptive capacity and vulnerability of these populations to changing growing conditions.

Conference presentation 7 (oral presentation). Natalini, F., Vázquez-Piqué, J., Alejano, R., 2016. Diverse growth-climate relationships and response to climate change of Mediterranean pine woodlands in the Iberian Peninsula. Third American Dendrochronology Conference, 28 March – 1 April 2016, Mendoza, Argentina, http://ameridendro2016.mendoza-conicet.gob.ar/

Abstract. In the Iberian Peninsula, Western Mediterranean, Pinus pinea woodlands have a great environmental and socio-economic value. There is a need to know the impacts of climate change on the ecology of this species and to develop management options that may improve its sustainability. In this work we provide an assessment of the acclimation capacity and vulnerability of Iberian P. pinea populations under changing climate. These studies also present the first application of dendroecology to growth dynamics in the Southernmost Iberian P. pinea forests.

We examined 237 tree-ring chronologies from 12 sites along altitudinal and latitudinal gradients. To characterize the spatiotemporal variability of climate, records from meteorological stations and gridded datasets were used. The growth-climate relationships were analyzed. We assessed the influence of the spatiotemporal variability of climate on tree growth.

We observed enhanced growth synchrony among chronologies, an increase in inter-annual ring-width variability, and changes in growth-climate correlations, that can be related to the increased mean temperatures in all regions in recent decades. Local-level differences in climate dynamics are also reflected in the dendroclimatic signals. In the southern (warmer) sites a distinctly reduced response to spring-summer climate was found. This suggests a phenological response of P. pinea to the greater water-stress risk at the lower latitudes in this season.

Although limited to Mediterranean-type environments, P. pinea is a plastic species able to growth within a variety of climatic conditions. This can be crucial for its conservation under future climatic contexts, probably characterized by higher temperatures and more limiting water conditions. Trees in the northern (milder) zones may acclimate to a further increase of drought, while the southern populations could further approach, or exceed, an ecological limit, which may threat their sustainability.