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Edmond Pasho

Tree growth responses to drought and climate variability analyzed at multiple scales

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TREE GROWTH RESPONSES TO DROUGHT AND CLIMATE VARIABILITY ANALYZED AT MULTIPLE SCALES

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Doctoral dissertation

Edmond Pasho

IPE
Instituto Pirenaico de Ecología
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Universidad de Zaragoza
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Respuesta del crecimiento forestal a la sequia y variabilidad climatica analizada a diferentes escalas

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Tesis Doctoral
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Dedicated to my family

Los Doctores Sergio M. Vicente-Serrano y Jesús Julio Camarero Martínez, Científicos del Consejo Superior de Investigaciones Científicas (CSIC) y de la Fundación Aragonesa para la Investigación y el Desarrollo (ARAID), en el Instituto Pirenaico de Ecología (IPE), Zaragoza, España,

CERTIFICAN:

Que Señor Edmond Pasho ha realizado bajo nuestra dirección el trabajo que, para optar al grado de Doctor en Geografía, presenta con el título:

´´ Tree growth responses to drought and climate variability analyzed at multiple scales´´, y

Que el trabajo se ajusta a los objetivos establecidos en el Proyecto de Tesis Doctoral aprobado el 28 de Enero 2010, por el Departamento de Geografía y ratificado por la Comisión de Doctorado el 11 de Junio de 2010.

Y para que así conste, firmamos la presente Certificación en Zaragoza a 03 de Septiembre de 2012 para los efectos que sean oportunos.

Fdo. Sergio M. Vicente-Serrano　　　　Fdo. J. Julio Camarero Martínez

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This thesis is a summary of the following scientific articles published in international peer-review journals:

I. Pasho E, Camarero JJ, De Luis M, Vicente-Serrano SM (2011). Spatial variability in large-scale and regional atmospheric drivers of *Pinus halepensis* growth in eastern Spain. Agricultural and Forest Meteorology 151: 1106–1119.

II. Pasho E, Camarero JJ, De Luis M, Vicente-Serrano SM (2011). Impacts of drought at different time scales on forest growth across a wide climatic gradient in north-eastern Spain. Agricultural and Forest Meteorology 151: 1800-1811.

III. Pasho E, Camarero JJ, Vicente-Serrano SM (2012). Climatic impacts and drought control of radial growth and seasonal wood formation in *Pinus halepensis*. Trees, DOI: 10.1007/s00468-012-0756-x.

IV. Pasho E, Camarero JJ, De Luis M, Vicente-Serrano SM (2012). Factors driving growth responses to drought in Mediterranean forests. European Journal of Forest Research, DOI: 10.1007/s10342-012-0633-6.

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1. Agriculture and Forest Meteorology	**3.228**
2. European Journal of Forest Research	**1.942**
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LIST OF ABBREVIATIONS

(in alphabetic order)

A = Anticyclone
AC1 = First-order Autocorrelation
AEMET = Agencia Estatal de Meteorología
AMiT = Mean minimum annual temperature
AMxT = Mean maximum annual temperature
C = Cyclone
DBH = Diameter at Breast Height
DTM = Digital Terrain Model
E = Elevation
EPS = Expressed Population Signal
EW = Earlywood Width
EVI = Enhanced Vegetation Index
GIS = Geographic Information System
GPS = Geographic Position System
IS = Inceptisol
ES=Entisol
AS=aridisol
JMiT = January mean minimum temperature
JMxT = July mean maximum temperature
LW = Latewood Width
MO = Mediterranean Oscillation
MODIS = Moderate Resolution Imaging Spectro-radiometer
MOPREDAS = Monthly Precipitation Dataset
MSx = Mean Sensitivity
MW = Mean tree-ring Width
NAO = North Atlantic Oscillation
NDVI = Normalized Difference Vegetation Index
PCA = Principal Component Analysis
PDSI = Palmer Drought Severity Index
PET = Potential Evapotranspiration
R = Radiation
S = Slope
SD = Standard Deviation
SE = Standard Error
SEA = Superposed Epoch Analysis
SPI = Standardized Precipitation Index
SPEI = Standardized Precipitation Evapotranspiration Index
TRW = Tree-Ring Width
UTM = Universal Transverse Mercator
WB = Water Balance
WeMO = Western Mediterranean Oscillation

RESUMEN

La cuenca mediterránea es una de las regiones del mundo más vulnerables a los procesos de cambio climático. La variabilidad y el cambio climático en esta región están muy afectados por los procesos de circulación atmosférica. Por lo tanto, se espera que la ocurrencia de cambios en los patrones de circulación atmosférica puedan afectar al crecimiento de los bosques. La mayoría de los estudios que analizan el impacto climático sobre el crecimiento de los bosques se han centrado, habitualmente, en las condiciones climáticas de superficie, sin tener en cuenta los patrones atmosféricos que controlan el clima en grandes regiones y que también puedan afectar los procesos de crecimiento de los árboles en el espacio y el tiempo. Debido a las proyecciones hacia un mayor calentamiento y una disminución de la precipitación en la región mediterránea, se espera un aumento del impacto de la sequía en estos bosques que afectaría a sus patrones de crecimiento. Por lo tanto, los bosques de esta región deberán adaptarse no sólo a una mayor variabilidad climática, sino también a fenómenos meteorológicos extremos, como la ocurrencia de sequías más severas y frecuentes.

En la actualidad existen algunas lagunas en el conocimiento de los impactos del cambio climático y de las sequías sobre el crecimiento de los bosques mediterráneos, teniendo en cuenta la diferente vulnerabilidad de las especies forestales frente a factores de estrés y la existencia de marcados contrates espaciales en las condiciones climáticas. Por lo tanto, conocer la respuestas del crecimiento forestal a los procesos de variabilidad climática en la cuenca del Mediterráneo resulta importante para entender la sensibilidad y la capacidad de adaptación de estos bosques a las tendencias hacia una mayor aridez previstas para finales del siglo XXI. Esto resulta de vital importancia para mejorar nuestra capacidad de predicción de las consecuencias del cambio climático sobre el crecimiento de los árboles y para desarrollar estrategias de silvicultura adecuadas para mitigar los impactos en los ecosistemas forestales mediterráneos.

Teniendo en cuenta las cuestiones antes mencionadas, la investigación que presenta esta tesis analizó en primer lugar la influencia de los patrones de circulación atmosférica general y regional,

resumidos a partir de diferentes índices atmosféricos y de series de frecuencias de tipos de tiempo, y de las temperaturas y precipitaciones sobre la variabilidad espacio-temporal en la formación de madera temprana (*earlywood,* EW) y madera tardía (*latewood*, LW) en bosques de *Pinus halepensis* del este de España. Además, la investigación también analizó el impacto de la sequía cuantificada a diferentes escalas temporales sobre el crecimiento radial de ocho especies arbóreas (*Abies alba, Pinus halepensis, Quercus faginea, Pinus sylvestris, Quercus ilex, Pinus pinea, Pinus nigra* y *Juniperus thurifera*) a lo largo de un amplio gradiente climático en el noreste de España. Los principales factores geográficos y ambientales que controlan la respuesta del crecimiento forestal a la sequía también fueron investigados e identificados.

Se utilizaron técnicas dendrocronológicas para cuantificar la variabilidad del crecimiento radial de todas las especies consideradas y analizar la influencia de los diferentes parámetros climáticos y de la sequía en el crecimiento de los árboles. En particular, la respuesta del crecimiento de los árboles a la variabilidad climática, incluyendo procesos de circulación atmosférica, se evaluó únicamente en bosques de *P. halepensis*, mientras que la respuesta espacio-temporal en el crecimiento de los árboles a la sequía y los factores que condicionan esa misma respuesta se analizaron teniendo en cuenta todas las especies antes mencionadas. La investigación se ha centrado principalmente en los bosques de *P. halepensis* porque se trata de la especie dominante en las zonas más secas del área de estudio y por estar esta especie bien representada en buena parte de la región. Los sitios de muestreo se seleccionaron para capturar la mayor parte de la variabilidad climática de la región. En cada sitio de muestreo se seleccionaron al azar y muestrearon entre 10 y 35 árboles. Se obtuvieron muestras a una altura aproximada de 1,3 m del suelo mediante una barrena de tipo Pressler. Las diferentes muestras de madera se procesaron utilizando métodos dendrocronológicos estándar con la finalidad de obtener información de la variabilidad de EW, LW y de la anchura del anillo de crecimiento anual.

Con respecto a la circulación general atmosférica, se ha analizado la influencia de los tres principales patrones de circulación atmosférica que afectan a la región mediterránea occidental: la

Oscilación del Atlántico Norte (*North Atlantic Oscillation,* NAO), la Oscilación del Mediterráneo Occidental (*Western Mediterranean Oscillation*, WeMO) y la Oscilación del Mediterráneo (*Mediterranean Oscillation*, MO). Se obtuvieron series estacionales para otoño (septiembre a noviembre), primavera (abril-mayo), verano (junio a agosto) e invierno (diciembre a marzo) de los índices mensuales de los tres patrones de circulación mencionados obtenidos a partir de series de presiones a nivel del mar (*Sea level pressure*, SLP). Además, se obtuvieron series de tipos de tiempo a partir de una rejilla de series de SLP del conjunto de la Península Ibérica para comprobar su influencia en el crecimiento radial de los bosques de *P. halepensis*. También se trabajó con series mensuales de precipitación total y temperatura media obtenidas a partir de dos bases de datos climáticos homogéneos y con una elevada densidad espacial de observatorios. Con ello se determinaron los mecanismos que condicionan la influencia de los procesos de circulación atmosférica en el crecimiento de los bosques de *P. halepensis* en la región y el impacto directo de las condiciones climáticas de superficie sobre el crecimiento radial de esta especie.

Para evaluar el impacto de la sequía sobre el crecimiento de diferentes especies arbóreas en el noreste de España, se utilizó el Índice de Precipitación Estandarizada (*Standardized Precipitation Index*, SPI), calculado a diferentes escalas temporales (de 1 a 48 meses). Además, se consideró un conjunto de factores abióticos (clima, topografía, tipo de suelo) y bióticos (Índices de Vegetación obtenidos mediante imágenes de satélite, diámetro de los árboles a 1,3 m, etc.) para identificar los principales factores que determinan las diferencias espaciales en el impacto de la sequía sobre el crecimiento forestal.

La dinámica estacional de la actividad cambial y la formación de la madera en los bosques de *P. halepensis* se analizó mediante el muestreo en un bosque sometido a condiciones climáticas semiáridas. Para ello, se llevó a cabo el muestreo y preparación de muestras radiales de madera tomadas periódicamente (*mini-cores*) con el propósito de describir el proceso de crecimiento intra-anual (xilogénesis) de forma detallada y para poder comprender cómo el crecimiento estacional puede estar respondiendo a los procesos de cambio climático. Esta información detallada ha

resultado crucial para corroborar los mecanismos que explican la respuesta del crecimiento radial a la variabilidad climática y a la sequía.

En la zona de estudio se han encontrado dos patrones de crecimiento diferentes en respuesta a la variabilidad en la circulación atmosférica, principalmente como consecuencia de la variabilidad en el crecimiento entre las sub-zonas del noreste y sureste de la zona de estudio. Ello se aprecia tanto para las series de EW como para las de LW. La formación de EW y LW en las áreas más septentrionales está muy condicionada por la variabilidad que la NAO muestra en invierno y primavera, mientras que en los bosques meridionales el crecimiento se ve afectado por el índice WeMO de invierno. La formación de EW en los bosques del norte de la zona de estudio está negativamente correlacionada con los índices NAO de diciembre y abril, mientras que la formación de LW estaba asociada negativamente con el índice de la WeMO en septiembre. También se ha comprobado que la frecuencia de diferentes tipos de tiempo en invierno, verano y otoño ejerce un importante control sobre el crecimiento radial. La formación de EW en los bosques del norte se ve favorecida por una alta frecuencia de tipos de tiempo del sudoeste y oeste, mientras que una alta frecuencia de tipos del este y sureste tiene un papel negativo en la formación de EW en estas áreas. En los bosques situados en el sur, la formación de EW se ve reforzada por una elevada frecuencia de tipos del este y sudeste. La formación de EW en las zonas del norte también se ha visto favorecido por la frecuencia invernal de tipos de tiempo del sur, sudoeste y anticiclónicos, mientras que en los bosques del sur, dicha formación se relaciona negativamente con la frecuencia de tipos del sudeste y sur. El índice NAO de invierno mostraba una correlación negativa significativa con la precipitación en los bosques del norte del área de estudio, mientras que durante el invierno y el otoño el índice de la WeMO se asociaba negativamente con la precipitación en los bosques del sur. Teniendo en cuenta los registros de temperatura, la NAO de invierno muestra una relación positiva con las temperaturas mientras que en primavera y otoño se observan fuertes correlaciones negativas entre el índice de la WeMO y la temperatura en el sector septentrional del área de estudio. La formación de EW y LW aumentó en respuesta a las precipitaciones del invierno previo y de la primavera del año en curso. Además, la formación LW también se correlacionaba positivamente con la precipitación de verano y otoño del año de formación del anillo, mientras que de junio a julio elevadas temperaturas limitaban el desarrollo del anillo del árbol, principalmente en los sectores más nororientales del área de estudio.

Se observó que la NAO y la WeMO ejercían un impacto significativo sobre la formación de EW y LW en *P. halepensis*. Esta influencia se ve propagada a través de su control sobre las condiciones climáticas de superficie: la temperatura y la precipitación. La respuesta en la formación de EW y LW a la variabilidad de los patrones de circulación atmosférica y a los diferentes tipos de tiempo presentaba una elevada variabilidad geográfica, lo que indica que los cambios previstos en la circulación atmosférica a lo largo del siglo XXI pueden traducirse en importante contrastes en cuanto a la respuesta en el crecimiento de los bosques del noroeste y suroeste del área de estudio. Teniendo en cuenta la influencia de las temperaturas y las precipitaciones sobre la formación de EW y LW en bosques de *P. halepensis,* se concluye que unas elevadas temperaturas de verano y la disponibilidad de agua en el invierno previo y la primavera del año de formación del anillo determinan de manera negativa y positiva, respectivamente, la formación de EW. Estos factores controlan en menor medida la formación de LW. Esto sugiere que en un escenario de calentamiento global, como el que se predice en la cuenca occidental del Mediterráneo, los bosques de *P. halepensis* pueden mostrar un mayor descenso en la formación de EW que en la de LW, causando una disminución en la anchura de los anillos de árboles y en la producción de madera, una reducción de la conductividad hidráulica e, indirectamente, una menor captación de carbono atmosférico.

Se ha comprobado que el impacto de la sequía sobre el crecimiento varía de forma importante entre las especies y en función de la localización geográfica. Se han observado claramente dos modelos de respuesta de las especies arbóreas estudiadas a la sequía. Las especies que viven en áreas semiáridas (por ejemplo *Pinus halepensis* y *Juniperus thurifera*) mostraron respuestas de su crecimiento al SPI a escalas temporales de entre 9 y 11 meses, mientras que las especies dominantes

en zonas más húmedas (por ejemplo, *Abies alba* y *Pinus sylvestris*) respondían a escalas temporales más cortas del SPI (alrededor de 5 meses). Se observaron correlaciones significativas entre el SPI y el crecimiento radial hasta escalas temporales del SPI de 30 meses en las zonas semiáridas, mientras que no se observó una asociación consistente a escalas de tiempo mayores. Existen importantes diferencias estacionales en la influencia de las sequías sobre el crecimiento forestal. El crecimiento de las especies de zonas semiáridas responde a los índices de sequía en primavera y verano, mientras que las que se distribuyen en sitios húmedos responden exclusivamente a las condiciones de verano. Considerando solamente los bosques de *P. halepensis*, la formación y el desarrollo de EW y LW muestran una fuerte asociación negativa con las condiciones de sequía en verano y otoño, respectivamente, a escalas temporales de 10 hasta 14 meses, hacer coincidir con las fases de menor producción de EW y LW traqueidas a nivel intra-anuales de las escalas.

El análisis de la influencia de diferentes variables abióticas y bióticas sobre la diferente respuesta en el crecimiento de los bosques a la sequía entre las áreas semiáridas y húmedas ha mostrado que aquellos parámetros relacionados con las características de los bosques (diámetro de los árboles, anchura del anillo), la actividad vegetal medida mediante imágenes de satélite, factores climáticos (balance hídrico, precipitaciones y temperatura) y las variables topográficas (tipo de suelo, pendiente, altitud) están inversamente correlacionados con las respuestas a la sequía en los bosques semiáridos y húmedos, respectivamente. La mayoría de las variables climáticas (evapotranspiración potencial, temperatura máxima y mínima, media de las máximas de julio y media de las mínimas de enero, radiación solar) se relacionaron negativamente con la respuesta del crecimiento a la sequía en los bosques húmedos. La respuesta a la sequía en los bosques semiáridos está asociada con la disponibilidad de agua, la temperatura, la elevación y el índice de vegetación normalizado (*Normalized Difference Vegetation Index*, NDVI). Los análisis de regresión linear han mostrado que la respuesta del crecimiento a la sequía en los bosques semiáridos está controlada por los valores medios de precipitación anual, el tipo de suelo, el NDVI de abril a junio y la pendiente topográfica, mientras que en los bosques húmedos los principales factores que determinan la respuesta a las

sequías son el balance hídrico anual, el índice de vegetación mejorado (*Enhanced Vegetation Index*, EVI) entre abril y junio, y el tipo de suelo. Sin embargo, los coeficientes de los modelos de regresión seleccionados mostraron que la respuesta del crecimiento forestal a la sequía en los bosques semiáridos ha estado principalmente determinada por la precipitación anual, mientras que en los bosques húmedos las diferencias en el balance climático medio fueron el factor más importante de control de la respuesta a la sequía.

El uso de índices de sequía a diferentes escalas temporales resulta particularmente útil para el análisis del impacto de la variabilidad climática sobre el crecimiento de los árboles debido a que la respuesta del crecimiento a la sequía es compleja y dependiente del tiempo. Las escalas temporales a las que se acumula el déficit hídrico y que afectan al crecimiento de los árboles varían entre especies y sitios dentro de la misma especie. Por esta razón, los índices de sequía deben estar asociados a una escala temporal específica y evaluarse teniendo en cuenta las condiciones locales para ser útiles en la cuantificación del impacto de las sequías sobre el crecimiento de los bosques. La elevada variabilidad espacial y temporal, en términos de respuesta en el crecimiento a la sequía, observada entre especies y localizaciones geográficas está determinada por diferentes variables climáticas, topográficas y bióticas. Todo ello indican que es la combinación de las diferentes variables la que determina la respuesta de las diferentes especies a la sequía. Estos resultados sugieren que el proceso de calentamiento global podría alterar la respuesta del crecimiento forestal a la sequía en los lugares húmedos o submediterráneos en relación a los bosques ubicados en las zonas de características semiáridas. El incremento de la aridez en el Mediterráneo occidental probablemente causará un descenso en el crecimiento de las diferentes especies más sensibles a la sequía. No obstante, la determinación de los posibles efectos de las sequías sobre el crecimiento, en un escenario en el que las temperaturas sean mayores y las precipitaciones desciendan, constituye un aspecto todavía sin resolver y que probablemente requiera de un enfoque basado en múltiples registros, desde datos de crecimiento radial, medidas de discriminación isotópica de carbono en la madera y variables referidas a actividad vegetal y obtenidas de imágenes de satélite.

Por último, destacar que los resultados obtenidos en este trabajo pueden ser muy útiles para entender las respuestas del crecimiento forestal al cambio climático, incluyendo en el mismo una mayor frecuencia y severidad de las sequías, pero también para adaptar las estrategias de gestión apropiadas de los bosques sometidos a un elevado estrés hídrico. La gestión de los bosques mediterráneos bajo condiciones más cálidas y secas debería focalizarse en los principales factores locales que modulan los efectos negativos de la sequía sobre el crecimiento de los bosques en lugares semiáridos y húmedos.

ABSTRACT

The Mediterranean Basin is one of the most vulnerable regions in the world affected by climate change. The climate variability and changes in this region are largely influenced by atmospheric circulation dynamics, therefore changes in atmospheric circulation patterns are expected to affect also forest growth. Most studies regarding climate impact on forest growth have focused on the surface climatic conditions with no consideration of the atmospheric patterns controlling the climate over large regions and therefore tree growth spatio-temporal patterns. Given the forecasted trends of warming and declining precipitation for the Circum-Mediterranean region, an increase of the drought impact on these forests is expected, which will affect their growth patterns. Therefore, forests in this region will have to adapt not only to increased climate variability but also to extreme weather events, such as prolonged and severe droughts.

Currently there are many research gaps regarding the impacts of climate and drought on growth of Mediterranean forests, considering species with different vulnerability against climatic stressors and areas with contrasting climatic conditions. Therefore, a deeper knowledge on tree growth responses to climate variability and drought in the Mediterranean Basin is crucial to understand the sensitivity and adaptive capacity of these forests to the predicted aridification trends by the end of the twentieth-first century. This is of critical importance in improving our ability to predict the consequences of climate on tree growth and to develop suitable forestry strategies for mitigating such impacts on Mediterranean forest ecosystems.

Considering the above issues, this research was firstly focused on the influence of general and regional atmospheric circulation patterns, summarized by several atmospheric indices and the frequency of weather types, and the surface climatic drivers (temperature, precipitation) on the spatio-temporal variability of earlywood (EW) and latewood (LW) growth in *Pinus halepensis* forests in eastern Spain. In addition, the research analyzed the impact of drought measured at different time-scales on radial growth of eight tree species (*Abies alba*, *Pinus halepensis*, *Quercus faginea*, *Pinus sylvestris*, *Quercus ilex*, *Pinus pinea*, *Pinus nigra*, *Juniperus thurifera*) growing across a wide climatic gradient in north-eastern Spain. The main drivers controlling such growth response to drought were also investigated and identified.

Dendrochronology was used to quantify the variability of radial growth of all species considered in the study and to analyze the influence of climatic drivers and drought on tree growth. In particular, the response of tree growth to climate variability was evaluated on annual EW and LW width series of *P. halepensis* while the spatio-temporal growth responses to drought and the main drivers influencing such responses were analyzed considering all of the aforementioned species. *P. halepensis* was particularly investigated because it is the dominant species in the driest sites of the study area subjected to semiarid climatic conditions. The selected sites were considered to capture most of the climatically mediated growth variability of the studied species in eastern Spain. At each sampled site, 10-35 dominant trees were randomly selected and cored at 1.3 m height by taking two radial cores using a Pressler increment borer. The wood samples were prepared following standard dendrochronological methods to obtain indexed EW, LW and tree-ring widths series.

With regard to general atmospheric circulation, three main patterns affecting the western Mediterranean region were analysed: the North Atlantic Oscillation (NAO), the Western Mediterranean Oscillation (WeMO) and the Mediterranean Oscillation (MO). Autumn (September to November), spring (April to May), summer (June to August) and winter (December to March) NAO, MO and WeMO atmospheric circulation indices were calculated using monthly northern hemisphere See Level Pressure (SLP) grids covering the Iberian Peninsula. In addition, the particular circulation patterns affecting eastern Spain were quantified using the frequency of weather types, which were related to *P. halepensis* growth. Monthly data of total precipitation and mean temperature, obtained from two homogeneous and spatially dense datasets of precipitation and temperature series of eastern Spain, were used to detect the mechanisms driving the influence of atmospheric circulation processes on *P. halepensis* growth and to quantify the direct impact of surface climatic conditions on the growth of this specie.

To calculate the impact of drought on growth of different tree species in north-eastern Spain, it was employed the Standardized Precipitation Index (SPI), calculated at different time scales (1-48 months). In addition, a set of abiotic (climate, topography, soil type) and biotic (Normalized Difference Vegetation Index (NDVI), Enhanced Vegetation Index (EVI), tree ring width, diameter at breast height) variables was used to identify the main factors determining the spatial differences in the drought impacts on forest growth.

The seasonal dynamics of cambial activity and wood formation in *P. halepensis* in a semi-arid site were explored by sampling and preparing minicores with the purpose of describing the process of intra-annual tree-ring formation (xylogenesis) and understanding the seasonal growth responses to climate. This mechanistic information is necessary to fully understand the radial-growth responses to climate variability and drought stress.

There were found two distinct growth patterns in response to atmospheric variability, reflecting the growth variability in northern and southern areas of eastern Spain, for both EW and LW growth series. The EW and LW growth in northern sites was determined by the winter-spring NAO variability whereas at the southern sites it was affected by the winter WeMO index. Considering monthly values, the EW growth at northern sites was negatively related to the previous December and the current April NAO indices whereas the LW growth was negatively associated with the current September WeMO. Winter, summer and autumn weather types also exerted a control on radial growth. The EW formation in the northern sites was enhanced by a high frequency of SW and W weather types whereas the high frequency of flows from the East and Southeast had a negative role on EW growth in these areas. In the southern sites, EW formation was enhanced by a high frequency of E and SE flows. The LW growth in the northern areas was also highly related to the winter frequency of S, SW and A weather types whereas in the southern sites it was negatively related with the frequency of SE and S weather types. Winter NAO showed a significant negative correlation with precipitation in northern sites whereas winter-autumn WeMO was negatively associated with precipitation in southern sites. Considering the temperature data, winter NAO showed a positive relationship with temperatures in the northern areas while spring-autumn WeMO influence on the temperatures presented strong negative correlations in the northern parts of the study area. The EW and LW growth was enhanced by winter-spring precipitation of the current year in the entire study area. In addition the LW formation was also positively correlated with summer-autumn precipitation whereas June-July temperatures constrained the development of both components of the tree ring, particularily in the north-eastern part of the study area.

It was found that both atmospheric circulation indices and weather types exert significant impact on the EW and LW formation in *P. halepensis* forests. This influence was expressed through their control of surface climate conditions, temperature and particularly precipitation. The response of EW and LW growth to atmospheric circulation patterns and weather types was found to be geographically variable, indicating that the predicted changes in atmospheric circulation will result in contrasting tree growth responses in the northwest and southeast parts of the study area. Considering the temperature and precipitation influences on *P. halepensis* EW and LW growth, it was concluded that high summer temperatures and winter-spring water availability affected EW formation in negative and positive ways respectively, and to a lesser extent controlled the LW growth. This suggests that in a warmer future scenario, as predicted for the Western Mediterranean Basin, this species will show a more pronounced decrease in EW than in LW development causing a decline in tree-ring width and wood production, a reduction in hydraulic conductivity and, indirectly, a hampered carbon uptake.

The impact of drought on growth varied noticeably among species and sites. Two distinct patterns were clearly observed considering spatial and temporal differences in the response of species to drought. Species growing in xeric sites (e.g., *Pinus halepensis* and *Juniperus thurifera*) showed the highest responses to SPI time-scales of 9-11 months while those located in mesic sites (e.g., *Abies alba*, *Pinus sylvestris*) responded more to SPI time scales shorter than 5 months. The SPI-growth correlations were significant, although weak, up to 30 months in xeric sites while no consistent association was observed at higher time scales. Important seasonal differences were noticed in the SPI-growth associations. Species growing in xeric areas responded to spring-summer SPI while those distributed in mesic sites responded more to summer SPI. Considering *P. halepensis*, EW and LW formation at inter-annual scales showed the strongest negative associations with mid-term cumulative drought stress recorded at time-scales from 10 up to 14 months, but these responses were observed in July and September, respectively, matching the phases of lowest EW and LW tracheid production at intra-annual scales.

The associations between abiotic and biotic variables and the growth responses to drought in xeric and mesic sites indicated that tree-related (diameter at breast height, tree-ring width), remote-sensing (NDVI, EVI), climatic (water balance, precipitation, temperature) and topographic variables (soil type, slope, elevation) were significantly and inversely correlated with the growth responses to drought in xeric and mesic sites, respectively. Most climatic variables (potencial evapotranspiration, mean maximum and minimum temperatures, July mean maximum and January mean minimum temperatures, solar radiation) were negatively related with the growth responses to drought in mesic sites. The growth responses to drought in xeric sites were strongly associated with water availability, temperature, elevation and NDVI. The regression analyses indicated that growth responses to drought in xeric forests were driven by the annual precipitation, inceptisol soils, April-June NDVI and slope while in mesic sites the major drivers of such responses were annual water balance, April-June EVI and inceptisol soils. However, the coefficients of the selected regression models showed that growth responses to drought in xeric forests were mainly driven by the annual precipitation while in mesic sites the annual water balance was the most important driver.

The use of multi-scalar drought indices is particularly useful for monitoring the impact of climate variability on tree growth because the growth responses to drought are complex and time-dependent. The time scales over which water deficit accumulates and affects noticeably tree growth, vary among species and sites within the same species. For this reason, drought indices must be associated with a specific time scale and assessed taking into account local conditions to be useful for monitoring impacts on tree growth. The high spatial and temporal variability in terms of growth responses to drought observed among species and sites in the Mediterranean forests was significantly driven by climatic, topographic and biotic variables, indicating that a combination of the above variables shaped the species behavior in response to drought. These findings suggest that warming-related drought stress might alter differently tree growth in mesic compared to xeric sites. Increasing aridity in the Western Mediterranean Basin is expected to cause selective growth decline in drought-sensitive species from mesic sites. However, disentangling the relative effects of warmer conditions and reduced precipitation on tree growth is an unsolved challenge which probably requires a multiproxy approach based on long-term data of radial growth, measures of carbon isotopic discrimination in wood and remote-sensing variables.

Finally, these findings should be useful to understand forest growth responses to climate change, including an increasing frequency of severe droughts, and to adapt appropriate management strategies such as selective thinning to mitigate the impact of drought on tree growth. The management of Mediterranean forests under the forecasted warmer and drier conditions should focus on the main local factors differently modulating the negative impacts of drought on tree growth in xeric and mesic sites.

CAPÍTULO I

INTRODUCCIÓN

En este capítulo se muestra una breve introducción sobre la dendrocronología y sus aplicaciones, haciendo especial hincapié en los efectos del clima sobre el crecimiento de los árboles. Además, se proporciona información básica sobre la variabilidad del clima y la sequía en la cuenca Mediterránea, en general, y en la Península Ibérica, en particular, mostrando una revisión actualizada sobre el actual estado de la cuestión e incidiendo en la influencia del clima sobre la dinámica de los bosques de la región . La última parte de este capítulo justifica la realización de este estudio, la principal hipótesis de trabajo y los diferentes objetivos planteados.

1.1. La dendrocronología

El término dendrocronología deriva de las palabras griegas "dendro", (madera) y "cronología" (tiempo). El término hace referencia a una disciplina científica basada en un conjunto de principios, técnicas y métodos fundamentados en la datación precisa y en el estudio de los anillos anuales de crecimiento formados por plantas leñosas en zonas de clima estacional. A partir de ello se extrae, ordena e interpreta la información que contienen dichos anillos para inferir los diferentes factores que influyen en el crecimiento de los árboles y en la formación de la madera (Fritts, 1976). La dendrocronología se comenzó a desarrollar formalmente durante la primera mitad del siglo XX por el astrónomo A.E. Douglass (Douglass, 1940), que fue el fundador del Laboratorio de Investigación en Dendrocronología de la Universidad de Arizona (Tucson, Arizona, EE.UU.). Hay que tener en cuenta que la mayoría de los árboles ubicados en zonas frías y templadas, sometidas a un clima estacional, presentan un incremento periódico en el crecimiento, con la formación de anillos anuales. De hecho, de cada anillo se puede obtener información relacionada con su estructura y formación. Para ello, se pueden extraer parámetros que representan las características específicas de cada anillo: anchura, anatomía, densidad máxima, composición isotópica y otros parámetros visuales o analíticos que pueden hacer que se produzcan diferencias entre unos anillos en función de una serie de factores ecológicos y climáticos (Schweingruber, 1988).

En las zonas con una marcada estacionalidad en el clima, el crecimiento de los árboles es discontinuo, pues éste se detiene en algunos periodos debido a la limitación impuesta por determinados factores climáticos externos. Ello explica la formación de anillos anuales de crecimiento. En muchas zonas del planeta con una marcada estacionalidad climática, el parón en el crecimiento de los árboles durante los períodos desfavorables (por ejemplo, el invierno frío en gran parte del hemisferio norte o el verano seco en zonas áridas) es habitual. De hecho, la actividad del cámbium se reinicia de nuevo cuando las condiciones climáticas vuelven a resultar favorables. Este patrón anual de actividad y crecimiento determina finalmente la estructura de la madera en forma de capas concéntricas anuales que, en sección transversal, se observan como anillos. En una escala intra-anual, la producción de nuevas células del xilema (xilogénesis o formación de la madera) es rápida en la primera fase de crecimiento, disminuye a medida que avanza el verano y se detiene cuando las condiciones climáticas empeoran. Estas diferencias en la tasa de formación de células se reflejan también en las características de los anillos de los árboles, ya que se pueden apreciar dos bandas de crecimiento: la madera temprana (*early wood*, EW), formada a principios del período de crecimiento (primavera, verano) y la madera tardía (*late wood*, LW) formada a finales de la estación de crecimiento (verano, otoño). En las coníferas (pinos, abetos, etc.) la EW es clara y está formada por traqueidas con lúmenes transversales anchos y paredes celulares delgadas, mientras que la LW es oscura y está formada por traqueidas estrechas con paredes celulares gruesas (Schweingruber, 1988). Las diferencias de tamaño, densidad y color entre la parte lignificada oscura de un anillo y la clara permiten la identificación y datación de los anillos.

La dendrocronología tiene aplicaciones en diferentes campos científicos debido a que los anillos contienen información sobre diferentes factores. Esta información se puede recuperar y analizar convenientemente, lo que permite el estudio y análisis de diferentes procesos ecológicos, geomorfológicos, climáticos, arqueológicos, etc., en el espacio y el tiempo a partir de una señal que pueda ser extraída de los anillos (Gutiérrez, 2008). Por ejemplo, los anillos de los árboles pueden registrar el efecto de los incendios forestales, terremotos, erupciones volcánicas, deslizamientos del terreno, caídas de rocas, avalanchas, inundaciones, el avance y retroceso de los glaciares, etc. Todos estos fenómenos pueden ser datados mediante las señales que dejan en los anillos, lo que permite determinar la frecuencia e intensidad con la que estos fenómenos ocurren en la zona afectada.

En ecología y siguiendo un enfoque retrospectivo, la dendrocronología es muy útil para estudiar procesos que ocurren a escalas de tiempo largas e implican a organismos longevos como los árboles. Por ejemplo, el estudio de los anillos de los árboles permite datar el año de germinación y muerte de los árboles, que son los dos procesos clave en la dinámica de las poblaciones y en la sucesión de los bosques. El análisis de las series de crecimiento anual permite la determinación de los regímenes de perturbaciones que pueden afectar la dinámica del bosque e incluso establecer la intensidad de la competencia entre árboles.

El clima es el factor ambiental más importante que influye en el crecimiento radial de las plantas leñosas y en particular en los árboles (Fritts, 1976). Cuando los diferentes factores climáticos limitan el crecimiento de los árboles, los anillos formados son normalmente más estrechos en la mayoría de los árboles de una región en particular. Como resultado de la estrecha relación entre el crecimiento radial y las condiciones climáticas, las series de anillos anuales formados por árboles que crecen bajo las mismas condiciones climáticas muestran una cierta sincronía, siendo su patrón de variación temporal muy similar entre árboles (Fritts, 1976). Esta señal climática que permanece en la madera constituye también una "firma" temporal, debido a que resulta muy poco probable que un determinado patrón temporal específico se repite exactamente igual en otro período. La señal climática registrada en los anillos de los árboles se puede así utilizar para reconstruir la evolución del clima en el pasado en períodos sin registros meteorológicos instrumentales. En particular, resulta posible reconstruir las variables climáticas que más limitan el crecimiento de los árboles, y que muestran una influencia significativa en la formación de los anillos anuales. Por ejemplo, es de esperar que las temperaturas y precipitaciones sean los principales factores de crecimiento en los bosques de climas fríos (por ejemplo, bosques subalpinos) y secos (por ejemplo, bosques en zonas semiáridas), respectivamente. Los estudios dendrocronológicos llevan a cabo la elaboración de cronologías de crecimiento formadas a partir de un gran número de series obtenidas de un gran número de árboles de la misma especie que crecen en el mismo lugar con el objetivo de maximizar la señal climática común (Cook y Kairiuktsis, 1990).

En resumen, la dendrocronología es una poderosa herramienta científica utilizada para mostrar cómo las condiciones climáticas determinan el crecimiento radial de los árboles (Schweingruber et al., 1988). Por esta razón, los anillos de árboles se han utilizado ampliamente como una aproximación válida en el estudio a largo plazo de los patrones de crecimiento de los árboles. Además, la anchura del anillo se puede utilizar como estima (*proxy*) de la producción primaria neta, o de la capacidad de captar carbono por parte de los bosques, y para evaluar el impacto de los cambios ambientales sobre los patrones de crecimiento. Ello se basa en la suposición general de que la relación entre el crecimiento de los árboles y el clima permanece aproximadamente constante a lo largo del tiempo (Fritts, 1976). Además, la variabilidad temporal en el ancho de los anillos de los árboles se ha utilizado para: reconocer posibles cambios en la sensibilidad del crecimiento de los árboles al clima (Andreu et al., 2007), estudiar la variabilidad regional en la relación entre el crecimiento de los árboles y el clima dentro de una especie a partir de redes dendrocronológicas (Tardif et al., 2003; Piovesan et al., 2005; Carrer et al., 2007) o identificar la reciente disminución del crecimiento asociada al calentamiento global y la sequía en las regiones mediterráneas (Salto et al., 2006; Sarris et al., 2007; Camarero et al., 2011).

1.2. Variabilidad climática y crecimiento forestal en la región mediterránea: el papel de las sequías.

A lo largo del siglo XX se han observado numerosos cambios en la cuenca mediterránea con relación a la amplitud ecológica, composición, dinámica y fenología de los bosques (Walther et al., 2002; Peñuelas y Boada, 2003). Estos fenómenos se conectan de forma significativa con el cambio climático observado en la región (Parmesan y Yohe, 2003; Linares et al., 2010). De forma natural, el clima de la cuenca mediterránea presenta frecuentes y severos períodos de sequía intensas (Briffa et al., 1994; Demuth y Stahl, 2001; Lloyd-Huges y Saunders, 2002a,b; Vicente-Serrano, 2006; González-Hidalgo et al., 2009) y una elevada variabilidad interanual de las precipitaciones (Palutikof et al., 1994; Trigo et al., 2000; Hasanean, 2004; Zveryaev, 2004; Giorgi y Lionello, 2008; González-Hidalgo et al., 2009). Los escenarios de cambio climático predicen un notable aumento de la temperatura (+2-4°C) y una disminución de la precipitación (cerca del -20%) en la cuenca mediterránea a lo largo del siglo XXI (Gibelin y Deque, 2003; IPCC, 2007). La tendencia prevista hacia un incremento de las condiciones de aridez estará asociada a un incremento de la frecuencia de condiciones anticiclónicas y un desplazamiento hacia el norte en la trayectoria de las borrascas atlánticas (Giorgi y Lionello, 2008). Por otra parte, también se espera un aumento en los gradientes de presión en superficie entre las regiones norte y sur del Atlántico Norte (Paeth y Pollinger, 2010), una disminución en la frecuencia e intensidad de los ciclones mediterráneos (Raible et al., 2010), y una disminución de los sistemas convectivos estivales (Brankovic et al., 2008; May, 2008). Estas condiciones conducirían a una intensificación de los episodios extremos de sequía, también como consecuencia del aumento de las tasas de evapotranspiración (Giorgi y Lionello, 2008). Ello podría llegar a modificar el crecimiento y la distribución de las especies arbóreas mediante una notable disminución del crecimiento y un aumento de la mortalidad, sobre todo en ecosistemas vulnerables a la sequía (Martínez-Vilalta y Piñol, 2002).

Los bosques son particularmente sensibles al cambio climático debido a que la larga vida de los árboles no permite una adaptación inmediata a cambios ambientales rápidos como es el caso del calentamiento actual (Kuparinen et al., 2010). Los bosques responden al calentamiento climático a través de cambios en el crecimiento y de la actividad vegetal (por ejemplo, mediante procesos de defoliación), actuando como sistemas de monitorización de los efectos del cambio climático sobre los ecosistemas terrestres (Bonan, 2008). En los bosques mediterráneos de coníferas de montaña, en los que la escasez de agua es además de la temperatura un importante factor limitante del crecimiento de los árboles, el calentamiento global podría afectar a la producción de madera debido a un aumento de la aridez (Martínez-Vilalta y Piñol, 2002; Macías et al. 2006; Camarero y Gutiérrez, 2007; Linares et al., 2010). En las regiones semiáridas, en las que la disponibilidad de agua es el principal factor limitante del crecimiento, la variabilidad de la precipitación es el principal factor determinante de la productividad de los árboles y de la dinámica de los bosques (Vicente-Serrano, 2007; Sarris et al., 2007). Por lo tanto, se pueden encontrar diferentes patrones de respuesta al cambio climático en función de las condiciones bioclimáticas y de los tipos de bosque. En general, se espera que los bosques ubicados en los límites de su distribución geográfica sean más vulnerables a la variabilidad climática que aquellos ubicados en áreas con condiciones ecológicas y climáticas más adecuadas para su crecimiento (Fritts, 1976). En consecuencia, se espera que los bosques mediterráneos de la Península Ibérica se vean muy afectados por la variabilidad espacio-temporal del clima ya que varias especies europeas de árboles tienen aquí su límite meridional de distribución, tales como *Pinus sylvestris*, *Abies alba*, *Pinus uncinata*, etc. (Camarero et al., 2005; Linares et al., 2009).

Los efectos derivados del cambio climático ya están siendo registrados en la Península Ibérica, afectando tanto a la frecuencia e intensidad de las precipitaciones como a las tendencias térmicas (González-Hidalgo et al., 2009). Varios estudios indican que la característica climática más notable de las últimas décadas del siglo XX en la Península Ibérica es la tendencia generalizada hacia un aumento de la temperatura y una elevada variabilidad en las precipitaciones (Abaurrea et al., 2001; Rodríguez-Puebla et al., 2004; El Kenawy et al., 2011). Brunet et al. (2007) analizaron las tasas de calentamiento estacional y anual en España durante el siglo XX, mostrando un mayor incremento en las temperaturas de primavera y verano en comparación con los periodos invernal y otoñal. Con respecto a la variabilidad de las precipitaciones, numerosos trabajos muestran una alta variabilidad espacial y temporal en la Península Ibérica (Esteban-Parra et al., 1998; González-Hidalgo et al., 2001; Muñoz-Díaz y Rodrigo, 2004a, Vicente-Serrano, 2006; López-Moreno y Beniston, 2008; Beguería et al., 2009; De Luis et al., 2009, 2010). López-Moreno y Beniston (2008) mostraron una disminución general de las precipitaciones en el Pirineo y López-Moreno et al. (2010) ampliaron el estudio en toda la fachada nororiental de la península Ibérica demostrando una disminución general en la frecuencia de los episodios de precipitación más copiosos. Estos resultados coinciden con los publicados por De Luis et al. (2009, 2010) quienes observaron un aumento en las precipitaciones de invierno en las zonas costeras, pero una disminución general de las lluvias de primavera en las zonas del interior durante la segunda mitad del siglo XX, así como una disminución en las precipitaciones de verano en el Pirineo central y la disminución en el otoño de la precipitación en las tierras bajas de la cuenca del Ebro.

La variabilidad climática en el este de España está determinada en gran medida por la circulación general atmosférica (Romero et al., 1999a,b; Martín-Vide y López-Bustins, 2006; Vicente Serrano y

López-Moreno, 2006; López-Bustins et al., 2008). Las variaciones espaciales y temporales de temperaturas y precipitaciones están determinadas por cambios en la circulación atmosférica que se cuantifican a diferentes escalas espaciales: desde los patrones de circulación atmosférica más generales que controlan el clima en Europa occidental y la región mediterránea (Hurrell y Van Loon, 1997; Rodríguez-Puebla et al., 1998; Pozo-Vázquez et al., 2004; Muñoz-Díaz y Rodrigo, 2004b; Martín Vide y López Bustins, 2006; Vicente-Serrano et al., 2009) hasta los tipos de tiempo que regulan el clima de determinadas regiones (Romero et al., 1999b;. Kahana et al., 2002, 2004; Esteban et al., 2005; Vicente-Serrano y López-Moreno, 2006). En concreto, la Península Ibérica representa uno de los casos más extremos de la variabilidad espacial en el clima en el sur de Europa. Debido a que la Península Ibérica está situada entre el Océano Atlántico y el Mar Mediterráneo, y tiene una topografía accidentada, dicha región presenta una marcada variabilidad espacial en la influencia de la circulación atmosférica sobre las precipitaciones (Rodríguez-Puebla et al., 1998; Vicente-Serrano y López-Moreno, 2006; González-Hidalgo et al., 2009) y las temperatura (Sáenz et al., 2001; Sigró et al., 2005; El Kenawy et al., 2011).

El análisis de los efectos de los procesos climáticos a gran escala en el crecimiento de los árboles permite inferir los mecanismos físicos que controlan la variabilidad del clima y el crecimiento radial a escalas regional y local. La Figura 1 muestra un modelo simplificado para ilustrar cómo los índices generales de circulación atmosférica pueden afectar el crecimiento de los bosques mediante la propagación de los efectos de los patrones de circulación atmosférica a escala regional (cuantificados mediante la frecuencia de diferentes tipos de tiempo), que controlan la variabilidad del clima en superficie (principalmente las variaciones espaciales y temporales de temperatura y precipitación), incluyendo las condiciones de sequía y, finalmente, el crecimiento de los árboles.

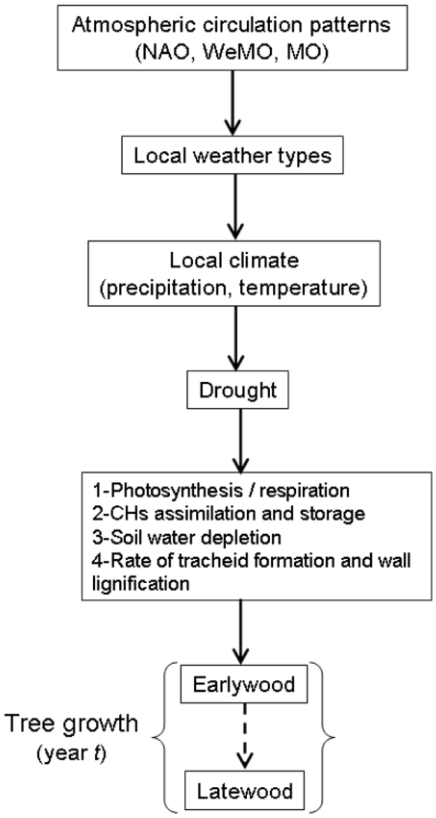

Figura 1. Diagrama esquemático de los procesos que relacionan la influencia de la circulación atmosférica sobre el crecimiento radial de los árboles durante el año de formación del anillo (año *t*) a través de cambios en las condiciones climáticas locales y la sequía. Abreviaturas: NAO, Oscilación del Atlántico Norte; WeMO, Oscilación del Mediterráneo Occidental; MO, Oscilación del Mediterráneo.

Entre los patrones de circulación atmosférica a gran escala, la Oscilación del Atlántico Norte (*North Atlantic Oscillation*, NAO) es uno de los principales modos de circulación atmosférica en el hemisferio norte (Hurrell et al., 2003), y afecta el clima en amplias regiones de Europa (Hurrell et al., 2003; Trigo et al., 2004) y la región mediterránea (Vicente-Serrano y Trigo, 2011). Por otra parte, la NAO se reconoce como el patrón más importante para explicar la variabilidad climática e hidrológica en la Península Ibérica (Vicente-Serrano et al., 2011; Lorenzo-Lacruz et al., 2011). La NAO se define a partir de un dipolo norte-sur que caracteriza las presiones a nivel del mar y los geopotenciales en la región del Atlántico Norte (Hurrell, 1995). La NAO determina la posición de la borrasca de Islandia y del sistema de altas presiones de las Azores. Por lo tanto, explica gran parte de la variabilidad climática en la zona del Atlántico Norte, incluyendo la dirección y la intensidad de los vientos del oeste en el sur de Europa, las trayectorias de las depresiones polares y la posición de los anticiclones (Lamb y Peppler, 1987; Hurrell et al., 2003). La NAO tiene una fuerte influencia sobre el clima de invierno en la Península Ibérica, donde el aumento de vientos del oeste (valores altos y positivos de la NAO) da lugar a condiciones secas y frías (Hurrell y Van Loon, 1997). Por lo tanto, valores altos (bajos) de la NAO están relacionados con niveles bajos (altos) de precipitaciones y elevadas (bajas) temperaturas en la Península Ibérica (Rodríguez-Puebla et al., 2001), que finalmente determinan la variabilidad de las condiciones de sequía en la región (López- Moreno y Vicente Serrano, 2008).

A pesar de que la NAO es de vital importancia para entender la variabilidad de las precipitaciones en la Península Ibérica, no es el único modo de variabilidad atmosférica con efectos significativos en la región (Trigo et al., 2006). En la región oriental de la Península Ibérica, cerca del Mar Mediterráneo, las condiciones climáticas también están determinadas por otros patrones de circulación atmosférica (González-Hidalgo et al., 2009; Vicente-Serrano et al., 2009). Estos patrones incluyen la Oscilación del Mediterráneo (*Mediterranean Oscillation*, MO) y la Oscilación del Mediterráneo Occidental (*Western Mediterranean Oscillation*, WeMO). El MO capta las anomalías en el gradiente de presión a nivel del mar entre la parte oriental y occidental de la cuenca mediterránea (Conte et al., 1989). Este patrón de circulación se enunció como la diferencia de anomalías estandarizadas de presión entre Gibraltar y Lod (Israel), para tener en cuenta los extremos de la cuenca mediterránea (Palutikof y Pollinger, 2003), proporcionando una buena estimación de los procesos de ciclogénesis mediterránea en el noreste de España. La WeMO se define como un dipolo que registra el gradiente de anomalía de presión entre el anticiclón de las Azores y la depresión en Liguria (Italia) (Martín-Vide y López Bustins, 2006). Este índice permite detectar la variabilidad de las precipitaciones con relación a la ciclogénesis mediterránea en las zonas adyacentes a la cuenca occidental del Mediterráneo y es superior a otros índices para explicar la variabilidad de las precipitaciones en amplias áreas de la costa mediterránea española (Martín-Vide y López Bustins, 2006; González-Hidalgo et al., 2009).

La variabilidad de la circulación atmosférica en general, bien representada en España por los patrones de circulación atmosférica definidos anteriormente, se propaga a nivel regional por medio de una serie de tipos de tiempo, que explican en términos físicos la intensidad y distribución espacial de la precipitación a escala local (Goodess y Jones, 2002; Vicente-Serrano y López-Moreno, 2006). La relación entre las tendencias de las precipitaciones y las tendencias en la frecuencia de diferentes tipos de tiempo ha sido analizada en estudios previos (por ejemplo, Vicente-Serrano y López-Moreno, 2006). Por lo general, se ha comprobado que una elevada frecuencia de tipos de tiempo ciclónicos y de flujos de componente SW y W resultan proclives a producir precipitaciones y condiciones más cálidas en invierno, mientras que aquellos tipos de tiempo que producen condiciones más estables, relacionados con situaciones anticiclónicas, se asocian a escasas precipitaciones y a la ocurrencia de sequías (Corte-Real et al., 1998; Goodess y Palutikof, 1998; Trigo y Da Camara, 2000; Martín-Vide, 2002; Goodess y Jones, 2002;. Esteban et al., 2005; Vicente-Serrano, 2006, 2007; Vicente-Serrano et al., 2009). La frecuencia y severidad de las sequías determinarán, en última instancia, las variaciones interanuales en el crecimiento de los árboles, y en general la actividad forestal en una amplia región (Martínez-Vilalta y Piñol, 2002; Vicente-Serrano et al., 2010a; Linares et al., 2010; Sánchez-Salguero et al., 2010; Pasho et al., 2011b).

La distribución espacial de las precipitaciones es uno de los principales limitantes de la distribución de los bosques y del crecimiento de los árboles en la Península Ibérica, como lo demuestran varios estudios basados en densas redes dendrocronológicas (Macías et al., 2006; Andreu et al., 2007). El impacto del déficit hídrico sobre el crecimiento de los árboles es mucho mayor en las zonas más áridas (véase por ejemplo, Vicente-Serrano et al., 2006; Andreu et al., 2007; Martínez-Vilalta et al., 2008), donde la disponibilidad de agua restringe en gran medida los procesos fisiológicos que controlan el crecimiento del árbol, como la captación de carbono mediante la fotosíntesis y la actividad de los meristemas como el cámbium. Sin embargo, la variabilidad de la precipitación no es el único factor que determina los patrones de crecimiento; la temperatura también juega un papel importante, ya que interactúa con la precipitación para determinar la disponibilidad real de agua para el crecimiento de los árboles (Vicente-Serrano et al., 2010a). Unas elevadas temperaturas generalmente tienen un efecto positivo sobre el crecimiento bajo condiciones mésicas, pero su influencia resulta negativa si no se registra el correspondiente aumento en la precipitación, es decir en condiciones xéricas.

La disminución de las precipitaciones, ya observada en la región mediterránea, está aumentando la frecuencia e intensidad de las sequías (Jones et al., 1996; Romero et al., 1998; Gibelin y Deque, 2003; Vicente-Serrano, 2006; IPCC, 2007; Giorgi y Lionello, 2008; García-Ruiz et al., 2011). Las sequías son el principal factor que limita el crecimiento y desencadena episodios relacionados con la mortalidad en los bosques, afectando de forma selectiva a diferentes especies y tipos de árboles (Allen et al., 2010; Koepke et al., 2010). La sequía produce una reducción en el crecimiento radial, conduce a alteraciones en la conductividad hidráulica (McDowell et al., 2008) y disminuye la productividad mediante una reducción en la actividad fotosintética y la captación de carbono (Hsiao, 1973; Flexas y Medrano, 2002). En particular, los déficits hídricos afectan el crecimiento del xilema en las coníferas reduciendo la turgencia celular durante la expansión inicial y la lignificación posterior de las traqeiadas (por ejemplo, Vysotskaya y Vaganov, 1989; Gindl, 2001), limitando la dinámica del cámbium y finalmente condicionando la formación de madera y el crecimiento secundario (Larson, 1963; Arend y Fromm, 2007).

La Figura 2 muestra un modelo conceptual que describe cómo la disminución de la precipitación a lo largo de un gradiente de sequía creciente, afecta negativamente al crecimiento y altera las características de las series de anchura del anillo en árboles (Fritts, 1976; Scharnweber et al., 2011). La zona izquierda de la gráfica representa los árboles que crecen en sitios templados y húmedos (por ejemplo, los bosques pirenaicos de montaña), donde la anchura de los anillos muestra los valores medios más altos, pero la menor variabilidad interanual, es decir, son zonas menos sensibles a la variabilidad climática. Por otro lado, la región de la derecha representa los árboles que crecen en sitios secos (por ejemplo, bosques semiáridos de la Depresión Media del Ebro), donde la serie de anchura de anillos muestra valores de crecimiento bajos y una mayor variabilidad interanual. Ello implica que son zonas muy sensibles a la variabilidad climática.

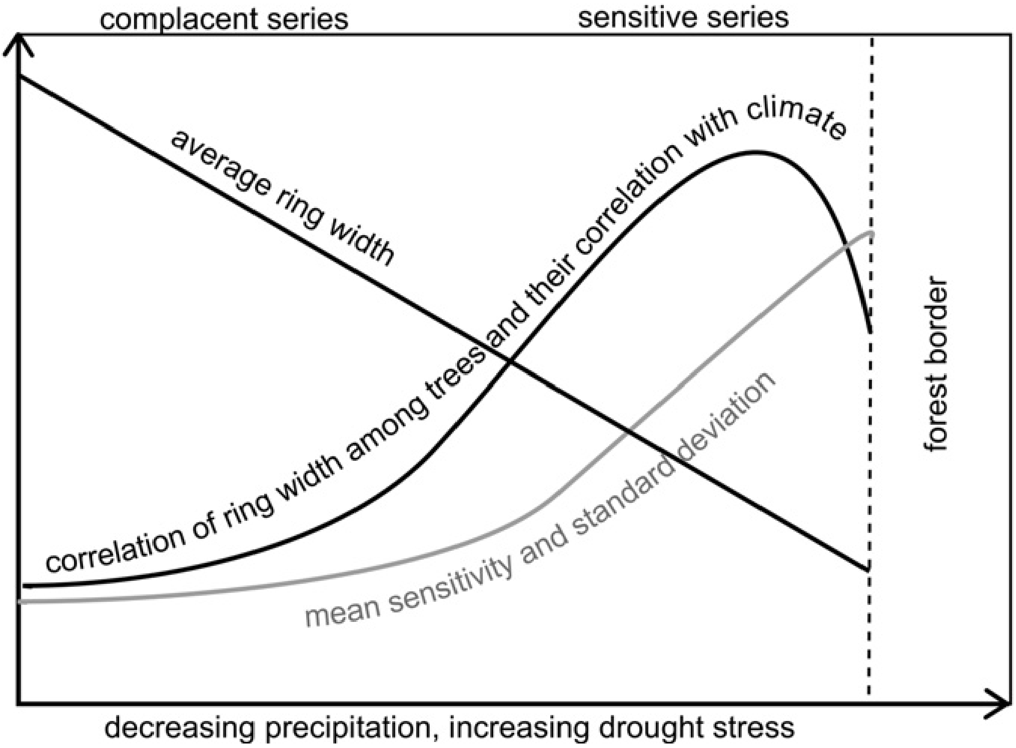

Figura 2. Variación teórica de las características dendrocronológicas a lo largo de un gradiente de estrés debido a un aumento de la sequía (modificado a partir de Fritts, 1976; Scharnweber et al., 2011). La línea punteada indica el límite xérico en la distribución de los árboles.

Sin embargo, los factores climáticos no son los únicos que condicionan los efectos de la sequía sobre el crecimiento del árbol. Las características geográficas de cada lugar, así como la elevación o las condiciones del suelo, determinan el grado en que los factores climáticos y la sequía afectan al crecimiento de los árboles (Fritts, 1976; Orwig y Abrams, 1997). Estos factores locales pueden suponer riesgos adicionales que incrementan el estrés causado por la sequía (suelos rocosos o pendientes pronunciadas) o que, en parte, pueden mitigar sus negativos efectos sobre el crecimiento de los árboles (suelos profundos o umbrías). Por ejemplo, los factores topográficos pueden determinar variaciones locales en la cantidad de agua retenida por los suelos y en la respuesta al clima (Tardif et al., 2003). Las diferencias en la exposición puede afectar la temperatura, el viento y la radiación, que, a su vez, influyen en la velocidad a la que la humedad se pierde por procesos de evapotranspiración (Fritts, 1976).

Por lo tanto, para comprender en profundidad cómo la variabilidad climática resulta determinante para explicar el crecimiento de los árboles en una región climáticamente compleja, como es el este de la Península Ibérica, resulta necesario seguir un enfoque metodológico que considere la variabilidad climática a diferentes escalas espaciales y temporales. Este enfoque debe permitir la comprensión de i) cómo los cambios en la circulación atmosférica y en el clima afectan el crecimiento de los árboles, ii) cómo es el impacto de la sequía sobre el crecimiento, iii) cómo este impacto varía en función de los tipos de bosques y las condiciones bioclimáticas de cada región y localidad, y, finalmente, iv) cómo las variaciones estacionales en la intensidad de la sequía determinan los procesos de formación de madera.

1.3. Justificación de la tesis, hipótesis y objetivos.

La mayoría de los estudios acerca del impacto del clima sobre el crecimiento de los bosques se han centrado en la influencia de las variables climáticas de superficie (Fritts, 1976). Sin embargo, los patrones de circulación atmosférica determinan la variabilidad del clima a lo largo de grandes regiones (Garfin, 1998; Girardin y Tardif, 2005). Por otra parte, se espera que los principales signos de cambio climático se identifiquen inicialmente a partir de cambios en la circulación atmosférica (Giorgi y Mearns, 1991; Räisänen et al., 2004), y que los cambios previstos en la circulación atmosférica y las condiciones climáticas afecten al crecimiento de los bosques en la cuenca mediterránea directamente a través de cambios en los patrones de circulación a gran escala e indirectamente a través de modificaciones en los patrones atmosféricos regionales que determinan el clima a escala local. Por lo tanto, es particularmente importante investigar tanto los efectos directos como los indirectos de los principales patrones de circulación atmosférica sobre el crecimiento forestal, especialmente en áreas sujetas a diversas condiciones climáticas. Este es el caso de la Península Ibérica, donde el clima varía de oceánico a continental y de condiciones húmedas a semi-áridas, dando lugar a diversas condiciones climáticas y tipos de bosques sometidos a limitaciones de crecimiento muy diferentes (Nahal, 1981). Además, las importantes diferencias espaciales en la respuesta de los bosques a la sequía (Andreu et al., 2007; Sarris et al., 2007; Martínez-Villalta et al., 2008; Sánchez-Salguero et al., 2010; Linares et al., 2010; Vicente-Serrano et al., 2010a), sugieren la importancia de analizar el crecimiento del bosque en relación a gradientes climáticos locales y la necesidad de considerar los bosques cercanos a su límite climático de distribución. Mientras que la tendencia prevista hacia condiciones progresivamente más secas es probable que cause una disminución en el crecimiento de los bosques mediterráneos, la extensión espacial y la magnitud del efecto de los factores atmosféricos y climáticos sobre el crecimiento de los árboles resulta muy incierta hoy en día (Andreu et al., 2007; Vicente- Serrano et al., 2010a).

Por otra parte, la elevada estacionalidad y variabilidad interanual que caracterizan las precipitaciones en la región del Mediterráneo y la diferente estacionalidad en el crecimiento forestal de los bosques de esta zona hacen difícil determinar los tiempos de respuesta en el crecimiento de los árboles a los déficits de precipitación. Pueden así aparecer desfases entre la escasez de agua y el crecimiento en función de diferentes estrategias funcionales o anatómicas y ajustes fenológicos y fisiológicos de los árboles para hacer frente a la sequía, pero también en función de la severidad de la sequía y en función del momento del año en que se produce el déficit hídrico más intenso. Todos estos mecanismos, ya sean aislados o actuando de forma sinérgica, pueden dificultar la identificación de los impactos de la sequía sobre el crecimiento del árbol. En la actualidad, resulta crucial ampliar el conocimiento existente sobre la respuesta de crecimiento de los árboles a la escasez de agua en la cuenca del Mediterráneo, pues los modelos generales de cambio climático predicen una gran reducción de las precipitaciones y un aumento de las tasas de evapotranspiración a finales del siglo XXI (Giorgi y Lionello, 2008; García-Ruiz et al., 2011). Existe también información contradictoria respecto a los impactos de la sequía sobre el crecimiento de las especies arbóreas a diferentes escalas temporales y en función de las condiciones bioclimáticas de cada lugar (Orwig y Abrams, 1997; Adams y Kolb, 2005). Por otra parte, la cuantificación del desarrollo intra- e inter-anual de la madera en respuesta a las condiciones de estrés hídrico cuantificadas a diferentes escalas de tiempo es crucial para entender la sensibilidad del crecimiento radial en respuesta a la variabilidad de las precipitaciones en la región (Andreu et al., 2007; Camarero et al., 2010).

Teniendo en cuenta las cuestiones mencionadas, se plantearon las siguientes hipótesis: (i) las respuestas de crecimiento de los bosques a los patrones de circulación atmosférica y la variabilidad climática en el noreste de España debe ser espacialmente estructurada y (ii) deben existir respuestas contrastadas en el crecimiento de los árboles a la sequía entre diferentes especies pero también entre bosques de una misma especie sometidos a diferentes condiciones ambientales. En particular, se planteó la hipótesis de que los bosques ubicados en los sitios xéricos mostrarán una mayor capacidad de respuesta a la sequía mediante la reducción en la formación de la madera en comparación con zonas más húmedas donde se espera que la temperatura sea el principal factor limitante del crecimiento. Sin embargo, estas respuestas pueden depender también de las tendencias climáticas estacionales y de la alta plasticidad fenológica del xilema en especies ibéricas de árboles (De Luis et al., 2007; Camarero et al., 2010).

Los objetivos de esta tesis son los siguientes:

- (i) el uso de métodos dendrocronológicos para caracterizar los patrones espaciales y temporales de crecimiento radial en una red de bosques ubicados en el noreste de España y sometidos a un amplio gradiente climático que abarca desde condiciones climáticas semiáridas hasta frías y húmedas. Los lugares de muestreo incluyen diversos tipos de bosques tales como bosques mediterráneos en sitios semi-áridos de la cuenca del Ebro y bosques subalpinos en sitios húmedos de los Pirineos;
- (ii) cuantificar la influencia de los patrones de circulación atmosférica a gran escala, la frecuencia de tipos de tiempo y las variables climáticas de superficie (temperatura y precipitación) sobre el crecimiento de los árboles;
- (iii) describir y analizar las respuestas espacio-temporales de crecimiento a la sequía por medio de un índice de sequía multi-escalar;
- (iv) detectar los principales factores geográficos y bioclimáticos que influyen en estas respuestas,

- (v) identificar el efecto de la clima y sequía en la formación de madera en bosques de *Pinus halepensis*, que es la especie forestal situada en los lugares más áridos de la región estudiada.

El estudio incluye ocho especies de árboles que crecen a lo largo de un gradiente climático muy contrastado, y que muestran diferentes vulnerabilidades a la variabilidad del clima: cuatro especies de pino (*Pinus halepensis*, *P. pinea*, *P. nigra*, *P. sylvestris*), el abeto (*Abies alba*), la sabina albar (*Juniperus thurifera*), el quejigo (*Quercus faginea*) y la carrasca (*Quercus ilex* subsp. *ballota*). Estas especies representan bosques de sitios templados y húmedos (por ejemplo, *A. alba*), sub-mediterráneos de transición (por ejemplo, *Q. faginea*) y sitios xéricos (por ejemplo, *P. halepensis*). Las respuestas de crecimiento a la sequía y los principales factores que influyen en este tipo de respuestas se analizaron teniendo en cuenta todas las especies antes mencionadas, mientras que la sensibilidad del crecimiento de los árboles a la variabilidad climática a escala general, regional y local, se evaluó mediante series de madera temprana (EW) y madera tardía (LW) en bosques de *P. halepensis* por varias razones. En primer lugar, esta conífera es una de las especies arbóreas dominantes en la cuenca del Mediterráneo Occidental y una de las especies ecológicamente más importantes en áreas semi-áridas (Ne'eman y Trabaud, 2000). En segundo lugar, las décadas finales del siglo XX se caracterizaron por una marcada variabilidad climática en la parte oriental de la Península Ibérica (De Luis et al., 2009), en cuyo ámbito el *P. halepensis* está bien representado, siendo la especie de coníferas dominante con una amplia distribución en el área de estudio. En tercer lugar, la aridez creciente en la región mediterránea podría tener importantes implicaciones para la dinámica de crecimiento a escalas inter- e intra-anual de los pinares de *P. halepensis*, sobre todo en zonas más secas. En cuarto lugar, ningún estudio ha investigado cómo diferentes factores climáticos afectan a la producción de EW y LW y cómo son las respuestas a largo plazo del crecimiento a la sequía, a pesar de las evidencias existentes sobre cómo las maderas temprana y tardía responden de manera diferente a diversas variables climáticas (De Luis et al., 2007; Camarero et al., 2010).

CHAPTER I

INTRODUCTION

In this chapter is briefly given an introduction on the dendrochronology and its applications, particularly focusing on climate effects on tree growth. In addition, this section provides basic information concerning climate variability and drought in the Mediterranean Basin in general and in the Iberian Peninsula in particular, based on the current state-of-the-art relevant literature, and their influence on forest growth in the region. The last part of this chapter justifies the undertaking of this study, the main hypothesis established and the objectives.

1.1. Dendrochronology

The term Dendrochronology, derived from the Greek words “dendro” –tree, wood– and “chronology” –time–, refers to a scientific discipline equipped with a set of principles, techniques and methods based on the precise dating and study of annual growth rings formed by woody plants to extract, sort and interpret information containing the different factors that influence their secondary growth, i.e. wood formation (Fritts, 1976). This science was formally developed during the first half of the 20th century by the astronomer A. E. Douglass (Douglass, 1940), the founder of the Laboratory of Tree-Ring Research at the University of Arizona (Tucson, Arizona, USA). Considering that the majority of trees form annual growth increments or tree rings in cold and temperate areas subjected to a seasonal climate, the information related to its formation and the factors influencing this process can be represented by the specific characteristics of each ring, namely width, anatomy, density, isotopic composition and other visual or analytical parameters that can differ from one ring to the other as a function of ecological and climatic constrains (Schweingruber, 1988).

The growth of trees is not a continuous process in areas with seasonal climate since it stops at some point due to the limitation imposed by external climatic factors, thus explaining the formation of annual tree rings. In many areas of the planet with a marked climatic seasonality, the tree growth arrests during unfavorable periods, for instance in cold winter sites from the northern hemisphere or dry periods in arid areas, and re-starts again when weather conditions become favorable. This annual pattern of activity and arrested growth is marked in the structure of wood, in the form of annual concentric layers which, in cross section, are seen as rings. At intra-annual scale, the production of new xylem cells (xylogenesis or wood formation) is fast in the early growing season, slows down as the summer progresses and eventually stops when climatic conditions worsen. These differences in the formation rate of the cells are also reflected in the characteristics of the tree rings in conifers and ring-porous woods, composed of two bands: the earlywood (EW) formed at the beginning of the growing period (spring, early summer) and the latewood (LW) formed at the end (late summer, autumn). In conifers (pines, firs, etc.) the EW is light and made up of tracheids with wide lumens and thin cell walls while the LW is dark and it is formed by narrow tracheids with thick cell walls (Schweingruber, 1988). The differences in size, density and color between the lignified dark LW part of a ring and the light EW of the next one allow identifying and dating of the rings.

Dendrochronology has applications in different fields of the science because the rings contain information on several factors. This information can be retrieved and analyzed conveniently, allowing the study and analyzes of various ecological, geomorphological, climatic, archaeological, etc., processes in space and time whenever they leave a signal in rings which can be adequately extracted (Gutiérrez, 2008). For instance, tree rings can record the effects of fires, outbreaks, earthquakes, volcanic eruptions, landslides, rock falls, avalanches, floods, advance and the retreat of glaciers, etc. All these phenomena can be dated by the signs engraved on tree rings which allows to determine the frequency and intensinty with which these phenomena occur over the affected area.

In ecology and following a retrospective approach, dendrochronology is very useful for studying processes that occur at long time scales and imply organisms with long lifespans such as trees. For instance, the study of tree rings allows dating the year of germination and death of trees, which are the two key processes of tree population dynamics and forest succession. The analysis of the annual growth series allows determining the disturbance regimes that might affect forest dynamics and infer tree-to-tree competition intensity. Climate is the most important environmental factor affecting radial growth in woody plants and particularly in trees (Fritts, 1976). When climatic drivers constrain tree growth, the rings formed are commonly narrow in most of the trees of a particular region. As a result of the close relationship between growth and climate, the series of annual rings formed by trees that grow under the same weather conditions show synchrony, its pattern of temporal variation in thickness is very similar among and within trees (Fritts, 1976). This “climatic signature in the wood” is also a “signature of time”, since it is unlikely that a specific temporal pattern is repeated exactly the same in another period. The climate signal recorded in tree rings can be used to reconstruct the evolution of the past climate for periods when meteorological records are not available. In particular, it is possible to reconstruct the climatic variables most limiting tree growth, which show a significant and strong influence on the formation of annual rings. For example, it is expected that temperature and precipitation are the main drivers of tree growth in cold (e.g., alpine treelines) and dry (e.g., semiarid woodlands) sites, respectively. Dendrochronological studies produce mean growth chronologies which are formed by a large number of series of many trees of the same species growing in the same site, which maximize the common climate signal (Cook and Kairiuktsis, 1990).

In summary, dendrochronology is a powerful tool used to show how climatic conditions determine radial growth in trees (e.g. Schweingruber et al., 1988). For this reason, tree rings have been widely used to study long-term patterns of tree growth, sometimes used as a proxy of net primary production or carbon uptake, and to assess the impact of environmental changes on growth patterns, based on the general assumption that the climate-tree growth relationships remain approximately constant over time (Fritts, 1976). For example, the temporal variability in tree-ring widths has been used to detect changes in the sensitivity of tree growth to climate (Andreu et al., 2007), to study the regional variability of the climate-tree growth relationships within a species based on dense dendrochronological networks (Tardif et al., 2003; Piovesan et al., 2005; Carrer et al., 2007) or to identify recent growth declines due to warming-related drought in Circum-Mediterranean regions (Jump et al., 2006; Sarris et al., 2007; Camarero et al., 2011).

1.2. Climate variability and forest growth in the Mediterranean region: the role of droughts.

In the late 20th century, many changes have been observed in the Mediterranean Basin regarding ecological amplitude, composition, dynamics and the phenology of forests (Walther et al., 2002; Peñuelas and Boada, 2003). These phenomena were significantly connected with the current climate changes already observed in the region (Parmesan and Yohe, 2003; Linares et al., 2010). As a matter of fact, climate in the Mediterranean basin is subjected to extended, frequent and intense dry periods (e.g., Briffa et al., 1994; Demuth and Stahl, 2001; Lloyd-Huges and Saunders, 2002a,b; Vicente-Serrano, 2006; González-Hidalgo et al., 2009) and a high inter-annual variability of precipitation (Palutikof et al., 1994; Trigo et al., 2000; Hasanean, 2004; Zveryaev, 2004; Giorgi and Lionello, 2008; González-Hidalgo et al., 2009). Climate change scenarios predict a large temperature rise (+2 to 4°C) and a precipitation decrease (ca. -20%) in the Basin during the 21st century (Gibelin and Dequé, 2003; IPCC, 2007). The forecasted drying trend will be partially determined by an increased frequency of anticyclonic conditions associated with a northward shift of the Atlantic storm track (Giorgi and Lionello, 2008). Moreover, it is expected that there will be an increase in the surface pressure gradient between the northern and southern parts of the North Atlantic region (Paeth and Pollinger, 2010), a decrease in the frequency and intensity of Mediterranean cyclones (Raible et al., 2010), and a decrease in summer convective systems (Brankovíc et al., 2008; May, 2008). These extreme climatic episodes are expected to be intensified in the future under warmer conditions, enhacing evapotranspiration and water deficit in many forested areas (Giorgi and Lionello, 2008), modifying the growth and distribution of tree species through growth decline and increased mortality, mostly in drought-prone ecosystems (e.g., Martínez-Vilalta and Piñol, 2002).

Forests are particularly sensitive to climate change because the long-life span of trees does not allow for an immediate adaptation to rapid environmental changes such as current climate warming (Kuparinen et al., 2010). Forests respond to climate warming through changes in growth and vigor (e.g, defoliation), acting as valuable monitors of the effects of climate change on terrestrial ecosystems (Bonan, 2008). For instance, in the Mediterranean mountain conifer forests, where water shortage is not a major constrain for tree growth, temperature rise could affect wood production by increasing aridity through enhanced evapotranspiration and water loss (Martínez-Vilalta and Piñol, 2002; Macias et al., 2006; Camarero and Gutiérrez, 2007; Linares et al., 2010). In semi-arid regions, in which water availability is the main limiting factor of growth, the precipitation variability is the main factor determining tree productivity and forest dynamics (Vicente-Serrano, 2007; Sarris et al., 2007). Therefore, different patterns of forest response to climate can be found as a function of bioclimatic conditions and forest types. In general, forests located at the limits of their environmental or geographical distribution are expected to be more vulnerable to climatic variability than those located in core areas where more suitable ecological and climatic conditions for tree growth are met (Fritts, 1976). Consequently, Iberian Mediterranean forests are expected to be highly sensitive to the spatio-temporal variability of climate, since several European tree species such as *Pinus sylvestris, Abies alba, Pinus uncinata*, etc. reach their southernmost distributional limit ("rear edge") in that area (Camarero et al., 2005; Linares et al., 2009).

Climate changes are already taking place in the Iberian Peninsula affecting both the frequency and intensity of precipitation and temperature trends (González-Hidalgo et al., 2009). Several studies indicated that the most remarkable climatic feature of the 20th century in the Iberian Peninsula was a general tendency of increasing temperature and year-to-year precipitation variability (Abaurrea et al., 2001; Rodríguez-Puebla et al., 2004; El Kenawy et al., 2011). Brunet et al. (2007) found high seasonal and annual warming in Spain for the 20th century, with greater increases in spring and summer minimum, maximum and mean temperatures compared to those for autumn and winter seasons respectively. With respect to precipitation variability, several papers concluded that this climatic factor is characterized by a high spatial and temporal variability in the Iberian Peninsula (Esteban-Parra et al., 1998; González-Hidalgo et al., 2001; Muñoz-Díaz and Rodrigo, 2004a; Vicente-Serrano, 2006; López-Moreno and Beniston, 2008; Beguería et al., 2009; De Luis et al., 2009, 2010). López-Moreno and Beniston (2008), revealed a general decrease in precipitation for the Pyrenees. López-Moreno et al. (2010) extended the study for the north-east Spain and showed a general decrease of the frequency of the most extreme precipitation events. This is in agreement with the results of De Luis et al. (2009, 2010), who indicated an increase in winter precipitation in the costal areas, but a general decrease of spring rainfall in inland areas during the second half of the 20th century, a decrease in summer precipitation in the central Pyrenees and decrease in autumn precipitation in low lands of the Ebro basin.

Climate variability in eastern Spain is largely determined by the general atmospheric circulation (e.g., Romero et al., 1999a,b; Martín-Vide and López-Bustins, 2006; Vicente-Serrano and López-Moreno, 2006; López-Bustins et al., 2008). The spatial and temporal variations of temperature and precipitation are determined by changes in the wind flows quantified on different spatial scales; i.e., from the general atmospheric circulation patterns that govern the climate of western Europe and the Mediterranean region (Hurrell and Van Loon, 1997; Rodríguez-Puebla et al., 1998; Pozo-Vázquez et al., 2004; Muñoz-Díaz and Rodrigo, 2004b; Martín-Vide and López-Bustins, 2006; Vicente-Serrano et al., 2009) to the weather types that control the climate of particular regions (Romero et al., 1999b; Kahana et al., 2002, 2004; Esteban et al., 2005; Vicente-Serrano and López-Moreno, 2006). Specifically, the Iberian Peninsula represents one of the most extreme cases of spatial variability in climate within southern Europe. Located between the Atlantic Ocean and the Mediterranean Sea, with a rugged topography, the Iberian Peninsula shows marked spatial variability in the influence of atmospheric circulation on precipitation (e.g., Rodríguez-Puebla et al., 1998; Vicente-Serrano and López- Moreno, 2006; González-Hidalgo et al., 2009) and temperature (Sáenz et al., 2001; Sigró et al., 2005; El Kenawy et al., 2011).

Analysing the effects of the large-scale climate processes on forest growth allows infering the physical mechanisms that control climate variability and growth at regional and/or local scales. Figure 1 shows a simplified model which illustrates how the general atmospheric circulation indices can affect forest growth by driving the patterns of regional atmospheric circulation (quantified by means of the frequency of different weather types), which control the variability of the surface climate (mainly the spatial and temporal variations in temperature and precipitation), including drought conditions, and finally tree growth.

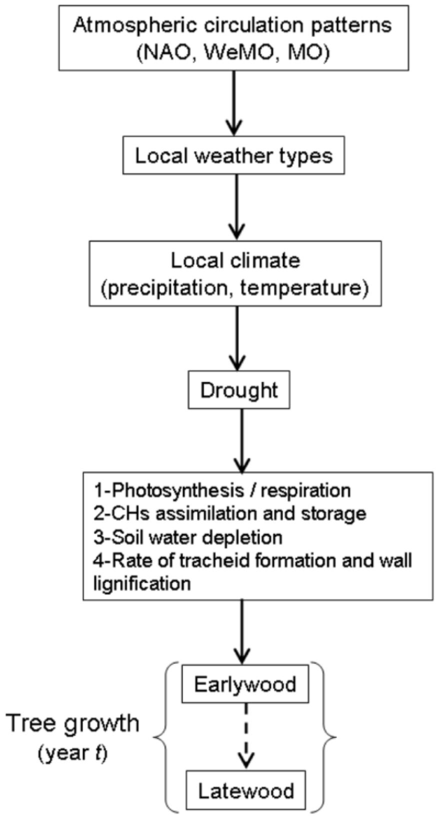

Figure 1. Schematic diagram of the processes linking the influence of atmospheric circulation on tree radial growth during the year of tree-ring formation (year *t*) through changes in local weather types, surface climate conditions and drought. NAO: North Atlantic Oscillation, WeMO: Western Mediterranean Oscillation, MO: Mediterranean Oscillation

Among the large-scale atmospheric circulation patterns, the North Atlantic Oscillation (NAO) is one of the main modes of atmospheric circulation in the northern hemisphere (Hurrell et al., 2003), which affects the surface climate across large parts of Europe (Hurrell et al., 2003; Trigo et al., 2004) and the Mediterranean region (Vicente-Serrano and Trigo, 2011). Moreover, it is widely recognised as the most important pattern for explaining the climatic and hydrological variability of the Iberian Peninsula (Vicente-Serrano et al., 2011; Lorenzo-Lacruz et al., 2011). The NAO is defined by a north-south dipole that characterizes the sea level pressures and geopotential heights in the North Atlantic region (Hurrell, 1995). It determines the position of the Icelandic low and the Azores high pressure systems, and therefore explains much of the climatic variability in the North Atlantic areas, including the direction and intensity of the westerly winds in southern Europe, the trajectories of polar depressions and the position of anticyclones (Lamb and Peppler, 1987; Hurrell et al., 2003). The NAO has a strong influence on winter climate in the Iberian Peninsula, where increased westerlies (high positive NAO values) lead to dry and cold conditions (Hurrell and Van Loon, 1997). Therefore, high (low) NAO values in winter are linked to low (high) levels of precipitation and high (low) temperatures in the Iberian Peninsula (Rodríguez-Puebla et al., 2001), governing drought variability in the region (López-Moreno and Vicente-Serrano, 2008).

Although the NAO is of prime importance to understand the precipitation variability in the Iberian Peninsula, it is not the only mode of atmospheric variability with significant effects in the region (Trigo et al., 2006). In the eastern Iberian Peninsula, close to the Mediterranean Sea, climatic conditions are also affected by other atmospheric circulation patterns (González-Hidalgo et al., 2009; Vicente-Serrano et al., 2009). These include the Mediterranean Oscillation (MO) and the Western Mediterranean Oscillation (WeMO). The MO captures the gradient in sea level pressure (SLP) anomalies between the eastern and western parts of the Mediterranean Basin (Conte et al., 1989). This index was developed as the difference in standardized geopotential height anomalies between Gibraltar and Lod (Israel) considering the extremes of the Basin (Palutikof and Pollinger, 2003), and it provides a good record of Mediterranean cyclogenesis over northeast Spain. The WeMO is defined as a dipole structure that records the SLP anomaly gradient between the anticyclone over the Azores and the depression over Liguria (Italy) (Martín-Vide and López-Bustins, 2006). This index enables the detection of variability in precipitation related to Mediterranean cyclogenesis in areas adjacent to the western Mediterranean Basin and is superior to other indices in explaining precipitation variability over large areas of the Spanish Mediterranean coast (Martín-Vide and López-Bustins, 2006; González-Hidalgo et al., 2009).

The general atmospheric circulation variability, well represented in Spain by the atmospheric circulation patterns defined above, are propagated regionally by means of a series of weather types, which explain in physical terms the intensity and spatial distribution of precipitation at local scales (Goodess and Jones, 2002; Vicente-Serrano and López-Moreno, 2006). The relationships between precipitation trends and the trends in the frequency of different weather types have been analysed previously (Vicente-Serrano and López-Moreno, 2006). Generally, a high frequency of weather types prone to cause precipitation and linked to cyclonic activity, mainly SW and W weather types, cause warmer and more humid conditions in winter than weather types characterized by more stable conditions, related to anticyclonic activity, which are associated with low precipitation, leading to drought occurrence (Corte-Real et al., 1998; Goodess and Palutikof, 1998; Trigo and Da Camara, 2000; Martín-Vide, 2002; Goodess and Jones, 2002; Esteban et al., 2005; Vicente-Serrano, 2006, 2007; Vicente-Serrano et al., 2009). Drought severity and frequency will ultimately determine the interannual variations of tree growth, vigor and forest activity across a region (Martínez-Vilalta and Piñol, 2002; Vicente-Serrano et al., 2010a; Linares et al., 2010; Sánchez-Salguero et al., 2010; Pasho et al., 2011b).

The spatial patterns of precipitation are among the main constraints for forest distribution and tree growth in the Iberian Peninsula, as evidenced by several tree-ring studies based on extensive dendrochronological networks (Macias et al., 2006; Andreu et al., 2007). The impact of water deficit on growth is supposed to be much higher in the most arid sites, where water availability largely constrains the physiological processes controlling tree growth, such as photosynthesis, carbon uptake and nitrogen use, than in mesic ones (e.g., Vicente-Serrano et al., 2006; Andreu et al., 2007; Martínez-Vilalta et al., 2008). However, precipitation variability is not the only factor driving growth patterns; temperature as well, plays an important role because it interacts with precipitation to determine actual water availability for tree growth (Vicente-Serrano et al., 2010a). High temperatures generally have a positive effect on growth under mesic conditions, but their influence can be negative if there is no corresponding increase in precipitation, as drought stress may occur.

The decrease in precipitation, already observed in the Circum-Mediterranean region, is increasing the frequency and intensity of droughts (Jones et al., 1996; Romero et al., 1998; Gibelin and Déqué, 2003; Vicente-Serrano, 2006; IPCC, 2007; Giorgi and Lionello, 2008; García-Ruiz et al., 2011) which are believed to be the main drivers of growth decline and related mortality episodes in forests, affecting selectively species, stands and trees (Allen et al., 2010; Koepke et al., 2010).

Drought causes reduction in radial growth, alterations in hydraulic conductivity (McDowell et al., 2008) and decreases productivity due to limitations in water use and photosynthesis (Hsiao, 1973; Flexas and Medrano, 2002). In particular, water deficit affects xylem growth by influencing initially cell turgidity during expansion (e.g., Vysotskaya and Vaganov, 1989; Gindl, 2001), reducing or preventing cell metabolism and indirectly limiting cambial dynamics, wood formation and secondary growth (Larson, 1963; Arend and Fromm, 2007).

Figure 2 shows a conceptual model describing how the decreasing precipitation along a climatic gradient increases drought stress, negatively affecting growth and altering the dendrochronological characteristics of tree-ring width series (Fritts, 1976; Scharnweber et al., 2011). The left area of the graph represents trees growing in mesic sites (e.g., humid mountain forests) where tree-ring width series show high mean values but the lowest year-to-year variability (mean sensitivity), i.e. they are complacent series, while the area to the right represents trees growing in dry sites (e.g., semi-arid woodlands) where tree-ring width series show low values but the highest mean sensitivities and variability, corresponding to sensitive series, and also the highest correlation in growth among co-existing trees and the highest response to climate.

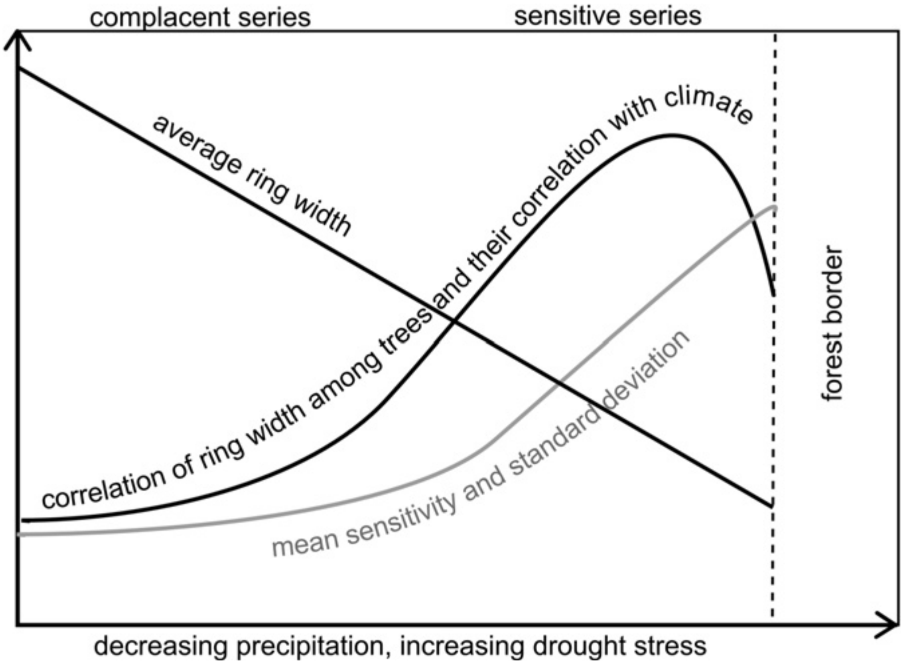

Figure 2. Theoretical variation of dendrochronological characteristics along a gradient of increasing drought stress (modified from Fritts, 1976; Scharnweber et al., 2011). The right dashed line indicates the xeric limit of tree distribution, i.e. the forest border.

However, climatic factors are not the only drivers which condition drought effects on tree growth. Site factors as well, such as elevation or topography or soil conditions, affect the degree to which climatic drivers and drought impact tree growth (Fritts, 1976; Orwig and Abrams, 1997). These local drivers may impose additional risks exacerbating drought stress (e.g., rocky soils or steep slopes) or they may partially mitigate its negative effects on tree growth (e.g., deep soils or northern aspects). For example, the topographic factors may impose local variations in the amounts of water retained by soils (Tardif et al., 2003). The differences in site exposure can affect temperature, wind and radiation, which, in turn, influence the rate at which moisture is lost by evapotranspiration processes leading to different drought conditions (Fritts, 1976).

Therefore, to understand in depth how climate variability processes are determining tree growth in a region so complex in climate and forest composition like the eastern Iberian Peninsula, it is necessary to follow a methodological approach that consider the climate variability on different spatial and temporal scales. This approach must allow understanding i) how the general atmospheric circulation drives changes in surface climate and affects tree growth, ii) how is the impact of drought on growth, iii) how this impact varies as a function of forest type and bioclimatic conditions of the region and, finally, iv) how seasonal variations of drought intensity impact wood formation.

1.3. Justification of the thesis, hypotheses and objectives.

Most analyses of climate impact on forest growth have focused on the influence of surface climate factors (Fritts, 1976). Nevertheless, atmospheric circulation patterns affect climate variability over large regions (Garfin, 1998; Girardin and Tardif, 2005). Moreover, it is expected that the main signs of climate change will be identified earlier through changes in atmospheric circulation (Giorgi and Mearns, 1991; Räisänen et al., 2004). The predicted changes in atmospheric circulation and climatic conditions are expected to affect forest growth in the Mediterranean Basin directly through changes in large-scale circulation patterns but also indirectly through modifications in regional atmospheric patterns and proximate local climate factors such as wind patterns and precipitation. Therefore, it is particularly important to investigate both the direct and indirect influences of large-scale atmospheric circulation paterns on tree growth, particularly in areas subjected to diverse climatic conditions. This is the case of the Iberian Peninsula, where climate ranges from mild to continental and from humid to semi-arid types, resulting in diverse climatic conditions and forest types subjected to different growth constraints (Nahal, 1981). In addition, the large spatial differences found at local scales in the response of forests to drought (Sarris et al., 2007; Andreu et al., 2007; Martìnez-Villalta et al., 2008; Sánchez-Salguero et al., 2010; Linares et al., 2010; Vicente-Serrano et al., 2010a), suggest the importance of analyzing forest growth in relation to local climatic gradients, and the need to consider forests near their limit of distribution, as the first impacts of climate change processes are expected to be observed in these ecotones (Neilson, 1993). While the predicted trend towards progressively drier conditions is likely to cause a decline in the growth of Mediterranean forests, the spatial extent and the magnitude of the effect of atmospheric and climatic drivers on tree growth is uncertain (Andreu et al., 2007; Vicente-Serrano et al., 2010a).

Moreover, the large seasonality and year-to-year variability that characterize precipitation in the Mediterranean region and the different site-dependent seasonality of tree growth in forests from this area could make very difficult to determine the time response of tree growth to the precipitation deficit. Lags between water shortages and growth can appear as a function of different anatomical and physiological adjustments of trees to cope with drought stress but also in response to drought severity and duration, and to the season in which water deficit occurs. All these mechanisms, either isolated or acting synergistically, can challenge the identification of drought impacts on tree growth. Currently, a deeper knowledge on the tree growth responses to water shortages in the Mediterranean Basin is a crucial task since General Climate Change Models predict a large reduction of precipitation and an increase of the evapotranspiration rates by the end of the twentieth-first century (Giorgi and Lionello, 2008; García-Ruiz et al., 2011). There exists also contradictory information regarding the drought impacts on growth of tree species at different time scales and across contrasting site conditions (Orwig and Abrams, 1997; Adams and Kolb, 2005). Moreover, the quantification of intra- and inter-annual wood development in response to drought stress assessed at different time scales is crucial for understanding the increased sensitivity of radial growth in response to the amplified precipitation variability detected in Mediterranean region during the past century (Andreu et al., 2007; Camarero et al., 2010).

Considering the aforementioned issues, it was hypothesized (*i*) that the growth responses of forests to the atmospheric circulation patterns and climate variability in north-eastern Spain must be structured, (*ii*) that there must be contrasting growth responses to drought among and within tree species and also among sites with different local conditions (xeric vs. mesic sites). In particular, it was hypothesized that forests located in xeric sites will show a higher responsiveness to drought by reducing the wood formation compared to mesic locations where temperature is expected to be the major constrain of growth. However, these responses may also depend on seasonal climatic trends and on the high phenological plasticity of xylogenesis in Iberian tree species (De Luis et al., 2007; Camarero et al., 2010).

The objectives of this thesis were:

- (*i*) to use dendrochronological methods to characterize the spatial and temporal patterns of radial growth in a network of forests located in north-eastern Spain, where a wide climatic gradient exists ranging from semi-arid to cold and wet climatic conditions. The sampled sites include diverse forest types such as Mediterranean woodlands under semi-arid conditions in the Middle Ebro Basin to mountain forests under humid conditions in the Pyrenees;
- (*ii*) to quantify the influence of large-scale circulation patterns, regional weather types and the surface climate variables (temperature and precipitation) on tree growth;
- (*iii*) to describe and analyze the spatio-temporal growth responses to drought by means of a multi-scalar drought index;
- (iv) to detect the main geographic and bioclimatic drivers influencing these responses;

- (*v*) to identify the effect of climate and drought on seasonal wood formation in *Pinus halepensis* which is the tree specie located in the most arid sites of the studied region.

The study includes eight tree species growing along a wide climatic gradient, showing contrasting vulnerability to climate variability: four pine species (*Pinus halepensis*, *P. pinea*, *P. nigra*, *P. sylvestris*), silver fir (*Abies alba*), Spanish juniper (*Juniperus thurifera*), and two oak species (*Quercus faginea*, *Q. ilex*). These species represent species typically associated with mesic sites and humid conditions (e.g., *A. alba*), transitional sub-Mediterranean locations (e.g., *Q. faginea*) and xeric sites (e.g., *P. halepensis*). The spatio-temporal growth responses to drought and the main drivers influencing such responses were analyzed considering all of the above mentioned species, while the sensitivity of tree growth to climatic variability at large, regional and local scales was evaluated on earlywood (EW) and latewood (LW) width series of *P. halepensis*, for several reasons. First, this conifer is one of the dominant tree species in the Western Mediterranean Basin and the most ecologically important species in semi-arid woodlands (Ne´eman and Trabaud, 2000). Second, the late 20th century was characterized by marked climatic variability in the eastern Iberian Peninsula (De Luis et al., 2009) and in all these areas *P. halepensis* is present, being the dominant conifer species with a broad distribution across the study area. Third, the increasing aridity in the Mediterranean region could have important implications for inter and intra-annual growth dynamics of *P. halepensis*, particularly in drought-prone areas. Fourth, no studies have investigated how climatic drivers affect EW and LW production and the long-term responses to drought of these components, despite ample evidence that each of these components of *P. halepensis* growth responds differently to diverse climatic variables (De Luis et al., 2007; Camarero et al., 2010).

CHAPTER II

METHODOLOGY

This chapter provides general information about the study area, the methodological possibilities to carry out the research and indicates the specific methods applied to investigate the responses of forests to climatic drivers and drought. In particular, this section describes the available dense network of tree ring samples, the climate dataset, the drought indices and the general statistical analysis employed.

2.1. Study sites and species

The study area includes forests in Aragón and Valencia regions, eastern Spain (Figure 3, Table 1). The Aragón region is subjected to continental Mediterranean conditions with a typical summer drought and it is characterized by a strong climatic gradient ranging from a semiarid climate in the Middle Ebro Basin (mean annual temperature 13.1 ºC, total annual precipitation 558 mm) to humid climates in the Pyrenees and Pre-Pyrenees (mean annual temperature 8.5 ºC, total annual precipitation 1750 mm). In the Middle Ebro Basin the average temperatures in January and July are about 6.7 ºC and 26.0 ºC, whereas in Pyrenean stations the means for both months are about 1.5 ºC and 16.8 ºC, respectively (Cuadrat et al., 2007).

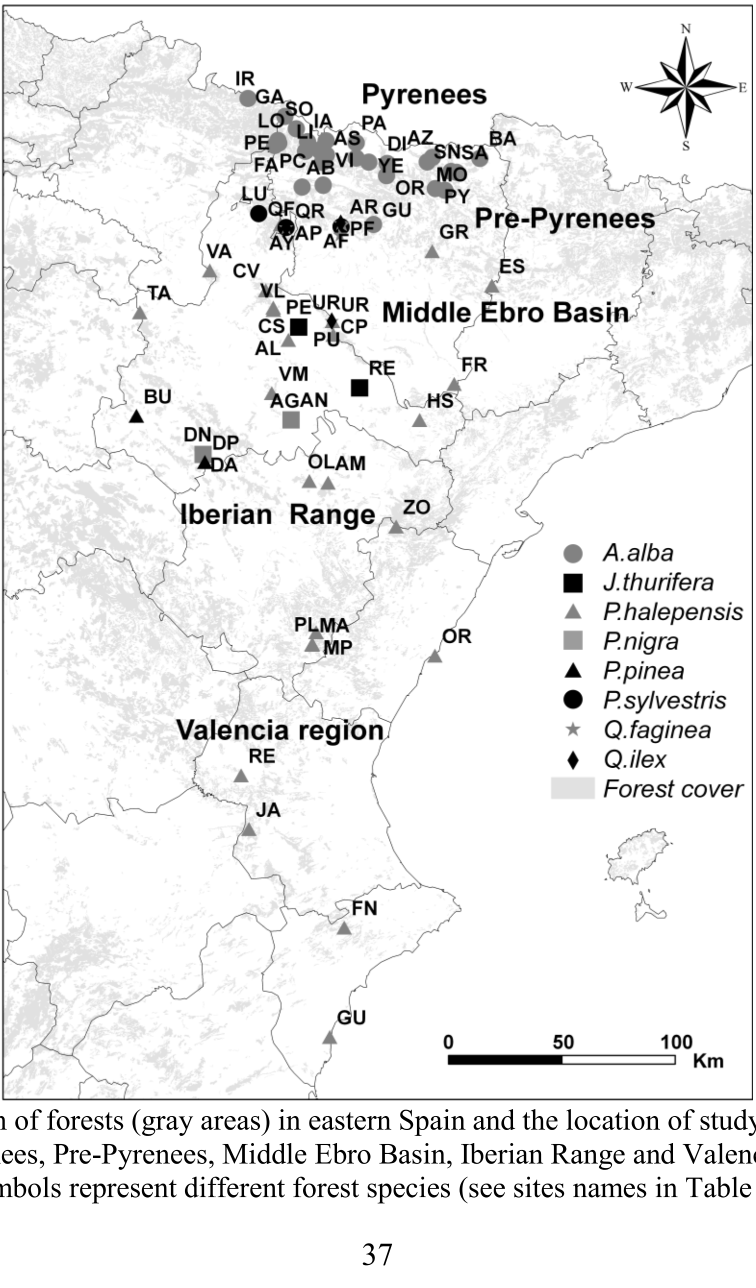

Figure 3. Distribution of forests (gray areas) in eastern Spain and the location of study sites grouped in five major regions (Pyrenees, Pre-Pyrenees, Middle Ebro Basin, Iberian Range and Valencia region). Different symbols represent different forest species (see sites names in Table 1).

In Valencia region the climate is typically Mediterranean with high daily, seasonal and inter-annual precipitation variability (De Luis et al., 2001). There, the mean annual temperature is about 15.7ºC and the mean annual sum of precipitation about 466mm (De Luis et al., 2009). Seasonal variability in precipitation is less pronounced in the Pyrenees and Pre-Pyrenees than in the Ebro Basin and Valencia region, although summer is the predominant dry season in all study sites. In the Middle Ebro Basin and Valencia region there is a negative water balance (precipitation minus evapotranspiration), as a consequence of the high potential evapotranspiration (PET) that occurs in summer. Annual PET reaches 1300 mm in some sectors of the Middle Ebro valley. Moreover, in the Middle Ebro Basin and Valencia region, the high temporal variability in precipitation constrains tree growth, as severe droughts are frequent (Vicente-Serrano and Cuadrat, 2007), and periods of more than 80 days without precipitation are common (Vicente-Serrano and Beguería, 2003). In the Middle Ebro Basin the lithology is characterized by millestones and gypsums (Peña et al., 2002), which contribute to aridity because there is poor retention of water by these soils (Navas and Machín, 1998). In the Pyrenees, soils are usually deep and basic and develop over limestone, sandstones and granites. The Pre-Pyrenees form a mountain chain characterized by a transitional sub-Mediterranean climate with a mean annual temperature of 11.1 ºC and mean annual precipitation of about 950 mm (Cuadrat et al., 2007). In the Valencia region the landscape shows widely contrasting geological features represented by a diversity of soils. The bedrock material is dominated by limestone, dolomites, calcareous substrates which produce shallow soils and marls characterized by deep soils (Kazanis et al., 2007).

The study area contains very different forest types (Figure 4) in terms of the dominant forest species and vegetation communities (Costa et al., 2005). Most of the studied forests are located in the mountain chains (Pyrenees and Pre-Pyrenees in the north, and the Iberian range in the south) forming pure conifer (e.g., silver fir, *Abies alba* Mill.) or mixed conifer-hardwood forests (e.g., silver fir-beech forests). In the northern study area, the Pyrenees and Pre-Pyrenees constitute transitional and mountainous areas between more humid conditions northwards or upwards and drier conditions southwards or downwards (Vigo and Ninot, 1987). In transitional areas of the Pre-Pyrenees and the Iberian range, forest landscapes comprise stands of *Pinus sylvestris* L., *Pinus pinea* L., *Pinus nigra* subsp. *salzmannii* (Dunal) Franco, *Quercus faginea* Lam., and *Quercus ilex* L. subsp. *ballota* (Desf.) Samp.

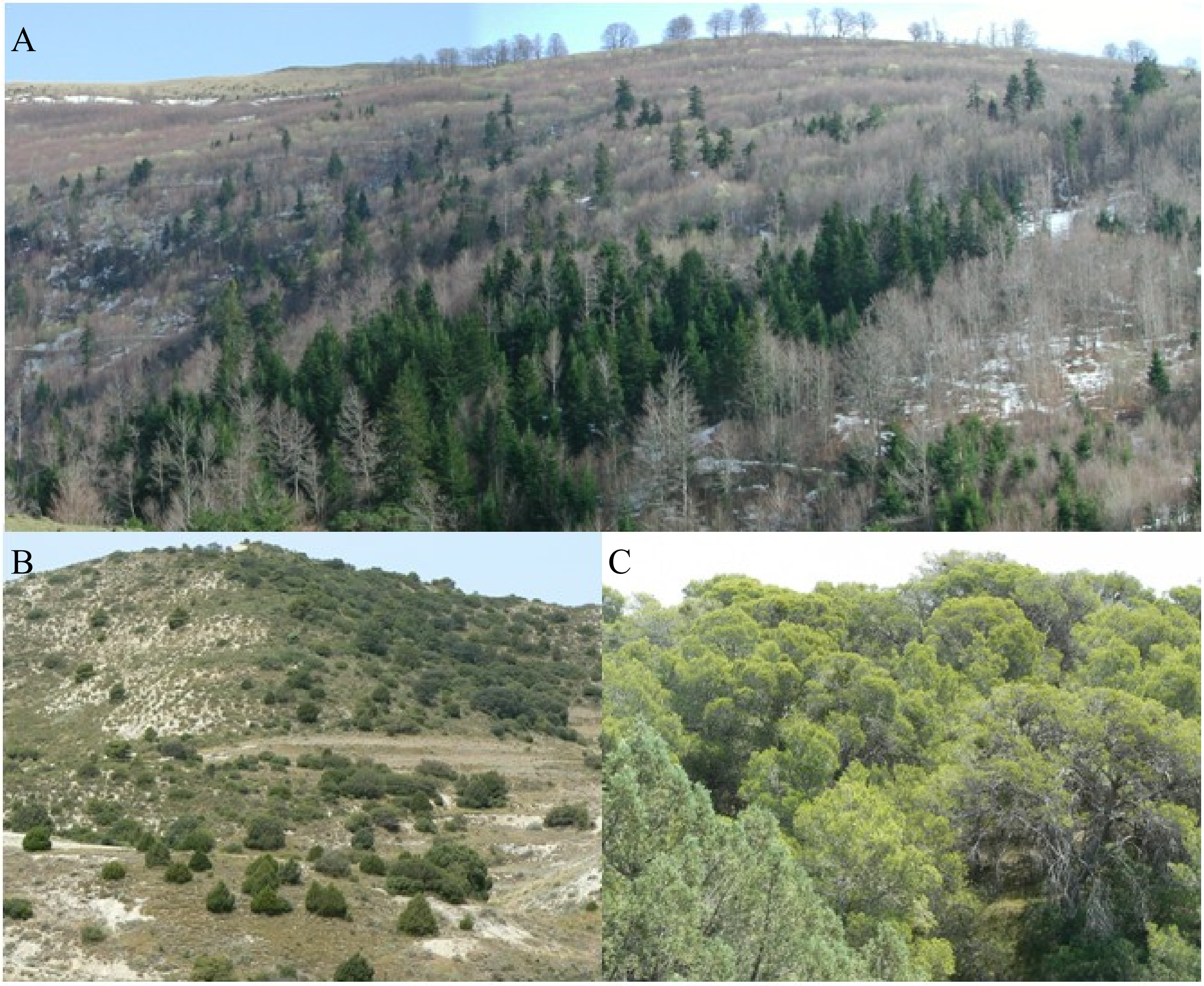

Figure 4. Contrasting types of studied forests dominated by (A) *A. alba* and *F. sylvatica* (Gamueta-Linza, Pyrenees), (B) *Q. ilex* and *J. thurifera* (Sierra de Alcubierre, Middle Ebro Basin) and (C) *P. halepensis* and *J. thurifera* (Vedado de Peñaflor, Middle Ebro Basin). Photographs were taken by J. J. Camarero.

In the semiarid Middle Ebro Basin, forests are open woodlands dominated by *Pinus halepensis* Mill., with scattered relict populations of *Juniperus thurifera* L. The *P. halepensis* forests in the Ebro Valley commonly occur on the top and slopes of structural platforms developed on Miocene carbonate and marl sediments, whereas the valley bottoms have been traditionally used for agriculture and livestock grazing. In the Valencia region, vegetation is also dominated by open *P. halepensis* Mill. forests. The understory species are mainly Mediterranean shrubs and sub-shrubs such as *Quercus coccifera* L., *Rosmarinus officinalis* L., *Linum suffruticosum* L., *Genista scorpius* L., *Thymus* species, etc (Bochet et al., 2009).

To summarize the main growth patterns of species included in the study, a dense network of tree-ring width chronologies (75 sites), covering a wide climatic gradient, was employed (Table 1). In particular, three datasets of radial growth data, summarizing the growth variability in northern, central and southern parts of the study area were involved in the research. The first dataset included mainly mesic forests of *A. alba* (29 sites) and *P. sylvestris* (3 sites) sampled in the Pre-Pyrenees and Pyrenees (see Figure 3; Table 1) by Dr. J.J. Camarero and colleagues during the period 2000-2009. In those areas, trees grow under humid and continental climatic conditions. In addition, this database provided samples of forests growing in the transitional sub-Mediterranean locations such as: *Q. faginea* (5 sites*)* and *Q. ilex* (3 sites) and a few sites located in the Middle Ebro Basin consisting of *P. halepensis* (AG, PH) and *J. thurifera* (PE, RE) species. The second dataset provided radial growth data for the *P. halepensis* forests growing in the Middle Ebro Basin (sites VM, CV, CS, VA, TA, AL, AU, PU) and the Iberian Range in Teruel province (sites MA, PL, MP) under semi-arid Mediterranean continental conditions and a *P.pinea* site (BU) also located in the Iberian Range, Zaragoza province. These sites were sampled and processed by the author (Edmond Pasho), assisted by Dr. Camarero team, and used in the framework of this study. The third dataset comprised mostly *P. halepensis* forests located in the Middle Ebro Basin (sites ES, GR, OL, AM, VL, DA, AY, CP, HS, FR) and Valencia region (sites OR, ZO, RE, JA, FN, GU) under mild Mediterranean conditions, as well as two sites of *P. nigra* (AN, DN) and a *P. pinea* site (DP) distributed in the transitional area between the Iberian Range and the Ebro Basin. These tree ring samples were collected and measured by Dr. M. de Luis during the period 2000-2008. In addition, for the *P. halepensis* sampled forests (except sites AL and AU), radial growth data consisted of ring width as well as EW and LW width series whereas for the rest of the species and sites only the annual tree-ring width was available.

Table 1. Study sites, location, dominant tree species and geographical and climatic conditions.

Site	Code	Species	UTMX	UTMY	Elevation (m a.s.l.)	Mean annual Temperature (ºC)[a]	Total annual Precipitation (mm)[b]
Castiello de Jaca	CA	*Abies alba*	701629.00	4724017.00	1034	9.86	1056
Collubert	CO	*Abies alba*	771980.25	4707884.05	1469	7.80	1078
Guara	GU	*Abies alba*	731016.00	4688155.00	1350	9.09	937
Orús	OR	*Abies alba*	738396.00	4716290.00	1354	9.18	1097
Peña Montañesa	PY	*Abies alba*	766430.83	4708874.57	1269	8.41	1076
Peña Oroel-high	OO	*Abies alba*	702131.00	4710695.00	1725	8.55	828
Peña Oroel-low	PO	*Abies alba*	702078.00	4710940.00	1440	8.88	823
San Juan de la Peña	JP	*Abies alba*	690030.00	4709767.00	1117	9.79	778
Yésero	YE	*Abies alba*	728301.00	4724042.00	1350	8.92	1308
Irati	IR	*Abies alba*	658986.46	4760808.99	1282	9.35	1271
Fago	FA	*Abies alba*	674245.00	4733646.00	1104	9.71	1109
Paco Ezpela	PE	*Abies alba*	676599.00	4735002.00	1305	9.38	1149
Lopetón	LO	*Abies alba*	676104.00	4736564.00	1041	9.93	1161
Gamueta	GA	*Abies alba*	680132.00	4750404.00	1427	7.59	1461
Selva de Oza	SO	*Abies alba*	686634.00	4743354.00	1418	8.32	1413
Paco Mayor	PM	*Abies alba*	691973.00	4730319.00	987	10.43	1129
Puente de los Corralones	PC	*Abies alba*	693160.00	4735909.00	1438	8.67	1385
Lierde	LI	*Abies alba*	700654.00	4730133.00	1433	8.68	1379
Los Abetazos	AB	*Abies alba*	701622.00	4732075.00	1468	8.44	1482
Izquierda del Aragón	IA	*Abies alba*	703750.00	4736367.00	1235	8.01	1664
Paco de Villanúa	VI	*Abies alba*	704012.00	4728255.00	1454	8.51	1330
Paco Asieso	AS	*Abies alba*	721065.00	4726463.00	1135	8.80	1256
Panticosa	PA	*Abies alba*	721103.00	4735234.00	1538	8.24	1348
Diazas	DI	*Abies alba*	738794.00	4723284.00	1575	7.70	1295
Montinier	MO	*Abies alba*	761808.27	4724145.98	1722	6.57	1263
Azirón	AZ	*Abies alba*	764833.03	4726762.55	1677	7.50	1196
Selva Negra	SN	*Abies alba*	775486.46	4718681.68	1529	6.92	1174
Collado de Sahún	SA	*Abies alba*	778703.41	4718191.99	1881	6.00	1188
Ballibierna	BA	*Abies alba*	792046.57	4726250.11	1388	6.65	1186
Agüero	AG	*Pinus halepensis*	683696.93	4575401.30	546	14.44	334
Vedado de Peñaflor	PH	*Pinus halepensis*	688040.00	4628966.00	313	14.17	385
Alcubierre	AL	*Pinus halepensis*	682125.00	4621587.00	235	14.73	348
Alcubierre-Trincheras	AU	*Pinus halepensis*	707390.92	4632435.42	597	13.38	485
Puerto de Alcubierre	PU	*Pinus halepensis*	707340.29	4632588.29	560	14.00	485
Tarazona	TA	*Pinus halepensis*	596865.47	4637574.52	795	12.52	520
Valareña	VA	*Pinus halepensis*	636953.56	4661620.32	520	14.40	448
Castejón de Valdejasa	CV	*Pinus halepensis*	669056.80	4650279.64	498	14.60	562
C. Valdejasa-Zuera	CS	*Pinus halepensis*	673445.71	4640263.00	565	14.50	441
Valmadrid	VM	*Pinus halepensis*	672553.01	4590958.15	648	14.30	465

Zorita	ZO	*Pinus halepensis*	743960.50	4514043.26	843	12.70	535
Estopiñan del Castillo	ES	*Pinus halepensis*	798913.95	4652943.19	492	13.13	504
El Grado	GR	*Pinus halepensis*	764638.95	4672814.33	478	13.50	583
Oliete	OL	*Pinus halepensis*	694144.72	4540298.96	530	14.30	368
Alloza	AM	*Pinus halepensis*	704847.10	4539335.96	595	13.70	387
Villanueva de Gállego	VL	*Pinus halepensis*	673478.45	4638872.29	452	14.70	422
Daroca	DA	*Pinus halepensis*	633119.39	4555501.05	937	12.20	429
Ayerbe	AY	*Pinus halepensis*	677634.94	4688192.68	924	12.20	699
Alcubierre-San Caprasio	CP	*Pinus halepensis*	707892.44	4624573.14	738	13.50	490
Caspe	HS	*Pinus halepensis*	757369.51	4575399.17	166	15.40	321
Fraga	FR	*Pinus halepensis*	777175.30	4596239.49	340	15.20	357
Mas de Puntar	MP	*Pinus halepensis*	698042.03	4453076.62	963	12.35	430
Pileto	PL	*Pinus halepensis*	695732.69	4446320.55	956	12.82	458
Mirador de la Atalaya	MA	*Pinus halepensis*	695720.99	4445857.40	855	13.12	461
Oropesa	OR	*Pinus halepensis*	766132.42	4439591.18	1	17.1	425
Requena	RE	*Pinus halepensis*	654961.25	4370550.69	721	13.9	407
Jalance	JA	*Pinus halepensis*	659418.38	4339557.75	571	15.5	447
Font Roja	FN	*Pinus halepensis*	714156.6	4282734.07	1022	14.5	779
Guardamar	GU	*Pinus halepensis*	705789.97	4219646.49	15	17.7	271
Agüero	AN	*Pinus nigra*	683696.93	4575401.30	546	14.44	334
Daroca	DN	*Pinus nigra*	633119.39	4555501.05	931	12.06	429
Bubierca	BU	*Pinus pinea*	594885.38	4577845.22	877	12.52	390
Daroca	DP	*Pinus pinea*	634170.19	4551185.84	803	12.37	418
Agüero	AP	*Pinus sylvestris*	680862.13	4686373.95	681	13.00	640
Luesia	LU	*Pinus sylvestris*	665077.29	4694417.31	993	10.60	839
Monrepos	PS	*Pinus sylvestris*	712363.31	4686855.15	1096	10.43	930
Retuerta de Pina	PE	*Juniperus thurifera*	688040.00	4628966.00	313	14.17	385
Peñaflor	RE	*Juniperus thurifera*	722972.00	4593912.00	294	14.87	337
Nueno	NF	*Quercus faginea*	711691.00	4682266.00	712	12.85	761
Agüero	QF	*Quercus faginea*	680860.00	4686435.00	702	12.94	642
Arguis	AF	*Quercus faginea*	712154.00	4688949.00	1112	10.39	969
Pico del Águila	PF	*Quercus faginea*	713207.00	4688209.00	1459	10.16	972
Alcubierre	UR	*Quercus faginea*	706972.00	4632515.00	589	13.30	488
Arguis	QR	*Quercus ilex*	680860.00	4686435.00	702	12.94	642
Agüero	AR	*Quercus ilex*	712154.00	4688949.00	1112	10.39	969
Alcubierre	UR	*Quercus ilex*	706972.00	4632515.00	589	13.30	488

[a,b] Climatic data are annual values and were obtained from two homogeneous and spatially dense datasets developed for the north-eastern Spain (Vicente-Serrano et al., 2010b; El Kenawy et al., 2011), MOPREDAS and AEMET dataset (Valencia and Alicante) and an interpolated grid (spatial resolution of 1 km) of existing local climate data for the Pre-Pyrenees and Pyrenees sampled forests.

With regard to the dendrochronological sampling procedure, which was similar for all datasets, forests were selected based on: (*i*) the species dominance in the canopy over at least 1 hectare of fully forested area (*ii*) the occurrence of harsh environmental conditions potentially constraining tree growth such as steep slopes or shallow or rocky soils and (*iii*) to capture most of the climatically mediated growth variability of the studied species. At each of the sampled sites, 10–35 dominant trees were randomly selected, separated by a distance at least 10 m from each other, and their diameter was measured at 1.3 m from the ground. At least two radial cores per tree were taken at 1.3 m using a Pressler increment borer.

2.2. Dendrochronological methods

All the samples provided by the three tree ring datasets were processed following standard dendrochronological methods (Fritts, 1976). Wood samples were carefully mounted with the tracheids or vessels as vertical as possible and sanded until tree-rings were clearly visible with a binocular microscope. All samples were visually cross-dated to ensure that each tree ring is assigned to a specific calendar year without error. The cross-dating was performed and evaluated using statistical comparisons among series incorporated in the COFECHA program (Holmes, 1983). The ring width as well as EW and LW widths (in the case of *P. halepensis*) were measured separately to a precision of 0.001 mm and accuracy of ± 0.0003 mm, using a LINTAB measuring device (Rinntech, Heidelberg, Germany) (Figure 5). The EW and LW were distinguished based on the cross-sectional area of tracheids and the thickness of their walls so as to define an objective threshold of change between both types of wood within the tree ring based on previous dendrochronological and xylogenesis studies on *P. halepensis* (De Luis et al., 2007, 2009; Camarero et al., 2010).

Tree-ring width usually decreases as trees age and enlarge. Because of that, the raw tree-ring width series were transformed into indexed by using a double detrending and a standardization process (Fritts, 1976). Each ring as well as EW and LW width series was double-detrended using a negative exponential function and a spline function with a 50% frequency response of 32 years to retain high-frequency variability.

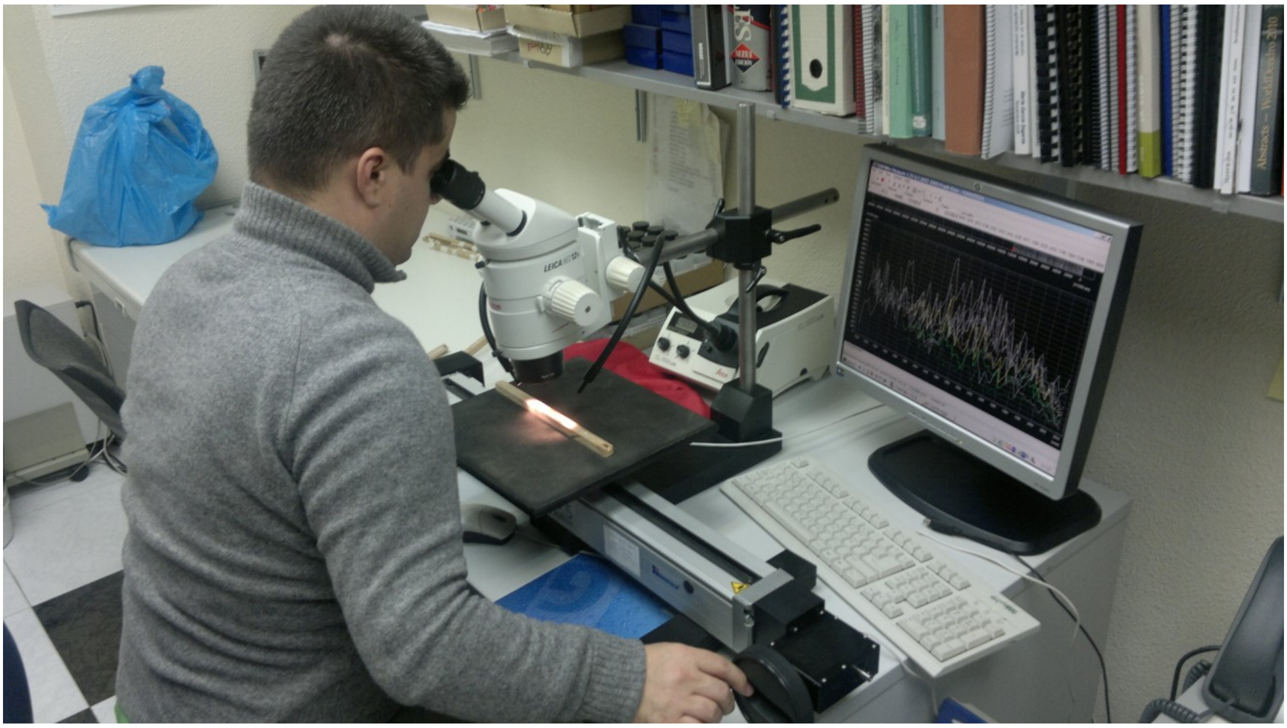

Figure 5. The author measuring wood cores with a LINTAB semiautomatic measuring device in the Instituto Pyrenaico de Ecologia (CSIC).

Standardization involved transforming the measured values into a dimensionless index by dividing the raw values by the expected ones given by the spline function. Autoregressive modeling was then carried out on each series to model and remove temporal autocorrelation. The indexed residual or pre-whitened series were then averaged for each site and species using a biweight robust mean to obtain mean chronologies of ring, EW and LW width which were used in all subsequent analyses. The detrending and standardization of all growth series (three datasets) was done by the author using the ARSTAN program (Cook, 1985).

The quality of the chronologies was evaluated using several dendrochronological statistics (Briffa and Jones, 1990): the mean width and standard deviation (SD) of the raw width series; the first-order autocorrelation (AC1) of these raw series, which measures the year-to-year persistence; the mean sensitivity (MSx) of the residual series, which quantifies the relative change in width among consecutive years; the expressed population signal (EPS) of residual series, which indicates to what extent the sample size is representative of a theoretical infinite population (Wigley et al., 1984) and the mean correlation (Rbar) among individual residual series within each site.

Dendrochronologycal methods provide useful information on climate-growth relationships based on year-to-year correlative approaches but these approaches are unable to capture intra-annual growth variability and delayed growth responses to climate (Camarero et al., 1998). Therefore, dendrochronological information is necessarily to be compared with xylogenesis studies which describe the process of xylem formation and capture the intra-annual growth responses to climate (Camarero et al., 1998; Rossi et al., 2006b). This analysis provides the necessary information to fully understand the dendrochronological patterns and provide mechanisms explaining radial-growth responses to climate variability and drought stress. Xylogenesis studies are now widely employed to provide new data to explain previously established climate–growth relationships (Deslauriers et al., 2003; Rossi et al., 2006b; Vaganov et al., 2006; De Luis et al., 2007; Camarero et al., 2010). Therefore, xylogenesis was also used in this study (see a more detailed methodological description of this approach in section 3.3).

2.3. Climatic data

Different climate information has been used in this study. Firstly, to characterize atmospheric circulation patterns on different spatial scales, several atmospheric circulation indices and weather types were employed. Secondly, to describe the spatial and temporal variability of the surface climatic conditions in the study area, precipitation and temperature data from different climatic databases were used. The following sections describe the climatic data available for this study and the importance of using them to study climate-growth relationships.

2.3.1 Atmospheric circulation

The large scale atmospheric circulation determines the regional atmospheric variability (frequency of weather types) and the surface climate conditions (spatio-temporal variations of temperature and precipitation) in the Iberian Peninsula (Muñoz-Díaz and Rodrigo, 2004b; Vicente-Serrano and López-Moreno, 2005; Martín-Vide and López-Bustins, 2006; Vicente-Serrano and Lopez-Moreno, 2006). Various studies have investigated the direct influence of the spatio-temporal variations of temperature and precipitation on tree growth variability in the Mediterranean region (Macias et al., 2006; Andreu et al., 2007). However, as the variations in temperature and precipitation are controlled by the atmospheric circulation, it is expected that apart from the local climatic conditions, atmospheric circulation as well should exert some influence on the spatial patterns of tree growth in the region. According to Bijak (2009), temperature and precipitation do not explain the whole variability observed in tree-ring width series. This may suggest that tree-ring formation could be partially under the influence of more general factors. In other words, it remains uncertain what is the magnitude of the effect of atmospheric circulation variability on tree growth in the Mediterranean region.

Most of the existing studues regarding the influence of atmospheric circulation on tree growth in the Mediterranean region have been focused on the North Atlantic Oscillation (NAO). For example, Piovesan and Schirone (2000) found high signals of NAO on tree-ring growth of *Fagus sylvatica* in Italy. Tree-ring widths of *Pinus sylvestris* trees in Fennoscandia were also significantly related to variations in the winter NAO (D'Arrigo et al., 1993). Solberg et al. (2002) found negative relationships between *Picea abies* growth and the NAO in central Norway. Moreover, links between tree rings and the NAO index have been used to reconstruct the NAO index using tree-rings as proxies (Cook et al., 1998; Jones et al., 2001; Cullen et al., 2001; Schultz et al., 2008).

In the Iberian Peninsula, only a few studies have investigated the impact of broad scale atmospheric patterns (mostly NAO) on forest growth (Bogino and Bravo, 2008; Roig et al., 2009; Rozas et al., 2009). In particular, Roig et al. (2009) used tree ring series from two deciduous species of western Iberia to reconstruct the NAO index. Rozas et al. (2009) studied the responses of two *Pinus* and *Quercus* species to NAO variations in north-western Spain. Bogino and Bravo (2008) analyzed the impact of NAO on *Pinus pinaster* growth in eastern Spain. However, the eastern Spain is also affected by other atmospheric circulation patterns such as Western Mediterranean Oscillation (WeMO) and the Mediterranean Oscillation (MO) (González-Hidalgo et al., 2009; Vicente-Serrano et al., 2009). In addition, the general atmospheric circulation variability is propagated regionally by means of a series of weather types which control the intensity and spatial distribution of precipitation at local scales (Goodess and Jones, 2002; Vicente-Serrano and López-Moreno, 2006). Therefore it is crucial to consider all these circulation patterns and the frequency of regional weather types as possible drivers of spatio-temporal variability of forest growth in the study area. For this purpose, *P. halepensis* forests, covering a wide climatic gradient in eastern Spain, were selected to investigate the sensitivity of tree growth to climate variability at broad and local scales. Details of the specific methodological approach implemented to obtain the atmospheric circulation indices used in this study are given in section 3.1.

2.3.2. Temperature and precipitation data

Various temperature and precipitation climatic datasets based on AEMET (Agencia Estatal de Meteorología, Spanish Meteorological Agency) data are available for Spain. Most of them consist of precipitation series (Romero et al., 1998; González-Rouco et al., 2001; González-Hidalgo et al., 2004, 2011; Brunetti et al., 2004; De Luis et al., 2009) and less deal with temperature data (Morales et al., 2005; Brunet et al., 2006, 2007). The main purpose behind these studies was to develop complete and homogeneous climatic datasets with improved quality. However, several problems such as spatial density, temporal coverage, quality control and homogenization are usually associated with the available climatic datasets in the region. For example, Brunet et al. (2006) developed a new daily adjusted dataset of 22 observatories of maximum and minimum temperatures in the whole Spain but the spatial coverage was inadequate for several spatial studies. Romero et al. (1998) created 410 complete daily precipitation series for the Spanish Mediterranean area, using information derived from 3366 individual series but the homogeneity of the resultant series was not checked and the dataset is temporally limited (period 1964-1993). To overcome these problems and to construct reliable databases of precipitation and temperature series, a full process of reconstruction, quality control and homogenization of the climatic data is needed (Vicente-Serrano et al., 2010b). Recently, this approach was followed by Vicente-Serrano et al. (2010b) and El Kenawy et al. (2011) to develop two complete, dense, reliable and homogeneous databases of daily precipitation and temperature series for north-eastern Spain.

Different climatic datasets, either based on local observatories or transformed into gridded values, were used to study climate-growth relationships in the study area. In this regard, for the sampled forests located near the populated areas (Middle Ebro Basin), where a considerable high number of local meteorological stations are available, two homogeneous and spatially dense datasets of daily precipitation and temperature series were employed (Vicente-Serrano et al., 2010b; El Kenawy et al., 2011). Since these datasets are covering only north-eastern Spain, additional climatic data of precipitation and temperature series obtained from the MOPREDAS dataset (González-Hidalgo et al., 2011) and the AEMET were used for the forest sites located in Valencia and Alicante provinces. Moreover, considering that many of the sampled forests are located in mountainous areas (Pre-Pyrenees and Pyrenees) where only few meteorological stations are available, the existing local precipitation data were interpolated at a spatial resolution of 1000 m (gridded data) and converted to monthly data to have a regular grid with information in each one of the sampled forest (Vicente-Serrano et al., 2010b). To take into account the effect of elevation on precipitation, and to have more reliable estimations for each forest, the interpolation was done using a Digital Terrain Model and a Geographic Information System (GIS)-assisted regression-based approach (Ninyerola et al., 2000,2007; Vicente-Serrano and Beguería, 2003; Vicente-Serrano, 2007). The precipitation in each 1000 m grid point was estimated, for each month between 1950 and 2006, by means of a stepwise-regression model, in which the independent variables were the elevation, the latitude and the longitude of each site. The residuals, i.e. the differences between the observed and modeled precipitation, were also included in the estimations by means of a local interpolation procedure (splines with tension - Mitasova and Mitas, 1993) to include the local precipitation features recorded each month, which were not well represented by the regression models.

The validation of the grid layers was done for each monthly layer by a jackknifing method, based on withholding, in turn, one station out of the network, estimating regression coefficients from the remaining observatories and calculating the difference between the predicted and observed value for each withheld observatory (Phillips et al., 1992). This method has been frequently used in climatology (e.g. Daly et al., 1994; Holdaway, 1996; Hofstra et al., 2008). The average Root Mean Square Error for the different months and years was 15.2 mm, being lower in summer (6.5 mm) than in winter (22.3 mm). The D agreement index (Willmott, 1982) showed an average of 0.94 for the different monthly layers, with a range between 0.82 and 0.99, which indicates a high reliability between the observed and modeled precipitation data.

2.4. Drought indexes

The drought severity is frequently quantified by drought indices which consider the complexity to determine the magnitude, duration and surface extent of droughts (Wilhite and Glantz, 1985; Redmond, 2002). For these reasons, numerous efforts have been made to develop methods for quantifying drought severity. The main efforts consisted of developing drought indices that enable earlier identification of droughts, quantification of their severity and spatial extent. Several drought indices, using diverse variables and parameters for drought quantification, were developed during the 20th century (Du Pisani et al., 1998; Heim, 2002). Most studies related to drought analysis have been conducted using either (*i*) the Palmer Drought Severity Index (PDSI; Palmer, 1965), based on a soil water balance equation, or (*ii*) the Standardized Precipitation Index (SPI; McKee et al., 1993), based on a precipitation probabilistic approach. The PDSI has numerous deficiencies (Vicente-Serrano et al., 2011) but its main shortcoming for the identification of drought impacts is the fixed temporal scale used to calculate it (Guttman, 1998). This is not in agreement with the frequently accepted fact that drought is a multi-scalar, i.e. time-dependent, phenomenon considering that the period from the water shortages to impacts in a given system differs noticeably. Consequently, drought indices must be associated with a specific time scale to be useful for monitoring drought impacts and be comparable in time and space (Guttman, 1998; Hayes et al., 1999).

Among the existing drought indices (Heim, 2002; Mishra and Singh, 2010) only the SPI and the Standardized Precipitation Evaporation Index (SPEI) can be obtained at different time scales. The SPI is calculated using precipitation data to identify the varied times of response of different hydrological systems to precipitation deficits in a better way than other indices like the PDSI (McKee et al.,1993). The SPEI was developed by Vicente-Serrano et al. (2010c) to include both precipitation and temperature influence on droughts by means of the evapotranspiration processes. Both indices have the advantage of allowing the determination of duration, magnitude and intensity of droughts and can be calculated at different time scales. The later is important in determining ecological impacts of droughts, considering the different time-dependent physiological strategies of vegetation to deal with water deficit (Hsiao, 1973).

However, in this study, only the SPI was employed to analyze the influence of drought on tree growth (all species) since the responses of forests to long-term temperature anomalies can be very different in mesic *vs*. xeric sites. For example, in mesic sites, where water availability is high, high temperatures can favor forest growth by increasing photosynthetic activity, whereas in xeric sites, characterized by frequent water deficit, the same process increases drought stress leading to growth decline and even die off (Jump et al., 2006; Martínez-Vilalta et al., 2008; Vicente-Serrano et al., 2010a). Therefore, depending on water availability, the effect of temperature increase can be positive or negative for forest growth in the respective sites. This is why the SPEI was not included in the drought-growth analysis, since the study considers both xeric and mesic sites. In addition, precipitation is a very important variable explaining the frequency, duration and severity of droughts (Chang and Cleopa, 1991; Heim, 2002) and its variations can markedly influence spatio-temporal patterns of tree growth, particularly in water-limited environments (Macias et al., 2006; Andreu et al., 2007).

2.5. Factors affecting growth-drought responses: climate, topography and vegetation activity

Remote sensing data and GIS-techniques were used in this study to evaluate the potential roles of the differences in vegetation activity and topographical variables in explaining the spatial differences in the growth responses to drought in each sampled forest. Remote sensing offers a feasible tool to objectively and systematically monitor vegetation condition by estimating photosynthetically active vegetation throughout the growing season. The major interest of remote sensing imagery lies on the possibility of extrapolating acquired data at pixel resolution, to get spatially continuous information less costly than ground surveys and in a relatively short time. The utility of remote sensing for vegetation monitoring is based on the response of vegetation cover to radiation in the visible and near-infrared regions of the electromagnetic spectrum (Myneni et al., 1995). Visible radiation is mainly absorbed by vegetation in photosynthesis processes while near infrared radiation is principally reflected, owing to the internal structure of leaves (Knipling, 1970). High vegetation activity is characterized by low reflectivity of solar visible radiation and high reflectivity in the near infrared region of the spectrum.

GIS-related technologies have been widely used in a variety of ecological applications. According to Booth and Tueller (2003), GIS is a powerful tool for integrating and analyzing data derived from remotely sensed imagery interpretations, soil surveys, vegetation maps, land ownership maps, utility maps, water resources, geology and many other potential themes that can be presented spatially. These geographically referenced data sets are spatially registered so that multiple themes of data can be quickly compared and analyzed together. According to Buchan (1997), satellite images are used to identify what is growing, while the GIS component is used to further analyze its position on the earth, measure area, etc, providing in this way a complete record of the site.

Different indices have been developed for monitoring and measuring vegetation status using spectral data (Bannari et al., 1995). Among them, the most widely used is the Normalized Differences Vegetation Index (NDVI) (Rouse et al., 1973). Numerous authors have pointed out the close relationship between NDVI, vegetation activity and tree radial growth (e.g., Wang et al., 2004; Pettorelli et al., 2005; Lopatin et al., 2006; Kaufmann et al., 2008; Khabarova et al., 2010; Vicente-Serrano et al., 2010a; Julien et al., 2011). The NDVI measures the fractional absorbed photosynthetically active radiation (Myneni et al., 1995) and exhibits a strong relationship with the green leaf-area index (Carlson and Ripley, 1997). In addition, the Enhanced Vegetation Index (EVI) enhances the vegetation signal with improved sensitivity in regions with high biomass (e.g, dense forests) and allows improved vegetation monitoring through a decoupling of the canopy background signal and a reduction in atmosphere influences (Huete et al., 2002).

NDVI is an excellent measure of the photosynthetic activity but it has some limitations to analyze vegetation activity in dense forests since the relationship between vegetation parameters (leaf area, annual net primary production (ANPP), vegetation coverage, etc.) and the NDVI are sometimes non-linear because the NDVI saturates before the maximum biomass is reached (Carlson et al., 1990). On the contrary, the EVI was developed to improve the vegetation signal and provide a more accurate measure of vegetation activity in dense biomass regions. Since the canopy cover of the forests located in the most arid sites of the study area (mainly *P. halepensis*) is not very dense while the opposite occurs with the Pyrenean silver fir stands, it is justified the use of both indices to provide complementary information as the best measure of photosynthetic activity in the respective areas. The data was obtained from the products of Moderate Resolution Imaging Spectro-radiometer (MODIS 13A1 product, 16-day at 500 m resolution; available at http://www. daac.ornl.gov /MODIS/modis.html in HDF format; see Huete et al., 2002) which provide significant refinements in spectral, radiometric, and geometric properties compared to previously available data sets with similar spatial resolution (Justice & Townshend, 2002; Zhang et al., 2004). Data processing included images re-projection from a Sinusoidal to a UTM-30N-S/IGN projection, images stacking to provide a full coverage of the study area and crossing of the images with forest sites location to extract the NDVI and EVI values at each sampled forest.

2.6. Statistical analyses

In this section are described the main statistical analysis applied in the framework of this study, providing also a justification of their use to investigate the relationships between the climatic variables, drought and the spatio-temporal variations of tree growth in the study area.

2.6.1. Principal component analysis (PCA)

The main purpose of the PCA analysis is to reduce the dimensionality of the data into a few, uncorrelated components, leading to more understandable and clearly interpretable dataset (Vicente-Serrano et al., 1999). There are six possible modes of the PCA called O, P, Q, R, S, and T (Richman, 1986). The modes differ according to which parameter is chosen as variable, which of them is considered as individual case and which as a fixed entity. In the case that the parameter has been fixed, there remain two options: the S and T modes. The T-mode is the result of choosing the individual observations as variables and sites as cases of those variables. When rotated, T-mode identifies subgroups of observations with similar spatial patterns. The S-mode considers the sites as variables and the observations as cases. The S-mode compares the sites and identifies those which show similarity in a particular observation. In other words, this method enables common features to be identified and specific relevant local characteristics to be detected (Richman, 1986). This is why the S-mode PCA was selected as the most appropriate one to be applied for this study to summarize the spatio-temporal variability of forest growth in the large data set used.

2.6.2. Correlation analyses

Correlation analysis is a widely used statistical technique for studying climate-growth relationships (Briffa and Cook, 1990). Among the several correlation coefficients available, in this study it was employed the parametric Pearson correlation because the climate and growth data used, fullefilled the requirements of normal distribution and homogeneity of the variance (Clark and Hosking, 1986). Therefore, this correlation coefficient was used for several purposes as detailed in the specific sections of the results chapter.

2.6.3. Superposed epoch analysis (SEA)

Superposed epoch analysis (SEA) is a non-parametric technique used to examine how punctual events modifiy the values of a continuously derived variable such as growth (Hoenig, 1989; Haurwitz and Brier, 1981). Since the statistical significance is determined by a randomization test, SEA is a robuts approach which does not rely on the usual assumptions (normality, homogeneity of variance, independence of observations) of parametric testing. In a previous dendrochronological study (Martín-Benito et al., 2008), SEA was used to assess the relationship between extreme climatic events (e.g. drought) and tree growth response in the corresponding and following years. For each drought occurrence, the tree ring data is selected from a window of years preceeding, including, and after the event occurs. In this regard, SEA was employed in this study to investigate the impacts of drought severity on EW and LW growth in *P. halepensis*, during the current and following (post-drought) two years of growth.

2.6.4. Regression analyses

Linear regression analysis is a statistical technique used to predict the response of a variable (predictand) as a function of another one (predictor) assuming they are linearly related. To explore such relationships, the data is organised into variables of interest and regression is applied to estimate the quantitative effect of the causal variables upon the variable that they influence. Regression analysis with a single explanatory variable is termed “simple regression”, while “multiple regression” is a technique that allows additional factors to enter the analysis separately so that the effect of each of them can be estimated. Multiple regression analysis has shown to be valuable among others for quantifying the impact of various climatic and site factors on spatio-temporal variations of tree growth (Suarez et al., 2004; Hogg and Wein, 2005; Sánchez-Salguero et al., 2010). Taking into account its efficiency and simplicity, this analysis was employed in the framework of this research to detect which abiotic and biotic factors (potential predictors) most affect growth responses to drought of all species considered in the study.

CHAPTER III

RESULTS

In this chapter are presented the main findings of the study. In particular, the first and third parts of this section deal with the results regarding the influence of large, regional and local scale climatic drivers and drought on *P.halepensis* growth. The second and fourth parts of the chapter show the findings concerning forest responses (all studied species) to drought (SPI index) and the main factors driving such responses.

3.1. Spatial variability in large-scale and regional atmospheric drivers of *Pinus halepensis* growth in eastern Spain

Introduction

Climatic projections predict strong warming (2–4°C) trends and a decrease in land water availability (ca. −20%) for the Mediterranean basin during the 21st century (IPCC, 2007). The forecasted drying trend will be in part determined by an increased frequency of anticyclone conditions associated with a northward shift of the Atlantic storm track (Giorgi and Lionello, 2008). Moreover, it is expected that there will be an increase in the surface pressure gradient between the northern and southern parts of the North Atlantic region (Osborn, 2004; Paeth and Pollinger, 2010), a decrease in the frequency and intensity of Mediterranean cyclones (Lionello et al., 2008; Raible et al., 2010), and a decrease in summer convective systems (May, 2008; Branković et al., 2010).

The predicted changes in atmospheric circulation are expected to affect the growth of trees in the Mediterranean region through changes in the characteristics of the dominant atmospheric flows, the frequency of particular weather types, and the surface climate (including precipitation and temperature). Most analyses of the impacts of climate on forest growth have only focused on the influence of surface climate factors (Fritts, 2001). Nevertheless, atmospheric circulation patterns affect climate variability over large regions. They allow determining the effects of large-scale climate processes and focusing in the physical mechanisms that control climate variability at regional and/or local scales.

Few studies have attempted to determine the direct and indirect influences of atmospheric circulation on tree growth (see Hirschboeck et al., 1996, Garfin 1998, Girardin and Tardif, 2005). This kind of information is lacking in areas with a Mediterranean climate. This is particularly the case of most Iberian Peninsula, where climatic conditions range from mild to continental, and from humid to semiarid, creating diverse constraints on tree growth (Nahal, 1981).

The climate variability of the Iberian Peninsula is under the influence of various atmospheric circulation patterns (Rodó et al., 1997; Rodríguez-Puebla et al., 1998; Trigo and Palutikoff, 1999, 2001; Trigo et al., 2004; González-Hidalgo et al., 2009). The influence of large-scale atmospheric patterns on Iberian tree growth reported previously (Bogino and Bravo, 2008; Roig et al., 2009; Rozas et al., 2009) may also reflect growth effects caused by precipitation variability, which is directly determined by local-scale climatic drivers (e.g. weather types), as has been suggested to occur in Canada (Girardin and Tardif, 2005) and Mexico (Brienen et al., 2010).

While the predicted trend towards progressively drier conditions is likely to cause a decline in the growth of Mediterranean forests, the spatial extent and the magnitude of the effect of atmospheric and climatic drivers on tree growth is uncertain (Andreu et al., 2007; Sarris et al., 2007; Vicente-Serrano et al., 2010a). Iberian forests of *Pinus halepensis* Mill., (Ne'eman & Trabaud, 2000), provide a useful model for evaluating the sensitivity of tree growth to climatic variability at broad and local scales. No studies have investigated how the climate drivers affect earlywood and latewood production, despite ample evidence that each of these components of *P. halepensis* growth respond differently to diverse climatic variables (De Luis et al., 2007; Camarero et al., 2010). Therefore, here it is analyzed the influence of large-scale atmospheric circulation patterns (NAO, MO and WeMO), as well as the role of the atmospheric circulation processes at regional scales (quantified by the frequency of various weather types) on the spatio−temporal patterns of tree growth in *P. halepensis* forests of eastern Spain (Figure 6).

The objectives of this study were: (*i*) to use dendrochronological methods to characterize the spatial and temporal patterns of radial growth (earlywood and latewood width) (*ii*) to quantify the influence of large-scale circulation patterns and regional weather types as atmospheric drivers of tree growth and (*iii*) to explain the surface climate processes that drive the influence of the atmospheric circulation on forest growth. It was hypothesized on a spatially structured response of forest growth to the atmospheric circulation patterns that determine the climate variability across the region.

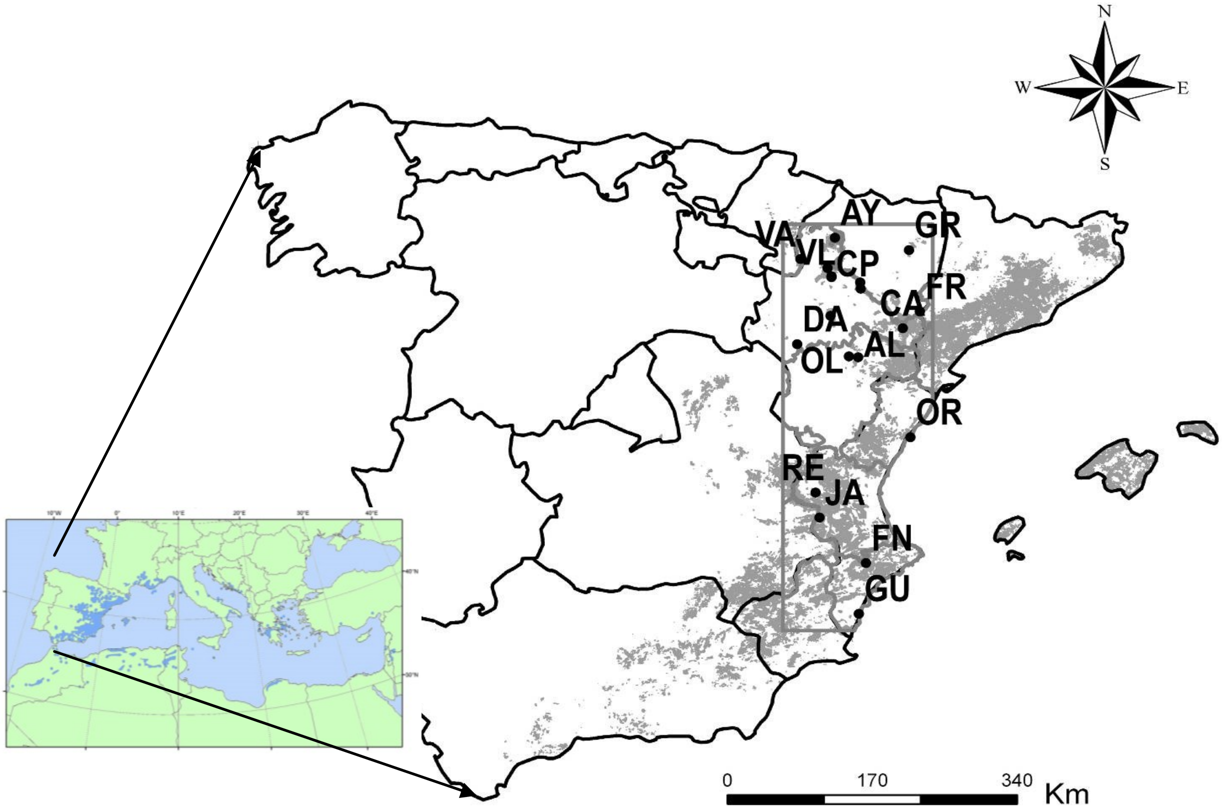

Figure 6. Distribution of *P. halepensis* in the Mediterranean Basin (map was taken from EUFORGEN, http://www.euforgen.org/distribution_maps.html) and eastern Spain (gray area) and the location of the study sites (black points). The sites codes are explained in Table 1.

Specific methods

Dendrochronological methods

The samples preparation, cross-dating and standartization were performed following standard dendrochronological methods (see section 2.2). The common period 1960-2003 was selected because all sites residual chronologies showed EPS values above the 0.85 threshold, which is widely used in dendrochronological studies (Wigley et al., 1984).

Atmospheric circulation patterns

The NAO, MO and WeMO atmospheric circulation patterns, which affect autumn and winter climatic conditions (particularly precipitation) over eastern Spain, were selected following Vicente-Serrano et al. (2009) and González-Hidalgo et al. (2009). Autumn (September to November), spring

(April to May), summer (June to August) and winter (December to March) indices were calculated. To calculate the seasonal circulation indices were used the monthly SLP grids from the NCEP-NCAR ds010.1 Monthly Northern Hemisphere Sea Level Pressure Grids (http://dss.ucar.edu/datasets/ds010.1/; Trenberth and Paolino, 1980). This dataset contains complete records for the study period (1960–2003), with a spatial resolution of 5°. The atmospheric circulation indices were calculated monthly from the differences between the series of standardized SLPs recorded at the two points closest to the sites most used to calculate these indices: Gibraltar (south of the Iberian Peninsula; 35° N, 5° W) and Rejkiavic in Iceland (65° N, 20° W) in the case of the NAO (Jones et al., 1997); Gibraltar and Lod in Israel (30° N, 35° E) in the case of MO (Palutikof, 2003); and Gibraltar and Padova (Italy) (45° N, 10° E) in the case of the WeMO (Martín-Vide and Lopez-Bustins, 2006). Seasonal atmospheric circulation indices were obtained from the average of the monthly series.

Classification of weather types

The general atmospheric circulation, well represented in East Spain by means of the general atmospheric circulation patterns cited above, is propagated regionally by means of different weather types that represent pressure fields and winter flows with a noticeable role on the surface climate conditions (e.g., precipitation and temperature) (Yarnal et al., 2001). On one hand, a high frequency of weather types prone to cause precipitation would tend to produce humid conditions. On the other hand, weather types characterized by stability conditions will be the direct cause of droughts. The influence of the frequency of weather types on the surface climate in eastern Spain (e.g., Vicente-Serrano and López-Moreno, 2006) justifies their use to investigate the possible influence on tree radial growth.

Several attempts have been made to develop classification methods based on different categories of weather type (see review in Yarnal et al., 2001). Among these, automatic methods allow the construction of homogeneous daily or monthly series of atmospheric climatic conditions, at local and regional scales. The most widely used automatic method to classify weather types is that formulated by Jenkinson and Collison (1977), which is based on the Lamb (1972) catalogue. This has been widely used to classify weather types in the Iberian Peninsula (Spellman, 2000; Trigo and DaCamara, 2000; Goodess and Jones, 2002; Vicente-Serrano and López-Moreno, 2006; López-Moreno and Vicente-Serrano, 2007). To obtain a daily classification of weather types it was used a sea surface pressure grid of 16 points centered over the Iberian Peninsula (see Figure 1 in Vicente-Serrano and López Moreno, 2006). From daily pressure data at these points over the period 1960–2003 were calculated the type and direction of winds (cyclonic/anticyclonic, directional and hybrid) on which to base a classification of weather types. For this purpose it was used again the NCEP–NCAR Northern Hemisphere Sea Level Pressure Grids, but at a daily time scale (http://dss.ucar.edu/datasets/ds010.0). Quantitative monthly series can be derived from the daily weather types using the sum of the number of weather types in each class during the month (Corte-Real et al., 1998). The 26 weather types obtained using Jenkinson and Collison's method were summarized by the elimination of hybrid types, which were reclassified at 50% to cyclonic (C), anticyclonic (A) or directional weather types (N, north; NE, northeast; E, east; SE, southeast; S, south; SW, southwest; W, west; and NW, northwest) (Trigo and DaCamara, 2000; Vicente-Serrano and López-Moreno, 2006). Seasonal series of the frequency of the 10 weather types from 1960 to 2003 were related to *P. halepensis* growth.

Climate data

To explain the mechanisms driving the influence of the atmospheric circulation processes on the EW and LW growth, were used data of monthly precipitation and temperature from 1960 to 2003 for each sampled forest. The monthly climatic data were grouped seasonally following the same approach as for the atmospheric circulation patterns: Autumn (September to November), spring (April to May), summer (June to August) and winter (December to March).

Statistical analyses

The PCA analysis (S-mode) was applied to determine the spatial patterns in the inter annual variability of EW and LW growth in *P. halepensis* forests across the study area for the period 1960−2003. The areas represented by each component, showing the spatial patterns of EW and LW growth, were identified by mapping the factorial loadings. The PCA was performed on a covariance matrix calculated among the chronologies (Legendre and Legendre, 1998). The number of components was selected using the criterion of an eigenvalue > 1, the components were rotated (Varimax) to redistribute the final explained variance and to obtain more stable and robust spatial patterns (Richman, 1986; Garfin, 1998). The spatial classification of EW and LW growth was carried out using the factorial loading values obtained for each component, with the forests being grouped using the maximum loading rule. Each forest was assigned to the component with the greatest loading value. This method has been applied in many climatic classification studies (e.g. Comrie and Glenn, 1998).

To explain the influence of variability in atmospheric circulation on the spatio-temporal patterns of EW and LW growth, correlation analyses were carried out (Briffa and Cook, 1990). To compare with the de-trended forest growth series and to avoid the possibility that atmospheric circulation trends could disrupt potential relationships, prior to assessing the correlations, the trend in each of the atmospheric circulation series was removed by fitting a linear trend in each series. Correlation analyses were performed between EW and LW residual indices, de-trended monthly and seasonally atmospheric circulation indices, and the de-trended series of the frequency of weather types for the period 1960–2003. The joint influence of climate and EW on LW was obtained by carrying out partial correlation analysis. Finally, to determine climate processes that drive the influence of atmospheric circulation on forest growth, it was calculated the correlation between the atmospheric circulation patterns and the surface climate as well as the correlation between EW, LW and the seasonal precipitation and temperature at each sampling site.

Results

Earlywood and latewood chronologies

Initially, the statistical characteristics of the EW and LW series in each *P. halepensis* forest used in this section are shown. EW growth varied more than LW growth among sites (EW, 0.62-2.29 mm; LW, 0.15-0.66 mm) (Table 2, Figure 7). The average values of first-order autocorrelation (AC1) and mean senistivity (MSx) were higher for the EW (AC1 = 0.64, MSx = 0.39) than for the LW (AC1 = 0.49, MSx = 0.33) chronologies. Similar results were obtained for the mean correlation (Rbar) among individual series within each site; and the expressed population signal (EPS), which were also higher for the EW (Rbar = 0.60, EPS = 0.97) than for the LW (Rbar = 0.40, EPS = 0.93) series.

Table 2. Dendrochronological statistics of earlywood (EW) and latewood (LW) *P. halepensis* chronologies for the common period 1960-2003. The column EW-LW shows the Pearson correlation coefficient calculated between the series of both variables.

				EW						LW					
Site	Trees (radii)	Period	EW-LW	MW (mm)	SD (mm)	AC1	MSx	Rbar	EPS	MW (mm)	SD (mm)	AC1	MSx	Rbar	EPS
AY	19 (33)	1946-2006	0.56	2.07	0.91	0.60	0.21	0.34	0.93	0.58	0.39	0.33	0.28	0.28	0.92
GR	15 (30)	1946-2006	0.46	1.78	1.02	0.69	0.29	0.54	0.97	0.51	0.29	0.35	0.32	0.33	0.93
VA	17 (31)	1925-2009	0.65	1.4	0.91	0.70	0.36	0.61	0.96	0.41	0.28	0.66	0.31	0.43	0.95
CV	13 (23)	1928-2009	0.42	1.79	1.07	0.74	0.28	0.48	0.92	0.56	0.38	0.70	0.29	0.33	0.90
CS	13 (23)	1900-2009	0.64	0.90	0.59	0.57	0.33	0.69	0.98	0.25	0.19	0.50	0.32	0.40	0.93
VL	15 (29)	1878-2006	0.68	0.94	0.65	0.55	0.44	0.55	0.96	0.27	0.23	0.48	0.38	0.39	0.93
PU	15 (22)	1943-2009	0.58	1.12	0.74	0.65	0.34	0.67	0.98	0.36	0.20	0.55	0.30	0.39	0.92
CP	14 (27)	1927-2006	0.62	1.58	1.05	0.70	0.36	0.57	0.96	0.42	0.26	0.55	0.26	0.31	0.91
FR	16 (29)	1844-2006	0.57	0.72	0.63	0.68	0.51	0.63	0.97	0.25	0.21	0.61	0.34	0.37	0.93
VM	17 (30)	1959-2009	0.57	1.43	0.83	0.62	0.34	0.8	0.99	0.40	0.23	0.55	0.28	0.52	0.96
CA	16 (28)	1845-2007	0.65	0.62	0.51	0.55	0.64	0.71	0.98	0.15	0.11	0.39	0.42	0.41	0.94
DA	14 (28)	1934-2006	0.54	1.62	1.0	0.48	0.46	0.82	0.99	0.44	0.28	0.25	0.43	0.65	0.98
OL	15 (27)	1960-2006	0.40	2.29	1.98	0.77	0.37	0.78	0.99	0.66	0.36	0.46	0.30	0.47	0.95
AL	15 (31)	1888-2006	0.63	1.11	0.83	0.69	0.43	0.66	0.98	0.34	0.25	0.60	0.23	0.33	0.93
OR	16 (30)	1921-2003	0.53	1.45	1.18	0.63	0.41	0.58	0.97	0.58	0.45	0.51	0.35	0.46	0.95
RE	15 (30)	1789-2003	0.40	0.93	0.64	0.58	0.41	0.39	0.94	0.36	0.31	0.47	0.37	0.26	0.89
JA	15 (35)	1863-2003	0.56	1.05	0.62	0.48	0.44	0.59	0.97	0.37	0.30	0.26	0.47	0.40	0.95
FN	15 (24)	1863-2006	0.68	1.06	0.75	0.69	0.40	0.53	0.93	0.27	0.20	0.51	0.35	0.41	0.9
GU	36 (75)	1912-2006	0.52	1.12	1.43	0.77	0.43	0.55	0.99	0.37	0.37	0.60	0.33	0.40	0.97

Statistics for raw-data series: MW, mean ring width; SD, standard deviation; AC1, first order autocorrelation. Statistics for residual series: MSx, mean sensitivity; Rbar, mean interseries correlation; EPS, expressed population signal. Sites names as in Table 1.

Consequently, EW growth showed a greater year-to-year persistence (AC1), a higher change among consecutive years (MSx) and a higher common signal (Rbar, EPS) than LW formation. The change in EW and LW width among consecutive years (MSx) increased as latitude decreased but these trends were not significant (EW, p = 0.15; LW, p = 0.10). The correlation between EW and LW series decreased significantly as the LW width increased (r = –0.67, p = 0.002).

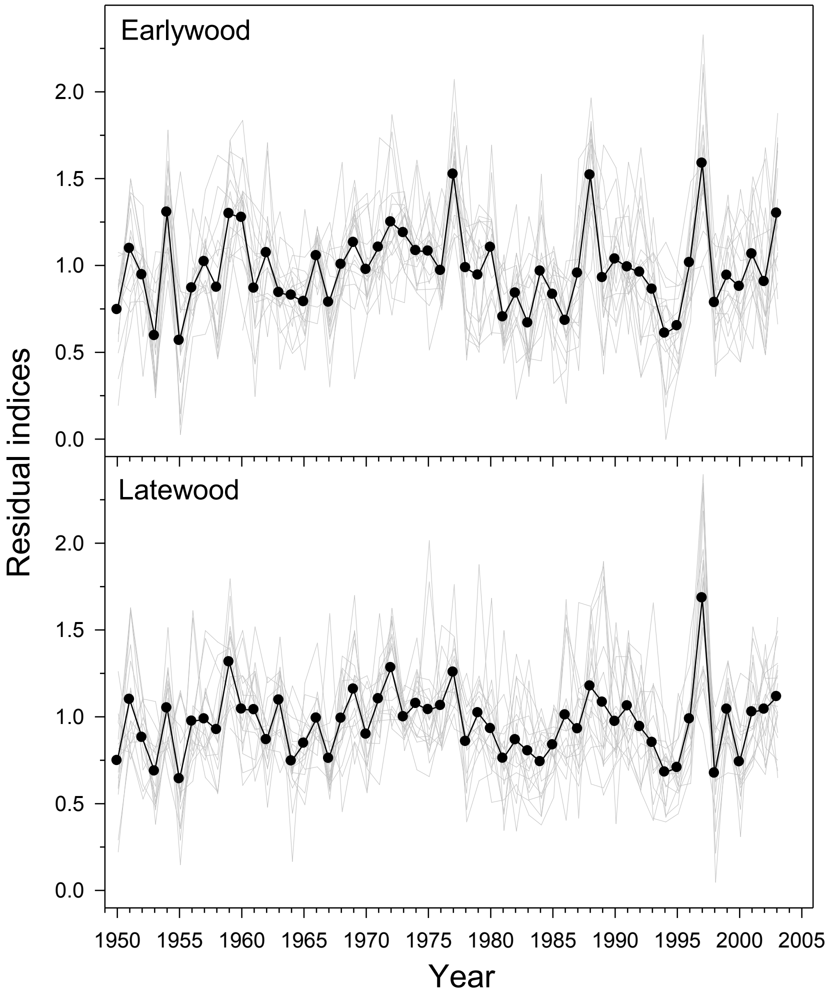

Figure 7. Residual chronologies of earlywood (EW) and latewood (LW) (gray lines) widths for the *P. halepensis* network developed in eastern Spain, and the overall mean for each variable (black lines).

Spatio-temporal patterns of P. halepensis growth

The PCA was used to summarise the EW and LW growth series and to retain the main patterns of spatio-temporal variability across the study area. PCA analysis revealed four and five components (PCs) for EW and LW, which accounted for 72% and 71% of the variance, respectively (Table 3). This indicates a slightly higher spatial variability for the LW formation, although the components retained, represent a high percentage of the total variance, which shows that tree growth in the region is not very heterogeneous and that coherent temporal patterns, representative of large regions can be found.

Table 3. Correlations (Pearson coefficient) calculated between the main principal components (PC) of EW and LW widths and atmospheric circulation indices (NAO: North Atlantic Oscillation; MO: Mediterranean Oscillation; WeMO: Western Mediterranean Oscillation) for winter (W), spring (Sp), summer (Su) and autumn (A). The third raw is the variance explained by each principal component.

	EW				LW				
	PC1	PC2	PC3	PC4	PC1	PC2	PC3	PC4	PC5
Variance (%)	33.58	15.62	12.9	10.1	20.9	17.97	11.8	12	8.6
NAO-W	-0.32*	0.05	-0.3	0.18	-0.28	0.05	-0.21	-0.13	0.17
MO-W	-0.25	-0.08	-0.21	-0.03	-0.29	0.02	-0.19	-0.21	-0.20
WeMO-W	0.12	-0.43**	-0.04	0.02	-0.04	-0.18	0.02	-0.22	-0.23
NAO-Sp	-0.45**	0.10	0.25	-0.20	-0.14	0.12	0.05	-0.16	-0.02
MO-Sp	0.10	-0.12	0.19	0.14	-0.31*	-0.16	0.16	-0.20	0.10
WeMO-Sp	-0.20	-0.30	-0.12	0.26	0.17	-0.13	0.16	-0.09	0.10
NAO-Su	–––	–––	–––	–––	0.14	0.23	0.33*	0.04	0.26
MO-Su	–––	–––	–––	–––	-0.01	-0.22	-0.24	0.04	-0.16
WeMO-Su	–––	–––	–––	–––	0.14	0.23	0.33	0.07	0.26
NAO-A	–––	–––	–––	–––	-0.13	-0.06	0.07	0.02	0.10
MO-A	–––	–––	–––	–––	-0.11	-0.35*	-0.06	-0.04	0.04
WeMO-A	–––	–––	–––	–––	-0.15	-0.36*	-0.03	0.19	0.08

Significance levels: ** $p < 0.01$, * $p < 0.05$.

Overall, EW chronologies showed greater correlation among nearby sites than LW series did. The spatial extend of these relationships was significant up to 300 and 380 km for EW and LW chronologies, respectively (Figure 8).

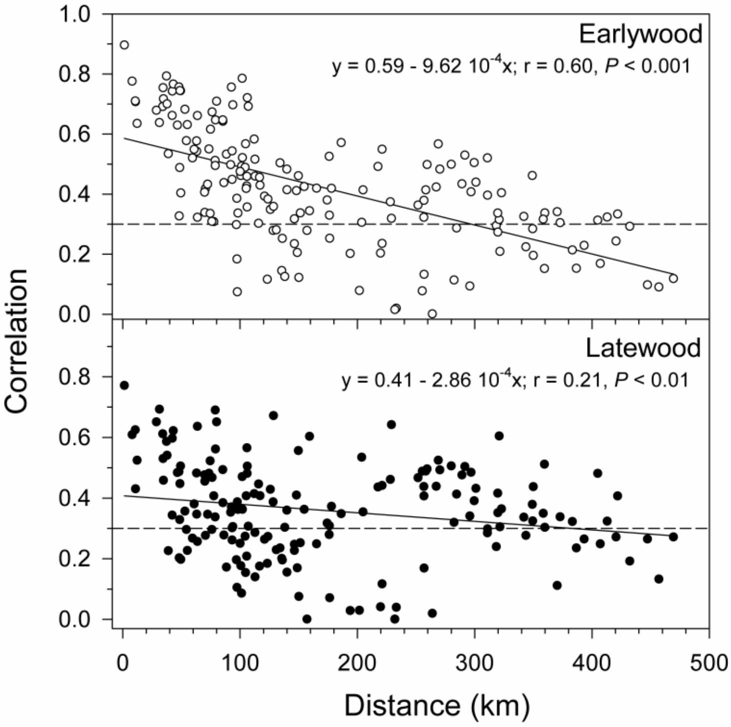

Figure 8. Spatial extent of earlywood (EW) and latewood (LW) chronologies. The diagonal lines represent the indicated linear regressions, whereas the dashed horizontal lines represent significance thresholds ($p < 0.05$) for the correlation values.

The spatial distribution of the PCA loadings, corresponding to the 4 and 5 retained components for EW and LW respecively, shows clear geographical patterns in tree growth across the study region (Figure 9 A).

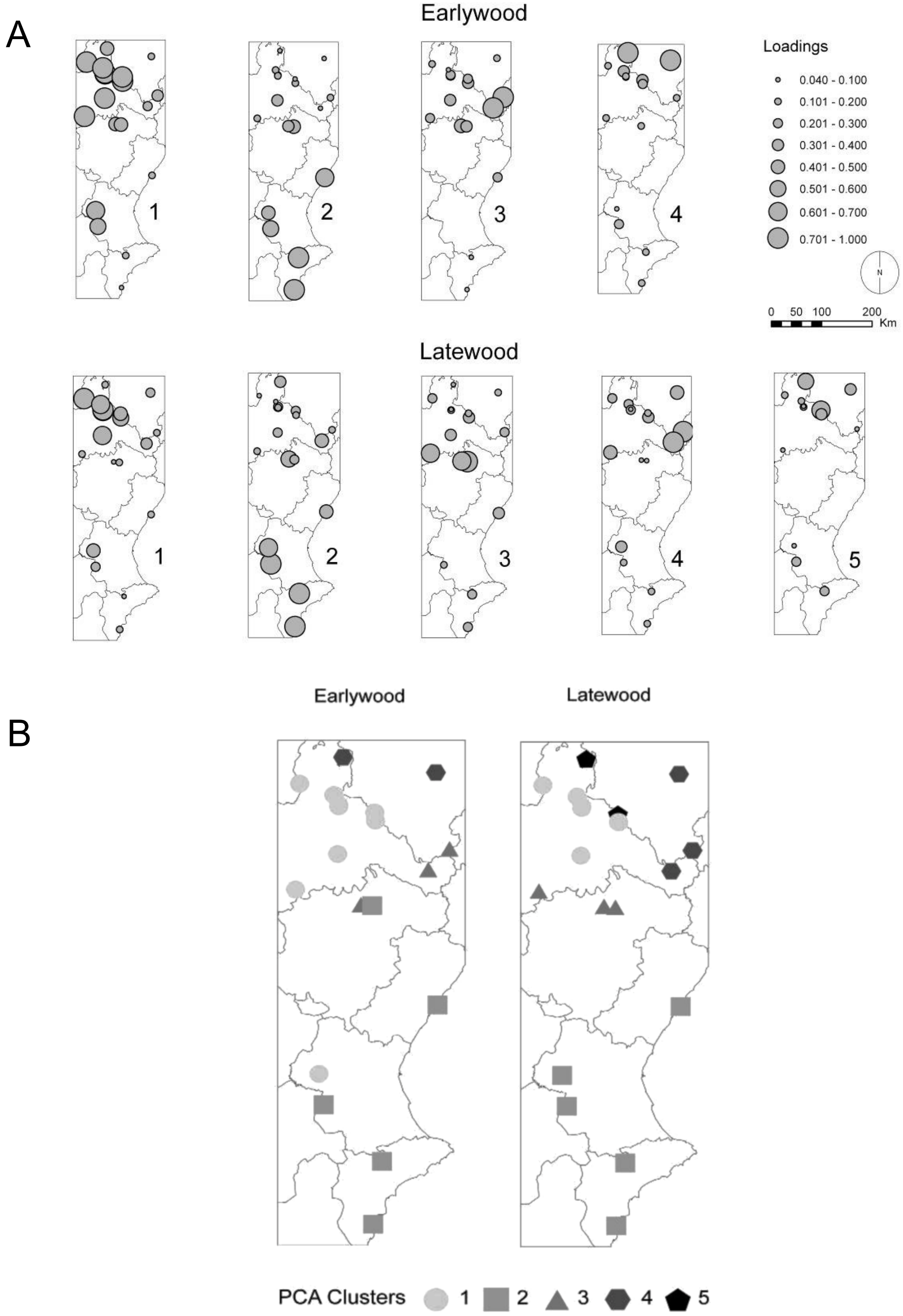

Figure 9. Spatial patterns of *P. halepensis* growth (earlywood (EW) and latewood (LW) chronologies) as revealed by PCA based on the loadings of the first four and five principal components, for earlywood (EW) and latewood (LW), respectively (A), and spatial classification based on the maximum loadings for each component (B).

According to the PCA loadings of the first components of EW and LW production, two main growth patterns, corresponding to PC1 and PC2, were found in northwestern and southeastern sites, respectively. These components group the 49.2% and the 38.9% of the total EW and LW variability, respectively (Table 3). This indicates that a high percentage of the tree-growth variance of the region is represented by these components. Additional sites were represented by the other components, but they account for a lower percentage of the total variance and they are found in transitional areas between the northwestern and southeastern locations, and in the northeastern part of the study area. The spatial classification of EW and LW variability based on the maximum loading rule shows clearly the distinction between the northwest and southeast sectors, both for EW and LW formation, with few differences among them (Figure 9 B).

Influence of atmospheric circulation on P. halepensis growth

The influence of atmospheric circulation patterns on *P. halepensis* growth was assessed by means of correlation analysis. In general, very few significant correlations were found between the seasonal atmospheric circulation patterns and the EW and LW series of the retained principal components (Table 3). Significant and negative relationships were found between the winter, spring NAO index and EW PC1, whereas the EW PC2 was negatively related to the WeMO winter index. For the LW, significant correlations were found between the PC1 and the MO in spring, between the PC3 and the summer NAO and between the autumn MO and WeMO and the LW PC2. These results clearly indicate that the two main components, which represent the major percentage of growth variability, are significantly correlated to some of the atmospheric circulation patterns at a seasonal scale. In addition, it was found a high temporal agreement between the variability of the atmospheric circulation patterns (winter and spring NAO, winter and autumn WeMO) and tree growth as represented by the first and second components of EW and LW (Figure 10). Such temporal agreement is coherent with spatial analyses between EW and LW growth and the seasonal atmospheric circulation patterns (Figure 11). The EW PC1 is significantly related to the winter and spring NAO in north and northwestern forests. In contrast, the effects of the winter and autumn WeMO indices on PC2 EW and LW formation were greater at southeastern sites.

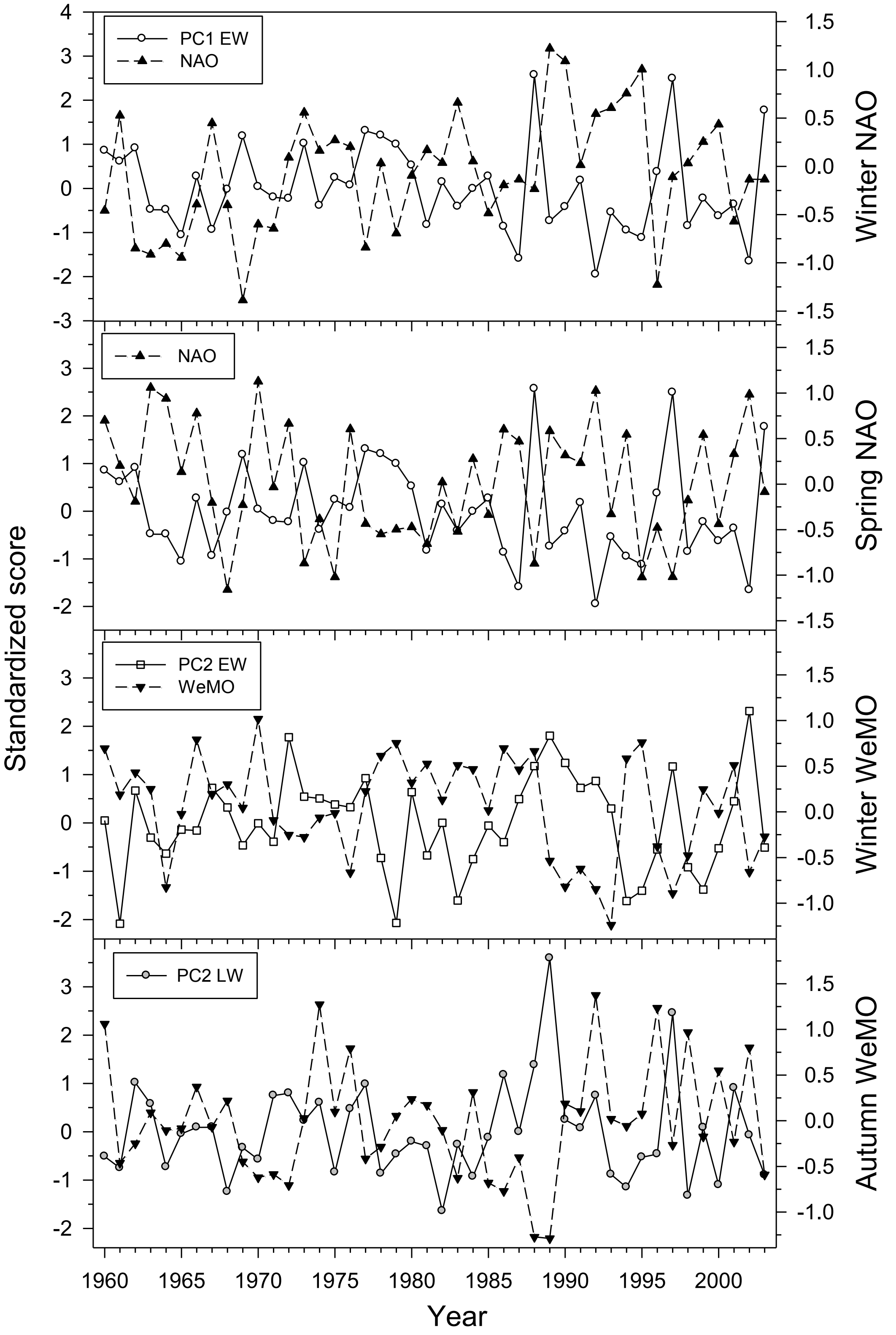

Figure 10. Temporal evolution of the first two principal components (PC1, PC2) of EW and LW *P. halepensis* chronologies, and related atmospheric circulation indices (NAO, WeMO) calculated from the previous winter to the current autumn.

At a monthly scale, there were significant ($p < 0.05$) negative correlations between the first principal component of EW and the previous December ($r = -0.40$) current April NAO indices ($r = -0.35$) but it is also noteworthy that the correlations between December and May were negative. Significant negative correlations were also found between the second component of the LW and the current September WeMO ($r = -0.37$, $p < 0.05$), whereas correlations with the October and November WeMO index were also negative.

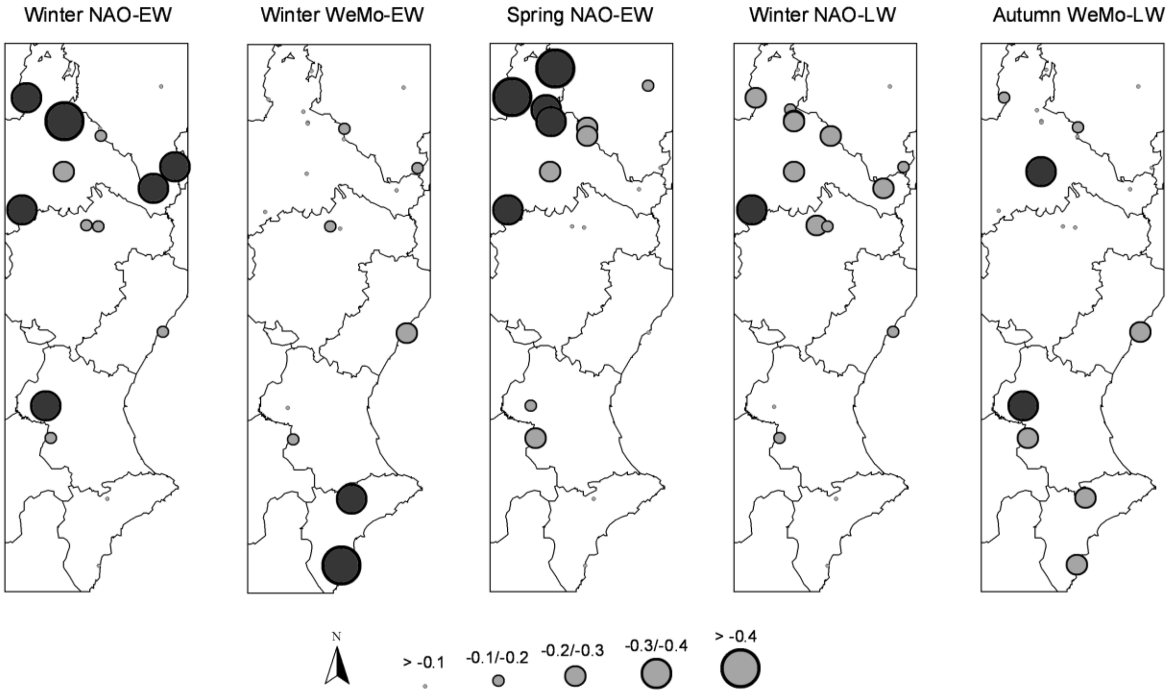

Figure 11. Geographic correlations of the atmospheric circulation indices (NAO, WeMO) in winter, spring and autumn with *P. halepensis* earlywood (EW) and latewood (LW) growth. The circles are proportional to the absolute correlation value; those filled dark gray indicate significant correlations ($p < 0.05$).

In summary, the described associations between atmospheric patterns and growth were highly spatially structured, showing that the NAO and WeMO are affecting both EW and LW formation in different parts of the study area: the NAO mainly in the North and the WeMO mostly in the South. These results are highly consistent with the analysis on the impact of weather types frequencies on forest growth (Table 4). Winter was the season with higher and more significant correlations between the EW and LW components and the seasonal frequency of weather types.

Table 4. Correlation of the principal components (PC) of earlywood (EW) and latewood (LW) with the seasonal frequency of weather types. Weather types: N, north; NE, northeast; E, east; SE, southeast; S, south; SW, southwest; W, west; NW, northwest; C, cyclonic; A, anticyclonic.

	N	NE	E	SE	S	SW	W	NW	C	A
Winter										
PC 1-EW	-0.06	-0.02	-0.31	-0.31*	0.22	0.36*	0.30*	0.10	0.29	-0.31
PC 2-EW	-0.35*	-0.04	0.17	0.33*	0.06	0.03	-0.09	-0.37	0.16	-0.03
PC 3-EW	-0.04	0.19	0.02	0.14	0.05	-0.01	0.02	-0.10	0.23	-0.26
PC 4-EW	-0.20	-0.09	0.06	-0.04	-0.12	0.03	0.22	0.02	-0.11	0.10
PC 1-LW	-0.02	-0.07	-0.28	-0.01	0.39**	0.33*	0.17	-0.02	0.28	-0.38**
PC 2-LW	-0.30*	0.02	0.10	0.05	-0.01	-0.03	-0.03	-0.07	0.12	0.01
PC 3-LW	0.12	-0.19	-0.14	-0.15	-0.18	0.07	0.21	0.04	0.38**	-0.22
PC 4-LW	-0.06	-0.01	0.04	0.14	0.27	-0.03	-0.23	-0.21	0.09	0.00
PC 5-LW	-0.15	-0.04	0.10	-0.10	0.03	0.06	0.07	0.04	0.09	-0.06
Spring										
PC 1-EW	-0.17	0.24	-0.08	-0.01	-0.06	-0.05	0.05	0.04	0.03	-0.06
PC 2-EW	0.13	0.11	0.13	0.12	-0.19	-0.26	-0.31*	-0.20	0.12	-0.03
PC 3-EW	-0.13	0.09	-0.17	0.04	0.10	0.11	-0.17	-0.07	-0.02	0.18
PC 4-EW	0.14	0.06	-0.17	-0.10	0.09	-0.13	0.15	0.24	0.01	-0.18
PC 1-LW	-0.01	0.23	0.09	-0.04	-0.11	0.14	-0.06	-0.07	-0.07	-0.06
PC 2-LW	0.12	-0.03	-0.12	0.05	-0.26	-0.32*	0.03	-0.12	0.25	-0.12
PC 3-LW	0.11	0.26	-0.01	-0.09	-0.14	-0.05	0.04	-0.03	-0.25	0.18
PC 4-LW	-0.46**	-0.05	-0.04	0.13	0.09	0.03	-0.20	-0.13	0.28	0.06
PC 5-LW	0.10	0.19	0.02	-0.13	-0.08	-0.08	0.14	0.11	-0.07	-0.14
Summer										
PC 1-LW	0.11	0.14	-0.27	-0.08	0.15	0.15	0.10	-0.03	-0.13	0.14
PC 2-LW	0.23	-0.13	-0.11	-0.38*	-0.35*	0.27	-0.07	0.07	0.16	-0.12
PC 3-LW	-0.06	0.34*	-0.03	0.06	-0.02	-0.11	-0.05	0.04	-0.27	0.09
PC 4-LW	-0.06	-0.18	0.03	0.06	-0.07	0.37*	0.11	0.15	-0.03	0.07
PC 5-LW	0.08	-0.01	-0.19	-0.11	0.10	0.25	0.09	0.03	-0.09	0.16
Autumn										
PC 1-LW	-0.20	-0.09	0.05	0.00	0.14	0.11	0.19	0.05	0.04	-0.12
PC 2-LW	-0.25	0.04	0.26	0.32*	0.19	0.18	-0.15	-0.45**	0.24	-0.29
PC 3-LW	0.04	-0.10	0.08	-0.13	-0.18	0.05	0.01	-0.10	0.15	-0.03
PC 4-LW	-0.02	-0.05	-0.21	0.00	0.00	0.01	0.25	0.06	0.06	-0.07
PC 5-LW	0.28	0.25	0.11	-0.03	-0.01	-0.03	-0.07	-0.12	-0.27	0.11

Significance levels: **$p < 0.01$, * $p < 0.05$.

The EW formation in the sites represented by the PC1 is enhanced by a high frequency of SW and W weather types, which are related to the advections of humid air from the Atlantic Ocean. On the contrary, a high frequency of flows from the East and Southeast has a negative role on the EW development. E and SE flows usually are less intense and have lower moisture than the W flows and they reach the central areas of the Ebro valley completely dry (Vicente-Serrano and López-Moreno, 2006). In addition, the EW formation in the sites represented by the PC2 is improved by a high frequency of E and SE flows since these forests are located in areas under the direct influence of these flows. The EW components PC3 and PC4 do not show any significant connection with the frequency of weather types in winter and spring.

The LW growth in areas represented by the PC1 was also highly related to the winter frequency of S, SW and A weather types. Nevertheless, the partial correlation between the frequency of these weather types and the LW PC1 was only significant for the S type ($r = 0.32$, $p = 0.04$) when the effect of EW was controlled for, whereas for the SE and A types partial correlation was not significant ($r = 0.17$, $p = 0.28$ and $r = -0.20$, $p = 0.20$, respectively). This would suggest that lagged effects of winter atmospheric circulation on LW in northern sites are mainly driven by an indirect influence determined by the winter circulation control of the EW formation. Areas represented by the LW PC2 did not show a noticeable influence of the frequency of winter and spring weather types on growth, but they were significantly correlated with the frequency of some weather types in summer and autumn. The LW PC2 showed a significant negative correlation with the frequency of summer SE and S weather types, which are characterized by African warm air advections arriving to the Iberian Peninsula and causing dry and persistent weather conditions. In addition, a positive correlation was found with the autumn SE weather type and a negative one with the NW type. This indicates that Mediterranean SE flows that commonly produce high precipitation in the Mediterranean coastland would enhance the development of LW in the southern sites.

The analyses based on the weather types allow quantifying some of the results obtained from the general atmospheric circulation patterns, but the main features of the weather types variability were well represented by the three different indices of atmospheric circulation. In winter season, strong and significant correlations are found between several weather types and atmospheric indices (Table 5).

Table 5. Correlations between the atmospheric circulation indices (NAO, North Atlantic Oscillation; MO, Mediterranean Oscillation; WeMO, Western Mediterranean Oscillation), for the previous winter and the current autumn, with weather types (N, north; NE, north-east; E, East; SE, south-east; S, south; SW, south-west; W, west; NW, north-west; C, cyclonic; A, anticyclonic).

	Winter			Spring			Summer			Autumn		
	NAO	MO	WeMO	NAO	MO	WeMO	NAO	MO	WeMO	NAO	MO	WeMO
N	-0.02	0.03	0.59**	0.14	0.03	0.35*	-0.13	0.08	0.49**	0.33*	0.28	0.58**
NE	0.15	0.22	-0.11	0.08	0.40**	0.10	0.14	-0.16	-0.06	0.15	0.16	0.17
E	0.19	-0.03	-0.55**	0.13	0.10	-0.23	0.20	0.00	-0.52**	-0.02	-0.09	-0.54**
SE	0.20	0.09	-0.56**	0.01	-0.29	-0.27	-0.04	0.11	-0.29	-0.11	-0.15	-0.68**
S	-0.12	-0.15	-0.39**	-0.25	-0.29	0.09	-0.20	-0.11	0.07	-0.15	-0.04	-0.47**
SW	-0.51**	-0.53**	0.19	0.03	0.03	-0.06	-0.05	-0.22	0.15	-0.33*	-0.14	0.24
W	-0.46**	-0.39*	0.51**	-0.08	0.15	0.22	-0.03	-0.03	-0.18	-0.27	-0.28	0.28
NW	-0.14	-0.11	0.53**	-0.29	-0.28	0.41**	-0.40*	-0.06	0.42**	0.01	0.03	0.55**
C	-0.68**	-0.72**	-0.14	-0.25	-0.49**	-0.33*	0.12	-0.18	-0.29	-0.18	-0.51**	-0.35*
A	0.76**	0.84**	-0.02	0.36*	0.54**	0.08	-0.08	0.29	0.25	0.32*	0.63**	0.30*

Significance levels: ** $p < 0.01$, * $p < 0.05$.

The NAO was negatively correlated with the frequency of SW, W and C types and positively associated with the frequency of anticyclones. The same pattern was also found for the MO. On the contrary, the WeMO represented mainly the frequency of the SE-NW flows, since it showed significant negative correlations with the frequency of E, SE and S types and positive correlations with the frequency of NW and W flows. In spring and summer months, the number of significant correlations was much lower, but in autumn, significant correlations between the WeMO and a number of weather types were found, similar to those obtained for the winter months. Except the summer SE and S types that showed a significant influence on the second LW component, the rest of the weather types showing a noticeable impact on the EW and LW formation in northern and southern sites are well represented by the general atmospheric circulation patterns used in this study. This would imply that, with very few exceptions, the regional circulation represented by the weather types and their impacts on tree growth are already represented by the general atmospheric circulation patterns. Therefore in the following section, the attention is focused only on the general atmospheric circulation patterns that have the main impacts on the EW and LW formation.

Connections with the surface climate variability

The analysis of the circulation influence on surface climate indicated that winter NAO and WeMO showed significant correlations with precipitation in a number of sites (Figure 12). Nevertheless, the spatial patterns showed a high variability. The impact of NAO on precipitation was recorded in northern areas whereas the WeMO affected precipitation mostly in southern sites.

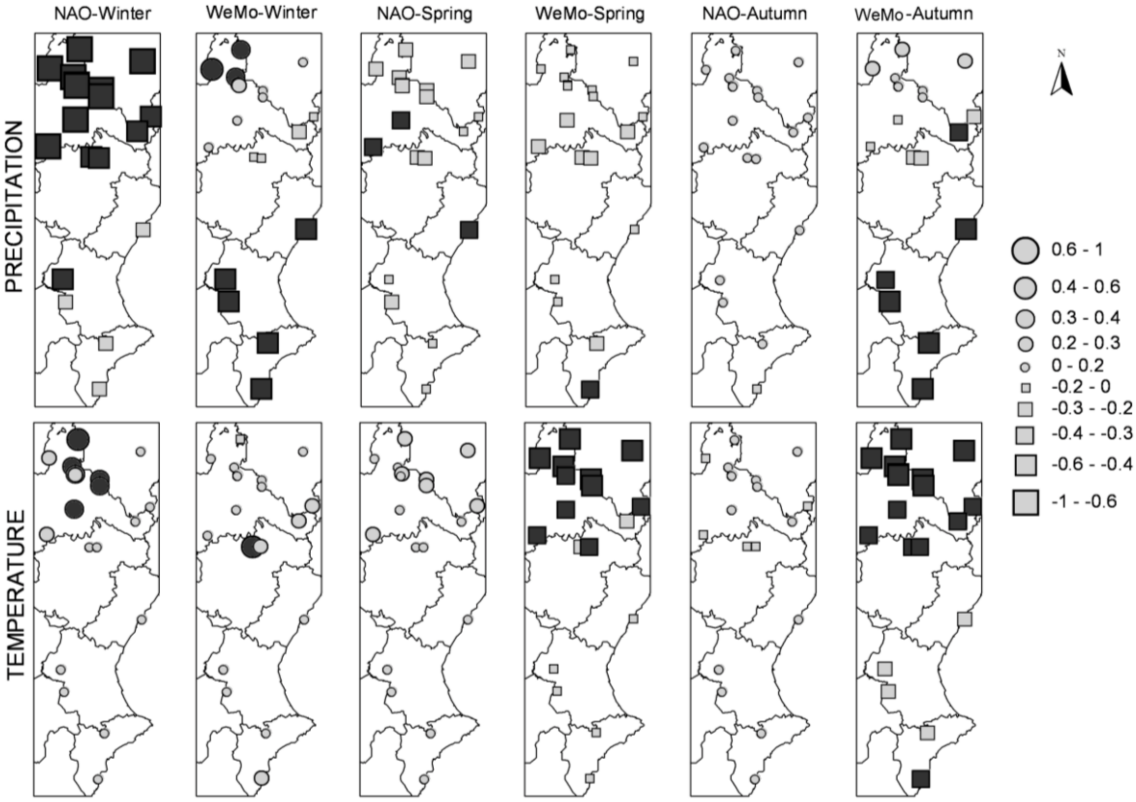

Figure 12. Geographic correlations of the atmospheric circulation indices (NAO, WeMO) in winter, spring and autumn with precipitation and temperature. The circles are proportional to the absolute correlation value; those filled dark gray indicate significant correlations ($p < 0.05$).

Consequently, this spatial configuration resembled the observed pattern of tree growth variability obtained by means of the PCA. Areas in which the EW was mainly determined by the winter NAO showed a direct control of precipitation by this circulation pattern. The same behavior was observed for the winter WeMO. In spring, correlations with NAO were lower than in winter, although magnitudes also tended to be higher in northern areas than elsewhere. Finally, the autumn NAO did not show a remarkable impact on precipitation but the impact of the autumn WeMO on precipitation indicated a clear spatial gradient with negative and significant correlations in the southern areas. This spatial pattern was similar to that found for the WeMO impact on the LW formation.

Some northern sites showed significant positive correlations between temperatures and the NAO in winter, which also would contribute to explain the influence of the NAO on the EW formation in these sites (Figure 12). Nevertheless, it is much more remarkable the WeMO influence on the temperatures of spring and autumn, which presented strong negative correlations in the northern parts of the study area. These results suggest that the spatial variability of forest growth across the region is directly driven by the distinct spatial influence of the atmospheric circulation processes mainly on precipitation.

The relationship between climate variability and EW and LW development showed significant correlations between the EW and the winter and spring precipitation in the entire study area (Figure 13). On the contrary, few sites showed significant correlations between EW and temperature variability.

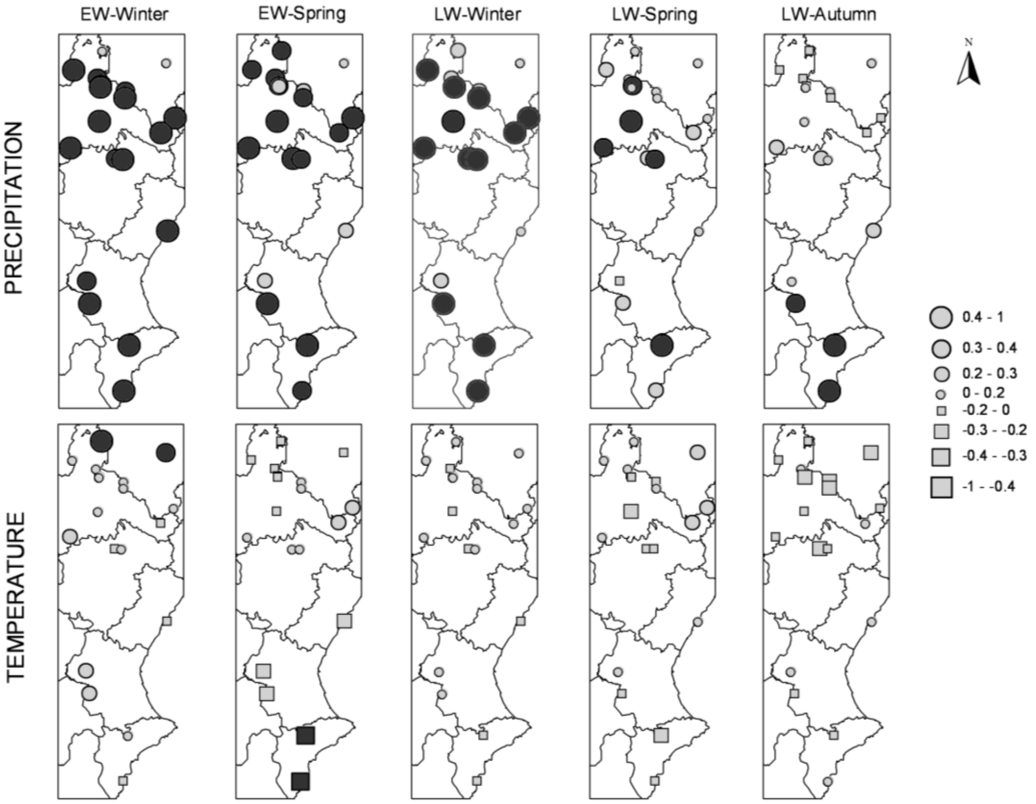

Figure 13. Geographic correlations between seasonal precipitation, temperature and earlywood (EW) and latewood (LW) formation in the *P. halepensis* sampled forests. The symbols are proportional to the absolute correlation value; those filled dark grey indicate significant correlations ($p < 0.05$).

There were also significant correlations between winter and spring precipitation and the LW width in most sites, which could suggest a lagged response of the winter climate on the forest growth in late summer and autumn, possibly driven by soil water storage. Nevertheless, for the forests showing significant correlations between LW and winter precipitation, it was found that partial correlations (considering the influence of EW on LW) between winter/spring precipitation and LW were not significant. In 11 of the 12 sites with significant correlation between winter precipitation and LW, no significant partial correlation was found, whereas 11 sites showed significant partial correlations ($p < 0.05$) between the EW and the LW variability. This would provide further evidence that the influence of the winter precipitation on LW is mainly driven through a direct influence on the EW formation.

Nevertheless, in the southern study area, the analysis also revealed a direct influence of the surface climate on the LW formation. Therefore, in the southern sites there was a significant correlation between the autumn precipitation and the LW formation. These sites also showed a significant association between the autumn precipitation and the WeMO, with a clear different behavior as compared with the rest of the sites. In addition, no significant correlations were found between LW PCs and temperature. This would explain that although spring and autumn WeMO are correlated with temperatures in northern sites, both EW and LW formation in these sites are not correlated with the WeMO, since tree growth in those sites is not mainly driven by temperatures. For the southern sites, the influence of the autumn WeMO on LW was directly driven by precipitation. Therefore, in the southern region both EW and autumn precipitation played a significant role in explaining the LW variability. EW and autumn precipitation showed significant partial correlations with the LW in the southern areas ($r = 0.65$ and $r = 0.43$, $p < 0.01$, for the EW and autumn precipitation, respectively). This indicates that EW formation and also autumn precipitation are affecting LW development.

Discussion

In *P. halepensis* the production of EW showed a greater year-to-year variability and a higher tree-to-tree common variance than did LW; these results are similar to those reported by De Luis et al. (2009). Thus, EW and LW covaried to some extent, indicating a strong temporal association, as suggested by xylogenesis studies of *P. halepensis* (De Luis et al., 2007; Camarero et al., 2010).

EW and LW responded to atmospheric circulation patterns and weather types in different ways, although for both variables were detected at least two groups of forests (those located in northwestern and southeastern sites) with contrasting responses. Such a geographically structured climatic response suggests that northwestern sites are more influenced by southwestern flows, which was indicated by the stronger relationships with the winter NAO index relative to that which occurred for southeastern sites near the Mediterranean coast, where *P. halepensis* growth was mainly affected by the winter–autumn WeMO and the autumn MO indices. These findings are consistent with the associations found between atmospheric patterns and weather types. For instance, the winter NAO and MO indices were negatively (positively) associated with the frequency of cyclones (anticyclones) in winter. The winter WeMO index was positively correlated with the frequency of N, W and NW weather types. High levels of the WeMO index in autumn were also associated with greater occurrence of N, NW and anticyclonic weather types, and a low frequency of E, SE, S and cyclonic weather types. These results confirm that the effects of atmospheric circulation patterns on *P. halepensis* growth in the study area are probably an indirect expression of their effects on local weather types and climatic factors, including precipitation, temperature and radiation (Garfin, 1998; Mäkinen et al., 2003). In agreement with the results obtained by Vicente-Serrano and López-Moreno (2006) and González-Hidalgo et al. (2009) for the same region, the same spatial gradient in the effect of NAO and WeMO on tree growth has been found for precipitation. Although NAO mainly affects the southwestern Iberian Peninsula, the southwest flows are reactivated when they reach the Pre-Pyrenean chains, explaining why the forests located in the Ebro valley are affected by this pattern. In contrast, the humid influence of the southwestern flows associated with the NAO does not reach the Mediterranean coastal region (Rodó et al., 1997; Rodríguez-Puebla et al., 1998), where the humid influences come from the east, as reflected by the WeMO index. Thus, the spatial pattern of *P. halepensis* forests in eastern Spain reflects the influence of atmospheric circulation patterns on precipitation, and clearly demonstrates that these effects act through the control of variability of local precipitation in the region.

Several studies have reported that, in addition to precipitation, the winter NAO also exerts a marked influence on surface air temperature, and that its association with tree growth varies from northern (positive) to southern (negative) Europe (Piovesan and Schirone, 2000; Linderholm et al., 2003; Schultz et al., 2008), but in eastern Spain the results indicate an insignificant influence of temperature variability on both EW and LW growth and support the view that most of the influence of the atmospheric circulation variability on tree growth is mainly driven through changes in precipitation.

The spatially constrained negative relationship between the winter NAO index and EW growth at northwestern sites in eastern Spain is consistent with results from earlier studies of Iberian conifer forests (Bogino and Bravo, 2008; Rozas et al., 2009). However, growth at xeric southwestern sites is also negatively related to the winter WeMO index, which can be explained by more winter precipitation, and consequent enhanced radial growth in spring during negative phases of the winter WeMO index (Martín-Vide and Lopez-Bustins, 2006; González-Hidalgo et al., 2009; Vicente-Serrano et al., 2009). A similar result has been reported for the WeMO index in spring and *P. halepensis* forests in the middle Ebro basin (Ribas et al., 2008). These results highlight the marked spatial variability in the effect of general atmospheric circulation patterns as drivers of tree growth, which may be a consequence of distance to the sea and the landscape relief.

LW formation in *P. halepensis* was negatively associated with the Mediterranean indices (WeMO, MO) at southeastern sites, suggesting a dependence on autumn precipitation. This finding suggests that autumn precipitation may be important for LW growth in *P. halepensis*, which is consistent with phenological observations that cambial activity in this species can be greatly enhanced after summer because of sporadic autumn rainfall, which is usually produced by Mediterranean cyclonic activity (De Luis et al., 2007; Camarero et al., 2010).

An important finding of this study is the distinct influence of winter atmospheric circulation patterns on LW formation in *P. halepensis*. Two explanations can be proposed for this observation. First, EW formation in *P. halepensis* is partly dependent on photosynthetic activity and moisture reserves supplied by precipitation prior to spring growth (Kagawa et al., 2006), and the amount of winter rainfall is inversely correlated with the NAO (Piovensan and Schirone, 2000). In *P. halepensis*, EW is usually formed between March and June whereas LW starts developing in July and ends its maturation in November (De Luis et al., 2007; Camarero et al., 2010). Thus, EW formation may be very dependent on the water supply and photosynthetic activity in late winter and early spring. Relative to southwestern sites, which are more subjected to Mediterranean cyclonic activity, a high winter NAO index may be associated with low winter rainfall and reduced EW formation at northwestern sites, under the strong influence of Atlantic westerlies. The greater degree of EW formation may result in an increase in hydraulic conductivity and the synthesis of more carbohydrates for LW formation in summer and autumn (Camarero et al., 2010). A second and much less plausible explanation is that in those years with abundant winter rainfall (low winter NAO index) water is stored in deep soil layers, providing surface soil water for LW growth in summer. The first explanation appears more likely, as xylogenesis studies support a functional link between EW and LW growth, which show plastic responses to climatic conditions. For instance, at coastal sites cambial activity may occur for longer than at inland sites, where trees are subject to low winter temperatures and summer droughts (De Luis et al., 2007; Camarero et al., 2010). According to these authors, the transition between EW and LW is linked to the temperature rise and the decline in soil water reserves between late spring and early summer (June-July), but xylogenesis processes are plastic. For instance, these studies indicate that EW may start late (e.g., April-May) in cold northwestern sites whereas LW maturation may last up to December in warm southeastern sites. This cambial plasticity is consistent with other features of *P. halepensis*, which is a species well adapted to drought because of its ability to rapidly reduce transpiration by stomatal closure (Borghetti et al., 1998), and its capacity to make efficient use of water reserves that become available several months prior to growth (Sarris et al., 2007). The first explanation is also consistent with findings of allometric relationships between tree ring width and maximum LW density (Kirdyanov et al., 2007).

The analyses indicate that weather types also exert a relatively strong influence on EW and LW growth, probably because of their indirect effect on local patterns of ultimate climatic drivers, including precipitation, solar radiation and temperature (Garfin, 1998). In winters characterized by extended periods of high pressure (i.e. a high frequency of N and anticyclonic weather types), EW formation was less than in other years. Explanations for these associations include the relationship of anticyclone weather types to dry and cold conditions in winter over the eastern Iberian Peninsula (Goodess and Jones, 2002). Very cold and dry winters may result in less photosynthetic activity in *P. halepensis*, and reduce the amount of carbohydrates available for EW growth during the following spring (Kagawa et al., 2006). In contrast, cyclonic activity linked to an increase in Atlantic westerlies (SW and W weather types) caused warmer and more humid conditions in winter than during anticyclonic periods, which enhanced EW formation and, probably through indirect effects, LW development. In autumn, LW development was enhanced by cyclonic conditions probably related to Mediterranean convection, as both E and SE (N and NW) weather types were positively (negatively) related to LW growth. In the eastern half of the Iberian Peninsula, autumn rainfall is usually associated with easterly and southeasterly winds, and Mediterranean storms (Goodess and Jones, 2002; Beguería et al., 2009). An increase in autumn precipitation may enhance cambial *activity* in *P. halepensis* and co-occurring tree species after the summer drought (Camarero et al., 2010), and mild conditions may provide a longer growing season, particularly at coastal southeastern sites (De Luis et al., 2007).

In conclusion, the results indicate that large-scale atmospheric patterns (NAO, MO, WeMO) and local weather types influence EW and LW formation in *P. halepensis* forests of eastern Spain.

However, across this dendrochronological network both EW and LW responded differently to atmospheric circulation patterns and weather types, suggesting that the predicted changes in atmospheric circulation will result in contrasting tree growth responses in the northwest and southeast areas of this Mediterranean region. Therefore, the forecasted trend of increasing winter anticyclonic conditions and reduced activity of westerlies (high NAO and WeMO indices) are expected to reduce EW production in northwestern sites, whereas an increase of autumn cyclonic Mediterranean conditions (low WeMO and MO indices) will enhance LW formation in southeastern sites.

3.2. Impacts of drought at different time scales on forest growth across a wide climatic gradient in north-eastern Spain

Introduction

Water availability is one of the main climatic constraints for tree growth in the Circum-Mediterranean forests. Thus, several studies have shown a strong correlation between precipitation and radial growth in different Mediterranean forests and tree species (Tardif et al., 2003; Macias et al., 2006; Andreu et al., 2007; Sarris et al., 2007; De Luis et al., 2009; Linares et al., 2010; Carrer et al., 2010; Lebourgeois et al., 2010; Mérian et al., 2010). The impact of water deficit on growth is much higher in the most arid sites, where water availability largely constrains the main physiological processes of vegetation (growth, photosynthesis, carbon and nitrogen use), than in mesic sites (e.g., Jump et al., 2006; Vicente-Serrano et al., 2006, 2010a; Sarris et al., 2007; Martínez-Vilalta et al., 2008). Although the main patterns of precipitation-growth relationships are well known, the large seasonality and year-to-year variability that characterize precipitation in the Mediterranean region and the different site-dependent seasonality of tree growth in forests from this area may make very difficult to determine the response times of tree growth to the precipitation deficit. Furthermore, lags between water shortages and growth can appear as a function of different anatomical and physiological adjustments of trees to cope with drought, but also in response to drought severity and to the season in which water deficit occurs. All these mechanisms, either isolated or acting synergistically, can challenge the identification of drought impacts on tree growth.

Commonly drought indices are used with the purpose of solving the current problems of quantifying drought severity since it is very complex to determine the magnitude, duration and surface extent of droughts (Wilhite and Glantz, 1985; Redmond, 2002). Different drought indices have been developed to quantify the water deficit in an objective way, which is usually better than using the precipitation information itself (Keyantash and Dracup, 2002; Heim, 2002; Mishra and Singh, 2010). Drought indices are based on the quantification of the cumulative water shortages over a period of time. Some of the indices are based on soil water balance equations. The best example of this type of indices is the Palmer Drought Severity Index (PDSI, Palmer, 1965; Wells et al., 2004). Different studies have analyzed the influence of the drought conditions on tree growth using the PDSI (Orwig and Abrams, 1997; Kempes et al., 2008; Bhuta et al., 2009; Mundo et al., 2010). Nevertheless, although the PDSI can be useful to determine the severity of a drought, the index has several deficiencies (Alley, 1984; Weber and Nkemdirim, 1998), being its main shortcoming that it can only be calculated at a unique time scale (Guttman, 1998; Vicente-Serrano et al., 2011). On the contrary, drought is a multi-scalar phenomenon, given the great variety of response times found in different hydrological, agricultural and environmental systems to the occurrence of water deficits (e.g., McKee et al., 1993; Ji and Peters, 2003; Vicente-Serrano and López-Moreno, 2005; Lorenzo-Lacruz et al., 2010; Quiring and Ganesh, 2010).

The problems involved with the use of PDSI have motivated the development of drought indices that can be calculated at different time-scales such as the Standardized Precipitation Index (SPI) (McKee et al., 1993) and the Standardized Precipitation Evapotranspiration Index (SPEI) (Vicente-Serrano et al., 2010c). The quantification of droughts at different time scales is crucial to determine their ecological impacts, given the different physiological strategies of vegetation to cope with water deficit. Studies analyzing the drought impacts on vegetation activity using the SPI have shown contrasting responses according to the time scales at which drought affected vegetation activity and also depending on vegetation types (Vicente-Serrano, 2007) and environmental conditions for the same vegetation type (e.g., Ji and Peters, 2003; Quiring and Ganesh, 2010). At present, most studies quantifying the vegetation response to different drought time-scales have been carried out using remote sensing data for mid-term (10-30 years) datasets, which is related to the potential photosynthetic activity of the canopy or the leaf area of the forest (Vicente-Serrano, 2007). Nevertheless, currently there are lack of studies analyzing the response of tree secondary growth to different time-scales of drought, which are quantified by means of multi-scalar drought indices.

This methodological approach could improve the knowledge of the long-term responses of tree growth to water availability better than using precipitation data itself or other drought indices.

Currently, a deeper knowledge of the tree growth responses to water shortages in the Mediterranean Basin is a crucial task. Forests are particularly sensitive to climate change because the long-life span of trees does not allow for a quick adaptation to rapid environmental changes such as current climate warming (Andreu et al., 2007). As a matter of fact, various studies have provided evidence on the direct effect of drought on forest decline, particularly in Mediterranean forest ecosystems where water shortage is the main factor constraining growth (Sarris et al., 2007; Linares et al., 2010; Sánchez-Salguero et al., 2010).

In this study it was analyzed the response of tree growth to different time scales of drought, quantified by means of the Standardized Precipitation Index (SPI), in forests from the Aragón region, in North-eastern Spain (Figure 14). Forests located in this region were particularly selected because they grow under a strong climatic gradient ranging from semiarid conditions in the Middle Ebro Basin to humid conditions in the Pyrenees. Furthermore, a trend towards more arid conditions was observed during the late 20th century in the study area (López-Moreno et al., 2010). Therefore, these forests represent an appropriate model to test the drought impact and the expected contrasting vulnerability to drought stress of species growing in the area.

The objective of this study was to determine whether the use of multi-scalar drought indices is an effective way to determine the impact of water deficit on growth, and whether this approach may detect different responses, in terms of magnitude and seasonality, in a variety of tree species and locations. The study includes eight tree species growing along the mentioned climatic gradient showing contrasting vulnerability to drought stress: four pine species (*Pinus halepensis*, *P. pinea*, *P. nigra*, *P. sylvestris*), silver fir (*Abies alba*), Spanish juniper (*Juniperus thurifera*), and two oak species (*Quercus faginea*, *Q. ilex*).

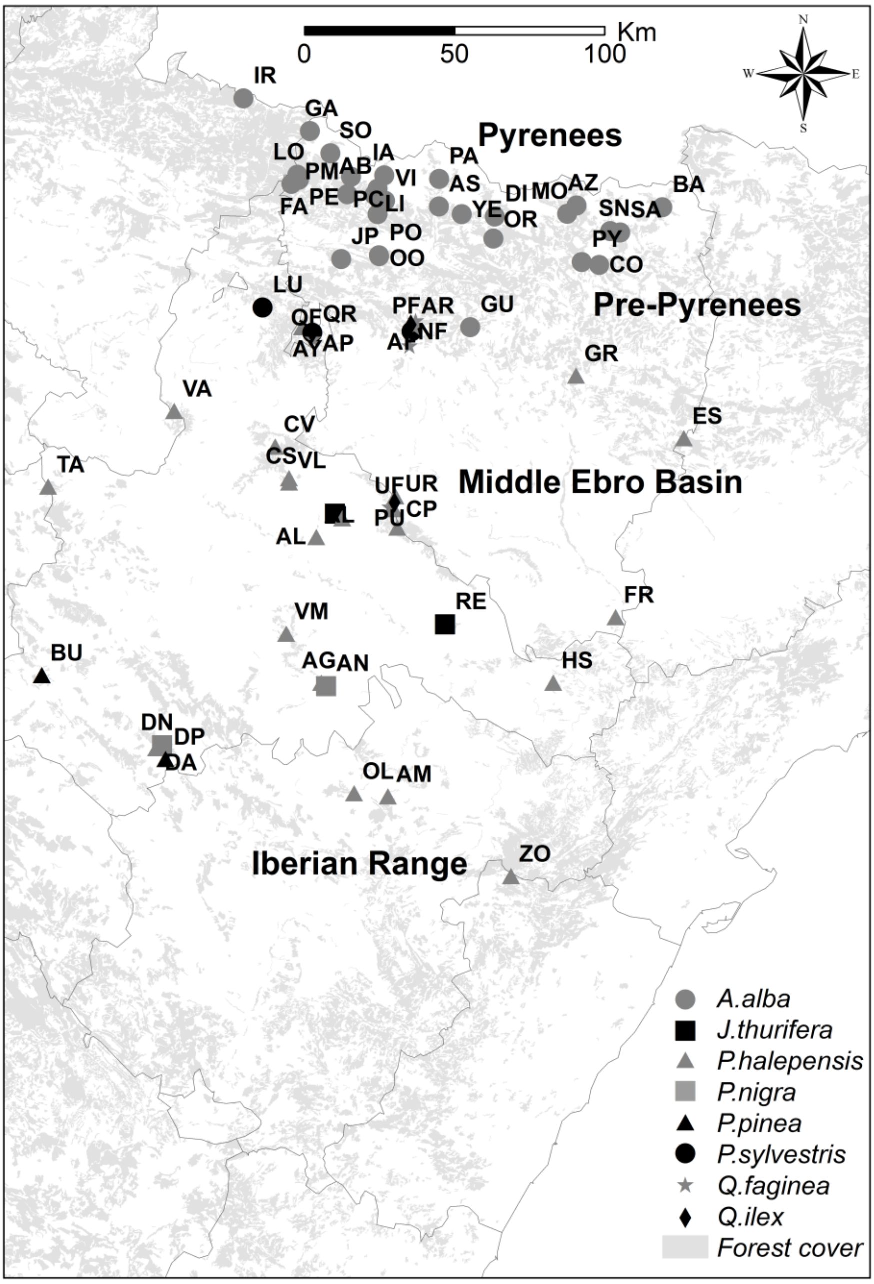

Figure 14. Distribution of forests (gray area) in the north-eastern Spain and the location of study sites. Different symbols represent different forest species. See sites names in Table 1.

These species represent species typically associated with mesic sites and humid conditions (e.g., *A. alba*), transitional locations (e.g., *P. sylvestris*) and xeric sites (e.g., *P. halepensis*). This is why all these species were considered in the study, to test if the responses to drought vary among species, sites and contrasting climate conditions found in the study area.

Methodology

Dendrochronological methods

The samples preparation, cross-dating and standartization were performed following standard dendrochronological methods (see section 2.2). The common period 1950–1999 was selected because all chronologies showed EPS values above the 0.85 threshold for this interval, and this threshold is widely used in dendrochronological studies (Wigley et al., 1984). The statistical characteristics of the chronologies are shown in Table 6.

Drought index calculation

The Standartized Precipitation Index (SPI) was used to analyze the influence of drought on growth of all species considered in the study. The precipitation data in the region has been obtained from a homogeneous and spatially dense dataset of daily observatories interpolated to a regular grid of 1000m (Vicente-Serrano et al., 2010b).

An average monthly precipitation series was obtained for each one of the 67 sites using the gridded monthly precipitation data. From each one of the series, the SPI was obtained at time scales from 1 to 48 months for having a range of time scales to be compared with radial growth. The SPI was calculated by adjusting the precipitation series to a given probability distribution. Initially, the Gamma distribution was used to calculate the SPI (McKee et al., 1993), but the Pearson III distribution was considered more robust due to its three parameters (Vicente- Serrano, 2006). The complete formulation of the SPI following the Pearson III distribution and the L-moments method for calculating parameters is described in Vicente-Serrano (2006), and López-Moreno and Vicente-Serrano (2008).

Statistical analyses

To determine the influence of drought severity on tree growth, but also the drought time-scales that are affecting radial growth of species and sites considered in the study, correlation analyses using the Pearson coefficient were carried out. Prior to calculating the correlations, the trend in each of the SPI time series was removed by fitting a linear evolution in each monthly series at the different time scales. Therefore, correlation analyses were performed between ring-width residual chronologies representing tree growth and detrended monthly SPI series representing drought severity for the period 1950-1999. To summarize the correlation analyses and to compare the drought impact among species, it was performed an average correlation for all sites corresponding to a particular species. The threshold for significant correlations was set at $p \leq 0.05$.

Results

Growth patterns

This section presents the growth patterns of all species considered in the study with the purpose of understanding their growth characteristics and variability all over the study area. The mean ring width ranged from 1.15 mm (*Q. ilex*) to 2.39 mm (*A. alba*) across the studied dendrochronological network (Table 6). The first-order autocorrelation (AC1) values were highest in *A. alba* (0.81) and lowest in *Q. ilex* (0.31), while the mean sensitivity (MSx) values were generally high for *P.nigra* (0.46), *P. pinea* (0.44), *Q. ilex* (0.43), *J. thurifera* (0.39) and *P. halepensis* (0.38), and low for *P. sylvestris* (0.33), *Q. faginea* (0.32) and *A. alba* (0.20). The highest correlations among individual series (Rbar) within each site and the Expressed Population Signal (EPS) values were observed for *P. halepensis* and the lowest ones for *A. alba*.

Table 6. Dendrochronological statistics of ring-width chronologies considering the 67 sites of the eight studied tree species for the common period 1950-1999.

Species	Code	No. trees (no. radii)	MW (mm)	SD (mm)	AC1	MSx	Rbar	EPS
A. alba	CA	10 (20)	1.23	0.63	0.81	0.24	0.41	0.93
A. alba	CO	12 (27)	2.75	1.2	0.83	0.17	0.33	0.92
A. alba	GU	10 (23)	2.92	1.18	0.7	0.2	0.55	0.96
A. alba	OR	11 (22)	1.73	0.63	0.73	0.2	0.51	0.95
A. alba	PY	12 (21)	2.33	1.08	0.81	0.2	0.41	0.93
A. alba	OO	12 (24)	2.8	1.19	0.79	0.2	0.55	0.96
A. alba	PO	11 (23)	2.59	0.95	0.76	0.18	0.51	0.96
A. alba	JP	13 (28)	2.16	1.18	0.85	0.22	0.23	0.9
A. alba	YE	12 (24)	3.44	1.43	0.77	0.2	0.43	0.94
A. alba	IR	13 (29)	1.83	0.89	0.87	0.17	0.36	0.94
A. alba	FA	11 (22)	1.34	0.73	0.71	0.29	0.54	0.97
A. alba	PE	11 (22)	1.63	0.87	0.81	0.23	0.41	0.95
A. alba	LO	10 (23)	1.42	0.84	0.79	0.27	0.44	0.94
A. alba	GA	13 (26)	1.99	0.95	0.83	0.2	0.4	0.94
A. alba	SO	13 (25)	2.01	1.4	0.91	0.19	0.37	0.92
A. alba	PM	10 (22)	1.97	0.78	0.65	0.25	0.52	0.96
A. alba	PC	14 (27)	3.49	1.61	0.82	0.19	0.36	0.92
A. alba	LI	11 (22)	2.96	1.37	0.86	0.18	0.45	0.94
A. alba	AB	12 (24)	4.46	1.95	0.97	0.16	0.33	0.9
A. alba	IA	13 (25)	2.7	1.1	0.84	0.17	0.41	0.94
A. alba	VI	21 (42)	1.99	0.88	0.83	0.18	0.4	0.96
A. alba	AS	10 (20)	3.05	1.5	0.86	0.22	0.47	0.94
A. alba	PA	12 (23)	2.39	1.23	0.8	0.27	0.57	0.96
A. alba	DI	12 (24)	2.66	1.12	0.82	0.21	0.54	0.96
A. alba	MO	21 (30)	1.54	0.71	0.85	0.18	0.35	0.94
A. alba	AZ	11 (22)	3.29	1.09	0.8	0.15	0.39	0.92
A. alba	SN	14 (29)	2.89	1.11	0.84	0.16	0.33	0.92
A. alba	SA	12 (29)	1.87	0.63	0.84	0.15	0.37	0.94
A. alba	BA	11 (29)	2.09	0.69	0.82	0.15	0.39	0.95
P. halepensis	AG	12 (24)	3.26	1.32	0.61	0.28	0.52	0.92
P. halepensis	PH	13 (29)	1.12	0.73	0.66	0.37	0.6	0.98
P. halepensis	AL	15 (31)	1.55	1.5	0.79	0.46	0.59	0.97
P. halepensis	AU	10 (14)	2.79	1.2	0.61	0.29	0.68	0.93
P. halepensis	PU	15 (22)	1.48	0.87	0.69	0.33	0.65	0.97
P. halepensis	TA	15 (30)	2.4	1.42	0.59	0.4	0.76	0.99
P. halepensis	VA	16 (31)	1.81	1.14	0.74	0.36	0.62	0.97
P. halepensis	CV	13 (23)	3.35	1.37	0.78	0.27	0.44	0.9
P. halepensis	CS	12 (23)	1.14	0.73	0.6	0.43	0.68	0.98
P. halepensis	VM	15 (30)	1.83	1	0.67	0.35	0.82	0.99
P. halepensis	ZO	15 (29)	1.18	0.69	0.64	0.38	0.69	0.98
P. halepensis	ES	15 (27)	2.84	2.43	0.85	0.37	0.52	0.96
P. halepensis	GR	15 (30)	2.29	1.17	0.7	0.3	0.53	0.97

P. halepensis	OL	15 (27)	2.95	2.17	0.81	0.35	0.82	0.99
P. halepensis	AM	15 (31)	1.45	1	0.72	0.39	0.73	0.99
P. halepensis	VL	15 (29)	1.2	0.82	0.58	0.52	0.58	0.98
P. halepensis	DA	14 (28)	2.06	1.17	0.5	0.44	0.82	0.99
P. halepensis	AY	16 (33)	2.65	1.11	0.6	0.27	0.34	0.93
P. halepensis	CP	14 (27)	2	1.24	0.72	0.34	0.58	0.96
P. halepensis	HS	16 (28)	0.76	0.59	0.56	0.65	0.72	0.99
P. halepensis	FR	16 (29)	0.97	0.79	0.72	0.5	0.6	0.98
Q. faginea	QF	22 (44)	1.51	0.87	0.72	0.28	0.31	0.91
Q. faginea	AF	10 (20)	1.72	0.62	0.46	0.29	0.47	0.93
Q. faginea	NF	10 (20)	1.61	0.79	0.53	0.3	0.58	0.95
Q. faginea	PF	10 (20)	1.83	0.62	0.32	0.3	0.5	0.98
Q. faginea	UR	33 (56)	1.61	1	0.43	0.44	0.7	0.99
Q. ilex	QR	10 (11)	1.34	0.56	0.37	0.34	0.32	0.91
Q. ilex	AR	10 (14)	1.16	0.6	0.32	0.44	0.46	0.92
Q. ilex	UR	10 (20)	0.95	0.73	0.26	0.51	0.52	0.94
J. thurifera	RE	35 (64)	1.09	0.71	0.61	0.42	0.56	0.9
J. thurifera	PE	11 (19)	1.47	1.18	0.74	0.37	0.41	0.93
P. sylvestris	AP	19 (37)	1.84	0.99	0.61	0.36	0.53	0.96
P. sylvestris	LU	11 (15)	2.21	1.43	0.77	0.34	0.52	0.93
P. sylvestris	PS	11 (23)	1.5	0.99	0.79	0.29	0.45	0.95
P. pinea	BU	19 (37)	3.07	1.78	0.53	0.42	0.63	0.98
P. pinea	DP	14 (28)	1.63	1.14	0.68	0.46	0.8	0.99
P. nigra	AN	19 (34)	2.6	1.36	0.55	0.4	0.48	0.92
P. nigra	DN	16 (33)	1.8	1.27	0.6	0.54	0.59	0.98

Statistics: Raw tree-ring width series: MW, mean ring width; SD, standard deviation; AC1, first-order autocorrelation. Residual ring-width series: MSx, mean sensitivity; Rbar, mean interseries correlation; EPS, expressed population signal. See sites names in Table 1.

Similar high-frequency growth patterns were observed for species from the xeric sites (*P. halepensis*, *P. pinea*, *P.nigra* and *J. thurifera*) with growth reductions in 1953, 1961, 1981, 1989 and 2005 (Figure 15). On the other hand, the periods characterized by substantial increase in radial growth included 1959, 1960, 1977, 1988 and 1997. Some of these sharp growth decreases and increases corresponded to severe droughts (e.g., 2005) and wet years (e.g., 1997), respectively. *A. alba* showed a more stable growth pattern with growth reductions in 1965, 1986, 1981, 1993 and 2001, while *P. sylvestris, Q. faginea* and *Q. ilex* showed high inter annual growth variability.

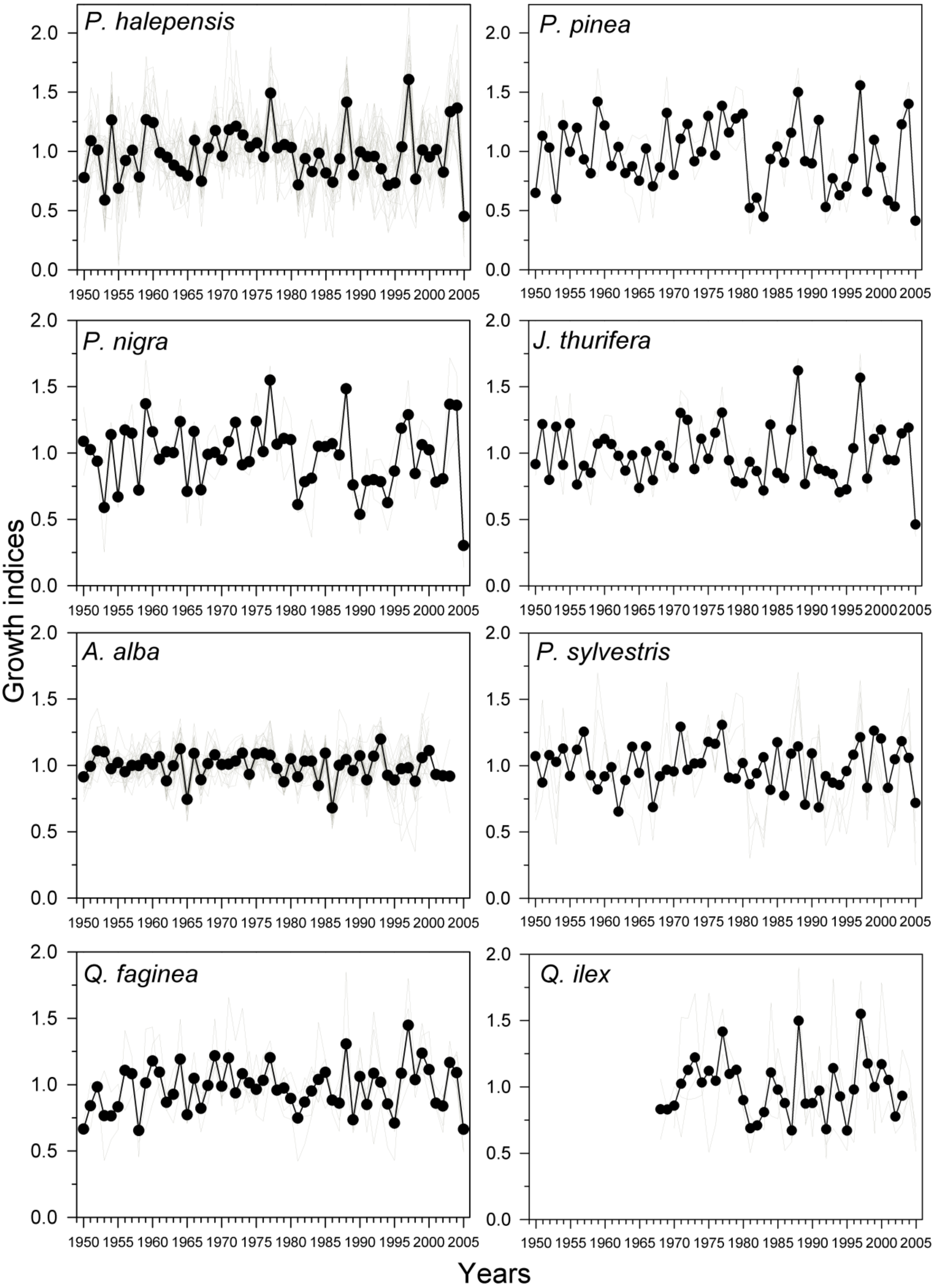

Figure 15. Residual chronologies of ring width (gray lines) of a dendrochronological network studied in north-eastern Spain, and the overall mean for each tree species (black lines).

Species- and site-dependent associations between growth and drought

In this section are presented the relationships between forest growth and drought at different time scale. The drought variability as represented by the Standardized Precipitation Index (SPI) showed high contrasted frequency as a function of the time scale (Figure 16). On the shortest time scales (e.g., 3 months), the dry and humid periods are short and occur at high frequencies. At long time scales (e.g., 24 and 48 months), droughts lasted longer, but were less frequent, with few dry or humid periods recorded.

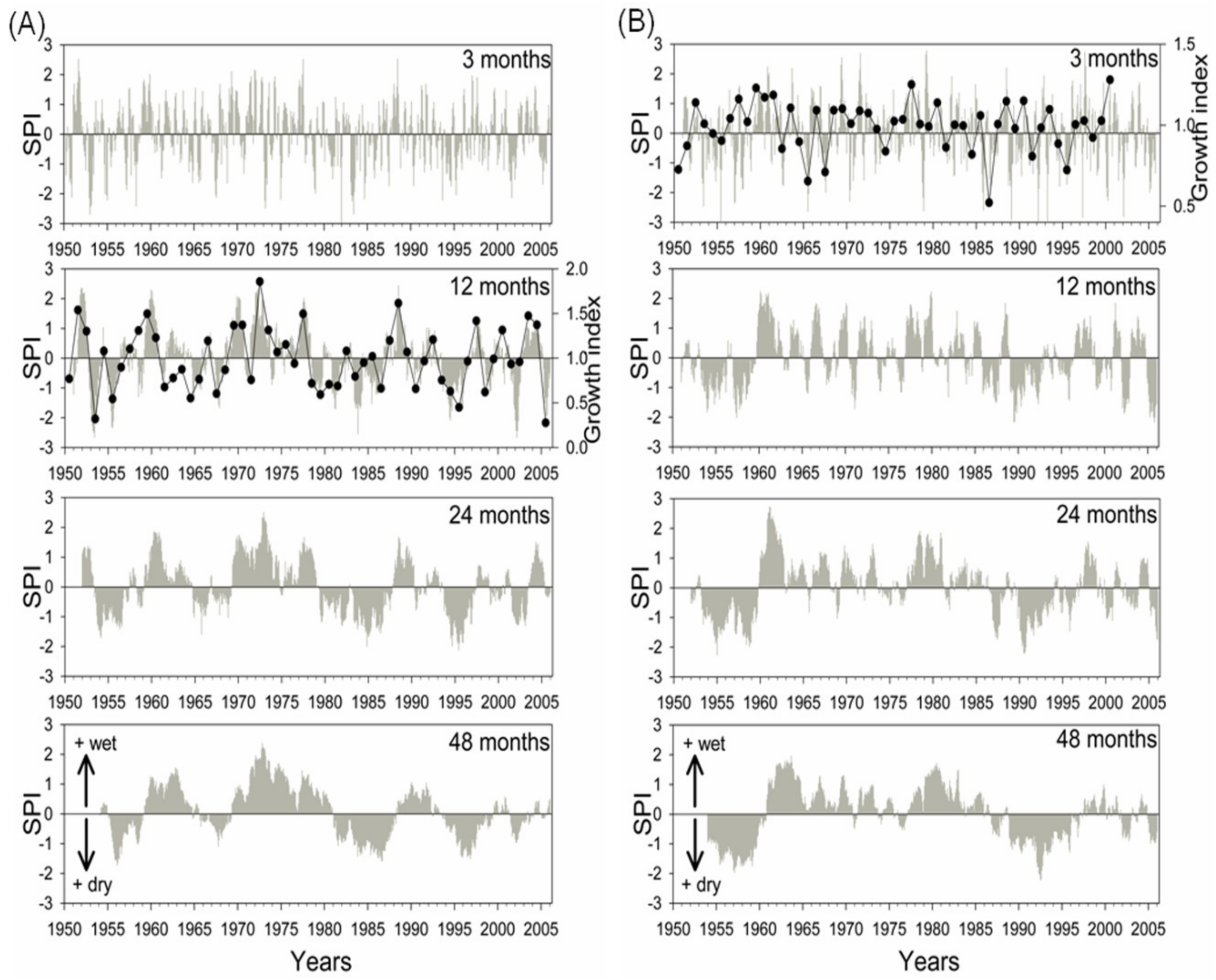

Figure 16. Evolution of the drought index (Standardized Precipitation Index, SPI) at different time scales (3, 12, 24 and 48 months) in *P.halepensis* (A, site AL) and *A.alba* (B, site FA) forests (see sites names in Table 1). Black lines with circles show the residual ring-width chronologies for the selected sites and they are drawn over the SPI time scale at which growth series showed the strongest response to the drought index obtained for that scale. Note that positive and negative SPI values indicate wet (high tree growth) and dry conditions (low tree growth), respectively.

In general, important differences were found in the responses of tree growth to the different time scales of the SPI (Figures 16 and 17).

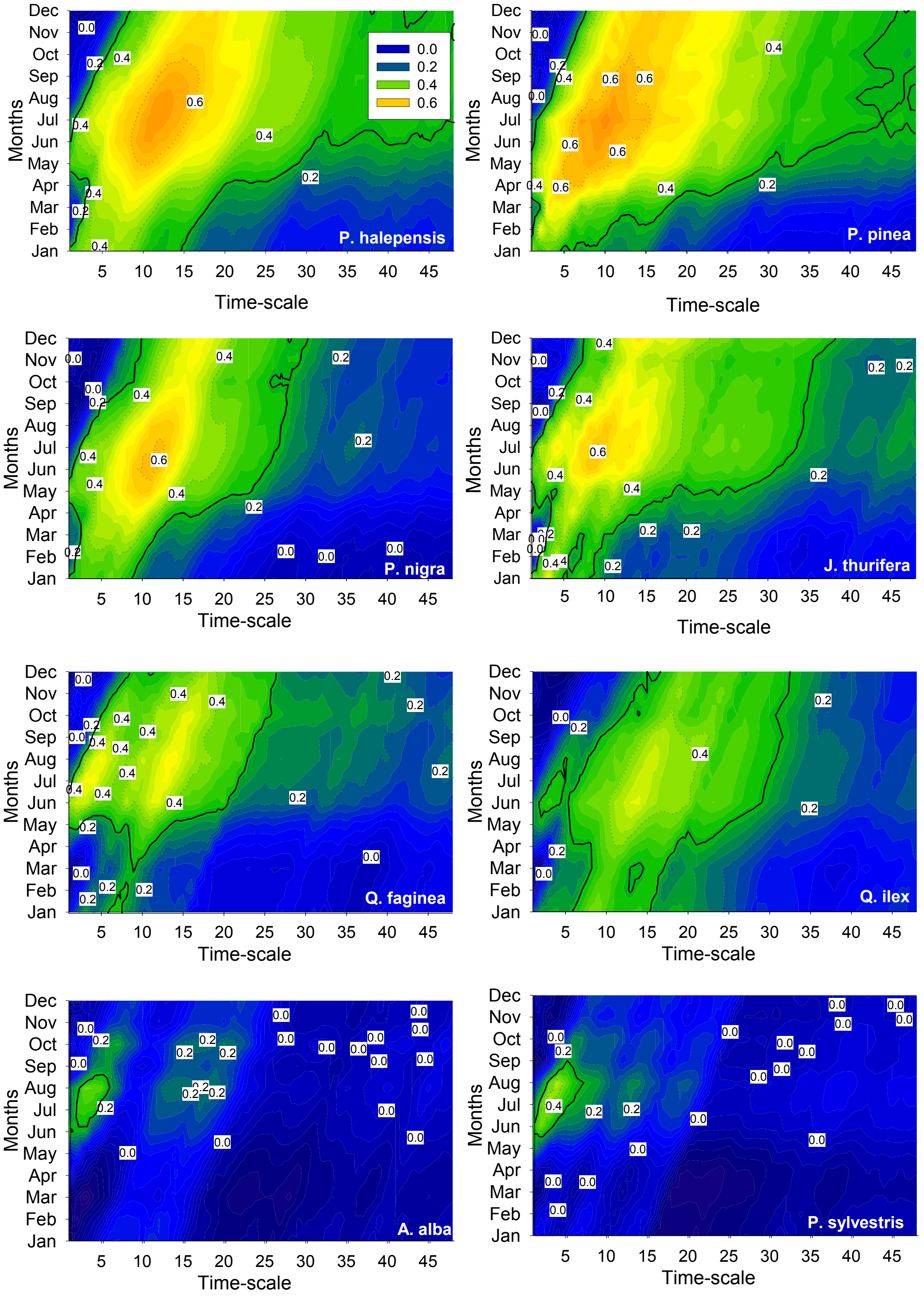

Figure 17. Mean correlation coefficients between ring-width chronologies and monthly SPI series at different time scales for the eight studied species. Bold lines frame significant correlations ($p \leq 0.05$).

In *P.halepensis* forests, significant correlations were revealed at time scales from 1 to 48 months. Nevertheless, at short time scales (1 to 3 months) significant correlations only appeared for the period May - July. In this specie the highest correlations (r = 0.60-0.70) were observed at time scales between 12 and 16 months during June, July and August. High correlations were also found between the SPI and the chronologies of *P. pinea* (maximum r = 0.70), *P. nigra* (maximum r = 0.62) and *J.thurifera* (maximum r = 0.61) considering spring (May), summer (June, July, August) and early-fall (September) months, particularly at time scales from 9 to 15 months. The remaining conifers (*A. alba*, *P. sylvestris*) did not show strong associations between growth and SPI, presenting low and significant correlation coefficients (r = 0.30-0.40) during summer months for time scales ranging between 2 and 5 months. A higher growth response to drought was observed for *Q. faginea* and *Q. ilex* based on the significant correlations they showed at time scales up to 25 months, mostly during summer and autumn months. *Q. ilex* indicated lower growth-SPI correlations than *Q. faginea*, with association being significant only at time scales between 8 and 25 months.

Geographically structured growth-drought relationships

Here is shown the spatial variability of the associations between forest growth and drought. A high site-to-site variability was detected in the growth response to drought within the same species across the study region (Figure 18). Consequently, a clear South-North gradient was observed in the maximum correlations between growth and SPI. This gradient corresponded to maximum correlation values for sites located in the Middle Ebro Basin in the case of Mediterranean conifers (*P. nigra*, r = 0.84; *P. halepensis*, r = 0.83; *P, pinea*, r = 0.81; *J. thurifera*, r = 0.75) and oaks (*Q. faginea*, r = 0.74; *Q. ilex*, r = 0.67), intermediate values in sub-Mediterranean *P. sylvestris* forests from the Pre-Pyrenees (r = 0.66) and minimum values in Pyrenean mesic *A. alba* forests (r = 0.64).

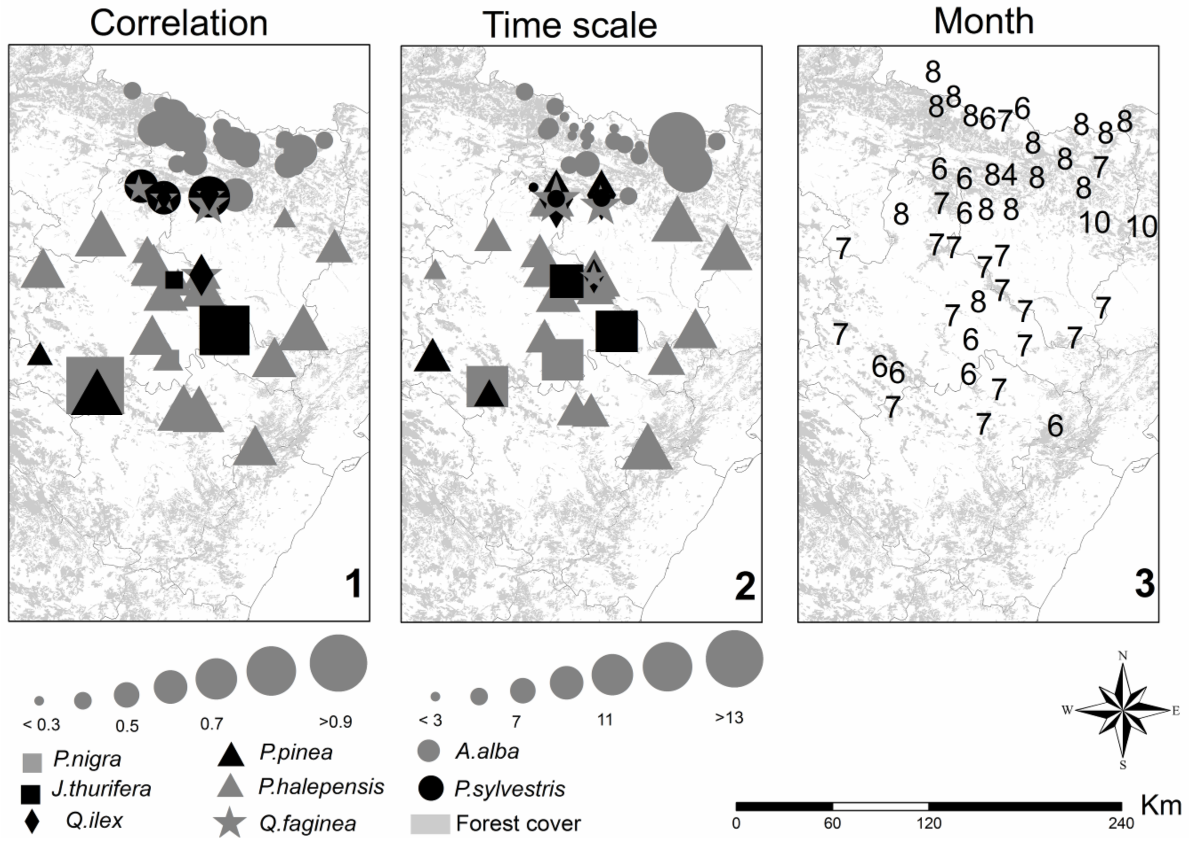

Figure 18. Geographic variability of the growth-drought associations showing (1) maximum Pearson correlations between ring-width chronologies for all sites and the monthly SPI series (the symbols are proportional to the absolute correlation value), (2) time scale (in months) at which the maximum correlation was achieved; and (3) month of the year at which the highest correlation was reached.

Most species reached the maximum growth-drought correlations at time scales varying from 9 to 11 months, except *A. alba* and *P. sylvestris* which showed the maximum association at time scales lower than 5 months in most of their sampled forests. Nevertheless, large differences were also noted in the time scales at which maximum correlation were observed for each sampled species without any clear spatial pattern. Finally, irrespective of the tree species, the study site, the magnitude of the SPI-tree growth correlations and the characteristic time scale, the maximum correlations were commonly obtained in summer months (June to August), which indicates the relevance of water availability for tree growth during the late growing season.

Discussion

This study evaluated the impact of droughts on eight tree species forming forests distributed along a wide climatic gradient in north-eastern Spain, by means of dendrochronological methods and using the Standardized Precipitation Index (SPI). This is the first investigation exploring the relationship between tree growth and drought using multi-scalar drought indices. Particularly, the research focused on the impact of different time scales characterizing drought intensity on radial growth, given that droughts may act on growth at different characteristic time scales. For instance, at short time scales dry and moist periods alter with a high frequency, while at long time scales droughts are less frequent but longer in duration (Hayes et al., 1999; Vicente-Serrano, 2006).

The analyses revealed two distinct patterns in terms of the growth sensitivity to drought, depending on the time scale of drought and the studied species. Species growing in the Middle Ebro Basin under Mediterranean semiarid conditions (all *Pinus* species excepting *P. sylvestris*, *Quercus* species, *J. thurifera*) showed stronger growth responses to drought compared to those growing in mountainous areas from the Pre-Pyrenees and Pyrenees (*A. alba*, *P. sylvestris*) characterized by a humid and cold climate. It has been found previously that in xeric Mediterranean areas tree growth is mainly limited by low precipitation, while in mesic Mediterranean areas the main factors constraining growth are low temperatures (Richter et al., 1991; De Luis et al., 2007; Vicente-Serrano, 2007; Camarero et al., 2010). The high level of dependence on water availability of north-eastern Spanish forests has been also reported before mainly in pine and oaks species (Corcuera at al., 2004a,b; Andreu et al., 2007; Montserrat-Martí et al., 2009; Gutiérrez et al., 2011). Overall, these studies reported marked spatial variations in the response of forests to drought as a function of climate conditions, confirming that forests located in the driest sites are the most sensitive to drought occurrence.

Tree species growing in the driest sites of the study area, i.e. the Middle Ebro Basin, showed robust relationships ($r > 0.60$) with the SPI drought series at time scales between 9 and 11 months, which is a remarkable finding since it indicates that cumulative precipitation conditions during one year impact tree growth as illustrated by Sarris et al. (2007). The response of growth to drought (SPI) time scales longer than 11 months decreased gradually but correlations were significant up to 30 months ($r > 0.30$). Beyond this threshold, growth responses to drought were very low, indicating that precipitation recorded for periods longer than 30 months is not significantly affecting radial growth. Other studies that analyzed the relationships between precipitation and growth in semiarid sites showed that the correlations between two variables increased when considering the cumulative precipitation over a period of consecutive months (De Luis et al., 2009; Linares and Tíscar, 2010). Thus, forest growth variability in similar drought-prone areas is determined by the precipitation recorded during the year of tree-ring formation but also by the precipitation that fell in the previous year (Sarris et al., 2007). The use of a multi-scalar drought indicator allowed confirming this question in the analyzed forests. In the semiarid Middle Ebro Basin, the previous-winter soil water reserves are crucial for supporting tree growth during spring (Pasho et al., 2011a). It has been found previously that spatio-temporal variations in soil moisture and related rainfall pattern determine the growth response to climate in most Iberian forests (Andreu et al., 2007). Soil types (limestone and gypsum) in the Ebro Basin valley may additionally intensify the effects of drought conditions on tree growth because they have low water holding capacity (Guerrero et al., 1999). All the studied species found in the Middle Ebro Basin showed the strongest growth response to drought during spring and summer months, which indicates that forest growth in the area is highly dependent on spring and summer cumulative water deficit. First, most of these species show their maximum radial-growth rates between May and June (Camarero et al., 2010). Second, water deficit starts to affect markedly vegetation activity and plausibly growth in the study area as early as June (Vicente-Serrano, 2007). In addition, in the driest sites it was found that the growth-drought correlation decreased at time scales lower than 9 months, indicating that these forests may show certain adaptative capacity in response to short droughts.

The response of tree growth to drought greatly varied among species, being the maximum growth-drought correlation very high for *P. halepensis, P. pinea*, *P. nigra* and *J. thurifera* (r = 0.60-

0.80), moderate for *Q. ilex* and *Q. faginea* (*r* = 0.50-0.60) and low for *P. sylvestris* and *A. alba* (*r* = 0.40-0.50). The variability of species responses to drought may indicate very different strategies and functional threshold in coping with droughts. The lower tree growth–drought correlations found in drought-tolerant oaks (e.g., *Q. ilex*) as compared with drought-avoiding pines (e.g., *P. halepensis*) could be related to the more efficient conductive elements (vessels in oaks *vs*. tracheids in conifers), a more conservative water and deeper root systems of the former as compared with the later species, which might mitigate the negative effects of short-term water shortages on tree growth (Hacke and Sperry, 2001; Willson et al., 2008). However, the results indicate that *Q. ilex* showed a higher growth plasticity in response to drought, i.e. low growth-SPI correlations, in comparison to *Q. faginea*, suggesting a greater resistance to water constrains of the former as compared with the later species, which is in agreement with the low phenological activity of *Q. faginea* in summer (Corcuera et al., 2004a,b; Montserrat-Martí et al., 2009). *J. thurifera* also appeared to be affected moderately by drought despite this species is considered a drought-resistant species among the Iberian conifers and its radial-growth dynamics are very plastic in response to drought and to episodic rains (Camarero et al., 2010).

Considering *Pinus* species from the most arid study sites (*P. halepensis, P. pinea*, *P. nigra*), it was detected a stronger response to cumulative droughts over a 11-months period, during spring and summer months in comparison to other co-existing species in the area. This indicates that tree growth in these pine species is sensitive to mid-term water deficits which agrees with the findings of Linares et al. (2010), who found that *P. halepensis* growth in south-eastern Spain can be limited by drought during the summer prior to growth. Although pine species as *P. halepensis* are considered as drought-avoiding species, they may show functional growth thresholds in response to lasting and severe drought leading to growth decline and death (Novak et al., 2011). For instance, *P. halepensis* is adapted to the scarcity of soil water in the short-term due to summer drought by ceasing secondary growth and recovering it rapidly when water becomes available (Borghetti et al., 1998; Nicault et al., 2001; Rathgeber et al., 2005; De Luis et al., 2007, 2011). However, its growth may be much vulnerable to mid- and long-term droughts as the results support. Moreover, considering the fact that some of the studied sites represent the southernmost populations of some of the studied species in Europe (e.g., *A. alba*) and these stands are growing near the species' climatic tolerance, they may be affected severely by strong and lasting droughts leading to forest decline (Macias et al., 2006; Camarero et al., 2011).

The results indicated no impact of long-term droughts on radial growth of mountain conifers from mesic sites (*A. alba*, *P. sylvestris*), which responded to short-term droughts of a duration lower than five months during summer. This association may be explained by the low water-use efficiency of *A. alba*, which is a species whose photosynthetic rates are very sensitive to atmospheric drought (Guehl et al., 1991) and its growth rates respond to short-term cumulative water deficit in late summer (Camarero et al., 2011). In the case of *P. sylvestris*, previous studies have clearly indicated that summer drought contrains growth and xylogenesis in *P. sylvestris* (Camarero et al., 2010; Gruber et al., 2010) and severe water deficit may even lead to drought-induced mortality (Martínez-Vilalta and Piñol, 2002; Sánchez-Salguero et al., 2010).

The response to drought was site-dependent and this variability among sites was greater in *P. nigra* and *Q. faginea* forests as compared with the other species. However, the number of sites sampled to capture the variability of both species was low in comparison to other well-replicated species such as *P. halepensis* and *A. alba*. In general, sites located in the driest areas of the Middle Ebro Basin showed a higher response to drought compared to those located in mesic mountainous areas where water availability is high. For example, it was observed that *P. halepensis* showed higher growth-drought correlations in the driest sites than in northern less xeric sites receiving more precipitation. Given the large intra-specific differences, in the section 3.4 are investigated the relative roles of local conditions (topography, soil type, etc.) on the growth responses to drought at different time scales.

Therefore, multi-scalar drought indices are particularly useful for monitoring the impact of climate variability on forest growth because the response of tree growth to droughts is complex. The time scales over which precipitation deficits accumulate affecting noticeably forest growth vary among species and sites within the same species. For this reason, drought indices must be associated with a specific time scale and assessed taking into account local conditions to be useful for monitoring impacts on forest growth as has been done with remote-sensing assessments of vegetation activity (Ji and Peters, 2003; Vicente-Serrano, 2007; Quiring and Ganesh, 2010). In the current context of climate warming, several climate models have indicated that drought frequency and intensity are expected to increase in the Western Mediterranean Basin (Giorgi and Lionello, 2008). Increasing aridity is expected to cause growth decline and enhance mortality particularly in drought-sensitive species (Linares et al., 2010; Gruber et al., 2010; Koepke et al., 2010). The approach used in this study for examining growth responses to drought at different time scales and considering multiple tree species and sites across a wide climatic gradient in north-eastern Spain may represent a first step in understanding and forecasting forest responses to future climate change. If climate warming causes more frequent and severe droughts in the future, many forests in the study area will be adversely and selectively affected.

3.3. Climatic impacts and drought control of radial growth and seasonal wood formation in *Pinus halepensis*

Introduction

In Circum-Mediterranean forests, drought is considered as the main driver of the tree growth variability (Sarris et al., 2007). Climate change models project a decrease in annual mean precipitation and rising air temperatures over the Mediterranean Basin for the late 21st century leading to an increase in evapotranspiration (IPCC, 2007; Giorgi and Lionello, 2008; García-Ruiz et al., 2011). These trends towards increasing arid conditions in the region are expected to cause more frequent episodes of forest growth decline and mortality events as those already observed by some authors (Macias et al., 2006; Linares et al., 2009; Galiano et al., 2010; Sánchez-Salguero et al., 2010).

Various studies indicate contrasting tree growth responses to drought (Martín-Benito et al., 2008; Koepke et al., 2010; Linares et al., 2010; Sánchez-Salguero et al., 2010). For instance, some authors (Abrams et al., 1998; Sarris et al., 2007) noted that trees growing in xeric sites showed declining radial growth trends and increased crown dieback and mortality in response to long-lasting droughts. However, other researchers argued that species growing in xeric locations develop adaptive features to withstand the negative effects of drought on growth by reducing water loss or increasing hydraulic efficiency, and by showing lagged growth responses or recovering rapidly after the drought (Bréda et al., 2006; McDowell et al., 2008; Eilmann et al., 2009).

Dendrochronology is a useful tool for providing information on climate-growth relationships based on year-to-year correlative approaches. However, these relationships must be compared with xylogenesis studies for capturing short term climatic influences on radial tree growth (Camarero et al., 1998; Rossi et al., 2008). Therefore, information regarding the phenology of xylem growth is required to better understand the processes underlying the effects of climate and drought stress on seasonal wood formation.

Pinus halepensis forests provide a valuable system to explore how drought measured at different time scales constrains radial growth. This conifer is one of the dominant tree species in the Western Mediterranean Basin and the most ecologically important species in semi-arid woodlands (Ne´eman and Trabaud, 2000). *P. halepensis* is considered as a species well adapted to withstand drought by reducing growth as water availability decreases (Serre-Bachet, 1992; Borghetti et al., 1998; Nicault et al., 2001; Rathgeber et al., 2005; De Luis et al., 2007; Camarero et al., 2010). The increasing aridity in the Mediterranean region could have important implications for the intra-annual growth dynamics of *P. halepensis* which could be reflected also in long-term (inter-annual) growth trends in this species. In addition, there are no studies analyzing jointly the intra and inter-annual long-term responses of earlywood (hereafter abbreviated as EW) and latewood (hereafter abbreviated as LW) formation to climate and drought in *P. halepensis* forests from semi-arid areas.

In Circum-Mediterranean drought-prone forests, a deeper knowledge on the EW and LW responses to recurrent water shortages at several time scales is important for understanding how amplified precipitation variability will drive radial growth trends (Andreu et al., 2007). In a previous study on growth-drought relationships assessed at multiple time scales, it was found that *P. halepensis* growth is highly sensitive to mid-term cumulative drought stress, particularly during summer (Pasho et al., 2011b). This study aims at understanding how drought and climate variability affects the patterns of seasonal wood formation (EW and LW widths) of *P. halepensis* forests from central (Middle Ebro Basin) and southern (Teruel) Aragón, north-eastern Spain (Figure 19). In addition, the research aims at providing a mechanistic basis concerning the long-term impacts of drought and climate on EW and LW production by studying xylogenesis processes (periods and production rates of different tracheid types) in a semi-arid *P. halepensis* forest. Moreover, the current and post-drought (up to two years later) effects on growth of both wood types are investigated to quantify possible lagged effects of water deficit on seasonal wood production.

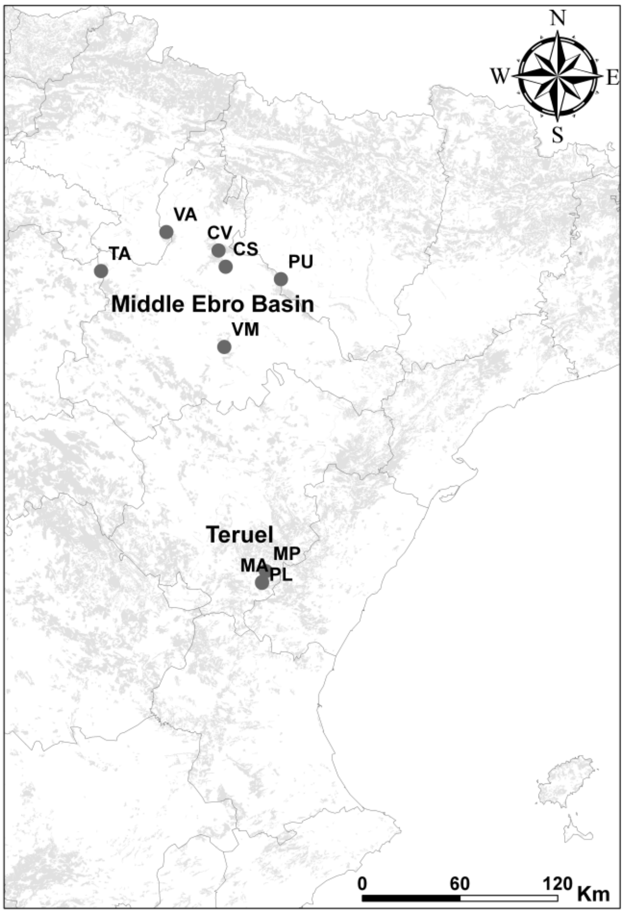

Figure 19. Location of *P. halepensis* sites (dark grey points) in the central (Middle Ebro Basin) and southern (Teruel) Aragón, north-eastern Spain. The grey area indicates forest cover in the region. The site codes are named as shown in Table 1.

The objectives were: (*i*) to quantify the long-term (inter-annual) effects of climate and drought on EW and LW growth in *P. halepensis* forests from north-eastern Spain and (*ii*) to describe the intra-annual xylogenesis processes, including the seasonal wood production, for explaining the differential long-term responses of EW and LW production to climate and drought. The hypothesis of this study was that severe and long-term drought conditions will impact more EW than LW formation since EW tracheids mature when water deficit usually starts and their number and transversal lumen size reflect well the theoretical hydraulic conductivity of the tree, and, consequently its potential capacity to uptake carbon and grow (von Wilpert, 1991). It is expected that the drought-induced reduction in EW production and hydraulic conductivity will lead to an indirect decrease in LW formation. The evaluation of these ideas is relevant for predicting the responses of Circum-Mediterranean *P. halepensis* forests from semi-arid areas to the forecasted aridification trends (IPCC, 2007).

Methodology

Climatic data

To quantify climate-growth relationships at local scale it was explored a large database of local meteorological stations and selected 14 of them located near the sampled sites (mean site-station distance is 14.5 km) with the longest climate series. From these stations, monthly and yearly variables of mean temperature (minimum, average and maximum) and total precipitation were collected for the period 1950-2005.

Drought index calculation

To quantify the impact of drought on *P. halepensis* EW and LW growth, it was employed again the Standardized Precipitation Index (SPI) (McKee et al., 1993). The SPI was calculated at time scales ranging from 1 to 48 months to be compared with EW and LW growth at each forest site (see section 3.2).

Xylogenesis

To understand the dendrochronological patterns and provide mechanisms explaining the influence of climate drivers and drought on EW and LW tracheid production rates at intra-annual scales, xylogenesis analysis were carried out. On March 2010, ten dominant *P. halepensis* trees were randomly selected in the site PU (Figure 19). They were tagged and their diameter at breast height (dbh) was measured. Then, wood micro-cores (15-mm long and 2-mm thick) were extracted beweekly from April until December using a Trephor puncher (Rossi et al., 2006a). Consecutive wood samples were collected 5-10 cm apart from each other, following a spiral up the stem (mean sampling height was 1.3 m) to avoid disturbance reactions caused by cambium wounds. Micro-cores contained at least the previous five tree rings and the developing cambial zone. Samples were placed in Eppendorf tubes containing a fixative solution (formalin-ethanol-acetic acid, 5:90: 5). Micro-cores were cut to obtain transversal sections for histological analyses (Antonova and Stasova, 1993). Before cutting, each micro-core was vertically oriented by marking the fibre orientation with a pencil under a stereomicroscope at x20 magnification. We obtained from four to six sections per micro-core with 10–20 µm thicknesses using a sliding microtome (Anglia Scientific AS 200, Cambridge, UK). The sections were stained with 0.05% cresyl violet. The mounted and fixed sections were examined under a light microscope (Olympus BH2; Olympus, Hamburg, Germany) within 10 minutes of staining at 100-500 magnification. Images were photographed with a digital camera (JVC 3.3 CCD GC-X3E; JVC, Yokohama, Japan) to verify cell counts and to distinguish EW and LW tracheids according to their lumen and cell wall thickness. To distinguish EW and LW tracheids, first we measured their lumens and double-wall thickness along five radial lines per tree using the November wood samples. Then, we followed Denne (1988) chriterion, i.e., LW tracheids were regarded as those whose single cell-wall thickness multiplied by four were greater or equal to their lumen widths.

For each analysed wood sample, the following cell types were distinguished and counted along the radial files: cambial cells, radially enlarging tracheids, wall-thickening tracheids and mature tracheids (Antonova and Stasova, 1993). The first cells with evident radial diameter increments, but still containing a protoplast enclosed by a thin primary wall, were regarded as the first radially enlarging tracheids. The end of radial-cell expansion and the onset of secondary cell wall formation were defined by the appearance of pit borders and cell corner rounding. Tracheid lignification corresponded to a colour change from violet to blue. The maturation zone ended when visible traces of cytoplasm were not observed within the tracheid lumen and also when tracheids exhibited completely blue cell walls. The onset of xylem formation was regarded as the date when at least five trees showed more than one row of cells in the cell-enlargement phase. The ending of xylogenesis was considered the date when all trees lacked tracheids corresponding to the wall thickening phase.

Dendrochronological methods

To quantify the temporal patterns of EW and LW widths in the studied sites, dendrochronological methods were used (see details in section 2.2). The common period 1970-2005 was selected because all chronologies showed EPS values above the 0.85 threshold for this interval and they were considered being well replicated (Wigley et al., 1984).

Statistical analyses

To quantify the climate-growth relationships, the residual EW and LW chronologies of each site and the detrended climate series of monthly mean temperatures, mean minimum and maximum temperatures and total precipitation were used. Correlations were computed over the common period 1970-2005 using a 15-month window from August of the year prior to growth (year *t-1*) until October of the year of tree-ring formation (year *t*). According to previous studies, this window encloses the most influential period for radial growth of *P. halepensis* (De Luis et al., 2007; Camarero et al., 2010). The percentage of EW and LW growth variability explained by climate (minimum, average, maximum monthly temperature and monthly precipitation) in each site (R^2adj, R^2 adjusted) was also obtained through multiple linear regressions, based on a stepwise forward selection of significant variables ($p \leq 0.05$), calculated between EW and LW indices and the local monthly climatic data.

To quantify the impact of drought severity on tree growth at different time scales were performed superposed epoch analysis (SEA) (Haurwitz and Brier, 1981) and correlation analyses with SPI based on the Pearson coefficient. SEA was used to detect the drought impacts on EW and LW formation by calculating deviations in EW or LW width two years after selected drought.

According to SPI data were selected four dry years (1967, 1986, 1994 and 2002) with values close to SPI = -1, i.e. experiencing mild to severe drought. The significance of mean tree growth response to these extremely dry years was then assessed (Orwig and Abrams, 1997). The software Resampling Stats was used to select 10,000 random sets of three years from each EW or LW width series and to estimate the confidence intervals ($p<0.05$) for the growth deviations (Bruce, 1991).

Prior to the assessment of the correlations between SPI and EW or LW width indices, the trend in each SPI time series was removed by assuming a linear tendency in each monthly series at the different time scales. This step avoided that possible SPI trends could disrupt potential relationships. Then, correlation analyses were performed for the period 1970-2005 between EW and LW residual chronologies representing forest growth at sampled locations and detrended monthly series of 1- to 48-month SPI representing drought severity. The threshold for significant correlations was set at $p \leq 0.05$ for all correlation analyses.

The periods of maximum intra-annual growth were identified by transforming the cumulative number of EW and LW tracheids into daily rates of tracheid production (cells d^{-1}). This was achieved by dividing the difference of the total number of tracheids formed in successive dates (ΔN) by the time interval (Δt) between both dates (Camarero et al., 1998).

Results

Growth patterns

Initially, the statistics of the EW and LW series in the selected *P. halepensis* forests are shown. In difference to the *P. halepensis* growth patterns presented in the section 3.1, here are also described the growth statistics of forests sampled in the Teruel region.The mean width values of EW varied among sites more than those of LW (EW, 0.68-1.91 mm; LW, 0.18-0.54 mm) (Table 7). The average values of AC1 and MSx were higher for the EW (AC1 = 0.65, MSx = 0.44) than for the LW (AC1 = 0.53, MSx = 0.43) chronologies. Similar results were obtained for Rbar and EPS, considering EW (Rbar = 0.70, EPS = 0.93) and LW (Rbar = 0.56, EPS = 0.89) width series. Thus, EW chronologies showed a greater year-to-year persistence (AC1), a higher relative change between consecutive years (MSx) and a higher common signal (Rbar, EPS) than LW ones. The within-site correlation between EW and LW series varied from 0.38 (site PL) to 0.75 (site CS) and it was always significant ($p \leq 0.05$). On average, 32% of LW width variability was related to EW width variability.

Similar high-frequency growth patterns were observed for EW and LW width series with growth reductions in 1955, 1958, 1962, 1981, 1986, 1994, 2000 and 2005 (Figure 20). The periods characterized by substantial increase in EW and LW width corresponded to the years 1954, 1959, 1977, 1988, 1997 and 2004. These sharp growth decreases and increases coincided with dry (SPI < 0) and wet conditions (SPI > 0), respectively.

Climate-growth relationships

In this section are shown the relationships between the climatic variables and EW-LW growth in the studied *P. halepensis* forests. The proportion of growth variance explained by climate was generally higher for EW (62.7%) than LW (45.3%) and varied among sites (Table 7). Mean correlation coefficients revealed positive responses of EW growth to current spring and summer precipitation (April, May and June) and negative ones to temperature variables, particularly to mean maximum temperatures in May, June and July (Figure 21). Wet conditions and high minimum temperatures in the previous December and the current January favored EW development whereas LW growth was also enhanced by high minimum temperatures in January.

Table 7. Dendrochronological statistics of earlywood (EW) and latewood (LW) *P. halepensis* chronologies for the common period 1970–2005.

				Earlywood						Latewood					
Site	No. trees (No. radii)	Period	Correlation EW-LW	MW ± SD (mm)	AC1	MSx	Rbar	EPS	R^2adj (%)	MW ± SD (mm)	AC1	MSx	Rbar	EPS	R^2adj (%)
VM	17 (30)	1959-2009	0.61	1.39 ± 0.81	0.59	0.44	0.80	0.99	80.30	0.39 ± 0.21	0.52	0.47	0.56	0.95	72.45
CV	13 (23)	1928-2009	0.47	1.75 ± 0.94	0.75	0.38	0.47	0.89	82.85	0.54 ± 0.33	0.71	0.34	0.50	0.86	64.06
CS	13 (23)	1900-2009	0.75	0.68 ± 0.37	0.41	0.47	0.64	0.97	40.04	0.18 ± 0.10	0.39	0.44	0.62	0.91	18.33
VA	17 (31)	1925-2009	0.74	1.28 ± 0.75	0.62	0.43	0.68	0.92	54.01	0.37 ± 0.22	0.58	0.43	0.51	0.86	41.92
TA	14 (27)	1927-2006	0.57	1.91 ± 1.22	0.59	0.50	0.78	0.97	44.68	0.43 ± 0.24	0.35	0.48	0.52	0.85	24.60
PU	15 (22)	1943-2009	0.58	0.85 ± 0.43	0.60	0.38	0.69	0.85	50.10	0.30 ± 0.16	0.56	0.40	0.54	0.88	29.10
MA	15 (28)	1963-2009	0.60	1.49 ± 1.27	0.75	0.53	0.81	0.94	64.51	0.38 ± 0.26	0.53	0.46	0.69	0.93	46.54
PL	15 (30)	1961-2009	0.38	1.35 ± 1.08	0.73	0.49	0.79	0.94	70.67	0.39 ± 0.25	0.53	0.44	0.61	0.92	50.87
MP	14 (29)	1965-2009	0.52	1.53 ± 1.26	0.81	0.37	0.68	0.93	77.61	0.38± 0.22	0.61	0.37	0.49	0.90	59.49
Mean	–––	–––	0.58	1.36 ± 0.86	0.65	0.44	0.70	0.93	62.75	0.37± 0.22	0.53	0.43	0.56	0.89	45.26

Statistics: EW–LW, Pearson correlation coefficient calculated between the residual earlywood and latewood chronologies for each site. Raw-data series: MW, mean width; SD, standard deviation of width; AC1, first order autocorrelation. Residual series: MSx, mean sensitivity; Rbar, mean interseries correlation; EPS, expressed population signal; R^2adj, adjusted R^2 obtained relating monthly climatic variables and EW, LW residual chronologies through stepwise linear regressions. The last line provides the mean values for all sites and considering statistics calculated for raw ring-width data (MW, SD, AC1) and residual chronologies (MSx, Rbar and EPS).

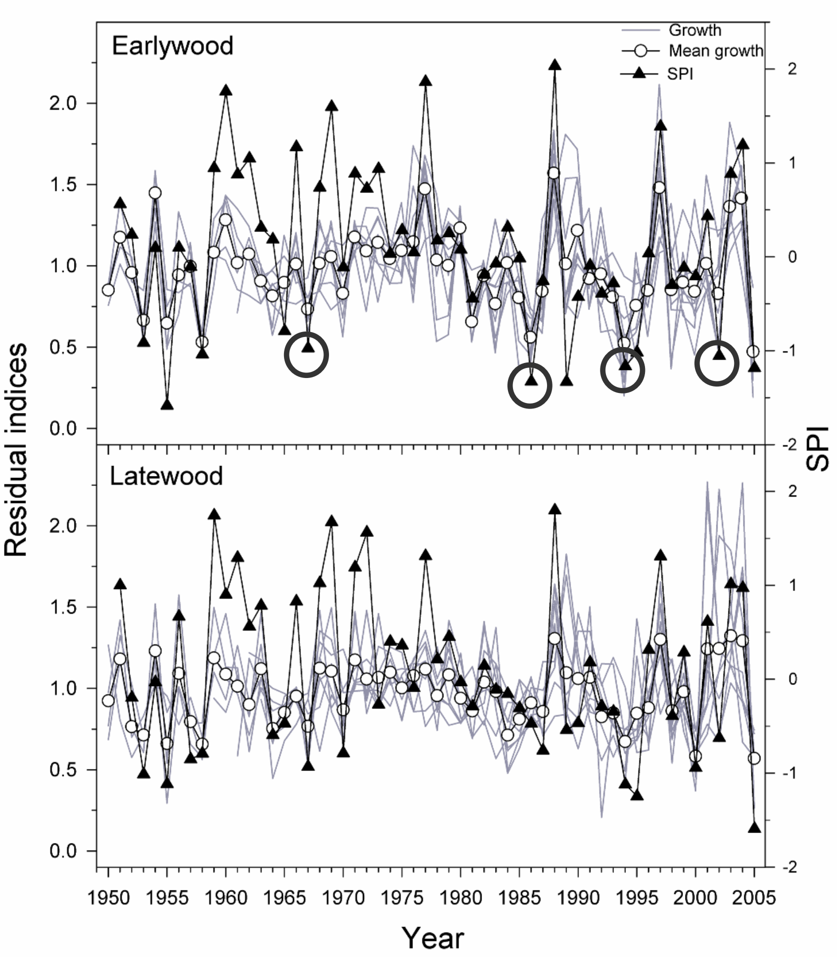

Figure 20. Residual chronologies of *P. halepensis* earlywood (EW) and latewood (LW) widths (gray lines) for the studied sites and their overall means (lines with empty circles). Black lines with triangles show the evolution of the drought index (Standardized Precipitation Index, SPI, mean of all sites) at time scales of 12 months in July and September, the scale at which EW and LW growth series showed the strongest response to the SPI drought index. Note that positive and negative SPI values indicate wet (high EW and LW indices) and dry conditions (low EW and LW indices), respectively. Selected dry years (1967, 1986, 1994 and 2002) for the study of growth departures are encircles in the upper graph.

Considering the variability in climate-growth associations among sites, strong positive correlations were found between May precipitation and EW growth in the sites MA, MP and PL whereas for the sites VA, VM and PU summer precipitation was found to be more important (Figure 22). The rest of sites did not show any particular correlation with spring-summer precipitation (except June). However, the growth in all sites was influenced considerably by winter precipitation (December-January). Considering the LW, there were found positive correlations between previous October precipitation and LW growth in the sites MA and PL.

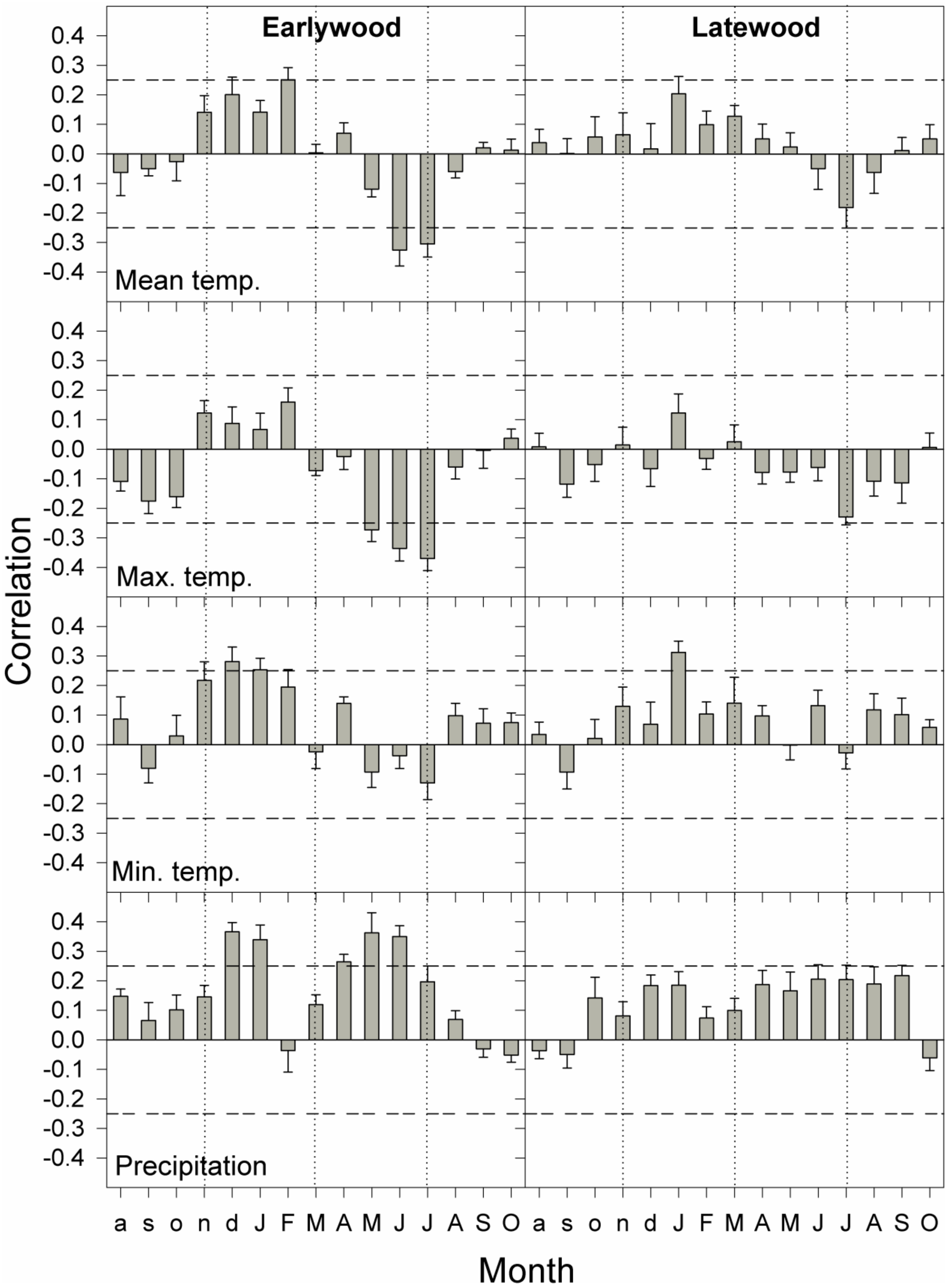

Figure 21. Mean (± SE) correlation coefficients calculated between earlywood and latewood width chronologies of the nine study sites and monthly climatic variables (mean temperature, mean maximum and minimum temperatures, and total precipitation). Growth is related with climate data from the previous August to current October, i.e. of the prior year (months abbreviated by lowercaste letters) and the year of tree-ring formation (months abbreviated by uppercaste letters). The significance level ($p \leq 0.05$) is indicated by dashed horizontal lines.

The remaining sites did not present any significant correlation with the previous autumn current winter precipitation. The spring precipitation was particulary important for the sites MP, VM and CS whereas the summer precipitation was positively and significantly correlated with almost all sites. The autumn precipitation in general did not show any particular influence on LW growth except September month which affected positively the growth in sites MP, VA and PU.

With regard to temperature, generally positive correlations were found between EW growth and minimum winter temperatures, particularly for the sites MA, MP, PL, CS and CV. The same can be commented for the mean and maximum temperature in winter but not for the summer months in which temperature excerted a high negative influence on EW growth in almost all sites (except site VA). The LW growth was enhanced by the winter minimum and mean temperatures, particularly at the sites MP, PL, VA, SC and CS whereas spring and autumn temperatures did not have any significant influence. Summer mean and maximum temperatures generally constrained the LW growth, specifically at the sites VM, CS and CV.

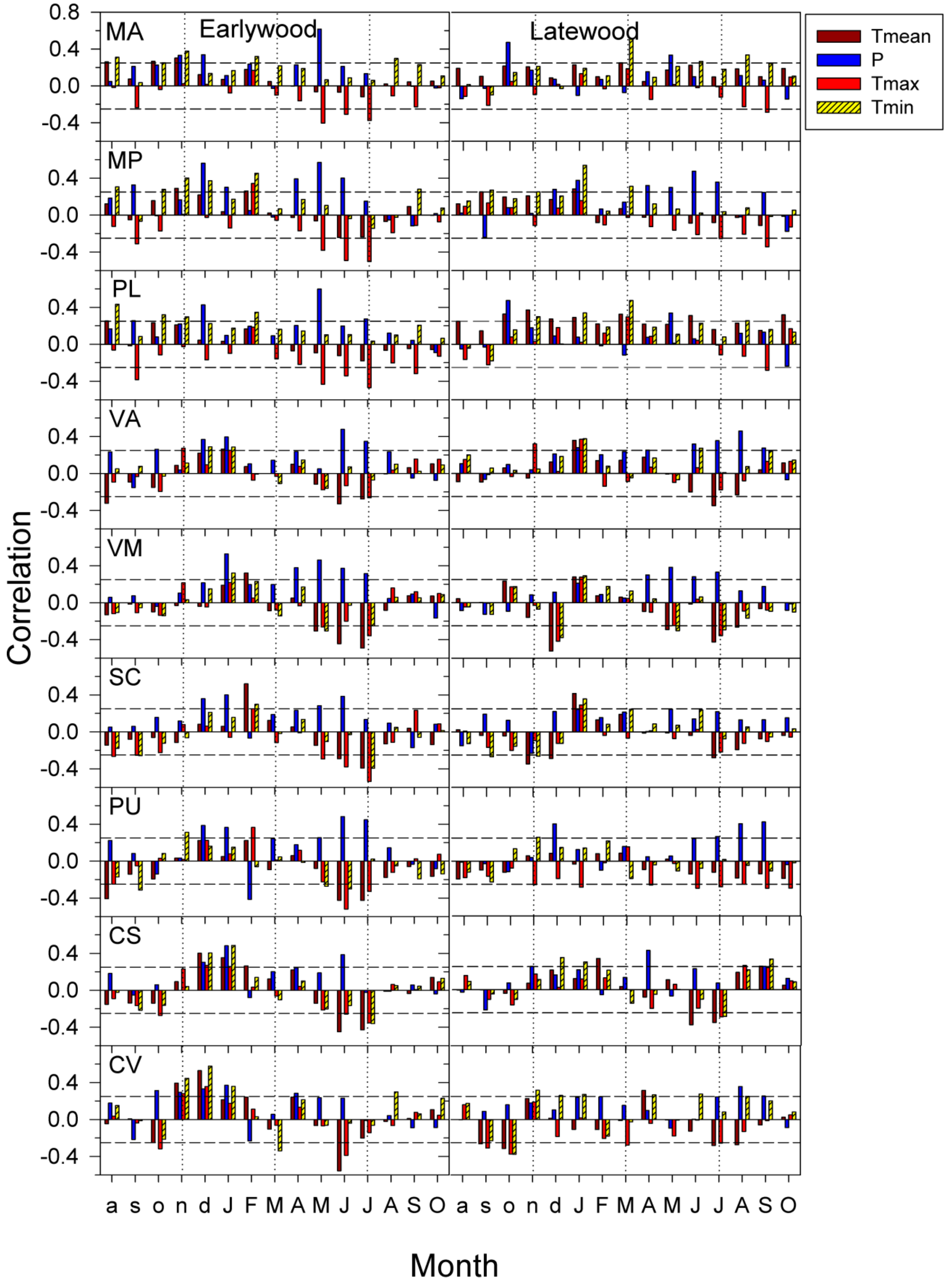

Figure 22. Relationships (Pearson correlation coefficients) between earlywood and latewood width indices and monthly climatic variables (mean, minimum, maximum temperature and total precipitation) for the nine study sites. Growth is related with climate data from the previous August to October of the year of tree-ring formation. The significance level ($p \leq 0.05$) is indicated by dashed horizontal lines.

Intra-annual dynamics of earlywood and latewood formation

In this section is described the intra-annual development of EW and LW formation in *P. halepensis* (site PU) as revealed by the xylogenesis analysis. In the selected site, climatic conditions during 2010 were within the range of the local long-term climatology with mean annual temperature of 15.3 ºC (long-term mean = 15.0 ºC) and total precipitation of 267 mm (long-term mean = 327 mm) (Figure 23). Considering monthly values in 2010, April and July temperatures and April rainfall amount were above long-term mean values whereas May precipitation was below historical means.

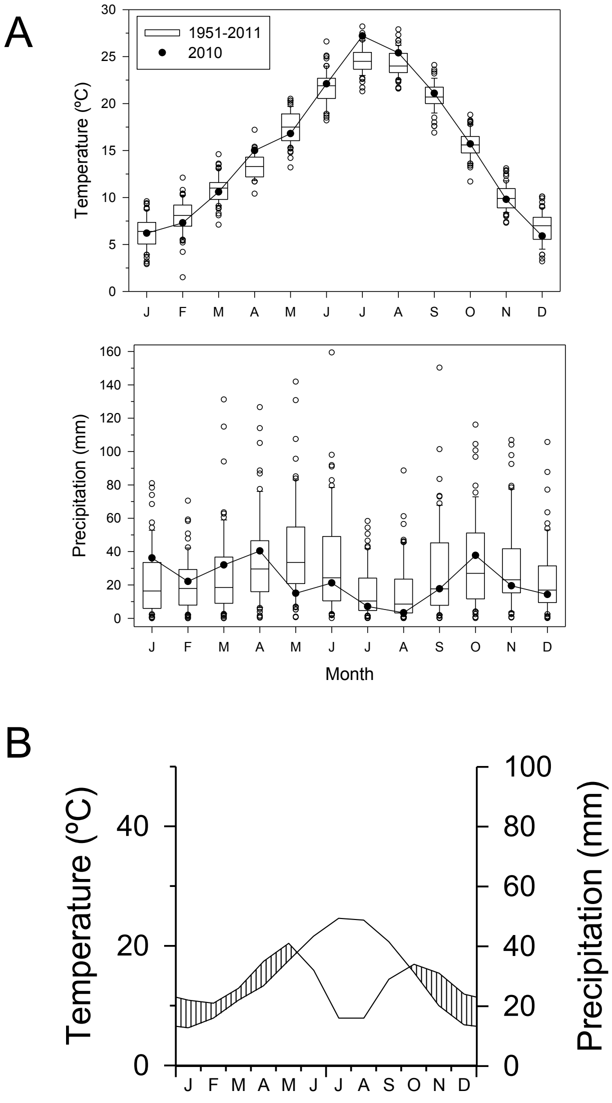

Figure 23. A. Climatic conditions (mean monthly temperature and total precipitation) at the site PU during the year 2010 as compared with historical data (period 1951-2011, boxplots showing the median values and outliers) from the Zaragoza-Aeropuerto meteorological station (latitude 41° 39' N, longitude 1° 00' W, elevation 263 m a.s.l.) located at ca. 24 km. **B.** Climatic diagram of Zaragoza-Aeropuerto station based on 1951-2011 data.

Xylem formation had already started in March and xylogenesis was active until November (Figure 24). The cambial activity followed a unimodal pattern, with two major peaks (May-June and mid July-August) of tracheid formation corresponding respectively to the enlargement and wall-thickening phase.

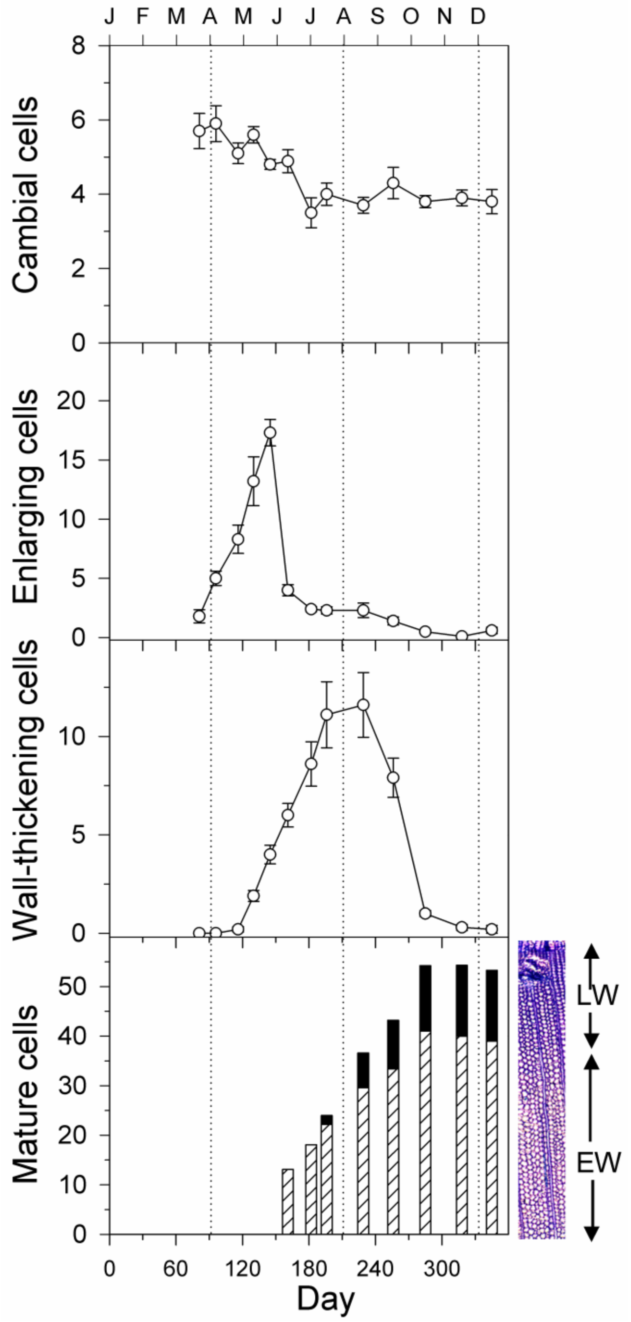

Figure 24. Number of cells of *P. halepensis* according to their development phase (cambial cells, radially enlarging tracheids, wall-thickening tracheids and mature tracheids −earlywood and latewood tracheids are shown as bars with different fill types) formed during the year 2010 in the site PU. The image shows the earlywood (EW) and latewood (LW) of a cross-section of a ring (total width = 1.22 mm) from a wood sample taken in mid November. Data are means (n = 10 trees).

These two phases match with the periods of maximum EW and LW formation in that order (Figure 25 B). The rate of EW tracheid production was higher (0.38 cells day^{-1}) than that of LW (0.22 cells day^{-1}). The EW tracheid formation started in late March and finished in September in most trees whereas the first LW tracheids were formed in July and the last ones were observed in November (Figure 24).

Drought-growth relationships

In this section are shown the results regarding drought-growth relationships as revealed by the SEA and SPI analysis. The SEA indicated differences in the annual deviations of EW and LW widths in response to drought. Significant decreases in EW width were observed in five out of nine sites during the year of drought whereas only one site showed significant reduction in LW width one year after the drought (Table 8). The mean deviations in EW and LW widths during the drought year were -0.48 and -0.31, respectively, whereas they showed similar responses up to two years after the drought.

Table 8. Annual earlywood (EW) and latewood (LW) width departures observed up to two years after the occurrence of a severe drought (in year "0"). Departures were calculated in response to selected severe droughts (1967, 1986, 1994 and 2002; see Figure 20). Significant ($p \leq 0.05$) values are in bold.

	EW			LW		
	Years after drought			Years after drought		
Site	0	1	2	0	1	2
VA	−0.35	−0.21	−0.14	−0.28	**−0.52**	0.17
CV	−0.34	−0.24	0.16	−0.30	−0.05	0.24
CS	**−0.46**	−0.04	0.23	−0.37	0.05	0.18
PU	−0.20	−0.26	0.09	−0.11	−0.26	−0.08
TA	**−0.74**	−0.42	0.01	−0.28	−0.18	−0.01
VM	**−0.56**	−0.18	0.28	−0.25	−0.12	−0.06
MP	**−0.45**	−0.15	−0.25	−0.38	−0.26	0.23
PL	**−0.85**	−0.43	−0.28	−0.44	−0.20	0.08
MA	−0.41	0.35	0.3	−0.35	−0.07	0.02
Mean	−0.48	−0.18	0.04	−0.31	−0.18	0.09

The correlations between EW and LW growth indices and the different SPI time-scales reached maximum values at similar time-scales (10-14 months), despite significant correlations were found up to 48 (EW) and 35 (LW) months (Figure 25 A). The strongest responses of EW to drought intensity (*r* = 0.70–0.72) were observed in July, whereas LW responded strongly (*r* = 0.54) to SPI September values. The months when the highest responses of EW and LW width to drought at inter-annual scales were detected, coincided with those in which were observed low production rates of EW (July) and LW (August-September) tracheids at intra annual scales (Figure 25 B). Finally, the maximum production rates of EW (May-June) and LW (mid July-August) tracheids occurred approximately one month before the strongest impact of drought on inter-annual EW and LW growth series was detected.

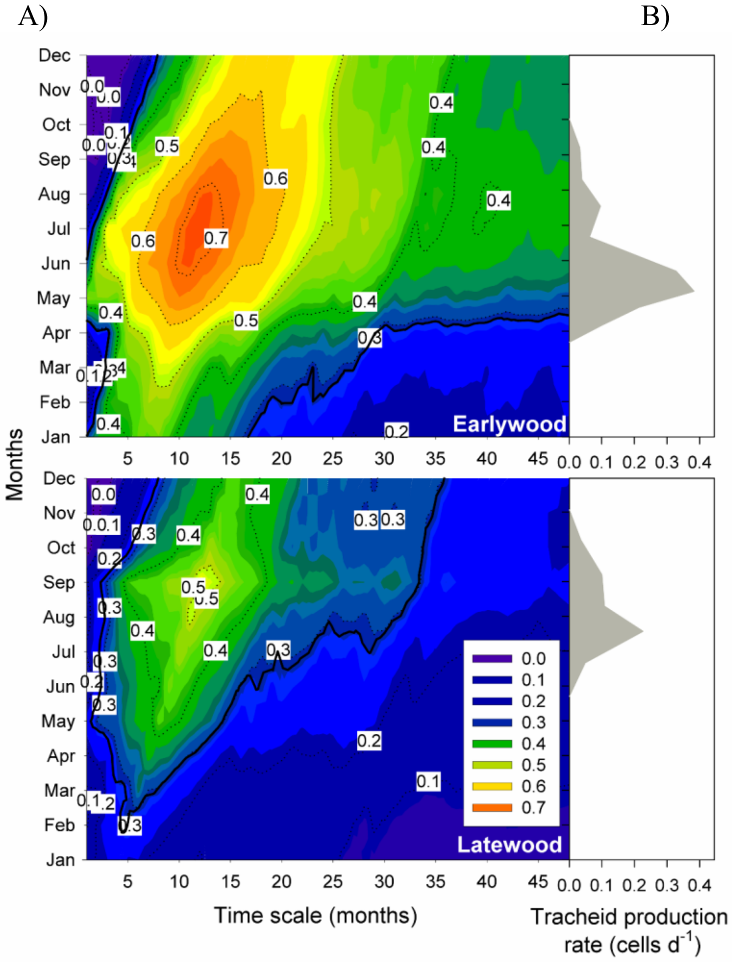

Figure 25. A) Mean correlation coefficients of earlywood (EW) and latewood (LW) width chronologies and the SPI drought index calculated at different time scales (1-48 months, *x* axis) from January to December (*y* axis) for the nine study sites. Bold lines frame significant correlations ($p \leq 0.05$). B) Calculated daily rates of EW and LW tracheids production in *P. halepensis* during the year 2010.

Certain variability among sites regarding EW and LW growth responses to drought was also detected (Figure 26), but these local responses matched the general patterns described before. However, the strongest response of EW growth to drought was found for the sites VM, CV, CS, VA whereas the sites TA, PU, MA, PL and MP were less affected by drought. The same pattern was also observed with respect to the LW.

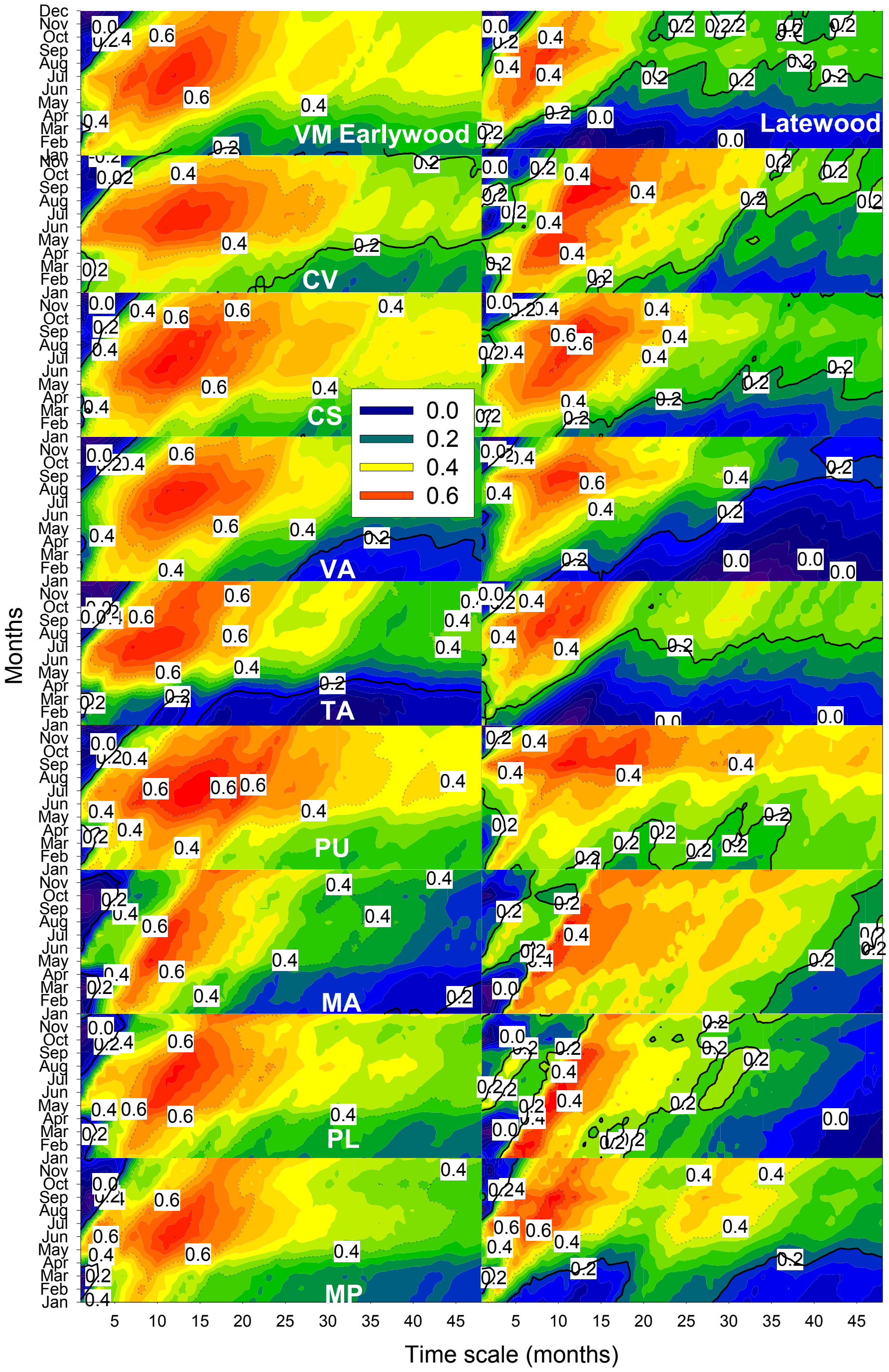

Figure 26. Pearson Correlation coefficients obtained relating earlwyood and latewood width indices *vs*. the monthly drought index (SPI) calculated at different time scales (1-48 months, *x* axis) from January up to December (*y* axis) in the nine study sites. Bold lines frame significant correlations ($p \leq 0.05$).

Discussion

This study evaluated the impact of climatic drivers and drought stress on earlywood (EW) and latewood (LW) formation at inter- and intra-annual scales in *P. halepensis* forests from semi-arid areas. Climatic factors and drought highly impacted both components of the tree ring in short and long terms, particularly EW production. At the intra-annual scale, the EW production was enhanced by relatively high rainfall amounts in April, May and June, whereas the production of radially enlarging tracheids, which are closely linked to the radial-growth rate (Larson, 1994), was sharply reduced during the dry period (July-August) (see Figure 23). Interestingly, the LW tracheid production was intensified as a response to high summer temperatures and low water availability. These climatic conditions are linked to the cessation of EW tracheid production and may trigger the formation of LW tracheids and enhance cell-wall lignification as reported previously (von Wilpert, 1991; Jyske et al., 2010).

In drought-stressed *P.halepensis* forests, water availability constrains the rate of EW tracheid production while temperature can be considered as the main climatic driver determining the onset and ending of tracheid production (Camarero et al., 2010). The low cambial activity of *P. halepensis* in summer appears to be triggered by high temperatures and the decrease of precipitation, i.e. low soil water availability (Camarero et al., 2010). However, the ability to maintain tracheid production, although at a reduced rate, during the dry summer months (Serre-Bachet, 1992) is most likely due to the high hydraulic activity and the deep root system of *P. halepensis* which enables it to make use of deep soil water reserves (Borghetti et al., 1998). The continuation of LW production also in late November is most likely favoured by wet conditions and mild temperatures in autumn as found in a previous study (Camarero et al., 2010).

The decrease of EW and LW production rates in July and August-September respectively, indicates that *P. halepensis* reduces tracheids formation when precipitation deficit surpasses a functional threshold. As a matter of fact, this relationship was also observed in the responses of EW and LW growth to long SPI time-scales, indicating that there may be a synchronized response of intra and inter-annual growth in this species to drought conditions. This response to drought stress might be linked to the physiological and growth adjustments of *P. halepensis* to cope with the scarcity of soil water, including a decline in phtosynthesis rates, carbon uptake, needle elongation and wood formation as shown previously (Borgetti et al., 1998; Camarero et al., 2010).

At the inter-annual scale, the regression analyses indicated that EW and LW series are responding to the limitations imposed by the climatic factors as shown by the relatively high values of adjusted R^2, particularly in the case of EW series. Comparing EW and LW chronologies, the former showed a greater year-to-year variability (MSx) and a higher tree-to-tree common variance (Rbar) than the later did. However, the EW and LW series presented a strong within-ring correlation indicating certain dependence of LW formation on previous EW growth. In general, the EW and LW chronologies of the nine sampled sites showed a strong common signal related to climatic factors, mostly in response to spring and early summer rainfall amounts. This is particularly the case of EW, whose formation in *P. halepensis* sites from semi-arid areas usually peaks in that period. This means that water availability in the period when the maximum rates of EW tracheid formation occur is among the most critical factors for radial growth with cascading effects on water conduction and carbon uptake. An improved production of EW tracheids with wide lumens in response to wet spring conditions may result in an increase of hydraulic conductivity and photosynthesis leading to the synthesis of more carbohydrates for LW formation in summer and autumn (Camarero et al., 2010).

The positive (negative) correlation between EW growth and April, May and June precipitation (maximum temperatures) suggest that this growth component of the ring may be very susceptible to water deficits during the early part of the growing season. High temperatures increase water deficit which affects photosynthetic and tracheid division rates, constraining radial growth (Hsiao, 1973; Linares and Tiscar, 2010; Vicente-Serrano et al., 2010a). The high sensitivity of EW to maximum July temperatures indicates that growth decline of the study species may be caused by warming-induced drought stress. On the other hand, the positive association of EW growth with

December and January minimum temperature and precipitation suggests that warm minimum (night) temperatures and wet conditions in winter can favour an earlier and longer growing season for *P. halepensis* as reported previously (De Luis et al., 2007; Camarero et al., 2010). The only explanation found for the significant positive influence of January minimum temperatures on LW development is based on a direct improvement of EW formation leading to an indirect LW enhanced growth. This indicates that the LW growth in *P. halepensis* is not only determined by weather conditions during the wall thickening process, mainly occurring in summer and autumn (Camarero et al., 2010), but it may be also modulated by the previous EW growth rates as shown by the high correlation between them.

The strong sensitivity of EW and LW growth to cumulative drought stress in July and September, respectively, indicates that summed (10-14 months) precipitation amounts during those periods are crucial for the development of both components of the tree ring. The EW growth appeared to depend more on water availability than LW did, showing two distinct patterns in terms of growth sensitivity to drought in *P. halepensis*. These patterns varied among sites indicating changing growth responses of *P. halepensis* EW and LW growth to different rainfall regimes at local scales. For instance, there was variability in terms of the EW and LW responses to drought when comparing the less xeric sites (TA, PU, MA, PL and MP) with the most xeric ones (VM, CV, CS, VA) showing a more intense and prolonged impact of drought on the formation of both wood types in the later as compared with the former sites. The higher impact of drought on EW growth as compared to the LW was also confirmed by the SEA analysis which clearly indicated significant EW growth reduction in most sites during the year of drought occurrence, a pattern that was not observed in the case of LW. The growth of both components during the two years after selected droughts did not significantly decrease, most likely due to soil water recharge after the drought event in those site. There was an exception to this in site VA, where drought negatively impacted LW production one year after the drought occurrence, possibly because of lagged effects on carbohydrates synthesis and growth or due to a poor water-holding capacity of soils.

P. halepensis is considered as a drought-avoiding species (Ferrio et al., 2003) but its inter-annual growth is very sensitive to lasting and severe droughts as our results support. Moreover, the vulnerability to drought may be aggravated by the soil types (e.g., aridisol, entisol) which may additionally intensify the negative effects of drought on *P.halepensis* growth. In the study area, a pronounced decline in winter and spring precipitation has also been observed during the late 20th century (González-Hidalgo et al., 2009) which has negatively influenced the EW formation, leading to denser wood, i.e. with less EW in relative terms, and thus causing a reduction in hydraulic conductivity but increasing the resistance to drought-induced xylem cavitation (Eilmann et al., 2011). Even if drought-stressed pines are able to form tracheids with wider lumens than non-stressed ones as it was shown by Eilmann et al. (2011), the production of less EW will undoubtedly induce a decrease in hydraulic conductivity, leading to local growth declines in the long term and reduction in carbon uptake at regional scales.

It is concluded that although *P. halepensis* is considered among the most drought-resistant Circum-Mediterranean conifers, its seasonal wood formation appears to be driven negatively by mid-term cumulative drought stress in semi-arid areas. In the short term, these influences were associated with a reduction of tracheid production, whereas in the long term they caused declining EW and LW formation. Therefore, under expected decreased winter and spring water availability in a warmer future world as predicted for continental areas in the Western Mediterranean Basin (IPCC, 2007), the studied forests may show a more intense reduction in the production of EW tracheids than in the case of LW ones. This selective reduction in EW formation may lead to several cascading effects, namely a decline of radial growth (including LW formation), a reduction in hydraulic conductivity and, indirectly, a hampered carbon uptake under semi-arid conditions.

3.4. Factors driving growth responses to drought in Mediterranean forests

Introduction

Warming-related water deficit is one of the major drivers of growth dieback and related mortality episodes in forests, affecting selectively tree species, stands and trees (Allen et al., 2010; Koepke et al., 2010). Drought causes reductions in radial growth, alterations in hydraulic conductivity (McDowell et al., 2008) and decreases productivity due to limitations in water use and photosynthesis (Hsiao, 1973; Flexas and Medrano, 2002). These effects are enhanced particularly in Mediterranean drought-prone forests where water availability is the main factor constraining growth (Pereira and Chaves, 1995; Vicente-Serrano et al., 2006; Sarris et al., 2007, 2011; Linares et al., 2009, 2010).

Different studies evidence that our understanding of the drought impact on growth of tree species at different time scales and across contrasting site conditions is still very limited (Orwig and Abrams, 1997; Adams and Kolb, 2005). Usually, radial growth of tree species and populations growing in xeric sites is more affected by drought than in mesic locations (Abrams et al., 1998). However, other researchers argued that species growing in xeric sites show adaptive features to withstand the negative effects of drought (De Luis et al., 2007; Mc Dowell et al., 2008; Linares et al., 2010). This implies that the drought-adapted species may be less vulnerable against drought stress, in terms of growth, than species inhabiting wet sites.

The lacking information regarding factors driving the spatial and temporal patterns of growth responses to drought may be partially obtained by quantifying growth trends across environmental and climatic gradients. Growth responses to drought can vary as a function of species’ responsiveness to water deficit (Orwig and Abrams, 1997; Bogino and Bravo, 2008), site features (Tardif and Bergeron, 1997; Macias et al., 2006; Linares and Tíscar, 2010), and characteristics of trees (size, age, competition, genetic differences) (De Luis et al., 2009; Kuparinen et al., 2010; Linares et al., 2010).

In Circum-Mediterranean forests, several studies have emphasized that the inter-annual variability of precipitation and drought occurrence are among the main constrains of tree growth (Andreu et al., 2007; Sarris et al., 2011). However, previous studies in mountain forests also found that the regional climatic conditions can be greatly modulated by site features such as elevation or topography (Rolland et al., 1999; Tardif et al., 2003). These local factors may impose additional risks exacerbating drought stress (e.g., rocky soils or steep slopes) or they may partially mitigate its negative effects on tree growth (e.g., deep soils or northern aspects). For instance, water deficit has been linked to growth decline of tree populations mainly located in xeric sites (Martínez-Vilalta and Piñol, 2002; Camarero et al., 2011).

This study aimed: (i) to describe the spatio-temporal growth responses to drought across a wide climatic gradient in north-eastern Spain (see Figure 27) and (ii) to detect the main drivers influencing these responses. The study included eight tree species with contrasting sensitivity to drought stress ranging from pine species in semi-arid areas (e.g., *Pinus halepensis*) to fir species dominating wet sites (e.g., *Abies alba*), thus providing a wide ecological gradient representative for many Mediterranean forests.

Methodology

Dendrochronological methods

The dendrochronological methods involved in this study are explained in details in section 2.2.

Drought index calculation

The procedure followed for the drought index calculation is explained in the section 3.2.

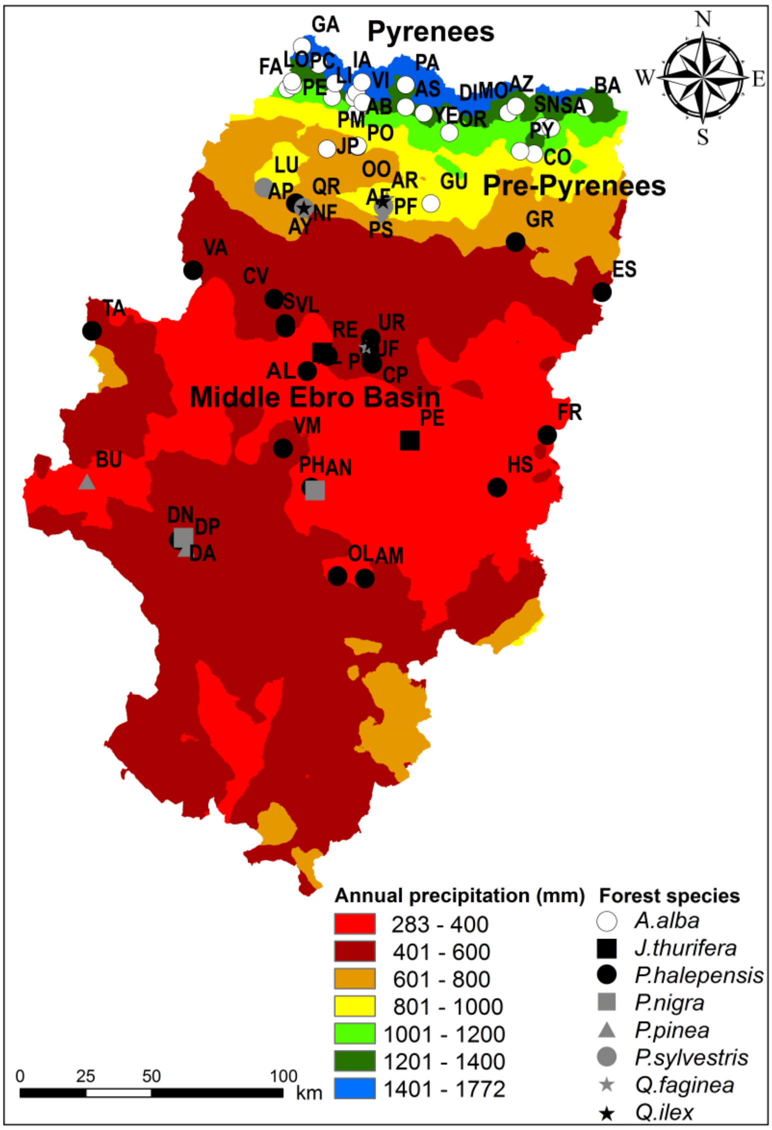

Figure 27. Location of sampled sites and annual precipitation values in Aragón, north-eastern Spain. Different symbols and colours represent different tree species and precipitation ranges, respectively. The three sub-areas studied (Pyrenees, Pre-Pyrenees and Middle Ebro Basin) are also indicated in the map. Sites codes are as in Table 1.

Factors affecting growth-drought responses: climate, topography, remote sensing data

In this section are introduced the variables considered as possible drivers of the spatial differences of growth responses to drought and their method of preparation for the analysis. In particular, climatologies for different variables obtained from the digital climatic atlas of Aragon at a spatial resolution of 1 km (Cuadrat et al., 2007) were employed. The climatic variables used in the study were: annual water balance, annual precipitation, annual potential evapo-transpiration, annual mean maximum temperature, annual mean minimum temperature, July mean maximum temperature, January mean minimum temperature and solar radiation. The incoming solar radiation, which provides information on the slope aspect was obtained using a terrain model (Pons and Ninyerola, 2008) implemented in the MiraMon Geographical Information System (Pons, 2011). For each sampled forest the average value of these variables was extracted.

The topographic data consisted of the following variables: elevation (m) and slope (%) derived by using a DTM of the area with a spatial resolution of 100 meters. The soil types were determined by using the Spanish soil map developed by the Spanish Geographic Institute following the Soil Taxonomy of the USDA (IGN, 2006). They included the following soil types: inceptisol, entisol and aridisol. The inceptisol soils are found mostly in the mesic areas (Pre-Pyrenees and Pyrenees) and are characterized by a generally developed soil horizont, with organic matter and relatively high capacity to store water in the deeper layers. The entisol and aridisol soils are distributed mainly in xeric areas (Middle Ebro Basin) and are generally shallow, with low organic matter on the surface and limited water holding ability.

Remote sensing data were used to evaluate the potential roles of the differences in leaf activity and leaf-area index in explaining the spatial variability in the growth responses to drought in each forest. In particular, time series of NDVI and EVI covering the period 2000-2010 were used in the study. The mean annual and April-June (period with the highest forest activity; see Vicente-Serrano et al., 2010a) NDVI and EVI values were calculated and used in further analysis.

Statistical analyses

The spatial variability of growth responses to the drought index (SPI) was analyzed by using a S-mode principal component analysis (PCA). Initially, a matrix of the correlations between the 1-48 time scales SPIs and the residual ring-width chronologies for all sites was prepared. The matrix was organized in a way that columns corresponded to a particular forest site and the rows indicated the specific correlation coefficient associated with that site at a particular time scale (ascending order 1-48) and month (1-12). Subsequently, the PCA was performed on a covariance matrix calculated from the correlation series mentioned above. The number of components was selected based on the criterion of eigenvalues greater than 1, and they were rotated (Varimax) to redistribute the final explained variance and to obtain more stable and robust spatial patterns (Richman, 1986). Components were presented in the non-standardized original units to make the interpretation easier, by using the coefficient scores of each principal component. In other words, the PC scores were converted to correlation values, summarizing the correlation series at all forest sites. The geographical variability in terms of forest response to drought was identified by mapping the factorial loadings.

To detect the factors which potentially affect the growth responses to drought, correlation and regression analysis were carried out between the PCs loadings and a set of abiotic (climatic and topographic variables, soil type) and biotic (Dbh, mean tree-ring width for the period 1970-1999, NDVI and EVI) variables. Categorical variables, like the soil type, were converted to binary variables to be included in the regression analyses. The importance of each variable was assessed by using a forward selection method which starts with no variables in the model, trying out the variables one by one and including them if they are significant ($p \leq 0.05$).

Results

Spatial patterns of the growth responses to drought

In this section are presented the spatial patterns of growth responses to drought as revealed by the PCA analysis. In particular, it was found that the first two components of the PCA accounted for 75.1 % (PC1, 41.3%; PC2, 33.8%) of the total amount of the growth responses to drought variability. The PCs correlation coefficients, summarizing the species' growth responses to drought at xeric and mesic areas, showed that tree species associated with the first principal component (PC1) presented significant correlations ($r > 0.29$) at all time scales, with the highest ones ($r > 0.80$) achieved at time scales ranging between 9 and 12 months, during summer months (Figure 28). The second principal component (PC2) captured significant growth responses to drought at 2-5 months scales, again during summer.

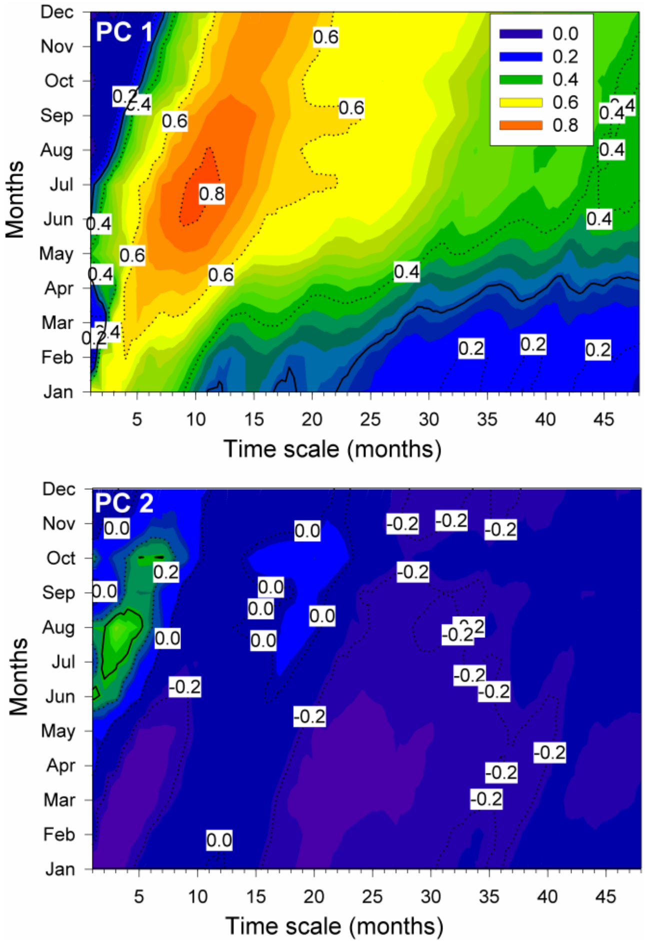

Figure 28. First (PC1) and second (PC2) principal components summarizing the correlations between all ring-width chronologies and monthly drought (Standardized Precipitation Index, SPI) series at different time scales. Bold lines frame significant correlations ($p \leq 0.05$).

The spatial distribution of the loadings of the PC1 and PC2 components shows two clear spatial patterns of responses to drought across the study area (Figure 29). The first pattern represented by PC1 was found in the southern part of the study area (Middle Ebro Basin), while the second one described by the PC2 corresponded to the northern study area (Pyrenees). The PC loadings of each forest indicated that the highest contribution to the PC1 variability was accounted for by species growing in xeric locations such as *P. halepensis*, *P. nigra*, *P. pinea*, *J. thurifera*, *Q. faginea* and *Q. ilex*. On the other hand, the PC2 captured the growth responses to drought expressed by species located in sub-Mediterranean and mesic sites (*A. alba, P. sylvestris)*.

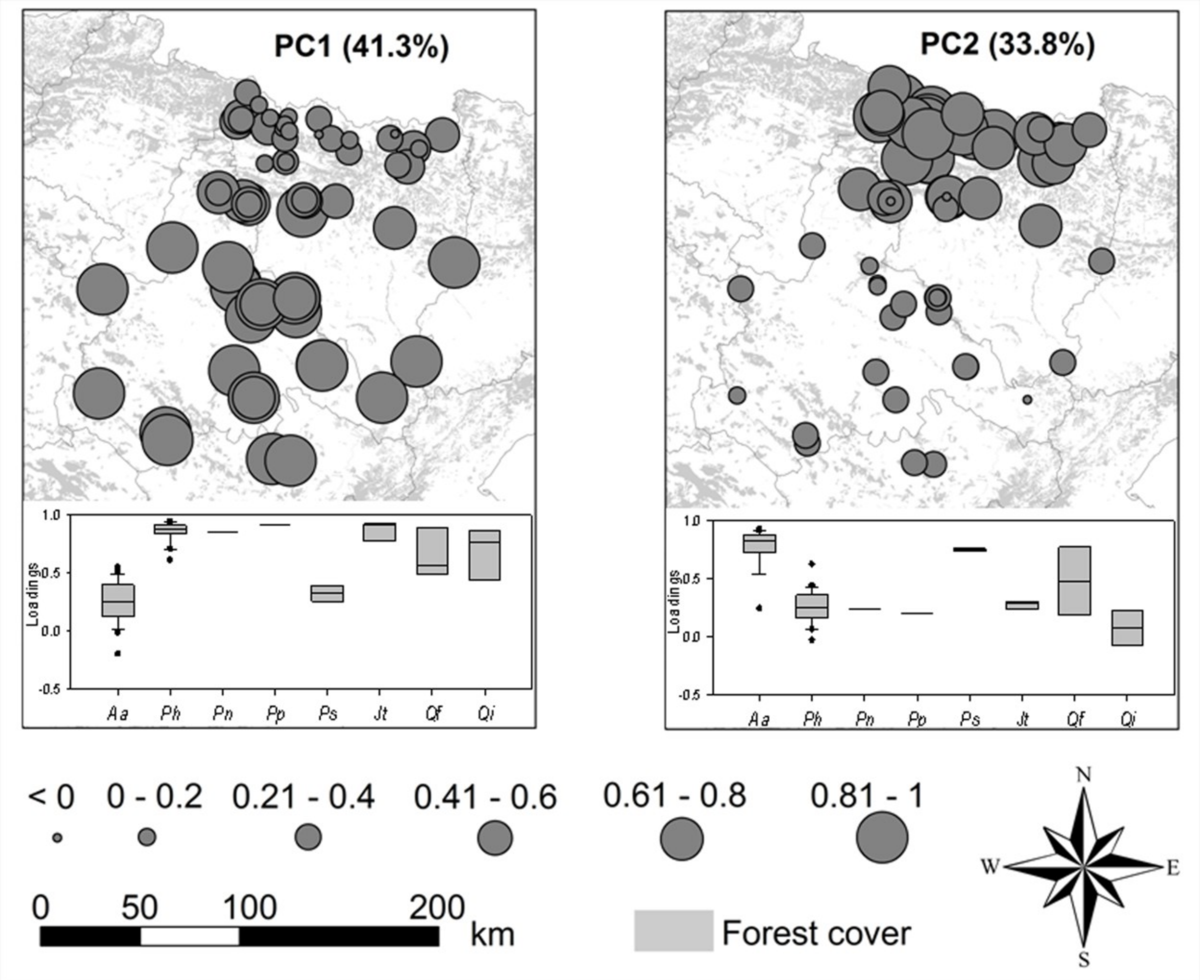

Figure 29. Spatial patterns of species' growth responses to drought as revealed by the loadings of the first (PC1) and second (PC2) principal components (upper graphs, the size of circles is proportional to the loadings) and within-species variability of these responses (lower graphs; box plots of species loadings in the two principal components, PC1 and PC2 respectively). Species codes: *Aa*, *Abies alba*; *Ph*, *Pinus halepensis*; *Pn*, *Pinus nigra*; *Pp*, *Pinus pinea*; *Ps*, *Pinus sylvestris*; *Jt*, *Juniperus thurifera*; *Qf*, *Quercus faginea*; *Qi*, *Quercus ilex*.

Drivers of the growth responses to drought

In this section are shown the factors influencing growth responses to drought in the studied forests. Firstly, here are presented the correlations between the growth responses to drought summarized by PC1, PC2 and the abiotic and biotic variables involved in the analysis. Secondly, here are shown the results of the regression analysis which identify the main drivers of forest growth responses to drought.

The associations between abiotic and biotic variables and the two first principal components (PC1, PC2) summarizing the growth responses to drought indicated that tree-related (DBH, tree-ring width), remote-sensing (NDVI, EVI), climatic (water balance, precipitation) and topographic variables were significantly (*p*<0.01) and inversely correlated with the PC1 (Table 9).

Table 9. Significant (*p*<0.01) correlations between explanatory variables and the first two principal components (PC1, first component; PC2, second component) summarizing the growth responses to drought.

Type of variables	Explanatory variables (abbreviation, units)	PC1	PC2
Tree variables	Diameter at breast height (DBH, cm)	-0.70	0.63
	Tree-ring width (TRW, mm)	-0.46	0.44
Remote-sensing variables	Annual NDVI (NDVI)	-0.73	0.64
	Annual EVI (EVI)	-0.66	0.62
	April-June NDVI (AJ NDVI)	-0.78	0.71
	April-June EVI (AJ EVI)	-0.71	0.71
Soil variables	Inceptisol soil (IS)	-0.72	0.72
	Entisol soil (ES)	0.56	-0.53
	Aridisol soil (AS)	0.30	-0.27
Climatic variables	Annual water balance (WB, mm)	-0.85	0.78
	Annual precipitation (AP, mm)	-0.85	0.75
	Annual potencial evapotranspiration (PET, mm)	0.64	-0.65
	Mean maximum annual temperature (AMxT, ºC)	0.80	-0.70
	Mean minimum annual temperature (AMiT, ºC)	0.79	-0.67
	July mean maximum temperature (JMxT, ºC)	0.79	-0.70
	January mean minimum temperature (JMiT, ºC)	0.74	-0.61
	Incoming solar radiation (R, W m^{-2})	0.38	-0.48
Topographic variables	Elevation (E, m)	-0.78	0.66
	Slope (S, %)	-0.70	0.54

Most climatic variables (potencial evapotranspiration, mean maximum and minimum temperatures, July mean maximum and January mean minimum temperatures, solar radiation) were negatively related to the PC2. The PC1 was mainly driven by water availability, temperature and elevation, while the PC2 was also strongly associated to these variables and to NDVI and EVI data. The regression analysis indicated that four variables (annual precipitation, inceptisol soils, April-June NDVI and slope) explained 78% of the total spatial variability accounted for by the PC1 and three variables (annual water balance, April-June EVI and inceptisol soils) determined 66% of the variance represented by PC2 (Table 10). The coefficients of the selected regression models (Table 11) showed that the main variable driving growth responses to drought in xeric sites represented by PC1 was annual precipitation ($p < 0.003$), followed by soil type (inceptisol), April-June NDVI and slope.

Table 10. Selected regression models explaining the patterns of the first (PC1) and second (PC2) principal components of growth responses to drought for all species and corresponding statistics (R^2adj, adjusted percentage of variability explained by models; *F*, *F*-ratio, *p*, probability level). The PCs were calculated from the matrix of correlations obtained between the 1-48 months drought index (Standardized Precipitation Index, SPI) and the residual ring-width chronologies. Abbreviations are as in Table 9.

Response variables	Explanatory variables	R^2adj (%)	*F*	*p*
PC1	1.240-0.001 AP-0.142 IS-0.471 AJ NDVI-0.002 S	77.7	58.44	<0.0001
PC2	0.064 + 0.001 WB + 1.245 AJ EVI + 0.163 IS	65.8	43.42	0.0001

Considering PC2, the main driver of growth responsiveness to drought was the annual water balance ($p < 0.002$), whereas April-June EVI and soil type (inceptisol) were less important. The partial correlations between the PCs and each predictor of the regression models were significant ($p<0.05$) when the effect of the other independent variables was accounted for, suggesting that the growth responses to drought in xeric and mesic sites were mainly driven by precipitation and the water balance, respectively.

Table 11. Statistics of the coefficients of the selected regression models (see Table 10) explaining the patterns of the first (PC1) and second (PC2) principal components of growth responses to drought for all tree species.

Model	Variable	Student *t*	*p*	Partial correlation
PC1	Constant	15.094	<0.0001	
	Annual Precipitation	-3.038	0.003	-0.360
	Inceptisol	-2.62	0.011	-0.316
	April - June NDVI	-2.152	0.035	-0.264
	Slope	-2.091	0.041	-0.257
PC2	Constant	0.417	0.678	
	Annual Water Balance	2.452	0.002	0.295
	April-June EVI	2.884	0.008	0.341
	Inceptisol	2.482	0.017	0.299

In fact, the PC loadings and the most important drivers of growth responses to drought confirmed the high dependence of the growth responsiveness on annual precipitation in xeric sites (Figure 32). The variability in the responses to drought of mesic forests characterized by the PC2 was driven by the annual water balance.

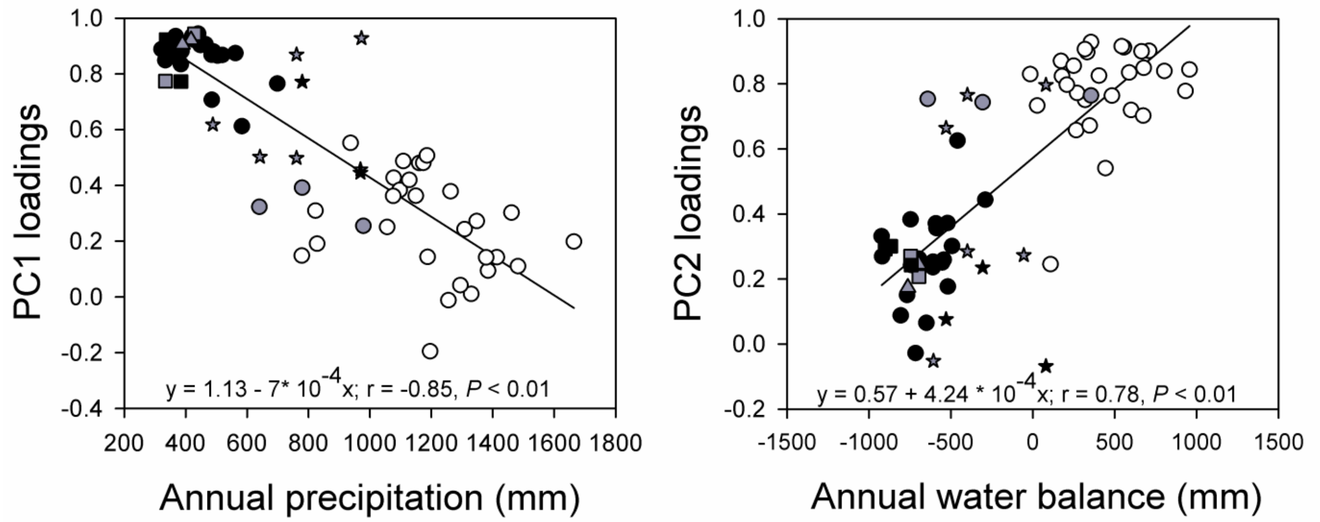

Figure 32. Scattergram of the loadings of the first two principal components and the main predictor variables as revealed by linear regressions (see Table 11). The different symbols in the graphs correspond to different species (white circles, *A. alba*; black squares, *J. thurifera*; black circles, *P. halepensis*; gray squares, *P. nigra*; gray triangles, *P. pinea*; gray circles, *P. sylvestris*; gray stars, *Q. faginea*; black stars, *Q .ilex*)

Discussion

In this study are evaluated the growth responses to drought and factors driving such responses in eight tree species growing across a wide climatic gradient, by means of dendrochronological methods and a quantitative assessment of drought at different time scales based on the multi-scalar Standardized Precipitation Index (SPI). This is the first investigation evaluating the factors responsible for the variable growth responses to drought in diverse Mediterranean forests. Particularly, it was investigated the role of biotic and abiotic variables at modulating the spatial and temporal variability within and among species in the growth responsiveness to drought focusing on contrasting environmental conditions in xeric and mesic sites.

The PCA analyses revealed two distinct spatial patterns in terms of growth response to drought across the study area corresponding to: (*i*) species growing in the Middle Ebro Basin (represented by PC1) under Mediterraneand semi-arid conditions (all *Pinus* species except *P. sylvestris*, *Quercus* species, and *J. thurifera*) and (*ii*) species distributed in mountainous areas (represented by PC2), from the Pre-Pyrenees and Pyrenees (*A. alba*, *P. sylvestris*) characterized by a humid and cold sub-Mediterranean climate.

The regression analyses showed that the annual precipitation is the main driver of forest growth sensitivity to drought in xeric sites indicating that in dry Mediterranean forests tree growth is mainly constrained by low water availability (Borghetti et al., 1998; De Luis et al., 2007; Vicente-Serrano, 2007; Camarero et al., 2010). This has been also confirmed by additional studies on growth and phenology of pine and oak species in nearby areas (Corcuera et al., 2004a,b; Andreu et al., 2007; Montserrat-Martí et al., 2009; Gutiérrez et al., 2011; Pasho et al., 2011a,b). In general, these studies found important spatial variations in the growth responses to drought of forests as a function of climate conditions, confirming that forests located in the driest sites are the most sensitive to drought occurrence and severity. Furthermore, these results suggest that growth declines in xeric areas, and plausibly dieback events and episodes of high mortality as those reported by Allen et al. (2010), will be observed in response to long-term dry conditions greatly reducing the water balance.

Contrastingly, it was found that even short-term summer drought, lasting between two and six months, can affect radial growth of mountain conifers from mesic sites such as *A. alba*. This association may be explained by the low water-use efficiency of *A. alba*, which is a species whose photosynthetic rates are very sensitive to atmospheric drought (Guehl et al., 1991) and its growth rates respond to cumulative water deficit in late summer and to temperature-related drought stress (Rolland et al., 1999; Camarero et al., 2011).

The growth responses to drought of mountain forests from mesic and wet sites such as Pyrenean silver fir forests was also determined by a combined influence of several drivers, with the most significant impact exerted by annual water balance and temperature variables. In mountain conifer forests, high temperatures can enhance evaporation rates which additionally decrease moisture content in the upper layers of the soil and reduce water reserves, influencing so the soil water balance negatively (Pichler and Oberhuber, 2007). Short-term warming-induced water deficits during late summer may cause growth decline and dieback of *A. alba* forests (Camarero et al., 2011). Therefore, growth declines in silver fir forests located in the less humid sites may be expected in response to warming-induced short term drought stress (Macias et al., 2006). In addition, the low temperatures in winter also affect growth responses to drought in mesic silver fir forests because they may cause frost-induced xylem embolism and reduce photosynthesis (Rolland et al., 1999, Aussenac, 2002).

The contribution of each site to the respective first two principal components was different, indicating a site- and species-dependent variability in terms of growth responses to drought (Orwig and Abrams, 1997). The species' responsiveness to drought seems to be conditioned by contrasting climatic conditions and local variability in soil water holding capacity. For example, Sánchez-Salguero et al. (2010) showed a more intense growth reduction of *P. pinaster* and *P.halepensis* in response to extreme droughts in xeric than in wet sites in south-eastern Spain. This is in line with the findings of Fekedulegn et al. (2003) who stressed that forest responses to drought may be affected by a combination of many factors including precipitation, temperature, inherent species' characteristics and site topographic features. These factors may impose additional constrains on the growth responses to drought. As revealed in this study, the growth sensitivity to drought was also affected by soil and topographic conditions. For instance, the soil types (aridisol and entisol) that characterize xeric environments in the study area enhance the negative effects of water deficit on growth since these soils are generally shallow, characterized by limited ability to hold adequate moisture (Guerrero et al., 1999; Vicente-Serrano, 2007), which increases the negative effects of drought on tree growth. In the Pyrenees, the dominant soils (e.g., inceptisol) had an inverse association with the growth responsiveness to drought, suggesting the presence of mitigating effects of the negative impacts of water deficit on growth, most likely due to the high capacity of these soils to hold water in the deeper layers. This is the case of many *A. alba* forests located in valley bottoms of the Pyrenees, characterized by deep soils and humid climatic conditions (Macias et al., 2006; Camarero et al., 2011).

In addition, it was expected that topographic factors such as elevation and slope would exert contrasting influences on the species responses to drought in xeric and mesic forest sites, respectively. However, it was found that the growth responses to drought were only affected by slope in the case of xeric sites (PC1), most likely due to its local influence on surface runoff and water retention by soils. The studied forests in xeric sites, mostly located in low elevation but topographically complex areas (plain localities have been mostly converted to croplands), grow under an exacerbated drought stress in undulating or moderate slopes since in these areas trees are more sensitive to the rapidly occurring water shortages (Fekedulegn et al., 2003). It is known that topographic position drives the soil water availability in areas subjected to seasonal droughts affecting tree growth and the species composition of diverse ecosystems as tropical forests (Engelbrecht et al., 2007).

Xeric sites are also characterized by low precipitation and high temperatures which enhance the drought impacts on growth (Camarero et al., 2010). In these areas, high temperatures in summer most likely deplete soil water reserves causing drought-induced embolism. Slope and aspect can also influence growth locally through changes in the radiation received by trees (Tardif et al., 2003; Leonelli et al., 2009). Generally, south facing slopes in xeric areas with low water holding capacity increase the drought impacts on tree growth (Sánchez-Salguero et al., 2010). The opposite was observed in *A. alba* forests located in north-oriented slopes with deep soils. Overall, topography acts as a local modulator of the effects of drought on growth but further research on this subject in Circum-Mediterranean forests is desirable.

The tree features such as tree size (diameter) or the growth rate (mean tree-ring width) and vegetation activity indices (NDVI, EVI) showed positive and negative associations with the growth responsiveness to drought in xeric and mesic sites, respectively. These associations indicate that low water availability associated with prolonged and intense drought lead to a decrease of the canopy growth (e.g., shoot extension, leaf production) and probably a decline in photosynthetic activity causing a reduction in cambial activity and hydraulic conductivity (Corcuera et al., 2004a,b; Linares et al., 2009; Montserrat-Martí et al., 2009; Vicente-Serrano et al., 2010a). Such growth decline may further enhance the species' vulnerability against drought stress.

In conclusion, the study highlights that Mediterranean forests show high spatial and temporal variability in terms of growth responses to drought. This variability observed among species and sites was significantly driven by climatic, topographic and biotic variables, indicating that a combination of these variables shape the species' behaviour in response to drought. Since climate models predict rising temperatures and enhanced evapotranspiration for the Mediterranean Basin, the findings suggest that warming-related drought stress might affect growth dynamics on different time scales in mesic and xeric forests. However, disentangling the relative effects of warmer conditions and reduced precipitation on tree growth is an unsolved challenge which probably requires a multiproxy approach based on long-term data of radial growth, isotopic discrimination in wood and remote-sensing variables.

CHAPTER IV

GENERAL DISCUSSION AND CONCLUSIONS

In this chapter, the main findings of the study are discussed, providing explanations, supported also by the relevant literature, on the responses of the studied forests to climatic drivers and drought as well as the factors modulating these responses. In addition, in this section of the thesis, the main conclusions based on the results obtained are also presented and, finally, the lines for future research are indicated.

4.1. General discussion

This study provided evidence on the influence of climatic drivers and drought on the spatio-temporal variations of tree growth across a wide climatic gradient in eastern Spain. With respect to the climatic drivers, it was found a very clear spatial gradient in the influence of large-scale atmospheric circulation patterns on *P. halepensis* EW and LW growth. The geographical structure detected in the growth of both components in this species was associated with two particular spatial patterns of atmospheric circulation affecting the study area, namely those represented by the NAO and WeMO indices. NAO and WeMO variabilty determined the spatial patterns of forest growth in northern and southern areas respectively, providing strong evidence that tree growth variability in the region do not only respond to the surface climatic variables such as temperature and precipitation, whose associations with tree-ring width have been well-established (Andreu et al., 2007; Martínez-Vilalta et al., 2008), but also to large-scale atmospheric drivers. The influence of NAO and WeMO indices on the spatially structured EW and LW growth patterns in *P. halepensis* forests was expressed indirectly through their control of precipitation patterns and the local weather types which also drove surface climate variability, particularly precipitation. The later suggestion was confirmed by the strong negative connection found between winter NAO and WeMO indices and the frequency of SW, W, SE and E weather types which are known to be associated with high precipitation events in northwestern and southeastern areas of the Iberian Peninsula respectively (Corte-Real et al., 1998; Martín-Vide, 2002; Vicente-Serrano and López-Moreno, 2006).

The geographical structure of both EW and LW growth patterns in terms of spatial variability, reflected a geographically structured response of the surface precipitation to the atmospheric variability associated mainly with winter NAO and WeMO indices. Both NAO and WeMO indices were negatively associated with winter-spring precipitation, the later positively correlated with both components of the tree growth, indicating the dependency of EW and LW development on moisture reserves supplied during these seasons. This is particulary the case of the

P. halepensis forests growing in semi-arid areas of north-eastern Spain which responded significantly to the influences of surface climatic variables, indicating a positive relationship of EW and LW with previous winter precipitation and a negative one with warm summer temperatures. The strong positive association, particularly with spring precipitation, is related to the maximum EW growth rate which occurs in this season as evidenced by the xylogenesis analysis performed in this study and in previous ones (De Luis et al., 2007; Camarero et al., 2010). However, the summer temperatures constrained the EW growth in *P. halepensis*, suggesting that high temperatures associated with a decrease in precipitation may impose drought stress and growth declines in this specie. This was also confirmed by the high drought impact during summer months on the tracheid production rate of *P. halepensis*. The unexpected dependency of LW growth on the winter-spring precipitation may be caused by an enhancement of EW formation leading to an indirect LW improved growth. The later component also showed high dependency to the autumn precipitation particularly in the southern sites, under the negative WeMO phase. Therefore, the forecasted trend of increasing winter anticyclonic conditions and reduced activity of westerlies (high NAO values) are expected to reduce EW production in northwestern sites, whereas an increase of autumn cyclonic Mediterranean conditions (low WeMO indices) will enhance LW formation in southeastern sites. Since the atmospheric variability affects the precipitation patterns in the region, it can indirectly control the physiological processes that determine tree growth, which are strongly connected to water availability (Andreu et al., 2007). Therefore, the drought impact on growth will be particulary negative for the northwestern sites, since water stress conditions are more frequent under positive NAO conditions (Vicente-Serrano and Heredia-Laclaustra, 2004), causing a reduction of photosintetic activity and production of carbohydrates which is associated with a decreased growth during spring and early summer (Kagawa et al., 2006; Roig et al., 2009). Contrarily, the WeMO is mostly affecting the southern sites and this index is associated with high precipitation amounts (Martín-Vide and López-Bustins, 2006; González-Hidalgo et al., 2009), leading to enhanced growth in those coastal areas.

The analysis of drought-growth associations for the studied forests in north-eastern Spain confirmed that the increasing drought occurrence under the NAO influence is highly affecting tree growth in these areas. As a matter of fact, the study indicated marked spatial variations in the response of forests to drought as a function of water availability indicating two patterns with contrasting growth responses to accumulated water deficits. The large spatial differences to different time-scale drought found between forests growing in the mesic sites (*A. alba*, *P.sylvestris*) and xeric locations (all *Pinus* species excepting *P. sylvestris*, *Quercus species, J. thurifera)* indicated contrasting growth responses and different physiological thresholds to water deficit. The species growing in the most arid sites, although adapted to short-term droughts (<9 months), showed functional growth thresholds in response to mid- (10-14 months) and long-term (> 14 months) droughts during summer, indicating that forest growth variability in these areas is controlled by the accumulated precipitation amounts since the previous year of the tree ring formation up to current summer. In addition, considering that the highest impact of drought on growth was detected in summer months, evidences how important is water availability during the late growing season for tree radial growth. A different pattern was observed for the conifers from mesic locations, which responded to short-term (<5 months) droughts, demonstrating the low water-use efficiency of these species, as compared with those from xeric sites, and thus a high sensitivity to available water in spring and summer. Although these forests are located in mountainous areas, which receive relatively high precipitation amounts in comparison to xeric locations and which currently do not suffer from long-term drought most likely due to the more rapid soil water recharge, they may be affected severely by strong and lasting droughts in the future, followed by growth decline and mortality episodes as reported previously in several studies (Martínez Villalta and Piñol, 2002; Sánches-Salguero et al., 2010; Camarero et al., 2011).

Important findings of this study were the large inter- and intra-specific differences found to the time scales over which cumulative precipitation deficits affected forest growth in the study area, indicating that apart from the physiological adaptations of species to deal with drought, other factors as well may be involved in determining the spatial variations in tems of growth responses to drought. As a matter of fact, the analysis indicated that not a single factor but a combination of climatic, topographic, and biotic variables shaped the species' behaviour in response to drought. All these factors exerted contrasting influences on growth responses to drought in xeric and mesic sites, being either constrains or mitigators of growth responses to drought. In this regard, although in xeric forests the mean precipitation was the main factor driving growth responses to drought, other factors such as soil types (limestone and gypsum) characterized by low water holding capacity (Guerrero et al., 1999; Vicente-Serrano, 2007) and high temperatures aggravated the negative impacts of drought on tree growth. In mesic sites, although precipitation was an important driver, other factors such as temperature had a significant effect on growth responses to drought. The most plausible involvement of temperature as a mitigating factor controlling growth responses to drought in these locations is in interaction with high precipitation amounts, influencing so positively the photosintetic activity and therefore enhancing growth (Martínez-Vilalta et al., 2008; Vicente-Serrano et al., 2010a). Apart from the climatic factors, soil type also influenced the tree growth responses to drought in mesic sites. In this regard, the inceptisol soil type mitigated drought impacts on growth in these areas, most likely due to the high capacity of these soils to hold water in the deepest soil layers. With regard to the topographic factors, slope was the most important driver having contrasting effects on growth responses to drought in semi-arid areas and humid locations respectively. These effects might be expressed in combination with other factors such as elevation, aspect, soil type etc, which, depending on the situation, may favour or constrain forest growth and exacerbate or mitigate the drought effects on growth.

In the context of future climate projections (IPCC, 2007), which show a trend towards warmer conditions and less precipitation in the next century for the Circum-Mediterranean region as related to an increased frequency of anticyclonic conditions (Giorgi and Lionello, 2008) and a decreased frequency and intensity of Mediterranean cyclones (Raible et al., 2010), the future growth and distribution of the studied tree species is expected to be modified as a consequence of subsequent pronounced decrease in growth and frequent die off events (Andreu et al., 2007; Camarero et al., 2011). It is well known that environmental and climatic conditions strongly influence species distribution patterns locally and regionally (Hawkins et al., 2003). As a matter of fact, this research provided evidence about the influence of climatic stressors, drought and site related factors on the spatial patterns of tree growth in the study area. The climatic drivers appeared to exert the strongest influence on growth, being one of the major challenges for forestry in the coming decades in the sense of managing climatic impacts on forest state, since they are expected to drastically modify growing conditions for trees (De Dios et al., 2007). Growth losses and decline will probably be greatest for trees on the limits of their natural distribution where a small change most likely will make the environment unsuitable for them. Therefore, some of the studied forests in the Iberian Peninsula will be particularly affected by climate changes since many European forest species reach their southern distributional limit in this area (Camarero et al., 2005; Linares et al., 2009). In particular, the mountainous conifer forests considered in this study (*A. alba* and *P.sylvestris*) growing near the species' climatic tolerance, will be more jeopardized by strong and lasting warming-induced drought stress (Macias et al., 2006; Camarero et al., 2011). The prediction towards more arid conditions will affect also species growing in the semi-arid areas (e.g., *P. halepensis*, *J. thurifera*, etc), which showed to be vulnerable to mid and long-term lasting droughts. Although these species show plasticity to cope with short-term droughts (< 9 months) and therefore predicted to lose less of their current distribuition area than species dominating mesic sites (Keenan et al., 2011), their growth and vitality are expected to suffer under long-term drought conditions as this study confirmed.

Therefore, active forest management is absolutely necessary to reduce global warming effects on tree growth and forest vitality (Allué-Andrade, 1995; Lindner, 2000; Montoya-Oliver, 2001). Without intervention and active management, it seems unlikely that many plant species in the region will survive a period of rapidly changing climate (Davis, 1989; De Dios et al., 2007; Benito-Garzón et al., 2008; Keenan et al., 2011). In this framework, new silvicultural techniques including also afforestation and reforestation with resistant genotypes (e.g., using seeds from drought-adapted stands) or species based on feedbacks from rapidly changing forest conditions are to be implemented for the future maintenance of Iberian forests. The observed influences of regional and local climatic conditions as well as prolonged droughts on the spatio-temporal patterns of tree growth in eastern Spain underlies the potential impact of climate change on future Iberian and European forests.

Future research lines

With respect to the influence of climatic drivers on *P. halepensis* growth, the results suggested the need for further study of EW and LW in dendrochronological networks of conifers growing under a wide range of climatic conditions, to provide critical information on the atmospheric drivers of tree growth and function. With regard to the drought impacts on forest growth and factors driving such response, the findings suggested the need for further investigation of drought impacts on forests under a wide range of climatic conditions to provide a current spatial analogue on the influence of drought on tree growth and function as well as the respective drivers.

4.2 Conclusiones

Las principales conclusiones de este estudio son las siguientes:

1. En relación a los factores de la circulación atmosférica que afectan al crecimiento de *P. halepensis* se encontró que:
    - El crecimiento de *P. halepensis* en el este de España estaba caracterizado por dos patrones espaciales diferentes que reflejaban la variabilidad del crecimiento de las maderas temprana y tardía en áreas septentrionales y meridionales. El crecimiento en las zonas septentrionales estaba principalmente influido por la NAO de invierno-primavera, mientras que en las zonas meridionales el crecimiento estaba controlado por el índice WeMO de invierno.
    - La influencia de los índices NAO y WeMO sobre la formación de las maderas temprana y tardía en *P. halepensis* se expresó de forma indirecta controlando la frecuencia regional de tipos de tiempo y de las condiciones climáticas de la superficie, principalmente la precipitación. El crecimiento en los sitios septentrionales estaba asociado positivamente con la frecuencia de tipos de tiempo del SW y W que están bajo la influencia de la NAO, mientars que en los sitios meridionales el crecimiento estaba asociado a tipos de tiempo del E y SE controlados por la variabilidad del WeMO.
    - Una precipitación elevada en invierno y primavera estimuló el crecimiento de las maderas temprana y tardía, mientras que la formación de madera tardía estaba favorecida por otoños húmedos. La influencia de la precipitación de invierno y primavera sobre el crecimiento de la madera tardía se expresó a través de una estimulación directa sobre el desarrollo de la madera temprana lo que condujo de forma indirecta a una mayor formación de madera tardía.

2. En relación al impacto de la sequía sobre el crecimiento de los árboles se encontró que:

- El uso de un índice de sequía multi-escalar (Índice Estandardizado de Precipitación) permitió detectar impactos de la sequía sobre el crecimiento dependientes de la escala temporal.
- Las especies de árboles de sitios xéricos (*Pinus halepensis, Pinus pinea, Pinus nigra, Quercus ilex, Quercus faginea, Juniperus thurifera*) respondieron principalmente a sequías de duración media y larga que persistieron de 9 a 12 meses, mientras que especies de sitios mésicos de los Pre-Pirineos y Pirineos (*Abies alba, Pinus sylvestris*) mostraron una respuesta a la sequía a corto plazo (1-5 meses). En todos los casos, la asociación máxima entre crecimiento y sequía se detectó durante los meses estivales.

3. En relación a los impactos climáticos y el control de la sequía sobre el crecimiento de *Pinus halepensis* se encontró que:

- La formación de madera temprana en *P. halepensis* respondió de forma positiva a condiciones frías y húmedas durante el invierno previo y la primavera y verano actuales y de forma negativa a temperaturas máximas elevadas en verano durante el año de formación del anillo de crecimiento.
- Los análisis de la xilogénesis indicaron dos episodios principales de formación de traqueidas en Mayo-Junio y medio Julio-Agosto correspondientes a las máximas tasas de formación de traqueidas en sus fases de expansión radial y de engrosamiento de sus paredes celulares, respectivamente. Estas fases de crecimiento activo estaban separadas por un periodo de escasa o nula actividad del cámbium en verano cuando el elevado déficit hídrico paraliza la producción de traqueidas.

- Tanto la formación de la madera temprana como la de la tardía mostraron cierta sensibilidad al déficit hídrico acumulado a medio plazo (10-14 meses) pero dicho impacto se produjo principalmente en verano y comienzos del otoño, respectivamente. En el corto plazo, estas influencias se asociaron con una reducción de la producción de traqueidas, mientras que en el largo plazo han causado disminución de la formación de EW y LW.
- La sequía afectó más negativamente el crecimiento de la madera temprana que tardía. Esta reducción selectiva en la formación de la EW puede dar lugar a varios efectos en cascada, a saber, una disminución del crecimiento radial (incluyendo la formación de LW) una reducción de la conductividad hidráulica e, indirectamente, una absorción de carbono obstaculizado en condiciones semi-áridas.

4. En relación a los factores que determinan las respuestas del crecimiento a la sequía en bosques mediterráneos se encontró que:

- La elevada variabilidad espacial en términos de las respuestas del crecimiento a la sequía observada entre especies y sitios en los bosques del nordeste de España estaba controlada por una combinación de variables climáticas, topográficas y bióticas.
- En bosques de sitios xéricos, donde el factor principal que afectaba las respuestas del crecimiento a la sequía era el déficit hídrico, otros factores como los tipos de suelo con poca capacidad de retención de agua y las elevadas temperaturas exacerbaron los impactos negativos de la sequía sobre el crecimiento.
- En bosques de sitios mésicos, los principales factores que mitigaron el impacto de la sequía sobre el crecimiento fueron un balance hídrico anual positivo, bajas temperaturas y la presencia de suelos profundos del tipo inceptisol con una elevada capacidad de retención de agua.

4.2. Conclusions

The main conclusions of this study are the following:

1. In relation to the atmospheric cuirculation drivers of *P. halepensis* growth it was found that:

   - *P. halepensis* growth in eastern Spain was characterized by two distinct spatial patterns reflecting the growth variability in northern and southern areas for earlywood and latewood growth. Tree growth in the northern sites was mainly influenced by the winter-spring NAO, whereas at the southern sites growth was driven by the winter WeMO index.
   - The influence of the winter NAO and WeMO index on *P. halepensis* earlywood and latewood growth was expressed indirectly through their control of the regional frequency of weather types and the surface climatic conditions, mainly precipitation. The northern sites were positively associated with the SW and W weather types frequency which are under the NAO influence whereas the southern sites were mainly associated with E and SE weather types, controlled by the WeMO variability.
   - A high winter-spring precipitation enhanced both earlywood and latewood growth, whereas latewood formation was also positively influenced by autumn precipitation. The influence of winter-spring precipitation on latewood growth was expressed through a direct improvement of earlywood formation leading to an indirect latewood improved growth.

2. In relation to the impact of droughts on tree growth it was found that:

   - The use of a multi-scalar drought index (Standardized Precipitation Index) allowed detecting time-dependent drought impacts on tree growth.

- Tree species growing in xeric sites (*Pinus halepensis*, *Pinus pinea*, *Pinus nigra*, *Quercus ilex*, *Quercus faginea*, *Juniperus thurifera*) responded strongly to mid-long-term droughts lasting from 9 to 12 months whereas species from mesic sites of the Pre-Pyrenees and Pyrenees (*Abies alba*, *Pinus sylvestris*) responded to drought in a short-term (1-5 months) period. In all cases, the maximum association between growth and drought was detected during summer months.

3. In relation to the climatic impacts and drought control on *Pinus halepensis* growth, it was found that:

- *P. halepensis* earlywood growth responded positively to wet (cold and humid) conditions during the previous winter and current spring-summer and negatively to warm maximum summer temperatures during the year of tree-ring formation.
- The xylogenesis analyses indicated two major peaks of tracheid formation in May-June and mid July-August corresponding to the maximum expressions of the tracheid enlargement and wall-thickening phases respectively. These peaks were separated by a period of reduced cambial activity in summer when a high water deficit stops tracheid production.
- Both earlywood and latewood growth showed sensitivity to the mid-term accumulated water deficit (10-14 months) but this impact mainly occurred in summer and early autumn respectively. In the short term, these influences were associated with a reduction of tracheid production, whereas in the long term they caused declining EW and LW formation.
- Drought affected more negatively the earlywood than latewood growth. This selective reduction in EW formation may lead to several cascading effects, namely a decline of radial growth (including LW formation) a reduction in hydraulic conductivity and, indirectly, a hampered carbon uptake under semi-arid conditions.

4. In relation to the factors driving growth responses to drought in Mediterranean forests, it was found that:

    - The high spatial variability in terms of growth responses to drought observed among species and sites in north-eastern Spain forests was driven by a combination of climatic, topographic and biotic variables.
    - In xeric forests, despite the main driver of the growth responses to drought was the water deficit, other factors such as soil types with a low water retention capacity and warm temperatures exacerbated the negative impacts of drought on tree growth.
    - In mesic forests, the main factors mitigating the drought impact on growth were a positive annual water balance, low temperatures and the presence of deep inceptisol soils with a high capacity to hold water.

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ORIGINAL ARTICLES

In the following section are attached the original articles performed in the context of this study, as they were published by international scientific journals corresponding to Forestry and Ecology subjects.

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Spatial variability in large-scale and regional atmospheric drivers of *Pinus halepensis* growth in eastern Spain

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ABSTRACT

In this study we analyzed the influence of general atmospheric circulation patterns and the frequency of weather types on the spatio-temporal variability of tree-ring growth in *Pinus halepensis* forests in eastern Spain. Three atmospheric circulation patterns affecting the western Mediterranean region were included in the study: the North Atlantic Oscillation (NAO), the Western Mediterranean Oscillation (WeMO) and the Mediterranean Oscillation (MO). In addition, the particular circulation pattern affecting eastern Spain was quantified using the frequency of weather types. The variability of radial growth (width) of earlywood and latewood in *P. halepensis* was quantified at 19 sites using dendrochronological methods. Two distinct patterns, reflecting growth variability in the northern and southern areas involved in the study, were identified for both earlywood and latewood tree-ring series. The influence of atmospheric circulation modes on tree growth resembled the spatial patterns identified, as earlywood and latewood formation in northern sites was determined by the NAO variability, whereas the WeMO dominated growth at the southern sites. Winter, summer and autumn weather types also exerted a control over tree radial growth. We conclude that both atmospheric circulation indices and weather types exert significant control on the formation of earlywood and latewood, because of their influence on precipitation patterns. The findings also suggest that wet and mild conditions during winter and the following autumn enhance *P. halepensis* earlywood and latewood formation, respectively. Thus, winter atmospheric patterns may indirectly influence latewood growth through direct effects on previous earlywood development driven by precipitation variability.

1. Introduction

Climatic projections predict strong warming (2–4 °C) trends and a decrease in land water availability (ca. −20%) for the Mediterranean basin during the 21st century (IPCC, 2007). The forecast drying trend will be in part determined by an increased frequency of anticyclone conditions associated with a northward shift of the Atlantic storm track (Giorgi and Lionello, 2008). Moreover, it is expected that there will be an increase in the surface pressure gradient between the northern and southern parts of the North Atlantic region (Osborn, 2004; Paeth and Pollinger, 2010), a decrease in the frequency and intensity of Mediterranean cyclones (Lionello et al., 2008; Raible et al., 2010), and a decrease in summer convective systems (Branković et al., 2010; May, 2008).

The predicted changes in atmospheric circulation are expected to affect the growth of trees in the Mediterranean region through changes in the characteristics of the dominant atmospheric flows, the frequency of particular weather types, and the surface climate (including precipitation and temperature). Fig. 1 shows a simplified mechanistic model to illustrate how the general atmospheric circulation can drive the patterns of the regional atmospheric circulation (quantified by means of the frequency of different weather types), which will finally drive the variability of the surface climate (mainly the spatial and temporal variations in temperature and precipitation). This variability will influence the patterns of tree radial growth, including the formation of earlywood and latewood, the latter affected both by previous earlywood development but also by the surface climate conditions. Most analyses of the impacts of climate on forest growth have only focused on the influence of surface climate factors (Fritts, 2001). Nevertheless, atmospheric circulation patterns affect climate variability over large regions.

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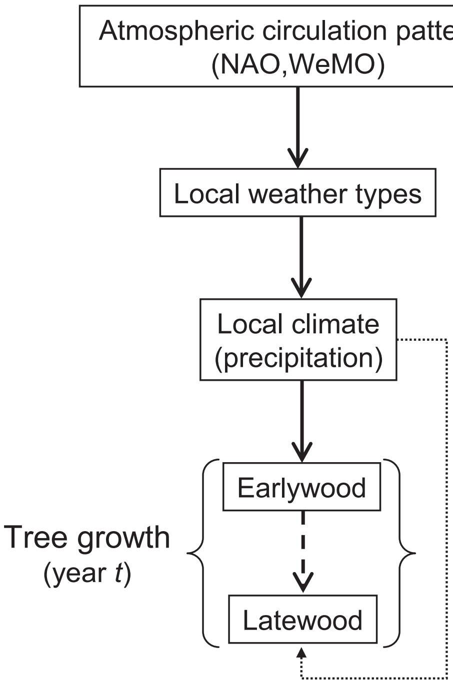

Fig. 1. Schematic diagram of the processes linking the influence of atmospheric circulation on growth of *P. halepensis* during the year (*t*) of tree-ring formation through changes in local weather types and climate conditions, mainly precipitation.

They allow determining the effects of the large-scale climate processes and focusing in the physical mechanisms that control climate variability at regional and/or local scales. Moreover, it is expected that the main signs of climate change will be identified earlier through changes in atmospheric circulation (Giorgi and Mearns, 1991; Räisänen et al., 2004).

Few studies have attempted to determine the direct and indirect influences of atmospheric circulation on tree growth (but see Hirschboeck et al., 1996; Garfin, 1998, Girardin and Tardif, 2005). Such information is lacking in areas with a Mediterranean climate. This is particularly the case for most of the Iberian Peninsula, where climatic conditions range from mild to continental, and from humid to semiarid, creating diverse constraints on tree growth (Nahal, 1981).

The climate variability of the Iberian Peninsula is under the influence of various atmospheric circulation patterns (Rodó et al., 1997; Rodríguez-Puebla et al., 1998; Trigo and Palutikof, 1999; Trigo and Palutikof, 2001; Trigo et al., 2004; González-Hidalgo et al., 2009). Among these is the North Atlantic Oscillation (NAO), which is one of the main modes of atmospheric circulation in the northern hemisphere (Hurrell et al., 2003). The NAO is defined by a north–south dipole that characterizes the sea level pressures and geopotential heights in the North Atlantic region. The NAO determines the position of the Icelandic low pressure and the Azores high pressure systems, and therefore the direction and strength of westerly winds in southern Europe (Hurrell, 1995). The NAO has a strong influence on winter climate in the Iberian Peninsula, where increased westerlies (high NAO values) lead to dry and cold conditions (Hurrell and Van Loon, 1997). Thus, high (low) NAO values in winter are linked to low (high) levels of precipitation and low (high) temperatures in the Iberian Peninsula, particularly in southwestern areas (Rodríguez-Puebla et al., 2001). In the eastern Iberian Peninsula, close to the Mediterranean Sea, climatic conditions are also affected by other atmospheric circulation patterns (González-Hidalgo et al., 2009; Vicente-Serrano et al., 2009). These include the Mediterranean Oscillation (MO), which captures the gradient in sea level pressure (SLP) anomalies between the eastern and western parts of the Mediterranean basin (Conte et al., 1989), and the Western Mediterranean Oscillation (WeMO), which reflects the variability in precipitation related to Mediterranean cyclogenesis in the western Mediterranean basin (Martín-Vide and López-Bustins, 2006). The negative phases of the WeMO and MO are linked to high levels of precipitation over the Spanish Mediterranean coast.

These broad-scale atmospheric circulation patterns influence local weather patterns, which are the main drivers of precipitation at local scales in the Iberian Peninsula (Goodess and Jones, 2002; Vicente-Serrano and López-Moreno, 2006). The local spatial patterns of precipitation are among the main constraints on tree growth in the region, as evidenced by several dendrochronological studies based on tree-ring networks (Macias et al., 2006; Andreu et al., 2007; Di Filippo et al., 2007). However, the influence of large-scale atmospheric patterns on Iberian tree growth reported previously (Bogino and Bravo, 2008; Roig et al., 2009; Rozas et al., 2009) may also reflect growth effects caused by precipitation variability, which is directly determined by local-scale climatic drivers (e.g. weather types), as has been suggested to occur in Canada (Girardin and Tardif, 2005) and Mexico (Brienen et al., 2010).

While the predicted trend towards progressively drier conditions is likely to cause a decline in the growth of Mediterranean forests, the spatial extent and the magnitude of the effect of atmospheric and climatic drivers on tree growth is uncertain (Andreu et al., 2007; Sarris et al., 2007; Vicente-Serrano et al., 2010a,b). Iberian forests of *Pinus halepensis* Mill., a drought tolerant species (Ne'eman & Trabaud, 2000), provide a useful model for evaluating the sensitivity of tree growth to climatic variability at broad and local scales. Several factors are relevant to such an evaluation. First, the late 20th century was characterized by marked climatic variability in the eastern Iberian Peninsula, where most of these forests occur (De Luis et al., 2009a). Second, tree growth in this region should be less sensitive to NAO than in southwestern Iberia, and respond more to other atmospheric patterns (MO, WeMO), but these hypotheses have not previously been tested. Third, no studies have investigated how the climate drivers affect earlywood and latewood production, despite ample evidence that each of these components of *P. halepensis* growth respond differently to diverse climatic variables (De Luis et al., 2007; Camarero et al., 2010).

We analyzed the influence of large-scale atmospheric circulation patterns (NAO, MO and WeMO), but also the role of the atmospheric circulation processes at regional scales (quantified by the frequency of various weather types) on the spatio-temporal patterns of tree growth in *P. halepensis* forests. Our objectives were: (i) to use dendrochronological methods to characterize the spatial and temporal patterns of radial growth (earlywood and latewood width) in a network of *P. halepensis* forests along a climate gradient in the eastern Iberian Peninsula; (ii) to quantify the influence of large-scale circulation patterns and regional weather types as atmospheric drivers of tree growth and (iii) to explain the surface climate processes that drive the influence of the atmospheric circulation on the forest growth. We hypothesized on a spatially structured response of the forest growth to the atmospheric circulation patterns that determine the climate variability across the region.

2. Materials and methods

2.1. Study area

The study area is located in eastern Spain (Aragón and Valencia regions), where a steep climate gradient occurs as a result of both geographical and topographical factors (Fig. 2; Table 1). In this area the influences of the Atlantic Ocean (high levels of winter and spring precipitation derived from the Atlantic Ocean storm

Table 1
Characteristics of the study sites.

Site (code)	UTM X	UTM Y	Elevation (m)	Dbh (cm)	Temperature (°C)[a]	Precipitation (mm)
Ayerbe (AY)	677,634.93	4,688,192.68	924	22.2 ± 0.6	12.2	880
El Grado (GR)	764,638.95	4,672,814.33	168	23 ± 0.4	13.5	768
Valareña (VA)	636,953.56	4,661,620.32	520	19.4 ± 0.4	14.4	496
Castejón - Zuera (CV)	669,056.80	4,650,279.64	565	18.8 ± 0.7	14.5	540
Castejón de Valdejasa (CS)	673,445.71	4,640,263.00	498	22.4 ± 0.4	14.6	390
Villanueva de Gállego (VL)	673,478.45	4,638,872.29	452	26 ± 0.8	14.7	380
Puerto de Alcubierre (PU)	707,340.29	4632588.29	560	15.4 ± 0.5	14.0	558
San Caprasio (CP)	707,892.44	4624573.14	738	20 ± 0.5	13.5	710
Fraga (FR)	777,175.30	4,596,239.49	340	25 ± 0.7	15.2	349
Valmadrid (VM)	672,553.01	4,590,958.15	648	15.4 ± 0.4	14.3	440
Caspe (CA)	757,369.51	4,575,399.17	166	20 ± 0.5	15.4	298
Daroca (DA)	633,119.39	4,555,501.05	937	25 ± 0.4	12.2	436
Oliete (OL)	694144.72	4,540,298.96	530	23.2 ± 0.5	14.3	437
Alloza (AL)	704,847.10	4,539,335.96	595	27 ± 0.8	13.7	450
Oropesa (OR)	766,132.42	4,439,591.18	1	27.2 ± 0.5	17.1	425
Requena (RE)	654,961.25	4,370,550.69	721	33.4 ± 0.9	13.9	407
Jalance (JA)	659,418.38	4,339,557.75	571	24.6 ± 0.6	15.5	447
Font Roja (FN)	714,156.60	4,282,734.07	1022	21.8 ± 0.6	14.5	779
Guardamar (GU)	705,789.97	4,219,646.49	15	23 ± 0.8	17.7	271

[a] Climatic data are annual values and were obtained for meteorological stations located at similar elevation and at less than 15 km from the closest sampling site.

track) and the Mediterranean Sea (high levels of autumn precipitation caused by the cyclonic influence from the Mediterranean Sea) increase northwestwards and southeastwards, respectively (Linés, 1981). Rainfall decreases from north to south and from the coast to inland areas (González-Hidalgo et al., 2009). A thermal gradient is also present from the southeastern coastal areas to northwestern inland areas, resulting in mild and continental conditions near and far from the Mediterranean coast, respectively. Thus, *P. halepensis* in this area grows under a wide variety of climate types ranging from mesic and mild conditions to semiarid and continental conditions (Gil et al., 1996).). In *P. halepensis*, earlywood is formed between spring and early summer whereas latewood is mostly formed between summer and late autumn (De Luis et al., 2007; Camarero et al., 2010). Most of the geological substrates in the study area are limestones and marls, which leads to the formation of basic soils.

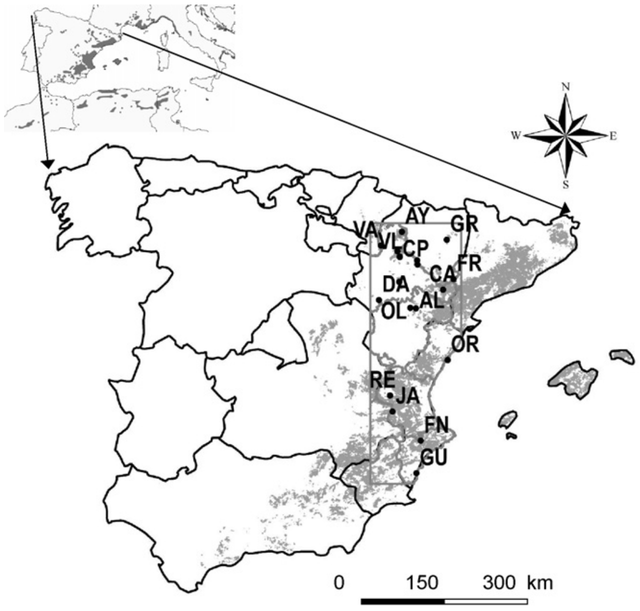

Fig. 2. Distribution of *P. halepensis* (gray area) in the western Mediterranean basin and in eastern Spain, and the location of the study sites (black points). The site codes are as shown in Table 1. The study area in eastern Spain is indicated by the gray rectangle.

2.2. Dendrochronological methods

Sites were selected based on the dominance of *P. halepensis* in the canopy over at least 1 ha of fully forested area. Sites were also selected based on the occurrence of stressing environmental conditions such as shallow or rocky soils and the absence of signals related to recent management (stumps) or local disturbances (fire scars, charcoal). The selected sites were considered to capture most of the climatically mediated growth variability of *P. halepensis* in eastern Spain. At each of 19 sampling sites we randomly selected 15–20 trees, separated by at least 50 m from each other, and measured their diameter at 1.3 m from the ground. At least two radial cores per tree were removed at 1.3 m height using a Pressler increment borer. The cores were prepared following standard dendrochronological methods (Fritts, 2001), and were mounted and sanded until tree rings were clearly visible with a binocular microscope. All samples were visually cross-dated, and the earlywood and latewood widths were measured separately to a precision of 0.001 mm and accuracy of ±0.0003 mm, using a LINTAB measuring device (Rinntech, Heidelberg, Germany). We distinguished earlywood and latewood based on the cross-sectional area of tracheids and the thickness of their walls so as to define an objective threshold of change between both types of wood within the tree ring based on previous dendrochronological and xylogenesis studies on *P. halepensis* (De Luis et al., 2007,2009b; Camarero et al., 2010). Cross-dating was evaluated using the COFECHA program (Holmes, 1983).

Each series was standardized using a spline function with a 50% frequency response of 32 years to retain high-frequency variability. Standardization involved transforming the measured values into a dimensionless index by dividing the raw values by the expected values given by the spline function. Autoregressive modeling was carried out on each series to remove temporal autocorrelation. The indexed residual series were then averaged using a biweight robust mean to obtain site residual chronologies of earlywood and latewood width. We used the ARSTAN program to obtain the residual chronologies of earlywood and latewood (Cook, 1985), and these were used in all subsequent analyses.

The quality of the chronology data was evaluated using several dendrochronological statistics (Briffa & Jones, 1990): the mean width and standard deviation (SD) of the earlywood and latewood raw width series; the first-order autocorrelation (AC1) of these raw series, which measures the year-to-year persistence; the mean sensitivity (MSx) of the residual series, which quantifies the relative change in width among consecutive years; the expressed population signal (EPS) of residual series, which indicates to what extent the sample size is representative of a theoretical infinite population; and the mean correlation (Rbar) among individual residual series within each site. The common period 1960–2003 was selected because all site residual chronologies showed EPS values above the 0.85 threshold, which is widely used in dendrochronological studies (Wigley et al., 1984).

2.3. Atmospheric circulation patterns

The NAO, MO and WeMO atmospheric circulation patterns, which affect autumn and winter climatic conditions (particularly precipitation) over eastern Spain, were selected following Vicente-Serrano et al. (2009) and González-Hidalgo et al. (2009). Autumn (September to November), spring (April to May), summer (June to August) and winter (December to March) indices were calculated. To calculate the three-monthly circulation indices for the winter, spring and autumn seasons we used monthly SLP grids from the NCEP-NCAR ds010.1 Monthly Northern Hemisphere Sea Level Pressure Grids (http://dss.ucar.edu/datasets/ds010.1/; Trenberth and Paolino, 1980). This dataset contains complete records for the study period (1960–2003), with a spatial resolution of 5°. The atmospheric circulation indices were calculated monthly from the differences between the series of standardized SLPs recorded at the two points closest to the sites most used to calculate these indices: Gibraltar (south of the Iberian Peninsula; 35° N, 5° W) and Rejkiavic in Iceland (65° N, 20° W) in the case of the NAO (Jones et al., 1997); Gibraltar and Lod in Israel (30° N, 35° E) in the case of MO (Palutikof, 2003); and Gibraltar and Padova (Italy) (45° N, 10° E) in the case of the WeMO (Martín-Vide and López-Bustins, 2006). Seasonal atmospheric circulation indices were obtained from the average of the monthly series.

2.4. Classification of weather types

The general atmospheric circulation, well represented in East Spain by means of the general atmospheric circulation patterns cited above are propagated regionally by means of different weather types that represent pressure fields and winter flows with a noticeable role on the surface climate conditions (e.g., precipitation and temperature) (Yarnal et al., 2001). On the one hand, a high frequency of weather types prone to cause precipitation would tend to produce humid conditions. On the other hand, weather types characterized by stability conditions will be the direct cause of droughts. The influence of the frequency of weather types on the surface climate in eastern Spain (e.g., Vicente-Serrano and López-Moreno, 2006) justifies the use of weather types to check their possible influence on tree radial growth.

Several attempts have been made to develop classification methods based on different categories of weather type (see review in Yarnal et al., 2001). Among these, automatic methods allow the construction of homogeneous daily or monthly series of atmospheric climatic conditions, at local to regional scales. The most widely used automatic method to classify weather types is that formulated by Jenkinson and Collison (1977), which is based on the Lamb (1972) catalogue. This has been widely used to classify weather types in the Iberian Peninsula (Spellman, 2000; Trigo and DaCamara, 2000; Goodess and Jones, 2002; Vicente-Serrano and López-Moreno, 2006; López-Moreno and Vicente-Serrano, 2007). To obtain a daily classification of weather types we used a sea surface pressure grid of 16 points centered over the Iberian Peninsula (seefig. 1 in Vicente-Serrano and López-Moreno, 2006). From daily pressure data at these points over the period 1960–2003 we calculated the type and direction of winds (cyclonic/anticyclonic, directional and hybrid) on which to base a classification of weather types. For this purpose we used again the NCEP–NCAR Northern Hemisphere Sea Level Pressure Grids, but at a daily time scale (http://dss.ucar.edu/datasets/ds010.0/). Quantitative monthly series can be derived from the daily weather types using the sum of the number of weather types in each class during the month (Corte-Real et al., 1998). The 26 weather types obtained using Jenkinson and Collison's method were summarized by the elimination of hybrid types, which were reclassified at 50% to cyclonic (C), anticyclonic (A) or directional weather types (N, north; NE, northeast; E, east; SE, southeast; S, south; SW, southwest; W, west; and NW, northwest) (Trigo and DaCamara, 2000; Vicente-Serrano and López-Moreno, 2006). Monthly and seasonal series of the frequency of the 10 weather-types series from 1960 to 2003 were related to *P. halepensis* growth.

2.5. Climate data

To explain the mechanisms that drive the influence of the atmospheric circulation processes on the earlywood and latewood, we have used data of monthly precipitation and temperature from 1960 to 2003 recorded in the closest meteorological stations to the 19 sampling sites. Precipitation and temperature were obtained from two daily dataset that followed a careful procedure of quality control and reconstruction to guarantee the reliability of the data. The high spatial density of stations allowed having a meteorological station at a distance lower than 15 km of the sampling point. Details on the datasets can be found in Vicente-Serrano et al. (2010a,b) and El Kenawy et al. (2011). The four southern sampling sites, located in the regions of Valencia and Alicante were out of the regions covered by the cited data sets. For these sites we used the MOPREDAS dataset (González-Hidalgo et al., 2011). In addition we also used the closest temperature stations from the available records of the Spanish Meteorological Agency (*Agencia Estatal de Meteorología*, AEMET). The monthly climatic data was grouped seasonally following the same approach than for the atmospheric circulation patterns: Autumn (September–November), spring (April–May), summer (June–August) and winter (December–March).

2.6. Statistical analyses

The spatio-temporal variability of earlywood and latewood chronologies for the period 1960–2003 was analyzed using an S-mode principal component analysis (PCA). This enabled common features to be identified and specific relevant local characteristics to be detected (Richman, 1986). The S-mode also enabled the general temporal patterns of forest growth to be identified. The areas represented by each component in the analysis were identified by mapping the factorial loadings. The PCA was performed on a covariance matrix calculated among the chronologies (Legendre and Legendre, 1998). The number of components was selected using the criterion of an eigenvalue >1, and the components were rotated (Varimax) to redistribute the final explained variance, and to obtain more stable and robust spatial patterns (Richman, 1986, Garfin, 1998). The spatial classification of earlywood/latewood growth was carried out using the factorial loading values obtained for each component, with the forests being grouped using the maximum loading rule. Each forest was assigned to the component with the greatest loading value. This method has been applied in many climatic classification studies (e.g. Comrie and Glenn, 1998).

To explain the influence of variability in atmospheric circulation on the spatio-temporal patterns of earlywood and latewood growth we carried out correlation analyses (Briffa and Cook, 1990). To compare with the de-trended forest growth series and to avoid the possibility that atmospheric circulation trends could disrupt potential relationships, prior to assessing the correlations the trend in each of the atmospheric circulation series was removed by

Table 2
Dendrochronological statistics of earlywood and latewood *P. halepensis* chronologies for the common period 1960–2003.

Site	Trees (radii)	Period	EW-LW	Earlywood						Latewood					
				MW (mm)	SD (mm)	AC1	MSx	Rbar	EPS	MW (mm)	SD (mm)	AC1	MSx	Rbar	EPS
AY	19 (33)	1946–2006	0.56	2.07	0.91	0.60	0.21	0.34	0.93	0.58	0.39	0.33	0.28	0.28	0.92
GR	15 (30)	1946–2006	0.46	1.78	1.02	0.69	0.29	0.54	0.97	0.51	0.29	0.35	0.32	0.33	0.93
VA	17 (31)	1925–2009	0.65	1.40	0.91	0.70	0.36	0.61	0.96	0.41	0.28	0.66	0.31	0.43	0.95
CV	13 (23)	1928–2009	0.42	1.79	1.07	0.74	0.28	0.48	0.92	0.56	0.38	0.70	0.29	0.33	0.90
CS	13 (23)	1900–2009	0.64	0.90	0.59	0.57	0.33	0.69	0.98	0.25	0.19	0.50	0.32	0.40	0.93
VL	15 (29)	1878–2006	0.68	0.94	0.65	0.55	0.44	0.55	0.96	0.27	0.23	0.48	0.38	0.39	0.93
PU	15 (22)	1943–2009	0.58	1.12	0.74	0.65	0.34	0.67	0.98	0.36	0.20	0.55	0.30	0.39	0.92
CP	14 (27)	1927–2006	0.62	1.58	1.05	0.70	0.36	0.57	0.96	0.42	0.26	0.55	0.26	0.31	0.91
FR	16 (29)	1844–2006	0.57	0.72	0.63	0.68	0.51	0.63	0.97	0.25	0.21	0.61	0.34	0.37	0.93
VM	17 (30)	1959–2009	0.57	1.43	0.83	0.62	0.34	0.80	0.99	0.40	0.23	0.55	0.28	0.52	0.96
CA	16 (28)	1845–2007	0.65	0.62	0.51	0.55	0.64	0.71	0.98	0.15	0.11	0.39	0.42	0.41	0.94
DA	14 (28)	1934–2006	0.54	1.62	1.00	0.48	0.46	0.82	0.99	0.44	0.28	0.25	0.43	0.65	0.98
OL	15 (27)	1960–2006	0.40	2.29	1.98	0.77	0.37	0.78	0.99	0.66	0.36	0.46	0.30	0.47	0.95
AL	15 (31)	1888–2006	0.63	1.11	0.83	0.69	0.43	0.66	0.98	0.34	0.25	0.60	0.23	0.33	0.93
OR	16 (30)	1921–2003	0.53	1.45	1.18	0.63	0.41	0.58	0.97	0.58	0.45	0.51	0.35	0.46	0.95
RE	15 (30)	1789–2003	0.40	0.93	0.64	0.58	0.41	0.39	0.94	0.36	0.31	0.47	0.37	0.26	0.89
JA	15 (35)	1863–2003	0.56	1.05	0.62	0.48	0.44	0.59	0.97	0.37	0.30	0.26	0.47	0.40	0.95
FN	15 (24)	1863–2006	0.68	1.06	0.75	0.69	0.40	0.53	0.93	0.27	0.20	0.51	0.35	0.41	0.90
GU	36 (75)	1912–2006	0.52	1.12	1.43	0.77	0.43	0.55	0.99	0.37	0.37	0.60	0.33	0.40	0.97

Statistics: EW–LW, Pearson correlation coefficient between the residual earlywood and latewood chronologies for each site. Raw-data series: MW, mean ring width; SD, standard deviation; AC1, first order autocorrelation. Residual series: MSx, mean sensitivity; Rbar, mean interseries correlation; EPS, expressed population signal. All statistics refer to residual chronologies excepting MW and SD.

assuming a linear trend in each series. Correlation analyses were performed between earlywood and latewood residual indices, de-trended monthly and seasonally atmospheric circulation indices, and the de-trended series of the frequency of weather types for the period 1960–2003. Also partial correlations were obtained to analyse the joint influence of climate and earlywood on latewood. Finally, to determine climate processes that drive the influence of atmospheric circulation on forest growth, we calculated the correlation between earlywood and latewood and the seasonal precipitation and temperature between the atmospheric circulation patterns and the surface climate at each sampling site.

3. Results

3.1. Earlywood and latewood chronologies

Earlywood growth varied more than latewood growth among sites (earlywood, 0.62–2.29 mm; latewood, 0.15–0.66 mm) (Table 2; Fig. 3). The average values of AC1 and MSx were higher for the earlywood (AC1 = 0.64, MSx = 0.39) than for the latewood (AC1 = 0.49, MSx = 0.33) chronologies. Similar results were obtained for Rbar and EPS, which were also higher for the earlywood (Rbar = 0.60, EPS = 0.97) than the latewood (Rbar = 0.40, EPS = 0.93) series. Hence, earlywood growth showed a greater year-to-year persistence (AC1), a higher change among consecutive years (MSx) and a higher common signal (Rbar, EPS) than latewood formation. The change in earlywood and latewood width among consecutive years (MSx) increased as latitude decreased but these trends were not significant (earlywood, $P = 0.15$; latewood, $P = 0.10$). The correlation between earlywood and latewood series decreased significantly as the latewood width increased ($r = -0.67$, $P = 0.002$).

3.2. Spatio-temporal patterns of *P. halepensis* growth

The PCA analysis revealed four and five components (PCs) for earlywood and latewood, which accounted for 72% and 71% of the variance, respectively (Table 3). This indicates a slightly higher spatial variability for the latewood formation, although the components retained represent a high percentage of the total variance, which shows that forest growth in the region is not very heterogeneous and that coherent temporal patterns, representative of large regions can be found. Overall, earlywood site chronologies showed greater correlation among nearby sites than did latewood series. The spatial correlation among sites was significant up to 300 and 380 km for earlywood and latewood chronologies, respectively (Fig. 4). The spatial extent of these relationships was approximately 300 and 380 km for earlywood and latewood chronologies, respectively.

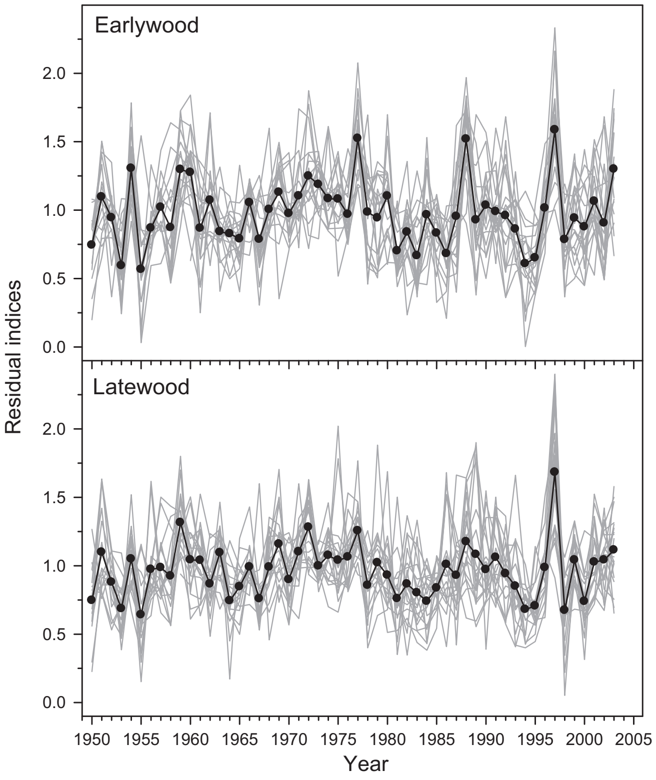

Fig. 3. Local residual chronologies of earlywood and latewood (gray lines) for the *P. halepensis* network in eastern Spain, and the overall mean for each variable (black lines).

Table 3
Correlation of the main principal components (PC) of earlywood and latewood width with atmospheric circulation indices (NAO: North Atlantic Oscillation; MO: Mediterranean Oscillation; WeMO: Western Mediterranean Oscillation) for winter (W), spring (Sp), summer (Su) and autumn (A).

	Earlywood				Latewood				
	PC1	PC2	PC3	PC4	PC1	PC2	PC3	PC4	PC5
Variance (%)	33.58	15.62	12.90	10.07	20.94	17.97	11.77	11.65	8.56
NAO-W	−0.32*	0.05	−0.25	0.18	−0.28	0.05	−0.21	−0.13	0.17
MO-W	−0.25	−0.08	−0.21	−0.03	−0.29	0.02	−0.19	−0.21	−0.20
WeMO-W	0.12	−0.43**	−0.04	0.02	−0.04	−0.18	0.02	−0.22	−0.23
NAO-Sp	−0.45**	0.1	0.25	−0.2	−0.14	0.12	0.05	−0.16	−0.02
MO-Sp	0.10	−0.12	0.19	0.14	−0.31*	−0.16	0.16	−0.2	0.1
WeMO-Sp	−0.2	−0.3	−0.12	0.26	0.17	−0.13	0.16	−0.09	0.1
NAO-Su	–	–	–	–	0.14	0.23	0.33*	0.07	0.26
MO-Su	–	–	–	–	−0.01	−0.22	−0.24	0.04	−0.16
WeMO-Su	–	–	–	–	0.14	0.23	0.33	0.07	0.26
NAO-A	–	–	–	–	−0.13	−0.06	0.07	0.02	0.10
MO-A	–	–	–	–	−0.11	−0.35*	−0.06	−0.04	0.04
WeMO-A	–	–	–	–	−0.15	−0.36*	−0.03	0.19	0.08

* Significance level: $P < 0.05$.
** Significance level: $P < 0.01$.

The spatial distribution of the PCA loadings corresponding to the 4-earlywood and 5-latewood retained components shows clear spatial patterns in forest growth across the region (Fig. 5A). According to the PCA loadings of the first components of earlywood and latewood production, two main growth patterns, corresponding to PC1 and PC2, were found in northwestern and southeastern sites forests, respectively. These components group the 49.2% and the 38.9% of the total earlywood and latewood variability, respectively. This indicates that a high percentage of the tree-growth variance of the region is represented by these components. Additional sites were represented by the other components, but they represent a lower percentage of the total variance and they are found in transitional areas between the northwestern and southeastern locations, and in the northeastern study area. The spatial classification of earlywood and latewood variability based on the maximum loading rule shows clearly the distinction between the northwest and southeast sectors, both for earlywood and latewood formation, with few differences among them (Fig. 5B).

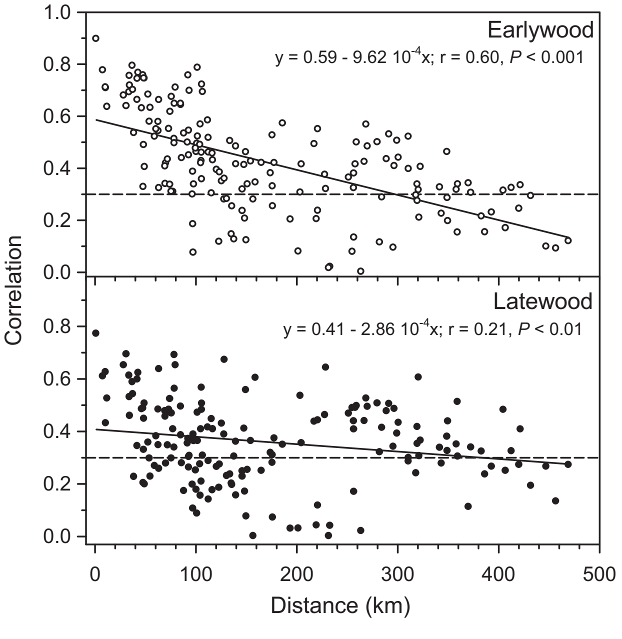

Fig. 4. Spatial extent of earlywood and latewood chronologies. The diagonal lines represent the indicated linear regressions, whereas the dashed horizontal lines represent significance thresholds ($P < 0.05$) for the correlation values.

3.3. *Influence of atmospheric circulation on P. halepensis growth*

In general, very few significant correlations are found between the seasonal atmospheric circulation patterns and the earlywood and latewood series of the retained principal components (Table 3). We found a negative and significant relationship between the winter and spring NAO index and earlywood first principal component, whereas the second earlywood component was negatively related to the WeMO winter index. For the latewood we found significant correlations between the first component and the MO in spring, between the third component and the summer NAO and between the autumn MO and WeMO and the second latewood component.

These results show clearly how the main two components, which represent the main percentage of forest growth variability, are significantly correlated to some of the patterns of atmospheric circulation at a seasonal scale. We found a high temporal agreement between the variability of the atmospheric circulation patterns (winter and spring NAO, winter and autumn WeMO) and the tree growth as represented by the first and second components of earlywood and latewood (Fig. 6). Such temporal agreement is coherent with spatial analyses between earlywood and latewood growth and the seasonal atmospheric circulation patterns (Fig. 7). The earlywood is significantly related to the winter and spring NAO in north and northwestern forests. In contrast, the effects of the winter and autumn WeMO indices on earlywood and latewood formation were greater at southeastern sites.

For monthly values we found significant ($P < 0.05$) negative correlations for the first principal component of earlywood with the previous December ($r = -0.40$) and the current April NAO indices ($r = -0.35$), but it is also noteworthy that the correlations between December and May were negative. At a monthly scale we also found a significant negative correlation between the second component for latewood and the current September WeMO ($r = -0.37$, $P < 0.05$); correlations with the October and November WeMO index were also negative.

In summary, the described associations between atmospheric patterns and growth were highly spatially structured, showing that the NAO and WeMO are affecting both earlywood and latewood formation in different parts of the study area: the NAO in the North and the WeMO in the South.

These results are highly consistent with the analysis on the impact of weather types frequencies on forest growth. The winter was the season with more significant correlations between the four earlywood components and the five latewood components and the seasonal frequency of weather types (Table 4). The earlywood formation in the sites represented by the component 1 is enhanced

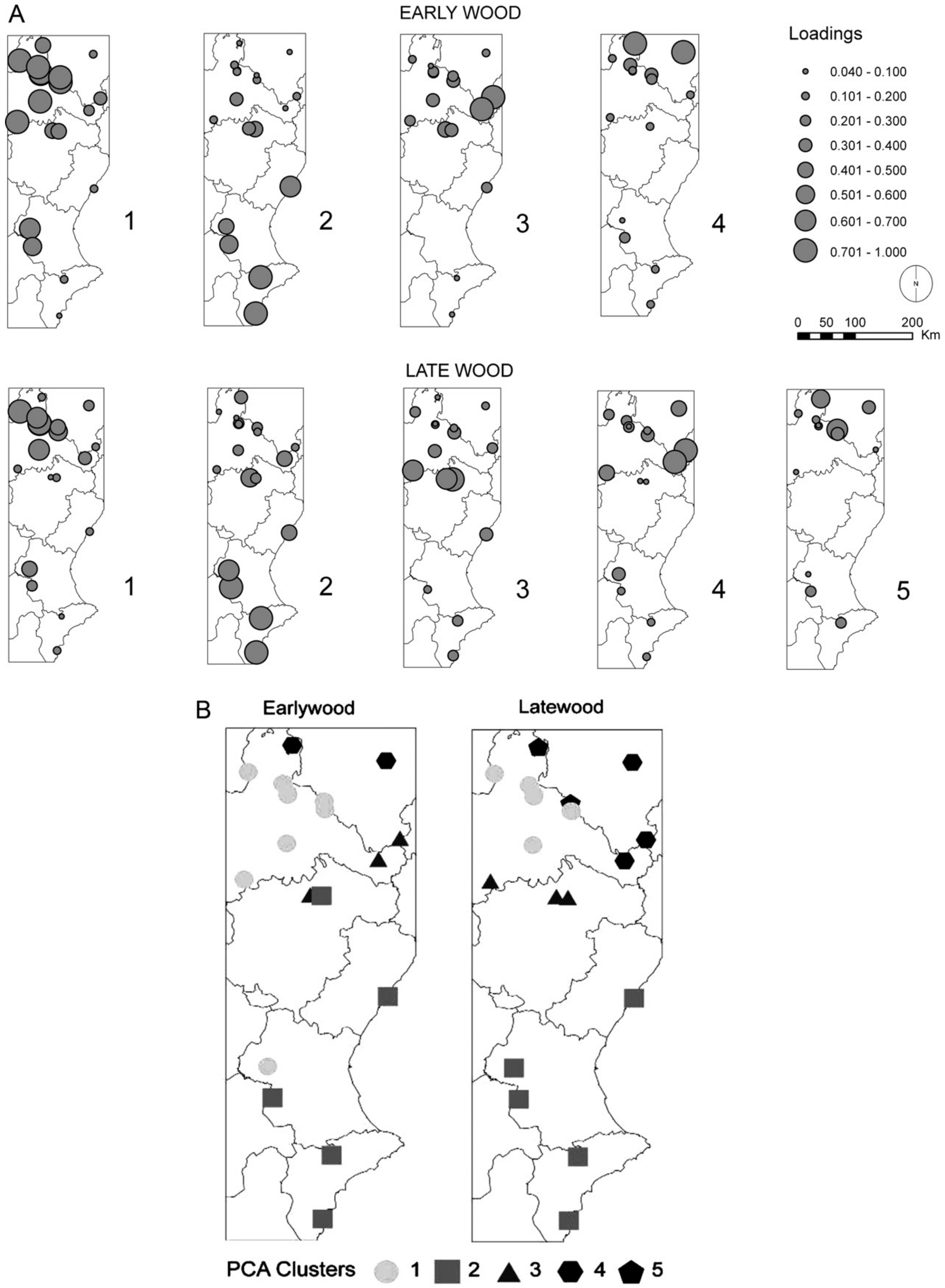

Fig. 5. Spatial patterns of *P. halepensis* growth (earlywood and latewood chronologies) as revealed by PCA based on the loadings of the first four and five principal components, for earlywood and latewood, respectively (A), and spatial classification based on the maximum loadings for each component (B).

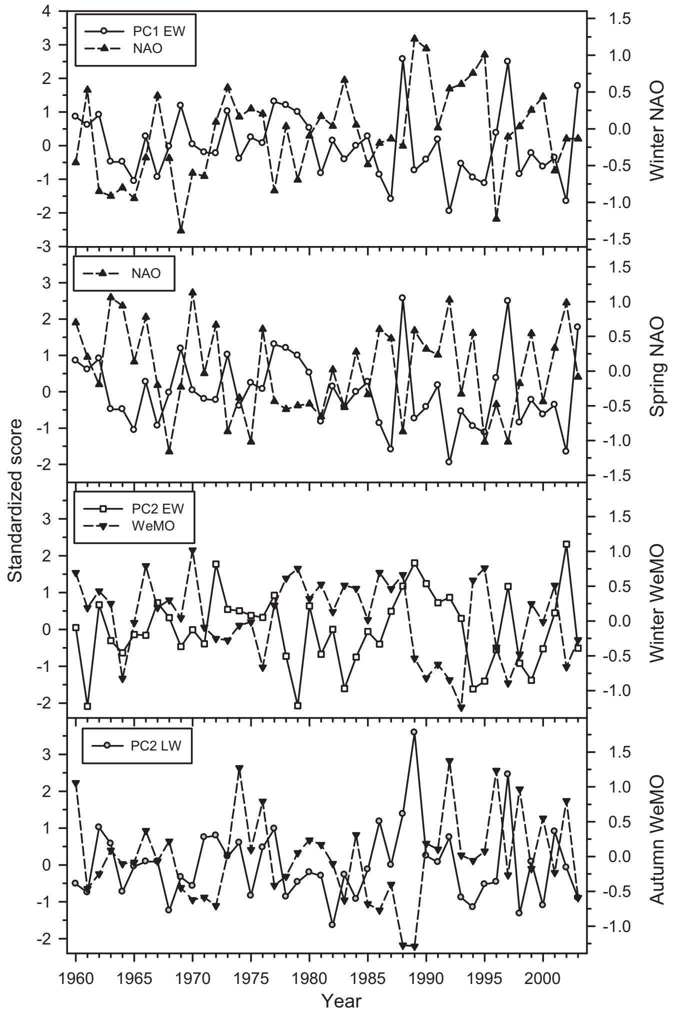

Fig. 6. Temporal evolution of the first two principal components (PC1, PC2) of earlywood (EW) and latewood (LW) *P. halepensis* chronologies, and related atmospheric circulation indices (NAO, WeMO) calculated for the previous winter or the current autumn.

by a high frequency of SW and W types, which are related to the advections of humid air from the Atlantic Ocean. On the contrary, a high frequency of flows from the East and Southeast has a negative role on the earlywood. E and SE flows usually are less intense and have lower moisture than the W flows and they reach the central areas of the Ebro valley completely dry. In addition, the earlywood formation in the sites represented by the component 2 is improved by a high frequency of E and SE flows since these forests are located in areas under the direct influence of these flows. The earlywood components 3 and 4 do not show any significant connection with the frequency of weather types in winter and spring.

Latewood in areas represented by the component 1 is also highly related to the winter frequency of S, SW and A weather types. Nevertheless, the partial correlation between the frequency of these weather types and the first latewood component was only significant for the S type ($r = 0.32$, $P = 0.04$) when the effect of the earlywood was controlled, whereas for the SE and A types partial correlation was not significant ($r = 0.17$, $P = 0.28$ and $r = -0.20$, $P = 0.20$, respectively). This would suggest that lagged effects of winter atmospheric circulation on latewood in northern sites are mainly driven by an indirect influence determined by the winter circulation control of the earlywood. Areas represented by the second earlywood component did not show a noticeable influence of the frequency of the winter and spring weather types on growth, but we found a significant correlation with the frequency of some weather types in summer and autumn. The second latewood component showed a significant negative correlation with the frequency of summer SE and S types, which are characterized by African warm air advections arriving to the Iberian Peninsula and causing dry and persistent weather conditions. In addition, a positive correlation was found with the autumn SE weather type and a negative one with the NW type. This would indicate that Mediterranean SE flows that commonly produce high precipitation in the Mediterranean coastland would enhance the development of latewood in the southern sites.

The analysis based on the weather types allows qualifying some of the results obtained from the general atmospheric circulation patterns, but the main features of the weather types variability were well represented by the three different indices of atmospheric circulation. In winter strong and significant correlations are found for a number of weather types (Table 5). The NAO was negatively

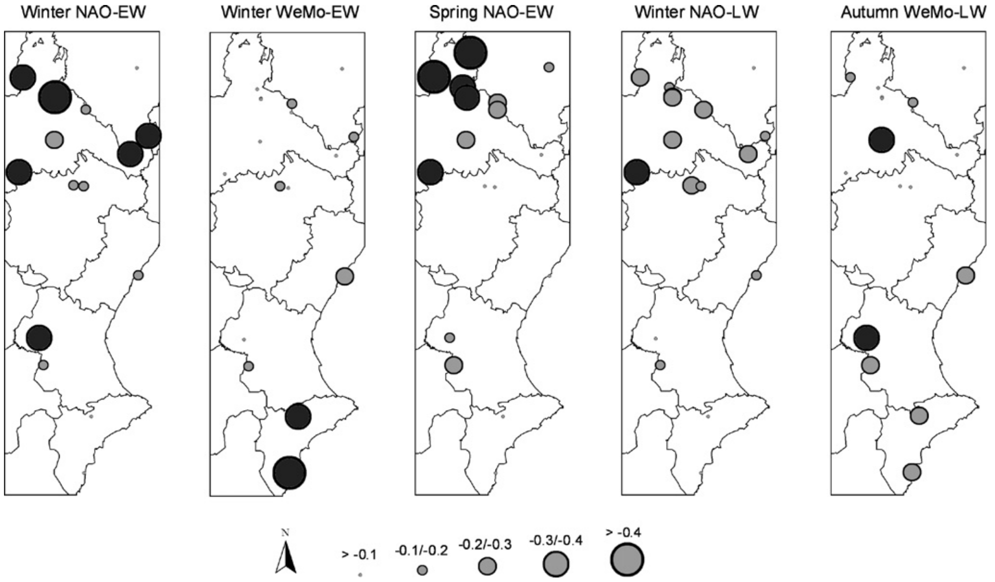

Fig. 7. Geographic correlations of the atmospheric circulation indices (NAO, WeMO) in winter, spring and autumn with *P. halepensis* growth for earlywood (EW) and latewood (LW). The circles are proportional to the absolute correlation value; those filled dark gray indicate significant correlations ($P < 0.05$).

Table 4
Correlation of the principal components (PC) of earlywood (EW) and latewood (LW) with the seasonal frequency of weather types. Weather types: N, north; NE, northeast; E, east; SE, southeast; S, south; SW, southwest; W, west; NW, northwest; C, cyclonic; A, anticyclonic.

	N	NE	E	SE	S	SW	W	NW	C	A
Winter										
PC 1-EW	−0.06	−0.02	−0.31	−0.31*	0.22	0.36*	0.30*	0.10	0.29	-0.31
PC 2-EW	−0.35*	−0.04	0.17	0.33*	0.06	0.03	−0.09	−0.37	0.16	−0.03
PC 3-EW	−0.04	0.19	0.02	0.14	0.05	−0.01	0.02	−0.10	0.23	−0.26
PC 4-EW	−0.20	−0.09	0.06	−0.04	−0.12	0.03	0.22	0.02	−0.11	0.10
PC 1-LW	−0.02	−0.07	−0.28	−0.01	0.39**	0.33*	0.17	−0.02	0.28	−0.38**
PC 2-LW	−0.30*	0.02	0.10	0.05	−0.01	−0.03	−0.03	−0.07	0.12	0.01
PC 3-LW	0.12	−0.19	−0.14	−0.15	−0.18	0.07	0.21	0.04	0.38**	−0.22
PC 4-LW	−0.06	−0.01	0.04	0.14	0.27	−0.03	−0.23	−0.21	0.09	0.00
PC 5-LW	−0.15	−0.04	0.10	−0.10	0.03	0.06	0.07	0.04	0.09	−0.06
Spring										
PC 1-EW	−0.17	0.24	−0.08	−0.01	−0.06	−0.05	0.05	0.04	0.03	−0.06
PC 2-EW	0.13	0.11	0.13	0.12	−0.19	−0.26	−0.31*	−0.20	0.12	−0.03
PC 3-EW	−0.13	0.09	−0.17	0.04	0.10	0.11	−0.17	−0.07	−0.02	0.18
PC 4-EW	0.14	0.06	−0.17	−0.10	0.09	−0.13	0.15	0.24	0.01	−0.18
PC 1-LW	−0.01	0.23	0.09	−0.04	−0.11	0.14	−0.06	−0.07	−0.07	−0.06
PC 2-LW	0.12	−0.03	−0.12	0.05	−0.26	−0.32*	0.03	−0.12	0.25	−0.12
PC 3-LW	0.11	0.26	−0.01	−0.09	−0.14	−0.05	0.04	−0.03	−0.25	0.18
PC 4-LW	−0.46**	−0.05	−0.04	0.13	0.09	0.03	−0.20	−0.13	0.28	0.06
PC 5-LW	0.10	0.19	0.02	−0.13	−0.08	−0.08	0.14	0.11	−0.07	−0.14
Summer										
PC 1-LW	0.11	0.14	−0.27	−0.08	0.15	0.15	0.10	−0.03	−0.13	0.14
PC 2-LW	0.23	−0.13	−0.11	−0.38*	−0.35*	0.27	−0.07	0.07	0.16	−0.12
PC 3-LW	−0.06	0.34*	−0.03	0.06	−0.02	−0.11	−0.05	0.04	−0.27	0.09
PC 4-LW	−0.06	−0.18	0.03	0.06	−0.07	0.37*	0.11	0.15	−0.03	0.07
PC 5-LW	0.08	−0.01	−0.19	−0.11	0.10	0.25	0.09	0.03	−0.09	0.16
Autumn										
PC 1-LW	−0.20	−0.09	0.05	0.00	0.14	0.11	0.19	0.05	0.04	−0.12
PC 2-LW	−0.25	0.04	0.26	0.32*	0.19	0.18	−0.15	−0.45**	0.24	−0.29
PC 3-LW	0.04	−0.10	0.08	−0.13	−0.18	0.05	0.01	−0.10	0.15	−0.03
PC 4-LW	−0.02	−0.05	−0.21	0.00	0.00	0.01	0.25	0.06	0.06	−0.07
PC 5-LW	0.28	0.25	0.11	−0.03	−0.01	−0.03	−0.07	−0.12	−0.27	0.11

* Significance level: $P < 0.05$.
** Significance level: $P < 0.01$.

Table 5
Correlations of the atmospheric circulation indices (NAO, North Atlantic Oscillation; MO, Mediterranean Oscillation; WeMO, Western Mediterranean Oscillation) for the previous winter and the current autumn with weather types (N, north; NE, north–east; E, East; SE, south–east; S, south; SW, south–west; W, west; NW, north–west; C, cyclonic; A, anticyclonic).

	Winter			Spring			Summer			Autumn		
	NAO	MO	WeMO	NAO	MO	WeMO	NAO	MO	WeMO	NAO	MO	WeMO
N	−0.02	0.03	0.59**	0.14	0.03	0.35*	−0.13	0.08	0.49**	0.33*	0.28	0.58**
NE	0.15	0.22	−0.11	0.08	0.40**	0.10	0.14	−0.16	−0.06	0.15	0.16	0.17
E	0.19	−0.03	−0.55**	0.13	0.10	−0.23	0.20	0.00	−0.52**	−0.02	−0.09	−0.54**
SE	0.2	0.09	−0.56**	0.01	−0.29	−0.27	−0.04	0.11	−0.29	−0.11	−0.15	−0.68**
S	−0.12	−0.15	−0.39**	−0.25	−0.29	0.09	−0.20	−0.11	0.07	−0.15	−0.04	−0.47**
SW	−0.51**	−0.53**	0.19	0.03	0.03	−0.06	−0.05	−0.22	0.15	−0.33*	−0.14	0.24
W	−0.46**	−0.39*	0.51**	−0.08	0.15	0.22	−0.03	−0.03	−0.18	−0.27	−0.28	0.28
NW	−0.14	−0.11	0.53**	−0.29	−0.28	0.41**	−0.40*	−0.06	0.42**	0.01	0.03	0.55**
C	−0.68**	−0.72**	−0.14	−0.25	−0.49**	−0.33*	0.12	−0.18	−0.29	−0.18	−0.51**	−0.35*
A	0.76**	0.84**	−0.02	0.36*	0.54**	0.08	−0.08	0.29	0.25	0.32*	0.63**	0.30*

* Significance level: $P < 0.05$.
** Significance level: $P < 0.01$.

correlated with the frequency of SW W and C types and positively correlated with the frequency of anticyclones. The same pattern was found for the MO. On the contrary, the WeMO represented mainly the frequency of the SE-NW flows, since it showed significant negative correlations with the frequency of E, SE and S types and positive correlations with the frequency of NW and W flows. In spring and summer the number of significant correlations was much lower, but in autumn significant correlations between the WeMO and a number of weather types were found, similar to those obtained for the winter. With the exception of the summer SE and S types that showed a significant influence on the second latewood component, the rest of the weather types showing a noticeable impact on the earlywood and latewood formation in northern and southern sites are well represented by the general atmospheric circulation patterns used here. This would imply that with very few exceptions, the regional circulation represented by the weather types and their impacts on tree growth are already represented by the general atmospheric circulation patterns. Therefore in the following section, we focus our attention only on the general atmospheric circulation patterns that have the main impacts on the earlywood and latewood formation.

4. Connection with the surface climate variability

Winter NAO and WeMO showed significant correlation with precipitation in a number of sites (Fig. 8). Nevertheless, the spatial

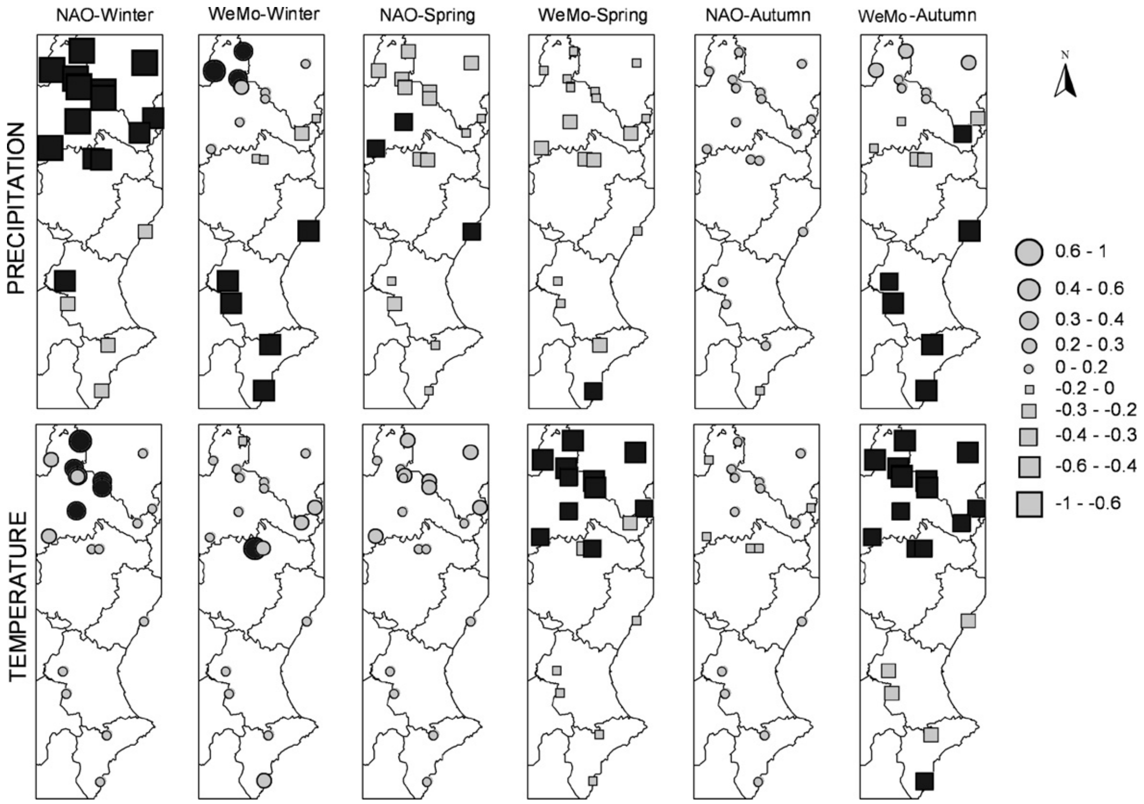

Fig. 8. Geographic correlations of the atmospheric circulation indices (NAO, WeMO) in winter, spring and autumn with precipitation and temperature. The circles are proportional to the absolute correlation value; those filled dark gray indicate significant correlations ($P < 0.05$).

patterns showed a high spatial variability. The impact of NAO on precipitation was recorded in northern areas whereas the WeMO affected precipitation in southern sites. Thus, this spatial configuration resembled the observed pattern of tree growth variability obtained by means of the PCA. Areas in which the earlywood was mainly determined by the winter NAO showed a direct control of precipitation by this circulation pattern. The same behavior was observed for the winter WeMO. In spring, correlations with the NAO were lower than in winter, although magnitudes also tended to be higher in northern areas than elsewhere. Finally, the autumn NAO did not show a remarkable impact on precipitation, but the impact of the autumn WeMO on precipitation showed a clear spatial gradient with negative and significant correlations in the southern areas. This again showed a spatial pattern similar to that found for the WeMO impact on the latewood formation.

Some northern forests showed significant positive correlations with the NAO in winter, which also could contribute to explain the influence of the NAO on the earlywood in these sites (Fig. 8). Nevertheless, it is much more remarkable the WeMO influence on the temperatures of spring and autumn, which presented strong positive correlations in the northern parts of the study area. These results suggest that the spatial variability of forest growth across the region is directly driven by the distinct spatial influence of the atmospheric circulation processes not on temperature, but mainly on precipitation.

The relationship between climate variability and earlywood and latewood showed significant correlations between the earlywood and the winter and spring precipitation in the entire study area (Fig. 9). On the contrary, few sites showed significant correlations between earlywood and temperature variability. Thus, the first earlywood component was significantly correlated with the winter ($r = 0.55$, $P < 0.01$) and spring precipitation ($r = 0.43$, $P < 0.01$). Also the second earlywood component showed a significant correlation with the winter precipitation ($r = 0.53$, $P < 0.01$). On the contrary, both first and second earlywood components did not show any significant correlation with temperature.

There were also significant correlations between winter and spring precipitation and the latewood width in most sites, which could suggest a lagged response of the winter climate on the forest growth in late summer and autumn, possibly driven by soil water storage. Nevertheless, in the forests with significant correlations between latewood and winter precipitation, we found that partial correlations (considering the influence of earlywood on latewood) between winter/spring precipitation and latewood were not significant. In 11 of the 12 sites with significant correlation between winter precipitation and latewood no significant partial correlation was found, whereas eleven of the sites showed a significant partial correlation ($P < 0.05$) between the earlywood and the latewood variability. This would provide evidence that the influence of the winter precipitation on the latewood would be mainly driven through a direct influence on the earlywood formation.

Nevertheless, in the southern study area we also found a direct influence of the surface climate on the latewood formation. Thus, in the southern sites there was a significant correlation between the autumn precipitation and the latewood formation. These sites showed a significant correlation between the autumn precipitation and the WeMO, with a clear different behavior as compared with the rest of the sites. Thus, only the second latewood component showed a significant correlation with the autumn precipitation ($r = 0.39$, $P < 0.05$) and, in addition, no significant correlations were found between any of the five latewood components and temperature. This would explain that although spring and autumn WeMO are correlated with temperatures in northern sites, both earlywood and latewood formation in these sites are not correlated with the WeMO, since tree growth in those sites is not mainly driven by temperatures. For the southern sites, i.e. the sites represented by the

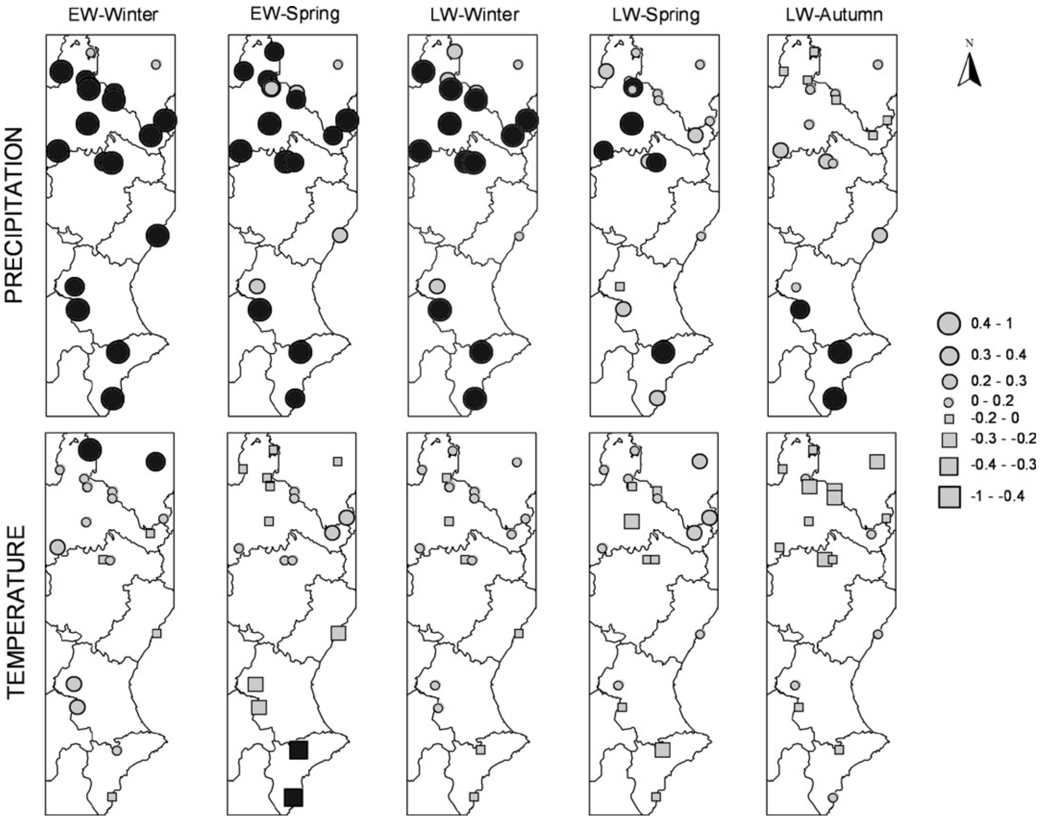

Fig. 9. Geographic correlations between seasonal precipitation and temperature and earlywood (EW) and latewood (LW) formation in *P. halepensis* sampled forests. The symbols are proportional to the absolute correlation value; those filled dark gray indicate significant correlations ($P < 0.05$).

second latewood component, the influence of the autumn WeMO on latewood was directly driven by precipitation. Thus, in opposite with the northern sites, in the southern region both earlywood and autumn precipitation played a significant role to explain the latewood variability. Earlywood and autumn precipitation showed significant partial correlations with the latewood in the areas represented by the second latewood component ($r = 0.65$ and $r = 0.43$, $P < 0.01$, for the earlywood and autumn precipitation, respectively). This indicates that earlywood conditions are affecting latewood but also autumn precipitation plays a significant role.

5. Discussion

In *P. halepensis* the production of earlywood showed a greater year-to-year variability and a higher tree-to-tree common variance than did latewood; these results are similar to those reported by De Luis et al. (2009b). Thus, earlywood and latewood covaried to some extent, indicating a strong temporal association, as suggested in xylogenesis studies of *P. halepensis* (De Luis et al., 2007; Camarero et al., 2010). Furthermore, at sites with wider latewood the positive association between the earlywood and latewood series was weaker, indicating that the development of more latewood tracheids was less reliant on prior formation of earlywood, which is dependent on the synthesis of carbohydrates during the previous winter (Kagawa et al., 2006). Therefore, our results suggest that growth at sites with more latewood development should show a greater response to current climatic conditions in late summer and autumn during the year of tree-ring formation, whereas the reverse is expected for sites with more earlywood formation, where the previous winter and current spring conditions should be more important.

Earlywood and latewood responded to atmospheric circulation patterns and weather types in different ways, although for both variables we detected at least two groups of forests (those located in northwestern and southeastern sites) with contrasting responses. In addition, the geographic pattern of associations among latewood site chronologies suggested the occurrence of these two homogeneous groups of forests with similar reactions to atmospheric conditions. Such a geographically structured climatic response suggests that northwestern sites are more influenced by southwestern flows, which was indicated by the stronger relationships with the winter NAO index relative to that which occurred for southeastern sites near the Mediterranean coast, where *P. halepensis* growth was mainly affected by the winter–autumn WeMO and the autumn MO indices. These findings are consistent with the associations found between atmospheric patterns and weather types. For instance, the winter NAO and MO indices were negatively (positively) associated with the frequency of cyclones (anticyclones) in winter. The winter WeMO index was positively correlated with the frequency of N, W and NW weather types. High levels of the WeMO index in autumn were also associated with greater occurrence of N, NW and anticyclonic weather types, and a low frequency of E, SE, S and cyclonic weather types. These results confirm that the effects of atmospheric circulation patterns on *P. halepensis* growth in the study area are probably an indirect expression of their effects on local weather types and climatic factors, including precipitation, temperature and radiation (Garfin, 1998; Mäkinen et al., 2003). In agreement with the results obtained by Vicente-Serrano and López-Moreno (2006) and González-Hidalgo et al. (2009) for the same region, the same spatial gradient in the effect of the NAO and WeMO on tree growth has been found for the precipitation. Although the NAO mainly affects the southwestern Iberian Peninsula, the southwest flows are reactivated when they reach the Pre-Pyrenean chains, explaining why the forests located in the Ebro valley are affected by this pattern. In contrast, the humid influence of the southwestern flows associated with the NAO does not reach the Mediterranean coastal region (Rodó et al., 1997; Rodríguez-Puebla et al., 1998), where the humid influences come from the east, as reflected by the WeMO index. Thus, the spatial pattern of *P. halepensis* forests in eastern Spain reflects the influence of atmospheric circulation patterns on precipitation, and clearly demonstrates that these effects act through the control of variability of local precipitation in the region.

Several studies have reported that, in addition to precipitation, the winter NAO also exerts a marked influence on surface air temperature, and that its association with tree growth varies from northern (positive) to southern (negative) Europe (Piovesan and Schirone, 2000; Linderholm et al., 2003; Schultz et al., 2008), but in eastern Spain our results indicate an insignificant influence of temperature variability on both earlywood and latewood growth and support the view that most of the influence of the atmospheric circulation variability on tree growth is mainly driven through changes in precipitation.

The spatially constrained negative relationship between the winter NAO index and earlywood growth at northwestern sites in eastern Spain is consistent with results from earlier studies of Iberian conifer forests (Bogino and Bravo, 2008; Rozas et al., 2009). However, growth at xeric southwestern sites is also negatively related to the winter WeMO index, which can be explained by more winter precipitation, and consequent enhanced radial growth in spring during negative phases of the winter WeMO index (Martín-Vide and López-Bustins, 2006; González-Hidalgo et al., 2009; Vicente-Serrano et al., 2009). A similar result has been reported for the WeMO index in spring and *P. halepensis* forests in the middle Ebro basin (Ribas Matamoros et al., 2007). In contrast, we did not find any consistent relationship with the winter NAO index in the previous two winters. These results highlight the marked spatial variability in the effect of general atmospheric circulation patterns as drivers of tree growth, which may be a consequence of distance to the sea and the landscape relief.

Latewood formation in *P. halepensis* was negatively associated with the Mediterranean indices (WeMO, MO) at southeastern sites, suggesting a dependence on autumn precipitation. This finding suggests that autumn precipitation may be important for latewood formation in *P. halepensis*, which is consistent with phenological observations that cambial activity in this species can be greatly enhanced after summer because of sporadic autumn rainfall, which is usually produced by Mediterranean cyclonic activity (De Luis et al., 2007; Camarero et al., 2010). Furthermore, this finding agrees with the observed geographical trend of greater change in latewood width among consecutive years in southeastern sites as compared with northwestern sites.

An important finding of this study is the distinct influence of winter atmospheric circulation patterns on latewood formation in *P. halepensis*. Two explanations can be proposed for this observation. First, earlywood formation in *P. halepensis* is partly dependent on photosynthetic activity and moisture reserves supplied by precipitation prior to spring growth (Kagawa et al., 2006), and the amount of winter rainfall is inversely correlated with the NAO (Piovensan and Schirone 2000). In *P. halepensis*, earlywood is usually formed between March and June whereas latewood starts developing in July and ends its maturation in November (De Luis et al., 2007; Camarero et al., 2010). Thus, earlywood formation may be very dependent on the water supply and photosynthetic activity in late winter and early spring. Relative to southwestern sites, which are more subject to Mediterranean cyclonic activity, a high winter NAO index may be associated with low winter rainfall and reduced earlywood formation at northwestern sites, under the strong influence of Atlantic westerlies. Consequently, the greater degree of earlywood formation may result in an increase in hydraulic conductivity and the synthesis of more carbohydrates for latewood formation in summer and autumn (Camarero et al., 2010). A second and much less plausible explanation is that in those years with abundant winter rainfall (low winter NAO index) water is stored in deep soil layers, providing surface soil water for latewood growth in summer. The first explanation appears more likely, as xylogenesis studies support a functional link between earlywood and latewood growth, which show plastic responses to climatic conditions. For instance, at coastal sites cambial activity may occur for longer than at inland sites, where trees are subject to low winter temperatures and summer droughts (De Luis et al., 2007; Camarero et al., 2010). According to these authors, the transition between earlywood and latewood is linked to the temperature rise and the decline in soil water reserves between late spring and early summer (June–July), but xylogenesis processes are plastic. For instance, these studies indicate that earlywood may start late (e.g., April–May) in cold northwestern sites whereas latewood maturation may last up to December in warm southeastern sites. This cambial plasticity is consistent with other features of *P. halepensis*, which is a species that is well adapted to drought because of its ability to rapidly reduce transpiration by stomatal closure (Borghetti et al., 1998), and its capacity to make efficient use of water reserves that become available several months prior to growth (Sarris et al., 2007). The first explanation is also consistent with findings of allometric relationships between tree-ring width and maximum latewood density (Kirdyanov et al., 2007). Finally, since wood formation is an important sink of carbohydrates it would be interesting to compare how climate variability affects photosynthate allocation within the tree. It may be speculated that wet springs enhance earlywood and latewood formation, whereas carbohydrate allocation to regeneration of fine roots is given priority in response to dry springs.

Our analyses indicate that weather types also exert a relatively strong influence on earlywood and latewood growth, probably because of their indirect effect on local patterns of ultimate climatic drivers, including precipitation, solar radiation and temperature (Garfin, 1998). In winters characterized by extended periods of high pressure (i.e. a high frequency of N and anticyclonic weather types), earlywood formation was less than in other years. Explanations for these associations include the relationship of anticyclone weather types to dry and cold conditions in winter over the eastern Iberian Peninsula (Goodess and Jones, 2002). Very cold and dry winters may result in less photosynthetic activity in *P. halepensis*, and reduce the amount of carbohydrates available for earlywood growth during the following spring (Kagawa et al., 2006). In contrast, cyclonic activity linked to an increase in Atlantic westerlies (SW and W weather types) caused warmer and more humid conditions in winter than during anticyclonic periods, which enhanced earlywood formation and, probably through indirect effects, latewood development. In autumn, latewood development was enhanced by cyclonic conditions probably related to Mediterranean convection, as both E and SE (N and NW) weather types were positively (negatively) related to latewood growth. In the eastern half of the Iberian Peninsula, autumn rainfall is usually associated with easterly and southeasterly winds, and Mediterranean storms (Goodess and Jones, 2002; Beguería et al., 2009). An increase in autumn precipitation may enhance cambial activity in *P. halepensis* and co-occurring tree species after the summer drought (Camarero et al., 2010), and mild conditions may provide for a longer growing season, particularly at coastal southeastern sites (De Luis et al., 2007).

6. Conclusions

Our results indicate that large-scale atmospheric patterns (NAO, MO, WeMO) and local weather types influence earlywood and latewood formation in *P. halepensis* forests of eastern Spain. However, across this dendrochronological network both earlywood and latewood responded differently to atmospheric circulation patterns and weather types, suggesting that the predicted changes in atmospheric circulation will result in contrasting tree growth responses in the northwest and southeast areas of this Mediterranean region.

Thus, the forecast trend of increasing winter anticyclonic conditions and reduced activity of westerlies (high NAO and WeMO indices) are expected to reduce earlywood production in northwestern sites, whereas an increase of autumn cyclonic Mediterranean conditions (low WeMO and MO indices) will enhance latewood formation in southeastern sites.

As any change in the latewood/earlywood ratio will affect the hydraulic and mechanical properties of wood, and thus the physiological status of trees, our results suggest the need for further study of earlywood and latewood in dendrochronological networks of conifers growing under a wide range of climatic conditions, to provide critical information on the atmospheric drivers of tree growth and function.

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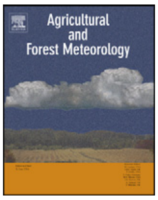

Impacts of drought at different time scales on forest growth across a wide climatic gradient in north-eastern Spain

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ABSTRACT

We analyzed the impact of drought measured on different time-scales on radial growth of eight tree species during the period 1950–2005 growing across a wide climatic gradient encompassing semiarid Mediterranean woodlands and wet mountain forests in north-eastern Spain. A drought index (standardized precipitation index, SPI) at different time scales (1–48 months) was correlated with chronologies of ring width to determine the significant time scale at which drought affected most tree growth. The findings indicated that the impact of drought on growth varied noticeably among species and sites. Two distinct patterns were clearly observed considering spatial and temporal differences in the response of species to drought. Species growing in xeric sites (*Pinus* and *Quercus* species and *Juniperus thurifera*) showed the highest responses to SPI time-scales of 9–11 months while those located in mesic sites (*Abies alba*, *Pinus sylvestris*) did respond more to SPI time scales shorter than 5 months. The SPI-growth correlations were significant, although weak, up to 30 months in xeric sites while no consistent association was observed at higher time scales. Important seasonal differences were noticed in the SPI-growth associations. Species growing in xeric areas responded to spring-summer SPI while those distributed in mesic sites responded more to summer SPI. Our findings should be useful to understand forest responses to climate change, including an increasing frequency of severe droughts, and to adapt appropriate management strategies to mitigate the impact of drought on tree growth.

1. Introduction

Water availability is one of the main climatic constraints for the tree growth in the Circum-Mediterranean forests. Thus, several studies have showed a strong correlation between precipitation and radial growth in different Mediterranean forests and tree species (Tardif et al., 2003; Macias et al., 2006; Andreu et al., 2007; Sarris et al., 2007; De Luis et al., 2009; Linares et al., 2010a; Carrer et al., 2010; Lebourgeois et al., 2010; Mérian and Lebourgeois, 2011). The impact of water deficit on growth is much higher in the most arid sites, in which the water availability largely constrains the main physiological processes of vegetation (growth, photosynthesis, carbon and nitrogen use), than in mesic sites (e.g., Vicente-Serrano et al., 2006, 2010a; Jump et al., 2006; Sarris et al., 2007; Martínez-Vilalta et al., 2008). Although the main patterns of precipitation-growth relationships are well known, the large seasonality and year-to-year variability that characterize precipitation in the Mediterranean region and the different site-dependent seasonality of tree growth in forests from this area may make very difficult to determine the response times of tree growth to the precipitation deficit. Furthermore, lags between water shortages and growth can appear as a function of different anatomical and physiological adjustments of trees to cope with drought, but also in response to drought severity and to the season in which water deficit occurs. All these mechanisms, either isolated or acting synergistically, can challenge the identification of drought impacts on tree growth.

Commonly drought indices are used with the purpose of solving the current problems of quantifying drought severity since it is very complex to determine the magnitude, duration and surface extent of droughts (Wilhite and Glantz, 1985; Redmond, 2002). Different drought indices have been developed to quantify the water deficit in an objective way, which is usually better than using the precipitation information itself (Keyantash and Dracup, 2002; Heim, 2002; Mishra and Singh, 2010). Drought indices are based on the quantification of the cumulative water shortages over a period of

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time. Some of the indices are based on soil water balance equations. The best example of this type of indices is the Palmer Drought Severity Index (PDSI, Palmer, 1965; Wells et al., 2004). Different studies have analyzed the influence of the drought conditions on tree growth using the PDSI (Orwig and Abrams, 1997; Kempes et al., 2008; Bhuta et al., 2009; Mundo et al., 2010). Nevertheless, although the PDSI can be useful to determine the severity of a drought, the index has several deficiencies (Alley, 1984; Weber and Nkemdirim, 1998), being its main shortcoming that it can only be calculated at a unique time scale (Guttman, 1998; Vicente-Serrano et al., 2010b). On the contrary, drought is a multi-scalar phenomenon, given the great variety of response times found in different hydrological, agricultural and environmental systems to the occurrence of water deficits (e.g., McKee et al., 1993; Ji and Peters, 2003; Vicente-Serrano and López-Moreno, 2005; Lorenzo-Lacruz et al., 2010; Quiring and Ganesh, 2010).

The problems involved with the use of PDSI have motivated the development of drought indices that can be calculated at different time-scales such as the standardized precipitation index (SPI) (McKee et al., 1993) and the standardized precipitation evapotranspiration index (SPEI) (Vicente-Serrano et al., 2010b). The quantification of droughts at different time scales is crucial to determine their ecological impacts, given the different physiological strategies of vegetation to cope with water deficit. Studies analyzing the drought impacts on vegetation activity using the SPI have showed contrasting responses according to the time scales at which drought affected vegetation activity and also depending on vegetation types (Vicente-Serrano, 2007) and environmental conditions for the same vegetation type (e.g., Ji and Peters, 2003; Quiring and Ganesh, 2010). At present, most studies that quantified the vegetation response to different drought time-scales have been carried out using remote sensing data for mid-term (10–30 years) datasets, which is related to the potential photosynthetic activity of the canopy or the leaf area of the forest (Vicente-Serrano, 2007). Nevertheless, presently there are a lack of studies analyzing the response of tree secondary growth to different time-scales of drought, which are quantified by means of multi-scalar drought indices. This methodological approach could improve the knowledge of the long-term responses of tree growth to water availability better than using precipitation data itself or other drought indices.

Currently, a deeper knowledge of the tree growth responses to water shortages in the Mediterranean Basin is a crucial task since General Climate Change Models predict a large reduction of precipitation and an increase of the evapotranspiration rates by the end of the twentieth-one century (Giorgi and Lionello, 2008; García-Ruiz et al., 2011). Forests are particularly sensitive to climate change because the long-life span of trees does not allow for a rapid adaptation to rapid environmental changes such as current climate warming (Andreu et al., 2007). As a matter of fact, various studies have provided evidence on the direct effect of drought on forest decline, particularly in Mediterranean forest ecosystems where water shortage is the main factor constraining growth (Sarris et al., 2007; Linares et al., 2010a; Sánchez-Salguero et al., 2010).

In this study we analyze the response of tree growth to different time scales of drought, quantified by means of the standardized precipitation index, in forests from north-eastern Spain, where a wide climatic gradient exists including diverse forest types such as Mediterranean woodlands under semiarid conditions to mountain forests under humid conditions. Furthermore, a trend towards more arid conditions (e.g., a decrease in spring precipitation) was observed during the late 20th century in the study area (González-Hidalgo et al., 2009, 2011; De Luis et al., 2010).

The objective of this study was to determine whether the use of multi-scalar drought indices is an effective way to determine the impact of the water deficit on growth, and whether this approach may detect different responses, in terms of magnitude and seasonality, in a variety of tree species and locations. The study includes eight tree species growing along the mentioned climatic gradient showing contrasting vulnerability to drought stress: four pine species (*Pinus halepensis*, *P. pinea*, *P. nigra*, *P. sylvestris*), silver fir (*Abies alba*), Spanish juniper (*Juniperus thurifera*), and two oak species (*Quercus faginea*, *Q. ilex*). These species represent species typically associated with mesic sites and humid conditions (e.g., *A. alba*), transitional locations (e.g., *P. sylvestris*) and xeric sites (e.g., *P. halepensis*).

2. Study area

The study area includes forests in Aragón, north-eastern Spain (Fig. 1). This area is subjected to Mediterranean influence with a typical summer drought and it is characterized by a strong climatic gradient ranging from semiarid conditions in the Middle Ebro Basin (mean annual temperature 15.0 °C, total annual precipitation 318 mm) to humid conditions in the Pyrenees (mean annual temperature 8.5 °C, total annual precipitation 1750 mm). In the Middle Ebro Basin the average temperatures in January and July are 6.7 °C and 26.0 °C, whereas in Pyrenean stations the means for both months are 1.5 °C and 16.8 °C, respectively (Cuadrat et al., 2007). Seasonal variability in precipitation is less pronounced in the Pyrenees than in the Ebro Basin, although summer is the predominant dry season in all study sites. In the Middle Ebro Basin there is a negative water balance (precipitation minus evapotranspiration), as a consequence of the high potential evapotranspiration (PET) that occurs in summer. Annual PET reaches 1300 mm in some sectors of this valley, which is the cause of very negative water balances. Moreover, in the Middle Ebro Basin the high temporal variability in precipitation introduces more limitations to vegetation growth, as severe droughts are frequent (Vicente-Serrano and Cuadrat, 2007), and periods of more than 80 days without precipitation are common (Vicente-Serrano and Beguería-Portugués, 2003). In the Middle Ebro Basin the lithology is characterized by millstones and gypsums (Peña et al., 2002), which contribute to aridity because there is poor retention of water by these soils (Navas and Machín, 1998). In the Pyrenees, soils are usually deep and basic and develop over limestone, sandstones and granites. The pre-Pyrenees form a mountain chain with a transitional sub-Mediterranean climate with a mean annual temperature of 11.1 °C and mean annual precipitation of about 950 mm (Cuadrat et al., 2007).

The study area contains very different forest types in terms of the dominant forest species and vegetation communities (Costa et al., 2005). Most of the studied forests are located in the mountain chains (Pyrenees and Pre-Pyrenees in the north, and the Iberian range in the south) forming pure mountain conifer (e.g., silver fir, *A. alba* Mill.) or mixed conifer-hardwood forests. In the northern study area, the Pyrenees and Pre-Pyrenees constitute transitional and mountainous areas between more humid conditions northwards or upwards and drier conditions southwards or downwards (Vigo and Ninot, 1987). In transitional areas of the Pre-Pyrenees and the Iberian range, forested landscapes comprise stands of *Pinus sylvestris* L., *Pinus pinea* L., *Pinus nigra* subsp. *salzmannii* (Dunal) Franco, *Q. faginea* Lam., and *Q. ilex* L. subsp. *ballota* (Desf.) Samp. In the semiarid Middle Ebro Basin the forests and open woodlands are dominated by *Pinus halepensis* Mill., with a few relict populations of *J. thurifera* L. The *P. halepensis* forests in the Ebro Valley commonly occur on the top and slopes of structural platforms developed on Miocene carbonate and marl sediments, whereas the valley bottoms have been traditionally used for agriculture and livestock grazing.

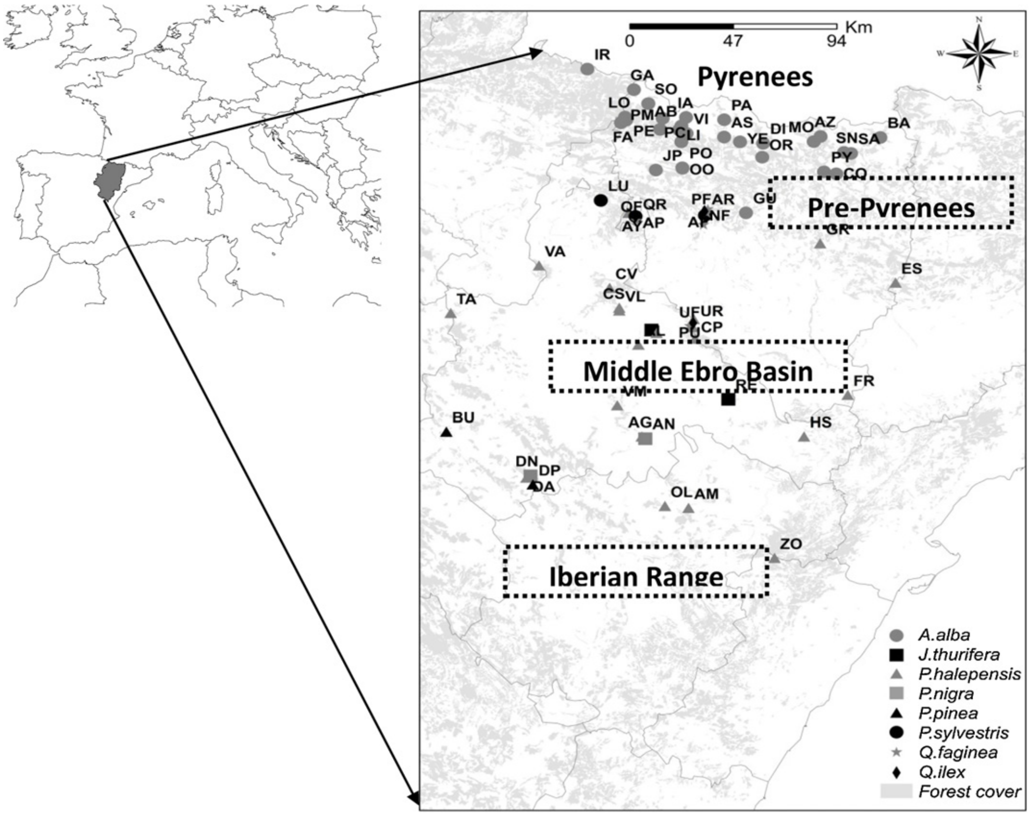

Fig. 1. Distribution of forests (gray area) in the north-eastern Spain and the location of study sites. Different symbols represent different forest species.

3. Methodology

3.1. Dendrochronological methods

Sites were selected based on the dominance of each species in the canopy over at least 1 hectare of fully forested area and the occurrence of stressing environmental conditions for tree growth such as steep slopes or shallow or rocky soils. The selected sites were considered to capture most of the climatically mediated growth variability of the studied species in north-eastern Spain. At each of the 67 sampled sites, 10–35 dominant trees were randomly selected and sampled (Table 1). At least two radial cores per tree were extracted at 1.3 m height using a Pressler increment borer. The cores were prepared following standard dendrochronological methods (Fritts, 2001). They were mounted and sanded until tree-rings were clearly visible with a binocular microscope. All samples were visually cross-dated and the ring width was measured to a precision of 0.001 mm and accuracy of ±0.0003 mm, using a LINTAB measuring device (Rinntech, Heidelberg, Germany). Cross-dating was evaluated using the COFECHA program (Holmes, 1983).

Each ring-width series was double-detrended using a negative exponential function and a spline function with a 50% frequency response of 32 years to retain high-frequency variability. Detrending and standardization involved transforming the measured values into a dimensionless index by dividing the raw values by the expected values given by the spline function. Autoregressive modeling was carried out on each series to remove temporal autocorrelation. The indexed residual series of all trees within each site were then averaged using a biweight robust mean to obtain mean site residual chronologies of ring width. We used the program ARSTAN to obtain the residual chronologies of ring width (Cook, 1985) which were used in all subsequent analyses. The quality of the chronologies was evaluated for the common period 1950–1999 using several dendrochronological statistics (Briffa and Cook, 1990): the mean width and standard deviation (SD) of the raw ring width series; the first-order autocorrelation (AC1) of raw ring width series, which measures the year-to-year persistence; the mean sensitivity (MSx) of the residual series, which quantifies the relative change in width among consecutive years; the mean correlation (R_{bar}) among individual series within each site; and the expressed population signal (EPS) of residual series, which indicates to what extent the sample size is representative of a theoretical infinite population. The common period 1950–1999 was selected because all chronologies showed EPS values above the 0.85 threshold for this interval, and this threshold is widely used in dendrochronological studies (Wigley et al., 1984). The statistical characteristics of the chronologies are shown in Table 1.

3.2. Drought index calculation

Among the existing drought indices (Heim, 2002; Mishra and Singh, 2010), only the SPI and the SPEI can be obtained at different time scales. The SPI is calculated using precipitation data exclusively. The index was developed by McKee et al. (1993) to identify the varied times of response of different hydrological systems to the precipitation deficits in a better way than other indices like the PDSI. The SPEI was developed by Vicente-Serrano et al. (2010b) to include both precipitation and temperature influence on droughts by means of the evapotranspiration processes. In this study, we used the SPI to analyze the influence of drought on tree growth since the responses of forests to long-term temperature anomalies can be very complex. An increase of evapotranspiration may have contrasting effects on tree growth depending on site conditions, the forest type and the amount of precipitation received. In drought-stressed areas an increase in the evapotranspiration rates will lead to a negative influence on tree growth, whereas in humid sites high evapotranspiration rates may enhance vegetation activity and

Table 1
Dendrochronological statistics of ring-width chronologies considering the 67 sites of the studied species for the common period 1950–1999.

Species	Site	Code	No. trees (no. radii)	MW (mm)	SD (mm)	AC1	MSx	R_{bar}	EPS
A. alba	Castiello de Jaca	CA	10 (20)	1.23	0.63	0.81	0.24	0.41	0.93
A. alba	Collubert	CO	12 (27)	2.75	1.20	0.83	0.17	0.33	0.92
A. alba	Guara	GU	10 (23)	2.92	1.18	0.70	0.20	0.55	0.96
A. alba	Orús	OR	11 (22)	1.73	0.63	0.73	0.20	0.51	0.95
A. alba	Peña Montañesa	PY	12 (21)	2.33	1.08	0.81	0.20	0.41	0.93
A. alba	Peña Oroel-high	OO	12 (24)	2.80	1.19	0.79	0.20	0.55	0.96
A. alba	Peña Oroel-low	PO	11 (23)	2.59	0.95	0.76	0.18	0.51	0.96
A. alba	San Juan de la Peña	JP	13 (28)	2.16	1.18	0.85	0.22	0.23	0.90
A. alba	Yésero	YE	12 (24)	3.44	1.43	0.77	0.20	0.43	0.94
A. alba	Irati	IR	13 (29)	1.83	0.89	0.87	0.17	0.36	0.94
A. alba	Fago	FA	11 (22)	1.34	0.73	0.71	0.29	0.54	0.97
A. alba	Paco Ezpela	PE	11 (22)	1.63	0.87	0.81	0.23	0.41	0.95
A. alba	Lopetón	LO	10 (23)	1.42	0.84	0.79	0.27	0.44	0.94
A. alba	Gamueta	GA	13 (26)	1.99	0.95	0.83	0.20	0.40	0.94
A. alba	Selva de Oza	SO	13 (25)	2.01	1.40	0.91	0.19	0.37	0.92
A. alba	Paco Mayor	PM	10 (22)	1.97	0.78	0.65	0.25	0.52	0.96
A. alba	Puente de los Corralones	PC	14 (27)	3.49	1.61	0.82	0.19	0.36	0.92
A. alba	Lierde	LI	11 (22)	2.96	1.37	0.86	0.18	0.45	0.94
A. alba	Los Abetazos	AB	12 (24)	4.46	1.95	0.97	0.16	0.33	0.90
A. alba	Izquierda del Aragón	IA	13 (25)	2.70	1.10	0.84	0.17	0.41	0.94
A. alba	Paco de Villanúa	VI	21 (42)	1.99	0.88	0.83	0.18	0.40	0.96
A. alba	Paco Asieso	AS	10 (20)	3.05	1.50	0.86	0.22	0.47	0.94
A. alba	Panticosa	PA	12 (23)	2.39	1.23	0.80	0.27	0.57	0.96
A. alba	Diazas	DI	12 (24)	2.66	1.12	0.82	0.21	0.54	0.96
A. alba	Montinier	MO	21 (30)	1.54	0.71	0.85	0.18	0.35	0.94
A. alba	Azirón	AZ	11 (22)	3.29	1.09	0.80	0.15	0.39	0.92
A. alba	Selva Negra	SN	14 (29)	2.89	1.11	0.84	0.16	0.33	0.92
A. alba	Collado de Sahún	SA	12 (29)	1.87	0.63	0.84	0.15	0.37	0.94
A. alba	Ballibierna	BA	11 (29)	2.09	0.69	0.82	0.15	0.39	0.95
P. halepensis	Agüero	AG	12 (24)	3.26	1.32	0.61	0.28	0.52	0.92
P. halepensis	Vedado de Peñaflor	PH	13 (29)	1.12	0.73	0.66	0.37	0.60	0.98
P. halepensis	Alcubierre	AL	15 (31)	1.55	1.50	0.79	0.46	0.59	0.97
P. halepensis	Alcubierre-Trincheras	AU	10 (14)	2.79	1.20	0.61	0.29	0.68	0.93
P. halepensis	Puerto de Alcubierre	PU	15 (22)	1.48	0.87	0.69	0.33	0.65	0.97
P. halepensis	Tarazona	TA	15 (30)	2.40	1.42	0.59	0.40	0.76	0.99
P. halepensis	Valareña	VA	16 (31)	1.81	1.14	0.74	0.36	0.62	0.97
P. halepensis	Castejón de Valdejasa	CV	13 (23)	3.35	1.37	0.78	0.27	0.44	0.90
P. halepensis	C. Valdejasa-Zuera	CS	12 (23)	1.14	0.73	0.60	0.43	0.68	0.98
P. halepensis	Valmadrid	VM	15 (30)	1.83	1.00	0.67	0.35	0.82	0.99
P. halepensis	Zorita	ZO	15 (29)	1.18	0.69	0.64	0.38	0.69	0.98
P. halepensis	Estopiñan del Castillo	ES	15 (27)	2.84	2.43	0.85	0.37	0.52	0.96
P. halepensis	El Grado	GR	15 (30)	2.29	1.17	0.70	0.30	0.53	0.97
P. halepensis	Oliete	OL	15 (27)	2.95	2.17	0.81	0.35	0.82	0.99
P. halepensis	Alloza	AM	15 (31)	1.45	1.00	0.72	0.39	0.73	0.99
P. halepensis	Villanueva de Gállego	VL	15 (29)	1.20	0.82	0.58	0.52	0.58	0.98
P. halepensis	Daroca	DA	14 (28)	2.06	1.17	0.50	0.44	0.82	0.99
P. halepensis	Ayerbe	AI	16 (33)	2.65	1.11	0.60	0.27	0.34	0.93
P. halepensis	Alcubierre-San Caprasio	CP	14 (27)	2.00	1.24	0.72	0.34	0.58	0.96
P. halepensis	Caspe	HS	16 (28)	0.76	0.59	0.56	0.65	0.72	0.99
P. halepensis	Fraga	FR	16 (29)	0.97	0.79	0.72	0.50	0.60	0.98
A. faginea	Agüero	QF	22 (44)	1.51	0.87	0.72	0.28	0.31	0.91
A. faginea	Arguis	AF	10 (20)	1.72	0.62	0.46	0.29	0.47	0.93
A. faginea	Nueno	NF	10 (20)	1.61	0.79	0.53	0.30	0.58	0.95
A. faginea	Pico del Águila	PF	10 (20)	1.83	0.62	0.32	0.30	0.50	0.98
A. faginea	Alcubierre	UR	33 (56)	1.61	1.00	0.43	0.44	0.70	0.99
A. ilex	Arguis	QR	10 (11)	1.34	0.56	0.37	0.34	0.32	0.91
A. ilex	Agüero	AR	10 (14)	1.16	0.60	0.32	0.44	0.46	0.92
A. ilex	Alcubierre	UR	10 (20)	0.95	0.73	0.26	0.51	0.52	0.94
J. thurifera	Retuerta de Pina	RE	35 (64)	1.09	0.71	0.61	0.42	0.56	0.90
J. thurifera	Peñaflor	PE	11 (19)	1.47	1.18	0.74	0.37	0.41	0.93
P. sylvestris	Agüero	AP	19 (37)	1.84	0.99	0.61	0.36	0.53	0.96
P. sylvestris	Luesia	LU	11 (15)	2.21	1.43	0.77	0.34	0.52	0.93
P. sylvestris	Monrepos	PS	11 (23)	1.50	0.99	0.79	0.29	0.45	0.95
P. pinea	Bubierca	BU	19 (37)	3.07	1.78	0.53	0.42	0.63	0.98
P. pinea	Daroca	DP	14 (28)	1.63	1.14	0.68	0.46	0.80	0.99
P. nigra	Agüero	AN	19 (34)	2.60	1.36	0.55	0.40	0.48	0.92
P. nigra	Daroca	DN	16 (33)	1.80	1.27	0.60	0.54	0.59	0.98

Statistics: Raw tree-ring width series: MW, mean ring width; SD, standard deviation; AC1, first order autocorrelation. Residual ring- width series: MSx, mean sensitivity; R_{bar}, mean interseries correlation; EPS, expressed population signal.

growth when soil moisture is not a constraining factor (Sabaté et al., 2002; Gaucherel et al., 2008; Vicente-Serrano et al., 2010a).

The precipitation data in the region has been obtained from a homogeneous and spatially dense dataset of daily observatories (Vicente-Serrano et al., 2010c). Nevertheless, since the available observatories are commonly located near populated areas, few stations are available in mountainous location where we sampled most of the forests. For this reason, the available punctual

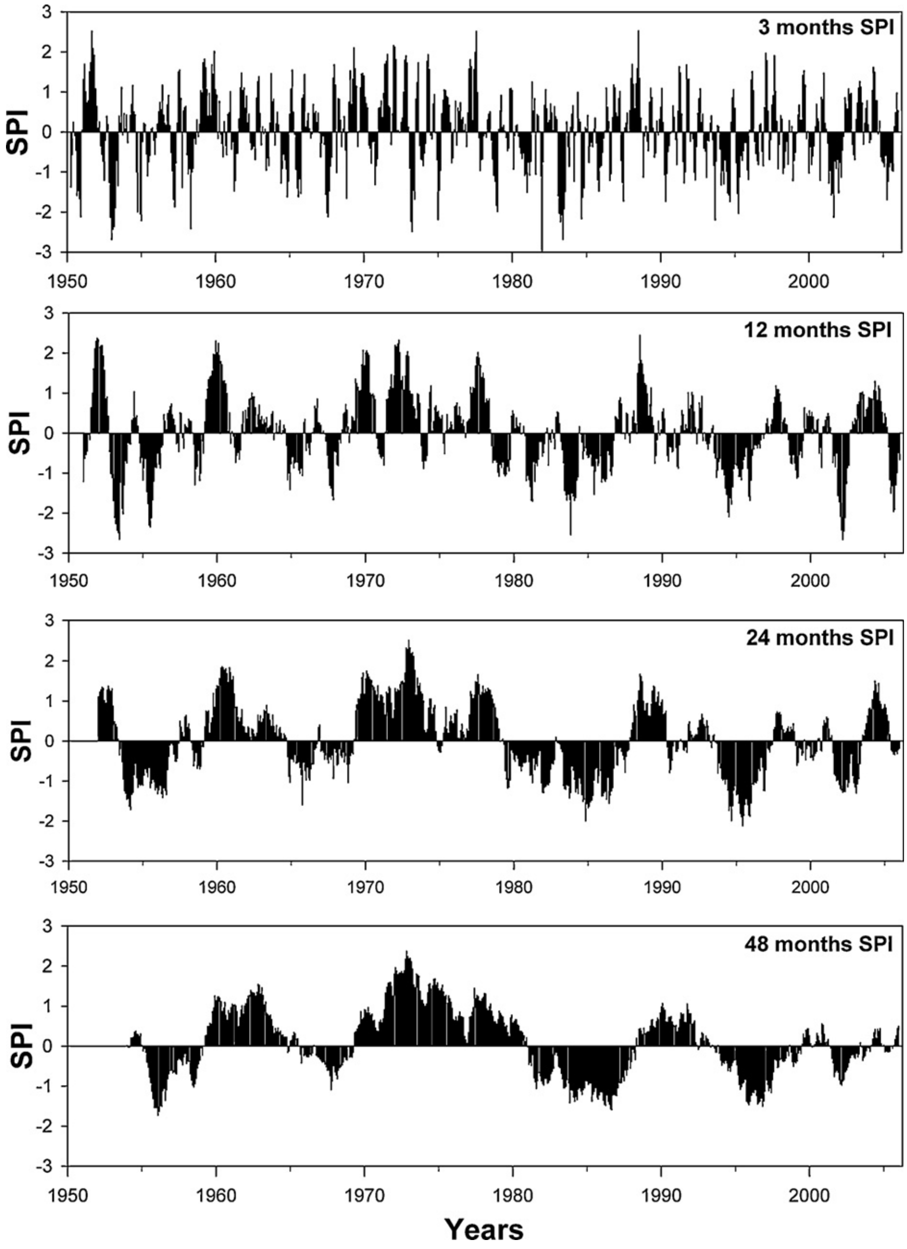

Fig. 2. Evolution of the drought index SPI at different monthly time scales in one of the forests of the study area (site AL, *P. halepensis* forest).

precipitation data was interpolated to have a regular grid with information in each one of the forests sampled. Monthly precipitation data between 1950 and 2006 was interpolated at a spatial resolution of 1000 m. To take into account the effect of the elevation on precipitation, and to have more reliable estimations for each forest, the interpolation was done using a Digital Terrain Model and a Geographic Information System (GIS)-assisted regression-based approach (Ninyerola et al., 2000, 2007; Vicente-Serrano et al., 2003, 2007). The precipitation in each 1000 m grid point was estimated, for each month between 1950 and 2006, by means of a stepwise-regression model, in which the independent variables were the elevation, the latitude and the longitude of each site. The residuals, i.e. the differences between the observations and the modeled precipitation, were also included in the estimations by means of a local interpolation procedure (splines with tension – Mitasova and Mitas, 1993) to include the local precipitation features recorded each month, which were not well represented by the regression models.

The validation of the grid layers was done for each monthly layer by a jackknifing method, based on withholding, in turn, one station out of the network, estimating regression coefficients from the remaining observatories and calculating the difference between the predicted and observed value for each withheld observatory (Phillips et al., 1992). This method has frequently been used in climatology (e.g. Daly et al., 1994; Holdaway, 1996; Hofstra et al., 2008). The average Root Mean Square Error for the different months and years was 15.2 mm, being lower in summer (6.5 mm) than in winter (22.3 mm). The D agreement index (Willmott, 1982) showed an average of 0.94 for the different monthly layers, with a range between 0.82 and 0.99, which indicates a high reliability between the observed and the modeled precipitation data.

We obtained an average monthly precipitation series for each one of the 67 sites using the gridded monthly precipitation data. From each one of the series, we obtained the SPI at time scales from 1 to 48 months for having a range of time scales to be compared with radial growth. The SPI was calculated by adjusting the

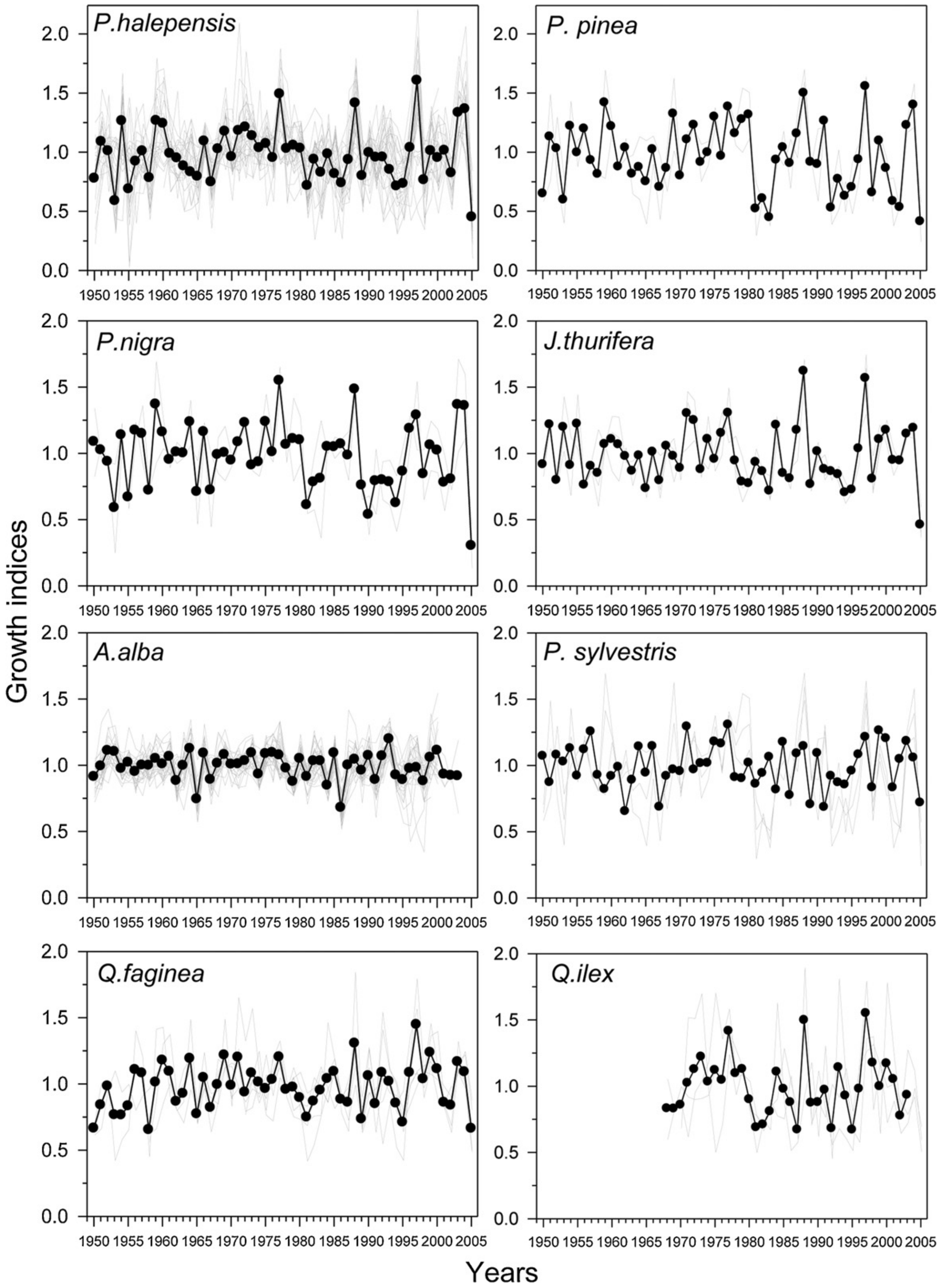

Fig. 3. Residual chronologies of ring width (gray lines) for all studied species network in north-eastern Spain, and the overall mean for each variable (black lines).

precipitation series to a given probability distribution. Initially, the Gamma distribution was used to calculate the SPI (McKee et al., 1993), but the Pearson III distribution was considered more robust due to its three parameters (Vicente-Serrano, 2006). The complete formulation of the SPI following the Pearson III distribution and the L-moments method for calculating parameters is described in Vicente-Serrano (2006) and López-Moreno and Vicente-Serrano (2008).

The Fig. 2 shows a representative example of the evolution of the SPI at the time scales of 3, 12, 24 and 48 months in one of the forest sites of the study area (site AL, *P. halepensis* forest). Droughts show high contrasted frequency as a function of the time scale. On

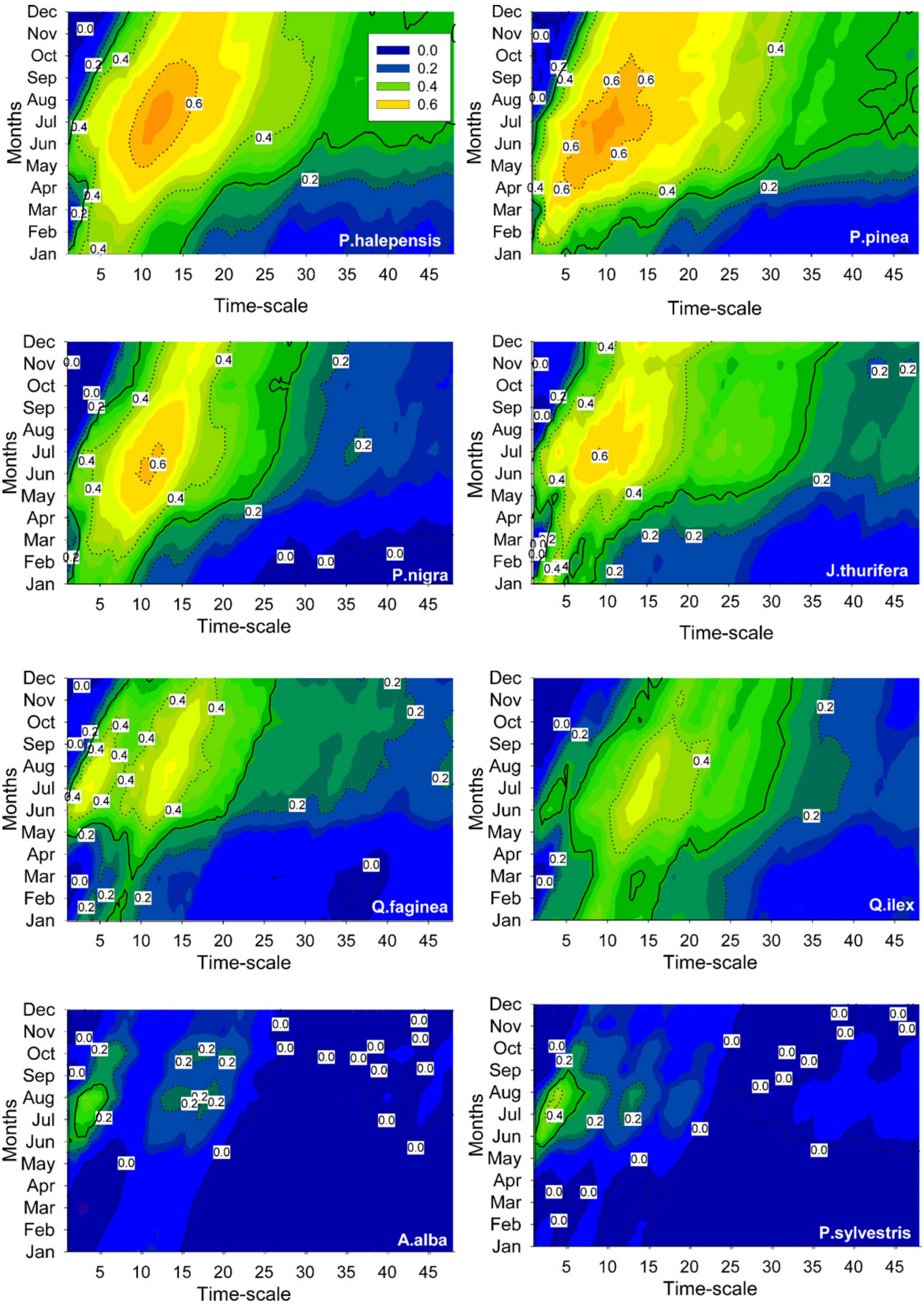

Fig. 4. Mean correlation coefficients between ring-width chronologies and monthly SPI series at different time scales and for the six species analyzed in this study. Bold lines frame significant correlations ($p < 0.05$).

the shortest time scales (e.g., 3 months), the dry and humid periods are short and occur at high frequencies. At long time scales (e.g., 24 and 48 months), droughts lasted longer, but were less frequent, with few dry or humid periods recorded.

3.3. Statistical analyses

To determine the influence of drought severity on tree growth, but also the drought time-scales that are affecting radial growth

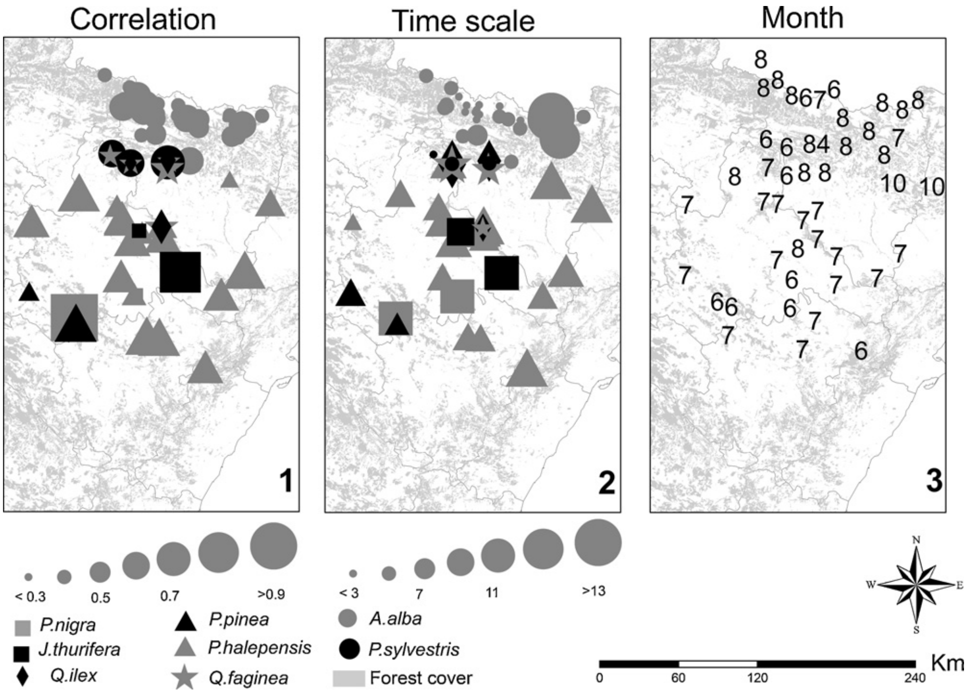

Fig. 5. Geographic variability of the growth-drought associations showing (1) maximum Pearson correlations between ring-width chronologies for all sites and the monthly SPI series (the symbols are proportional to the absolute correlation value), (2) time scale (in months) at which the maximum correlation was achieved; and (3) month of the year at which the highest correlation was reached. Symbols are as in Fig. 1.

of species and sites considered in the study, we carried out correlation analyses using the Pearson coefficient. Prior to calculating the correlations, the trend in each of the SPI time series was removed by assuming a linear evolution in each monthly series at the different time scales. Therefore, correlation analyses were performed between ring-width residual chronologies representing tree growth and detrended monthly SPI series representing drought severity for the period 1950–1999. To summarize the correlation analyses and to compare the drought impact among species, we also obtained an average correlation for all sites corresponding to a particular species. Moreover, the variability within species in terms of drought impact on growth was illustrated by selecting representative sites. The threshold for significant correlations was set at $P \leq 0.05$.

4. Results

4.1. Growth patterns

The mean ring width ranged from 1.15 mm (*Q. ilex*) to 2.39 mm (*A. alba*) across the studied dendrochronological network (Table 1). The AC1 values were highest in *A. alba* (0.81) and lowest in *Q. ilex* (0.31), while the MSx values were generally high for *P. nigra* (0.46), *P. pinea* (0.44), *Q. ilex* (0.43), *J. thurifera* (0.39) and *P. halepensis* (0.38), and low for *P. sylvestris* (0.33), *Q. faginea* (0.32) and *A. alba* (0.20). The highest R_{bar} and EPS values were observed for *P. halepensis* and the lowest were found for *A. alba*.

We observed similar high-frequency growth patterns for species from xeric sites (*P. halepensis*, *P. pinea*, *P.nigra* and *J. thurifera*) with growth reductions in 1953, 1961, 1981, 1989 and 2005 (Fig. 3). On the other hand, the periods characterized by substantial increase in radial growth included 1959, 1960, 1977, 1988 and 1997. Some of these sharp growth decreases and increases corresponded to severe droughts (e.g., 2005) and very wet years (e.g., 1997), respectively. *A. alba* showed a more stable growth pattern with growth reductions in 1965 and 1986, 1981, 1993 and 2001, while *P. sylvestris*, *Q. faginea* and *Q. ilex* showed inter annual variability in radial growth.

4.2. Species- and site-dependent associations between growth and drought

We found important differences in the responses of tree growth to the different time scales of the SPI (Fig. 4). In *P. halepensis* forests, significant correlations were found for time scales from 1 to 48 months. Nevertheless, for short time scales (1 to 3 months) significant correlations only appeared between May and July. In this specie the highest correlations ($r = 0.60–0.70$) were observed at time scales between 12 and 16 months during June, July and August. High correlations were also found between the SPI and the growth chronologies of *P. pinea* (maximum $r = 0.70$), *P. nigra* (maximum $r = 0.62$) and *J. thurifera* (maximum $r = 0.61$) considering spring (May), summer (June, July, August) and early-fall (September) months, particularly at time scales from 9 to 15 months. The remaining conifers (*A. alba*, *P. sylvestris*) did not show strong associations between growth and SPI and presented low and significant correlation coefficients ($r = 0.30–0.40$) during summer months for time scales between 2 and 5 months. A higher growth response to drought was observed for *Q. faginea* and *Q. ilex* since they showed significant correlations at time scales up to 25 months, mostly during summer and autumn months. *Q. ilex* showed lower growth-SPI correlations than *Q. faginea*, with association being significant only at time scales between 8 and 25 months. Independently of the magnitude of the association and the SPI time scale analyzed, the highest correlation coefficients between growth and the drought index were obtained in late-spring (May) and early-summer (June) months, the period when growth rates are usually maximum, and when water deficit is noticeable in most study sites.

4.3. Geographically structured growth-drought relationships

We detected a high site-to-site variability in the growth response to drought within the same species across the study region (Fig. 5). We observed a clear south-north gradient in the maximum correlations between growth and SPI. This gradient corresponded to maximum correlation values for sites located in the Middle Ebro Basin in the case of Mediterranean conifers (*P. nigra*, $r = 0.84$; *P. halepensis*, $r = 0.83$; *P. pinea*, $r = 0.81$; *J. thurifera*, $r = 0.75$) and oaks (*Q. faginea*, $r = 0.74$; *Q. ilex*, $r = 0.67$), intermediate values in sub-Mediterranean *P. sylvestris* forests from the Pre-Pyrenees ($r = 0.66$) and minimum values in Pyrenean mesic *A. alba* forests ($r = 0.64$).

Most species reached the maximum growth-drought correlations at time scales varying from 9 to 11 months, excepting *A. alba* and *P. sylvestris* which showed the maximum association at time scales lower than 5 months in most of their forests. Nevertheless, we also noted large differences of the maximum correlation time scales within species without any clear spatial pattern. Finally, irrespective of the tree species, the study site, the magnitude of the SPI-tree growth correlations and the characteristic time scale, the maximum correlations were commonly obtained in summer months (June to August), which indicates the relevance of water availability during the late growing season for tree growth.

5. Discussion

This study evaluated the impact of droughts on eight tree species forming forests distributed along a wide climatic gradient of north-eastern Spain by means of dendrochronological methods and using the standardized precipitation index. To the best of our knowledge, this is the first investigation exploring the relationship between tree growth and drought using multi-scalar drought indices. Particularly, the research has focused on the impact of different time scales characterizing drought intensity on radial growth, given that droughts may act on growth at different characteristic time scales. For instance, at short time scales dry and moist periods alter with a high frequency, but at long time scales droughts are less frequent but longer in duration (Hayes et al., 1999; Vicente-Serrano, 2006).

Our analyses revealed two distinct patterns in terms of the growth sensitivity to drought, depending on the time scale of drought and the studied species. Species growing in the Middle Ebro Basin under Mediterranean semiarid conditions (all *Pinus* species excepting *P. sylvestris*, *Quercus* species, *J. thurifera*) showed stronger growth responses to drought compared to those growing in mountainous areas from the Pre-Pyrenees and Pyrenees (*A. alba*, *P. sylvestris*) characterized by a humid and cold climate. It has been found previously that in xeric Mediterranean areas tree growth is mainly limited by low precipitation, while in mesic Mediterranean areas the main factors constraining growth are low temperatures (Richter et al., 1991; De Luis et al., 2007; Vicente-Serrano, 2007; Camarero et al., 2010). The high level of dependence on water availability of north-eastern Spanish forests has been also reported before mainly in pine and oaks species (Corcuera et al., 2004a,b; Andreu et al., 2007; Montserrat-Martí et al., 2009; Gutiérrez et al., 2011). Overall, these studies reported marked spatial variations in the response of forests to drought as a function of climate conditions, confirming that forests located in the driest sites are the most sensitive to drought occurrence.

Tree species growing in the driest sites of our study area, i.e. the Middle Ebro Basin, showed robust relationships ($r > 0.60$) with the SPI drought series at time scales between 9 and 11 months, which is a remarkable finding since it indicates that cumulative precipitation conditions during one year impact tree growth as illustrated by Sarris et al. (2007). The response of growth to drought time scales longer than 11 months decreased gradually but correlations were significant up to 30 months ($r > 0.30$). Beyond this threshold, the growth responses to drought was very low, indicating that precipitation recorded for periods longer that 30 months is not significantly affecting radial growth. Other studies that analyzed the relationships between precipitation and growth in semiarid sites showed that the correlations between two variables increased when considering the cumulative precipitation over a period of consecutive months (De Luis et al., 2009; Linares et al., 2010b). Thus, forest growth variability in similar drought-prone area is determined by the precipitation recorded during the year of tree-ring formation but also by the precipitation that fell in the previous year (Sarris et al., 2007). The use of a multi-scalar drought indicator allowed confirming this question in the analyzed forests. In the semiarid Middle Ebro Basin, the previous-winter soil water reserves are crucial for supporting tree growth during spring (Pasho et al., 2011). It has been found that spatio-temporal variations in soil moisture and related rainfall pattern determine the growth response to climate in most Iberian forests (Andreu et al., 2007). Soil types (limestone, gypsum) in the Ebro Basin valley may additionally intensify the effects of drought conditions on tree growth because they have low water holding capacity (Guerrero et al., 1999). All the studied species found in the Middle Ebro Basin showed the strongest growth response to drought during spring and summer months, which indicates that forest growth in the area is very dependent on spring and summer cumulative water deficit. First, most of these species show their maximum radial-growth rates between May and June (Camarero et al., 2010). Second, water deficit starts to affect markedly vegetation activity and plausibly growth in the study area as early as June (Vicente-Serrano, 2007). In addition, in the driest sites we found that the growth-drought correlation decreased at time scales lower than 9 months, showing that these forests may show certain adaptive capacity in response to short droughts.

The response of tree growth to drought greatly varied among species, being the maximum growth-drought correlation very high for *P. halepensis, P. pinea*, *P. nigra* and *J. thurifera* ($r = 0.60–0.80$), moderate for *Q. ilex* and *Q. faginea* ($r = 0.50–0.60$), and low for *P. sylvestris* and *A. alba* ($r = 0.40–0.50$). The variability of species responses to drought may indicate very different strategies and functional threshold in coping with droughts. The lower tree growth–drought correlations found in drought-tolerant oaks (e.g., *Q. ilex*) as compared with drought-avoiding pines (e.g., *P. halepensis*) could be related to the more efficient conductive elements (vessels in oaks *vs.* tracheids in conifers), a more conservative water and deeper root systems of the former as compared with the later species, which might mitigate the negative effects of short-term water shortages on tree growth (Hacke and Sperry, 2001; Willson et al., 2008). However, our results suggests that *Q. ilex* have showed a higher growth plasticity in response to drought, i.e. low growth-SPI correlations, in comparison to *Q. faginea*, suggesting a greater resistance to water constrains of the former as compared with the later species, which is in agreement with the low phenological activity of *Q. faginea* in summer (Corcuera et al., 2004a,b; Montserrat-Martí et al., 2009). *J. thurifera* also appeared to be affected moderately by drought despite this species is considered a drought-resistant species among the Iberian conifers and its radial-growth dynamics are very plastic in the response to drought and to episodic rains (Camarero et al., 2010).

Considering the *Pinus* species from the most arid study sites (*P. halepensis, P. pinea*, *P. nigra*), we detected a stronger response to cumulative droughts over a 11-months period and during spring and summer months in comparison to other co-existing species in the area. This indicates that tree growth in these pine species is sensitive to mid-term water deficits which agrees with the findings of Linares et al. (2010b), who found that *P. halepensis* growth in south-eastern Spain can be limited by drought during the summer prior to growth. Although pine species as *P. halepensis* are considered as drought-avoiding species, they may show functional growth thresholds in response to lasting and severe drought leading to growth decline and death (Novak et al., 2011). For instance, *P. halepensis* is adapted to the scarcity of soil water in the short-term due to summer drought by ceasing secondary growth and recovering it rapidly when water becomes available (Borghetti et al., 1998; Nicault et al., 2001; Rathgeber et al., 2005; De Luis et al., 2007, 2011). However, its growth may be much vulnerable to mid- and long-term droughts as our results support. Moreover, considering the fact that some of the studied sites represent the southernmost populations of some of the studied species in Europe (e.g., *A. alba*) and these stands are growing near the species' climatic tolerance, they may be affected severely by strong and lasting droughts leading to forest decline (Macias et al., 2006; Camarero et al., 2011).

We found no impact of long-term droughts on radial growth of mountain conifers from mesic sites (*A. alba*, *P. sylvestris*) which responded to short-term droughts of a duration lower than five months during summer. This association may be explained by the low water-use efficiency of *A. alba* which is a species whose photosynthetic rates are very sensitive to atmospheric drought (Guehl et al., 1991) and its growth rates respond to short-term cumulative water deficit in late summer (Camarero et al., 2011). In the case of *P. sylvestris* previous studies have clearly indicated that summer drought contrains growth and xylogenesis in *P. sylvestris* (Camarero et al., 2010; Gruber et al., 2010) and severe water deficit may even lead to drought-induced mortality (Martínez-Vilalta and Piñol, 2002; Sánchez-Salguero et al., 2010).

The response to drought was site-dependent and this variability among sites was greater in *P. nigra* and *Q. faginea* forests as compared with the other species. However, the number of sites sampled to capture the variability of both species was low in comparison to other well-replicated species such as *P. halepensis* and *A. alba*. In general, sites located in the driest areas of the Middle Ebro Basin showed a higher response to drought compared to those located in mesic mountainous areas where water availability is high. For example, growth in *P. halepensis* showed higher growth-drought correlations in the driest sites than in northern less xeric sites receiving more precipitation. Given the large intra-specific differences found in the study area, further studies are necessary to assess the relative roles of local conditions (topography, soil type, management history, etc.) on the growth responses to drought at different time scales particularly in those species with more sampled forests.

6. Conclusions

We have provided compelling evidence that multi-scalar drought indices are particularly useful for monitoring the impact of climate variability on forest growth because the response of tree growth to droughts is complex. The time scales over which precipitation deficits accumulate affecting noticeably forest growth vary among species and among sites within the same species. For this reason, drought indices must be associated with a specific time scale and assessed taking into account local conditions to be useful for monitoring impacts on forest growth as has been done with remote-sensing assessments of vegetation activity (Ji and Peters, 2003; Vicente-Serrano, 2007; Quiring and Ganesh, 2010).

In the current context of climate warming, several climate models have indicated that drought frequency and intensity are expected to increase in the Western Mediterranean Basin (Giorgi and Lionello, 2008). Increasing aridity is expected to cause growth decline and enhance mortality particularly in drought-sensitive species (Linares et al., 2010b; Gruber et al., 2010; Koepke et al., 2010). The approach used in this study for examining growth responses to drought at different time scales and considering multiple tree species and sites across a wide climatic gradient in north-eastern Spain may represent a first step in understanding and forecasting forest responses to future climate change.

7. Summary

The use of multi-scalar drought indices such as the standardized precipitation index is useful in determining and quantifying the drought impacts on tree growth. The eight tree species considered in this study across a wide climatic gradient in north-eastern Spain showed a high inter- and intra-specific (site-dependent) variability in terms of growth responses to drought, suggesting different mechanisms in coping with drought. Growth of tree species from in xeric sites responded strongly to mid- to long-term droughts lasting from 9 to 12 months, whereas species from mesic sites showed a lower short-term (1–5 months) response. In most cases the maximum association between growth and drought was detected from June up to August. The variability among species and sites to drought acting at different time scale could be attributed to species characteristics and local conditions of the sampled sites. If future climate warming causes more frequent and severe droughts in the future, many forests in the study area will be adversely and selectively affected. Our finding suggest the need for further studies of drought impacts on forests under a wide range of climatic conditions to provide a current spatial analogue on the influence of forecasted severe drought on tree growth and function in the future.

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ORIGINAL PAPER

Climatic impacts and drought control of radial growth and seasonal wood formation in *Pinus halepensis*

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Abstract Short- and long-term growth responses to drought and climatic influences still remain poorly understood. In this study, we investigated the impact of climatic drivers (temperature, precipitation) and drought, using the Standardized Precipitation Index (SPI) calculated at different time scales (1–48 months), on earlywood (EW) and latewood (LW) widths in *Pinus halepensis.* Nine forests subjected to dry summer conditions were sampled in Mediterranean semi-arid areas from north-eastern Spain. In addition, we explored the seasonal dynamics of cambial activity and wood formation in relation to short-term climate variability. We found two peaks of tracheid cell production corresponding to EW (May–June) and LW (mid-July–August) growth phases, associated with a sharp decrease in enlarging cells in early July in response to low water availability. In the period of analysis (1970–2005), EW growth was positively correlated with precipitation in previous December and current January, April, May and June, while it was negatively correlated with temperature in June and July. LW was correlated positively with minimum temperatures in January. Probably this was an indirect relationship as a consequence of increased EW width at higher January temperatures. Drought affected more negatively EW than LW formation as evidenced the higher SPI-EW correlation ($r = 0.72$) than the SPI-LW one ($r = 0.54$). The strongest EW response to drought was observed in July, whereas the highest LW response to drought occurred in September; and this seasonal pattern matched the phases of lowest EW and LW tracheid production. Under a future reduction of winter and spring precipitation, the studied forests may show a decrease in tracheid cell production, causing a decline of radial growth, a reduction in hydraulic conductivity and, indirectly, a hampered carbon uptake in such semi-arid woodlands.

Keywords Climate · Drought · Earlywood · Latewood · *Pinus halepensis* · Standardized Precipitation Index · Xylogenesis

Introduction

In Circum-Mediterranean forests, drought is considered as the main driver of the tree growth variability (Sarris et al. 2007). Climate change models project a decrease in annual mean precipitation and rising air temperatures over the Mediterranean Basin for the late twenty-first century leading to an increase in evapotranspiration (IPCC 2007; Giorgi and Lionello 2008; García-Ruiz et al. 2011). These trends towards increasing arid conditions in the region are expected to cause more frequent episodes of forest growth decline and mortality events as those already observed by some authors (Macias et al. 2006; Linares et al. 2009; Galiano et al. 2010; Sánchez-Salguero et al. 2010).

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Various studies indicate contrasting tree growth responses to drought (Martín-Benito et al. 2008; Koepke et al. 2010; Linares et al. 2010; Sánchez-Salguero et al. 2010). For instance, some authors (Abrams et al. 1998; Sarris et al. 2007) noted that trees growing in xeric sites showed declining radial growth trends and increased crown dieback and mortality in response to long-lasting droughts. However, other researchers argued that species growing in xeric locations develop adaptive features to withstand the negative effects of drought on growth by reducing water loss or increasing hydraulic efficiency, and by showing lagged growth responses or recovering rapidly after the drought (Bréda et al. 2006; Eilmann et al. 2009; McDowell et al. 2008).

Dendrochronology is a useful tool for providing information on climate–growth relationships based on year-to-year correlative approaches. However, these relationships must be compared with xylogenesis studies for capturing short term climatic influences on radial tree growth (Camarero et al. 1998; Rossi et al. 2008). Therefore, information regarding the phenology of xylem growth is required to better understand the processes underlying the effects of climate and drought stress on seasonal wood formation.

Pinus halepensis forests provide a valuable system to explore how drought measured at different time scales constrains radial growth. This conifer is one of the dominant tree species in the Western Mediterranean Basin and the most ecologically important species in semi-arid woodlands (Néeman and Trabaud 2000). *P. halepensis* is considered as a species well adapted to withstand drought by reducing growth as water availability decreases (Serre-Bachet 1992; Borghetti et al. 1998; Nicault et al. 2001; Rathgeber et al. 2005; De Luis et al. 2007; Camarero et al. 2010). The increasing aridity in the Mediterranean region could have important implications for the intra-annual growth dynamics of *P. halepensis* which could be reflected also in long-term (inter-annual) growth trends in this species. In addition, there are no studies analyzing jointly the intra- and inter-annual long-term responses of earlywood (hereafter abbreviated as EW) and latewood (hereafter abbreviated as LW) formation to climate and drought in *P. halepensis* forests from semi-arid areas.

In Circum-Mediterranean drought-prone forests, a deeper knowledge on the EW and LW responses to recurrent water shortages at several time scales is important for understanding how amplified precipitation variability will drive radial growth trends (Andreu et al. 2007). In a previous study on growth–drought relationships assessed at multiple time scales, we found that *P. halepensis* growth is highly sensitive to mid-term cumulative drought stress, particularly during summer (Pasho et al. 2011b). In this study, we aim at understanding how drought and climate variability affects the patterns of seasonal wood formation (EW and LW widths) of this species. We aim at providing a mechanistic basis concerning the long-term impacts of drought and climate on EW and LW production by studying xylogenesis processes (periods and production rates of different tracheid types) in a semi-arid *P. halepensis* forest. In addition, the current and post-drought (up to 2 years later) effects on growth of both wood types are investigated to quantify possible lagged effects of water deficit on seasonal wood production.

Our objectives were (1) to quantify the long-term (inter-annual) effects of climate and drought on EW and LW growth in *P. halepensis* forests from north-eastern Spain, and (2) to describe the intra-annual xylogenesis processes, including the seasonal wood production, for explaining the differential long-term responses of EW and LW production to climate and drought. The hypothesis of this study was that severe and long-term drought conditions will impact more EW than LW formation since EW tracheids mature when water deficit usually starts and their number and transversal lumen size reflect well the theoretical hydraulic conductivity of the tree, and, consequently its potential capacity to uptake carbon and grow (von Wilpert 1991). We also expect that the drought-induced reduction in EW production and hydraulic conductivity will lead to an indirect decrease in LW formation. The evaluation of these ideas is relevant for predicting the responses of Circum-Mediterranean *P. halepensis* forests from semi-arid areas to the forecasted aridification trends (IPCC 2007).

Materials and methods

Study sites

The study sites are located in central (Middle Ebro Basin) and southern (Teruel) Aragón, north-eastern Spain (see Table S1 in Supporting Information). The area is characterized by semi-arid Mediterranean continental conditions with a seasonal variability in precipitation and temperature, mostly evidenced in the Middle Ebro Basin (mean annual temperature is 13.1 °C, total annual precipitation is 558 mm) and less pronounced in southern Teruel (mean annual temperature is 10.6 °C, total annual precipitation is 1,021 mm) although summer is the predominant dry season in all studied sites. In the Middle Ebro Basin the water balance is strongly negative, as a consequence of the high potential evapotranspiration which reaches annual values of 1,300 mm in some of the driest sectors of this valley (Vicente-Serrano and Beguería 2003) and up to 800 mm in Teruel sites (Peña Monné et al. 2002). Moreover, the high year-to-year temporal variability in precipitation introduces additional constraints on tree growth, since severe droughts are frequent and periods of more than 80 days without precipitation are common (Vicente-Serrano and Beguería 2003). Furthermore, some of the forests in the Middle Ebro Basin grow on gypsum substrates which improve water penetration into soil, contributing to local aridity (Navas and Machín 1998).

Pinus halepensis Mill. is the dominant forest tree species in the study sites. This species commonly occurs in semi-arid sites, on the top and slopes of structural platforms developed on Miocene carbonate and marl sediments. The understory species are mainly Mediterranean shrubs and sub-shrubs such as *Quercus coccifera* L., *Rosmarinus officinalis* L., *Linum suffruticosum* L., *Genista scorpius* L. and *Thymus* species. In the less xeric sites (TA, PU, MP, PL and MA) (see Table S1), *P. halepensis* co-exists with other tree species such as *Quercus ilex* L. subsp. *ballota* (Desf.) Samp., *Quercus faginea* Lam., *Juniperus thurifera* L., *Pinus pinaster* Ait. and *Pinus nigra* Arn. subsp. *salzmannii* (Dunal) Franco.

Climatic data

To quantify climate–growth relationships at a local scale, we explored a large database of local meteorological stations and selected 14 of them located near the sampled sites (mean site–station distance is 14.5 km) with the longest climate series. From these stations, monthly and yearly variables of mean temperature (minimum, average and maximum) and total precipitation were collected for the period 1950–2005. We carefully controlled the data quality, including the reconstruction and homogenization processes to guarantee the data reliability. Details on the dataset can be found in Vicente-Serrano et al. (2010b) and El Kenawy et al. (2011). Trends in temperature and precipitation series were analysed by means of non-parametric Spearman's rank correlation test ($p < 0.05$) because it is less affected by the presence of outliers and non-normality of the series than parametric coefficients (Lanzante 1996).

Drought index calculation

To quantify the impact of drought on EW, LW growth we employed the Standardized Precipitation Index (SPI) (McKee et al. 1993), which has been accepted by the World Meteorological Organization as the universal meteorological drought index for effective drought monitoring and climate risk management (Hayes et al. 2011). The SPI allows determining the duration, magnitude and intensity of droughts at different time scales. The SPI is calculated using precipitation data and it allows identifying the different times of response of hydrological and ecological systems to the precipitation deficit. The SPI was computed by fitting the precipitation series to a given probability distribution. Initially, the SPI was calculated following a Gamma distribution (McKee et al. 1993), but further analyses indicated that the Pearson III distribution was more robust (see Vicente-Serrano 2006; Quiring 2009). We obtained for each forest the SPI at time scales ranging from 1 to 48 months to be compared with radial growth. Values of SPI above and below zero correspond to wet and dry conditions, respectively. Details of the method to calculate the SPI can be found in Vicente-Serrano (2006).

Xylogenesis

On March 2010, ten dominant *P. halepensis* trees were randomly selected in site PU (see Table S1). They were tagged and their diameter at breast height (dbh) was measured. Then, wood micro-cores (15-mm long and 2-mm thick) were extracted biweekly from April until December using a Trephor puncher (Rossi et al. 2006). Consecutive wood samples were collected 5–10 cm apart from each other, following a spiral up the stem (mean sampling height was 1.3 m) to avoid disturbance reactions caused by cambium wounds. Micro-cores contained at least the previous five tree rings and the developing cambial zone. Samples were placed in Eppendorf tubes containing a fixative solution (formalin–ethanol–acetic acid, 5:90:5). Micro-cores were cut to obtain transversal sections for histological analyses (Antonova and Stasova 1993). Before cutting, each micro-core was vertically oriented by marking the fibre orientation with a pencil under a stereomicroscope at 20 × magnification. We obtained from four to six sections per micro-core with 10–20 μm thicknesses using a sliding microtome (Anglia Scientific AS 200, Cambridge, UK). The sections were stained with 0.05 % cresyl violet. The mounted and fixed sections were examined under a light microscope (Olympus BH2; Olympus, Hamburg, Germany) within 10 min of staining at 100–500 magnification. Images were photographed with a digital camera (JVC 3.3 CCD GC-X3E; JVC, Yokohama, Japan) to verify cell counts and to distinguish EW and LW tracheids according to their lumen and cell wall thickness. To distinguish EW and LW tracheids, first we measured their lumens and double-wall thickness along five radial lines per tree using the November wood samples. Then, we followed Denne (1988) criterion, i.e., LW tracheids were regarded as those whose single cell-wall thickness multiplied by four were greater or equal to their lumen widths.

For each analysed wood sample, the following cell types were distinguished and counted along the radial files: cambial cells, radially enlarging tracheids, wall-thickening tracheids and mature tracheids (Antonova and Stasova 1993). The first cells with evident radial diameter increments, but still containing a protoplast enclosed by a thin primary wall, were regarded as the first radially enlarging tracheids. The end of radial-cell expansion and the onset of secondary cell wall formation were defined by the appearance of pit borders and cell corner rounding. Tracheid lignification corresponded to a color change from violet to blue. The maturation zone ended when visible traces of cytoplasm were not observed within the tracheid lumen and also when tracheids exhibited completely blue cell walls. The onset of xylem formation was regarded as the date when at least five trees showed more than one row of cells in the cell-enlargement phase. The ending of xylogenesis was considered the date when all trees lacked tracheids corresponding to the wall thickening phase.

Dendrochronological methods

Dendrochronological methods were used to quantify the temporal patterns of EW and LW widths in the studied sites. Forests were selected based on: (1) the dominance of *P. halepensis* in the canopy over at least 1 ha of fully forested area, and (2) the occurrence of harsh environmental conditions potentially constraining tree growth such as steep slopes, shallow or rocky soils. At each of the nine sampling sites, we randomly selected 15–20 trees within a 1,500 m long and 100 m wide transect randomly located within the stand and measured their dbh (Table S1). Distance between trees was always greater than 10 m to avoid capturing local effects on tree growth due to spatial autocorrelation. Two radial cores per tree were extracted at 1.3 m height using a Pressler increment borer. The cores were prepared following standard dendrochronological methods (Fritts 2001). They were air-dried, mounted and sanded with sandpapers of progressively finer grains until EW and LW were clearly visible under a stereomicroscope. All samples were visually cross-dated and the EW and LW widths were measured to a precision of 0.001 mm (accuracy ± 0.0003 mm), using a LINTAB measuring device (Rinntech, Heidelberg, Germany). We distinguished EW and LW based on the cross-sectional area of tracheids and the thickness of their walls and following previous dendrochronological and xylogenesis studies on *P. halepensis* (De Luis et al. 2007; Camarero et al. 2010). The visual cross-dating was evaluated using the COFECHA program (Holmes 1983).

To retain the high-frequency variability of growth, each EW or LW series was double-detrended using a negative exponential function and a spline function with a 50 % frequency response of 32 years. Detrending and standardization involved transforming the measured values into dimensionless indices by dividing the raw values by the expected ones given by the negative exponential and spline functions. Autoregressive modelling was carried out on each series to remove the temporal autocorrelation. The indexed pre-whitened residual series of all trees within each site were then averaged using a biweight robust mean to obtain mean site residual chronologies of ring width, which were used in subsequent analyses. We used the program ARSTAN to obtain the residual site chronologies (Cook 1985).

The characteristics of the chronologies were evaluated for the common period 1970–2005 using several dendrochronological statistics (Briffa and Cook 1990): the mean width and standard deviation (SD) of the EW and LW raw width series; the first-order autocorrelation (AC1) of these raw series, which measures the year-to-year persistence; the mean sensitivity (MSx) of the residual series, which quantifies the relative change in EW or LW width among consecutive years; the mean correlation (Rbar) among individual series within each site; and the expressed population signal (EPS) of residual series, which indicates to what extent the sample size is representative of a theoretical infinite population. The common period 1970–2005 was selected as the interval for which all chronologies showed EPS values above the 0.85 threshold for this interval and were considered being well replicated (Wigley et al. 1984).

Statistical analyses

The climate–growth relationships were quantified using the residual EW and LW chronologies of each site and the detrended climate series of monthly mean temperatures, mean minimum and maximum temperatures and total precipitation. Correlations were computed over the common period 1970–2005 using a 15-month window from August of the year prior to growth (year $t-1$) until October of the year of tree-ring formation (year t). According to the previous studies, this window encloses the most influential period for radial growth of *P. halepensis* (De Luis et al. 2007; Camarero et al. 2010). We also obtained the percentage of EW and LW growth variability explained by climate (minimum, average, maximum monthly temperature and monthly precipitation) in each site (R^2adj, adjusted R^2) through multiple linear regressions, based on a stepwise forward selection of significant variables ($P \leq 0.05$), calculated between EW and LW indices and the local monthly climatic data.

To quantify the impact of drought severity on tree growth at different time scales, we performed superposed epoch analysis (SEA) (Haurwitz and Brier 1981) and correlation analyses with SPI based on the Pearson's coefficient. SEA was used to detect the drought impacts on EW and LW formation by calculating deviations in EW or LW width 2 years after selected droughts. According to SPI data, we selected four dry years (1967, 1986, 1994 and 2002) with values close to SPI $= -1$, i.e., experiencing mild to severe drought. We assessed the significance of mean tree growth response to these extremely dry years (Orwig and Abrams 1997). We used the software *Resampling Stats* to select 10,000 random sets of 3 years from each EW or LW width series and to estimate the confidence intervals ($P < 0.05$) for the growth deviations (Bruce 1991).

Before assessing the correlations between SPI and EW or LW width indices, the trend in each SPI time series was removed by fitting a linear tendency in each monthly series at the different time scales (for details see Pasho et al. 2011a). This step avoided that possible SPI trends could disrupt potential relationships. Then, correlation analyses were performed for the period 1970–2005 between EW and LW residual chronologies representing forest growth at sampled locations and detrended monthly series of 1 to 48 months SPI representing drought severity. The threshold for significant correlations was set at $P \leq 0.05$ for all correlation analyses.

The periods of maximum intra-annual growth were identified by transforming the cumulative number of EW and LW tracheids into daily rates of tracheid production (cells day^{-1}). This was achieved by dividing the difference of the total number of tracheids formed in successive dates (ΔN) by the time interval (Δt) between both dates (Camarero et al. 1998).

Results

Climatic trends

The annual climatic series showed opposite trends for annual mean temperature (increasing) and annual precipitation (decreasing) since 1950, suggesting an aridification trend in the study area during the last half of the twentieth century (see Fig. S1, Supporting Information). The mean annual temperature rose significantly ($P \leq 0.05$) between +0.01 and +0.03 °C in all sites while the annual precipitation declined from −0.75 to −2.88 mm year^{-1}, although this decrease was not significant. Warm and dry conditions prevailed in the 1960 s, 1980 s and 1990 s, whereas low temperatures were recorded in the early 1970 s. Minimum annual precipitation values were detected in the period 1991–1995 for most sites but similar low water records also occurred before (e.g., 1985).

Growth patterns

The mean width values of EW varied among sites more than those of LW (EW, 0.68–1.91 mm; LW, 0.18–0.54 mm) (Table 1). The average values of AC1 and MSx were higher for the EW (AC1 = 0.65, MSx = 0.44) than for the LW (AC1 = 0.53, MSx = 0.43) chronologies. Similar results were obtained for Rbar and EPS, considering EW (Rbar = 0.70, EPS = 0.93) and LW (Rbar = 0.56, EPS = 0.89) width series. Thus, EW chronologies showed a greater year-to-year persistence (AC1), a higher relative change between consecutive years (MSx) and a higher common signal (Rbar, EPS) than LW ones. The within-site correlation between EW and LW series varied from 0.38 (site PL) to 0.75 (site CS) and it was always significant ($P \leq 0.05$). On an average, 32 % of LW width variability was related to EW width variability.

We observed similar high-frequency growth patterns for EW and LW width series with growth reductions in 1955, 1958, 1962, 1981, 1986, 1994, 2000 and 2005 (Fig. 1). The periods characterized by substantial increase in EW and LW width corresponded to the years 1954, 1959, 1977, 1988, 1997 and 2004. These sharp growth decreases and increases coincided with dry (SPI < 0) and wet conditions (SPI > 0), respectively.

Climate–growth relationships

On average the proportion of growth variance explained by climate was generally higher for EW (62.7 %) than for LW (45.3 %) and varied among sites (Table 1). Mean correlation coefficients revealed positive responses of EW growth to current spring and summer precipitation (April, May and June) and negative ones to temperature variables, particularly to mean maximum temperatures in May, June and July (Fig. 2). Wet conditions and high minimum temperatures in the previous December and the current January favored EW development whereas LW growth was also enhanced by high minimum temperatures in January.

Intra-annual dynamics of wood formation

Climatic conditions during 2010 were within the range of the local long-term climatology based on the data from a nearby meteorological station with mean annual temperature of 15.3 °C (long-term mean = 15.0 °C) and total precipitation of 267 mm (long-term mean = 327 mm) (see Fig. S3A in the Supporting Information). Considering monthly values in 2010, April and July temperatures and April rainfall amount were above long-term mean values, whereas May precipitation was below climate normal periods. Xylem formation had already started in March and xylogenesis was active until November (Fig. 3). The cambial activity followed a unimodal pattern, with two major peaks (May–June and mid July–August) of tracheid formation corresponding respectively to the enlargement and wall-thickening phase (Fig. 3). These two phases match with the periods of maximum EW and LW formation in that order (Fig. 4). The rate of EW tracheid production was higher (0.38 cells day^{-1}) than that of LW

Table 1 Dendrochronological statistics of earlywood (EW) and latewood (LW) *P. halepensis* chronologies for the common period 1970–2005

Site	No. trees (No. radii)	Period	Correlation EW–LW	Earlywood						Latewood					
				MW ± SD (mm)	AC1	MSx	Rbar	EPS	R^2adj (%)	MW ± SD (mm)	AC1	MSx	Rbar	EPS	R^2adj (%)
VM	17 (30)	1959–2009	0.61	1.39 ± 0.81	0.59	0.44	0.80	0.99	80.30	0.39 ± 0.21	0.52	0.47	0.56	0.95	72.45
CV	13 (23)	1928–2009	0.47	1.75 ± 0.94	0.75	0.38	0.47	0.89	82.85	0.54 ± 0.33	0.71	0.34	0.50	0.86	64.06
CS	13 (23)	1900–2009	0.75	0.68 ± 0.37	0.41	0.47	0.64	0.97	40.04	0.18 ± 0.10	0.39	0.44	0.62	0.91	18.33
VA	17 (31)	1925–2009	0.74	1.28 ± 0.75	0.62	0.43	0.68	0.92	54.01	0.37 ± 0.22	0.58	0.43	0.51	0.86	41.92
TA	14 (27)	1927–2006	0.57	1.91 ± 1.22	0.59	0.50	0.78	0.97	44.68	0.43 ± 0.24	0.35	0.48	0.52	0.85	24.60
PU	15 (22)	1943–2009	0.58	0.85 ± 0.43	0.60	0.38	0.69	0.85	50.10	0.30 ± 0.16	0.56	0.40	0.54	0.88	29.10
MA	15 (28)	1963–2009	0.60	1.49 ± 1.27	0.75	0.53	0.81	0.94	64.51	0.38 ± 0.26	0.53	0.46	0.69	0.93	46.54
PL	15 (30)	1961–2009	0.38	1.35 ± 1.08	0.73	0.49	0.79	0.94	70.67	0.39 ± 0.25	0.53	0.44	0.61	0.92	50.87
MP	14 (29)	1965–2009	0.52	1.53 ± 1.26	0.81	0.37	0.68	0.93	77.61	0.38 ± 0.22	0.61	0.37	0.49	0.90	59.49
Mean	–	–	0.58	1.36 ± 0.86	0.65	0.44	0.70	0.93	62.75	0.37 ± 0.22	0.53	0.43	0.56	0.89	45.26

Statistics: *EW–LW* Pearson correlation coefficient calculated between the residual earlywood and latewood chronologies for each site. Raw-data series: *MW* mean width, *SD* standard deviation of width, *AC1* first-order autocorrelation. Residual series: *MSx* mean sensitivity, *Rbar* mean interseries correlation, *EPS* expressed population signal, R^2adj adjusted R^2 obtained relating monthly climatic variables and EW, LW residual chronologies through stepwise linear regressions. The last line provides the mean values for all sites, considering statistics calculated for raw ring-width data (MW, SD, AC1) and residual chronologies (MSx, Rbar and EPS)

(0.22 cells day^{-1}). The EW tracheid formation started in late March and finished in September in most trees whereas the first LW tracheids were formed in July and the last ones were observed in November (Fig. 3).

Drought–growth relationships

The SEA revealed differences in the annual deviations of EW and LW widths in response to drought. Significant decreases in EW width were observed in five out of nine sites during the year of drought whereas only one site showed a significant reduction in LW width 1 year after the drought (Table 2). The mean deviations in EW and LW widths during the drought year were −0.48 and −0.31, respectively, whereas they showed similar responses up to 2 years after the drought.

The correlations between EW and LW growth indices and the different SPI time scales reached maximum values at similar time scales (10–14 months), despite significant correlations were found up to 48 (EW) or 35 (LW) months (Fig. 4). The strongest responses of EW to drought intensity ($r = 0.70$–0.72) were observed in July, whereas LW responded strongly ($r = 0.54$) to SPI September values. We also detected certain variability among sites in the EW and LW growth responses to drought (Fig. S2). The strongest response of EW growth to drought was found for the sites VM, CV, CS, VA, whereas the sites TA, PU, MA, PL and MP were less affected by drought. The same pattern was also observed with respect to LW growth. The months when we detected the highest responses of EW and LW width to drought at inter-annual scales coincided with those in which we observed low production rates of EW (July) and LW (August–September) tracheids at intra-annual scales (Fig. 4). Finally, the maximum production rates of EW (May–June) and LW (mid July–August) tracheids occurred approximately one month before the strongest impact of drought on inter-annual EW and LW growth series was detected.

Discussion

In this study, we evaluated the impact of climatic drivers and drought stress on earlywood (EW) and latewood (LW) formation at inter- and intra-annual scales in *P. halepensis* forests from semi-arid areas. Climatic factors and drought highly impacted both components of the tree ring in the short and long terms, particularly EW production. At the intra-annual scale, the EW production was enhanced by relatively high rainfall amounts in April, May and June, whereas the production of radially enlarging tracheids, which are closely linked to the radial-growth rate (Larson 1994), was sharply reduced during the dry period (July–August) (see Fig. S3B in the Supporting Information). Interestingly, the LW tracheid production was intensified as a response to high summer temperatures and low water availability. These climatic conditions are linked to the cessation of EW tracheid production and may trigger the formation of LW tracheids and enhance cell-wall lignification as reported previously (von Wilpert 1991; Jyske et al. 2010).

In drought-stressed *P.halepensis* forests, water availability constrains the rate of EW tracheid production while temperature can be considered as the main climatic driver

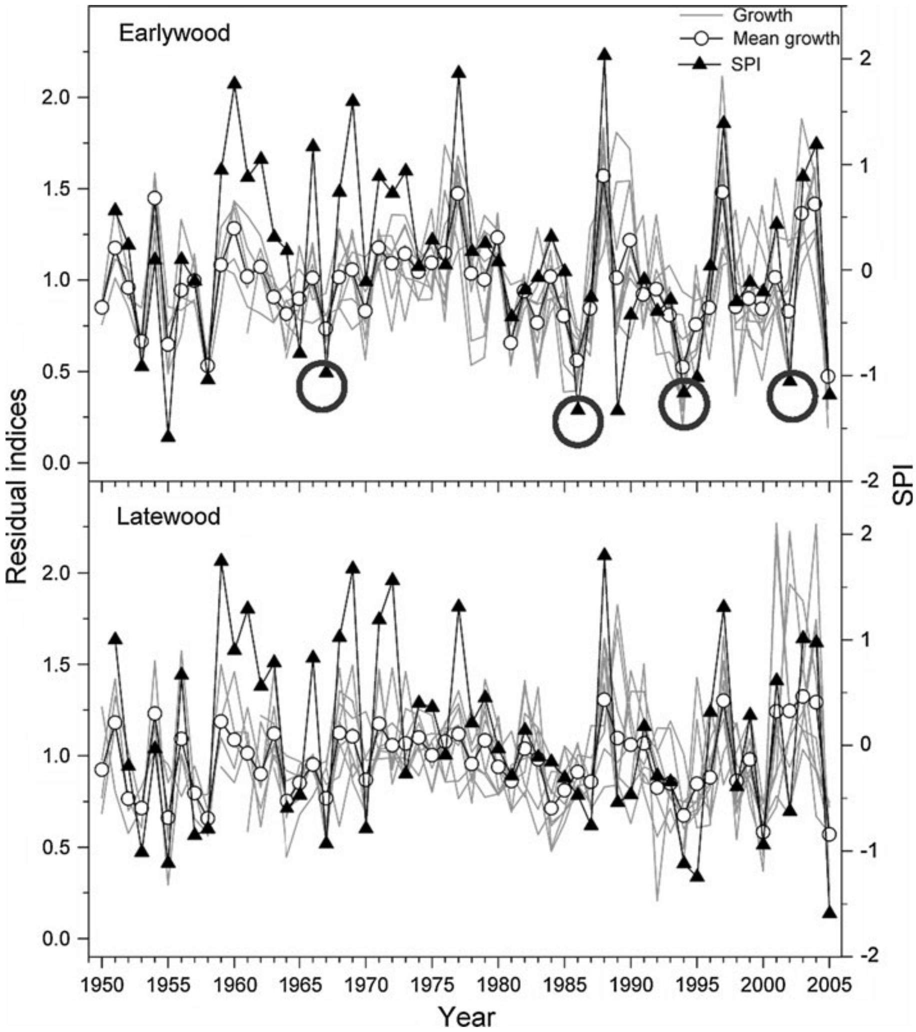

Fig. 1 Residual chronologies of *P. halepensis* earlywood (EW) and latewood (LW) width (*gray lines*) for the studied sites and their overall means (*lines with empty circles*). *Black lines* with *triangles* show the evolution of the drought index (SPI, mean of all sites) at time scales of 12 months in July and September, the scale at which EW and LW growth series responded more strongly to the SPI drought index. Note that positive and negative SPI values indicate wet (high EW and LW indices) and dry conditions (low EW and LW indices), respectively. Selected dry years (1967, 1986, 1994 and 2002) for the study of growth deviations are *encircled* in the *upper graph*

determining the onset and ending of tracheid production (Camarero et al. 2010). The low cambial activity of *P. halepensis* in summer appears to be triggered by high temperatures and the decrease of precipitation, i.e. low soil water availability (Camarero et al. 2010). However, the ability to maintain tracheid production, although at a reduced rate, during the dry summer months (Serre-Bachet 1992) is most likely due to the high hydraulic activity and the deep root system of *P. halepensis* which enables it to make use of deep soil water reserves (Borghetti et al. 1998). The continuation of LW production also in late November is most likely favoured by wet conditions and mild temperatures in autumn as found in a previous study (Camarero et al. 2010).

The decrease in EW and LW production rates in July and August–September respectively, indicates that *P. halepensis* reduces tracheids formation when precipitation deficit surpasses a functional threshold. As a matter of fact, this relationship was also observed in the responses of EW and LW growth to long SPI time scales indicating that there may be a synchronized response of intra- and inter-annual growth in this species to drought conditions. This response to drought stress might be linked to the physiological and growth adjustments of this species to cope with the scarcity of soil water, including a decline in photosynthesis rates, carbon uptake, needle elongation and wood formation as shown previously (Borghetti et al. 1998; Camarero et al. 2010).

At the inter-annual scale, the regression analyses indicate that EW and LW series are responding to the limitations imposed by the climatic factors as shown by the relatively high values of adjusted R^2, particularly in the case of EW series. Comparing EW and LW chronologies, the former showed a greater year-to-year variability (MSx) and a higher tree-to-tree common variance (Rbar) than the later did. However, the EW and LW series presented a strong within-ring correlation indicating a dependence of LW formation on previous EW growth. In general, the EW and LW chronologies of the nine sampled sites showed a strong common signal related to climatic factors, mostly in response to spring and early summer rainfall amounts. This is particularly the case of EW, whose formation in

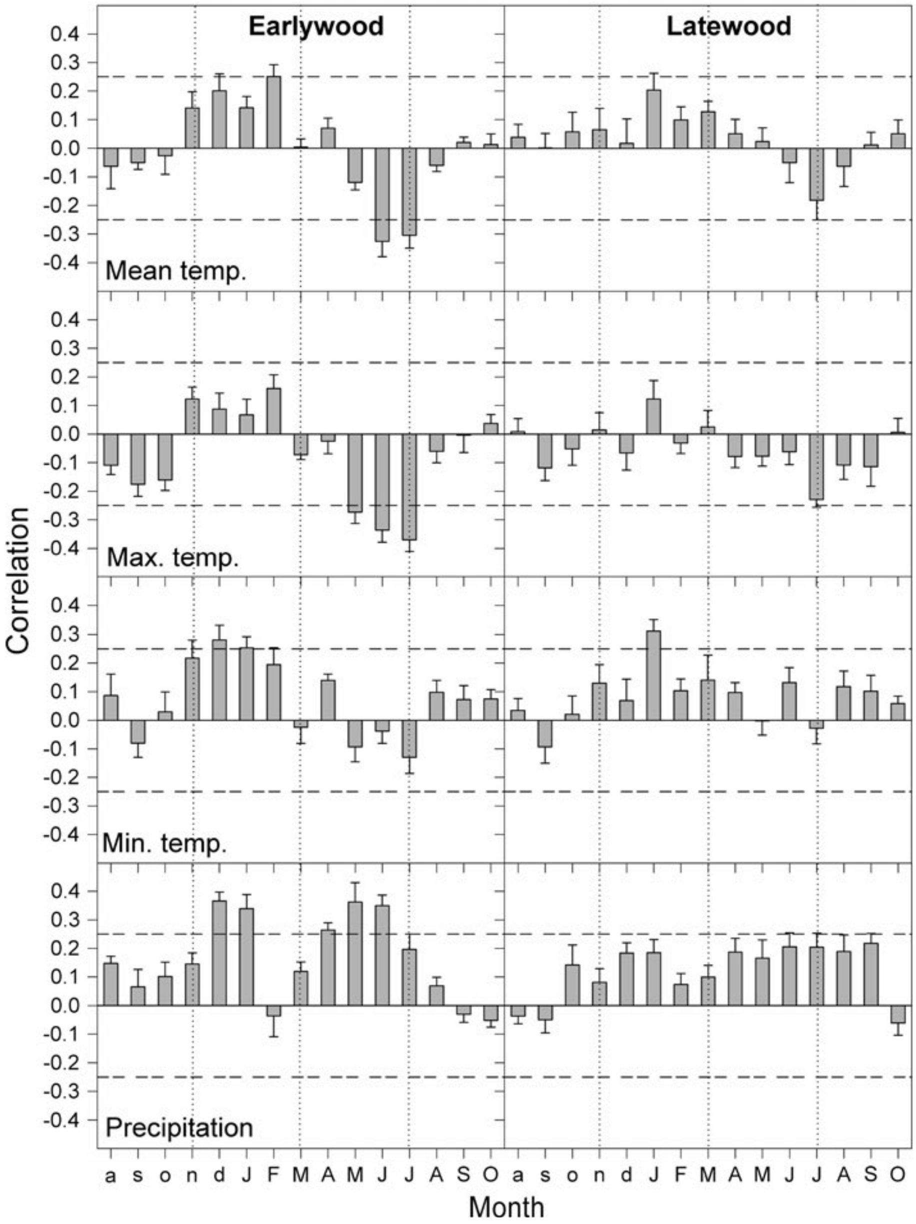

Fig. 2 Mean (±SE) correlation coefficients calculated between earlywood and latewood width chronologies of the nine study sites and monthly climatic variables (mean temperature, mean maximum and minimum temperatures, and total precipitation). Growth is related with climate data from the previous August to current October of EW and LW formation. The significance level ($P \leq 0.05$) is indicated by *dashed horizontal lines*

P. halepensis sites from semi-arid areas usually peaks in that period. This means that water availability in the period when the maximum rates of EW tracheid formation occur is among the most critical factors for radial growth with cascading effects on water conduction and carbon uptake. An improved production of EW tracheids with wide lumens in response to wet spring conditions may result in an increase of hydraulic conductivity and photosynthesis leading to the synthesis of more carbohydrates for LW formation in summer and autumn (Camarero et al. 2010).

The positive (negative) correlation between EW growth and April, May and June precipitation (maximum temperatures) suggest that this growth component of the ring may be very susceptible to water deficits during the early part of the growing season. High temperatures increase water deficit which affects photosynthetic and tracheid division rates, constraining radial growth (Hsiao 1973; Linares and Tiscar 2010; Vicente-Serrano et al. 2010a). The high sensitivity of EW to maximum July temperatures indicates that growth decline of the study species may be caused by warming-induced drought stress. On the other hand, the positive association of EW growth with December and January minimum temperature and precipitation suggests that warm minimum (night) temperatures and wet conditions in winter can favour an earlier and longer growing season for *P. halepensis* as reported previously (De Luis et al. 2007; Camarero et al. 2010). The only explanation we found for the significant positive influence of January minimum temperatures on LW development is based on a direct improvement of EW

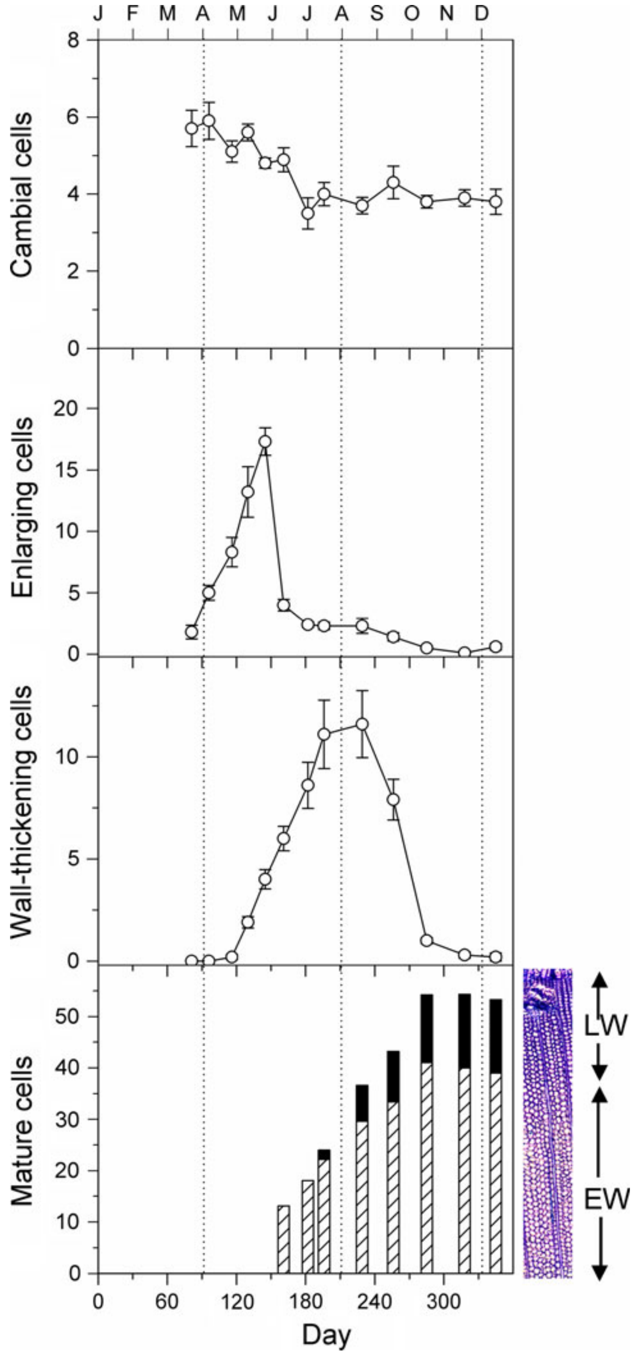

Fig. 3 Number of cells of *P. halepensis* according to their development phase (cambial cells, radially enlarging tracheids, wall-thickening tracheids and mature tracheids—earlywood and latewood tracheids are shown as bars with different fill types) formed during the year 2010 in the site PU. The image shows the earlywood (EW) and latewood (LW) of a cross-section of a ring (total width = 1.22 mm) from a wood sample taken in mid November. Data are means ($n = 10$ trees)

formation leading to an indirect LW enhanced growth. This indicates that the LW growth in *P. halepensis* is not only determined by weather conditions during the wall thickening process, mainly occurring in summer and autumn (Camarero et al. 2010), but it may be also modulated by the previous EW growth rates as shown by the high correlation between them.

The strong sensitivity of EW and LW growth to cumulative drought stress in July and September, respectively, indicates that summed (10–14 months) precipitation amounts during those periods are crucial for the development of both components of the tree ring. The EW growth appeared to depend more on water availability than LW did, showing two distinct patterns in terms of growth sensitivity to drought in *P. halepensis*. These patterns varied among sites indicating changing growth responses of *P. halepensis* EW and LW growth to different rainfall regimes at local scales. For instance, there was variability in terms of the EW and LW responses to drought when comparing the less xeric sites (TA, PU, MA, PL and MP) vs. the most xeric ones (VM, CV, CS, VA) showing a more intense and prolonged impact of drought on the formation of both wood types in the later as compared to the former sites. The higher impact of drought on EW growth as compared to the LW was also confirmed by the SEA analysis which clearly indicated significant EW growth reduction in most sites during the year of drought occurrence, a pattern that was not observed in the case of LW. The growth of both components during the 2 years after selected droughts did not significantly decrease, most likely due to soil water recharge after the drought event in those sites. There was an exception to this in site VA, where drought negatively impacted LW production 1 year after the drought possibly because of lagged effects on carbohydrates synthesis and growth or due to a poor water-holding capacity of soils.

P. halepensis is considered as a drought-avoiding species (Ferrio et al. 2003), but its inter-annual growth is very sensitive to lasting and severe droughts as our results support. Moreover, the vulnerability to drought may be aggravated by the soil types (e.g., gypsum) which may additionally intensify the negative effects of drought on *P. halepensis* growth. In the study area, a pronounced decline in winter and spring precipitation has also been observed during the late twentieth century (González-Hidalgo et al. 2009) which has negatively influenced the EW formation, leading to denser wood, i.e. with less EW in relative terms, and thus causing a reduction in hydraulic conductivity but increasing the resistance to drought-induced xylem cavitation (Eilmann et al. 2011). Even if drought-stressed pines are able to form tracheids with wider lumens than non-stressed pines as it was shown by Eilmann et al. (2011), the production of less EW will undoubtedly induce a decrease in hydraulic conductivity and, it is plausible that this will lead to local growth declines in the long term and a reduction in carbon uptake at regional scales.

Fig. 4 Mean correlation coefficients of earlywood and latewood width chronologies and the SPI drought index calculated at different time scales (1–48 months) from January up to December for the nine study sites. *Bold lines* frame significant correlations ($P \leq 0.05$). The *right area figure* shows the calculated daily rates of earlywood and latewood tracheids production in *P. halepensis* during the year 2010 (see also Fig. 3)

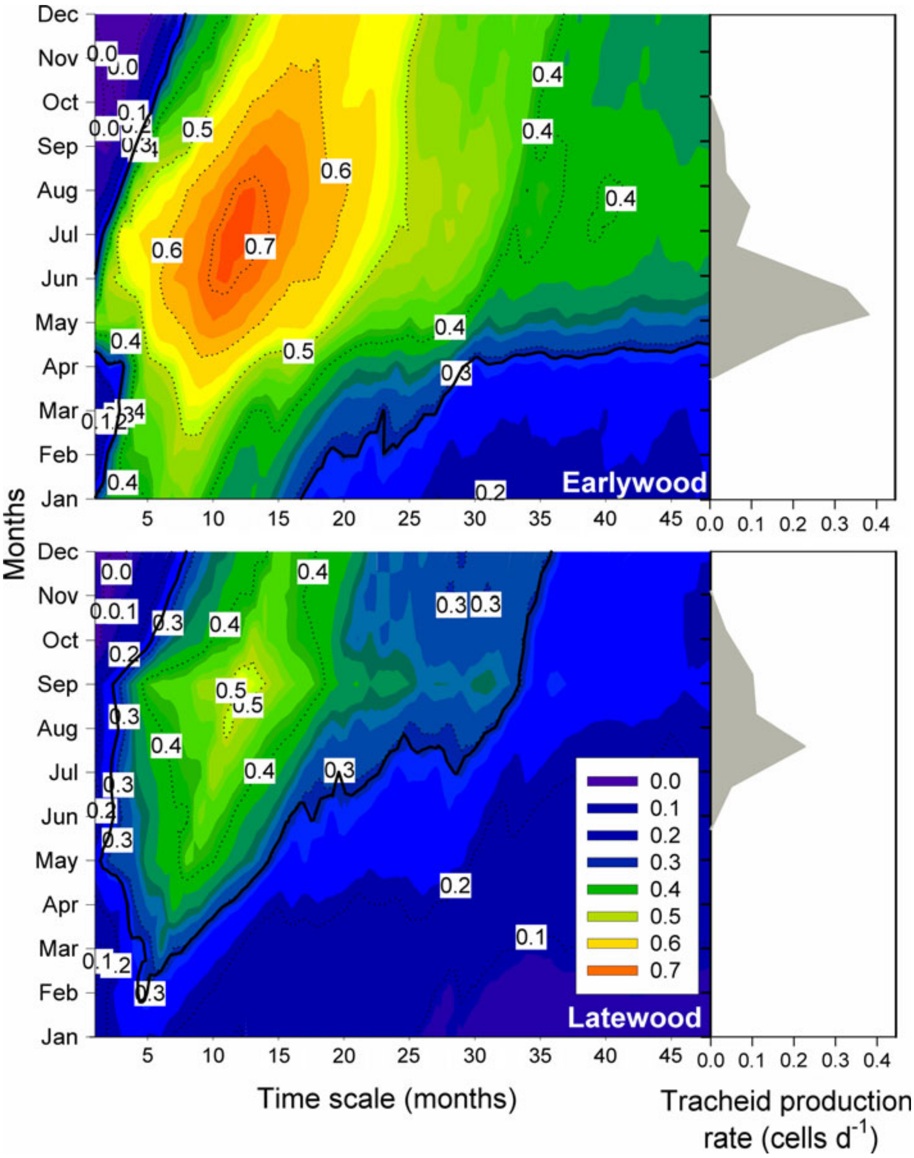

Table 2 Annual earlywood and latewood width deviations observed up to 2 years after the occurrence of a severe drought (year 0) (deviations were calculated in response to selected severe droughts (1967, 1986, 1994 and 2002; see Fig. 1); significant ($P \leq 0.05$) values are in bold)

Site	Earlywood			Latewood		
	Year 0	Year 1	Year 2	Year 0	Year 1	Year 2
VM	**−0.56**	−0.18	0.28	−0.25	−0.12	−0.06
CV	−0.34	−0.24	0.16	−0.30	−0.05	0.24
CS	**−0.46**	−0.04	0.23	−0.37	0.05	0.18
VA	−0.35	−0.21	−0.14	−0.28	**−0.52**	0.17
TA	**−0.74**	−0.42	0.01	−0.28	−0.18	−0.01
PU	−0.20	−0.26	0.09	−0.11	−0.26	−0.08
MA	−0.41	0.35	0.03	−0.35	−0.07	0.02
PL	**−0.85**	−0.43	−0.28	−0.44	−0.20	0.08
MP	−0.45	−0.15	−0.25	−0.38	−0.26	0.23
Mean	−0.48	−0.18	0.04	−0.31	−0.18	0.09

We conclude that despite *P. halepensis* is considered among the most drought-resistant Circum-Mediterranean conifers, its seasonal wood formation appears to be driven negatively by mid-term cumulative drought stress in semi-arid areas. In the short term, these influences were associated with a reduction of tracheid production, whereas in the long term they caused declining EW and LW formation. Therefore, under expected decrease of winter and spring water availability in a warmer future world as predicted for continental areas in the Western Mediterranean Basin (IPCC 2007), the studied forests may show a more intense reduction in the production of EW tracheids than in the case of LW ones. This selective reduction in EW formation may lead to several cascading effects, namely a decline of radial growth (including LW formation) a reduction in hydraulic conductivity and, indirectly, a hampered carbon uptake under semi-arid conditions.

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ORIGINAL PAPER

Factors driving growth responses to drought in Mediterranean forests

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Abstract We lack information regarding the main factors driving growth responses to drought in tree species with different vulnerability against this stressor and considering sites with contrasting climatic conditions. In this paper, we identify the main drivers controlling growth response to a multi-scalar drought index (Standardized Precipitation Index, SPI) in eight tree species (*Abies alba*, *Pinus halepensis*, *Quercus faginea*, *Pinus sylvestris*, *Quercus ilex*, *Pinus pinea*, *Pinus nigra*, *Juniperus thurifera*). We sampled forests growing across a pronounced climatic gradient under Mediterranean conditions in north-eastern Spain. To summarize the patterns of growth responses to drought, we used principal component analysis (PCA). To determine the main factors affecting growth responses to drought, correlation and regression analyses were carried out using a set of abiotic (climate, topography, soil type) and biotic (Normalized Difference Vegetation Index, Enhanced Vegetation Index, tree-ring width, diameter at breast height) predictors and the PCs loadings as response variables. The PCA analysis detected two patterns of growth responses to drought corresponding to xeric and mesic sites, respectively. The regression analyses indicated that growth responses to drought in xeric forests were mainly driven by the annual precipitation, while in mesic sites the annual water balance was the most important driver. The management of Mediterranean forests under the forecasted warmer and drier conditions should focus on the main local factors modulating the negative impacts of drought on tree growth in xeric and mesic sites.

Keywords Dendrochronology · Drought · Iberian Peninsula · Radial growth · Standardized precipitation index

Introduction

Warming-related water deficit is one of the major drivers of growth dieback and related mortality episodes in forests affecting selectively tree species, stands, and trees (Allen et al. 2010; Koepke et al. 2010). Drought causes reductions in radial growth and alterations in hydraulic conductivity (McDowell et al. 2008) and decreases productivity due to limitations in water use and photosynthesis (Hsiao 1973; Flexas and Medrano 2002). These effects are enhanced particularly in Mediterranean drought-prone forests where water availability is the main factor constraining growth (Pereira and Chaves 1995; Vicente-Serrano et al. 2006; Sarris et al. 2007, 2011; Linares et al. 2009, 2010).

Different studies evidence that our understanding of the drought impact on growth of tree species at different time scales and across contrasting site conditions is still very limited (Orwig and Abrams 1997; Adams and Kolb 2005).

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Usually, radial growth of tree species and populations growing in xeric sites are more affected by drought than in mesic locations (Abrams et al. 1998). However, other researchers argued that species growing in xeric sites show adaptive features to withstand the negative effects of drought (De Luis et al. 2007; McDowell et al. 2008; Linares et al. 2010). This implies that these drought-adapted species may be less vulnerable against drought stress, in terms of growth, than species inhabiting wet sites.

The lacking information regarding the factors driving the spatial and temporal patterns of growth responses to drought may be partially obtained by quantifying growth trends across environmental and climatic gradients. Growth responses to drought can vary as a function of the species' responsiveness to water deficit (Orwig and Abrams 1997; Bogino and Bravo 2008), site features (Tardif and Bergeron 1997; Macias et al. 2006; Linares and Tíscar 2010), and characteristics of trees (size, age, competition, genetic differences) (De Luis et al. 2009; Kuparinen et al. 2010; Linares et al. 2010).

During the second half of the twentieth century, climate trends in the Western Mediterranean Basin were characterized by remarkably high air temperatures and an increase in both the frequency and severity of droughts (Houghton et al. 2001; García-Ruiz et al. 2011; Xoplaki et al. 2006). These conditions are expected to be intensified in the future under warmer conditions enhancing evapotranspiration and water deficit in many forested areas (Giorgi and Lionello 2008). In Circum-Mediterranean forests, several studies have emphasized that the inter-annual variability of precipitation and drought occurrence are among the main constrains of tree growth (Andreu et al. 2007; Sarris et al. 2011). However, previous works in mountain forests also found that the regional climatic conditions can be greatly modulated by site features such as elevation or topography (Rolland et al. 1999; Tardif et al. 2003). These local factors may impose additional risks exacerbating drought stress (e.g., rocky soils or steep slopes) or they may partially mitigate its negative effects on tree growth (e.g., deep soils or northern aspects). For instance, water deficit has been linked to growth decline of tree populations mainly located in xeric sites (Martínez-Vilalta and Piñol 2002; Camarero et al. 2011).

In this study, we aimed: (i) to describe the spatio-temporal growth responses to drought across a wide climatic gradient in north-eastern Spain and (ii) to detect the main drivers influencing these responses. We studied eight tree species with contrasting sensitivity to drought stress ranging from pine species in semi-arid areas (e.g., *Pinus halepensis*) to fir species dominating wet sites (e.g., *Abies alba*), thus providing a wide ecological gradient representative for many Mediterranean forests.

Materials and methods

Study area

The study area includes forests located in Aragón, north-eastern Spain (Fig. 1; see sites in Table 1 in Pasho et al. 2011). This area is under Mediterranean influence with a strong climatic gradient ranging from semi-arid conditions in the Middle Ebro Basin (mean annual temperature 15.0 °C, total annual precipitation 318 mm) to humid conditions northwards in the Pyrenees (mean annual temperature 8.5 °C, total annual precipitation 1,750 mm). The seasonal variability in precipitation is more pronounced in the Middle Ebro Basin than in the Pyrenees and severe summer droughts (periods of more than 80 days without precipitation) are common in the former area (Vicente-Serrano and Beguería 2003). In the Middle Ebro Basin, the lithology is characterized by millstones and gypsums (Peña

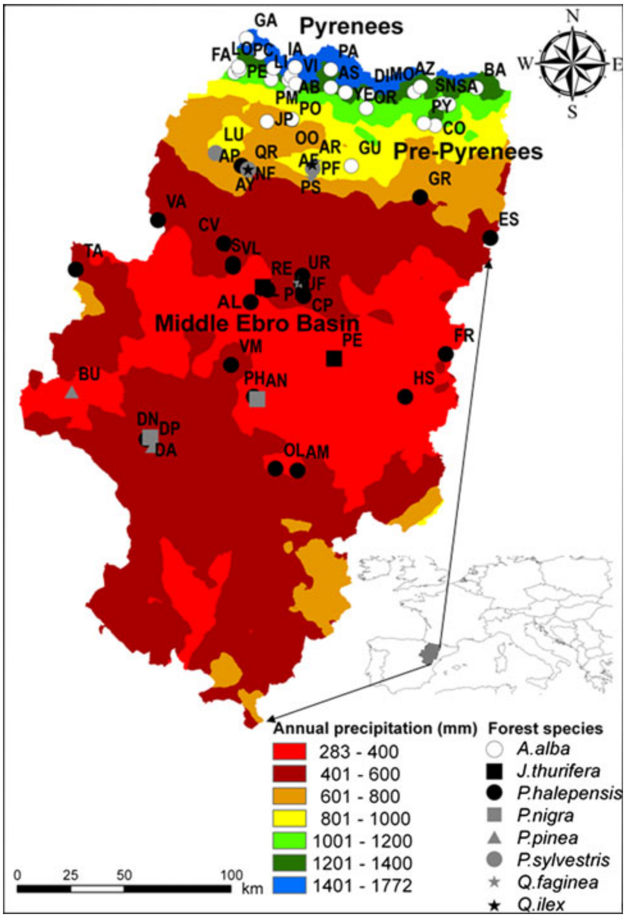

Fig. 1 Location of sampled sites and annual precipitation values in Aragón, north-eastern Spain. *Different symbols* and *colors* represent different tree species and precipitation ranges, respectively. The three sub-areas studied (Pyrenees, Pre-Pyrenees, and Middle Ebro Basin) are also indicated in the map. Sites' codes are as in Table 1 in Pasho et al. 2011

Table 1 Significant ($P < 0.01$) correlations between explanatory variables and the first two principal components (PC1, first component; PC2, second component) summarizing the growth responses to drought

Type of variables	Explanatory variables (abbreviations, units)	PC1	PC2
Tree variables	Diameter at breast height (DBH, cm)	−0.70	0.63
	Tree-ring width (TRW, mm)	−0.46	0.44
Remote sensing variables	Annual NDVI (NDVI)	−0.73	0.64
	Annual EVI (EVI)	−0.66	0.62
	April-June NDVI (AJ NDVI)	−0.78	0.71
	April-June EVI (AJ EVI)	−0.71	0.71
Soil variables	Inceptisol (IS)	−0.72	0.72
Climatic variables	Annual water balance (WB, mm)	−0.85	0.78
	Annual precipitation (AP, mm)	−0.85	0.75
	Annual potential evapotranspiration (PET, mm)	0.64	−0.65
	Mean maximum annual temperature (AMxT, °C)	0.80	−0.70
	Mean minimum annual temperature (AMiT, °C)	0.79	−0.67
	July mean maximum temperature (JMxT, °C)	0.79	−0.70
	January mean minimum temperature (JMiT, °C)	0.74	−0.61
	Incoming solar radiation (R, W m^{-2})	0.38	−0.48
Topographic variables	Elevation (E, m)	−0.78	0.66
	Slope (S, %)	−0.70	0.54

et al. 2002), which contribute to aridity due to their poor ability to retain water (Navas and Machín 1998). In the Pyrenees, soils are usually deep and basic and develop over limestone, sandstones, and granites.

The study area is characterized by a variety of forest types and vegetation communities mostly determined by climate (Costa et al. 2005). Most of the studied sites are located in the mountainous Pyrenean area forming pure stands or mixed conifer-hardwood forests (e.g., silver fir, *Abies alba* Mill.). Southwards, in sub-Mediterranean areas of the Pre-Pyrenees, forested landscapes comprise stands of *Pinus sylvestris* L., *Pinus pinea* L., *Pinus nigra* subsp. *salzmannii* (Dunal) Franco., *Quercus faginea* Lam., and *Quercus ilex* L. subsp. *ballota* (Desf.) Samp. In the semi-arid Middle Ebro Basin, the forests and woodlands are dominated by *Pinus halepensis* Mill., with a few relict populations of *Juniperus thurifera* L. The *P. halepensis* forests in the Middle Ebro Basin commonly occur on plateaus and slopes of structural platforms developed on Miocene carbonate and marl sediments, whereas the valley bottoms have been traditionally used for agriculture and livestock grazing.

Dendrochronological methods

To reconstruct recent growth trends in the studied sites, we used dendrochronological methods. Forests were selected based on: (i) the species dominance in the canopy over at least 1 hectare of fully forested area and (ii) the occurrence of harsh environmental conditions potentially constraining tree growth such as steep slopes or shallow or rocky soils. The selected sites were considered to capture most of the climatically mediated growth variability of the studied species in north-eastern Spain (see Pasho et al. 2011). In addition, the sampling strategy was adjusted according to the biogeography of the investigated species. In this regard, we only sampled one *A. alba* stand near the southernmost distribution limit of the species because similar populations may be more drought stressed than other located in more mesic sites at higher latitudes. The sampled *A. alba* sites are considered mesic in terms of the species' distribution across Europe since the climatic conditions and the coexisting species (e.g., *Fagus sylvatica* L.) are similar to other mixed silver fir stands in mesic areas from Central Europe. At each of 65 sites visited in the field, 10–35 dominant trees separated by at least 10 m were randomly selected, their diameter at 1.3 m (Dbh) was measured, and they were sampled (see Table 1 in Pasho et al. 2011). Two radial cores per tree were extracted at 1.3 m height using a Pressler increment borer. The cores were prepared following standard dendrochronological methods (Fritts, 2001). They were air dried, mounted, and sanded with sandpapers until tree rings were clearly visible with a binocular microscope. All samples were visually cross-dated and the ring width was measured to a precision of 0.001 mm (accuracy ± 0.0003 mm), using a LINTAB measuring device (Rinntech, Heidelberg, Germany). Cross-dating was evaluated using the COFECHA program (Holmes 1983).

To retain the high-frequency variability of growth, each ring-width series was double-detrended using a negative exponential function and a spline function with a 50 % frequency response of 32 years. Detrending and standardization involved transforming the measured values into dimensionless indices by dividing the raw values by the expected values given by the negative exponential and spline functions. Autoregressive modeling was carried out on each series to remove the temporal autocorrelation. The indexed residual (pre-whitened) series of all trees within each site were then averaged using a biweight robust mean to obtain mean site residual chronologies of ring width which were used in further analyses. We used the program ARSTAN to obtain the residual site chronologies (Cook 1985).

The quality of the chronologies was evaluated for the common period 1970–1999 using several dendrochronological statistics (Briffa and Cook 1990): the mean width and standard deviation (SD) of the raw ring-width series; the first-order autocorrelation (AC1) of raw series, which measures the year-to-year persistence; the mean sensitivity (MSx) of the residual series, which quantifies the relative change in width among consecutive years; the mean correlation (Rbar) among individual series within each site; and the expressed population signal (EPS) of residual series, which indicates to what extent the sample size is representative of a theoretical infinite population. The common period 1970–1999 was selected because all chronologies showed EPS values above the 0.85 threshold for this interval, and such threshold is widely recognized in dendrochronological studies for accepting mean growth series as being well replicated (Wigley et al. 1984).

Drought index calculation

To quantify the impact of drought on forest growth, we employed the Standardized Precipitation Index (SPI). The SPI has the advantage of allowing the determination of duration, magnitude, and intensity of droughts and can be calculated at different time scales (Hayes et al. 1999). The quantification of droughts at different time scales is important in determining their ecological impacts, considering the different physiological strategies of vegetation to deal with water deficit (Hsiao 1973).

The SPI is calculated using precipitation data and it was developed by McKee et al. (1993) to identify the varied times of response of different hydrological systems to precipitation deficits. The precipitation data in the region have been obtained from a homogeneous and spatially dense dataset of local observatories (Vicente-Serrano et al. 2010). Nevertheless, since the available observatories are commonly located near populated areas, few stations are available in mountainous locations where we sampled many of the studied forests. For this reason, the available local precipitation data were interpolated at a spatial resolution of 1,000 m and converted to monthly data for the period 1950–2006 to have a regular grid with information in each one of the sampled forests. To take into account the effect of elevation on precipitation, the interpolation was done using a Digital Terrain Model (DTM) and a Geographic Information System assisted regression-based approach (Vicente-Serrano et al. 2003, 2007; Ninyerola et al. 2007). The precipitation in each 1,000-m grid point was estimated by means of a stepwise-regression model in which the independent variables were the elevation, the latitude, and the longitude of each site. The residuals, that is, the differences between the observations and the modeled precipitation, were also included in the estimations by means of a local interpolation procedure (splines with tension, see Mitasova and Mitas 1993) to include the local precipitation features which were not well captured by the regression models.

The validation of the gridded monthly layers was done for each layer by a jackknifing method, based on withholding, in turn, one station out of the network, estimating regression coefficients from the remaining observatories and calculating the difference between the predicted and observed value for each withheld observatory (Phillips et al. 1992). The average root mean square error for the different months and years was 15.2 mm, being lower in summer (6.5 mm) than in winter (22.3 mm). The D agreement index (Willmott 1982) showed an average of 0.94 for the different monthly layers, with a range between 0.82 and 0.99, which indicates a high reliability between the observed and the modeled precipitation data.

An average monthly precipitation series was obtained for each one of the 65 sites using the gridded monthly precipitation data. From each series, we obtained the SPI at time scales ranging from 1 to 48 months to obtain a wide range of time scales to be compared with growth. Positive and negative SPI values correspond to wet and dry conditions, respectively. SPI values below −2.0 indicate extreme droughts. The SPI was calculated by adjusting the precipitation series to a given probability distribution. Initially, the SPI was calculated following a Gamma distribution (McKee et al. 1993), but further analyses indicated that the Pearson III distribution was more robust (see Vicente-Serrano 2006).

Factors affecting growth-drought responses: climate, topography, remote sensing data

We used climatologies for different variables obtained from the digital climatic atlas of Aragon at a spatial resolution of 1 km (Cuadrat et al. 2007). The climatic variables used in the study were: annual water balance, annual precipitation, annual potential evapotranspiration, annual mean maximum temperature, annual mean minimum temperature, July mean maximum temperature, January mean minimum temperature, and solar radiation. The incoming solar radiation, which provides information on the slope aspect, was obtained using a terrain model (Pons and Ninyerola 2008) implemented in the MiraMon Geographical Information System (Pons 2011). For each sampled forest, the average value of these variables was extracted.

The topographic data consisted of the following variables: elevation (m) recorded at each sample plot by using a GPS and slope (%) derived by using a DTM of the area with a spatial resolution of 100 m. The soil types were determined by using the Spanish soil map developed by the Spanish Geographic Institute following the Soil Taxonomy of the USDA (IGN 2006).

To evaluate the potential roles of the differences in leaf activity and leaf-area index in explaining the spatial differences in the growth responses to drought, we used remote sensing data to quantify these variables in each forest. The utility of remote sensing for vegetation monitoring is based on the response of vegetation cover to radiation in the visible and near-infrared regions of the electromagnetic spectrum (Myneni et al. 1995). Visible radiation is mainly absorbed by vegetation in photosynthesis processes while near-infrared radiation is principally reflected, owing to the internal structure of leaves (Knipling 1970). High vegetation activity is characterized by low reflectivity of solar visible radiation and high reflectivity in the near-infrared region of the spectrum.

Different indices have been developed for monitoring and measuring vegetation status using spectral data (Bannari et al. 1995). Among them, the most widely used is the Normalized Difference Vegetation Index (NDVI) (Rouse et al. 1973). Numerous authors have pointed out the close relationship between NDVI and several ecological parameters (e.g., Vicente-Serrano et al. 2010). The NDVI measures the fractional absorbed photosynthetically active radiation (Myneni et al. 1995) and exhibits a strong relationship with vegetation parameters such as green leaf-area index (Carlson and Ripley 1997). In addition, we also used the Enhanced Vegetation Index (EVI) since this index enhances the vegetation signal with improved sensitivity in high biomass regions and allows improved vegetation monitoring through a decoupling of the canopy background signal and a reduction in atmosphere influences (Huete et al. 2002).

Time series of NDVI and EVI covering the period 2000–2010 were used in the study. The data were obtained from the products of Moderate Resolution Imaging Spectro-radiometer (MODIS 13A1 product, 16-day at 500-m resolution; available at http://www.daac.ornl.gov/MODIS/modis.html in HDF format; see Huete et al. 2002). Data processing included images re-projected from a Sinusoidal to a UTM-30 N–S/IGN projection, images stacking to provide a full coverage of the study area, and crossing of the images with forest sites location to extract the NDVI and EVI values at each sampled forest. Subsequently, the mean annual and April-June (period with the highest forest activity; see Vicente-Serrano et al. 2010) NDVI and EVI values were calculated and used in further analysis.

Statistical analyses

The spatial variability of growth responses to the drought index (SPI) was analyzed by using a S-mode principal component analysis (PCA) which enabled common features to be identified and relevant local characteristics to be detected (Richman 1986). The PCA was performed on a covariance matrix calculated from the correlations between the 1–48 time scales SPIs and the residual ring-width chronologies for all sites (Legendre and Legendre 1998). The number of components was selected based on those with eigenvalues greater than 1, and the components were rotated (Varimax) to redistribute the final explained variance and to obtain more stable and robust spatial patterns (Richman 1986). Components were presented in the non-standardized original units to make the interpretation easier. For this purpose, the loadings at each forest site were multiplied by the coefficient scores of each principal component and summed up by rows. In other words, the PC scores were converted to correlation values, summarizing the correlation series at all forest sites. The geographical variability in terms of forest response to drought was identified by mapping the factorial loadings.

To detect the factors which potentially affect the growth responses to drought, correlation and regression analysis were carried out between the PCs loadings and a set of abiotic (climatic and topographic variables, soil type) and biotic (Dbh, mean tree-ring width for the period 1970–1999, NDVI, and EVI) variables. Categorical variables, like the soil type, were converted to binary variables to be included in the regression analyses. The importance of each variable was assessed by using a forward selection method which starts with no variables in the model, trying out the variables one by one, and including them if they were significant ($P \leq 0.05$).

Results

Spatial patterns of the growth responses to drought

The first two components of the PCA accounted for 75.1 % (PC1, 41.3 %; PC2, 33.8 %) of the total amount of the variability of growth responses to drought. The PCs correlation coefficients, summarizing the species' growth responses to drought at xeric and mesic areas, showed that

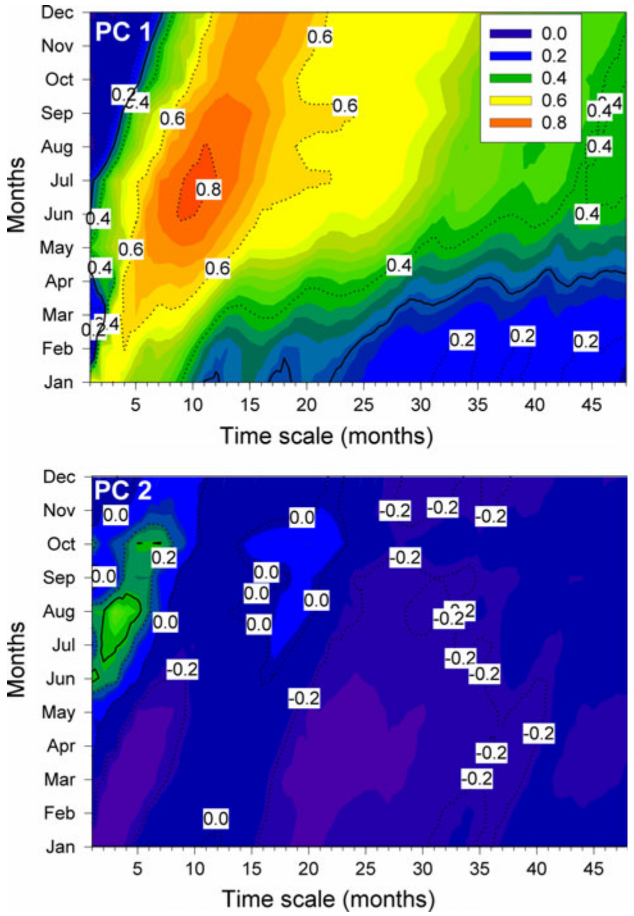

Fig. 2 First (PC1) and second (PC2) principal components summarizing the correlations between all ring-width chronologies and monthly drought (SPI) series at different time scales. *Bold lines* frame significant correlations ($P \leq 0.05$)

tree species associated with the first principal component (PC1) presented significant correlations ($r > 0.29$) at all time scales, with the highest ones ($r > 0.80$) achieved at time scales ranging between 9 and 12 months, during summer months (Fig. 2). The second principal component (PC2) captured significant growth responses to drought at 2–5 month scales, again during summer.

The spatial distribution of the loadings of the PC1 and PC2 components shows two clear spatial patterns of responses to drought across the study area (Fig. 3). The first pattern represented by PC1 was found in the southern study area (Middle Ebro Basin), while the second one described by the PC2 corresponded to the northern study area (Pyrenees). The PC loadings of each forest indicated that the highest contribution to the PC1 variability was accounted for by species growing in xeric locations such as *P. halepensis*, *P. nigra*, *P. pinea*, *J. thurifera*, *Q. faginea*, and *Q. ilex*. On the other hand, the PC2 captured the growth responses to drought expressed by species located in sub-Mediterranean and mesic sites (*A. alba*, *P. sylvestris*).

Drivers of the growth responses to drought

The associations between abiotic and biotic variables and the two first principal components (PC1, PC2) summarizing the growth responses to drought indicated that tree-related (Dbh, tree-ring width), remote sensing (NDVI, EVI), climatic (water balance, precipitation) and topographic variables were significantly ($P < 0.01$) and inversely correlated with the PC1 (Table 1). Most climatic variables (potential evapotranspiration, mean maximum and minimum temperatures, July mean maximum and January mean minimum temperatures, solar radiation) were negatively related to the PC2. The PC1 was mainly driven by water availability, temperature, and elevation, while the PC2 was also strongly associated to these variables and to NDVI and EVI data.

The regression analysis indicated that four variables (annual precipitation, inceptisol soils, April-June NDVI, and slope) explained 78 % of the total spatial variability accounted for by the PC1 and three variables (annual water balance, April-June EVI, and inceptisol soils) determined 66 % of the variance represented by PC2 (Table 2).

The coefficients of the selected regression models (Table 3) showed that the main variable driving growth responses to drought in xeric sites represented by PC1 was annual precipitation ($P < 0.003$), followed by the soil type (inceptisol), April-June NDVI, and slope. Considering the PC2, the main driver of growth responsiveness to drought was the annual water balance ($P < 0.002$), whereas April-June EVI and soil type (inceptisol) influences were less important.

The partial correlations between the PCs and each predictor of the regression models were significant ($P < 0.05$) when the effect of the other independent variables was controlled, suggesting that the growth responses to drought in xeric and mesic sites were mainly driven by precipitation and the water balance, respectively. In fact, the PC loadings and the most important drivers of growth responses to drought confirmed the high dependence of the growth responsiveness on annual precipitation in xeric sites (Fig. 4). The variability in the responses to drought of mesic forests characterized by the PC2 was driven by the annual water balance.

Discussion

We have evaluated the growth responses to drought and factors driving this responsiveness in eight tree species growing across a wide climatic gradient by means of

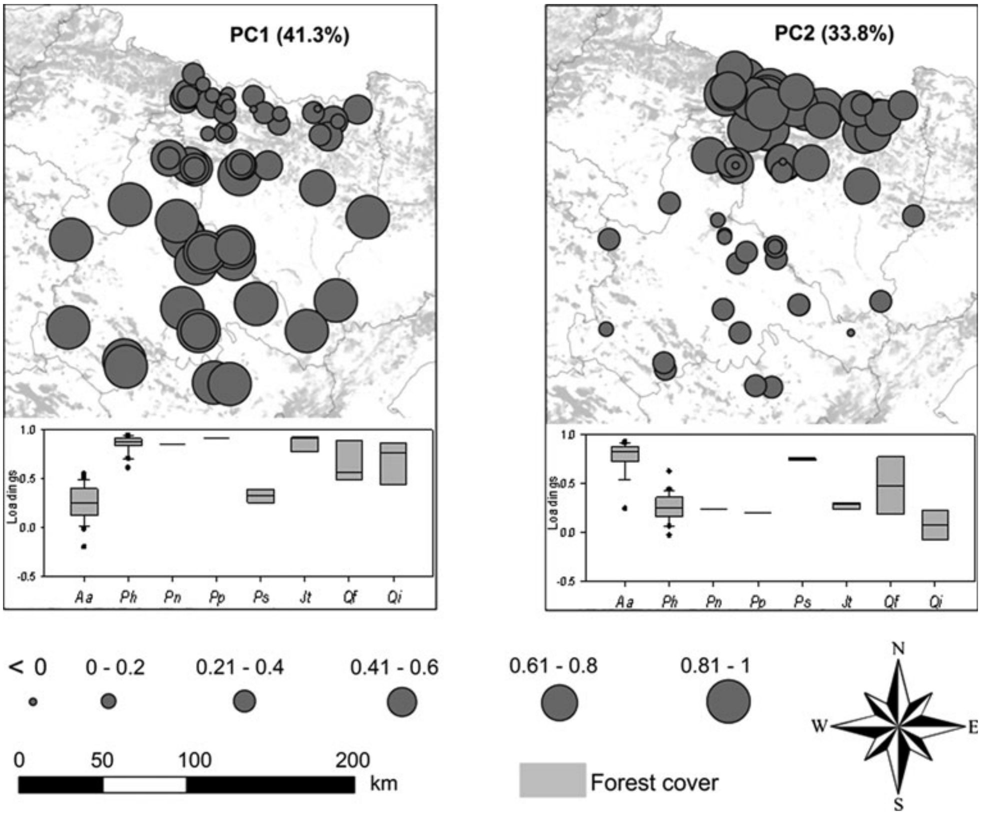

Fig. 3 Spatial patterns of species' growth responses to drought as revealed by the loadings of the first (PC1) and second (PC2) principal components (*upper graphs* the size of *circles* is proportional to the loadings) and within-species variability of these responses (*lower graphs* box plots of species loadings in the two principal components, PC1 and PC2, respectively). Species codes: *Aa*, *Abies alba*; *Ph*, *Pinus halepensis*; *Pn*, *Pinus nigra*; *Pp*, *Pinus pinea*; *Ps*, *Pinus sylvestris*; *Jt*, *Juniperus thurifera*; *Qf*, *Quercus faginea*; *Qi*, *Quercus ilex*

Table 2 Selected regression models explaining the patterns of the first (PC1) and second (PC2) principal components of growth responses to drought for all species and corresponding statistics (R^2adj, adjusted percentage of variability explained by models; *F*, *F*-ratio, *P*, probability level)

Response variables	Explanatory variables	R^2adj (%)	*F*	*P*
PC1	1.240 − 0.001 AP − 0.142 IS − 0.471 AJ_NDVI − 0.002 S	77.7	58.44	<0.0001
PC2	0.064 + 0.001 WB + 1.245 AJ_EVI + 0.163 IS	65.8	43.42	0.0001

The PCs were calculated from the matrix of correlations obtained between the 1–48 months drought index (SPI) and the residual ring-width chronologies. See variables abbreviations in Table 1

dendrochronological methods and a quantitative assessment of drought at different time scales based on the multi-scalar Standardized Precipitation Index (SPI). This is the first investigation evaluating the factors responsible for the variable growth responses to drought in diverse Mediterranean forests. Particularly, we evaluated the role of biotic and abiotic variables on modulating the spatial and temporal variability within and among species in the growth responsiveness to drought focusing on contrasting environmental conditions in xeric and mesic sites.

The PCA analyses revealed two distinct spatial patterns in terms of growth response to drought across the study area corresponding to: (i) species growing in the Middle Ebro Basin (represented by PC1) under Mediterranean semi-arid conditions (all *Pinus* species excepting *P. sylvestris*, *Quercus* species, and *J. thurifera*) and (ii) species distributed in mountainous areas, (represented by PC2, from the Pre-Pyrenees and Pyrenees (*A. alba*, *P. sylvestris*)) characterized by a humid and cold sub-Mediterranean climate.

The regression analyses showed that the annual precipitation is the main driver of forest growth sensitivity to drought in the xeric sites, indicating that in dry Mediterranean forests tree growth is mainly constrained by low water availability (Borghetti et al. 1998; De Luis et al. 2007; Vicente-Serrano 2007; Camarero et al. 2010). This has been also confirmed by additional studies on growth and phenology of pine and oaks species in nearby areas (Corcuera et al. 2004a, b; Andreu et al. 2007; Montserrat-Martí et al. 2009; Gutiérrez et al. 2011; Pasho et al. 2011). In general, these studies found important spatial variations in the growth responses to drought of forests as a function of climate conditions, confirming that forests located in the driest sites are the most sensitive to drought occurrence and

Table 3 Statistics of the coefficients of the selected regression models (see Table 2) explaining the patterns of the first (PC1) and second (PC2) principal components of growth responses to drought for all tree species

	Student *t*	*P*	Partial correlation
PC1			
Constant	15.094	<0.0001	
Annual precipitation	−3.038	0.003	−0.360
Inceptisol	−2.620	0.011	−0.316
April–June NDVI	−2.152	0.035	−0.264
Slope	−2.091	0.041	−0.257
PC2			
Constant	0.417	0.678	
Annual water balance	2.452	0.002	0.295
April–June EVI	2.884	0.008	0.341
Inceptisol	2.482	0.017	0.299

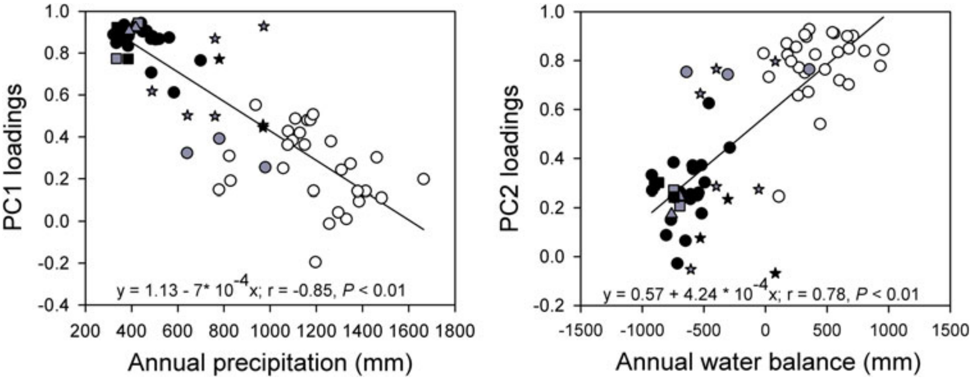

Fig. 4 Scattergram of the loadings of the first two principal components and the main predictor variables as revealed by linear regressions (see Table 3). The *different symbols* correspond to different species (see symbols in Fig. 1)

severity. Furthermore, these results suggest that growth declines in xeric areas, and plausibly dieback events and episodes of high mortality as those reported by Allen et al. (2010), will be observed in response to long-term dry conditions greatly reducing the water balance.

Contrastingly, we found that even short-term summer drought, lasting between 2 and 6 months, can affect radial growth of mountain conifers from mesic sites such as *A. alba*. This association may be explained by the low water-use efficiency of *A. alba*, which is a species whose photosynthetic rates are very sensitive to atmospheric drought (Guehl et al. 1991) and its growth rates respond to cumulative water deficit in late summer and to temperature-related drought stress (Rolland et al. 1999; Camarero et al. 2011).

The growth responses to drought of mountain forests from mesic and wet sites such as Pyrenean silver fir forests were also determined by a combined influence of several drivers, with the most significant impact exerted by annual water balance and temperature variables. In mountain conifer forests, the high temperatures in combination with strong radiation can intensify evaporation rates that additionally decrease moisture content in the upper layers of the soil and deplete moisture reserves, influencing so the soil water balance negatively (Pichler and Oberhuber 2007; Vicente-Serrano et al. 2010). Short-term warming-induced water deficits during late summer may cause growth decline and forest dieback of *A. alba* forests (Camarero et al. 2011). Hence, growth declines in silver fir forests located in the less humid sites may be expected in response to warming-induced short-term drought stress (Macias et al. 2006). In addition, the low temperatures in winter also affect growth responses to drought in mesic silver fir forests because they may cause frost-induced xylem embolism and reduce photosynthesis (Rolland et al. 1999, Aussenac 2002).

The contribution of each site to the respective first two principal components was different, indicating a site- and species-dependent variability in terms of growth responses to drought (Orwig and Abrams 1997). The species' responsiveness to drought seems to be conditioned by contrasting climatic conditions and local variability in soil water holding capacity. For example, Sánchez-Salguero et al. (2010) showed a more intense growth reduction of *P. pinaster* and *P.halepensis* in response to extreme droughts in xeric than in wet sites in south-eastern Spain.

This is in line with the findings of Fekedulegn et al. (2003) who stressed that forest responses to drought may be affected by a combination of many factors including precipitation, temperature, inherent species' characteristics, and site topographic features. These factors may impose additional constrains on the growth responses to drought. As revealed in this study, the growth sensitivity to drought was also affected by soil and topographic conditions. For instance, the lithology (millstones and gypsums) that characterize xeric environments in the study area enhance the negative effects of water deficit on growth since soils are generally shallow, characterized by limited ability to hold adequate moisture (Guerrero et al. 1999; Vicente-Serrano 2007), which increase the negative effects of drought on tree growth. In the Pyrenees, the dominant soils (e.g., inceptisol) had an inverse association with the growth responsiveness to drought, suggesting the presence of mitigating effects of the negative impacts of water deficit on growth, most likely due to the high capacity of these soils to hold water in the deeper layers. This is the case of many *A. alba* forests located in valley bottoms of the Pyrenees, characterized by deep soils and humid climatic conditions (Macias et al. 2006; Camarero et al. 2011).

We expected that topographic factors such as elevation and slope would exert contrasting influences on the species responses to drought in xeric and mesic forest sites, respectively. However, we found that the growth responses to drought were only affected by slope in the case of xeric sites (PC1), most likely due to its local influence on surface runoff and water retention by soils. The studied forests in xeric sites, mostly located in low elevation but topographically complex areas (plain localities have been mostly converted to croplands), grow under an exacerbated drought stress in undulating or moderate slopes since in these areas trees are more sensitive to the rapidly occurring water shortages (Fekedulegn et al. 2003). Topographic position has already been shown to drive the soil water availability in areas subjected to seasonal droughts affecting tree growth and the species composition of diverse ecosystems as tropical forests (Engelbrecht et al. 2007).

Xeric sites are also characterized by low precipitation and high temperatures which enhance the drought impacts on growth (Camarero et al. 2010). In these areas, high temperatures in summer most likely deplete soil water reserves causing drought-induced embolism. Slope and aspect can also influence growth locally through changes in the radiation received by trees (Tardif et al. 2003; Leonelli et al. 2009). Generally, south-facing slopes in xeric areas with low water holding capacity increase the drought impacts on tree growth (Sánchez-Salguero et al. 2010). The opposite was observed in *A. alba* forests located in north-oriented slopes with deep soils. Overall, topography acts as a local modulator of the effects of drought on growth but further research on this subject in Circum-Mediterranean forests is desirable.

The tree features such as tree size (diameter) or the growth rate (mean tree-ring width) and vegetation activity indices (NDVI, EVI) showed positive and negative associations with the growth responsiveness to drought in xeric and mesic sites, respectively. These associations indicate that low water availability associated with prolonged and intense drought lead to a decreasing canopy growth (e.g., shoot extension, leaf production) and probably a decline in photosynthetic activity causing a reduction in cambial activity and hydraulic conductivity (Corcuera et al. 2004a, b; Linares et al. 2009; Montserrat-Martí et al. 2009; Vicente-Serrano et al. 2010). Such growth decline may further enhance the species' vulnerability against drought stress.

In conclusion, our study highlights that Mediterranean forests show high spatial and temporal variability in terms of growth responses to drought. This variability observed among species and sites was significantly driven by climatic, topographic variables, and biotic variables indicating that a combination of variables shape the species' behavior in response to drought. Since climate models predict rising temperatures and enhanced evapotranspiration for the Mediterranean Basin (Giorgi and Lionello 2008), our findings suggest that warming-related drought stress might affect growth dynamics on different time scales in mesic than in xeric forests. However, disentangling the relative effects of warmer conditions and reduced precipitation on tree growth is an unsolved challenge which probably requires a multiproxy approach based on long-term data of radial growth, isotopic discrimination in wood, and remote sensing variables.

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