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TESIS DOCTORAL:

# Tree growth dynamic and thinning response in Mediterranean pine-oak forest stands

Presentada por Jorge Aldea para optar al grado de Doctor por la Universidad de Valladolid

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# Tree growth dynamic and thinning response in Mediterranean pine-oak forest stands

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# List of Acronyms

| | |
|---|---|
| AEMET | Spanish State Meteorological Agency |
| AIC | Akaike information criterion |
| AR | autoregressive serial model |
| ARIMA | mixed autoregressive and moving average serial model |
| BA | basal area ($m^2$/ha) |
| C | Concurrency |
| DBH, dbh | diameter at breast height mm |
| ha | hectare |
| $H_0$ | dominant height (m) |
| HT | heavy thinning (40-50% basal area removed) |
| IADFs | intra-annual density fluctuations |
| LdM | Loreau and de Mazancourt's metric |
| MA | moving average serial model |
| m.a.s.l. | meters above sea level |
| MT | moderate thinning (25% basal area removed) |
| P | rainfall per daily cycle (mm) |
| Q | Phase synchrony metric |
| RHmin | minimum relative air humidity (%) |
| SR | solar radiation (10KJ/$m^2$) |
| Tair | mean air temperature (ºC) |
| Tmin | minimum air temperature (ºC) |
| Treat. | thinning treatment intensity |
| VPD | mean vapor pressure deficit (kPa) |
| W | Kendall's concordance metric |
| WAI | Walter-Lieth annual aridity index |
| Wd | water deficit (mm) |

# Note to readers

This thesis is based on three original works, see Appendix D, published or under revision in different international journals and one manuscript under preparation. The text is written in English, so decimals are represented by a point and thousands by comma according to English grammar. Previously to the presentation of text, a summary of thesis was written in English and Spanish (*Resumen*), which highlights the methodologies, analyses employed and the main results. Similarly, final conclusions were written at the end of the thesis with a respective translate into Spanish language (*Conclusiones*).

# Abstract

Climate change forecasts are particularly severe for the western Mediterranean Basin, where rising temperatures and decreased precipitation could increase the frequency of drought events. Mixed forest stands via species niche complementarity may lead to greater functional services, over-yielding or increased temporal stability compared to monospecific stands. Controlling competition through thinning may also provide a drought adaptation tool to minimize potentially adverse ecological and socio-economic impacts of climate change.

In this study, we sought to better understand temporal complementarity among intra-annual radial increment and thinning effect in Mediterranean pine-oak coexisting species. Besides, we required to uncover differences in the weather drivers of radial variation for the two co-existing species. The forest stands under study were originated by pine forestation, which were diversified over time due to the recovery and sprout of initially oak coppice stands. Nowadays, they present a pine-oak mixed stands structure where pine species dominates the oak coppice trees.

We studied species differences in stem daily radial variation cycles, intra-annual cumulative radial increment pattern and thinning response of *Pinus pinaster-Quercus pyrenaica* mixed stands over climatically contrasted years (2010-2014) at two sites with dissimilar drought conditions. Moreover, intra-annual cumulative radial increment pattern and thinning response of *Pinus sylvestris-Quercus pyrenaica* mixed stands were evaluated for two contrasted year (2016-2017). A severe drought event occurred during 2012 and 2017 years in both sites respectively.

Nine rectangular plots were established in a Latin square design at the three study sites. The experimental design consisted of two thinning treatments with different intensity and unthinned control with three replicates each. Thinning treatment comprised moderately and heavy thinning removing 25% and 40-50 % of initial basal area. Thinning treatment was focused only on pine in maritime pine-oak mixed stands, while both species were harvested in Scots pine-oak mixed stand. Band and high-resolution point dendrometers were installed in oak and pine trees sample, so that stem radial variation was analyzed. Site weather variables were continuously monitored using a variety of sensors, a specifically weather station and via the Spanish State Meteorological Agency automatic network stations.

Non-linear mixed models were fitted to show species differences in intra-annual cumulative radial increment pattern: bi-logistic, a Richards curve for spring and autumn period and a double-Richards curve. Linear mixed models were fitted to analyze species-specific response to weather. Besides, linear and non-linear statistical metrics were also used to evaluate radial variation synchrony.

Radial increment commenced on 30 March for maritime pine, while deciduous oak stem increment began 1–3 weeks later coinciding in time with leaf budburst. Air temperature

leads to radial stem-size changes in daily variation cycles with different species responses, while precipitation increased daily amplitude and cycle duration in the same way for both species. Daily radial increment and number of cycles with increment phase during spring were mostly higher for maritime pine than oak, being water availability the most important control factor. Accordingly, intra-annual cumulative patterns showed greater radial increment for maritime pine than oak regardless year and site. Species differences in intra-annual cumulative radial increment patterns also revealed a possible species-specific complementarity growth strategy in certain periods, despite synchronization of radial variation.

Heavy thinning resulted in the greatest annual radial increment for maritime pine regardless drought episode. Besides, heavy thinning positively affected the intra-annual pattern for pine increasing spring and autumn asymptotes. Thinning treatment, independently of intensity, had also a slight positive effect on inter- and intra-annual radial increment for oak species, but not under drought conditions. Species-specific differences on intra-annual cumulative radial increment patterns showed an obvious asynchrony of radial growth for Scots pine-oak mixed stand. Only heavy thinning increased, but not prolonged, spring radial increment for both species in regardless climatic conditions. These results suggest a species niche complementarity, involving an efficient use of resources, which could release abiotic stress compared to monospecific stands. Besides, heavy thinning enhances the species-specific radial increment response to drought in Mediterranean pine-oak stands, so may be recommended to mitigate climate change impacts.

# Resumen

Las previsiones sobre el cambio climático son especialmente graves para la cuenca del Mediterráneo occidental, donde el aumento de las temperaturas y la disminución de las precipitaciones podrían acrecentar la frecuencia de los episodios de sequía. Las masas mixtas, a través de la complementariedad de nichos de las especies que la componen, pueden conducir a la obtención de mayores servicios ambientales, sobre-producción o mayor estabilidad temporal en comparación con masas monoespecíficas. Controlar la competencia mediante las claras puede proporcionar, asimismo, una herramienta de adaptación a la sequía, minimizando los impactos ecológicos y socioeconómicos potencialmente adversos generados por el cambio climático.

En el presente estudio, se pretende esclarecer la complementariedad temporal, de acuerdo con los patrones de incremento radial intra-anual, y el efecto de las claras en las especies de pino y rebollo que coexisten en clima Mediterráneo. Además, se evaluaron las diferencias en la variación radial de las especies en respuesta a las variables climáticas. Las masas objeto de estudio proceden de repoblación (inicialmente eran masas de pino, con las características típicas de las masas artificiales), las cuales se diversificaron con el tiempo debido a la recuperación y rebrote de las originales masas de monte bajo de rebollo. En la actualidad son masas mixtas con una en estructura en las que domina el pino con subpiso de rebollo.

Se estudiaron las diferencias entre especies de los ciclos de variación radial diaria, en el patrón intra-anual del incremento radial acumulado y en la respuesta de la clara de las masas mixtas de *Pinus pinaster-Quercus pyrenaica* en años climáticamente contrastados (2010-2014) y en dos sitios con condiciones de sequía diferentes. Asimismo, se evaluó el patrón intra-anual del incremento radial acumulado y la respuesta de la clara de una masa mixta de *Pinus sylvestris-Quercus pyrenaica* durante dos años distintos climáticamente (2016-2017). Se produjo un evento de sequía grave durante los años 2012 y 2017 en ambas masas, respectivamente.

Se establecieron nueve parcelas rectangulares en un diseño cuadrado latino en los tres sitios de estudio. El diseño experimental consistió en dos tratamientos de clara con diferente intensidad y un control (sin aclarar) con tres réplicas cada uno. El tratamiento de clara por lo bajo consistió en una intensidad moderada y fuerte, eliminando el 25% y el 40-50% del área basal inicial respectivamente. La clara se realizó solamente eliminando el pino en rodales mixtos de pino negral y rebollo, mientras que ambas especies fueron cortadas en rodales mixtos de pino albar y rebollo. Para el análisis de la variación radial, se instalaron dendrómetros de banda y electrónicos de alta resolución temporal en una muestras de los pies de pino y rebollo. Las variables meteorológicas de cada sitio se registraron de forma continua utilizando una variedad de sensores, una estación meteorológica al uso y estaciones automáticas de red de la Agencia Estatal de Meteorología.

Se ajustaron varios modelos mixtos no lineales para mostrar las diferencias entre especies en el patrón intra-anual del incremento radial acumulado: modelo bi-logístico, un modelo de Richards para el período de primavera y otro para otoño, y un doble modelo de

Richards. Se emplearon modelos mixtos lineales para analizar la respuesta de cada especie al clima. Además, se utilizaron estadísticos lineales y no lineales para evaluar la sincronía en la variación radial de las especies.

El incremento radial comenzó de media el 30 de marzo para el pino negral, mientras que para el rebollo fue entre 1-3 semanas más tarde coincidiendo con el brote de la hoja. La temperatura del aire generó variaciones radiales en los ciclos diarios con diferentes respuestas de las especies, mientras que la precipitación aumentó la amplitud y la duración del ciclo diario de igual forma para ambas especies. El incremento radial diario y el número de ciclos con dicha fase fueron mayores para el pino negral que para el rebollo durante la primavera, siendo la disponibilidad de agua el factor más importante para dicho incremento. En consecuencia, el patrón intra-anual mostró un mayor incremento radial para el pino negral que para el roble independientemente del año y el sitio. Las diferencias de las especies en el patrón intra-anual del incremento radial acumulado también revelaron una posible estrategia de complementariedad en el crecimiento en ciertos períodos, a pesar de la sincronización en la variación radial.

Las claras fuertes generaron el mayor incremento radial anual para el pino negral sin importar el episodio de sequía. Además, afectó positivamente el patrón intra-anual del pino aumentando la asíntota de primavera y otoño. Las claras, independientemente de su intensidad, también tuvieron un ligero efecto positivo en el incremento radial inter e intra-anual para el rebollo, pero no se observaron en condiciones de sequía. Las diferencias de las especies en el patrón intra-anual mostraron una evidente asincronía en el incremento radial para la masa mixta de pino albar y rebollo. Solo la clara fuerte incrementó, pero no prolongó, el incremento radial de primavera para ambas especies, independientemente de las condiciones climáticas. Estos resultados sugieren una complementariedad de nicho de las especies estudiadas, lo que implica un uso más eficiente de los recursos y una posible liberación del estrés abiótico en comparación con las masas monoespecíficas. Además, las claras fuertes aumentaron la respuesta de incremento radial de las especies frente a la sequía en masas mixtas de pino y rebollo en ambiente Mediterráneo, por lo que podría recomendarse como estrategia para mitigar los impactos del cambio climático.

# Introduction

## 1.1. Climate change impact on Mediterranean forest

Climate change could influence biodiversity and ecosystem functioning through phenological alterations (Gordo and Sanz, 2009; Rossi et al., 2011), species-specific distribution range shifts (Peñuelas et al., 2007), changes in forest production (Linares and Camarero, 2012; Pretzsch et al., 2014) and subsequent changes in carbon storage (Vayreda et al., 2012).

Thereby, climate change could entail severe loss in the economic value of forest land in southern Europe which might affect the provision of goods and forest services (Hanewinkel et al., 2012). This in turn may lead to changes in traditional timber harvesting or diversification in the use of non-woody forest products and other forest resources (Bravo et al., 2008; Hanewinkel et al., 2012). Thus, forest management plans must take into account future drought risk and water resource management strategies as adaptation measures for climate change (Botterill and Hayes, 2012).

Moreover, climate change may impact specially Mediterranean forests harshly (Dankers and Hiederer, 2008; Luterbacher et al., 2012) resulting in soil water deficits that could alter tree growth according to species sensitivity (Lara et al., 2013; Michelot et al., 2012). Although fertilize effect from $CO_2$ increment could enhance net primary productivity, low evidence was observed in Mediterranean stands (Camarero et al., 2015; Rathgeber et al., 2000). Several studies demonstrated an increment of plant mortality rates and die-off events, reduced seedling recruitment, long-term shifts in vegetation composition, reduced radial growth, and increased crown defoliation responses (Allen et al., 2010; Andreu et al., 2007; Carnicer et al., 2011).

Similarly, modeling approaches predict a large growth increase in mid-high latitudes of the Northern Hemisphere due to more benign temperatures, but a decrease in growth and survival in southern stands due to potentially warm-temperature induced drought-stress (Huang et al., 2013; Reich and Oleksyn, 2008). In Mediterranean ecosystems, forest growth is primarily constrained by water availability, changing tree-growth pattern and climatic response of Iberian pine forest since the mid-20th century(Andreu et al., 2007; Büntgen et al., 2013; Shestakova et al., 2017). Despite tree acclimation to cope with climate change through phenological changes and increased water-use efficiency (Hartmann et al., 2015; Natalini et al., 2016; Peñuelas et al., 2011), tree decline and die-back was evidenced for Mediterranean species studied here (Gea-izquierdo et al., 2013; Prieto-Recio et al., 2015; Voltas et al., 2013).

## 1.2. Forest management for climate change adaptation

Different temporal scales of management strategies must be considered for forest adaptation to climate change. The strategies should be executed towards achieving short-term objectives (as decreasing the immediate risk of a particular disturbance), and also towards the promotion of resilience for long-term adaptation. Different management strategies are expected to induce short/mid-term or long-term effects, and it can be implemented before disturbance (e.g. to improve resistance to drought) or after disturbance (e.g. to improve forest recovery after fire). According to Vilà-Cabrera et al., (2018) the management strategies to cope to climate change could be classified as follow:

1. Promoting mixed forests via species or genotype levels, or actions focused for the promotion of forest structural diversity as uneven-aged forests to raise stability to disturbances (Martín-Alcón et al., 2016).

2. Reduction of stand density. Thinning treatments increase growth, health and value of the remaining trees. Besides, reduces fire risk losses (Hurteau et al., 2008), and stimulates resistance to drought (D'Amato et al., 2013a) and pests (Waring and O'Hara, 2005).

3. Changing species or genetic composition better adapted to the conditions forecasted under global warming.

4. Management of the understory by breaking vertical and horizontal fuel continuity, or promoting spatial heterogeneity for disturbance prevention and enhancing connectivity.

The present study is focused on the first two strategies, which effects are expected to induce long and short/mid-term effects, respectively. Mixed-species stands present some advantages over monospecific ones with regard to ecological functions and services (Forrester, 2017; Knoke et al., 2008; Pretzsch and Forrester, 2017). Several recent studies have identified mixed forest stands as a possible adaptation strategy in forest management, to cope with climate change, increase resistance and recovery to biotic and abiotic factors (Forrester, 2015; Guyot et al., 2016; Pretzsch et al., 2013) and enhance temporal stability (del Río et al., 2017b; Jucker et al., 2014). Mixtures could increase resilience in extreme drought conditions through complementary use of water resources based on species niche partitioning and modifications in water-use efficiency (Forrester, 2014). Although studies have shown contrasting results depending on species composition and site conditions, the positive effect of mixing species seems relevant to drought-prone sites (Forrester et al., 2016; Grossiord et al., 2014). Mixed forest stands might also increase diversify production and reduce the risk of damage from pests or diseases (e.g. Condés et al., 2013; Griess and Knoke, 2011; Kelty, 2006; Pretzsch et al., 2015; Pretzsch and Schütze, 2009).

At the same time, the promotion of diversity and species interactions can benefit key ecosystem functions such as productivity, researching over-yielding and supporting higher stand density compared to monospecific stands (del Río and Sterba, 2009; Nunes et al., 2013; Riofrío et al., 2017a). This could be important for the Mediterranean region, where pine species have generally been re-introduced into oak coppice stands. Successional and phenological trait differences could involve different species growth, offset the usual low production of Mediterranean pure oak coppices and promote mixed composition as a possible adaptation strategy for climate change.

Thinning treatment is a management strategy planned to have short- or mid-term effects on forest responses. Thinning reduce tree-to-tree competition for resources and to improve survival and fruit production (Olivar et al., 2014; Sanchez-Humanes and Espelta, 2011), the physiological performance of individuals (Matteo et al., 2010), and alters forest functions such as C sequestration (Bravo-Oviedo et al., 2017), as well as the reduction of drought vulnerability via increasing water availability and water use efficiency (Cotillas et al., 2009; D'Amato et al., 2013b; Magruder et al., 2013) and fire risk (Hurteau et al., 2008).

Trees growing in conditions of low competition enhance tree growth and prevent stand growth stagnation and are less vulnerable to the drought events predicted by climate change scenarios (Fernández-de-Uña et al., 2015; Martín-Benito et al., 2010; Martínez-Vilalta et al., 2012). Concretely, thinning improve radial growth recovery but scarcely to resistance of drought Sohn et al., (2016b). Controlling competition through thinning may also provide a drought adaptation tool that would minimize potentially adverse ecological and socio-economic impacts of climate change (J. A. Sohn et al., 2016a, 2016b; Sohn et al., 2013). Therefore, understanding growth dynamics in mixed forest stands under different competition conditions may serve to establish a combined strategy for adapting forest stands to climate change.

## 1.3. The use of dendrometer devices for tree growth dynamics

Tree or stand growth can be measure by several methodologies attend to forestry science, which varies according temporal scale and precision. The common methodology used to evaluate tree growth is by difference of forest inventories. It is largely used in National Forest Inventories along the globe by comparing stocks in temporal field plots in different times. Growth is calculated by the difference of target variable (diameter, high, basal area, volume, biomass, etc.) for a same place (plot) in different times at long-term (years).

Tree diameter growth is a typical measure in forestry because it correlates with biomass, and therefore carbon uptake, as well as with pathogen damage, nutrient availability, and the influence of climate on photosynthesis among others (Barford et al., 2001). Accordingly, stem growth analyses can provide valuable information about how Mediterranean ecosystems will respond to forecasted climate change (Martín et al., 2014). Thus, increment cores are frequently used for foresters and dendrocronologists to assess tree growth. Inter-annual diameter growth is estimated by tree ring-width increments measured from increment cores, which are usually extracted at stem height of 1.30 m and taken from most trees of target plots. This methodology permits correlate climate and basal area increments at tree or stands level.

To examine relationships between growth and short-term climatic variability in tree species mixtures, inter-annual measurements usually provide a better basis than inventories or intra-annual measurements for analyzing ecosystem processes such as synchrony (Bauhus et al., 2017b). However, intra-annual data can improve predictions of potential tree growth response to climate by identifying particular climatic events that may escape a classical dendroclimatic approach (Duchesne and Houle, 2011). Monitoring intra-annual stem radial variations can provide insight into climate impacts on tree physiology and growth processes (Deslauriers et al., 2007; Duchesne and Houle, 2011; Zweifel, 2016). Accordingly, micro-cores let wood formation monitoring by sampling small wood samples (2 mm in diameter and 15-20 mm long) from the stem of the selected trees. Micro-cores are collected weekly at breast height following an ascending spiral pattern and spacing out each sampling from about 2 cm of the previous one to avoid wound reaction. Cross micro-sections are prepared from micro-cores to allow microscopic observation of cambial activity and tree growth.

Moreover, intra-annual radial variation patterns may reveal species-specific resource capture and growth, and repot tree interaction differences between mixed and monospecific stands (Forrester, 2014; Pretzsch, 2017). In view of that, band dendrometers are typically used to read manually using vernier measurement scales or similar. They can theoretically be used to detect small changes in stem size, when read very frequently. However, they require that an operator read this scale periodically and readings should be taken in the early morning when stem size is at a maximum to avoid mistakes. The advantages of band dendrometers for measuring tree diameter are that measured are taken easily with precision, and offer a low-cost. Thereby, they can be installed in a lot of trees, so they have most often been used for developing precise estimates of intra-annual growth. Drew and Downes, (2009) defined band dendromters as high-spatial and low temporal resolution measuring tools. Some examples of intra-annual uses of dendrometer bands include investigation of seasonal dynamics and growth phenology. Band dendrometer studies have generally analyzed relationships between stem size variations and climate (Duchesne and Houle, 2011; Oberhuber et al., 2014; Vieira et al., 2013), as well as species-specific responses (King et al., 2013; Oberhuber et al., 2015). Studies based on band dendrometer diameter measurement in Mediterranean mixed forests are scarce. Riofrío et al., (2017b) found proportion in species composition to be an important factor affecting intra-annual radial increment patterns in maritime pine-Scots pine mixed stands.

A second category of dendrometers has been developed to measure stem size regular and automatically, removing the need to manually read with high spatial and high temporal resolution. Consequently, this kind of dendrometers are now widely used to provide high-resolution stem variation data on coniferous and broadleaf trees from boreal to tropical forests (Biondi and Rossi, 2015; Deslauriers et al., 2007; Duchesne and Houle, 2011).

Continuous or high-resolution dendrometers are commonly used for studying seasonal tree growth dynamics, uncovering the environmental parameters that drive tree growth, and monitoring aspects of tree water balance such as water use and drought stress (Van der Maaten et al., 2016; Zweifel, 2016; Zweifel et al., 2016). They also make it possible to evaluate the onset of radial increment from daily stem variation cycles and radial variation synchrony between species. Radial increment onset from dendrometer recordings could be related with xylogenesis, i.e, radial growth development (Oberhuber and Gruber, 2010; Vieira et al., 2014; Vieira et al., 2015). Generally, forest synchrony analyses focus on inter-annual radial growth concurrence in the timing of ring formation over several years (Fajardo and Mcintire, 2012; Hayles et al., 2007; Lyu et al., 2016) or flowering and seed tree phenology (Bogdziewicz et al., 2017), but very little is known about intra-annual radial variation synchrony between species from dendrometer measurements. Moreover, several authors have also studied leaf phenology and *Quercus pyrenaica* Willd. cambial activity dynamics (Fernández-De-Uña et al., 2017; González-González et al., 2013; Pérez-de-Lis et al., 2013), but dendrometer records have seldom been used to explore the relation between leaf phenology and radial increment.

The handful of studies that have reported on seasonal variations in tree stem radius in Mediterranean areas mostly confirm the dominant role of temperature as the major constraint on radial increment in short time scales, and of precipitation effects in monthly scales (Camarero et al., 2010; Gutiérrez et al., 2011; Vieira et al., 2013). However, high-resolution stem diameter variation studies on mixed forests in this region are infrequent. Sánchez-Costa et al., (2015) found contrasting growth and water use strategies in four co-occurring Mediterranean species. Besides, reports of radial variation cycles focusing on the species studied here are insufficient, with the exception of Vieira et al. (2013), who worked with matirime pine for one year only (2010). Camarero et al., (2010) described also species-specific differences in xylogenesis patterns in mixed stands of *Juniperus thurifera* L., *Pinus halepensis* Mill., and *Pinus sylvestris* L. by high-resolution dendrometers.

Because intra-annual analyses often involve short observation periods, they do not accurately capture radial variations under contrasting weather conditions (Drew and Downes, 2009; King et al., 2013). However, in this study we evaluated a long period for *Pinus pinaster* Ait.-*Q.pyrenaica* stands (2010-2014) and two contrasted years for *P.sylvestris-Q.pyrenaica* mixed forest (2016-2017) with a severe drought episode in both cases.

### 1.4. Mediterranean pine-oak mixed forests

The maritime pine (*Pinus pinaster*) is a widespread medium-size tree native to the western Mediterranean basin (Figure 1). Most of the surface occupied in Europe by maritime pine is in the Iberian Peninsula, approximately 1.7 million ha in monospecific and mixed stands (Serrada et al., 2008). Maritime pine in Spain is at 600-1300 m.a.s.l. in a sub-humid and continental Mediterranean climate. Mean annual precipitation is 400-800 mm and summer precipitation is between 20-125 mm (Serrada et al., 2008). It is ecologically versatile, showing a wide range of expressive traits regarding growth characteristics, frost resistance, adaptation to summer drought and shows preference for siliceous and sandy soils.

Maritime pine is a light demanding (does not tolerate shade) and fast-growing species, so it has been used for soils protection, reforestation of degraded areas and dunes stabilization and also in intensive plantations. It has a deep root system with highly developed horizontal secondary roots. Its wood is appreciated for producing construction wood, poles and furniture. The maritime pine has been also traditionally utilized for the extraction of resin obtaining turpentine and rosin.

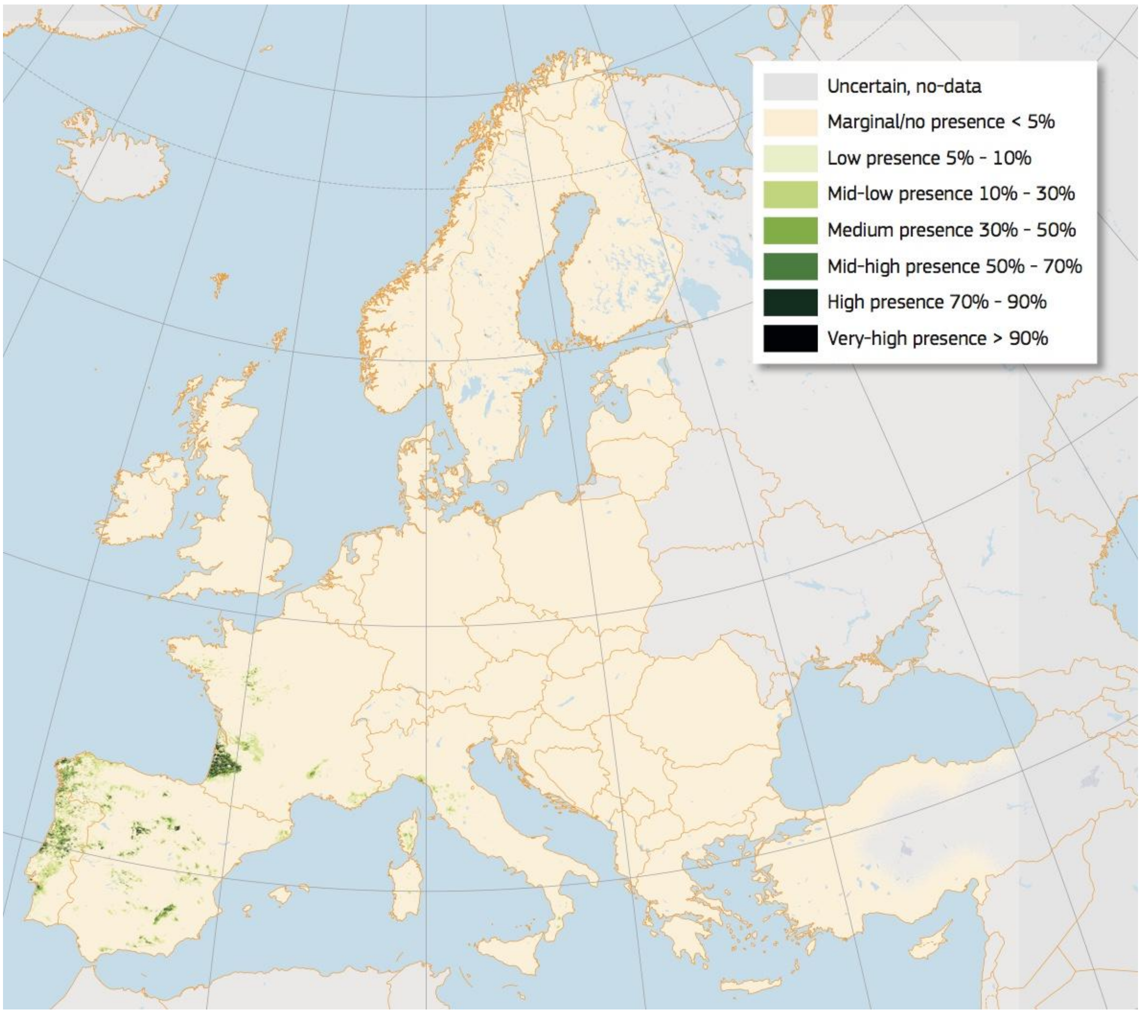

*Figure 1. High resolution distribution map for Pinus pinaster estimating the relative probability of presence. Source:*(Abad Viñas et al., 2016)

*Pinus sylvestris* (Scots pine) is the most widely distributed pine species in the world, can be found all the way across Eurasia. The mountains of Sierra Nevada in southern Spain (37° N) are the southern latitudinal limit of the species. In Europe, Scots pine forests now exceed 28 million ha (Figure 2) and in Spain is approximately 1.3 million ha (Serrada et al., 2008). Although the altitudinal distribution of Scots pine in Spain is at 800-2000 m.a.s.l., it is mainly found in montane climate: mean annual precipitation of 600-1200 mm and summer precipitation higher than 100 mm (Serrada et al., 2008).

Scots pine is a light-demanding pioneer species (but also can be found in partially shaded sites), frost and drought tolerant and able to grow on very poor soils, so it can be found in many ecologically diverse habitats. The root system is deep with dominant oblique and long secondary roots. Its timber is valued for its good strength to weight ratio and it is both commercially and culturally a very important species in a number of European countries, particularly in the more northerly regions.

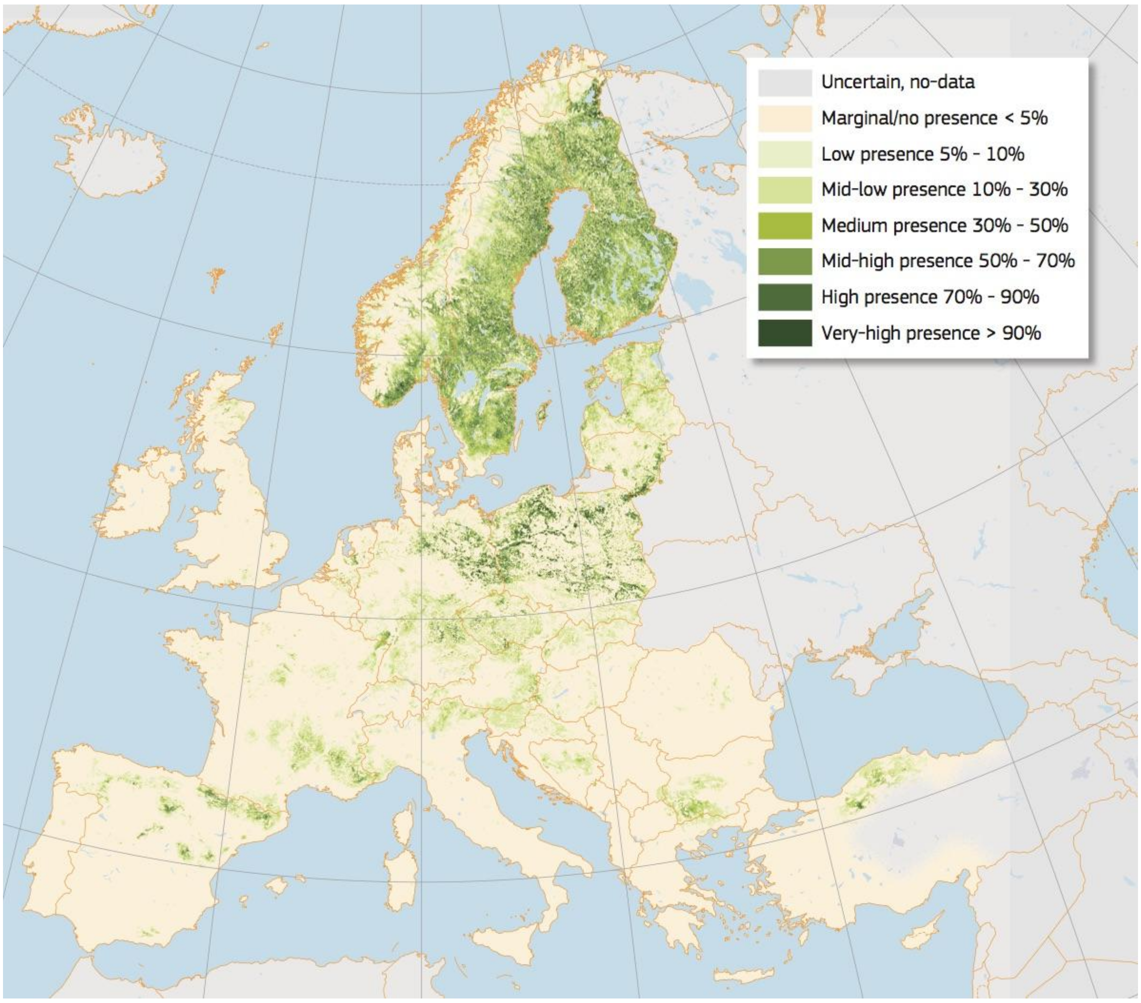

*Figure 2. High resolution distribution map for Pinus sylvestris estimating the relative probability of presence. Source:* (Houston Durrant et al., 2016)

Pyrenean oak (*Quercus pyrenaica* Willd.) is a deciduous and mercescent species distributed throughout the western Atlantic Mediterranean regions: West France, Portugal, Spain and North Morocco (Figure 3). In Spain it occupies 214,000 and 375,300 ha in seedling and coppice forest system respectively (Serrada et al., 2008). Castilla y Leon region in Spain hoard the largest area of the species (67% of its natural distribution area). This oak species is at 400-1600 m.a.s.l. in a sub-humid and continental Mediterranean climate. Mean annual precipitation is 600 mm and summer precipitation is higher than 125 mm (Serrada et al., 2008). It has a short growing season, which may determine its distribution. Summer drought is one of its limiting factors, and it avoids the driest areas. Hereafter we will refer to *Q. pyrenaica* as oak.

Oak is a partially shade-tolerant and intermediate tree between temperate and Mediterranean species, growing prevalently in mid mountain areas on siliceous soils. The root system is strong, equipped with numerous shallow, spreading, stoloniferous secondary roots, and reaches a depth of 50 cm. Thanks its high resprouting capability, the oak forests have been widely managed as coppice with silvo-pastoral uses, such as firewood, livestock grazing and charcoal production.

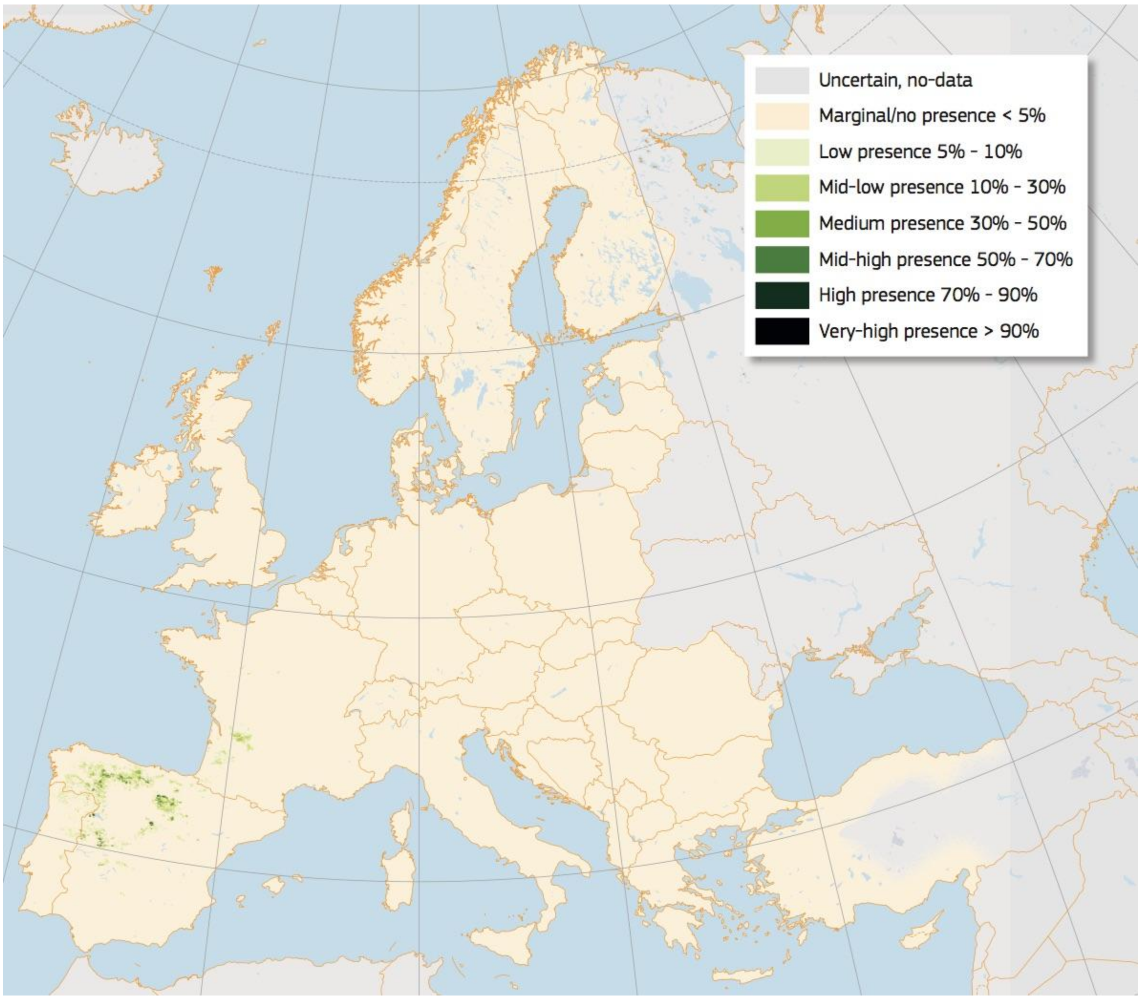

*Figure 3. High resolution distribution map for Quercus pyrenaica estimating the relative probability of presence. Source:* (Nieto Quintano et al., 2016)

Oak and both pines (*P. pinaster* and *P. sylvestris)* usually establish spontaneous mixed stands where its natural distribution area coincides. Consequently, forest management strategies during the second half of the twentieth century included re-introducing pine into oak coppice stands as a method of forest restoration and to increase stand productivity. This is the case of the mixed forest stands of the present study. These co-occurring species show different successional and phenological traits which enhance complementarity: light-demanding pine species are dominant in early successional stages, while deciduous oak is a moderately shade-tolerant tree that predominates in the late-successional stage. *P.pinaster* and *Q.pyrenaica* species are widely distributed throughout the Western Spain and occupy approximately 105,325 ha in mixed forest stands (Ministerio de Agricultura y Pesca, 2006; Figure 4). *P.sylvestris* and *Q.pyrenaica* co-exist in moderate slopes of mountain areas sited in continental and mountain climate of western Spain with an approximate surface of 97,300 ha (Ministerio de Agricultura y Pesca, 2006; Figure 5). In addition to their wide distribution and forest area, they hold great ecological and socio-economic value, although there is not a specifically silviculture or forest management for the mixed stands studied here.

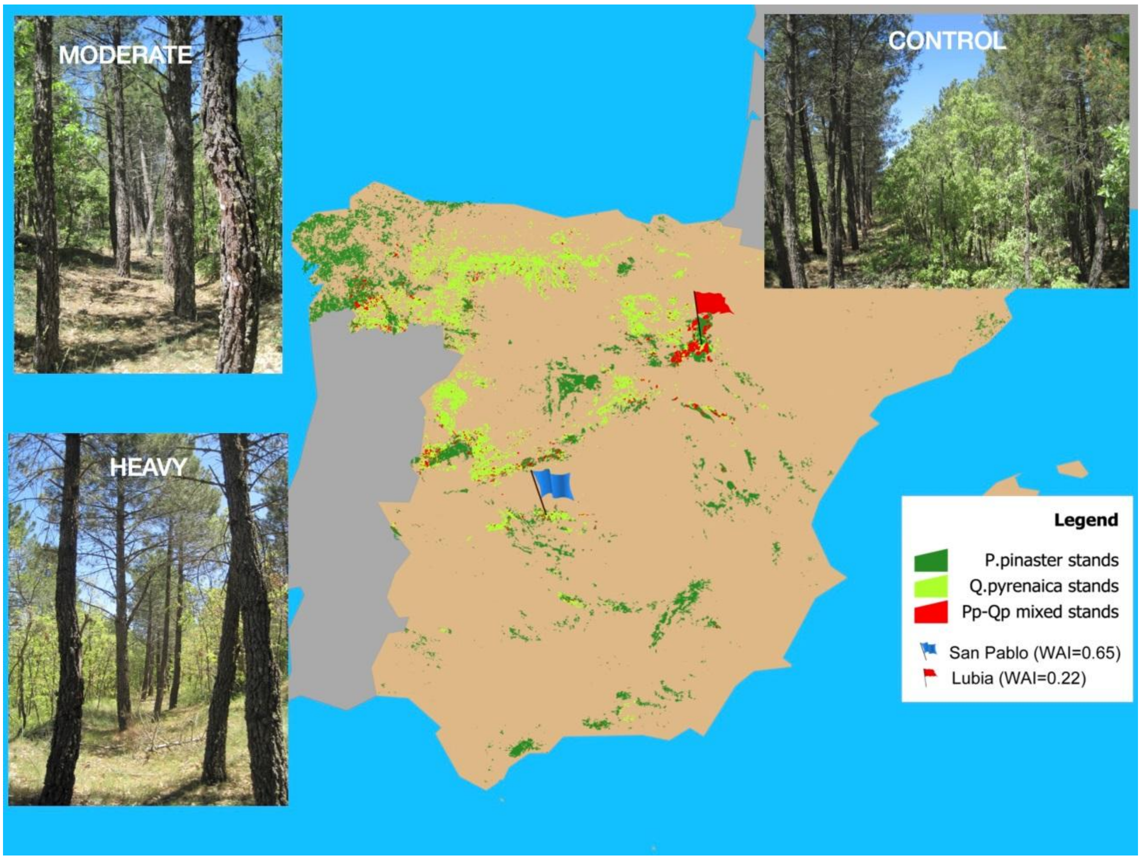

*Figure 4 Distribution map for Pinus pinaster, Quercus pyrenaica and mixed forest stands of both species in Spain. The study sites are marked with a different color flag. Pictures show thinning intensity.*

Vieira et al., (2013) studied growth dynamic for maritime pine based on season and daily variations in stem radius. They mainly determined that radial variation is related with the course of transpiration and thus dependent on temperature and tree water status. Bogino and Bravo, (2008) found that tree-ring growth of maritime pine was positively correlated with rainfall during the growing season and with summer rainfall of previous year, while temperature had a negative effect.

Caminero et al., (2018) reports a high plasticity in the growth responses of maritime pine to climate and drought conditions. Accordingly, recent studies of maritime pine are focused in wood formation monitoring and cambial dynamics, due to the capacity to quickly adjust cambial activity to the current environmental conditions (Vieira et al., 2014b). Cambium cells started to divide and differentiate earlier in years with a warmer winter (Vieira et al., 2014a). Young trees usually have a longer growing season and respond faster to climate conditions (Bogino and Bravo, 2009), presenting a higher frequency of intra-annual density fluctuation (IADFs) compared with old trees. Besides, the climatic signal of autumn growth seems to be mediated by stem size (Campelo et al., 2013). Most of the IADFs were located in latewood and were positively correlated to low previous winter and high late summer precipitation events (De Micco et al., 2007; Vieira et al., 2015, 2009). Similarly Campelo et al., (2013) reports that latewood IADFs were triggered by the combination of dry June, wet September, and warm December, supporting the previous dendrochronological studies in maritime pine which related it with September-October precipitation (Rozas et al., 2011).

*Figure 5. Distribution map for Pinus sylvestris, Quercus pyrenaica and mixed forest stands of both species in Spain. The study site is marked by colored flag. Pictures show thinning intensity.*

Despite having the ability to reactivate the cambium in autumn season, competition and water deficit appeared to operate as predisposing factors for maritime pine decline in the center of the Iberian Peninsula (Bravo-Oviedo et al., 2006; Prieto-Recio et al., 2015). Accordingly, Bogino et al., (2014) show an inverse significant correlation between δ13C and tree-ring growth for maritime and Scots pine suggesting the negative influence of water deficit on growth. Studies focused on tree response to climatic conditions for maritime pine in mixed forest are scarce. Recent studies evaluated changes in structural heterogeneity, stand productivity and species-specific competition for maritime and Scots pine mixed forest (Riofrío et al., 2017a, 2017b).

Because of its extended distribution area and economic importance, numerous studies were focused on the relationships between climate and tree-ring width for Scots pine. Studies from Central-Europe highlighted the significance of precipitation just before and at the beginning of the growing season to promote radial growth (Oberhuber and Gruber, 2010b; Rigling et al., 2001). Relative air humidity may increase radial increments, while soil water content and air temperature had no influence (Oberhuber et al., 2014; Oberhuber and Gruber, 2010b). Actually, even IADFs were detected in Scots pine due to moist-cool conditions in the middle of the growing season (Rigling et al., 2001).

However the results from studies focused on Scots pine in Mediterranean region are quite distinct, probably due to the large distribution area of the species with high variability in its response to climatic conditions (del Río et al., 2017a). Accordingly, the climate short-term effects should be negative in the warmest climates but strongly positive in the coldest (Rehfeldt et al., 2002). Warm late summer temperatures constrained growth of Scots pine (Sánchez-Salguero et al., 2015), but without cambium reactivation (IADFs) in autumn season as other Mediterranean endemic conifers (Camarero et al., 2010). Although mean day-length seems to be the key factor for wood formation (Camarero et al., 2010), nowadays, Scots pine is also suffering a process of growth decline in marginal areas of its distribution at Mediterranean region, mainly as a result of drought stress (Büntgen et al., 2013; Martínez-Vilalta et al., 2012). The resilience to drought was found to be lower in recent years regardless the tree vigor (Camarero et al., 2018), resulting in reduce latewood density as a way to enhance hydraulic conductivity during dry summers (Candel-Pérez et al., 2018).

Studies of mixed forest stands composed by Scots pine are currently spreading in Europe due to functional advantages compared to monospecific stands. Mixing effect on individual tree structure or crown morphology has been reported by several researches (Pretzsch, 2017, 2014; Pretzsch and Schütze, 2016). Besides, tree species mixing can increase maximum stand density and promote over-yielding (Pretzsch and Biber, 2016; Pretzsch and Schütze, 2016, 2009). Similar results were confirmed in mixed forest stands of Scots pine in Spain (Condés et al., 2013; del Río and Sterba, 2009; Riofrío et al., 2017a). Scots pine-oak mixed stands support higher volume increment per occupied area compared to pure stands suggesting a species interaction with reduced levels of competition in the former (del Río and Sterba, 2009).

In spite of its large distribution area in Spain, the studies of *Q.pyrenaica* growth are relatively scarce. The effect of climate on spring growth and early wood vessel area for oak species was closely related to precipitation during April and May (García-González and Souto-Herrero, 2017; González-González et al., 2013). According to xylem and wood formation monitoring earlywood growth onset occurred between late-March and early-April, while latewood enlargement ceased at the end of July-mid-August (Fernández-De-Uña et al., 2017; González-González et al., 2013). However, over-aging commonly caused a steep decline in latewood production, acting as a predisposing factor in the decline episode of oak coppice stands (Corcuera et al., 2006). Growth projections reveal local vulnerability of Mediterranean oaks with rising temperatures, resulting in declining trees characterized by a very low production of latewood and a decrease in lumen area of the widest earlywood vessels, suggesting a potential reduction of hydraulic conductivity (Gea-izquierdo et al., 2013; Gentilesca et al., 2017)

Nunes et al., (2013) reported that maritime pine-oak mixed stands had a significantly higher mean aboveground biomass and aboveground net primary production than pine or oak monospecific stands, being the foliage the component with the greater distribution of biomass. Oak tree-ring width is reported to be less affected by summer drought because parts of the earlywood are built in early spring, whereas xylem formation for co-existed Scots pine ceased 1–3 weeks earlier in mixed forest stands during drought conditions (Eilmann et al., 2009; Fernández-De-Uña et al., 2017). Accordingly, Cotillas et al., (2009) showed that oak coppice mixed stands did not suffer earlywood hydraulic diameter changes under rainfall exclusion, but experienced a cumulative reduction in latewood width.

Thinning improves the growth of the remaining trees by releasing competition for above and belowground resources, including water. Tree respond to thinning treatments depends on the thinning regime (age at the first thinning), intensity, type, and frequency. Thinning treatment for maritime pine forests commonly reduced the density to 150-200 trees per ha when it was 25 years old to ensure a fast growth diameter for resin extraction. Stand density after thinning coincided with the final density of regeneration cutting, but assuming a loss of timber yield in favor of resin production (Serrada et al., 2008).

In pure stands from reforestation, thinning treatments become more important due to the structural characteristics of the stand, even-aged and high densities. The first thinning is made at 20-40 years depending on the site index in a semi-systematic way(del Río et al., 2006). Thinning from below is usually employed due to common low site index, although co-dominant misshapen trees could be also removed. Thinning intensity of first cutting is moderate-heavy removing 25-30 % of initial basal area and chosen 300-400 trees per ha as final crop trees(del Río et al., 2006).

Thinning frequency depends of site index, from 7 years when young trees and high site index for timber production, to 15 years for old trees and low site index (del Río et al., 2006). When thinning frecuency is 5-6 years tree diameter increases from 3-4% to 6-8% of current annual growth (Serrada et al., 2008). The final number of thinning treatments in a stand is usually 3-4 for low or high site index respectively. The usual low wood quality of stems, resinated trees or elevated distance to processing factories, have generated a lack of demand for maritime pine wood and, as a result, a low number of thinning treatments (Serrada et al., 2008).

A large number of thinning experiments were established for Scots pine in the last century across Europe due to the importance of timber quality (del Río et al., 2017a). Occasionally, competition overrides climate as a driver of tree growth for Scots pine (Sánchez-Salguero et al., 2015), hence, highlight the thinning importance. In some experiments, accelerated basal area and volume growth was found for thinning treatments at young stand ages (del Río et al., 2008; Montero et al., 2001). Thinning from below commonly has no effect on the dominant height of the stand (del Río et al., 2008), although significant height growth reductions, as spacing decreases, have been reported for several species (del Río et al., 2017a). Conversely, heavy thinning from below significantly increases the quadratic mean diameter of the stand, but part of this increase is due to the shift caused by eliminate smaller trees (del Río et al., 2017a). Thinning selection from above and heavy intensity, result in greater tree radial increments but usually with associated yield loss at stand level for Scots pine (del Río et al., 2017a, 2008).

Heavy thinning significantly improve radial growth recovery after drought events, but scarcely affected the resistance for Scots pine stands (J. Sohn et al., 2016; J. A. Sohn et al., 2016a, 2016b). The effect on growth recovery was also greater after the first thinning and in recently and heavy thinned stands. However, drought induced changes in wood density that are not prevented by thinning treatment in Scots pine stands (Candel-Pérez et al., 2018) Besides, the time elapsed since the last thinning had the opposite effect on tree resistance (J. A. Sohn et al., 2016b; Sohn et al., 2013)Although mixed stands are often promoted because of the expected improvement in the provision of ecosystem services and greater stability (del Río et al., 2017b; Pretzsch et al., 2015), thinning experiments in mixed Scots pine stands are currently scarce (Primicia et al., 2016)

Similarly, there are not too much studies amog thinning treatment effect on oak growth. In Spain, traditional coppice management has declined rapidly since the 1960's, when the rural population and charcoal demand greatly decreased(Corcuera et al., 2006). These structural changes have also led to new management strategies such as the conversion from overaged coppice stands into high forests and open woodlands through selective thinning, a task which is not always successfully accomplished (Amorini et al., 1996).

Cañellas et al., (2004) reported that the higher oak tree growth was observed under heavy thinning treatment in coppice stands, although no differences were found for stand yield (total basal area and biomass). Remained oak trees from thinning treatment form wider tree-rings, more latewood and multiseriate tree-rings than overaged trees (Corcuera et al., 2006). Besides, the growth enhancement remained 8 years after thinning. Cotillas et al., (2009) also found that selective thinning (20–30% of total stump basal area) improved tree growth for oak mixed coppice stands under natural and under reduced rainfall conditions. Nevertheless, the positive effects of thinning rapidly declined during three years. Moreover, thinning may altere the early-decomposition rate and nutrient immobilization of foliar litter in Mediterranean oak-pine mixed stands (Bravo-Oviedo et al., 2017). The unknown clone factor could mask the results of thinning on oak radial increment. Accordingly, Salomón et al. (2013) proposed thinning or clonal silvicultural treatments in managed oak coppice stands, to control root aging and increase stem growth.

In spite of the amount of studies of thinning effect on monospecific stands, forest management recommendations or silvicultural information for mixed stands studied here are scarce or absent.

### 1.5. Motivation

We evaluated species differences in intra-annual radial increment patterns of co-occurring Mediterranean pine-oak species from mixed stands. Studying intra-annual radial increment allows to gain new insight into species growth differences in drought conditions and assess potential species-specific complementary growth strategies (Forrester et al., 2013). These complementary effects, as facilitation/reduce competition, typical from species with different functional traits are more important in adverse habitats where climate is the main driver of productivity. Radial increment measurements could be used to estimate ecological consequences and production alterations stemming from climate change, which has caused serious damage to Mediterranean pine and oak species in Spain (Gea-Izquierdo et al., 2013; Prieto-Recio et al., 2015). Understanding radial increment differences in co-existing species makes it possible to evaluate stand stability or predict change species composition in mixed forests. However, intra-annual radial variation studies focused on mixed forests in the Mediterranean region are still scarce. The important role of mixed forest and thinning effect as feasible adaptation strategies to cope to global change can contribute to promote social, economic and environmental functions towards an adaptive Mediterranean forest management.

# Objectives

## 2.1 General objective

The main objective of present study was to investigate the radial variation differences among species in Mediterranean pine-oak mixed forest stands. Specifically, we studied the species-specific tree responses to different meteorological conditions and how thinning affects radial increment for coexisting species.

## 2.2 Specific objectives

Exactly we studied the specific objectives shown as follow:

1. **Species differences in daily radial variation cycles.**
   To uncover species-specific weather responses in daily radial variation cycles and to identify the weather variables that drove radial increment. We tested the hypotheses that (i) daily radial variation cycles varied according to seasons and species; (ii) differences were due to species responding differently to daily weather conditions and (iii) temperature and water availability were the main factors limiting radial increment, as expected in Mediterranean areas.

2. **Temporal complementarity among species**
   To decipher temporal complementarity between studied species by species differences in intra-annual cumulative radial increment patterns, and to identify and quantify radial variation synchrony between time series of species. We tested the hypotheses that (i) radial increment onset occurred later for deciduous oak species than for pine, (ii) cumulative radial increment patterns differed by species, with greater radial increment for pine than oak, giving plausible indication of temporal complementarity at certain periods and (iii) we expected that radial variation synchrony was lower between species than within the species.

3. **Responses of pine-oak mixed stands to thinning**
   To evaluate the effects of thinning and weather on inter and, especially, on intra-annual radial increment patterns. We tested the hypotheses that moderate and, particularly, heavy thinning intensity promotes tree radial increment for co-existing species.

## 2.3 Graphic schedule of present research

The research activity of the thesis is showed in the Figure 6 as a linear evolution. Orange rounded rectangles show the beginning of the process and are variables that affect or condition growth records. Diamonds identify the decision to evaluate contrasted weather conditions by diverse years or different sites with distinct drought environments. The yellow parallelograms represent the input of data, which are constrained by species composition (maritime/Scots pine–oak mixed forest) or climate (humid/drought conditions). Blue rectangles identify the tools installed on trees to record stem radial measurements: band or electronic high-resolution point dendrometers. Rounded dark and light green rectangles represents the end of the process until intra-annual radial variation measurements in different temporal scales: daily radial variation cycles or cumulative radial increment patterns. Besides, thinning effect is tested via band dendrometer measurements in different competition situation.

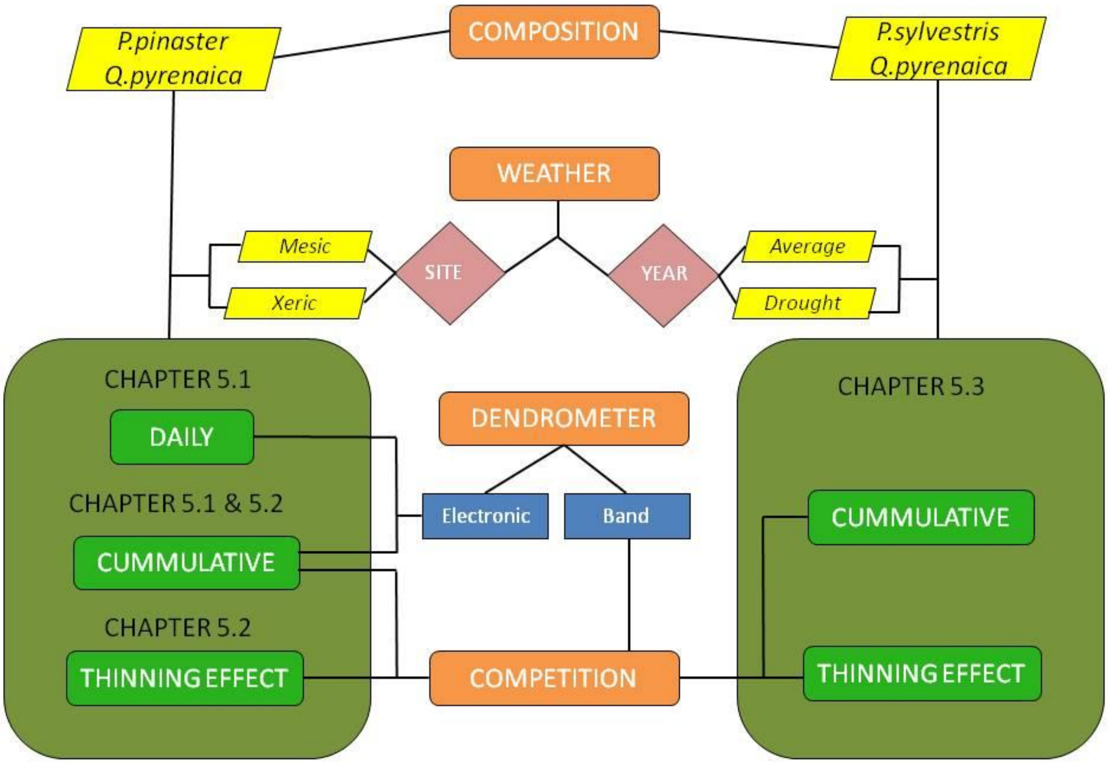

*Figure 6. Thesis workflow process to evaluate species temporal complementarity and thinning response based on intra-annual radial variation of pine-oak mixed forest.*

# Data

## 3.1. Study sites and experimental design

The field work has been executed in three experimental sites, where different thinning intensities were compared. Two sites where placed in maritime pine-oak mixed forest and another one in Scots pine-oak mixed stand. These mixed stands have a similar history: originally as monospecific pine forestation that has been diversifying over time, allowing the colonization of other species or the recovery of old and previous oak coppice stands. This evolution created mixed stands structure with different situations of dominance between pine and oak trees.

### *3.1.1.Pinus pinaster -Quercus pyrenaica mixed forest*

The study was located at two sites with different drought conditions in central Spain: Lubia (Soria; 41° 39' N, 2° 29' W) and San Pablo de los Montes (Toledo; 39° 31' N, 4° 16.6'W). The Lubia experimental site was located in the Duero Basin at an altitude of 1,134 m.a.s.l. on a continental plateau. This site is characterized by a sub-humid continental Mediterranean climate with an annual rainfall of 512 mm, of which 100 mm falls during the summer drought period, between June and August (AEMET, 2016; Spanish State Meteorological Agency). July is the driest month, with 30 mm rainfall, and May is the wettest month, with 67 mm rainfall. Annual mean temperature is 10.0 ºC, with frost occurring from September to May. The hottest month is July, with an average temperature of 18.9 °C, and the coldest is January, with a mean temperature of 2.3 °C. The soils are regosols and arenosols, characterized by a slightly acidic pH (5–6), sandy texture and low fertility, composed of predominately tertiary and quaternary materials (IGN, 1991). The experimental site was on a flat land.

The other study site was established in the Montes de Toledo mountain range, which separates the drainage basins of the Tagus and Guadiana rivers at 1,102 m.a.s.l. This site has a continental Mediterranean climate, with an average rainfall of 469 mm and a marked summer drought between June and August, with 49 mm recorded rainfall (AEMET, 2016). The driest month is July, with 8 mm, while the month with the highest rainfall is May, with 55± 32 mm. Annual mean temperature is 12.9 ºC and the hottest month is July, with an average temperature of 23.9 ºC. January is the coldest month of the year, with an average temperature of 4.1 ºC. The geological composition of the soil is mainly sandstones and quartzites from the mesozoic period that have given rise to slightly acidic arenosol soils (pH 5-6) (IGN, 1991). The site has a northwest facing aspect and the slope is 21.5%.

The Walter-Lieth annual aridity index (WAI), defined as the quotient between the dry and wet season areas from climogram based on historical climate records (1981-2010;AEMET, 2016), was calculated using the 'BIOdry' R package (Lara et al., 2013). WAI index revealed drought differences between sites: WAI of 0.22 for Lubia and 0.65 for San Pablo de los Montes (Figure S1). Hereafter, we will refer to these sites as WAI-0.22 and WAI-0.65

The forest stands at both sites had a similar origin: a plantation in rows of maritime pine (*Pinus pinaster* ssp. *mesogeensis*) was incorporated into the stand in 1970's after the removal of standing oaks. Between the plantation rows, oak sprouts have grown and the stand is currently a mixed stand in rows with a dominant canopy of maritime pine and an understory of oak. Today stand looks as pine-oak even-aged mixed stand of 35-40 years old, although real cambial age differs between species.

Nine rectangular plots (600-800 $m^2$) were established at each site, using a Latin square design. The experimental design consisted of an unthinned control and two treatments with three replicates each. Moderately and heavy thinning treatment consisted in 25 % and 40% of initial basal area removed respectively (Figure 4).

Only maritime pine was removed, applying thinning from below, which involved logging the suppressed or intermediate trees (Table 1). Harvest logs and branches were removed from plots. Thinning was carried out at the end of 2009, applying a buffer zone of 10 m around each plot. There were no statistical differences between treatments for each species and site before thinning. However, statistical differences were evident after thinning for pine density and basal area, though mean height and diameter at breast height from each site were not statistically different for moderate and heavy thinning (Table 1). Initial density of stand was higher for WAI-0.22 than WAI-0.65 site for both species.

*Table 1. Main stand characteristics before and after thinning for the two study sites. Data shown are mean and standard deviation values. Different letters denote significant differences for each site after thinning at the 0.05 significance level.*

| | | ***Quercus pyrenaica*** | | | | ***Pinus pinaster*** | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | **Before thinning** | | | | **After thinning** | | |
| **Site** | **Treat.** | **$H_o$ (m)** | **Density (n·ha$^{-1}$)** | **DBH (mm)** | **BA (m$^2$·ha$^{-1}$)** | **$H_o$ (m)** | **Density (n·ha$^{-1}$)** | **DBH (mm)** | **BA (m$^2$·ha$^{-1}$)** | **Density (n·ha$^{-1}$)** | **DBH (mm)** | **BA (m$^2$·ha$^{-1}$)** |
| **WAI-0.22** | Control | 4.8±1.2 | 2,203±399 | 45.4±17.9 | 5.1±1.4 | 11.0±0.7 | 1,388±225 | 182.8±55.6 | 38.9±5.2 | 1,388±225**c** | 182.8±55.6**a** | 38.9±5.2**c** |
| | Moderate | 5.7±1.8 | 2,284±401 | 55.1±22.9 | 6.7±1.8 | 11.0±1.1 | 1,257±69 | 185.2±58.7 | 39.5±6.0 | 681±77**b** | 221.3±39.9**b** | 29.5±4.3**b** |
| | Heavy | 5.1±1.6 | 2,406±484 | 46.5±19.6 | 6.7±2.8 | 11.3±1.0 | 1,228±235 | 187.7±57.7 | 39.3±4.9 | 482±112**a** | 225.5±40.5**b** | 23.4±2.9**a** |
| **WAI-0.65** | Control | 5.8±1.6 | 2,013±458 | 65.5±18.6 | 6.7±1.7 | 10.9±1.5 | 591±46 | 258.8±49.4 | 32.2±2.8 | 591±46**c** | 258.8±49.4**a** | 32.2±2.8**c** |
| | Moderate | 5.4±1.5 | 1,725±366 | 58.7±17.6 | 5.5±0.4 | 11.1±0.8 | 574±98 | 252.1±54.0 | 30.2±1.6 | 394±63**b** | 272.6±46.0**b** | 23.5±1.1**b** |
| | Heavy | 5.3±1.5 | 1,633±313 | 60.6±17.4 | 5.5±2..1 | 11.1±1.2 | 606±45 | 263.8±51.3 | 34.2±3.1 | 301±21**a** | 289.2±37.9**b** | 20.1±0.7**a** |

*Treat.: thinning treatment intensity; $H_0$: dominant height; DBH: diameter at breast height; BA: basal area.*

### *3.1.2. Pinus sylvestris-Quercus pyrenaica mixed forest*

The experiment was located in Palacio de Valdellorma (León, 42º 45' 42.4" N, 05º 12' 39.6" W) in north-western Spain (Figure 5). The experimental site was sited at 990 m.a.s.l. in a continental Mediterranean climate. The average annual rainfall is 515 mm with a marked summer drought episode between July and August, when 42 mm of precipitation are usually recorded (AEMET, 2016; Spanish State Meteorological Agency. 2661 weather station code, based on 1981-2010 historical records). Annual mean temperature is 11.1 ºC and the hottest month is July, with an average temperature of 27.4 ºC. The probability of frost period is from December to February. Topography was moderate with a slope of 16% and soils consisted in acid conglomerates based on Miocene clay sediments (IGN, 1991).

Similarly, initially oak coppice stand was harvested during 1970's and reforestation was carried out by planted pines in rows. Oak coppice sprouts grew again via asexual reproduction between pine rows, so today stand looks as pine-oak even-aged mixed stand of 40 years old, although real cambial age differs between species.

Nine rectangular plots (50 x 40 m) were established in a Latin square design. The experimental design consisted of two thinning treatments with different intensity and unthinned control with three replicates each. Thinning treatment consisted in moderately and heavy thinning removing 25% and 50 % of initial basal area (Table 2). Both species were removed applying thinning from below, which involved logging the suppressed and intermediate trees. Thinning was carried out at the end of 2015 and the felled logs and branches were removed from plots. There were no statistical differences between treatments for each species before thinning (Table 2). However, statistical differences were identified after thinning. Pine density differed between all three treatments, although there were no differences in tree diameter for moderate and heavy thinning either between moderate thinning and control basal area. There were not statistical differences between moderate and heavy thinning for density, diameter and basal area of oak trees after thinning (Table 2).

*Table 2. Main stand characteristics before and after thinning for Scots pine-oak mixed forest. Data shown are mean and standard deviation values. Different letters denote significant differences after thinning at the 0.05 significance level.*

|  |  |  | **Before thinning** |  |  | **After thinning** |  |  |
|---|---|---|---|---|---|---|---|---|
| **Species** | **Treat.** | **$H_o$ (m)** | **Density (n·ha$^{-1}$)** | **DBH (mm)** | **BA (m$^2$·ha$^{-1}$)** | **Density (n·ha$^{-1}$)** | **DBH (mm)** | **BA (m$^2$·ha$^{-1}$)** |
| **Pinus sylvestris** | Control | 12.5±1.2 | 1,415±130 | 122.1±43.4 | 19.6±2.3 | 1,415±130**c** | 122.1±43.4**a** | 19.6±2.3**b** |
|  | Moderate | 10.7±1.9 | 1,575±90 | 120.6±45.0 | 19.5±3.9 | 710±240**b** | 160.1±33.5**b** | 13.7±5.5**b** |
|  | Heavy | 11.7±1.7 | 1,580±130 | 118.3±42.5 | 20.9±3.3 | 390±197**a** | 151.6±35.5**b** | 9.0±4.6**a** |
| **Quercus pyrenaica** | Control | 10.9±1.1 | 2,960±710 | 59.3±32.6 | 12.6±1.6 | 2,960±710**b** | 59.3±32.6**a** | 12.6±1.6**b** |
|  | Moderate | 10.7±0.7 | 2,855±366 | 66.0±35.8 | 12.1±1.4 | 1,195±286**a** | 92.7±46.2**b** | 8.8±1.7**a** |
|  | Heavy | 11.3±1.8 | 2,005±760 | 66.3±41.0 | 8.7±5.0 | 430±427**a** | 93.1±63.4**b** | 4.0±2.9**a** |

*Treat.: thinning treatment intensity; $H_0$: dominant height; DBH: diameter at breast height; BA: basal area.*

## 3.2. Stem radial variation and climatic measurements

### *3.2.1.Leaf phenological records*

Leaf phenological events were visually observed on the main lower branches every two weeks throughout the year for maritime pine-oak mixed forest stands. These events included budburst (breaking up of the scales after bud swelling), twig enlargement (bud elongation and leaf unfolding) and leaf expansion (final stage of leaf extension). Because not all buds or leaves presented the same stage at any given moment during the season, especially at the beginning, we recorded a particular event when more than 50 % of the buds/leaves on the main branches were in the same stage.

### *3.2.2.Band dendrometer measurements*

After thinning, and three months before sampling (in order to ensure tool stabilization), dendrometer bands (DB 20, EMS Brno) were placed on ten trees per species and plot in maritime pine-oak mixed forest stands (Figure 7 and Table 3). A total of 360 dendrometer bands were fitted at breast height (1.30 m) after smoothing and removal of the outermost dead bark to avoid the influence of hygroscopic bark swelling and shrinkage on dendrometer measurements. Trees were selected within the plot using a stratified sampling approach that took diameter distribution into account and were carefully chosen attempting that local competition was representative to the plot thinning treatment. Dendrometer bands were read every two weeks throughout the year to the nearest 0.1 mm from April 2010 to December 2012.

*Table 3. Main characteristics of sampled trees with band dendrometer for maritime pine-oak mixed stands. Data shown are mean values and standard deviation in brackets. DBH: diameter at breast height;* $H_m$*: mean height. Letters denote significant differences between species, thinning treatments and site at the 0.05 significance level.*

| | | DBH (mm) | | $H_m$ (m) | |
|---|---|---|---|---|---|
| **Species** | **Treat.** | **WAI-0.22** | **WAI-0.65** | **WAI-0.22** | **WAI-0.65** |
| | Control | 216.3 (42.9)**d** | 279.4 (32.0)**e** | 10.1 (0.9)**c** | 11.1 (1.1)**d** |
| ***Pinus pinaster*** | Moderate | 218.7 (38.5)**d** | 264.7 (35.5)**e** | 10.5 (1.1)**cd** | 10.7 (1.1)**cd** |
| | Heavy | 222.5 (37.6)**d** | 288.6 (32.6)**e** | 10.5 (1.2)**cd** | 11.2 (1.5)**d** |
| | Control | 86.9 (11.4)**a** | 100.2 (11.0)**c** | 6.2 (0.7)**a** | 7.4 (1.0)**b** |
| ***Quercus pyrenaica*** | Moderate | 99.3 (17.1)**bc** | 90.6 (10.0)**ab** | 7.1 (1.4)**b** | 7.0 (1.0)**b** |
| | Heavy | 92.3 (17.4)**ab** | 88.0 (16.4)**ab** | 6.6 (1.2)**ab** | 6.9 (1.1)**ab** |

Accordingly, we installed also band dendrometers (DB 20, EMS Brno) after thinning treatment on five trees per species and plot in the Scots pine-oak mixed stand. A total of 90 bands dendrometer were fitted to trees selected considering also diameter distribution (Table 4). Band dendrometers were read every two weeks from March to December along 2016 and 2017 years with a resolution of 0.1 mm.

*Table 4. Main characteristics of sampled trees with band dendrometer for Scots pine-oak mixed stand. Data shown are mean values and standard deviation in brackets. DBH: diameter at breast height; $H_m$: mean height. Letters denote significant differences between species and thinning treatment at the 0.05 significance level.*

| Species | Treat. | DBH (mm) | $H_m$ (m) |
|---|---|---|---|
| ***Pinus sylvestris*** | Control | 131.9 (34.2) **a** | 11.7 (1.1) **ab** |
| | Moderate | 138.2 (29.2) **a** | 12.6 (1.8) **b** |
| | Heavy | 145.7 (33.1) **a** | 11.1 (0.7) **ab** |
| ***Quercus pyrenaica*** | Control | 117.8 (30.0) **a** | 9.7 (1.5) **ab** |
| | Moderate | 119.8 (26.6) **a** | 10.3 (0.5) **a** |
| | Heavy | 118.2 (28.6) **a** | 10.2 (1.1) **ab** |

Measurements were taken in the morning to reduce diurnal bias, which is caused by stem shrinkage from transpiration. The measurements were corrected for temperature effects and dendrometer thermal expansion (11.2 x $10^{-6}$ mm/ºC). Finally, girth increment data were transformed to radial increments based on a hypothetic cylindrical tree shape.

*Figure 7. Band dendrometer installed in maritime pine-oak mixed forest stands*

### *3.2.3. High-resolution point dendrometers*

Three dominant trees per species and site (twelve trees in total) were selected for installation of electronic point dendrometers in control plots of maritime pine-oak mixed forest. The pine trees chosen for sampling were 268.8 ± 15.3 mm diameter at breast height and 11.2 ± 0.7 m high, while the oaks were 94.5 ± 7.3 mm diameter and 7.4 ± 0.8 m high (Table 5). There were no significant differences in species diameter, height or age between sites.

*Table 5. Main characteristics of sampled trees with high-resolution dendrometer for the two study sites. Data shown are mean values and standard deviation in brackets. DBH: diameter at breast height; $H_m$: mean height. Letters denote significant differences between species and sites at the 0.05 significance level.*

| | **DBH (mm)** | | **$H_m$ (m)** | |
|---|---|---|---|---|
| | **WAI-0.22** | **WAI-0.65** | **WAI-0.22** | **WAI-0.65** |
| ***Pinus pinaster*** | 262.7 (21.2)**b** | 274.7 (5.5)**b** | 10.9 (0.9)**b** | 11.5 (0.5)**b** |
| ***Quercus pyrenaica*** | 90.7 (9.1) **a** | 98.3 (2.5) **a** | 7.0 (0.3) **a** | 8.0 (0.6) **a** |

In autumn 2011, we installed electronic point dendrometers (Depfor, University of Huelva, details are available in Vázquez-Piqué et al., 2009) in the selected trees to measure stem radial variation at breast height with a resolution of 1 μm (Figure 8). Dead outermost layers of the bark were carefully removed to avoid cambium damage and to eliminate hygroscopic influences from bark (shrinking and swelling due to change in air humidity) on dendrometer measurements. Data loggers were programmed to record measurements every 15 min for the entire 2012-2014 study period.

*Figure 8. Electronic high-resolution point dendrometer installed in maritime pine-oak mixed forest stands*

### *3.2.4. Weather devices and climatic information*

Site weather variables were continuously monitored using a variety of sensors for maritime pine-oak mixed forest. Air temperature, relative humidity and dew point were recorded at 15 min resolution using a data logger (HOBO U12 4-External Channel) placed at the WAI-0.22 site. A weather station (HOBO) was installed at the WAI-0.65 site to record air temperature, relative humidity, rainfall, solar radiation and wind speed. Additionally, temperature, precipitation and radiation records were compiled using hourly data from the AEMET automatic network stations (Lubia-Ceder 2044B and San Pablo de los Montes 3298X) located 6 km and 5 km from the WAI-0.22 and WAI-0.65 sites, respectively, to fill gaps in the climate information. Correlation between on-site meteorological records and network station was 0.978 and 0.969 for WAI-0.65 and WAI-0.22 sites respectively. The percentage of records filled from network stations with respect to the total was 9.2 % (9.729 hourly records) and 29.6% (31.169 hourly records) for WAI-0.65 and WAI-0.22 respectively. Mean vapor pressure deficit was also estimated from former weather measurements. We applied indirect method described by Zweifel et al., (2005), to calculate tree water deficit by tree and year, using dendrometer records to quantify drought stress based on potential linear growth (Zweifel et al., 2016).

Drought was limited during the summer of 2010 (dotted red area in Figure 9 and 10), but low autumn rainfall in 2011 and scarce spring precipitation revealed a severe summer drought in 2012 at both sites. 2013 and 2014 years had high winter and autumn rainfall, so summer drought was moderate, but more accused in WAI-0.65 site.

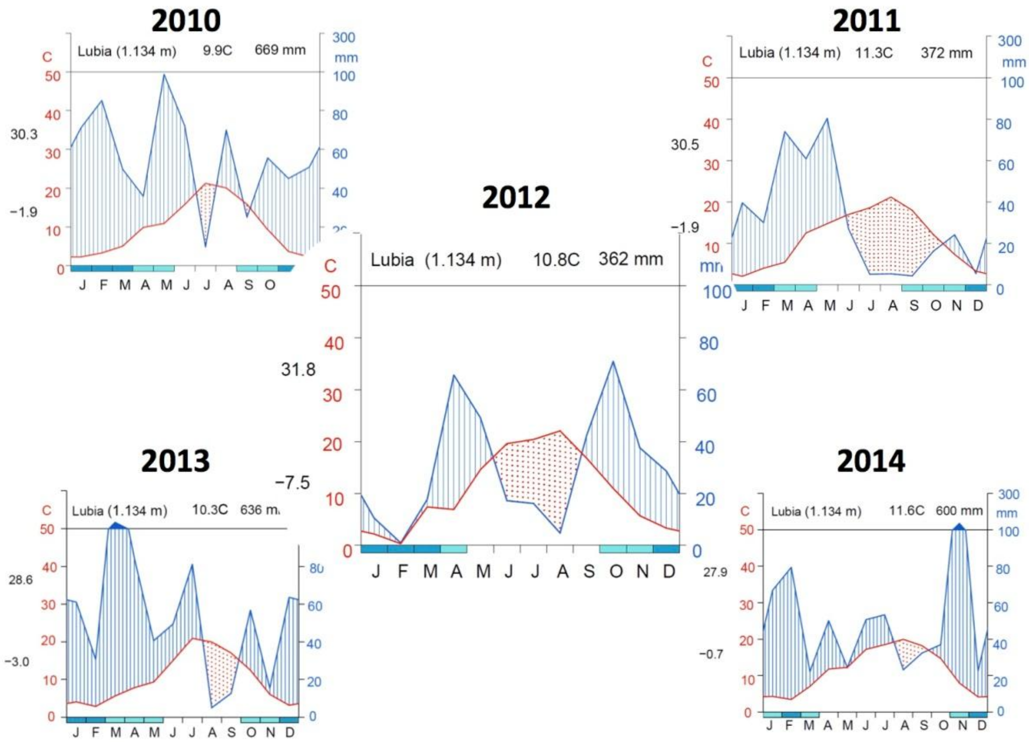

*Figure 9. Climograms of sampling years for maritime pine-oak mixed forest in WAI-0.22 site. Digits sited on the left side of y-axis are average of daily maximum temperatures of warmest month and average of daily minimum temperatures of coldest month from top to bottom respectively*

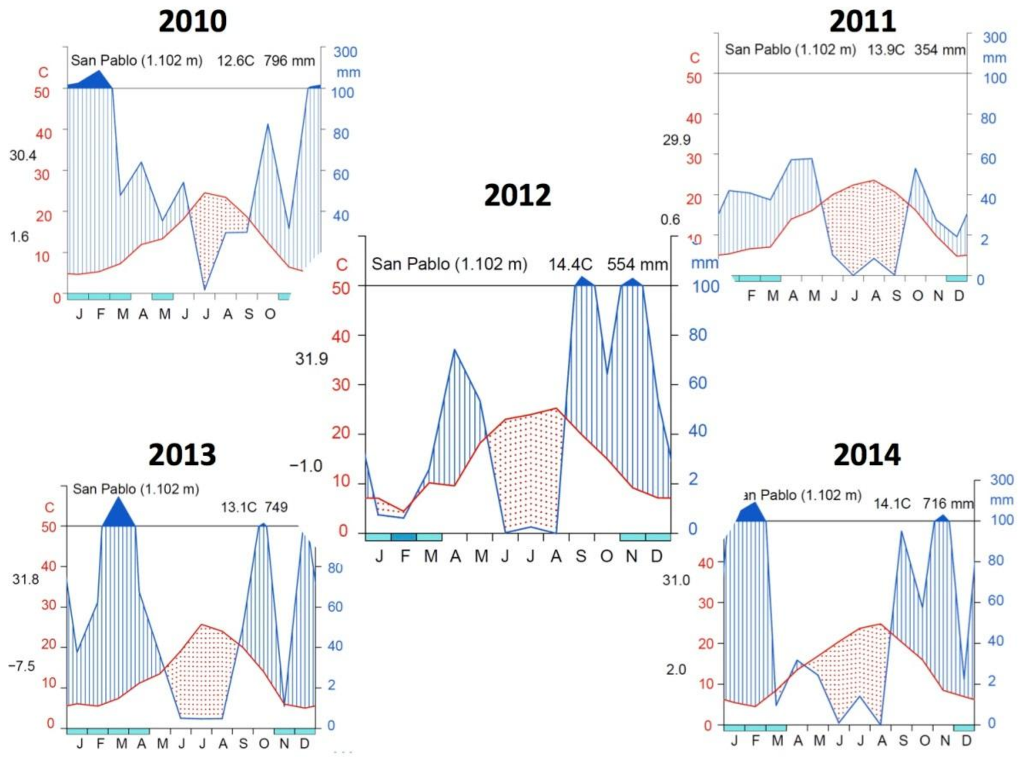

*Figure 10. Climograms of sampling years for maritime pine-oak mixed forest in WAI-0.65 site. Digits sited on the left side of y-axis are average of daily maximum temperatures of warmest month and average of daily minimum temperatures of coldest month from top to bottom respectively*

Temperature and precipitation records were compiled using data from the AEMET automatic network stations (León, Virgen del Camino, 2661). The weather of sampling years (2016-2017) for Scots pine-oak mixed stand was characterized by severe summer drought (Figure 11). However, 2017 was a very dry year due to a low precipitation at the beginning of spring (March-April) and at the end of autumn (October). Besides, average of daily maximum temperatures for warmest month was higher than mean historical records (29.4-28.4 vs. 27.4ºC).

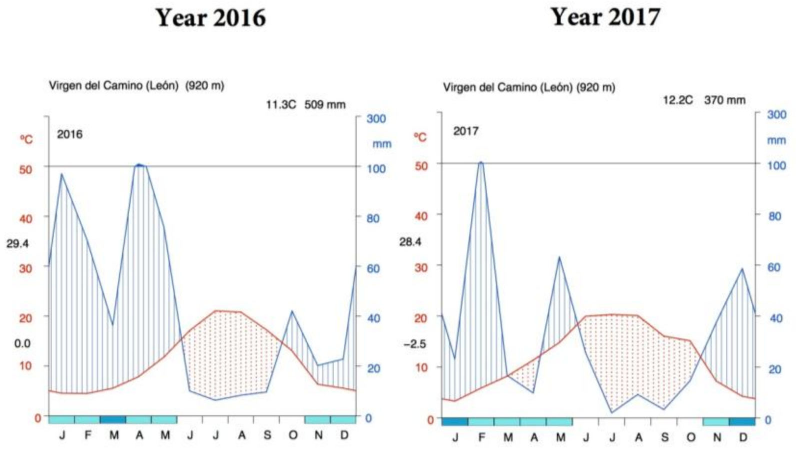

*Figure 11. Climograms of sampling years for Scots pine-oak mixed forest. Digits sited on the left side of y-axis are average of daily maximum temperatures of warmest month and average of daily minimum temperatures of coldest month from top to bottom respectively.*

# Methods

## 4.1. Spring radial increment onset

With the aim of check species differences and from high-resolution dendrometer data., we defined radial increment onset for trees in maritime pine-oak mixed stands as the first increment observed in the spring season and after that continuous positive daily radial increment took place. Radial increment onset observations generally occurred immediately after a negative radial increment period, which could be driven by the beginning of active water movement in the stem towards upper crown areas (Oberhuber et al., 2014; Zweifel et al., 2000). Conversely, radial increment onset could be masked by rehydration processes, though this generally takes place within a short period of time. We also compared radial increment onset with leaf phenological phases to uncover species functional adjustments.

Species differences in radial increment onset were tested by applying non-parametric statistic for the Behrens-Fisher problem, which computes simultaneous confidence intervals and adjusted p-values based on a studentized permutation test for small samples.

## 4.2. Stem radial variation cycle approach

The sub-hourly values from high-resolution point dendrometers were averaged to hourly resolution to link them with environmental variables, as well as to identify and correct errors or wrong measurements. Gaps of short duration (lower than a day) and abrupt jumps were corrected using an ARIMA model for the trend series from the same tree and season (Van der Maaten et al., 2016). Longer gaps remained unfilled.

Daily radial variation series for each tree and year were processed individually according to the stem cycle approach (Deslauriers et al., 2011; Drew and Downes, 2009; Van der Maaten et al., 2016, 2013), which splits radial variation cycles into three different phases: (1) contraction, the period between the first maximum radius and the next minimum radius; (2) expansion, the period from the minimum to the next morning maximum; and (3) stem radial increment, part of the expansion phase from the time when the stem radius exceeds the morning maximum until the subsequent maximum (Figure 12).

Stem radial increment (mm) and duration (hours) of the radial increment phase in the daily variation cycles were calculated for each tree and year. We also defined several metrics based on sinusoidal waveform characteristics, in order to explore features of full daily radial variation cycles (Figure 12). The difference between local maximum and minimum stem radius in the daily cycle is the amplitude of the cycle (mm), i.e., the maximum daily radial variation for a full cycle. Similarly, the period variable was defined as the duration, or the time (hours) required to complete a full cycle. The statistics extraction from cycle, gap filled and environmental linked was performed using 'dendrometeR' R package (Van der Maaten et al., 2016).

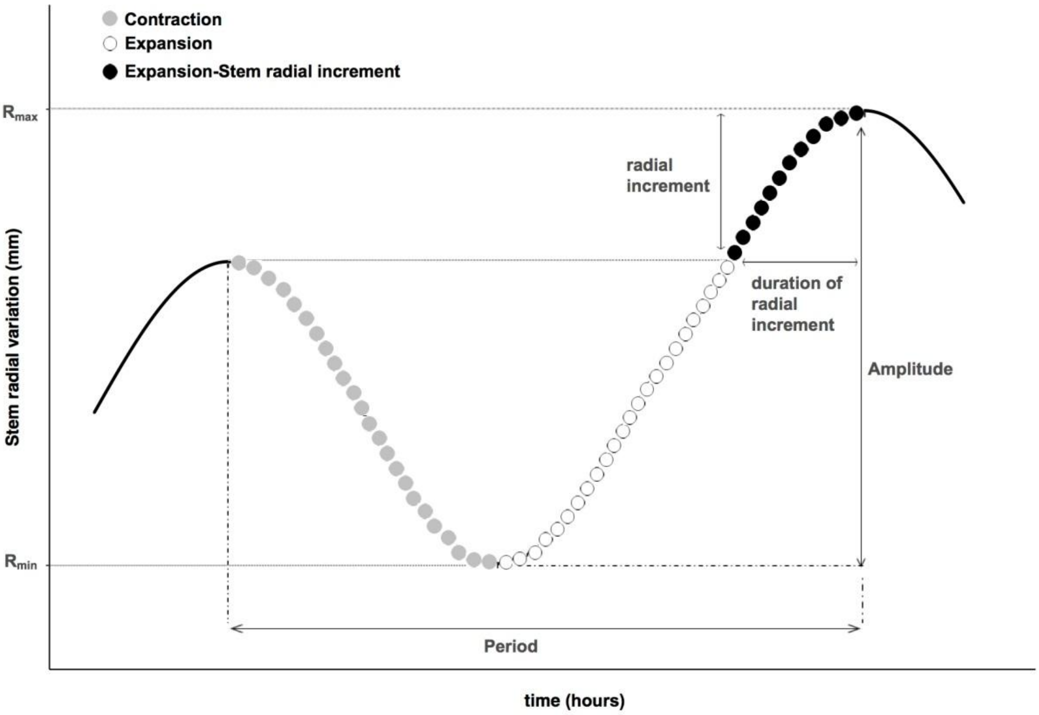

*Figure 12. Schematic representation of stem daily radial variation cycle, divided into three distinct phases: contraction (grey dots), expansion (white and black dots) and stem radial increment (black dots). Daily amplitude coincides with the magnitude of radial expansion (Rmax - Rmin). Period is the duration of full cycle.*

To better describe stem radial variation throughout the year, dendrometer series were divided into five periods or seasons according to Vieira et al., (2013): winter dormancy, during which radius variation was around zero; spring growth, from the start of positive radial increment until the spring maximum; pre-summer contraction, when the daily increment was negative; summer dormancy, when radial increment ceased and autumn, when rehydration occurred and radial increment increased rapidly in a short period of time. Radial variation cycles were defined as a symmetrical sinusoidal waveform for better visualization of daily seasonal cycles.

Species and season differences in amplitude and period for full daily cycles were calculated by applying non-parametric statistics based on global rankings, which compute simultaneous confidence intervals and adjusted p-values based on Tukey contrasts for repeated measurements. Similarly, we calculated species and year differences in magnitude (mm), duration (hours) and number of cycles with the radial increment phase.

## 4.3. Weather effect on stem radial variation

### *4.3.1. Weather effect on daily radial variation cycle and increment phase*

Linear mixed models were fitted to determine the influence of meteorological variables on the amplitude and period of radial variation cycles, and on the magnitude of the increment phase recorded by high-resolution point dendrometers. To better understand the influence of meteorological variables on the increment phase, especially when growth takes place, the model was fitted for two different time scales: annual and spring. Mean, sums (when necessary), maximum, and minimum values of meteorological variables were calculated and explored for full daily cycles.

Additionally, previous scatter plots were analyzed to check for possible non-linear relationships between response and weather variables. In this way, exponential model was estimated by means of a logarithmic transformation for respond variable which reduces the model to a linear form. Besides, when logarithm transformation of temperature was considered into account, the value of 5 was added to temperature variable to avoid that the minimum mean hourly temperature value (above -5 ºC) forced a mathematical indeterminacy. We considered three nested random effects: tree nested in site which is nested in year. They are assumed to be with mean 0 and variance defined as positive constant into a diagonal variance-covariance matrix. The final structure for the linear mixed model was as follows:

$$log(\rho_{ijk} + 1) = \alpha_0 + f(weather) + (\alpha_1 + f(weather)) * oak + \omega_k + u_{jk} + v_{ijk} + \varepsilon_{ijk} \quad [1]$$

where $\rho_{ijk}$ is the amplitude (mm), period (hours) of full radial variation cycle or daily radial increment (mm), for tree i in site j and year k (mm); $\alpha_0$ and $\alpha_1$ are the intercept regression coefficients for pine and oak, respectively; $f(weather)$ is a linear function of weather variables; *oak* is a dummy variable with values of 1 for oak and 0 for pine; $\omega_k$ ~N (0, $\sigma_k$) is the year random effect; $u_{jk}$ ~N (0, $\sigma_{jk}$) is the site random effect; $v_{ijk}$~N (0, $\sigma_{ijk}$) is the tree random effect and $\varepsilon_{ijk}$~N (0, $\sigma_e$) is the error term for each individual i in each site j for year k.

### *4.3.2. Weather effect on radial increment rate*

Linear mixed models were fitted per species and site to estimate weather and thinning effect on intra-annual radial increment rate based on band dendrometer measurement from maritime pine-oak mixed stand. Meteorological variables were calculated for different ranges of days before the sampling measurement: cumulative or mean weather variables over five, ten, fifteen, and twenty days before each measurement. Multicollinearity was controlled by variance inflation factor values, autocorrelation was assessed by autocorrelation function plot and AIC was employed to find the most parsimonious model. The final structure of the linear mixed model was as follows:

$$\mathrm{rir}_{ijk} = \beta_0 + \beta_1 \mathrm{MT} + \beta_2 \mathrm{HT} + \beta_3 \mathrm{dbh}_{ij} + \mathrm{f(weather)} + \omega_k + u_{jk} + v_{ijk} + \varepsilon_{ijk} \quad [2]$$

where $rir_{ijk}$ is the radial increment rate for tree *i* in plot *j* and year *k* (mm); $\beta_i$ are the regression coefficients*;* $MT$ and $HT$ are dummy treatment variables; $dbh_{ij}$ is the diameter at breast height (mm); $f(weather)$ is a linear function of weather variables; $\omega_k$ ~N (0, $\sigma_k$) is the year random effect; $u_{jk}$ ~N (0, $\sigma_{jk}$) is the plot random effect; $v_{ijk}$~N (0, $\sigma_{ijk}$) is the tree random effect and $\varepsilon_{ijk}$~N (0, $\sigma_e$) is the error term for each individual *i* in each plot *j* for year *k*. Finally, we did a *post-hoc* analysis based on multiple comparisons of means, using

Tukey contrasts to identify differences between thinning intensities when necessary necessary (see 4.6).

## 4.4. Radial variation synchrony

We identified and quantified temporal correlation of radial variability between time series for the same species and between species for each site from high-resolution point dendrometers records. Specifically, hourly radial variation and daily radial increment time series were analyzed to check tree radial increment synchrony. A 'caterpillar' randomization procedure was employed to avoid the typical violation of independence assumption used in classical statistics from temporal and spatial data set tests. This procedure preserves the temporal within-tree autocorrelation but destroys cross-correlation among trees, as it displaces the time series by a random amount for each randomization (Purves and Law, 2002).

The level of temporal synchrony was assessed with several metrics: mean correlation coefficient, Kendall's W non-parametric statistic (Legendre, 2005) and the Loreau and de Mazancourt (2008) metric. The last two statistics are bound between 0 and 1, so they cannot distinguish asynchrony (negatively correlated fluctuations) from lack of synchrony (independent fluctuation). We also calculated concurrency (Buonaccorsi et al., 2001) and phase synchrony (Cazelles and Stone, 2003) to evaluate phased species differences. The first evaluates the proportion of current local maxima and minima between series, and the second estimates modal distribution of phase differences. Concurrency metric varies between 0, when the time series never peak and trough together, and 1, when the time series always peak and trough simultaneously. The Monte Carlo randomization procedure was used to determine the statistical significance of Concurrency. The phase synchrony metric converts a time series of amplitudes into a time series of phases, then evaluates whether time series exhibit modal distribution with a prominent peak at a given phase difference and are therefore phase-synchronized. This metric varies between 0 (no phase synchrony) and 1 (full phase synchrony).

## 4.5. Intra-annual cumulative radial increment pattern

Different methodology based on non-linear mixed models was used to show species differences in intra-annual cumulative radial increment pattern: bi-logistic, a Richards curve for spring and autumn period and a double-Richards curve.

### *4.5.1. Bi-logistic model*

An initial visual analysis of scatter plots for band dendrometer measurements from maritime pine-oak mixed forest confirmed a bimodal pattern of radial increment for both species, as a consequence of the typical summer drought in Mediterranean environments (Albuixech et al., 2012; Camarero et al., 2010; Pacheco et al., 2018): stem growth in spring season, contraction during the summer due to depletion of stored water (concurrent with increasing water deficit) and stem rehydration (with growth for certain species) after autumn rainfall. Therefore, the function fitted for cumulative radial increment was the result of the sum of two logistic functions (Eq. 3). The first part of the sigmoid function represented the cumulative radial increment for spring time and the second part represented the autumnal increment.

$$cri_{ijk}(t) = \left\{\beta_1 + \frac{\beta_2-\beta_1}{(1+e^{(t-\beta_3)/\beta_4})}\right\} + \left\{(\beta_5-\beta_1) + \frac{\beta_1-\beta_5}{(1+e^{(t-\beta_6)/\beta_7})}\right\} + \varepsilon_{ijk} \qquad [3]$$

where $cri_{ijk}$ is the cumulative radial increment for tree $i$ in plot $j$ and year $k$ (mm); $\beta_i$ are the regression coefficients: $\beta_1$ is the spring radial increment asymptote, $\beta_2$ is the initial asymptote (null), $\beta_3$ is Julian days transpired since 1 January at the spring inflection point, $\beta_4$ is a spring scale parameter on the time-axis which represents the time when three-quarters of the distance from $\beta_1$occurs (the smaller it is, the greater the radial increment rate), $\beta_5$ is the autumnal radial increment asymptote or radial increment reach at the end of autumn, $\beta_6$ is the Julian days transpired since 1 January at the autumn inflection point and $\beta_7$ is an autumnal scale parameter on the time axis that represents the time when three-quarters of the distance from $\beta_1$ to $\beta_5$ occurs, (the smaller it is, the greater the radial increment rate) , $t$ is the Julian day transpired since 1 January and $\varepsilon_{ijk}$~N (0, $\sigma_e$) is the error term (for clarification of parameters, see Figure S2).

Due to the spatial and temporal dependence of measurements, the model was extended with a random structure that only affects (to avoid over-parameterization) the $\beta_1$parameter. The structure, which resulted in the lowest value of the Akaike information criterion (AIC) with respect to other parameters tested, is the following (Eq. 4).

$$cri_{ijk}(t) = \left\{(\beta_1 + \omega_k + u_{jk} + v_{ijk}) + \frac{\beta_2-(\beta_1+\omega_k+u_{jk}+v_{ijk})}{(1+e^{(t-\beta_3)/\beta_4})}\right\} + \left\{(\beta_5 - (\beta_1 + \omega_k + u_{jk} + v_{ijk})) + \frac{(\beta_1+\omega_k+u_{jk}+v_{ijk})-\beta_5}{(1+e^{(t-\beta_6)/\beta_7})}\right\} + \varepsilon_{ijk} \qquad [4]$$

where $\omega_k$ ~N (0, $\sigma_k$  is the year random effect; $u_{jk}$ ~N (0, $\sigma_{jk}$) is the plot random effect; $v_{ijk}$~N (0, $\sigma_{ijk}$) is the tree random effect. The other parameters are the same as in Equation 3.

### *4.5.2. Single Richards model for spring and autumn period*

According bi-modal data observed from high-resolution point dendrometers records, non-linear equation curves were fitted separately for spring and autumn periods to avoid the lack of analytical solutions with biphasic curves, such as convergence difficulties and high calculation time requirements. The spring period was reckoned from the beginning of the year to the decrease triggered by summer drought and generalized at 15 August to ensure final and initial spring and autumn asymptotes, respectively. The autumn period referred to the rest of the year.

We used a flexible Richards curve for each period and a random effects structure to include the spatial and temporal dependence of measurements. In this way, site and tree (nested in site) random effects were added to the model, affecting the intercept of asymptote ($A_{ij}$) and inflection point ($I_{ij}$). This proved to be the best random structure: the models were fitted by maximizing the restricted log-likelihood and then compared by likelihood ratio test, which is the lowest value of the Akaike information criterion (AIC). Year and species fixed effects were also included to evaluate their effects on model parameters, which allowed us to estimate our original query: species differences in intra-annual cumulative radial increment patterns. We compared all possible fixed model structures including permutation in the input of the variables in the model, combination of variables affecting several parameters and interaction among them. The final model was as follows:

$$y_{ij} = \frac{A_{ij}}{\left[1+m_{ij}e^{\left(-k_{ij}\left(t-I_{ij}\right)\right)}\right]^{\frac{1}{m_{ij}}}} + \varepsilon_{ij} \qquad [5]$$

$$A_{ij} = \alpha_1 + \alpha_2 2013 + \alpha_3 2014 + \alpha_4 * pine + u_j + v_{ij}$$

$$I_{ij} = \beta_1 + \beta_2 2013 + \beta_3 2014 + \beta_4 * pine + u_j + v_{ij}$$

$$k_{ij} = \gamma_1 + \gamma_2 2013 + \gamma_3 2014 + \gamma_4 * pine$$

$$m_{ij} = \tau_1 + \tau_2 2013 + \tau_3 2014 + \tau_4 * pine$$

where $y_{ij}$ is the cumulative radial increment for tree i in site j; $A_{ij}$, $I_{ij}$, $k_{ij}$ and $m_{ij}$ are the asymptote, inflection point (Julian days), rate parameter and shape parameter of Richards curve; t is time variable; $\alpha_i, \beta_i, \gamma_i$ and $\tau_i$ are the asymptote, inflection point, rate and shape parameter regression covariate coefficients (for clarification of parameters, see Figure S3); 2013 and 2014 are year dummy variables; pine is a dummy variable with a value of 0 for oak and 1 for pine species; $u_j \sim N(0, \sigma_j)$ is the site random effect; $v_{ij} \sim N(0, \sigma_{ij})$ is the tree random effect and $\varepsilon_{ij} \sim N(0, \sigma_e)$ is the error term.

#### *4.5.3. Double-Richards model*

The statistical approach was used to explain intra-annual cumulative radial increment for band dendrometer measurements from Scots pine-oak mixed forest. Based on flexible double-Richards curves (Eq.6), we determined the most appropriate model (number of necessary parameters) for our data. We compared all possible positive-negative Richards non-linear models by ranking competing model and then compare nested models using extra sum of squares F-Tests (Oswald, 2015). Accordingly, the best model structure resulted as five parameter model (all parameters from first Richards curve and asymptote of second Richards curve) and three fixed parameters (inflection point, rate and shape parameter from second Richards curve). The fixed parameters took the mean value across all trees in the dataset, reducing complexity and computation, due to these parameters did not vary across group levels (trees from plots).

Moreover, a random effect structure was generated to consider the spatial and temporal dependence of measurements. In this way, plot and tree (nested in plot) random effects were added to the model affecting intercept of asymptote ($A_{ij}$). This was the best random structure, which was evaluated as follow: first, the different models (with a diverse random structure) were fitted by maximizing the restricted log-likelihood and then, compared them by likelihood ratio test, that is, the lowest value of the Akaike information criterion (AIC). Besides, species, thinning treatment and year fixed effects and diameter covariate were included to evaluate their effect on model parameters. We compare all possible fixed model structures including permutation in the input of the variables in the model, combination of variables affecting several parameters and interaction among variables. The final model was selected according the most parsimonious (low AIC) and biological sense model, as follow (Eq.6):

$$y_{ij} = \frac{A_{ij}}{\left[1+m_{ij}e^{\left(-k_{ij}(t-I_{ij})\right)}\right]^{\frac{1}{m_{ij}}}} + \frac{RA_{ij}}{\left[1+Rm_{ij}e^{\left(-Rk_{ij}(t-Ri_{ij})\right)}\right]^{\frac{1}{Rm_{ij}}}} + \varepsilon_{ij} \qquad [6]$$

$$A_{ij} = \alpha_0 + \alpha_1 2017 + (\alpha_2 + \alpha_3 2017) * pine + \alpha_4 dbh + \alpha_5 MT + \alpha_6 HT + u_j + v_{ij}$$

$$I_{ij} = \beta_0 + \beta_1 * pine$$

$$k_{ij} = \gamma_0 + \gamma_1 * pine$$

$$m_{ij} = \tau_0$$

$$RA_{ij} = \rho_0 + \rho_1 2017$$

$$Ri_{ij} = 349$$

$$Rk_{ij} = 0.043$$

$$Rm_{ij} = 0.521$$

where $y_{ij}$ is the cumulative radial increment for tree *i* in plot *j;* $\alpha_i$, $\beta_i$, $\gamma_i$ and $\tau_i$ are the asymptote, inflection point, rate and shape parameter regression of fixed effect variables for the first Richards curve and $\rho_i$ are the amplitude parameters for the second one (for clarification of parameters, see Figure S4); *2017* is a year dummy variable with value 0 for year 2016 and 1 for 2017; *pine* is also a dummy variable with value 0 for oak and 1 for pine species; *dbh* is diameter at breast height (mm); *MT* is a dummy variable with value 1 for moderate thinning and 0 otherwise; *HT* is a dummy variable with value 1 for heavy thinning and 0 otherwise (see 4.6. for more details); $u_j$~N(0, $\sigma_j$) is the plot random effect; $v_{ij}$~N(0, $\sigma_{ij}$) is the tree random effect and $\varepsilon_{ij}$~N(0, $\sigma_e$) is the error term. $Ri_{ij}$, $Rk_{ij}$ and $Rm_{ij}$ are the inflection point, rate and shape fixed parameters from second Richards curve which took the mean value of all trees.

## 4.6. Thinning effect on radial increment

### *4.6.1. Thinning effect on intra-annual radial increment*

Weather influence and thinning effect on radial increment rate was evaluated by linear mixed model according to 4.3.2 section based on band dendrometer measurements in maritime pine-oak mixed forest.

Besides, effect of thinning on intra-annual cumulative radial increment was assessed through bi-logistic models fitted according 4.5.1 section. Species differences for each thinning treatment were tested from parameters of fitted models by nonparametric relative effects based on global rankings, simultaneous confidence intervals and adjusted p-values via Tukey contrasts.

Moreover, thinning treatment was included as fixed effect on parameters of double-Richards model for Scots pine-oak mixed forest (see 4.5.3 section).

### 4.6.2. *Thinning effect on inter-annual radial increment*

We analyzed the seasonal (spring and autumn) and the annual radial increment in order to study inter-annual variation of thinning effect in maritime pine-oak mixed forest. The spring increment period was reckoned from the beginning of the year to the decrease triggered by the summer drought (generalized as Aug. 1), while the autumn period referred to the rest of the year. Linear mixed models were used to avoid time-space dependence from the experimental design. Size of the tree was added as covariate and the final model was fitted for each species and site, as follows:

$$ri_{ijsk} = \alpha_k + \beta_s + \gamma_{sk} + \delta_i dbh_{ij} + u_j + v_{ij} + \varepsilon_{ijsk} \qquad [7]$$

$$\alpha_k = \alpha_1 2010 + \alpha_2 2011 + \alpha_3 2012$$

$$\beta_s = \beta_1 MT + \beta_2 HT$$

$$\gamma_{sk} = \gamma_{11} MT2011 + \gamma_{12} MT2012 + \gamma_{21} HT2011 + \gamma_{22} HT2012$$

where $ri_{ijsk}$ is the spring, autumn or annual radial increment for tree $i$ in plot $j$ subjected to thinning treatment $s$ and year $k$ (mm); $\alpha_k$ is the year effect vector, with $\alpha_1, \alpha_2, \alpha_3$ regression coefficients for the 2010, 2011 and 2012 dummy variables, respectively; $\beta_s$ is the treatment effect vector, $\beta_1, \beta_2$ are the regression coefficients for MT and HT thinning treatment dummy variables; $\gamma_{sk}$ is the treatment-year interaction vector, with $\gamma_{11}\ \gamma_{12}, \gamma_{21}, \gamma_{22}$ regression coefficients; $dbh_{ij}$ is the diameter at breast height (mm), with $\delta_i$ as the regression coefficient; $u_j \sim N(0, \sigma_j)$ is the plot random effect; $v_{ij} \sim N(0, \sigma_{ij})$ is the tree random effect and $\varepsilon_{ijsk} \sim N(0, \sigma_{ijsk})$ is the error term. Additionally, we did a *post-hoc* analysis based on simultaneous tests for general linear hypothesis through multiple comparisons of means, using Tukey contrasts when necessary to identify differences between thinning intensities.

## 4.7. Statistical methods summary

In all the fitted models, we evaluated different variance-covariance matrix structure, diverse random and fixed effect constructions, multicollinearity, heteroscedasticity and the existence of residual autocorrelation.

Different-patterned variance-covariance matrices were evaluated for random effects from linear and non-linear mixed models, such as the multiple of an identity, diagonal, and general positive-definite matrices. The block diagonal variance-covariance matrix was mainly chosen to fit the most parsimonious convergent model, based on AIC values. This assumes that random effects are independent of each other and have the same variance at each random level.

The best random and fixed effect structures were fitted by restricted and maximum likelihood, respectively. Explanatory variables for linear mixed models were chosen based on stepwise model selection using Akaike information criterion (AIC) to find the most parsimonious model. Multicollinearity of model variables was controlled by variance inflation factor values. When fixed parameters and covariates were included in parameters of non-linear mixed models, we compared all possible fixed model structures via AIC including permutation in the input of the variables in the model, combination of variables affecting several parameters and interaction among them.

Additionally, residual and autocorrelation function plots were used as diagnostic tools for identifying heteroscedasticity and residual autocorrelation. Several variance function (exponential, power and constant plus power of the absolute value of the variance covariate) were evaluated  to correct heteroscedasticity (Pinheiro and Bates, 2000). Serial autocorrelation was assessed by partial and autocorrelation function plots, and several serial correlation structures were evaluated (autoregressive, moving average, and a mixed autoregressive moving average model) to account for residual autocorrelation.

Linear and bi-logistic mixed models were fitted by 'nlme' R package (Pinheiro et al., 2015), while 'pn.mod.compare' and 'pn.mod.select.step' functions from 'FlexParamCurve' R package (Oswald, 2015) were used to select the best double-Richards model. The former and 'nlme'(Pinheiro et al., 2015) R packages were also used to  fit single and double-Richards models. All analyses were performed using the R statistical environment (R Development Core Team, 2017).

Species differences in radial increment onset, amplitude and period for daily cycles and thinning treatment (linear and bi-logistic model; before/after thinning stand features) were calculated by applying non-parametric statistics based on global rankings, which compute simultaneous confidence intervals and adjusted p-values based on Tukey contrasts. We used '*npar.t.test*', '*mctp.rm*' and '*mctp*' functions from '*nparcomp*' R package (Konietschke et al., 2015) for these calculation.

The statistics extraction from cycle, gap filled and environmental linked was performed using '*dendrometeR*' R package (Van der Maaten et al., 2016).

The level of temporal synchrony was assessed with several metrics: mean correlation coefficient, Kendall's W non-parametric statistic (Legendre, 2005) and the Loreau and de Mazancourt (2008),  which were calculated using '*synchrony*' R package (Gouhier and Guichard, 2014).Summary of statistical methods used for the thesis are collected in Table 6.

*Table 6. Summary of statistical methods and R packages used in relation to thesis objectives.*

| **Statistic Method** | | **Objective** | | | **R package** |
|---|---|---|---|---|---|
| | | **Species differences in daily radial cycles** | **Species temporal complementarity** | **Response to thinning** | |
| Linear mixed models | | X | | X | *‘nlme’* |
| Non-linear mixed models | Bi-logistic | | X | X | *‘nlme’* |
| | Single Richards | | X | | *‘nlme’*<br>*‘FlexParamCurve’* |
| | Double-Richards | | X | X | *‘nlme’*<br>*‘FlexParamCurve’* |
| Time series | | X | X | X | *‘nlme’*<br>*‘dendrometeR’* |
| Non-parametric test | | X | X | X | *‘nparcomp’* |
| Other parametric statistics | | | X | | *‘synchrony’* |

# Results

## 5.1. *Pinus pinaster* and *Quercus pyrenaica* daily radial increment dynamics

### 5.1.1. *Spring radial increment onset*

Pine radial increment onset was earlier than oak at both sites (P<0.05; Figure 13). Pine radial onset at WAI-0.65 was earlier than at the WAI-0.22 site (30 March vs 12 April) but presented no significant differences (P=0.08). The mean radial increment onset date for the oak species was 18 April without differences between sites (P=0.43). Radial increment onset almost coincided in time with leaf budburst for oak but occurred before twig or leaf expansion (Figure 13). Species leaf phenological differences only occurred for leaf expansion at theWAI-0.22 site (P<0.01); no significant differences (P=0.28) were found at the WAI-0.65 site.

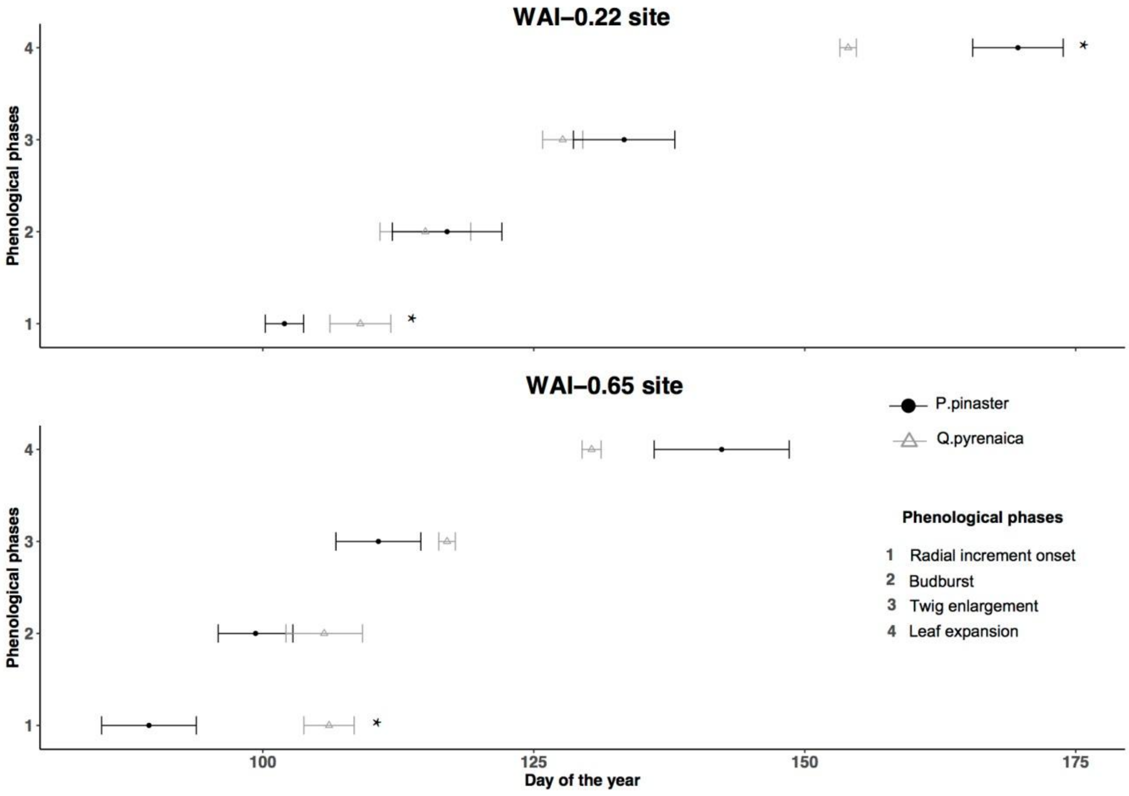

*Figure 13. Species radial increment onset and leaf phenological phases for maritime pine-oak mixed forest by site. Error bars show standard error. Asterisk denotes significant differences (P<0.05).*

### 5.1.2. *Seasonal differences in daily radial variation cycles*

Comparisons of daily cycles throughout the year reveal variation among seasons and species (Figures 14 and 15). The lowest amplitudes were observed in winter, regardless of species (P < 0.01). Oak had the highest amplitude during pre-summer and summer, while amplitude was greatest for pine in spring, when growth occurs (P < 0.01 for both cases). Amplitude was higher for pine than oak during winter and spring, but the opposite occurred in pre-summer and summer (P < 0.01). However, period was always lower for pine than oak (P < 0.01), except in pre-summer and summer, when there were no differences between species (P = 0.65). The cycle period was higher during winter and autumn, and lower in summer (P < 0.05).

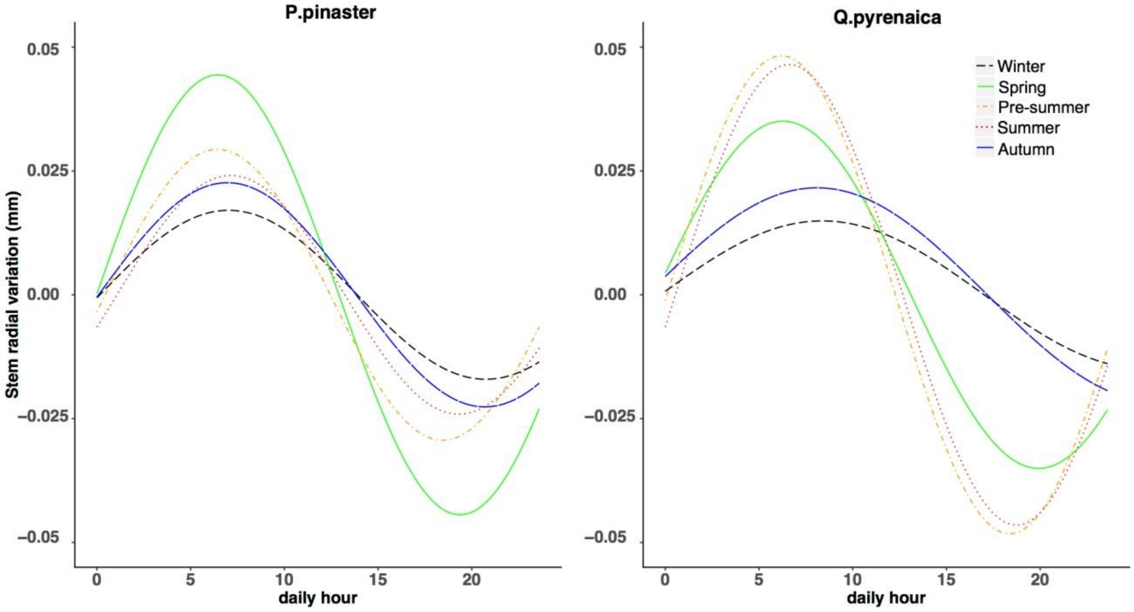

*Figure 14. Mean daily radial variation cycles by season for maritime pine-oak mixed forest.*

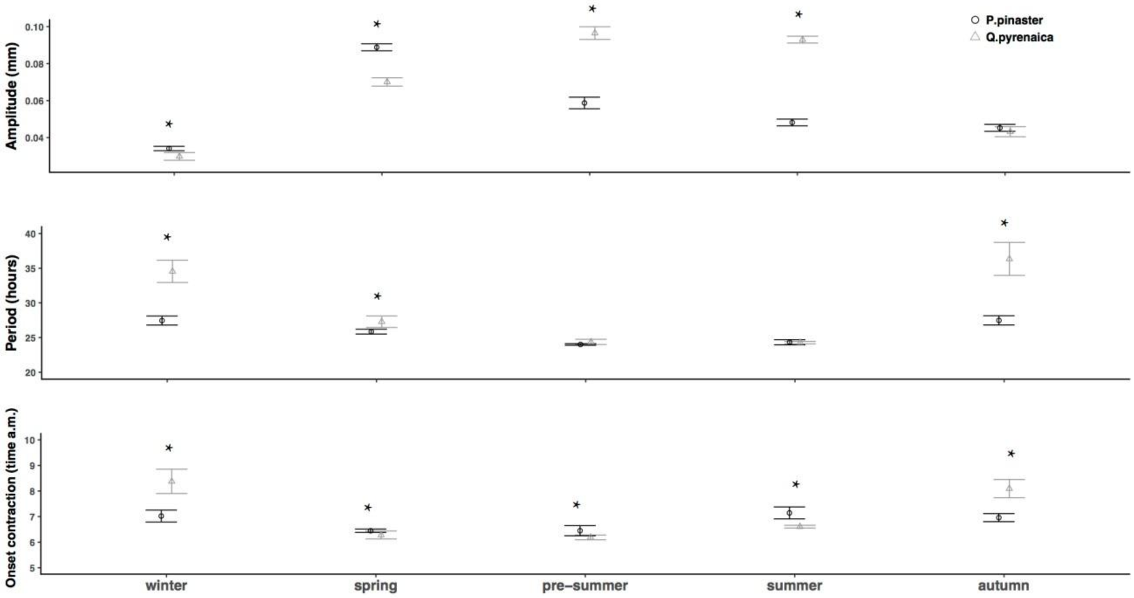

*Figure 15. Differences in amplitude (mm), period (hours) and onset of contraction phase for daily radial variation cycles by species and season. Error bars indicate confidence intervals (95%) and asterisk denotes significant differences between species.*

### *5.1.3. Weather influence on daily radial variation cycles*

#### *Influence on amplitude and period*

Models fitted for weather drivers of amplitude and period showed the importance of air temperature and rain (Table 7 and Figure 16). Water deficit was also related to high radial cycle amplitude, which supports summer observations. The effect of air temperature on the amplitude of daily cycles differed between species. In both species, amplitude increased with increasing air temperature (from 6º C for oak), though pine presented a more moderate trend (Figure 16). Amplitude also increased in oak species at air temperatures below 6.0 ºC, according to the fitted model in Table 7. Besides, daily amplitude raised with precipitation for both species. Furthermore, though period was affected by air temperature, precipitation had higher impact on both species. Differences on daily period between species were almost evidenced according to Figure 15 (P=0.06). Heteroscedasticity and residual autocorrelation were corrected by variance functions and, autoregressive and moving average model respectively.

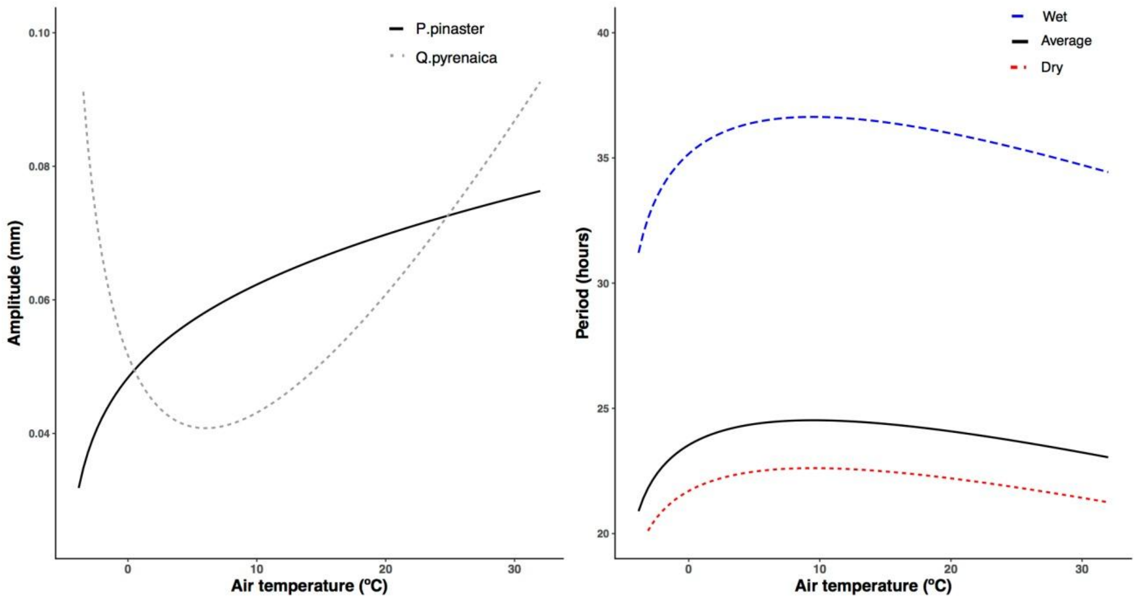

*Figure 16. Species-specific effect of air temperature on amplitude of daily radial variation cycles (left). Air temperature and precipitation effects on period of radial variation cycles for maritime pine-oak mixed forest (right). Simulation from the fitted linear mixed models for the air temperature and precipitation range. "Wet" weather corresponded to the 95th percentile of daily precipitation range and "Dry" weather corresponded to no rain.*

*Table 7. Linear mixed model fitted for weather effect on amplitude and period of stem radial variation cycles in maritime pine-oak mixed forest (Eq. 1). n.s., not significant.*

| **Parameter** | **Amplitude** | | **Period** | |
|---|---|---|---|---|
| | **Coefficient** | **p-value** | **Coefficient** | **p-value** |
| $\boldsymbol{\alpha_0}$ (pine) | n.s. | n.s. | 2.995 | <0.001 |
| $\boldsymbol{T_{air}}$(pine) | n.s. | n.s. | $-7.32 \cdot 10^{-3}$ | 0.002 |
| $\boldsymbol{log(T_{air}+5)}$ (pine) | $1.05 \cdot 10^{-4}$ | 0.021 | $9.94 \cdot 10^{-2}$ | 0.005 |
| $\boldsymbol{\alpha_1}$ (oak) | $8.85 \cdot 10^{-2}$ | <0.001 | $2.25 \cdot 10^{-1}$ | 0.065 |
| $\boldsymbol{T_{air}}$(oak) | $3.69 \cdot 10^{-3}$ | <0.001 | n.s. | n.s. |
| $\boldsymbol{log(T_{air}+5)}$ (oak) | $-5.30 \cdot 10^{-2}$ | <0.001 | n.s. | n.s. |
| $\boldsymbol{P}$ | $1.52 \cdot 10^{-3}$ | <0.001 | $4.34 \cdot 10^{-2}$ | <0.001 |
| $\boldsymbol{Wd}$ | $1.70 \cdot 10^{-1}$ | <0.001 | n.s. | n.s. |
| $\boldsymbol{\sigma_k}$ (year) | $1.14 \cdot 10^{-6}$ | | $1.26 \cdot 10^{-6}$ | |
| $\boldsymbol{\sigma_{jk}}$(site) | $1.15 \cdot 10^{-6}$ | | $2.76 \cdot 10^{-2}$ | |
| $\boldsymbol{\sigma_{ijk}}$(tree) | $2.34 \cdot 10^{-7}$ | | $2.31 \cdot 10^{-2}$ | |
| $\boldsymbol{\sigma_e}$(error) | $1.62 \cdot 10^{-2}$ | | $2.78 \cdot 10^{-5}$ | |
| $\boldsymbol{\varphi}$ | 0.961 | | -0.340 | |
| $\boldsymbol{\theta}$ | -0.663 | | 0.285 | |
| $\boldsymbol{\delta_1}$ | 11.151 | | $2.06 \cdot 10^{-6}$ | |
| $\boldsymbol{\delta_2}$ | ---- | | 7.668 | |

*$\boldsymbol{\alpha_0}$ and $\boldsymbol{\alpha_1}$ are the intercept regression coefficients for pine and oak respectively; $T_{air}$ is air temperature (ºC); P is daily precipitation(mm); Wd is water deficit (mm); $\boldsymbol{\sigma_k}$ is standard deviation for year random effect; $\boldsymbol{\sigma_{jk}}$ is standard deviation for site random effect; $\boldsymbol{\sigma_{ijk}}$ is standard deviation for tree random effect; $\boldsymbol{\sigma_e}$ is standard deviation for error term; $\boldsymbol{\varphi}$ and $\boldsymbol{\theta}$ are autoregressive and moving average for ARMA(1,1) residual serial correlation parameters; $\boldsymbol{\delta_1}$ and $\boldsymbol{\delta_2}$ are function parameters used to model residual variance as an exponential function of the variance covariate vector ($\boldsymbol{g_{ijk}}$) for amplitude: $\boldsymbol{Var(\varepsilon_{ijk}) = \sigma_e^2 \cdot e^{2\delta_1 g_{ijk}}}$ or constant plus a power for period: $\boldsymbol{Var(\varepsilon_{ijk}) = \sigma_e^2(\delta_1 + |g_{ijk}|^{\delta_2})^2}$*

### *Influence on radial increment phase*

Daily radial increment and number of cycles with a radial increment phase varied with years and species in spring (Figure 17). However, no differences in the duration of the increment phase between species were found (results not shown). Daily radial increment showed significant differences between species (higher for pine) during 2013 and 2014 at the WAI-0.65 site ($P < 0.01$, Figure 17), and only in spring 2013 at the WAI-0.22 site ($P = 0.02$). The number of cycles with increment phase was always higher for pine, regardless of site and year ($P < 0.01$), except in 2013 at the WAI-0.65 site (Figure 17). The number of cycles with increment phase was also lower in the 2012 drought year, regardless of species and site ($P < 0.01$), but with no significant differences for oak at the WAI-0.22 site.

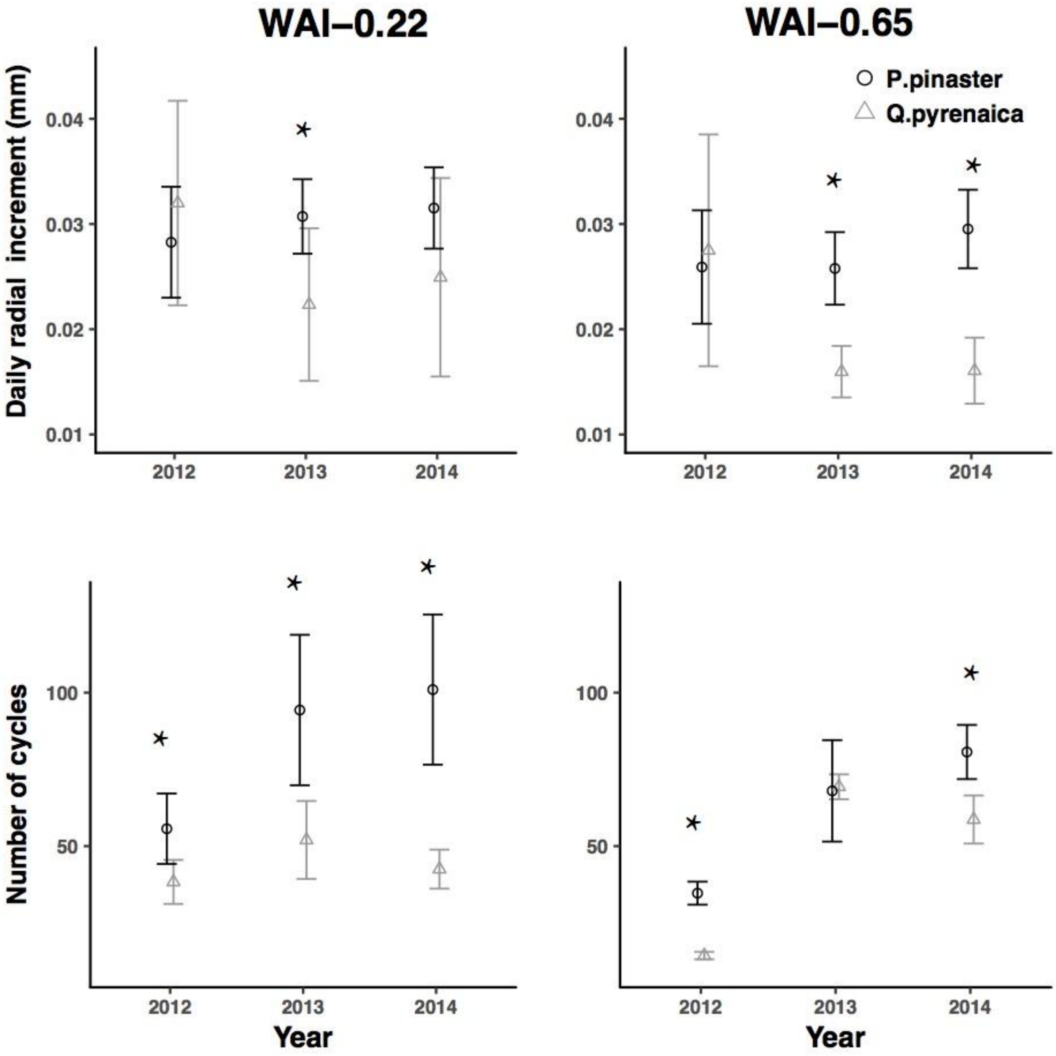

*Figure 17. Differences of daily radial increment and number of cycles with increment phase in spring by site, year, and species. Error bars indicate confidence intervals (95%), asterisk denotes significant differences between species.*

The results from the fitted model for daily radial increment (Eq. 1) are shown in Table 8. Statistically significant weather variables that were included in the final model for spring time were mean air temperature (Tair; ºC), solar radiation (SR; 10KJ/m$^2$), and accumulated rainfall per daily cycle (P; mm). Two additional variables, water deficit (Wd; mm) and mean vapor pressure deficit (VPD; kPa), were significant when all annual period was taken into account. Mean air temperature, solar radiation, and the amount of rainfall caused higher radial increments. In the annual analysis, however, was negatively affected by water deficit and high vapor pressure deficit values, which were especially acute during summer time.

*Table 8. Linear mixed model fitted for weather effect on annual and spring daily radial increment of maritime pine-oak mixed forest (Eq. 1). n.s., not significant.*

| Parameter | Annual | | Spring | |
|---|---|---|---|---|
| | Coefficient | p-value | Coefficient | p-value |
| $\boldsymbol{\alpha_0}$ (pine) | $7.38\cdot10^{-3}$ | <0.001 | $5.98\cdot10^{-3}$ | 0.002 |
| $\boldsymbol{T_{air}}$ | $5.15\cdot10^{-4}$ | <0.001 | $9.76\cdot10^{-4}$ | <0.001 |
| $\boldsymbol{SR}$ | $4.33\cdot10^{-4}$ | <0.001 | $6.38\cdot10^{-4}$ | <0.001 |
| $\boldsymbol{Wd}$ | $-1.68\cdot10^{-2}$ | <0.001 | n.s. | n.s. |
| $\boldsymbol{VPD}$ | $-4.39\cdot10^{-3}$ | <0.001 | n.s. | n.s. |
| $\boldsymbol{P}$ | $2.55\cdot10^{-3}$ | <0.001 | $1.68\cdot10^{-3}$ | <0.001 |
| $\boldsymbol{\alpha_1}$ (oak) | $-2.57\cdot10^{-3}$ | 0.002 | $-8.12\cdot10^{-3}$ | <0.001 |
| $\boldsymbol{\sigma_k}$ (year) | $3.36\cdot10^{-7}$ | | $1.46\cdot10^{-3}$ | |
| $\boldsymbol{\sigma_{jk}}$(site) | $1.08\cdot10^{-3}$ | | $4.08\cdot10^{-8}$ | |
| $\boldsymbol{\sigma_{ijk}}$(tree) | $7.88\cdot10^{-4}$ | | $3.17\cdot10^{-7}$ | |
| $\boldsymbol{\sigma_e}$(error) | 1.58 | | 2.18 | |
| $\boldsymbol{\varphi}$ | 0.43 | | $8.77\cdot10^{-1}$ | |
| $\boldsymbol{\theta}$ | ---- | | $-6.29\cdot10^{-1}$ | |
| $\boldsymbol{\delta_1}$ | $2.01\cdot10^{-3}$ | | $1.96\cdot10^{-3}$ | |
| $\boldsymbol{\delta_2}$ | 1.15 | | 1.32 | |

$\boldsymbol{\alpha_0}$ *and* $\boldsymbol{\alpha_1}$ *are the intercept regression coefficients for pine and oak, respectively;* $T_{air}$ *is air temperature (ºC);SR is solar radiation (10KJ/*$m^2$*); Wd is water deficit (mm); VPD is mean vapor pressure deficit (kPa); P is daily precipitation(mm);* $\boldsymbol{\sigma_k}$ *is standard deviation for year random effect;* $\boldsymbol{\sigma_{jk}}$ *is standard deviation for site random effect;* $\boldsymbol{\sigma_{ijk}}$ *is standard deviation for tree random effect;* $\boldsymbol{\sigma_e}$ *is standard deviation for error term;* $\boldsymbol{\varphi}$ *and* $\boldsymbol{\theta}$ *are autoregressive and moving average for annual and spring residual serial correlation parameters from AR(1) and ARMA(1,1), respectively;* $\boldsymbol{\delta_1}$ *and* $\boldsymbol{\delta_2}$ *are function parameters used to model residual variance as constant plus a power of the absolute value of the variance covariate (*$\boldsymbol{g_{ijk}}$*):* $\boldsymbol{Var(\varepsilon_{ijk}) = \sigma_e^2(\delta_1 + |g_{ijk}|^{\delta_2})^2}$

Interaction between weather variables and species was not significant, so the species dummy variable only affected the intercept ($\alpha_1$). The value of this coefficient was negative regardless of the analysis time scale, showing the species growth effect of lower radial increment for oak than pine. Therefore, species responded to identical weather variables in the same way (linearly) but with higher radial increment reaction for pine species. Heteroscedasticity and residual autocorrelation were corrected by variance functions and, autoregressive and moving average model respectively.

### *5.1.4. Species radial variation synchrony*

The pine and oak species showed high radial variation synchrony, regardless of the response variable, according mean correlation, Kendall's W and Loreau and de Mazancourt's metrics (Table 9). The synchrony metrics values were lower for daily radial increment than for hourly radial variation. Lower Concurrency values (when significant) between species could indicate that pine and oak series are locked in different phases. However, low phase synchrony values were similar when both species were compared and when same species where analyzed. As we expected, same-species synchrony was also elevated for each site according mean correlation, Kendall's W and Loreau and de Mazancourt's metrics (Table 9). Conversely, we found that same-species concurrency and phase metrics values were small, which could be related to noisy real world observational data.

*Table 9. Synchrony of radial variation between time series of maritime pine-oak mixed forest. Significance of p-value of observed synchrony data is shown as follows: '***' <0.001, '**' <0.01, '*' <0.05.*

| Response variable | Site | Series | Mean correlation (ϱ) | Kendall's concordance (W) | LdM(φ) | Concurrency (C) | Phase synchrony (Q) |
|---|---|---|---|---|---|---|---|
| Hourly radial variation | WAI-0.22 | Pine | $0.995^{***}$ | $0.992^{***}$ | $0.997^{***}$ | $0.207^{**}$ | $0.164^{***}$ |
| | | Oak | $0.870^{***}$ | $0.931^{***}$ | $0.936^{***}$ | $0.367^{***}$ | $0.233^{***}$ |
| | | P vs O | $0.921^{***}$ | $0.936^{***}$ | $0.980^{***}$ | $0.091^{**}$ | $0.162^{***}$ |
| | WAI-0.65 | Pine | $0.984^{***}$ | $0.983^{***}$ | $0.990^{***}$ | $0.109^{***}$ | $0.129^{***}$ |
| | | Oak | $0.848^{***}$ | $0.906^{***}$ | $0.925^{***}$ | $0.350^{***}$ | $0.218^{***}$ |
| | | P vs O | $0.948^{***}$ | $0.968^{***}$ | $0.980^{***}$ | $0.085^{***}$ | $0.161^{***}$ |
| Daily radial increment | WAI-0.22 | Pine | $0.869^{***}$ | $0.871^{***}$ | $0.914^{***}$ | $0.576^{***}$ | $0.120^{***}$ |
| | | Oak | $0.779^{**}$ | $0.896^{***}$ | $0.892^{***}$ | $0.539^{***}$ | $0.155^{***}$ |
| | | P vs O | $0.625^{**}$ | $0.751^{***}$ | $0.813^{***}$ | $0.345^{*}$ | $0.127^{***}$ |
| | WAI-0.65 | Pine | $0.759^{***}$ | $0.788^{***}$ | $0.839^{***}$ | $0.372^{**}$ | $0.094^{***}$ |
| | | Oak | $0.809^{***}$ | $0.892^{***}$ | $0.871^{***}$ | $0.774^{***}$ | $0.211^{***}$ |
| | | P vs O | $0.629^{***}$ | $0.792^{***}$ | $0.815^{***}$ | 0.332 | $0.067^{***}$ |

*LdM : Loreau and de Mazancourt's. 'P vs O' denotes comparison of pine and oak temporal series.*

### *5.1.5. Inter-annual variation in intra-annual cumulative radial increment pattern*

High-resolution point dendrometers evidenced differences on cumulative intra-annual radial increment patterns between species and among years (Figure 18). Results for single Richards model are shown in Table 10. Pine species always presented a higher asymptote ($\alpha_4$) and increment rate ($\gamma_4$) than oak, regardless of season (Eq.5 and Table 10). The spring asymptotic parameter was lower in 2012 ($\alpha_1$) than in 2013 and 2014, due to lower winter-spring rainfall and severe summer drought (Figure 9, 10 and 18).

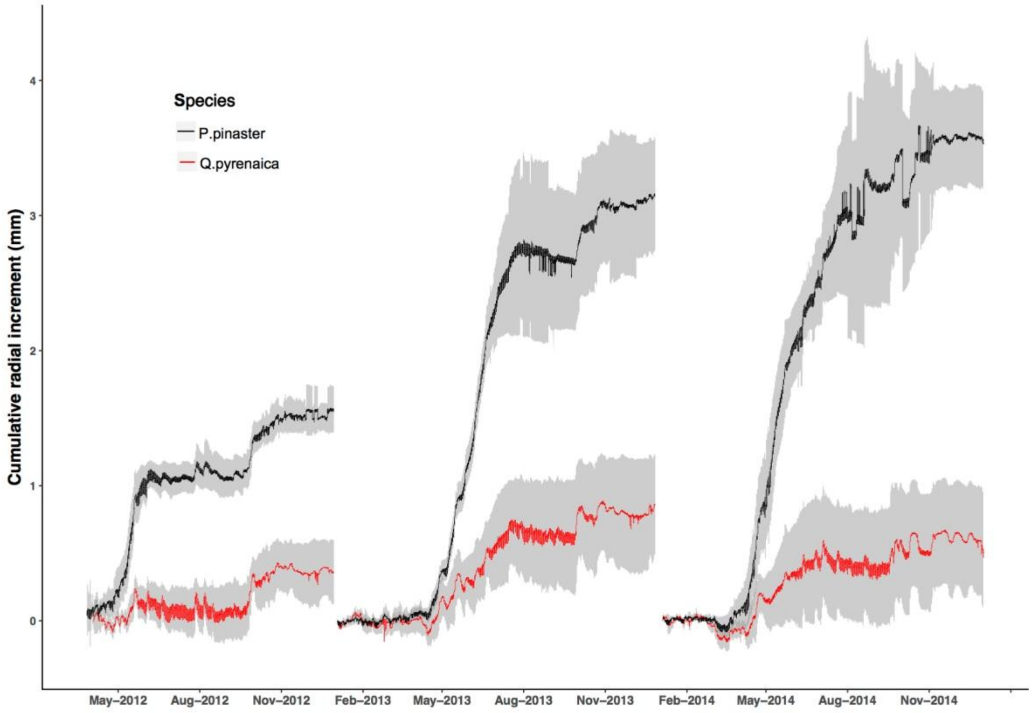

*Figure 18. Intra-annual cumulative radial increment patterns of maritime pine-oak mixed stands recorded by high-resolution point dendrometers. For each species, the line represents the mean radial increment of six monitored trees, and the grey shadowed area delimits the 95% confidence intervals.*

There was no significant difference between species and year at the spring inflection point ($\beta_4$), which was reached on 19 May. Conversely, species differences appeared in the Richards shape parameter ($\tau_4$), which showed a longer exponential period of radial increment for pine than oak.

Year effect did not affect to any autumn parameter, but species differences were observed in this period. Asymptotic ($\alpha_4$) and increment rate ($\gamma_4$) parameters were higher again for pine than oak. Additionally, the autumn inflection point ($\beta_4$) occurred later for pine (3 October) than oak (23 September). Though the shape parameter ($\tau_4$) also differed between species, low values for both species reflected a sudden change in radial increment that might correspond to rehydration processes.

*Table 10. Single Richards model fitted for spring and autumn cumulative radial increment pattern for maritime pine-oak mixed forest (Eq. 5). n.s.: not significant.*

| **Parameter** | **Spring** | | **Autumn** | |
|---|---|---|---|---|
| | **Coefficient** | **p-value** | **Coefficient** | **p-value** |
| $\boldsymbol{\alpha_1}$ (A$_{2012}$) | -0.528 | 0.029 | 0.184 | 0.023 |
| $\boldsymbol{\alpha_2}$ (A$_{2013}$) | 1.394 | <0.001 | n.s. | n.s. |
| $\boldsymbol{\alpha_3}$ (A$_{2014}$) | 1.858 | <0.001 | n.s. | n.s. |
| $\boldsymbol{\alpha_4}$ (A$_{pine}$) | 1.846 | <0.001 | 0.389 | <0.001 |
| $\boldsymbol{\beta_1}$ (I$_{2012}$) | 139.657 | <0.001 | 266.816 | <0.001 |
| $\boldsymbol{\beta_2}$ (I$_{2013}$) | n.s. | n.s. | n.s. | n.s. |
| $\boldsymbol{\beta_3}$ (I$_{2014}$) | n.s. | n.s. | n.s. | n.s. |
| $\boldsymbol{\beta_4}$ (I$_{pine}$) | n.s. | n.s. | 9.919 | <0.001 |
| $\boldsymbol{\gamma_1}$ (k$_{2012}$) | 0.019 | <0.001 | 0.049 | <0.001 |
| $\boldsymbol{\gamma_2}$ (k$_{2013}$) | n.s. | n.s. | n.s. | n.s. |
| $\boldsymbol{\gamma_3}$ (k$_{2014}$) | n.s. | n.s. | n.s. | n.s. |
| $\boldsymbol{\gamma_4}$ (k$_{pine}$) | 0.021 | <0.001 | 0.018 | <0.001 |
| $\boldsymbol{\tau_1}$ (m$_{2012}$) | -0.079 | <0.001 | -0.328 | <0.001 |
| $\boldsymbol{\tau_2}$ (m$_{2013}$) | n.s. | n.s. | n.s. | n.s. |
| $\boldsymbol{\tau_3}$ (m$_{2014}$) | n.s. | n.s. | n.s. | n.s. |
| $\boldsymbol{\tau_4}$ (m$_{pine}$) | 0.401 | <0.001 | 0.278 | <0.001 |
| $\boldsymbol{\sigma_j}$ (A$_{site}$) | 0.228 | | $2.61\cdot10^{-4}$ | |
| $\boldsymbol{\sigma_{ij}}$(A$_{tree}$) | 0.358 | | 0.161 | |
| $\boldsymbol{\sigma_j}$ (I$_{site}$) | 11.259 | | $1.42\cdot10^{-4}$ | |
| $\boldsymbol{\sigma_{ij}}$(I$_{tree}$) | 9.604 | | 2.962 | |
| $\boldsymbol{\sigma_e}$(error) | 0.154 | | 0.061 | |
| $\boldsymbol{\delta_1}$* | ----- | | 0.576 | |

*Variance function parameter used to model variance residual structure to correct heteroscedasticity as an exponential value of the variance covariate ($\boldsymbol{g_{ijk}}$): $\boldsymbol{Var(\varepsilon_{ijk}) = \sigma_e^2 \cdot e^{(2\delta_1 g_{ijk})}}$

Moreover, species differences were evidenced also according to bi-logistic model, although differed a slightly with those explained above. Higher spring and autumnal accumulated radial increment (asymptotes $\beta_1$ and $\beta_5$) and generally lower scale parameter ($\beta_4$ and $\beta_7$) for pine confirm again a more pronounced radial increment for this species than for oak (Table 12). Conversely, the spring and autumn inflection point ($\beta_3$and $\beta_6$) was generally lower for pine than oak (22 May vs. 5 June respectively).

## 5.2. *Pinus pinaster* and *Quercus pyrenaica* radial increment response to thinning

### *5.2.1. Thinning and weather influence on radial increment rate*

The results from fitted models for radial increment rate (Eq. 2) are shown in Table 11. The autocorrelation function plot showed that it was not necessary to correct the correlation. Weather variables for the five days prior to measuring were included in the models, based on the lowest AIC index analysis, which coincides this of similar studies for Mediterranean species (Camarero et al., 2010). Statistically significant weather variables that were included in the final fitted model were cumulative rainfall (P; mm), solar radiation (SR; 10KJ/m$^2$) and mean vapor pressure deficit (VPD; kPa). Two additional variables, minimum air temperature (Tmin; ºC) and minimum relative air humidity (RHmin; %), were incorporated into the oak model.

All weather variables from fitted models were positively correlated with increment rate except for vapor pressure deficit, which was especially acute in the summer (Figure S5 and S6). Solar radiation, as well as the amount and frequency of rainfall, caused higher increment rates in spring than in autumn. Additionally, the minimum temperature variable penalized low temperatures, and relative air humidity improved the radial increment rate for the oak species (Table 11).

Tree size (diameter at breast height) was also a significant explanatory variable in the model for all species and sites. Positive thinning treatment effects were found for the pine species at both sites, especially for heavy thinning (Table 11 and Figures S5 and S6). However, there were no differences in the radial increment rate between the moderate thinning treatment and the control at the WAI-0.22 site. The results for oak also pointed to a positive effect from thinning treatments at the WAI-0.65 site, although there were no differences between thinning intensities (P=0.917 according to the Tukey test). However, exclusively moderate thinning had a significant effect on the radial increment rate of oak at the WAI-0.22 site, compared to the control treatment (Table 11).

*Table 11. Linear mixed model fitted for weather and thinning effect on radial increment rate of maritime pine-oak mixed forest by site (Eq. 2). Significant parameters are shown as follows: '***' <0.001, '**' <0.01, '*' <0.05, n.s., not significant.*

| | **WAI-0.22** | | **WAI-0.65** | |
|---|---|---|---|---|
| **Parameter** | **Q.pyrenaica** | **P.pinaster** | **Q.pyrenaica** | **P.pinaster** |
| $\boldsymbol{\beta_0}$ | $-8.00 \cdot 10^{-3***}$ | $-1.52 \cdot 10^{-2***}$ | $-1.06 \cdot 10^{-2***}$ | $-5.71 \cdot 10^{-3**}$ |
| $\boldsymbol{\beta_1(MT)}$ | $1.07 \cdot 10^{-3**}$ | n.s. | $1.26 \cdot 10^{-3**}$**a** | $2.52 \cdot 10^{-3**}$**a** |
| $\boldsymbol{\beta_2(HT)}$ | n.s. | $8.15 \cdot 10^{-4*}$ | $1.11 \cdot 10^{-3*}$**a** | $3.49 \cdot 10^{-3***}$**b** |
| $\boldsymbol{\beta_3(dbh_{ij})}$ | $3.52 \cdot 10^{-5***}$ | $3.17 \cdot 10^{-5***}$ | $5.37 \cdot 10^{-5***}$ | $1.78 \cdot 10^{-5**}$ |
| $\boldsymbol{\beta_4(P)}$ | $6.11 \cdot 10^{-5***}$ | $3.49 \cdot 10^{-4***}$ | $7.02 \cdot 10^{-5***}$ | $2.55 \cdot 10^{-4***}$ |
| $\boldsymbol{\beta_5(SR)}$ | $6.24 \cdot 10^{-6***}$ | $4.39 \cdot 10^{-5***}$ | $6.17 \cdot 10^{-6***}$ | $5.47 \cdot 10^{-5***}$ |
| $\boldsymbol{\beta_6(VPD)}$ | $-2.24 \cdot 10^{-3***}$ | $-1.83 \cdot 10^{-2***}$ | $-3.18 \cdot 10^{-3***}$ | $-2.14 \cdot 10^{-2***}$ |
| $\boldsymbol{\beta_7(T_{min})}$ | $2.77 \cdot 10^{-4***}$ | n.s. | $4.25 \cdot 10^{-4***}$ | n.s. |
| $\boldsymbol{\beta_8(RH_{min})}$ | $5.13 \cdot 10^{-5***}$ | n.s. | $5.79 \cdot 10^{-5***}$ | n.s. |
| $\boldsymbol{\sigma_k}$(year) | $1.73 \cdot 10^{-7}$ | $1.44 \cdot 10^{-3}$ | $1.71 \cdot 10^{-4}$ | $8.80 \cdot 10^{-4}$ |
| $\boldsymbol{\sigma_{jk}}$(plot) | $3.97 \cdot 10^{-8}$ | $2.83 \cdot 10^{-4}$ | $4.91 \cdot 10^{-4}$ | $1.07 \cdot 10^{-3}$ |
| $\boldsymbol{\sigma_{ijk}}$(tree) | $1.46 \cdot 10^{-3}$ | $3.02 \cdot 10^{-7}$ | $1.52 \cdot 10^{-3}$ | $2.03 \cdot 10^{-7}$ |
| $\boldsymbol{\sigma_e}$(error) | $4.49 \cdot 10^{-3}$ | $1.06 \cdot 10^{-2}$ | $5.09 \cdot 10^{-3}$ | $1.52 \cdot 10^{-2}$ |

*Letters denote significant differences between thinning treatments according post-hoc Tukey analysis.*

### *5.2.2. Thinning effect on intra-annual radial increment pattern*

The results from the Eq. 4 fitted for band dendrometer measurements can be seen in Table S1. Figures 19 and 20 highlight the species and thinning treatment differences according fitted models over the sampling years.

Table 12 show significant differences between the fitted model set parameters for each species, treatment and site. The spring and autumn radial increments ($\beta_1$ and $\beta_5$) were higher at WAI-0.65 than at WAI-0.22 for the two species (P< 0.05 in all cases except for $\beta_1$ oak control; results not shown). In general, the spring radial increment $(\beta_1)$ exceeded the autumnal increment ($\beta_5 - \beta_1$) regardless of site and species (radial increment rate from Figures 19 and 20).

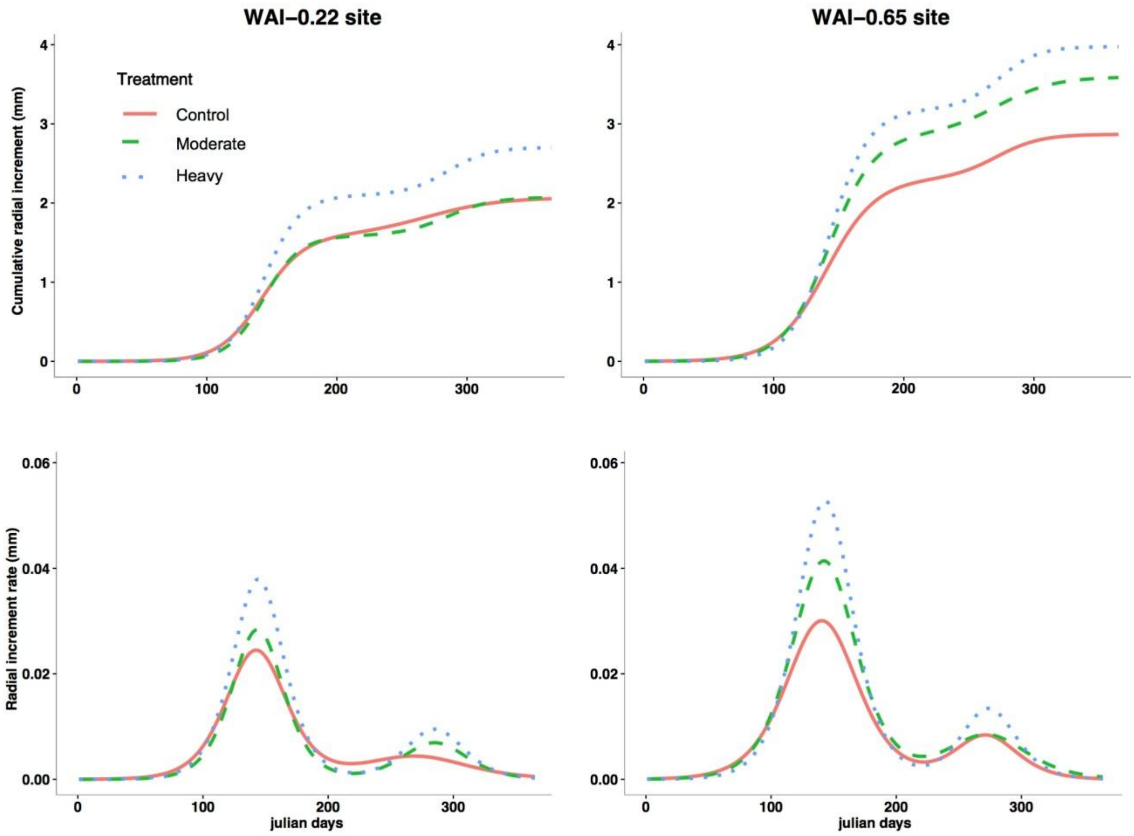

*Figure 19. Cumulative radial increment and radial increment rates from bi-logistic model for P.pinaster.*

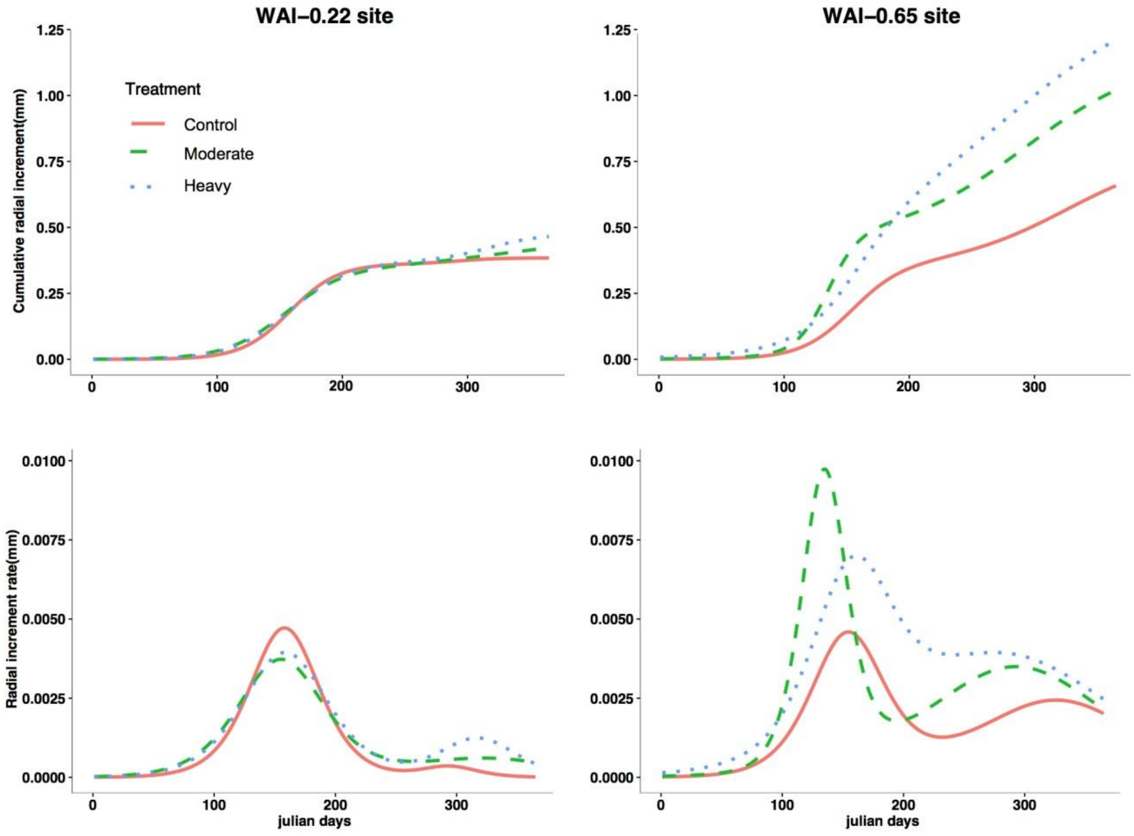

*Figure 20. Cumulative radial increment and radial increment rates from bi-logistic model for Q.pyrenaica.*

Heavy thinning increased radial increment in spring and autumn ($\beta_1$ and $\beta_5$) and prolonged the increment period ($\beta_3$ and $\beta_6$ at the WAI-0.22 site, $\beta_3$ at the WAI-0.65 site) for pine, though the increment period was lower than the sampling frequency (every two weeks). Additionally, the scale parameter ($\beta_4$ and $\beta_7$) was lower for heavy thinning, again reflecting a higher radial increment rate. Moderate thinning also had a positive effect, enhancing radial increment ($\beta_1$, $\beta_4$ and $\beta_5$) for pine at the WAI-0.65 site, but had no effect on the spring and autumn asymptotes ($\beta_1$ and $\beta_5$) at the WAI-0.22 site.

Heavy thinning also increased radial increment in spring ($\beta_1$) and prolonged the increment period ($\beta_3$) at the WAI-0.65 site for oak species. The autumn radial increment for oak ($\beta_5$) was also higher for thinning treatments, regardless of site, and increased with thinning intensity, but with no statistically significant differences between moderate and heavy thinning.

*Table 12. Intra-annual bi-logistic model parameter set differences between treatment and species for each site of maritime pine-oak mixed forest (Eq. 4). Different letters denote significant differences at the 0.05 significance level.*

| | | | **WAI-0.22** | | | **WAI-0.65** | |
|---|---|---|---|---|---|---|---|
| **Parameter** | **Species** | **Treat.A** | **Treat.D** | **Treat.E** | **Treat.A** | **Treat.D** | **Treat.E** |
| $\boldsymbol{\beta_1}$ | *P.pinaster* | 1.581 **b** | 1.581 **b** | 2.098 **c** | 2.308 **c** | 2.867 **d** | 3.184 **d** |
| | *Q.pyrenaica* | 0.362 **a** | 0.351 **a** | 0.372 **a** | 0.353 **a** | 0.456 **ab** | 0.479 **b** |
| $\boldsymbol{\beta_2}$ | *P.pinaster* | - 0.032 a**b** | -0.052 **a** | -0.0253**b** | 0.063 **d** | 0.060 **d** | 0.046 **d** |
| | *Q.pyrenaica* | -0.001**d** | -0.012 **bc** | -0.010**c** | -0.069 **b** | -0.036 **c** | -0.137 **a** |
| $\boldsymbol{\beta_3}$ | *P.pinaster* | 142.333 **a** | 143.618**ab** | 144.157**b** | 140.528**b** | 142.172**bc** | 142.928**c** |
| | *Q.pyrenaica* | 158.050**cd** | 154.981 **c** | 158.660**d** | 153.803**d** | 134.597 **a** | 157.655**e** |
| $\boldsymbol{\beta_4}$ | *P.pinaster* | 16.271 **b** | 13.973 **a** | 13.842 **a** | 19.204 **d** | 17.349 **c** | 15.080 **b** |
| | *Q.pyrenaica* | 19.229 **c** | 23.762 **d** | 23.595 **d** | 20.077**de** | 12.400 **a** | 21.839 **e** |
| $\boldsymbol{\beta_5}$ | *P.pinaster* | 2.069 **c** | 2.073 **c** | 2.703 **d** | 2.868 **c** | 3.594 **d** | 3.976 **e** |
| | *Q.pyrenaica* | 0.384 **a** | 0.448 **b** | 0.475 **b** | 0.783 **a** | 1.150 **b** | 1.392 **b** |
| $\boldsymbol{\beta_6}$ | *P.pinaster* | 269.335 **a** | 284.969**bc** | 285.014**b** | 271.508**a** | 272.277 **a** | 273.701**a** |
| | *Q.pyrenaica* | 293.703 **c** | 325.002 **d** | 317.600**d** | 326.000**b** | 292.690**ab** | 283.090**a** |
| $\boldsymbol{\beta_7}$ | *P.pinaster* | 27.918 **b** | 17.528 **a** | 15.943 **c** | 16.905**ab** | 21.643 **b** | 14.755 **a** |
| | *Q.pyrenaica* | 15.499 **a** | 40.631 **c** | 21.098 **a** | 44.121 **c** | 49.637 **c** | 59.093 **c** |

### 5.2.3. *Thinning effect on inter-annual variation of seasonal and annual radial increment*

Results for the treatment-year interaction from band dendrometer measurements for spring, autumn and annual radial increment (Eq. 7) are compiled in Table 13 and 14.

*Table 13. Linear mixed model fitted for thinning effect on spring, autumn and annual radial increment of Pinus pinaster by site (Eq. 7). Significant parameters are in bold with significance level as follows: '***' <0.001, '**' <0.01, '*' <0.05, '·' 0.1).*

| | **WAI-0.22** | | | **WAI-0.65** | | |
|---|---|---|---|---|---|---|
| **Parameter** | **Spring** | **Autumn** | **Annual** | **Spring** | **Autumn** | **Annual** |
| $\boldsymbol{\delta_i(dbh_{ij})}$ | **0.007$^{***}$** | **0.002$^{***}$** | **0.009$^{***}$** | 0.003 | **0.001$^{*}$** | **0.004·** |
| $\boldsymbol{\alpha_1(2010)}$ | 0.364 | 0.019 | 0.570 | **1.545$^{**}$** | **0.321$^{**}$** | **2.020$^{**}$** |
| $\boldsymbol{\alpha_2(2011)}$ | **0.611·** | -0.079 | 0.577 | **2.062$^{***}$** | **0.375$^{***}$** | **2.320$^{***}$** |
| $\boldsymbol{\alpha_3(2012)}$ | **-0.805$^{*}$** | **0.111$^{*}$** | **-0.854$^{*}$** | 0.571 | **0.866$^{***}$** | **1.247$^{*}$** |
| $\boldsymbol{\beta_1(TrtD)}$ | -0.187 | 0.001 | -0.158 | **0.691$^{*}$** | 0.042 | **0.815$^{*}$** |
| $\boldsymbol{\beta_2(TrtE)}$ | -0.053 | -0.005 | -0.003 | 0.782$^{*}$ | 0.080 | **1.056$^{**}$** |
| $\boldsymbol{\gamma_{11}(TrtD2011)}$ | 0.102 | -0.005 | 0.087 | 0.017 | -0.051 | -0.085 |
| $\boldsymbol{\gamma_{12}(TrtD2012)}$ | **0.280$^{*}$** | 0.002 | -0.218 | **-0.278$^{*}$** | 0.011 | **-0.315$^{*}$** |
| $\boldsymbol{\gamma_{21}(TrtE2011)}$ | **0.454$^{***}$** | -0.019 | **0.372$^{*}$** | **0.336$^{**}$** | **-0.099$^{**}$** | 0.046 |
| $\boldsymbol{\gamma_{22}(TrtE2012)}$ | **0.358$^{**}$** | 0.010 | **0.289$^{*}$** | -0.027 | 0.021 | -0.126 |
| $\boldsymbol{\sigma_j}$(plot) | 0.132 | $9.49 \cdot 10^{-6}$ | 0.122 | 0.200 | 0.019 | 0.204 |
| $\boldsymbol{\sigma_{ij}}$(tree) | 0.439 | 0.071 | 0.489 | 0.522 | 0.102 | 0.649 |
| $\boldsymbol{\sigma_{ijk}}$(error) | 0.350 | 0.076 | 0.404 | 0.338 | 0.090 | 0.344 |

In 2010 there were no thinning effects on radial increment, regardless of species, at the WAI-0.22 site ($\beta_1$ and $\beta_2$). However, the effect of thinning was greater in all years for pine at the WAI-0.65 site. Radial increment of oak for moderate thinning was also higher at the WAI-0.65 site ($\beta_1$).

A large spring radial increment occurred for both species in 2011 (Figure 21) coinciding with a period of high spring rainfall (see Figure 9 and 10). During this period, the effect of heavy thinning on pine increased ($\gamma_{21}$) at both sites (Table 13 and Figure 21). There was also a positive thinning effect for oak compared to the control ($\gamma_{11}, \gamma_{21}$, $\beta_1$), but there were no differences between thinning intensities at either site (Figure 21).

*Table 14. Linear mixed model fitted for thinning effect on spring, autumn and annual radial increment of Quercus pyrenaica by site (Eq. 7). Significant parameters are in bold with significance level as follows: '***' <0.001, '**' <0.01, '*' <0.05, '·' 0.1).*

| | **WAI-0.22** | | | **WAI-0.65** | | |
|---|---|---|---|---|---|---|
| **Parameter** | **Spring** | **Autumn** | **Annual** | **Spring** | **Autumn** | **Annual** |
| $\boldsymbol{\delta_i(dbh_{ij})}$ | **0.002**$^{*}$ | **0.001**$^{***}$ | **0.003**$^{*}$ | **0.012**$^{***}$ | **0.003**$^{***}$ | **0.012**$^{**}$ |
| $\boldsymbol{\alpha_1(2010)}$ | -0.061 | -0.036 | -0.002 | **-0.771**$^{*}$ | **-0.220**$^{***}$ | -0.532 |
| $\boldsymbol{\alpha_2(2011)}$ | 0.047 | -0.006 | 0.095 | **-0.732**$^{*}$ | **-0.123**$^{*}$ | -0.480 |
| $\boldsymbol{\alpha_3(2012)}$ | -0.086 | 0.023 | -0.027 | **-1.017**$^{**}$ | -0.025 | **-0.774**$^{*}$ |
| $\boldsymbol{\beta_1(TrtD)}$ | -0.014 | -0.003 | -0.028 | **0.308·** | 0.009 | **0.344·** |
| $\boldsymbol{\beta_2(TrtE)}$ | 0.011 | 0.006 | 0.041 | 0.241 | -0.004 | 0.231 |
| $\boldsymbol{\gamma_{11}(TrtD2011)}$ | **0.086**$^{*}$ | -0.028 | **0.095**$^{*}$ | 0.242 | 0.021 | 0.215 |
| $\boldsymbol{\gamma_{12}(TrtD2012)}$ | 0.043 | -0.014 | 0.051 | -0.169 | 0.014 | -0.189 |
| $\boldsymbol{\gamma_{21}(TrtE2011)}$ | **0.067·** | **-0.036·** | 0.034 | **0.270·** | **0.036**$^{*}$ | **0.294·** |
| $\boldsymbol{\gamma_{22}(TrtE2012)}$ | -0.001 | -0.025 | -0.025 | -0.042 | **0.045**$^{**}$ | 0.037 |
| $\boldsymbol{\sigma_j}$(plot) | 0.058 | $1.26 \cdot 10^{-6}$ | 0.052 | 0.115 | 0.013 | 0.097 |
| $\boldsymbol{\sigma_{ij}}$(tree) | 0.110 | 0.027 | 0.138 | 0.256 | 0.049 | 0.325 |
| $\boldsymbol{\sigma_{ijk}}$(error) | 0.092 | 0.046 | 0.111 | 0.379 | 0.040 | 0.431 |

In 2012, spring radial increment was lower at both sites regardless of species $(\alpha_3)$, coinciding with a period of low rainfall (Figures 9 and 10). Heavy thinning had a positive effect, similar to the previous year, for pine during the drought event and the effect increased for moderate thinning at the WAI-0.22 site ($\gamma_{12}$ and $\gamma_{22}$; Table 13). Thinning effect was also maintained in 2012 but was reduced for moderate thinning at the WAI-0.65 site $(\gamma_{12})$. No differences between thinning treatments were identified for oak in 2012 ($\gamma_{12}$, $\gamma_{22}$; Table 14 and Figure 3), although moderate thinning effects were similar over time at the WAI-0.65 site ($\beta_1$).

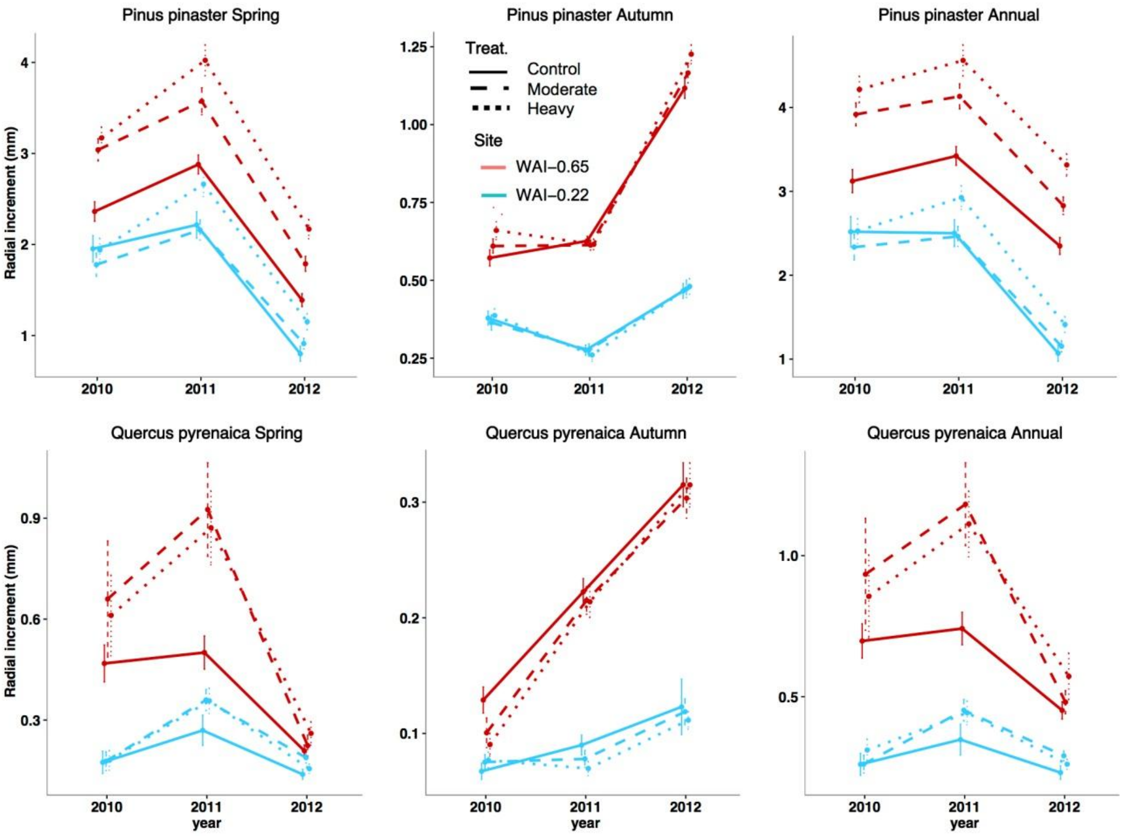

*Figure 21. Spring, autumnal and annual radial increment differences between treatments, years, species and sites in maritime pine-oak mixed forest. Note the different scales on the ordinate axis.*

There were no significant differences in autumn radial increment between thinning treatments each year for either species ($\beta_1$ and $\beta_2$) during the study period (Table 13 and 14), though their effects varied over time according to the amount of autumn rainfall ($\alpha_1, \alpha_2, \alpha_3,$ Figure 21 and Figure 9 and 10). Heavy thinning had a positive effect on annual radial increment for pine species, regardless of site and year, though the difference was not significant in 2010 at the WAI-0.22 site (Table 13). This effect remained almost constant over time at both sites ($\gamma_{21}$, $\gamma_{22}$ for WAI-0.22 and $\beta_2$ for WAI-0.65 site).The annual radial increment for oak differed between sites: moderate thinning had a positive effect during the entire study period at the WAI-0.65 site ($\beta_1$; Table 14), but only in 2011 at the WAI-0.22 site($\gamma_{11}$). The effect of heavy thinning was only significant in 2011 at WAI-0.65 site($\gamma_{21}$).

## 5.3. *Pinus sylvestris* and *Quercus pyrenaica* radial increment response to thinning

### *5.3.1. Thinning effect on intra-annual cumulative radial increment pattern*

Intra-annual cumulative radial increment patterns differed between species, thinning treatments and among years according to double-Richards approach (Table 15 and Figure 22). Pine species presented a higher increment rate ($\gamma_1$), but lower inflection point ($\beta_1$) than oak regardless year. The inflection point was in 14 May and 16 June for pine and oak species respectively. Thinning treatment affected to spring asymptote regardless year, although there were no differences between unthinned and moderate thinning ($\alpha_5$). Year fixed effect influenced to spring and autumn asymptotes. Spring asymptote for oak species was lower for each thinning treatment in the severe dry year 2017 than 2016 ($\alpha_1$), but inversely, during year 2017 it was higher for pine species compared to 2016 ($\alpha_3$). In year 2016 there were no difference between species ($\alpha_2$) and only the size of diameter ($\alpha_4$) and thinning treatment ($\alpha_6$) evidenced tree differences. In this regard, oak in thinned stands surpassed pine in unthinned stand spring asymptote for a mean diameter size of each species (Figure 22). However, in year 2017 pine always presented a higher spring asymptote ($\alpha_3$) compared to oak for a mean diameter size of both species. Autumn asymptote increased in 2016 (but with no statistical significance, P= 0.065) and negative trend happened during year 2017($\rho_1$). No differences were found on shape parameter among species ($\tau_0$).

*Table 15. Double-Richards model fitted for intra-annual cumulative radial increment pattern of Scots pine-oak mixed stand (Eq.6). n.s., not significant*

| Parameter | Coefficient | p-value |
|---|---|---|
| $\boldsymbol{\alpha_0}$ ($\mathrm{A}_{2016}$) | -0.839 | <0.001 |
| $\boldsymbol{\alpha_1}$ ($\mathrm{A}_{2017}$) | -0.159 | <0.001 |
| $\boldsymbol{\alpha_2}$ ($\mathrm{A}_{2016pine}$) | n.s. | n.s. |
| $\boldsymbol{\alpha_3}$ ($\mathrm{A}_{2017pine}$) | 0.432 | <0.001 |
| $\boldsymbol{\alpha_4}$ ($\mathrm{A}_{dbh}$) | 0.101 | <0.001 |
| $\boldsymbol{\alpha_5}$ ($\mathrm{A}_{MT}$) | n.s. | n.s. |
| $\boldsymbol{\alpha_6}$ ($\mathrm{A}_{HT}$) | 0.374 | 0.002 |
| $\boldsymbol{\beta_0}$ (I) | 167.274 | <0.001 |
| $\boldsymbol{\beta_1}$ ($\mathrm{I}_{pine}$) | -32.592 | <0.001 |
| $\boldsymbol{\gamma_0}$ (k) | 0.032 | <0.001 |
| $\boldsymbol{\gamma_1}$ ($\mathrm{k}_{pine}$) | 0.012 | <0.001 |
| $\boldsymbol{\tau_0}$ (m) | 0.307 | 0.032 |
| $\boldsymbol{\rho_0}$ ($\mathrm{RA}_{2016}$) | n.s. | n.s. |
| $\boldsymbol{\rho_1}$ ($\mathrm{RA}_{2017}$) | -0.337 | 0.002 |
| $\boldsymbol{\sigma_j}$ ($\mathrm{A}_{plot}$) | $2.160\cdot10^{-4}$ | |
| $\boldsymbol{\sigma_{ij}}$($\mathrm{A}_{tree}$) | 0.409 | |
| $\boldsymbol{\sigma_e}$(error) | 0.195 | |
| $\boldsymbol{\delta}$ | 0.304 | |
| $\boldsymbol{\theta}$ | 0.683 | |

$\boldsymbol{\alpha_i}$, $\boldsymbol{\beta_i}$, $\boldsymbol{\gamma_i}$ *and* $\boldsymbol{\tau_i}$ *are the asymptote, inflection point, rate and shape parameter regression of fixed effect variables for the first Richards curve and* $\boldsymbol{\rho_i}$ *are the amplitude parameters for the second one;* $\boldsymbol{\sigma_j}$ *is standard deviation for plot random effect;* $\boldsymbol{\sigma_{ij}}$ *is standard deviation for tree random effect;* $\boldsymbol{\sigma_e}$ *is standard deviation for error term;* $\boldsymbol{\theta}$ *is the residual serial correlation parameter for moving average model MA(1);* $\boldsymbol{\delta}$ *is function parameter used to model residual variance as a power of the absolute value of the variance covariate (*$\boldsymbol{g_{ijk}}$*):* $\boldsymbol{Var(\varepsilon_{ijk}) = \sigma_e^2(|g_{ijk}|^{\delta})^2}$

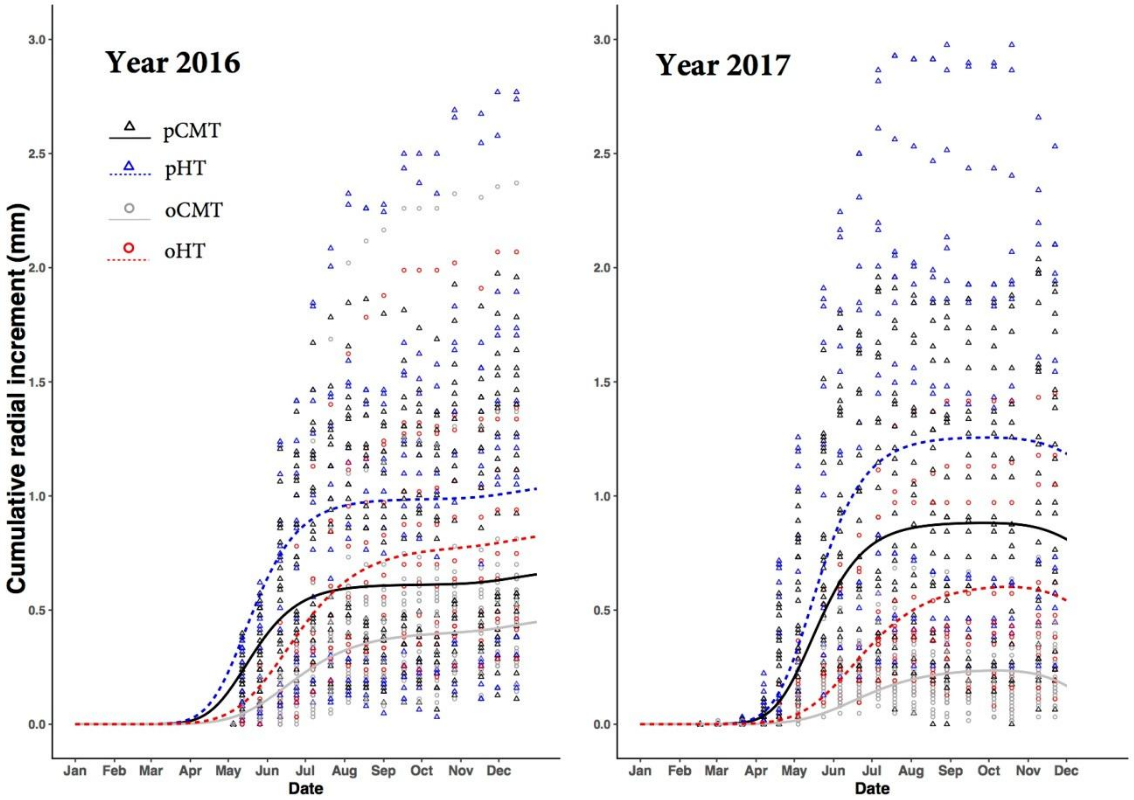

*Figure 22. Thinning treatment and year effect on species-specific intra-annual cumulative radial increment patterns from double-Richards fitted model for Scots pine-oak mixed stand. Diameter size was the mean for each species. 'pCMT' denotes control and moderate thinning for pine, 'pHT' is heavy thinning for pine, 'oCMT' is control and moderate thinning for oak and 'oHT' is heavy thinning for oak.*

# Discussion

## 6.1. Meteorological drivers of radial variation

Differences observed in amplitude and period features from radial variation daily cycles provide valuable information about tree water status (reversible process) and radial tree growth (irreversible process) (Turcotte et al., 2011; Vieira et al., 2013; Zweifel, 2016). We found species differences between maritime pine and oak in radial variation cycles across seasons, due to they responded differently to weather conditions. Temperature drove species differences in amplitude of daily cycles, whereas the effect of precipitation was similar for both species (Figure 16 and Table 7). Stem contraction was observed generally from early morning until evening, reflecting the daily cycle of water uptake and loss, similar to previous studies (Oberhuber et al., 2015; Vieira et al., 2013).

The relation between air temperature and stem cycle amplitude showed clear increases in amplitude with increased temperature, as found by King et al., (2013). This suggests a higher contraction phase due to the depletion of stem water reserves in response to greater evaporative demand, which is driven by warmer temperatures. Increased transpiration due to high air temperatures leads to elevated demand for water, which is scarce in summer time and provokes extreme contraction from shrinkage (Sánchez-Costa et al., 2015; Vieira et al., 2015; Zweifel et al., 2016). Accordingly, intra-annual cumulative radial increment patterns confirmed a marked bimodal pattern for both species regardless of the year (Figure 18) as a consequence of summer drought, which is typical in Mediterranean environments (Albuixech et al., 2012; Camarero et al., 2010). Thus, daily amplitude differences between species (Figure 16) at high temperatures (above 25ºC) during summer time could be related to distinct canopy transpiration rates and water demands. Higher leaf surface area of oak implies greater evapotranspiration during the diurnal period, hence, could exploit their internal stem water reserves more quickly than pine. Stem water store capacity could be higher for maritime pine due to greater conductivity area in sapwood and bark compared to oak (Oberhuber et al., 2014), which is accentuated by bigger pine diameter. Similarly, increased water deficit resulted in a greater amplitude of the radial variation cycle (Table 7), which could also explain the high amplitude during summer time (Figures 14 and 15). Turcotte et al., (2011) reported that water deficit during the day led to a pronounced contraction phase for boreal black spruce.

However, during winter, the circadian cycle of stem size becomes irregular, i.e., with marked phase shifts, due to temperature is the dominant factor determining stem size fluctuations in the absence of growth (Biondi and Rossi, 2015). Amplitude of radial variation cycles during winter time was related to different species specific responses to freezing events (Figure 16 and Table 7): pine decreased in amplitude, while oak increased below approximately 6 ºC. This minimum daily amplitude coincides with temperature thresholds for the beginning of xylogenesis and general vegetative biological activity (Rossi et al., 2008). Vieira et al., (2013) reported a similar pattern for maritime pine in a Mediterranean area, while King et al., (2013) reported amplitude increment for spruce and larch at freezing temperatures, which resembled the behavior of oak. Low temperatures makes extra-cellular water begins to freeze inducing the osmotic withdrawal of intra-cellular water and thus cell and ultimately stem shrinkage (Pearce, 2001; Strimbeck et al., 2008; Zweifel and Häsler, 2000). Thereby, we hypothesize that daily amplitude divergence at low temperatures may be due to a species differences in the sap freezing point. An alternative and perhaps more simple hypothesis relates to the difference in bark width, which could serve as a thermal insulation. We also observed (results not shown) sudden large decreases in stem size for pine species at low temperatures according the same physiological process. However, very rare winter temperatures below 0ºC at both sites made impossible to find a significant statistical relationship which showed increase amplitude with lower temperatures for pine species.

Moreover, only weather variables (temperature and rain) controlled the period of daily radial variation cycles, as reported by Vieira et al., (2013), without species differences (Table 7). We found that period decreased with increased temperature. Thus, when temperatures are especially high and the days are longer during pre-summer and summer, transpiration rates may be also high, causing faster contraction resulting in a compressed wave period (Figures 14 and 15). Deslauriers et al., (2007) demonstrated that vapor water deficit had a direct effect on the duration of the contraction phase, which corroborate our results. However, according to Figure 15 and almost significant value for species (P=0.06; Table 7) we theorize species differences-higher for oak than pine – in daily cycle duration, expect in summer time. Anatomical differences (sapwood, cell walls, and vessels) that govern water relocation and are directly related to the higher hygroscopicity of oak compared to pine (Popper et al., 2005) could explain these results. Additionally, the fitted model (Table 7) indicated that the period of radial variation cycles decreased at air temperatures below 8.5 ºC. We suggest that temperatures close to freezing may generate a faster contraction phase due to thermal response, leading to radial variation cycles with a compressed period. Although air temperature certainly plays a role in the radial variation cycle period, precipitation is more closely linked to higher period duration because of rehydration (Figure 16).

We also found that rain increased the amplitude cycles (Table 7) and could be related again to rehydration processes (Deslauriers et al., 2007; Vieira et al., 2013). However, the increase in daily stem diameter variation in spring time is partly a result of refilling of the internal stem storage pool in addition to stem growth (Steppe et al., 2006). In this sense, species-specific potential pressure increment in the stem storage compartment and growth could drive spring amplitude differences. Pine is an early successional and light-demanding species, so higher growth was expected (Sánchez-Costa et al., 2015) and corroborated during spring time (Table 8). Accordingly, the greatest daily radial amplitude for maritime pine was in spring season, which coincides with a large temperature range (Figure 16).

Anyway, maritime pine and oak species responded to the same weather variables and in the similar way (linearly) modifying daily radial increment (Table 8). This finding agrees with that of Sánchez-Costa et al., (2015) who reported coordinated responses of transpiration, water storage dynamics, and growth-based water use efficiency in Mediterranean pine and oak species. These evidences could suggest a strong functional convergence between co-existing species, resulting in competition for resources at least in some periods. Conversely, weather influence on radial increment rate showed species-specific radial increment responses (Table 11). Although precipitation, solar radiation and vapor pressure deficit influenced at both species, radial increment of oak trees were also sensitive to minimum temperature and relative air humidity. This may be explained by methodological and precision differences in estimating radial increment (daily cycle vs. biweekly rate analysis).

Overall, pine responded to weather with higher radial increment compared to oak (Table 8). These differences are showed also in Figure 17 depending on the year and site. Years with low spring precipitation as in 2012 and 2014 at WAI-0.22 and 2012 at WAI-0.65 (Figure 9 and 10), the difference between species seem to disappear. However, the number of daily cycles with increment phase was always higher for pine, except in 2013 at WAI-0.65, indicating probable species-specific growth strategy (evergreen vs. deciduous). This might be related to earlier radial increment onset (Figure 13) for pioneer pine species as a greater resource expender, developing riskier life strategies to capture resources (Cuny et al., 2012).

Several authors have found positive correlations between air temperature and radial increment (Deslauriers et al., 2003; King et al., 2013; Van der Maaten et al., 2013), though other works report the opposite due to elevated transpiration rates, especially in summer (Deslauriers et al., 2007; Oberhuber et al., 2014). Our results corroborated that water availability is an important factor in radial increment in Mediterranean areas, as it allows growth and/or replenishment of internal water reserves in trees. Precipitation events increase available soil water, which is essential for photosynthesis and growth, but there is also evidence that rain plays a role in the stem rehydration process. The difficulty in differentiating these two effects with dendrometers leads to overestimation of the role of rain (Biondi and Rossi, 2015; Turcotte et al., 2011; Zweifel et al., 2016). At the tree physiological level, the negative effect of high vapor pressure deficit concurs with other studies (Oberhuber et al., 2014; Van der Maaten et al., 2013) and can be explained by increased evapotranspiration, which inhibits cell enlargement and growth (Oberhuber et al., 2014). Water deficit is also related to climate variables which influence transpiration (Oberhuber et al., 2015). This suggests that drought from June to August is a highly prominent factor in limiting growth for both species, as we observed for 2012. Though solar radiation promotes radial increment and could be related to photosynthesis and eventual growth, under water deficit, these relationships weaken or are modified (Muller et al., 2011) suggesting that may also increase transpiration rates, close stomata and subsequent stem contraction (Duchesne and Houle, 2011).

## 6.2. Growth temporal complementarity

### *1.2.1. Maritime pine and oak species*

Intra-annual radial variation synchrony for maritime pine and oak species confirmed results explained above that species respond to the same weather conditions. The absence of significant differences between species at the spring inflection point ($\beta_4$ from single Richards approach, Table 10) may also be a consequence of species synchrony. These suggest that species competition for resources would primarily occur in spring. However, species differences would also confirm temporal complementarity evidenced by several points: Concurrency values (Table 9), differences in radial increment onset (Figure 13) and cumulative radial increment patterns (Table 10).

Lower Concurrency values when pine and oak radial variation are compared might also suggest species phase differences in radial variation. These results also agree with differences in the begging of contraction phase for daily radial cycles through the seasons (Figure 15). However, Concurrency and Phase metrics were small even when compared trees from the same species, which could indicate that neither of those non-linear metrics was able to adequately identify the strength of phase-locking. This shows that there is no 'magic bullet' method for quantifying phase synchrony in noisy observational data, especially if multiple factors are operating simultaneously (Gouhier and Guichard, 2014).

Species differences in radial increment onset could also indicate species niche complementarity, although it can be masked by water-related swelling from stem rehydration after frost-induced shrinkage during winter (Oberhuber et al., 2015; Turcotte et al., 2011; Zweifel et al., 2000). Prior research has reported notably earlier onset of xylem differentiation for the species analyzed here. Studies on *Q.pyrenaica* (Fernández-De-Uña et al., 2017; González-González et al., 2013; Pérez-de-Lis et al., 2013) recorded xylem differentiation onset from March to early April; while Vieira et al., (2015) observed the onset of *P.pinaster* differentiation in March, but with high yearly variability. Our radial increment onset dates for both species agree with the onset of tracheid and vessel enlargement, as reported by Vieira et al. (2015) and Fernández-De-Uña et al. (2017) for the same species in Mediterranean areas. This corroboration increases our confidence that we indeed observed the first stage of cell enlargement. Similarly, Oberhuber and Gruber (2010) reported that the onset and maximum stem diameter increments from dendrometer recordings of *Pinus sylvestris* corresponded to the start and maximum number of cells observed in the enlargement phase.

The coincidence of bud-burst and radial increment onset (Figure 13) supports the hypothesis of Rossi et al. (2011), that wood formation and several physiological activities (leaf phenological phases here) are closely interconnected. In this sense, González-González et al., (2013) showed a close relationship between bud burst and the completion of the first row of earlywood vessels for *Q.pyrenaica*, while initial cambium activity occurred before bud break involving carbon reserves.

Differences detected in radial increment onset between the co-occurring species could reveal dissimilar endogenous control involving species-specific temperature and/or photoperiod thresholds. Maritime pine and oak would respond to the first and second strategy, respectively. Bud-burst and growth onset after winter dormancy in temperate and boreal trees are known to be highly responsive to temperature (Hänninen and Tanino, 2011; Rossi et al., 2011). Several studies in the Mediterranean region have also documented earlier onset of cambial activity in response to higher winter temperatures (Camarero et al., 2010; Linares et al., 2009; Vieira et al., 2014a). In our study, the earliest radial increment onset occurred in 2014, which coincided with higher minimal temperatures from January to March (results not shown). The early radial increment onset of pine species is reflected in the higher spring shape parameter of the single Richards model ($\tau_4$), which may also increase the spring asymptote (Table 10). Maritime pine could get ahead in the use of soil water reserves in early spring at expense of oak due to leaf phenology differences (Fernández-De-Uña et al., 2017).

In this regard, species differences in intra-annual cumulative radial increment pattern, especially for the shape parameter ($\tau_4$) and autumn inflection point ($\beta_4$) from the single Richards model (Table 10), would confirm asynchronous growth response magnitude of both species at certain periods, indicating a distinct use of resources. The spring asymptote and rate parameter were higher for maritime pine, which corroborates faster growth for early successional and light-demanding species. However, Cuny et al., (2012) affirm that late successional species utilize resources more efficiently and, hence, higher increment rate is expected. We think that reproduction method (coppice) and tree competition (higher for oak trees) could influence these results.

Mediterranean tree species generally experience seasonal stem shrinkage in response to drought (increasing water deficit) and subsequent stem rehydration after rainfall (Sánchez-Costa et al., 2015). In this context, the Richards shape parameter ($\tau_4$) showed a longer exponential period of radial increment for pine at the beginning of autumn, which could suggest faster recovery from summer drought for pine than oak or even a different autumn growth strategy. Besides, autumn radial increment patterns showed higher asymptote and rate parameters for maritime pine, but also a delayed inflection point. We think these differences could indicate not just rehydration, but growth in pine during the autumn season. In fact, Vieira et al., (2014) verified that maritime pine in Mediterranean areas can present long-lasting xylem enlargement through mid-October, or even autumn cambial reactivation (Vieira et al., 2015). We did not observe intra-annual density fluctuations (IADFs) from core increments (results not shown), but direct measurements of intra-annual growth (i.e., repeated micro-coring or pinning) would be needed to evaluate this statement (Mäkinen et al., 2008).

Furthermore, the spring asymptote parameter showed differences in the cumulative radial increment among years (Table 10). In this sense, we observed extreme spring and summer shrinkage in 2012 (Figure 18) related to lower winter and spring precipitation. Drought drastically affected oak trees which radial growth was nearly suppressed, indicating higher susceptibility to water stress. The better pine response to drought could be related to higher availability to soil water reserves due to mainly lower intra-specific competition compared to oak trees. Besides, oak species may cease radial growth with a shift in the allocation of resources under stress, favoring carbon storage in root system or fine root growth over stem secondary growth (Eilmann et al., 2009).

Results from band dendrometer measurements (Table 12 and Table S1) agree with higher radial increment (asymptotes and rate) for maritime pine compared to oak. The inflection point for pine trees almost coincides for both analyses (19 and 22 May for single Richards and bi-logistic model respectively), but differed for oak species (19 May vs. 5 June). These differences may be due to several conditions: different sampling years (2010-2012 years vs. 2012-2014), different type of dendrometer (band vs. point electronic high-resolution) and distinct statistical approach (bi-logistic vs. single Richards model). According to results above (radial synchrony and response to same weather variables), we theorized that results from higher-resolution dendrometer records are closer to reality. Bi-logistic approach could be more rigid and inflexible method compared to Richards model and, finally, results for inflection point could be altered.

### 6.2.2. *Scots pine and oak species*

Species-specific differences in the intra-annual cumulative radial increment patterns (Table 15) showed an apparent asynchrony of radial growth, which could evidence a species niche complementarity. In this way, interactions such as facilitation or reduced competition generated by mixed forest stand as the presented here, may involve a complementary and efficient use of resources over time (Forrester, 2014). This may be demonstrated by species differences in spring inflection point ($\beta_1$from Table 15). Early inflection point of pine trees could involve a greater resource expenders and develop riskier life strategies to capture resources, while shade-tolerant oak species develop safer life strategies(Cuny et al., 2012). Additionally, a tighter stomatal control and higher intrinsic water use efficiency for Scots pine (Fernández-De-Uña et al., 2017) may restrict growth earlier. The date of inflection point for Scots pine was earlier to maritime pine in mixed forest stand with oak according Table 10 (14 vs 19 May respectively). Besides, it was previous to maximum formation rate of early-wood cell production (2 June) found by Camarero et al., (2010) in a Scots pine mixed forest with *Juniperus thurifera* species. On the other hand, the inflection point for oak trees was delayed compared to that oak exhibited in maritime pine mixed forest (16 June vs 19 May; Table 10). At this regard, temporal diversification or space occupation of tree species in mixed forest may relax resource competition according to morphological and physiological specific traits differences by complementary exploitation of light and water via crown and root space (Williams et al., 2017). Thereby, del Río and Sterba, (2009) found that Scots pine-oak mixed stands support higher volume increment per occupied area compared to pure stands.

Moreover, the mean diameters of Scots pine and oak were 14.3 cm and 12.2 cm, and the mean heights were 11.0 and 10.2 m, respectively, indicating that pine was slightly ahead of oak in terms of size growth. These differences were evidenced by higher radial increment rate for pine compared to oak ($\gamma_1$ form Table 15), which could be related to species-specific growth strategies. Deeper roots and light-demanding features, typical of pioneer species, provide Scots pine the possibility to rise quickly radial increment (Sánchez-Costa et al., 2015). On the other hand, shade-tolerant oak trees utilize resources more efficiently and could result even in higher radial increment rates (Cuny et al., 2012). We theorized that lower radial increment of oak trees may be related to differences in reproduction methods (seed vs. coppice). However, in years with an average spring weather conditions, as 2016, we did not found difference on asymptote parameter between species ($\alpha_2$) and only the tree size ($\alpha_4$) and thinning treatment ($\alpha_6$) drove radial increment (Table 15). This agree with Rathgeber et al., (2011) who reported a growth advantage for dominant trees than suppressed ones producing longer cambial activity. Higher internal stem water reserves due to greater conductivity area, i.e., more water reserves stored in sapwood, may prolong radial increment for bigger trees of both species (Oberhuber et al., 2014). Anyway, former results suggest that final spring growth is similar for both species in average weather conditions, which was possible by functional divergence between co-existing species and resulting in a complementary and efficient use of resources.

However, the net effect of competition and facilitation may vary over time as we showed in year 2017. Lower precipitation in March and April (Figure 11) resulted in a higher spring asymptote for pine trees ($\alpha_3$) compared to oak for a mean diameter size (Table 15). Pine could take advantage of soil water reserves during spring droughts due leaf budburst and foliation differences: oak is still leafless in early spring and lives from the reserves of the previous year (Bauhus et al., 2017a; Fernández-De-Uña et al., 2017). Besides, as a pioneer species, pine has deeper root systems than oak, which may allow access to additional soil water resources. In this way, we hypothesized that, when oak photosynthesis begins, scarce water was available due to it was largely consumed by pine species. They could be the main reasons why spring asymptote for oak trees was lower during 2017 than 2016 for a same thinning treatment. Therefore, in drought spring years, scots pine could benefit from co-existence with oak species in a mixed forest stand. However, we expect that shallow rooting, shade tolerance and slower growth provide oak species a competitive advantage over pine in low rainy days from advanced spring when water-saturated soil is reduced just to the top soil strata. Besides, oak tree-ring width is expected to be less affected than Scots pine by summer drought because parts of the earlywood are built in early spring (Eilmann et al., 2009). Accordingly, Fernández-De-Uña et al., (2017) evidenced that xylem formation ceased 1–3 weeks earlier in Scots pine than oak during severe drought episodes. Anyway, we conjecture that, for both species, intraspecific competition would be partially liberated in mixed compared to pure stands, so spatiotemporal differences may relax resource competition. Accordingly, several studies found that in years and sites with adverse growth conditions, interspecific competition was released, resulting in lower growth reduction than in respective monospecific stands (Miren del Río et al., 2014; Grossiord et al., 2014; Pretzsch et al., 2013b).

The lack of difference in Richards shape parameter among species ($\tau_0$, Table 15) suggests a similar radial increment onset for both species, but with a hypothetical different mechanism: beginning of photosynthesis and carbohydrate reserves use for pine and oak respectively. Although Fernández-De-Uña et al., (2017) evidenced an earlier xylem formation for oak trees, we theorize that, for both species, growth was largely controlled by day length (Camarero et al., 2010) and could occur synchronized. However, growth monitoring via xilogenesis analysis should be used to confirm former hypothesis.

The influence of year on autumn asymptote ($\rho_0$ and $\rho_1$), but without significance for species, suggest a probably diameter swelling/shrinkage in absence of growth (Table 15). Accordingly, Camarero et al., (2010) and Fernández-De-Uña et al., (2017) reported that cambial reactivation, typical of Mediterranean species (Pacheco et al., 2018; Vieira et al., 2015), was absent in *P.sylvestris* and *Q.pyrenaica* respectively. Accordingly, we observed that low rain from October month (Figure 11) prolonged summer drought, and finally, diameter shrinkage for both species ($\rho_1$; Table 15). This conduct is usual in Mediterranean tree species which generally experiment seasonal stem shrinkage in response to increasing water deficit (Albuixech et al., 2012; Sánchez-Costa et al., 2015).

### *6.2.3. Temporal complementarity consequences*

Differences in radial increment onset and intra-annual cumulative patterns would indicate distinct resource use at certain periods. This intra-annual species asynchrony can be thought of as a form of temporal complementarity and reflects niche differences among species (Pretzsch and Forrester, 2017). In this regard, species interactions such as facilitation or reduced competition between species can enable the use of more site resources and with greater efficiency (Forrester, 2014). Pretzsch and Zenner (2017) found the complementary use of resources – mixing light-demanding with shade-tolerant species, deep-rooting with shallow-rooting species or evergreen with deciduous species – to be the main cause of over-yielding from mixed stands. Accordingly, evergreen and deciduous temperate tree species with different moments for leaf flush and the onset of spring growth might be dissimilarly affected by spring droughts (Bauhus et al., 2017a). Scots/maritime pine and oak seem to meet all these requirements, respectively. Pine species may have a more advantageous growth strategy, as they are fast-growing in spring time, pioneering, light-demanding and may experience autumn growth (cell enlargement or xylem differentiation for maritime pine). Growth of dominant pine trees might be accelerated permanently thanks to reduced competition from oak (the effect of a rather translucent species) or facilitation (hydraulic water redistribution), and this superiority may extend over the entire tree lifespan (Pretzsch, 2017). Intra-specific competition may be released in pine-oak mixed than in monospecific stands, resulting in more soil water availability. This leads us to suggest that shallow rooting and shade tolerance provide also oak with a competitive advantage due to temporal diversification of space occupation, which may relax resource competition via morphological and physiological trait differences.

The asynchronous growth responses of mixed tree species based on facilitation/reducing competition can also decrease abiotic stress, diminish temporal growth variation and stabilize productivity over time (del Río et al., 2017b; M del Río et al., 2014; Jucker et al., 2014). According to our results, the net effect of competition and facilitation may vary according to the climatic year conditions. Facilitation or reduce competition in pine-oak mixed is expected to occurs in drought events compared to monospecific stands.

## 6.3. Intra and inter-annual thinning effect

Our results show a positive effect of thinning on cumulative intra-annual radial increment patterns for both species affecting the amount (asymptote) of radial increment (Table 12 and 15). Although heavy thinning also seems to prolong radial increment for maritime pine (Table 12)-according to found by van der Maaten (2013) for beech-, it was lower than the sampling frequency (every two weeks), so it could not be truly verified. Heavy thinning enhanced also maritime pine increment rate in spring and in autumn, regardless of site (Table 12), which is consistent with previous thinning studies. Linares et al. (2009) and van der Maaten (2013), for example, reported that thinning provides a useful management tool for reducing stand transpiration and interception, increasing water availability and temporarily accelerating spring radial increment. On the other hand, only spring asymptote was influenced for thinning in Scots pine-oak mixed stand (Table 15).

Although moderate thinning promote also spring asymptote for maritime pine in drought site (WAI-0.65), no statistical differences were found between moderate and unthinning stands for WAI-0.22 site and for Scots pine-oak mixed stand. The lack of these differences could be related to initial tree size and competition for maritime pine (higher competition for WAI-0.22 than WAI-0.65, Table 1) or a high local tree competition where band dendrometers were installed to monitoring moderate thinning treatment in Scots pine-oak mixed stand. The thinning effect based on intra- or inter-specific tree competition may be the subject of future work.

Thinning effect was similar for Scots pine and oak species ($\alpha_6$ from Table 15), but oak trees responded slightly to thinning (regardless intensity) in mixed stands with maritime pine. The main reason for that may reside in the fact that only pine trees were removed in the thinning treatments applied. Thus, a thinning treatment that also focused on oak could enhance the growth of the remaining trees in maritime pine-oak mixed stands as we observed for Scots pine-oak mixed stand (Cañellas et al., 2004; Corcuera et al., 2006; Cotillas et al., 2009). However, selective thinning is not always successfully accomplished in oak coppice stands (Amorini et al., 1996) and is further complicated by intense root sprouting. The unknown clone factor could also mask the results of thinning on oak radial increment. Accordingly, Salomón et al., (2013) proposed thinning or clonal silvicultural treatments in managed Q.pyrenaica coppice stands, to control root aging and increase stem growth.

The small differences we observed in autumn radial increment parameters between thinning treatments for maritime pine (Table 12) suggest that, the diameter shrinkage which occurs during a relatively long summer drought, is recovered in autumn and is probably water-related. It agrees with xylem anatomy studies for maritime pine in the Iberian Peninsula (Vieira et al., 2014a, 2013), who reported that rehydration may involve mere cell enlargement rather than the differentiation of new xylem cells by the cambium in common climate conditions. The absence of species and thinning differences, but affirmative for year influence, in autumn asymptote confirms also a probably diameter variation by water-related for Scots pine-oak mixed forest.

According to the above mentioned, heavy thinning led to the greatest annual radial increment for maritime pine, regardless of site and year, albeit with clear inter-annual variation (Table 13 and Figure 21). In 2010, there was higher precipitation but a lower response to thinning at the WAI-0.22 site. This might be due to the aforementioned higher initial tree competition level for this site, which was probably reflected in greater decompensation between subterranean and aerial parts of trees in the first year after thinning, pointing to a lag in root growth response (Vincent et al., 2009).

Our results also revealed that heavy thinning had a positive effect for maritime pine – similar to that of the previous year – during the drought event, regardless of site (Table 13). These results agree with those of many other studies in confirming that increasing the availability of growing space through thinning can enhance tree resistance and resilience in terms of height, diameter, and volume growth (D'Amato et al., 2013b; Rais et al., 2014). Differences in drought resistance may be related to water availability or adjustments in water use efficiency, so an unthinned stand is more likely to be more vulnerable to drought due to higher competition (Bogino et al., 2014; J. A. Sohn et al., 2016a, 2016b; Sohn et al., 2013). Sohn et al., (2016b, 2013) found that thinning treatments also improve growth recovery following drought events, so greater drought resilience might also be expected in species subjected to heavy thinning (Magruder et al., 2013). A longer study period would be required to determine stand resilience to the extreme drought of 2012 and 2017. Besides, heavy thinning could also report some trade-offs, such as a negative effect on biomass growth at stand level or affect nutrient dynamics (Bravo-Oviedo et al., 2017; Vilà-Cabrera et al., 2018). Anyway, our results showed that the positive effect of heavy thinning identified at both mixed stands during drought episode, especially for pine species, suggests that it could provide a useful adaptation strategy for densely mixed forest stands and to released competition in dominated oak coppice trees.

# Conclusions

1. Daily radial variation cycles varied according to seasons and species for *Pinus pinaster-Quercus pyrenaica* mixed forest stands. Species-specific responses to air temperature involved amplitude differences. Precipitation and water deficit increased amplitude regardless species. Only temperature and precipitation controlled the period of radial variation cycles in the same way for both species.

2. Daily radial increment was higher for *Pinus pinaster* than *Quercus pyrenaica*, although both species responded to the same weather variables and in the similar way (linearly). Air temperature, solar radiation and precipitation raised radial increment, while water deficit and vapor pressure deficit values decreased it.

3. Species radial variation synchrony for coexisting *Pinus pinaster-Quercus pyrenaica* confirmed that both species responded to same weather conditions, involving also a possible species competition at certain periods. However, species differences on functional traits, as leaf phenology, radial increment onset or intra-annual cumulative radial increment pattern evidenced also a temporal complementarity, and hence, a feasible resources competition reduction or an increment in the efficiency to utilize them.

4. Species-specific differences on intra-annual cumulative radial increment patterns showed an obvious asynchrony of radial growth for *Pinus sylvestris-Quercus pyrenaica* mixed stand. This result suggests a species niche complementarity involving an efficient use of resources over time.

5. Heavy thinning resulted in the greatest annual radial increment for *Pinus pinaster* regardless drought episode. Besides, heavy thinning positively affected the intra-annual pattern for pine increasing spring and autumn asymptotes. Thinning treatment, independently of intensity and removing only pine trees, had also a slight positive effect on inter- and intra-annual radial increment for oak species, but not in drought conditions.

6. Only heavy thinning increased, but not prolonged, spring radial increment for both species in *Pinus sylvestris-Quercus pyrenaica* mixed forest stands regardless climatic conditions.

7. Heavy thinning and species niche complementarity from Mediterranean pine-oak mixed forest may enhance response to drought and release abiotic stress compared to monospecific stands, so they could be recommended to mitigate climate change impacts.

# Conclusiones

**1.** Los ciclos diarios de variación radial cambiaron según las estaciones y las especies para la masa mixta de *Pinus pinaster-Quercus pyrenaica*. La amplitud de los ciclos diarios varió en función de la diferente respuesta de las especie a la temperatura del aire. La precipitación y el déficit hídrico aumentaron la amplitud de la misma manera para ambas especies. Solamente la temperatura y la precipitación controlaron el período de ciclos diarios sin diferencias entre especies.

**2.** El incremento radial diario fue mayor para *Pinus pinaster* que para *Quercus pyrenaica*, aunque ambas especies respondieron a las mismas variables climáticas de forma similar (linealmente). La temperatura del aire, la radiación solar y la precipitación aumentaron el incremento radial, mientras que el déficit de agua y el déficit de presión de vapor lo disminuyeron.

**3.** La sincronía en las variaciones radiales de *Pinus pinaster* y *Quercus pyrenaica* confirmó que ambas especies respondieron a las mismas condiciones climáticas, involucrando también una posible competencia en ciertos períodos. Sin embargo, las diferencias entre especies de rasgos funcionales, como la fenología foliar, el inicio de incremento radial o el patrón intra-anual del incremento radial acumulado evidenciaron también una complementariedad temporal y, por lo tanto, una reducción de la competencia por los recursos o un incremento en la eficiencia para utilizarlos.

**4.** Las diferencias entre las especies en el patrón intra-anual del incremento radial acumulado mostraron una evidente asincronía en el incremento radial para la masa mixta de *Pinus sylvestris-Quercus pyrenaica*. Esto sugiere una complementariedad de nicho de las especies, lo que implica un uso eficiente de los recursos a lo largo del tiempo.

**5.** Las claras fuertes generaron el mayor incremento radial anual para *Pinus pinaster* independientemente del episodio de sequía. Además, afectó positivamente el patrón intra-anual del pino aumentando la asíntota de primavera y otoño. Las claras, independientemente de la intensidad y con la única eliminación de los pinos, también tuvo un ligero efecto positivo en el incremento radial inter e intra-anual para el rebollo, pero no en las condiciones de sequía.

**6.** Solamente las claras fuertes aumentaron, pero no prolongaron, el incremento radial de primavera para ambas especies en masas mixtas de *Pinus sylvestris-Quercus pyrenaica,* independientemente de las condiciones climáticas.

**7.** Las claras fuertes y la complementariedad en el crecimiento de las especies que conforman las masas mixtas de pino y rebollo en ambiente Mediterráneo, pueden mejorar la respuesta a la sequía y liberar estrés abiótico en comparación con las masas monoespecíficas, por lo que podrían recomendarse para mitigar los impactos del cambio climático.

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# Appendix A: Supplementary Figures

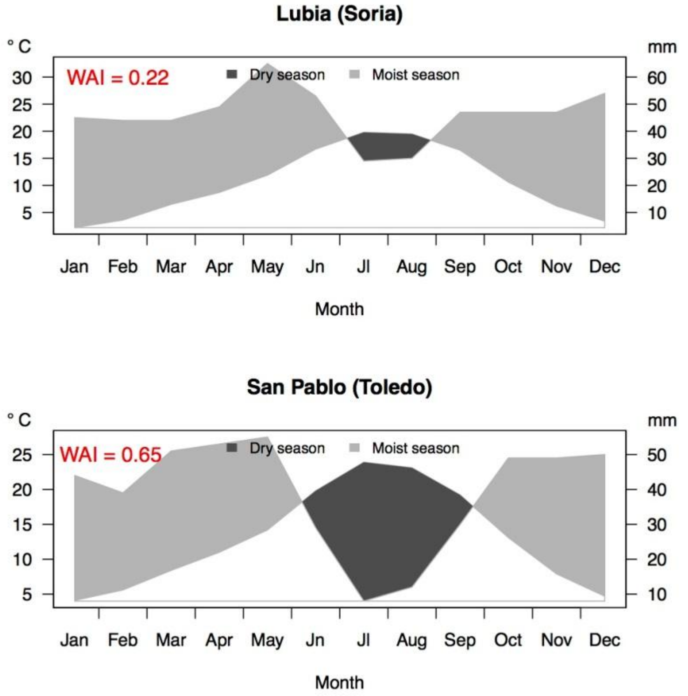

*Figure S1. Walter-Lieth annual aridity index (WAI), defined as the quotient between the dry and wet season areas, based on historical climate records (1981-2010) for the sampling sites. The figure and the WAI index were calculated using BIOdry software (Lara et al., 2013).*

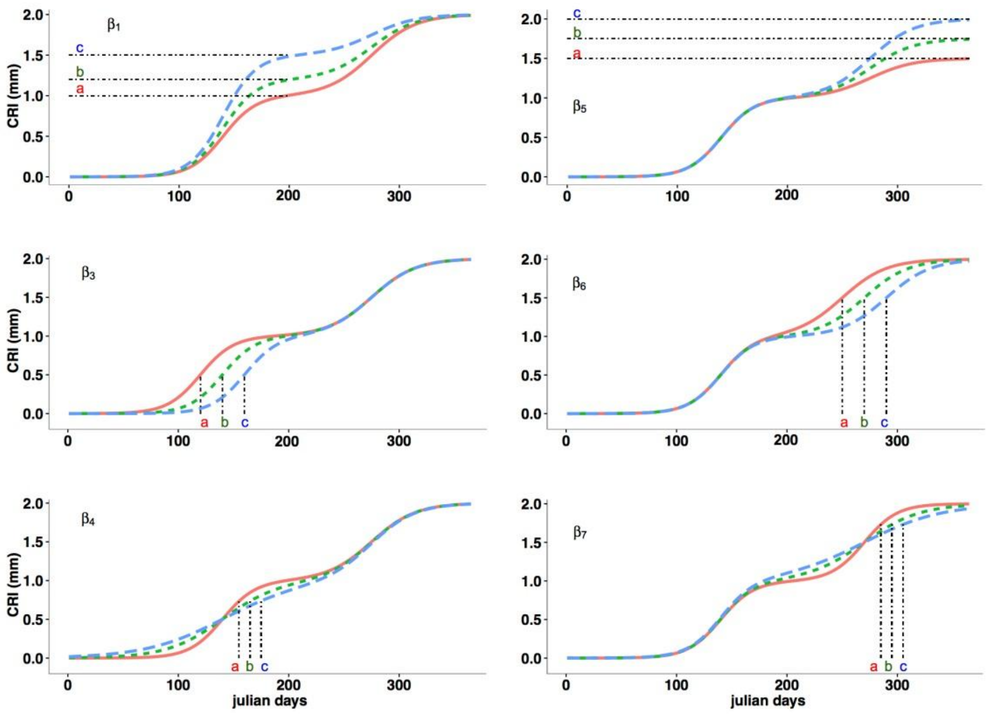

*Figure S2. Shift value display in parameter (a<b<c) for bi-logistic model (Eq.3 and 4).* $\beta_2$ *shift values denote the null initial asymptote and therefore are not shown. For further information, see Pinheiro and Bates (2000).*

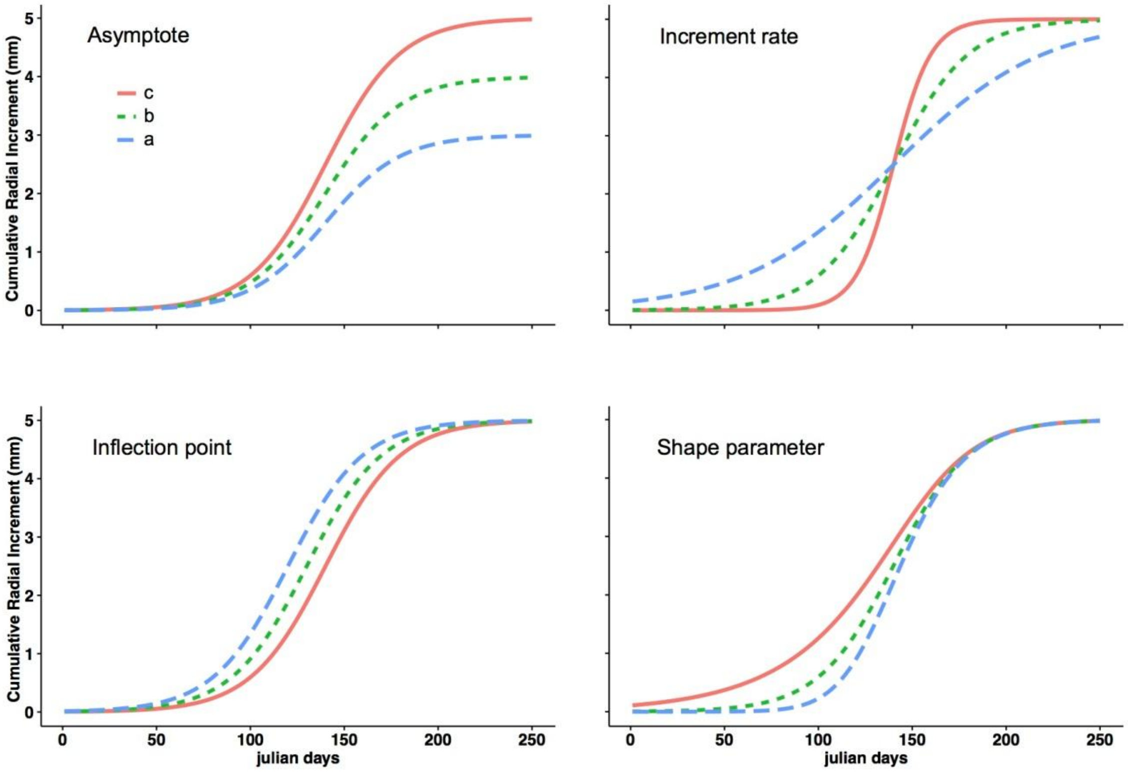

*Figure S3. Shift value display in parameter (a<b<c) for the single Richards model (Eq.5).*

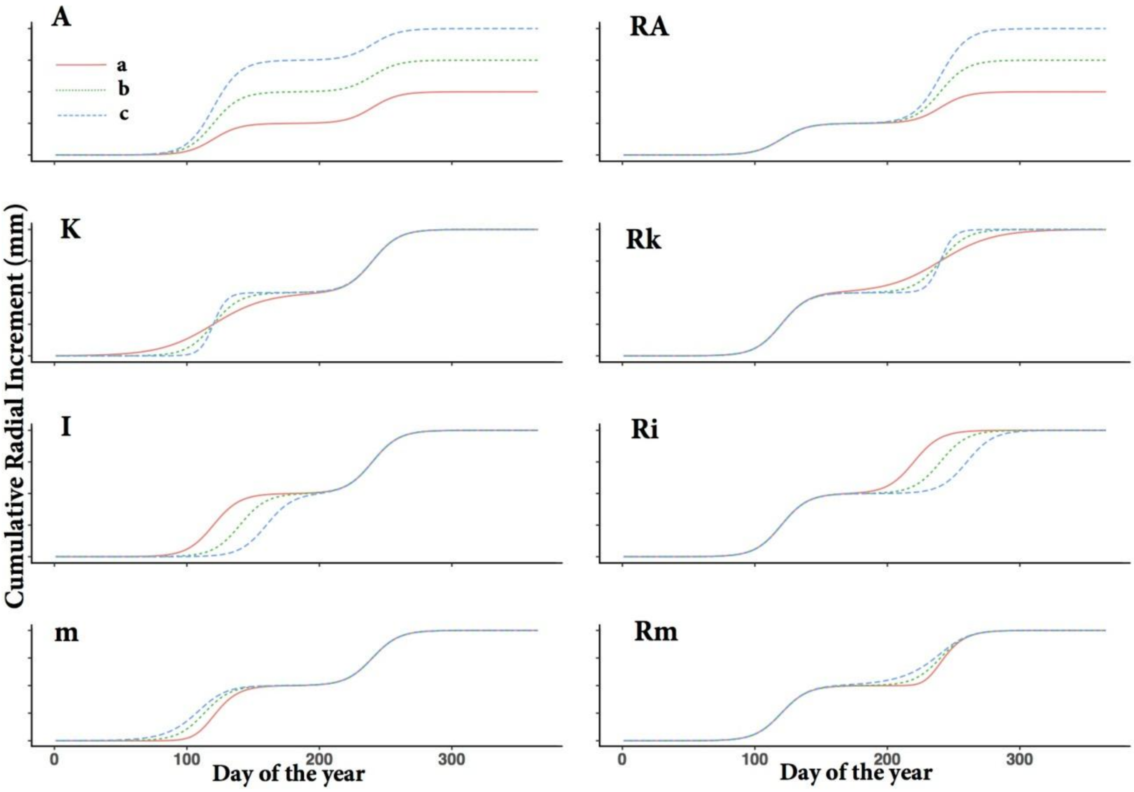

*Figure S4. Shift value display in parameter (a<b<c) for the double-Richards model (Eq.6).*

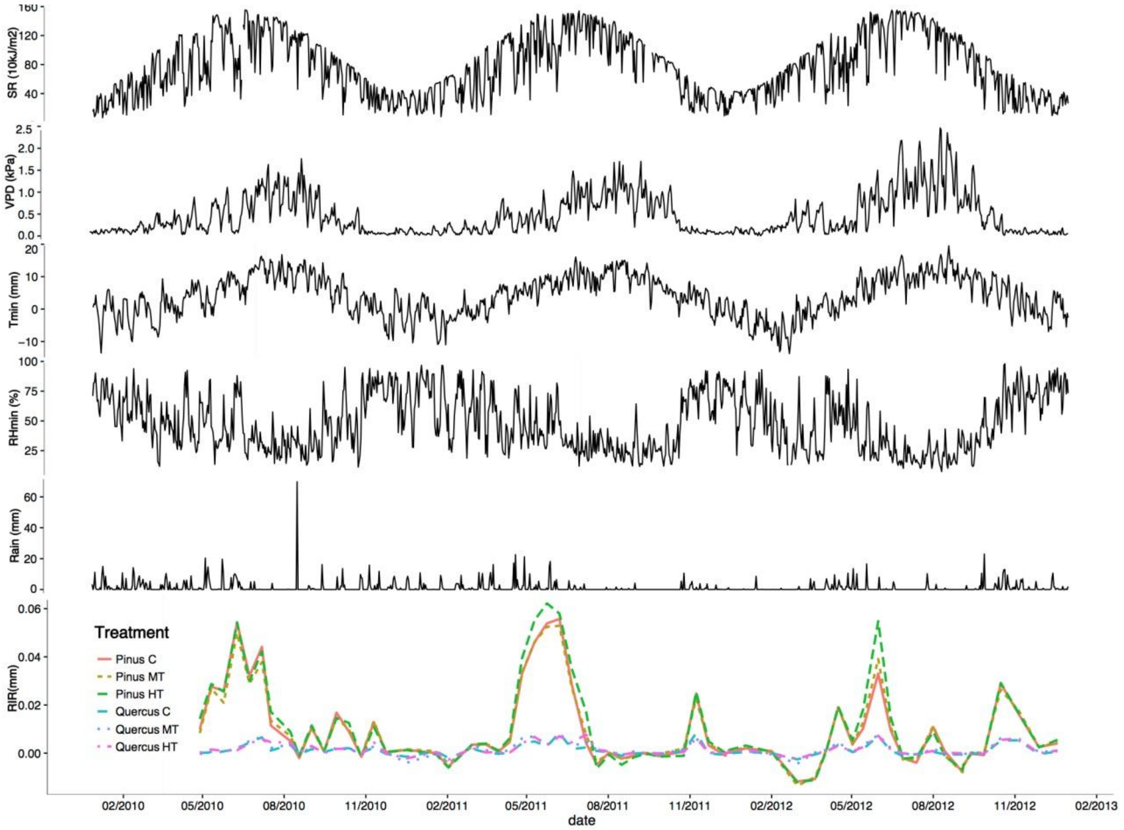

*Figure S5. Solar radiation (10kj/m²), vapor pressure deficit(kPa), minimum air temperature (ºC), minimum relative humidity (%), rain (mm) and mean radial increment rate (mm) by treatment and species in WAI-0.22 site.*

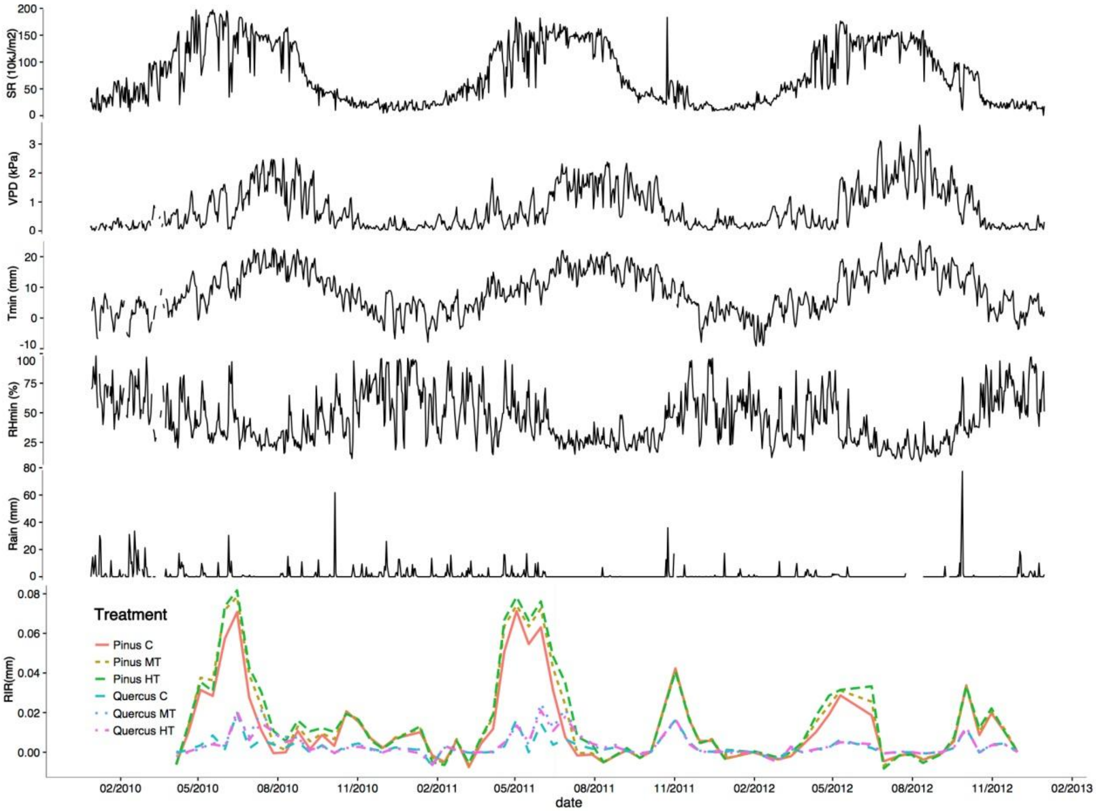

*Figure S6. Solar radiation (10kj/m2), vapor pressure deficit(kPa), minimum air temperature (ºC), minimum relative humidity (%), rain (mm) and mean radial increment rate (mm) by treatment and species in WAI-0.65 site.*

# Appendix B: Supplementary Tables

*Table S1. Bi-logistic model fitted for intra-annual cumulative radial increment for maritime pine-oak mixed forest by site and thinning treatment (Eq. 4). Significance level is as follow: ‘’ <0.001, ‘*’ <0.01, ‘**’ <0.05.*

| | | WAI-0.22 | | | WAI-0.65 | | |
|---|---|---|---|---|---|---|---|
| **Species** | **Parameter** | **A treat.** | **D treat.** | **E treat.** | **A treat.** | **D treat.** | **E treat.** |
| *P.pinaster* | $\boldsymbol{\beta_1}$ | 1.581$^{*}$ | 1.581 | 2.098 | 2.308 | 2.867 | 3.184 |
| | $\boldsymbol{\beta_2}$ | - 0.0328 | -0.0528 | -0.0253 | 0.0633 | 0.0601 | 0.0455 |
| | $\boldsymbol{\beta_3}$ | 142.333 | 143.618 | 144.157 | 140.528 | 142.172 | 142.928 |
| | $\boldsymbol{\beta_4}$ | 16.271 | 13.973 | 13.842 | 19.204 | 17.349 | 15.080 |
| | $\boldsymbol{\beta_5}$ | 2.069 | 2.073 | 2.703 | 2.868 | 3.594 | 3.976 |
| | $\boldsymbol{\beta_6}$ | 269.335 | 284.969 | 285.014 | 271.508 | 272.277 | 273.701 |
| | $\boldsymbol{\beta_7}$ | 27.918 | 17.528 | 15.943 | 16.905 | 21.643 | 14.755 |
| | $\boldsymbol{\sigma_k}$(year) | 0.728 | 0.690 | 0.657 | 0.549 | 0.550 | 0.914 |
| | $\boldsymbol{\sigma_{jk}}$(plot) | 0.169 | 0.00108 | $1.16 \cdot 10^{-4}$ | 0.257 | 0.329 | $4.64 \cdot 10^{-4}$ |
| | $\boldsymbol{\sigma_{ijk}}$(tree) | 0.712 | 0.596 | 0.670 | 0.504 | 0.517 | 0.868 |
| | $\boldsymbol{\sigma_e}$(error) | 0.0822 | 0.429 | 0.155 | 0.295 | 0.350 | 0.00494 |
| | $\boldsymbol{\delta_1}^{*}$ | 1.246 | - | 0.580 | - | - | 1.517 |
| | $\boldsymbol{\delta_2}^{*}$ | 1.256 | - | 0.766 | - | - | 0.847 |
| *Q.pyrenaica* | $\boldsymbol{\beta_1}$ | 0.362 | 0.351 | 0.372 | 0.353 | 0.456$^{**}$ | 0.479$^{*}$ |
| | $\boldsymbol{\beta_2}$ | -0.00103 | -0.0126$^{**}$ | -0.0108$^{**}$ | -0.0688 | -0.0358 | -0.137 |
| | $\boldsymbol{\beta_3}$ | 158.050 | 154.981 | 158.660 | 153.803 | 134.597$^{**}$ | 157.655 |
| | $\boldsymbol{\beta_4}$ | 19.229 | 23.762 | 23.595 | 20.077 | 12.400 | 21.839 |
| | $\boldsymbol{\beta_5}$ | 0.384 | 0.448 | 0.475 | 0.783 | 1.150 | 1.392 |
| | $\boldsymbol{\beta_6}$ | 293.703 | 325.002 | 317.600 | 326.000 | 292.690 | 283.090 |
| | $\boldsymbol{\beta_7}$ | 15.499 | 40.631 | 21.098 | 44.121 | 49.637 | 59.093 |
| | $\boldsymbol{\sigma_k}$(year) | $3.02 \cdot 10^{-5}$ | 0.0689 | 0.0433 | 0.143 | 0.285 | 0.221 |
| | $\boldsymbol{\sigma_{jk}}$(plot) | 0.0418 | 0.0940 | $2.51 \cdot 10^{-5}$ | 0.0785 | 0.211 | 0.178 |
| | $\boldsymbol{\sigma_{ijk}}$(tree) | 0.218 | 0.117 | 0.192 | 0.219 | 0.494 | 0.465 |
| | $\boldsymbol{\sigma_e}$(error) | 0.109 | 0.0562 | 0.0629 | 0.0709 | 0.0296 | 0.107 |
| | $\boldsymbol{\delta_1}^{*}$ | 0.260 | - | - | - | 2.553 | - |
| | $\boldsymbol{\delta_2}^{*}$ | 0.615 | - | - | - | 3.958 | - |

*Variance function parameter used to model variance residual structure to correct heterocedasticity as constant plus a power of the absolute value of the variance covariate ($|\boldsymbol{g_{ijk}}|$, fitted model values): $\boldsymbol{Var}(\boldsymbol{\varepsilon}_{\mathbf{ijk}}) = \boldsymbol{\sigma_e}\,(\boldsymbol{\delta_1} + |\boldsymbol{g_{ijk}}|^{\boldsymbol{\delta_2}}$

# Appendix C: Statistical Scripts Summary

All the statistical analyses of present study were performed using the R statistical software (R Development Core Team, 2017). The R packages used in relation to statistical methods and thesis objectives were summarized in Table 6. This section summarizes the main scripts developed in methodological section that I hope will be useful to future readers.

**1. Species differences in spring radial increment onset ----------------------------**

```
library(nparcomp)
data(onset)

sp_dif<-npar.t.test(DOY~Species, data = onset, method = "permu",
alternative="two.sided", info=T)
summary(sp_dif)
plot(sp_dif)
```

**2. Daily stem radial variation cycle analysis -----------------------------------------**

```
require(dendrometeR)
data(dmSoria)

###Check input data

is.dendro(dmSoria)

###Phases definition

dm.phase <- phase_def(dmSoria, resolution = dendro.resolution(dmSoria),
                shapeSensitivity = 0.6, minmaxDist = 0.2, minmaxSD = 2,
                radialIncrease = "max")

###Cycle statistic for sensor 1

dm.stats <- cycle_stats(dmSoria, dm.phase,sensor = 1, smooth.param = 1)

### Linking weather variables with phases of sensor 1

data(envED)
clim.phase <- climate_seg(envED, dm.stats, value = "mean")
summary(clim.phase)
```

**3. Weather effect on amplitude of daily radial variation cycle (Eq. 1)--------------**

```
require(nlme)
library(faraway)
data(data_A)

###Linear model solution and multicollinearity control
```

```
lm0<-lm(log(magnitude+1)~(Tair+log(Tair+5)+RH+SR+Wd+VPD+P)*Species,
data=na.omit(data_A))
vif(lm0)
stepAIC(lm0)
###Random effect structure for linear mixed model

lme1<-lme(log(magnitude+1)~(Tair+log(Tair+5)+SR+Wd+VPD+P)*Species,
random=~1|Site,method="REML",data=na.omit(data_A))
lme2<-lme(log(magnitude+1)~(Tair+log(Tair+5)+SR+Wd+VPD+P)*Species,
random=~1|dmID,method="REML",data=na.omit(data_A))
lme3<-lme(log(magnitude+1)~(Tair+log(Tair+5)+SR+Wd+VPD+P)*Species,
random=~1|Year,method="REML",data=na.omit(data_A))
lme4<-lme(log(magnitude+1)~(Tair+log(Tair+5)+SR+Wd+VPD+P)*Species,
random=~1|Site/dmID,method="REML",data=na.omit(data_A))
lme5<-lme(log(magnitude+1)~(Tair+log(Tair+5)+SR+Wd+VPD+P)*Species,
random=~1|Year/Site,method="REML",data=na.omit(data_A))
lme6<-lme(log(magnitude+1)~(Tair+log(Tair+5)+SR+Wd+VPD+P)*Species,
random=~1|Year/Site/dmID,method="REML",data=na.omit(data_A))
anova(lme1,lme2,lme3,lme4,lme5,lme6)


###Fixed effect structure for linear mixed model

lme7<-lme(log(magnitude+1)~(Tair+log(Tair+5)+SR+Wd+VPD+P)*Species-
1,random=~1|Year/Site/dmID,,method="ML",data=na.omit(data_A))
stepAIC(lme7)
summary(lme7)

###Solve final linear mixed model

lme7<-lme(log(magnitude+1)~(Tair+log(Tair+5))*Species+Wd+P,
random=~1|Year/Site/dmID,method="ML",data=na.omit(data_A))
summary(lme7)

###Autocorrelation correction

plot(ACF(lme7), maxLag = 15, alpha = 0.05)
acf(residuals(lme7, retype="normalized"))
pacf(residuals(lme7, retype="normalized"))
ModA1 <- update(lme7, corr = corARMA(p=1, q=1) )
ModA2 <- update(lme7, corr = corARMA(p=1, q=2) )
ModA3 <- update(lme7, corr = corARMA(p=2, q=1) )
ModA4<- update(lme7, corr = corARMA(p=1, q=0) )
ModA5 <- update(lme7, corr = corARMA(p=0, q=1) )
AIC(ModA1,ModA2,ModA3,ModA4,ModA5)
anova(ModA1,ModA2,ModA3,ModA4,ModA5)
summary(ModA1)


###Heteroscedasticity correction

plot(ModA1, resid(.) ~fitted(.), abline = 0)
plot(ModA1, resid(.) ~fitted(.)|dmID, abline = 0)
```

```
hist(resid(ModA1), main="Histogram of residuals", xlab="Residuals",col="blue")
qqnorm(resid(ModA1))
ModF1 <- update(ModA1, weights = varPower(form = ~ fitted(.)))
ModF2 <- update(ModA1, weights = varConstPower(form=~fitted(.)))
ModF3 <- update(ModA1, weights = varExp(form=~fitted(.)))
anova(ModF1,ModF2,ModF3)
summary(ModF3)
```

## 4. Radial variation synchrony ------------------------------------------------------------

```
library(synchrony)

###Data construction

pinemean<-rowMeans(subset(pine, select = c(incrementT1, incrementT2,incrementT3)),
na.rm = FALSE)
aokmean<-rowMeans(subset(oak, select = c(incrementT4, incrementT5, incrementT6)),
na.rm = FALSE)
pineoak<-cbind(pinemean,oakmean)

###Synchrony metrics

        #Mean correlation coefficient

meancorr(data=na.omit(pineoak),nrands=999,alternative="two.tailed",type=2,quiet=T)

        # Kendall's W non-parametric statistic (Legendre, 2005)

kendall.w(data= na.omit(pineoak),nrands=999,type=2, quiet= TRUE)

        # Loreau and de Mazancourt (2008) metric

community.sync(data=na.omit(pineoak),nrands=999,alternative="greater",type=1,quiet=T)

        # Concurrency (Buonaccorsi et al., 2001)

peaks(pineoak[,1],pineoak[,2],nrands=999,type= 2,quiet=TRUE)

        # Phase synchrony (Cazelles and Stone, 2003)

fase<-phase.sync(pineoak[,1],pineoak[,2],nrands=999,quiet=TRUE)
fase$Q.obs
fase$pval
```

## 5. Intra-annual cumulative radial increment analysis---------------------------------

### 5.1. Bi-logistic model (Eq.4)--------------------------------------------------

```
library(nlme)
library(faraway)


###Data construction

C_P_L<-subset(dat,data$Treat=="Control" & data$Species == "P.pinaster" & data$Site
== "Lubia")
Newdata<- groupedData( CRI ~ Date |year/plot/tree,data = C_P_L)
```

```
###Construction of bi-logistic function

bilogist <- deriv( ~a1+(a2-a1)/(1 + exp(-(a3-x)/a4))+(a5-a1)+(a1-a5)/(1 + exp(-(a6-x)/a7)),c("a1", "a2", "a3","a4", "a5", "a6","a7"), function(x, a1, a2, a3,a4,a5,a6,a7){} )

###Solve bi-logistic mixed model

CPL<-nlme( CRI ~ bilogist(Date,a1,a2,a3,a4,a5,a6,a7),data = Newdata,
fixed=a1+a2+a3+a4+a5+a6+a7 ~ 1,
random = a1 ~ 1,
start = c(a1=0.7,a2=-0.1,a3=145,a4=10,a5=1.35,a6=250,a7=15),
control=c(maxIter = 10000, pnlsMaxIter=1000, msMaxIter=1000, niterEM=50,
pnlsTol=5, tol = 1e-05, minFactor = 1/100000000),
weights = varConstPower(form=~Date)  )
intervals(CPL)
summary(CPL)
```

### 5.2. Single Richards model for spring period (Eq.5)-----------------------

```
library(nlme)
library(FlexParamCurve)
data(springdata)

###Data construction

Gt<- na.omit(groupedData(increment ~ doy|tree, data=springdata))

###Seed parameters estimation

modpar(Gt$doy, Gt$increment,force4par = TRUE,pn.options = "myoptions.spring")
startval <- c(0.7686947,1.7370271,1.7960807,2.197302,0.04031, 0.00401,143.3135,0, 0.26092,0)

###Solve single Richards mixed model with fixed effects

springRichards<-nlme(model = increment ~ SSposnegRichards(Doy, Asym = Asym,
K = K, Infl = Infl,M = M, modno =12,pn.options = "myoptions.spring"), data = Gt,
        random =Asym+Infl~1|site/tree,
        fixed = list(Asym~year+species, K~species, Infl~species, M~species),
        start =list(fixed=c(startval)),na.action = na.exclude)
summary(springRichards)
plot(springRichards)
```

### 5.3. Double Richards model (Eq.6)----------------------

```
library(nlme)
library(FlexParamCurve)

###Data construction

data(datanual)
G<-groupedData(increment ~ doy|tree,data=datanual)

###Seed parameters estimation

modpar(G$doy, G$increment,pn.options = "myoptions")

###Model selection

compar1 <- pn.mod.compare(G$doy, G$increment,
                G$tree, existing = FALSE, pn.options = "myoptions")
compar2 <- pn.modselect.step(G$doy, G$increment,
                G$tree, existing = FALSE, pn.options = "myoptions")

###Solve double-Richards mixed model with fixed effects and covariates

startval <- c(0.71977,0,0,0,0,0,0,0.05531,0,146.98231,0,1.10116,0.34679,0)
MdR<-nlme(model = increment ~ SSposnegRichards(doy, Asym = Asym, K = K, Infl =
Infl,M = M, RAsym = RAsym,
modno =11,pn.options = "myoptions"), data = G,
random =Asym~1|plot/tree,
fixed = list(Asym~dbh+treat+species*year, K~species, Infl~species, M~1,RAsym~year),
start =list(fixed=c(startval)),na.action = na.exclude)
summary(MdR)

###Heteroscedasticity correction

plot(MdR)
qqnorm(MdR)
ModA1 <- update(MdR, weights = varPower(form=~fitted(.)))
ModA2 <- update(MdR, weights = varConstPower(form=~fitted(.)))
ModA3 <- update(MdR, weights = varExp(form=~fitted(.)))
anova(MdR,ModA1,ModA2,ModA3)
summary(ModA1)

###Autocorrelation correction

acf(residuals(ModA1, retype="normalized"))
pacf(residuals(ModA1, retype="normalized"))
ModA1c <- update(ModA1, corr = corARMA(p=1, q=0) )
ModA2c <- update(ModA1, corr = corARMA(p=1, q=1) )
```

```
ModA3c <- update(ModA1, corr = corARMA(p=0, q=1) )
anova(ModA1c,ModA2c,ModA3c)
summary(ModA3c)
```

## 6. Thinning and weather influence on radial increment rate (Eq2)---------------------

```
require(nlme)
library(faraway)
data(rate_QLubia)

###Linear model solution and multicollinearity control

lm0<-lm(rate~Treat+dbh+Tmin+RHmin+SR+VPD+P,data=na.omit(rate_QLubia))
vif(lm0)
stepAIC(lm0)

###Random effect structure for linear mixed model

lme1<-lme(rate~Treat+dbh+Tmin+RHmin+SR+VPD+P,random=~1|year,
method="REML",data=na.omit(rate_QLubia))
lme2<-lme(rate~Treat+dbh+Tmin+RHmin+SR+VPD+P,random=~1|plot,
method="REML",data=na.omit(rate_QLubia))
lme3<-lme(rate~Treat+dbh+Tmin+RHmin+SR+VPD+P,random=~1|tree,
method="REML",data=na.omit(rate_QLubia))
lme4<-lme(rate~Treat+dbh+Tmin+RHmin+SR+VPD+P,random=~1|plot/tree,
method="REML",data=na.omit(rate_QLubia))
lme5<-lme(rate~Treat+dbh+Tmin+RHmin+SR+VPD+P,random=~1|year/plot,
method="REML",data=na.omit(rate_QLubia))
lme6<-lme(rate~Treat+dbh+Tmin+RHmin+SR+VPD+P,random=~1|year/plot/tree,
method="REML",data=na.omit(rate_QLubia))
anova(lme1,lme2,lme3,lme4,lme5,lme6)

###Fixed effect structure for linear mixed model

lme7<-lme(rate~Treat+dbh+Tmin+RHmin+SR+VPD+P,random=~1|year/plot/tree,
method="ML",data=na.omit(rate_QLubia))
stepAIC(lme7)
summary(lme7)

###Solve final linear mixed model

lmeF<-lme(rate~Treat+dbh+Tmin+RHmin+SR+VPD+P,random=~1|year/site/tree,
method="ML",data=na.omit(rate_QLubia))
summary(lmeF)
```

# Appendix D: Peer-reviewed articles

This thesis is based on three original works published or under revision in different international journals and one manuscript in preparation. These manuscripts are the following:

Aldea, J., Bravo, F., Bravo-Oviedo, A., Ruiz-Peinado, R., Rodríguez, F., Del Río, M., 2017. Thinning enhances the species-specific radial increment response to drought in Mediterranean pine-oak stands. Agric. For. Meteorol. 237, 371–383. doi:10.1016/j.agrformet.2017.02.009

Aldea, J., Bravo, F., Vázquez-Piqué, J., Rubio-Cuadrado, A., Del Río, M., 2018. Species-specific weather response in the daily stem variation cycles of Mediterranean pine-oak mixed stands. Agric. For. Meteorol. 256-257, 220–230. doi:10.1016/j.agrformet.2018.03.013

Aldea, J., Bravo, F., Vázquez-Piqué, J., Ruiz-Peinado, R., del Río, M., 2018. Intra-annual radial increment of Mediterranean pine-oak mixed stands: species-specific but synchronized patterns. Eur. J. For. Res. Under review.

Aldea, J., Bravo, F., del Río, M., 2018. Drought and thinning effect on species with different growth strategies: example of a Mediterranean Scots pine-oak mixed stand based on intra-annual cumulative radial increment patterns. In preparation.