Universidad
de Alcalá
COMISIÓN DE ESTUDIOS OFICIALES
DE POSGRADO Y DOCTORADO

ACTA DE EVALUACIÓN DE LA TESIS DOCTORAL

Año académico 2018/19

DOCTORANDO: **DIOS GARCÍA, JAVIER DE**
D.N.I./PASAPORTE: ******6186F**

PROGRAMA DE DOCTORADO: **D413-ECOLOGÍA. CONSERVACIÓN Y RESTAURACIÓN DE ECOSISTEMAS**
DPTO. COORDINADOR DEL PROGRAMA: **CIENCIAS DE LA VIDA**
TITULACIÓN DE DOCTOR EN: **DOCTOR/A POR LA UNIVERSIDAD DE ALCALÁ**

En el día de hoy 12/07/19, reunido el tribunal de evaluación nombrado por la Comisión de Estudios Oficiales de Posgrado y Doctorado de la Universidad y constituido por los miembros que suscriben la presente Acta, el aspirante defendió su Tesis Doctoral, elaborada bajo la dirección de **RAFAEL CALAMA SAINZ // MARTA PARDOS MÍNGUEZ.**

Sobre el siguiente tema: *ESTUDIO DE LAS MASAS MIXTAS DE PINUS PINEA L. EN LA MESETA NORTE. CRECIMIENTO Y DINÁMICA EN UN CONTEXTO DE CAMBIO GLOBAL*

Finalizada la defensa y discusión de la tesis, el tribunal acordó otorgar la CALIFICACIÓN GLOBAL[1] de (**no apto, aprobado, notable y sobresaliente**): Sobresaliente

Alcalá de Henares, 12 de julio de 2019

EL PRESIDENTE

Fdo.: LLUÍS COLL MIR

EL SECRETARIO

Natalia

Fdo.: NATALIA VIZCAÍNO PALOMAR

EL VOCAL

Fdo.: MIREN DEL RÍO GAZTELURRUTIA

Con fecha 24 de Julio de 2019 la Comisión Delegada de la Comisión de Estudios Oficiales de Posgrado, a la vista de los votos emitidos de manera anónima por el tribunal que ha juzgado la tesis, resuelve:

☐ Conceder la Mención de "Cum Laude"
☒ No conceder la Mención de "Cum Laude"

La Secretaria de la Comisión Delegada

FIRMA DEL ALUMNO,

Javier de Dios

Fdo.: DIOS GARCÍA, JAVIER DE

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[1] La calificación podrá ser "no apto" "aprobado" "notable" y "sobresaliente". El tribunal podrá otorgar la mención de "cum laude" si la calificación global es de sobresaliente y se emite en tal sentido el voto secreto positivo por unanimidad.

INCIDENCIAS / OBSERVACIONES: Nada que reseñar

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Y TRANSFERENCIA

En aplicación del art. 14.7 del RD. 99/2011 y el art. 14 del Reglamento de Elaboración, Autorización y Defensa de la Tesis Doctoral, la Comisión Delegada de la Comisión de Estudios Oficiales de Posgrado y Doctorado, en sesión pública de fecha 24 de julio, procedió al escrutinio de los votos emitidos por los miembros del tribunal de la tesis defendida por ***DIOS GARCÍA, JAVIER DE***, el día 12 de julio de 2019, titulada *ESTUDIO DE LAS MASAS MIXTAS DE PINUS PINEA L. EN LA MESETA NORTE. CRECIMIENTO Y DINÁMICA EN UN CONTEXTO DE CAMBIO GLOBAL*, para determinar si a la misma se le concede la mención "cum laude", no habiendo obtenido la unanimidad de los miembros del Tribunal.

Por lo tanto, la Comisión de Estudios Oficiales de Posgrado y Doctorado **resuelve no otorgar la Mención de "cum laude"** a dicha Tesis.

EL VICERRECTOR DE INVESTIGACIÓN Y TRANSFERENCIA
F. Javier de la Mata de la Mata
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Copia por e-mail a:
Doctorando: DIOS GARCÍA, JAVIER DE
Secretario del Tribunal: NATALIA VIZCAÍNO PALOMAR
Director/a de Tesis: RAFAEL CALAMA SAINZ//MARTA PARDOS MÍNGUEZ

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DILIGENCIA DE DEPÓSITO DE TESIS.

Comprobado que el expediente académico de D./Dª Javier de Dios García reúne los requisitos exigidos para la presentación de la Tesis, de acuerdo a la normativa vigente, y habiendo presentado la misma en formato: ☒ soporte electrónico ☐ impreso en papel, para el depósito de la misma, en el Servicio de Estudios Oficiales de Posgrado, con el nº de páginas: 250 se procede, con fecha de hoy a registrar el depósito de la tesis.

Alcalá de Henares a 17 de mayo de 2019

Aurora Juárez Abril

Fdo. El Funcionario

Universidad de Alcalá

Programa de Doctorado en Ecología, conservación y restauración de ecosistemas

ESTUDIO DE LAS MASAS MIXTAS DE *PINUS PINEA* L. EN LA MESETA NORTE. CRECIMIENTO Y DINÁMICA EN UN CONTEXTO DE CAMBIO GLOBAL

Tesis Doctoral presentada por

JAVIER DE DIOS GARCÍA

Director/a: DR. RAFAEL CALAMA
Co-directora: DRA. MARTA PARDOS

Alcalá de Henares, 2019

GOBIERNO
DE ESPAÑA

MINISTERIO
DE CIENCIA, INNOVACIÓN
Y UNIVERSIDADES

INIA
Instituto Nacional de Investigación
y Tecnología Agraria y Alimentaria

Dña. Marta Pardos Mínguez y D. Rafael Calama Sainz, Científicos Titulares en el Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria, como codirectores de esta Tesis Doctoral,

Hacen constar:

Que el trabajo descrito en la presente memoria, titulado "**Estudio de las masas mixtas de *Pinus pinea* L. en la Meseta Norte. Crecimiento y dinámica en un contexto de cambio global**", ha sido realizado por Javier de Dios García bajo su dirección en el Centro de Investigación Forestal (INIA-CIFOR), dentro del Programa de Doctorado "Ecología, Conservación y Restauración de Ecosistemas" (D330), reuniendo todos los requisitos necesarios para su aprobación como Tesis Doctoral.

Madrid, 7 de mayo de 2019

Marta Pardos

Rafael Calama Sainz

Marta Pardos Minguez

Universidad
de Alcalá

UNIVERSIDAD DE ALCALÁ. PATRIMONIO DE LA HUMANIDAD

D. MIGUEL ÁNGEL DE ZAVALA GIRONÉS, Catedrático del Departamento de Ciencias de la Vida de la Universidad de Alcalá y tutor de esta Tesis Doctoral,

HACE CONSTAR:

Que el trabajo descrito en la presente memoria, titulado "**Estudio de las masas mixtas de *Pinus pinea* L. en la Meseta Norte. Crecimiento y dinámica en un contexto de cambio global**", ha sido realizado por Javier de Dios García en el Centro de Investigación Forestal (INIA-CIFOR) bajo su tutorización en el Departamento de Ciencias de la Vida de la UAH, dentro del Programa de Doctorado "Ecología. Conservación y Restauración de Ecosistemas" (D330), reuniendo todos los requisitos necesarios para su aprobación como Tesis Doctoral.

Para que así conste y surta los efectos oportunos, se firma el presente informe en Alcalá de Henares a 07 de Mayo de 2019.

Miguel A Zaval

Universidad
de Alcalá

UNIVERSIDAD DE ALCALÁ, PATRIMONIO DE LA HUMANIDAD

D. MIGUEL ÁNGEL DE ZA VALA GIRONÉS, Coordinador de la Comisión Académica del Programa de Doctorado en ECOLOGÍA, CONSERVACIÓN Y RESTAURACIÓN DE ECOSISTEMAS,

INFORMA que la Tesis Doctoral titulada “Estudio de las masas mixtas de *Pinus pinea* L. en la Meseta Norte. Crecimiento y dinámica en un contexto de cambio global”, presentada por D/Dª JAVIER DE DIOS GARCÍA, bajo la dirección del / de la Dr/a. Marta Pardos y Rafael Calama, reúne los requisitos científicos de originalidad y rigor metodológicos para ser defendida ante un tribunal. Esta Comisión ha tenido también en cuenta la evaluación positiva anual del doctorando, habiendo obtenido las correspondientes competencias establecidas en el Programa.

Para que así conste y surta los efectos oportunos, se firma el presente informe en Alcalá de Henares a 07 de Mayo de 2019.

Fdo.: Miguel Ángel de Zavala Gironés

Agradecimientos

Quiero empezar este apartado agradeciendo a mis directores de tesis, Rafa y Marta por darme la oportunidad de hacer la tesis con vosotros en un momento de crisis económica brutal. Gracias a vosotros para mí se abrió una ventana al mundo de la ciencia. Sobre todo, quiero agradeceros a los dos vuestra implicación en esta última fase de la tesis, mandándome vuestros comentarios hasta en los fines de semana y los puentes que creo que han mejorado mucho este trabajo. Y en concreto quiero darle las gracias a Rafa Calama porque siento que sin ti esta tesis no habría salido adelante y me has demostrado todos estos años que en los momentos críticos siempre estás.

También quiero dar las gracias a Javier Gordo por todo el apoyo que nos diste para montar los dispositivos experimentales en El Carrascal. A Guille, Quique y Mar por acompañarme en un montón de viajes a El Carrascal y a las parcelas de las garrapatas y por ocuparos del trabajo de campo en todas las estancias que he hecho. A Quique en particular sabes que te tengo un gran aprecio personal y quiero agradecerte todo el trabajo en la sombra que haces. Digo en la sombra porque considero que haces un gran trabajo montando y lijando los cores y las rodajas y porque gran parte de los trabajos de dendro que salen en el Inia salen gracias a tu labor, que en mi opinión no es suficientemente reconocida.

A Rubén y Mathieu. Tengo un gran recuerdo de la estancia que hice con vosotros en Nancy. Sin duda ha sido la estancia predoctoral más provechosa de las que he hecho y eso fue gracias a vosotros. Recuerdo con mucho cariño la excursión a los Vosgos que organizaste Rubén, con Nacho, Marta y Leti. Creo que además de ser un gran investigador, que arrimas el hombro en todo lo que hace falta, eres una excelente persona y da gusto poder contar contigo.

A Richard Kobe y a Valerie Lemay quiero darles las gracias por acogerme en sus laboratorios de la MSU y UBC. A Richard por enseñarme a ser crítico con los artículos que leo y por hacerme ver que un Nature, un Ecology o un PNAS son trabajos igualmente criticables. Espero que pronto el trabajo que empezamos juntos se vea reconocido. De Valerie no olvidaré nunca tu consejo el primer día de mi estancia en Vancouver con Giulia que nos dijiste cómo protegernos de pumas, osos grizzlies y coyotes y que sin duda fue determinante para pasarme el primer finde de Vancouver encerrado en St. John's College.

De la gente del INIA sóis muchísima buena gente los que habéis pasado por aquí y que aún no he nombrado y pido disculpas de antemano de los que me pueda olvidar. Alicia, Carolina, Dani, Maria Jo, Edu, Jose Pablo, Raquel, Mario, Ana, César, Quique, Katha, Gregor, Mario, Natalia, Ruth, Isa, Luis, Marina, Maje, las Lauras Hernández y Fernández, Itziar, Álvaro, Marta Vergarechea, Antonio, Nerea, Macarena e Isa. Gracias a vosotros el INIA ha sido un sitio mejor para trabajar y no olvidaré nunca las galletas caseras de Gregor, las decoraciones de las tartas de las tesis, el concurso de postres, el de tortillas de patata y el reparto de naranjas en el parking del INIA.

A mis compis del FiDBosc y de Solsona. A Lluis por darme la oportunidad de trabajar con vosotros en un momento en que de verdad lo necesitaba, por ser comprensivo y una de las personas con más empatía que conozco. Y a Aitor, a Martina y a Mireia por estar en mi día a día de Solsona porque compartir despacho con vosotros ha sido una experiencia muy enriquecedora y muy guay. Guardo un gran recuerdo también de Hassan, de Diego, de la gran Sonia, de las tres Carlas, de las barbacoas de Edu y de los partidos de pádel con Mónica, Quim, Ana y Joan.

A Miren y a Elena quiero daros las gracias por revisar versiones preliminares del trabajo de competencia. Y a Elena en particular por apoyarme, por ser la amiga que siempre está tanto para hablar del crecimiento del cambium como para escucharme en los momentos difíciles.

Mi familia también me habéis apoyado mucho todo este tiempo y sin las croquetas y las albóndigas de mi madre y las torrijas de Charo este final no habría sido el mismo. Y en especial quiero agradecer a mi madre, a Ken, a Bego y a Manolo por estar tan pendientes de mi padre en los meses previos a mi vuelta de Solsona, porque gracias a vuestro esfuerzo todo fue más fácil. A Geli y Ken por darnos la oportunidad de vivir en la casa maravillosa en la que vivimos, por entender nuestra situación y por ser siempre tan generosos con nosotros, os queremos mucho.

Y por último a Tamara por estar siempre ahí y escucharme cuando te necesito; porque contigo me río cada día; por ocuparte de gran parte de las tareas de casa en mi última etapa de la tesis; por ayudarme a distinguir los problemas importantes de los que no lo son. Porque la experiencia tan dura que hemos vivido juntos estos últimos meses ha reforzado mucho nuestra relación y me ha hecho darme cuenta de que vas a ser la mejor madre del mundo.

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Resumen general

En un contexto de cambio global las masas mixtas mediterráneas han cobrado gran relevancia dado que la mezcla de especies arbóreas puede hacerlas más resistentes que las masas con poca riqueza específica. La mezcla de especies arbóreas puede aportar estabilidad a estas masas haciéndolas más productivas en comparación con las masas puras. Pese a esto existen muy pocos modelos de gestión específicos para masas mixtas en la cuenca mediterránea. Entre las hipótesis que pueden explicar una mayor estabilidad, crecimiento o productividad en masas mixtas frente a las puras están la hipótesis de la complementariedad de nichos y la hipótesis del gradiente de estrés. En el marco de esta Tesis Doctoral nos hemos centrado en analizar las interacciones entre tres especies arbóreas que cohabitan en las masas mixtas de *Pinus pinea* L. de los páramos calizos de la Meseta Norte de la Península Ibérica. Se ha analizado cómo estas interacciones pueden modular la respuesta al clima en términos de crecimiento y supervivencia. Estas especies son *Pinus pinea*, *Quercus ilex* subsp. *ballota* y *Juniperus thurifera*. Para ello se ha hecho una aproximación mediante modelos de crecimiento lineales y no lineales y técnicas de análisis de vida que han permitido integrar las relaciones bióticas con los principales factores climáticos que afectan a estos dos procesos a distintas escalas temporales. Para ello se ha estimado el crecimiento radial mediante canutillos de crecimiento y se ha medido el crecimiento en circunferencia mediante dendrómetros de banda en arbolado adulto de las 3 especies y se ha evaluado la supervivencia de estas tres especies en una plantación a lo largo de un gradiente de disponibilidad de recursos simulando un escenario de reducción de precipitación. De estos modelos se infiere que a igualdad de densidad de masa el efecto de la competencia sobre el crecimiento de *P. pinea* es menor en masas mixtas que en puras, efecto que se ve acentuado en años secos. La competencia intraespecífica en *P. pinea* y en *J. thurifera* tiene un mayor efecto sobre la reducción del

crecimiento que la interespecífica en masas mixtas. En rodales de masas puras de *P. pinea* más vulnerables a las nuevas condiciones climáticas, se plantea promover la mezcla abriendo espacios para el regenerado avanzado de especies complementarias que ya esté instalado de forma natural y que presente una mayor plasticidad en respuesta a las condiciones climáticas durante el periodo de crecimiento. En el caso de que estas especies no estén instaladas se plantea recurrir a la siembra directa. Entre estas especies más plásticas están *Q. ilex* subsp. *ballota, Quercus faginea* o *J. thurifera*. Las masas mixtas objeto de estudio se transformarán muy probablemente a largo plazo en un monte bajo de *Q. ilex*, con pies aislados de *P. pinea* y una mayor abundancia de *J. thurifera*. La regeneración de *Q. ilex* quedará ligada a sus rebrotes de cepa, viéndose la supervivencia de sus plántulas procedentes de bellota seriamente comprometida. *J. thurifera* indudablemente continuará colonizando estas masas mixtas dado que se ve menos afectada por factores climáticos extremos en todos los niveles de luz que se han evaluado.

Summary

In a global change context Mediterranean mixed stands have gained significant attention as tree species mixture can promote resistance over stands with a lower species richness. Tree species mixture can provide stability making these stands more productive compared to pure stands. However, specific management models for mixed stands are scarce in the Mediterranean basin. Among the hypothesis that can explain these increases in stability, growth and productivity in mixed vs. pure stands are the niche complementarity theory and the stress gradient hypothesis. The aim of this PhD dissertation has been to analyse the tree species interactions between three species that cohabit in *Pinus pinea* L. mixed stands in the limestone plains of the Iberian Peninsula. We have analysed how these interactions can modulate the response to climate in terms of growth and survival. These species are *Pinus pinea, Quercus ilex* subsp. *ballota* and *Juniperus thurifera*. This has been approached through linear and non-linear growth models and lifetime analysis techniques that allow to integrate biotic interactions with the main climatic factors affecting these processes at different temporal scales. Radial growth has been estimated through coring and measuring girth increment on adult trees of the three species with band dendrometers. Seedling survival of the three species was evaluated in a plantation experiment along a gradient of resource availability simulating a climatic scenario of precipitation reduction. From these models we can infer that at equal density levels the effect of competition on *P. pinea* growth is lower in mixed vs. pure stands, with a higher effect in dry years. Intraspecific competition in *P. pinea* and *J. thurifera* has a deeper effect on growth reduction than interspecific competition in mixed stands. In the *P. pinea* pure stands more vulnerable to the new climatic conditions, we propose to promote tree species mixing opening spaces to the advanced regeneration of the complementary species that are naturally installed and have a more plastic response to climatic conditions

during the growing season. If these species are not present direct seeding can be applied. Amongst these more plastic species are *Q. ilex* subsp. *ballota*, *Quercus faginea* or *J. thurifera*. These Mediterranean mixtures will very likely be transformed in the long term into a *Q. ilex* coppice forest with sparse *P. pinea* trees and a wider abundance of *J. thurifera*; *Q. ilex* regeneration will rely on its ability to resprout, being its seedlings survival severely compromised. *J. thurifera* will undoubtedly keep colonising these Mediterranean mixtures, being less affected by extreme climatic factors in all levels of light availability that we evaluated.

Chapter 1

General introduction and methodological overview

1.1. Relevancia de las masas mixtas en un contexto de cambio global

Los bosques son proveedores netos de servicios ecosistémicos. Entre estos servicios destacan la producción de madera y de productos forestales no maderables, pero también proporcionan otros servicios de importancia para la sociedad como la protección del suelo (Lü et al., 2012), la diversidad animal y vegetal o la fijación de carbono (Coll et al., 2018). Sin embargo, el cambio global parece que pueda estar contribuyendo a una merma en la provisión de estos servicios, generando episodios de mortalidad arbórea inducida por sequía y altas temperaturas, plagas más abundantes o mayor recurrencia de incendios (Allen et al., 2010; Carnicer et al., 2011; Scholze et al., 2006). En este contexto de cambio las masas mixtas han cobrado gran relevancia dado que la mezcla de especies arbóreas parece que puede contribuir a mejorar o garantizar la provisión de servicios ecosistémicos (Gamfeldt et al., 2013; Plas et al., 2016b) haciéndolos más resistentes que los bosques con poca riqueza específica (Pretzsch et al., 2013). Entre los servicios que pueden verse incrementados aumentando la diversidad arbórea están la calidad y la producción de madera, la regeneración, la producción de biomasa radical, el stock de carbono del suelo, la resistencia a la sequía, la resistencia al daño por patógenos o la resistencia a las plagas por insectos defoliadores y perforadores (Plas et al., 2016a).

El estudio de las masas mixtas ha sido el objeto de muchas publicaciones recientes por el efecto que la mezcla de especies arbóreas puede tener sobre la estabilidad de estas masas y su mayor productividad en comparación con las masas puras, en un contexto de cambio global (Liang et al., 2016; Río et al., 2017, 2016). Entre las hipótesis que pueden explicar una mayor estabilidad, crecimiento o productividad en masas mixtas frente a las puras están la hipótesis de la complementariedad de nichos (Hooper et al., 2005; Tillman, 1999) y la hipótesis del gradiente de estrés (Bertness and Callaway, 1994). De acuerdo a estas dos teorías, la mezcla de especies que presentan distintos rasgos funcionales y diferente capacidad de captación y uso de los recursos que necesitan puede permitir hacer frente a situaciones de estrés climático de forma más eficiente de la que lo haría cada especie por separado en una masa pura (Lebourgeois et al., 2013).

El crecimiento y la dinámica de los ecosistemas forestales compuestos por diversas especies arbóreas depende de los patrones de disponibilidad de nutrientes, agua y luz y de la capacidad de cada especie de obtenerlos haciendo frente a distintos factores de estrés (Gómez-Aparicio et al., 2011; Zavala et al., 2000). La disponibilidad de recursos necesarios para el crecimiento de las especies forestales varía a distintas escalas espacio-temporales. Asimismo, cada especie difiere en su plasticidad para afrontar la escasez de recursos (Pardos et al., 2005) y esta capacidad de adaptación se ve modulada por las interacciones entre especies (García-Cervigón et al., 2013).

De esta forma, diferencias en términos de supervivencia y crecimiento en masas mixtas a lo largo de gradientes de recursos dan lugar a patrones contrastados de abundancia y desarrollo a nivel del regenerado (Moreno-Fernández et al., 2018; Olmo et al., 2014; Sánchez-Gómez et al., 2006) y de crecimiento a nivel del arbolado adulto (Cotillas et al., 2009; Gómez-Aparicio et al., 2011). Estas diferencias pueden alterar la estructura futura de la masa afectando a su crecimiento y condicionando su dinámica.

1.2. Tipos de interacciones entre especies forestales y su efecto sobre el crecimiento y la dinámica

La riqueza en especies arbóreas es de gran relevancia para garantizar la multifuncionalidad de las masas forestales (Gamfeldt et al., 2013; Plas et al., 2016a, 2016b), funciones entre las que destacan el crecimiento y la productividad. En este trabajo nos hemos centrado en analizar las interacciones entre especies arbóreas por ser las que más condicionan el crecimiento del arbolado adulto y la supervivencia del regenerado.

Existen tres tipos de interacciones entre especies arbóreas que deben considerarse para explicar los incrementos en el crecimiento y la productividad en masas mixtas, comparado con las masas puras: Competencia, reducción competitiva y facilitación (Forrester et al., 2006).

1.2.1. Competencia

La competencia es la influencia que ejercen entre sí los individuos arbóreos de una masa, independientemente de su especie, que se traduce en una lucha por la utilización del espacio, la luz y los nutrientes y agua del suelo (Serrada et al., 2008) y que implica una limitación del crecimiento potencial de cada individuo (Holmes and Reed, 1991). Se han realizado numerosas aproximaciones para analizar el efecto de la competencia sobre el crecimiento, tanto a nivel de masa como a nivel de árbol individual, mediante el cálculo de índices de competencia (Daniels, 1976; Tomé and Burkhart, 1989). El objetivo de estos índices es evaluar y cuantificar la influencia de los vecinos mediante relaciones alométricas que tienen en cuenta la radiación incidente, el tamaño de los árboles sujeto y de los vecinos y la distancia de los árboles sujeto a los árboles que se consideran competidores. Existen dos tipos de índices que han sido muy utilizados para analizar las relaciones de competencia, los índices de competencia dependientes de la distancia y los independientes de la distancia (Biging and Dobbertin, 1995; Tomé and Burkhart, 1989). El cálculo de los índices de competencia dependientes de la distancia implica un mayor esfuerzo de inventario para posicionar los árboles de interés, determinar las especies e inventariarlas. A cambio, proporcionan una información más detallada del entorno competitivo cuando se pretende hacer modelos de árbol individual (Ledermann and Stage, 2001).

1.2.2. Reducción competitiva

La reducción competitiva es también una interacción negativa que implica una inhibición del crecimiento del árbol, pero es una interacción de menor intensidad que puede explicarse por una complementariedad de nichos espacio-temporal. La complementariedad espacial puede deberse a una estratificación en la formación de las copas, por el hecho de que dos especies que cohabitan en un mismo espacio busquen maximizar la captación de luz (Jucker et al., 2015; Riofrío et al., 2017), o a una estratificación en la disposición de los sistemas radicales que permitan maximizar el aprovechamiento de los recursos disponibles en el suelo (Grossiord et al., 2014). Encontramos ejemplos de complementariedad temporal en el Sistema Central de la Península Ibérica, debido a diferencias funcionales en el regenerado de especies con distintas amplitudes ecológicas. Este es el caso del regenerado de *Quercus ilex* subsp. *ballota* que es capaz de abrir estomas y fijar carbono en verano cuando las temperaturas son muy elevadas y hay poca disponibilidad de agua en el suelo, mientras que los juveniles de *P. pinea*, más sensibles a la sequía, se ven obligados a interrumpir el intercambio de gases y detener su crecimiento (Mayoral et al., 2015). Otro ejemplo de complementariedad espacio-temporal lo encontramos en el semiárido mediterráneo continental de la provincia de Zaragoza (Camarero et al., 2010) en el que *Pinus halepensis* y *Juniperus thurifera* comparten nicho ecológico. Ambas especies tienen un crecimiento radial bimodal característico de algunas coníferas de ambientes mediterráneos continentales, coincidente con los dos periodos del año con clima más suave y lluvioso (la primavera y el otoño). En esta zona, *P. halepensis* Mill. puede mantener la formación de traqueidas en verano, época en la que *J. thurifera* detiene su crecimiento radial. Sin embargo, *Juniperus thurifera* es capaz de reanudar su crecimiento de manera más intensa que *P. halepensis* con las lluvias de otoño formando fluctuaciones de densidad en la madera tardía. Este mayor crecimiento en otoño de *J. thurifera* podría estar relacionado con la disposición de sus raíces. Las especies del género *Juniperus* cuentan con una ventaja adaptativa en ambientes sometidos a estrés por sequía al disponer de un sistema radical más somero y fasciculado que el de otras especies con las que comparten nicho (Williams and Ehleringer, 2000). Este sistema radical se ha sugerido que puede permitir aprovechar lluvias tardías de verano y del otoño para crecer, dado que estas lluvias humedecen las capas superficiales del suelo, que no son ocupadas por otras especies forestales vecinas (Camarero et al., 2010).

1.2.3. Facilitación

Por último, la facilitación es un tipo de interacción positiva en el sentido de que una especie favorece el crecimiento de otra. Este tipo de interacciones son comunes en masas mixtas que incluyen especies forestales leguminosas como las del género *Acacia*. Los nódulos de las raíces de las acacias favorecen la fijación de nitrógeno en el suelo, que puede ser aprovechado por las especies forestales colindantes. Otros ejemplos los encontramos en el bombeo de agua de capas profundas del suelo a capas más superficiales que hacen ciertas especies en momentos de sequía y que puede ser aprovechada por otras especies. Este mecanismo ha sido observado en especies como *Acer saccharum* en el estado de Nueva York (Dawson, 1993), y en especies forestales mediterráneas de la Península Ibérica como *Quercus suber, Q. ilex* o *Pinus nigra* (David et al., 2007; Kurz-Besson et al., 2006; Peñuelas and Filella, 2003). Otro ejemplo clásico de facilitación en ambientes mediterráneos continentales es el que llevan a cabo las plantas nodriza sobre el regenerado de individuos conespecíficos o heteroespecíficos (Gimeno et al., 2014). Un ejemplo de ello es la sombra del dosel de especies como *Pinus pinea*, cuyas copas amplias y aparasoladas crean un microambiente sombreado de temperaturas más bajas en el suelo que favorece la supervivencia y el reclutamiento del regenerado de distintas especies arbóreas (Vergarechea et al., 2019).

1.3. Impacto del cambio climático en el crecimiento y la dinámica de los bosques mediterráneos

El cambio global está incidiendo en la región mediterránea con aumentos generalizados de las temperaturas, olas de calor más frecuentes, sequías más severas y recurrentes y cambios en el régimen de precipitaciones (IPCC, 2013). Existe un amplio consenso sobre el ascenso de las temperaturas futuras en la cuenca Mediterránea, sin embargo, las proyecciones sobre las precipitaciones difieren mucho entre modelos climáticos (Mestre et al., 2015). Estos modelos en promedio predicen un declive de las precipitaciones, que en el escenario de mayores emisiones de gases de efecto invernadero (escenario RCP 8.5) podría llegar a ser del 30% en el caso de las precipitaciones estivales, pasando la estación más lluviosa a ser el otoño frente a la primavera (de Luis et al., 2010).

Los impactos del cambio global están siendo bien ilustrados a través de cambios en la fenología y la morfología de las plantas y cambios latitudinales y altitudinales en la distribución de la biota mediterránea (Peñuelas and Boada, 2003; Richardson et al., 2013). Asimismo, daños directos al arbolado en la cuenca Mediterránea por eventos climáticos extremos causados por el cambio climático están bien documentados en la literatura forestal (Lindner et al., 2010; Lloret et al., 2004). Temperaturas más elevadas unidas a un declive de las precipitaciones pueden inducir un aumento de la demanda evaporativa y la evapotranspiración que muy probablemente harán disminuir la humedad edáfica provocando mayor estrés hídrico y creando condiciones más limitantes para el desarrollo de las plantas (Cotillas et al., 2009; Valladares et al., 2005). En este contexto de cambio global uno de los principales retos es determinar la influencia que los cambios en las condiciones ambientales pueden tener sobre el crecimiento y la dinámica de los ecosistemas forestales mediterráneos (Chapin et al., 2001) que podrían conllevar cambios en la distribución y en la abundancia de las especies arbóreas mediterráneas (Benito Garzón et al., 2008), y una disminución en la provisión de los distintos servicios ecosistémicos.

1.4. Gestión forestal en masas mixtas mediterráneas

La gestión de la composición y la competencia mediante la aplicación de claras y cortas de mejora son las principales herramientas que proponen los gestores forestales en ambientes mediterráneos para adaptar la dinámica forestal a los efectos negativos del cambio climático (Lindner and Calama, 2013). Las referencias a prácticas específicas de gestión forestal en masas mixtas en la cuenca Mediterránea son escasas (Pach et al., 2018), aplicándose en la mayor parte de los casos los mismos esquemas de selvicultura desarrollados para las masas puras de cada especie. En muchos casos, la no disponibilidad de esquemas de selvicultura para las masas mixtas está asociada a un desconocimiento de la dinámica de regeneración y crecimiento en este tipo de masas (Coll et al., 2018). Es posible encontrar excepciones, como son los modelos de gestión aplicables a distintas tipologías forestales del Mediterráneo subhúmedo en Cataluña (Piqué et al., 2014) que están siendo revisados en el marco del actual proyecto LIFE MixForChange (http://www.mixforchange.eu/es/) para adaptarlos a los escenarios más probables de cambio climático. En este sentido, se plantean criterios de gestión multiobjetivo buscando incrementar la resiliencia, asegurando la conservación y mejorando las funciones productiva, social y ambiental. Asimismo, García-Güemes y Calama (2015) identifican cómo la aplicación de claras selectivas pueden alterar la composición en pinares de *Pinus sylvestris* en el Sistema Ibérico. Otra práctica de gestión asociada a las masas mediterráneas es la diversificación de las repoblaciones monoespecíficas realizadas con especies del género *Pinus* mediante la aplicación de cortas aclaratorias que permitan la puesta en luz de rebrotes de *Quercus sp.* y el posterior resalveo de los mismos (Arrechea Veramendi, 2012), o la realización de plantaciones de diversificación y enriquecimiento bajo la cubierta, tal y como se está planteando en los proyectos FORADMIT (http://blogs.upm.es/foradmit/) de la UPM y OLDPINE (entre el INIA y la Universidad de Huelva).

1.5. Masas forestales de *Pinus Pinea* de la Meseta Norte

En la Meseta Norte destacan por su importancia ecológica y económica las masas forestales dominadas por pino piñonero (*Pinus pinea* L.). Estas masas ocupan unas 74,000 ha, principalmente en la provincia de Valladolid, y se asientan sobre dos tipos de suelos: las arenas silíceas continentales y los páramos calizos. Las arenas continentales tienen porcentajes de arenas superiores al 90% y una baja capacidad de retención del agua (CRA < 100 mm $\cdot$ m^{-1}), mientras que los páramos calizos alcanzan porcentajes de arcilla y limos superiores al 40-50% y valores de CRA promedios de 176 mm$\cdot$ m^{-1} (Calama et al., 2019).

Los bosques de pino piñonero en esta región han tenido una gestión multifuncional desde finales del siglo XIX (Romero-Gilsanz, 1886). Desde ese momento hasta mediados de 1970 la gestión selvícola en la Meseta Norte se centró en favorecer la producción de madera, manteniendo una producción secundaria de piña. Para lograr este objetivo se buscó alcanzar altas densidades de masas puras coetáneas mediante cortas a hecho por fajas seguidas de siembra (Gordo, 1999; Montero et al., 2008). Mediante estas cortas a hecho se eliminaron otras especies forestales, como *Quercus ilex* subsp. ballota (Desf.) Samp., *Quercus faginea* subsp. *faginea* Lam. y otras cupresáceas en los páramos, que en zonas que no fueron gestionadas con este objetivo están presentes de forma natural (De-

Dios-García et al., 2018; Manso, 2013). Este tipo de selvicultura fue llevada a cabo hasta la década de 1980, en la que coincidiendo con los altos precios que alcanzó el piñón en los mercados internacionales se promovió un cambio de objetivos para favorecer la producción de piña, lo que llevó a mantener densidades bajas del arbolado adulto. Para esto se planificaron claras fuertes y regeneración por aclareo sucesivo. Estas bajas densidades permiten un amplio desarrollo de las copas y garantizan una buena producción de piñón que es uno de los principales productos forestales no maderables de la Península Ibérica, con un alto valor de mercado y que se exporta a distintos países de nuestro entorno (Calama et al., 2008).

La aplicación de esta gestión resultó en la apertura de grandes claros en las masas puras, en las que actualmente el piñonero tiene grandes problemas de regeneración (Manso et al., 2012). Además, planteaba un problema en un contexto de baja disponibilidad de recursos que hacían necesario garantizar una regeneración natural sin tener que recurrir a siembra (Gordo et al., 2012). Asimismo, las masas puras en líneas generales se consideran más vulnerables frente a perturbaciones bióticas y menos resistentes y resilientes que las masas mixtas. En este contexto, el favorecimiento de las masas mixtas supone una alternativa de gestión eficaz para mejorar la resistencia y la resiliencia individual del arbolado adulto (Lebourgeois et al., 2013) tamponando el efecto de las plagas, los incendios forestales y los efectos del cambio climático (Jactel et al., 2017).

Las masas mixtas de *P. pinea* de la Meseta Norte aparecen tanto en arenas continentales como en los páramos calizos. La composición específica del arbolado varía en las dos tipologías. *P. pinea* se mezcla con *Pinus pinaster* Aiton, en arenales y con *Quercus ilex* subsp. *ballota*, *Quercus faginea* subsp. *faginea*, *Juniperus thurifera* y *Juniperus communis* en las parameras; estando los páramos en zonas ligeramente más elevadas (altitud media 800-850 m s.n.m.) que las arenas continentales (altitud media 700-750 m s.n.m.) (Calama et al., 2019).

La historia selvícola de las masas mixtas de los páramos es relativamente reciente y está íntimamente ligada a la propiedad forestal. La mayoría de estas masas perteneció a propietarios privados hasta mediados de los años 80. La falta de planes de gestión contribuyó a la conservación de estas masas. Gran parte de estas masas fueron compradas por la Junta de Castilla y León a mediados de los años 80. Desde entonces la gestión ha tenido un objetivo multifuncional orientado a promover el crecimiento y regeneración de todas las especies priorizando la conservación de la biodiversidad junto a la producción de piña, madera, biomasa, setas y un uso recreativo del monte (de-Dios-García et al., 2015). En la actualidad, la gestión propuesta en estas masas tiene como objetivo el mantenimiento y regeneración de todas las especies, aplicando cortas de regeneración mediante entresaca en el pinar, resalveo sobre el monte bajo de *Quercus* y liberación de individuos de *Juniperus*, favoreciendo la presencia de algunos pinos de gran tamaño, que jugarán un papel preponderante como árboles percha para la dispersión de las semillas de *Juniperus* (García-Güemes and Calama, 2015).

1.6. Zona de estudio

La zona de estudio de la presente Tesis Doctoral se encuentra en la Meseta Norte de la Península Ibérica. La Meseta Norte es una extensión de unos 50,000 km^2 situados a una altitud media de 700 m s. n. m. Se trata de una zona con clima Mediterráneo continental caracterizado por una sequía estival de 4 meses (junio a septiembre), coincidente con el periodo del año en el que las temperaturas son más altas. Las temperaturas medias anuales son de 11ºC, pero pueden alcanzar los 40ºC en verano y los -12ºC en invierno (Fig. 1.1).

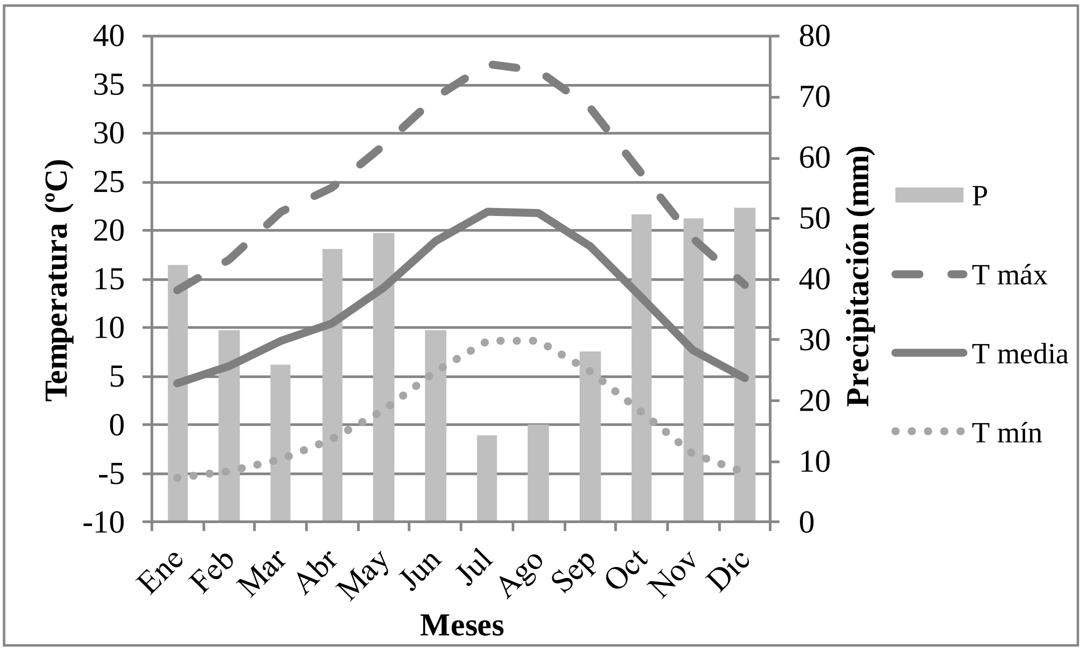

Fig. 1.1. Climodiagrama del área central de la Meseta Norte del periodo 1973-2010. Las líneas discontinua, continua y punteada corresponden a las temperaturas máxima, media y mínima respectivamente (ºC) y las barras representan la precipitación total mensual (Estación meteorológica 2422 de la AEMET, Valladolid).

Asimismo, es una región con una elevada variabilidad interanual en el régimen de precipitaciones (220-630 mm anuales) que afecta a la producción de semilla (Calama et al., 2011), a la supervivencia del regenerado (Calama et al., 2015) y al crecimiento del arbolado adulto (De-Dios-García et al., 2018); crecimiento que se ve modulado por interacciones entre especies arbóreas y cuya intensidad cambia en función de la climatología (de-Dios-García et al., 2015).

1.7. Dispositivos experimentales

Para lograr los objetivos de esta Tesis Doctoral se diseñaron tres experimentos independientes para poder estudiar la influencia de la competencia sobre el crecimiento interanual e intraanual y determinar los factores climáticos con mayor influencia en ambos procesos y en la supervivencia del regenerado. Los sitios de estudio están ubicados en montes de titularidad pública (M.U.P) de la provincia de Valladolid, y fueron seleccionados de forma que fuesen representativos de los pinares de *P. pinea* de los páramos calizos. Para poder analizar las diferencias en el crecimiento entre masas puras y mixtas era necesario recabar datos de crecimiento en ambas tipologías (Fig. 1.2.).

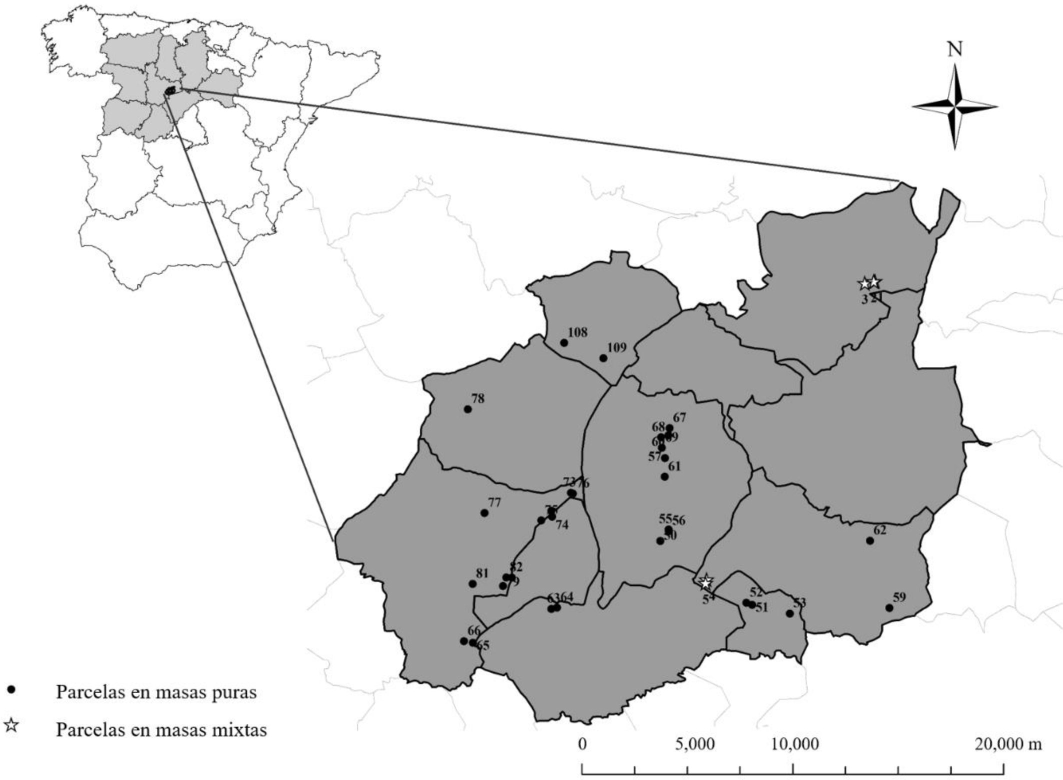

Fig. 1.2. Localización del área de estudio y de las parcelas experimentales.

En ambos casos se trató de cubrir todo el rango de edades, densidades y calidades de estación presentes en el territorio. En el caso de las masas puras se aprovechó la red de parcelas permanentes del INIA asentadas sobre terrenos calizos en las que se monitoriza el crecimiento y la producción de piña. Estas parcelas replanteadas en masas puras son de radio variable (Fig.1.3) e incluyen entre 10 y 20 árboles. Las parcelas se instalaron en el año 1996, y han sido reinventariadas en 2008, 2011 y 2016 (Fig. 1.4). En el momento de su instalación se marcaron y posicionaron todos los pies de la parcela, midiendo además el diámetro normal (a 1.30 m sobre el suelo), altura total y de copa, y el diámetro de copa, repitiendo estas mediciones en los siguientes inventarios. Asimismo, se tomó una muestra de edades a la altura del tocón mediante barrena de Pressler, y se tomaron canutillos de crecimiento radial en distintos pies en 2001, 2008 y 2011 (Fig. 1.5).

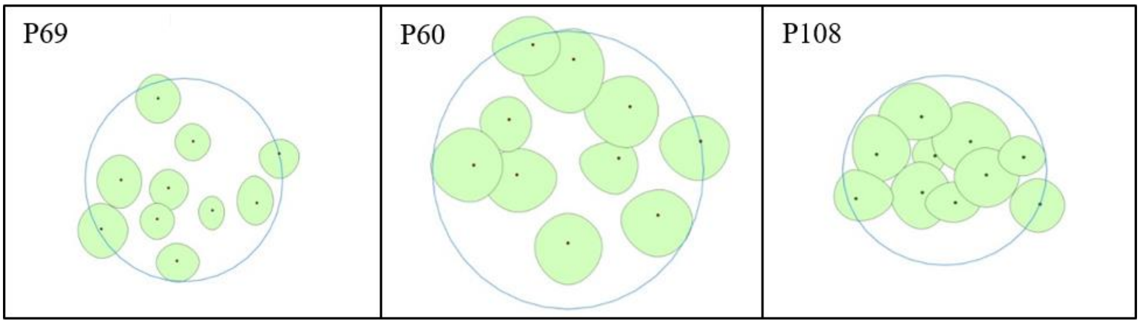

Fig. 1.3. Mapas de tres parcelas de producción de *P. pinea* localizadas en masas puras de los páramos calizos. Los puntos representan los tocones de cada árbol y las superficies en verde las proyecciones de sus copas. Fuente INIA.

Fig. 1.4. Fotografía de dos de las parcelas INIA (60 y 69) ubicadas en masas puras en el páramo calizo.

Fig. 1.5. Toma de muestras de crecimiento radial con barrena de Pressler en parcela INIA localizada en masa pura de *Pinus pinea* en el páramo calizo.

En el caso de las masas mixtas se establecieron dos tipos de parcelas. Por un lado, se replantearon cinco parcelas en masas mixtas con arbolado adulto al objeto de analizar la dinámica de crecimiento del arbolado, la instalación de regenerado, las relaciones de competencia entre el arbolado y el efecto del clima sobre estos procesos. Estas parcelas de arbolado son parcelas rectangulares de 50 m x 60 m, y se seleccionaron al objeto de cubrir distintos rangos de espesura dentro de las mezclas más habituales de la región de estudio. En el Monte de U.P. 110, El Carrascal (masa mixta), se montaron tres parcelas de arbolado (códigos P1, P2 y P3 de Fig. 1.2 y Fig. 1.6.). En el Monte U.P. 117 (masa mixta) se instalaron otras dos parcelas de seguimiento del arbolado adulto (códigos P4 y P5 de Fig. 1.2). En estas parcelas se procedió a marcar y posicionar todo el arbolado con altura superior a 50 cm, procediendo a medir diámetros normales, altura total y hasta la base de la copa, y diámetro de copa en los pies con altura superior a 1.30 m, y altura total, diámetro de tocón y de copa en los pies menores. En una muestra de entre 35 y 49 pies por parcela, de todas las especies presentes, se extrajeron con barrena de Pressler en 2011 canutillos de incremento radial. En el caso del monte U.P. 110, se apearon 3-4 encinas por parcela para extraer rodajas y determinar su incremento radial.

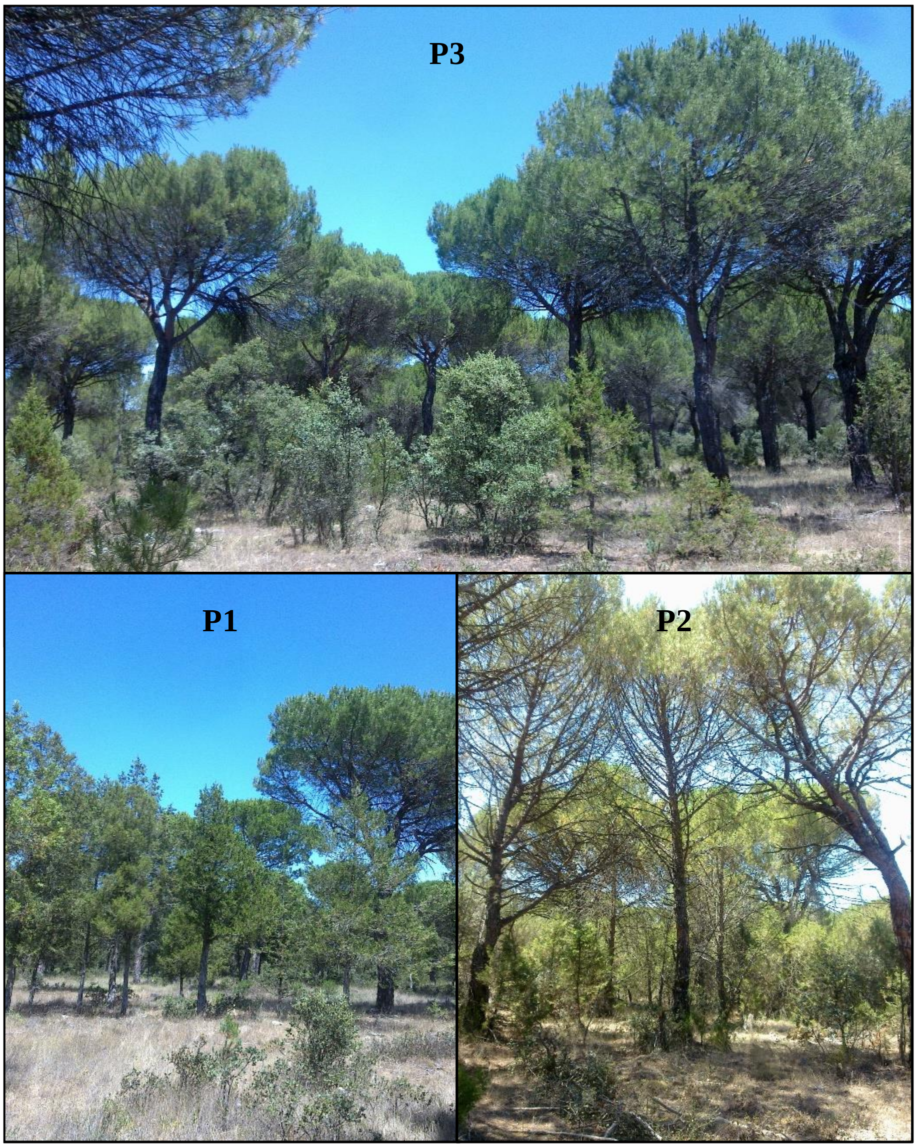

Fig. 1.6. Parcelas de arbolado en masas mixtas de monte U.P 110, El Carrascal, establecidas en tres niveles de espesura (P1 = 10, P3 = 15 y P2 = 20, $m^2 \cdot ha^{-1}$).

En las parcelas 1 y 2 del sitio de ensayo de "El Carrascal" se seleccionaron 30 pies por parcela (12 *P. pinea*, 12 *J. thurifera* y 8 *Q. ilex*), cubriendo el rango de clases diamétricas identificadas, sobre los que se procedió a instalar en el año 2012 dendrómetros de banda, que permitieron realizar un seguimiento del crecimiento en circunferencia con una periodicidad mensual, y que han permitido definir el patrón de respuesta intraanual en crecimiento secundario para las tres especies y su relación con parámetros climáticos y de competencia (Fig. 1.7).

Fig. 1.7. Dendrómetros de banda instalados en las parcelas 1 y 2 del sitio de ensayo de "El Carrascal".

Adicionalmente, y dentro del sitio de ensayo del MUP 110 "El Carrascal" se instalaron en 2012 12 parcelas en la que se realizó una plantación experimental bajo cubierta arbórea, al objeto de evaluar el efecto de la luz, la exclusión de lluvia y el clima sobre la supervivencia y crecimiento de plántulas de *P. pinea, Q. ilex* y *J. thurifera* (Fig. 1.8. y 1.9). Estas parcelas son rectangulares, de 5 x 9 m y están valladas. Se encuentran instaladas bajo un gradiente natural de disponibilidad lumínica, y en ellas se ha instalado un dispositivo de exclusión de la precipitación. En las mismas se ha realizado un seguimiento periódico de la supervivencia y del crecimiento del regenerado.

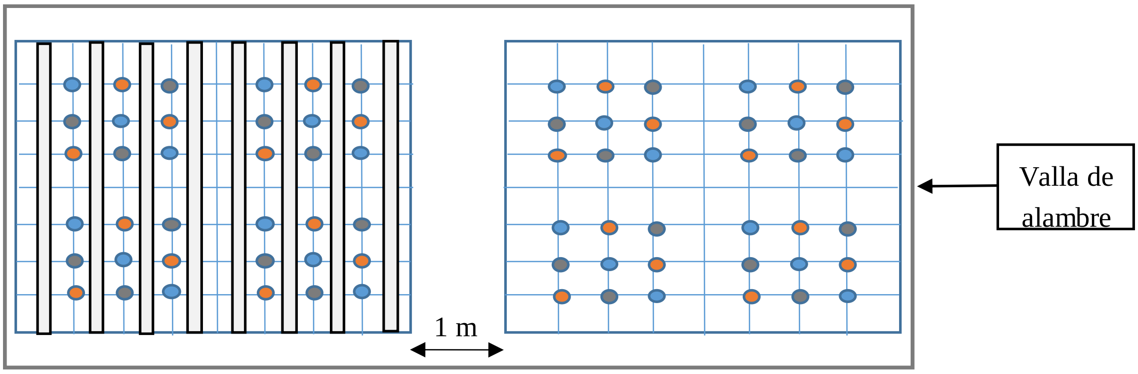

Fig. 1.8. Esquema de una parcela de plantación formada por dos subparcelas. En la suparcela de la izquierda figuran unas bandas longitudinales que representan unos canalones de exclusión de lluvia. Cada punto coloreado hace referencia a una plántula (Azul: *P. pinea*; Rojo*: Q. ilex* subsp. *ballota*; Verde: *J. thurifera*).

Fig. 1.9. Detalle de una parcela de plantación y su dispositivo de exclusión de precipitación.

1.8. Métodos estadísticos

En la presente Tesis Doctoral se ha hecho uso de distintas herramientas estadísticas en función de las preguntas específicas que se querían responder y de las particularidades que presentaban los datos de análisis y que se considera que son asimismo relevantes para el proceso de aprendizaje de una tesis doctoral. Entre ellas, el empleo de técnicas de modelización para analizar el crecimiento y la supervivencia permiten identificar los principales factores ecológicos implicados en estos procesos, así como elaborar predicciones de ayuda en la toma de decisiones para los gestores forestales incluyendo distintos escenarios climáticos. Entre las técnicas utilizadas están:

1.8.1. Modelos mixtos lineales

Un modelo mixto lineal, también llamado modelo de parámetros aleatorios, es la expresión de una relación lineal entre una variable dependiente (en general de tipo continuo), como por ejemplo el crecimiento en diámetro y una serie de variables independientes, continuas o categóricas. Un modelo mixto lineal se caracteriza porque tiene tanto efectos fijos, como efectos aleatorios. Los efectos fijos son comunes para toda la muestra de estudio y definirán el comportamiento medio del conjunto de datos, mientras que los efectos aleatorios son efectos propios de cada una de las unidades de muestreo (Calama, 2004)

Las aproximaciones mediante modelos aleatorios permiten analizar datos con una estructura espacial jerárquica (árboles que crecen dentro de parcelas y parcelas que se encuentran en distintos rodales) y con una variabilidad intrínseca al periodo de estudio. Asimismo tienen en cuenta la posible correlación en los datos obtenidos de un mismo árbol, parcela y periodo, que tienden a parecerse más entre sí que datos de distintos árboles y parcelas que se hayan medido en periodos diferentes (Henttonen et al., 2009; Pesonen et al., 2009). La no consideración de efectos aleatorios en un modelo sobre datos altamente correlacionados puede conducir a un sesgo en la estimación de los intervalos de confianza de los parámetros.

En la presente Tesis se han utilizado modelos mixtos lineales de tipo regresión en el capítulo 2 para analizar el efecto de distintos tipos de competencia intraespecífica e interespecífica sobre el incremento en área basimétrica anual en una serie de 15 años con condiciones climáticas contrastadas en masas puras y en masas mixtas de *P. pinea*. En estos modelos de regresión las variables independientes son de tipo continuo (u ocasionalmente categóricas), y el valor de la variable dependiente queda definido por el producto de una serie de variables independientes por unas constantes (también llamadas parámetros) más una serie de efectos aleatorios y un término de error aleatorio.

La dependencia inherente entre las observaciones, al corresponderse con medidas de crecimiento anual repetidas en los mismos árboles, que a su vez se localizan dentro de parcelas y se refieren a años comunes, justifica la utilización de los modelos mixtos lineales.

1.8.2. Modelos mixtos no lineales

Los modelos mixtos no lineales pueden entenderse como un caso particular de los modelos mixtos lineales, caracterizado porque la relación entre la variable dependiente y las posibles variables independientes y efectos aleatorios es de tipo no-lineal (Davidian and Giltinan, 2003). La formulación de este tipo de relaciones no-lineales permite expresar relaciones complejas entre las variables de estudio, como puede ser una relación con un máximo o relaciones de tipo potencial y exponencial. En este tipo de modelos se considera la inclusión de un efecto aleatorio al objeto de minimizar el efecto de la potencial dependencia entre las observaciones procedentes de la misma unidad de muestreo.

En la presente Tesis se han utilizado modelos mixtos no lineales en el capítulo 3, al objeto de modelizar el patrón de crecimiento intraanual en individuos de *P. pinea, Q. ilex* y *J. thurifera* en respuesta a factores climáticos y competencia intra e interespecífica. La dependencia entre las mediciones procedentes de un mismo árbol, y el patrón observado de respuesta no lineal del crecimiento a determinados factores climáticos, como son la temperatura media o el número de días sin precipitación, justifican el uso de esta técnica.

1.8.3. Técnicas de análisis de vida

Las técnicas de análisis de vida (también conocidas como *modelos de supervivencia*) permiten modelizar el tiempo transcurrido hasta la ocurrencia de un evento determinado, como puede ser la muerte de una planta o la germinación de una semilla (Manso et al., 2013). Los modelos de análisis de vida estudian la relación entre el tiempo transcurrido hasta la ocurrencia del evento y una serie de posibles variables predictoras, normalmente a través de la denominada función de riesgo, que representa la probabilidad instantánea de ocurrencia del evento. Un tópico común en este tipo de modelos es la censura por la derecha, que se refiere a la posibilidad de que durante el tiempo del experimento en determinados individuos no llegue a producirse el evento.

En la presente Tesis Doctoral se han usado modelos de técnicas de análisis de vida en el capítulo 4, al objeto de modelizar la supervivencia de plántulas de *Q. ilex, J. thurifera* y *P. pinea* a distintos niveles de luz, exclusión de precipitación y condiciones climáticas. El tipo de dato, correspondiente con un seguimiento periódico de la supervivencia en plantas con fecha de implantación conocida, justifica el empleo de esta técnica estadística.

1.8.4. Análisis de la varianza

El Análisis de la Varianza (ANOVA) es una técnica que permite descomponer la variabilidad detectada en una variable aleatoria en distintas componentes independientes que pueden asignarse a diferentes causas o fuentes. El Análisis de la Varianza se ha utilizado para analizar los diseños experimentales clásicos, en los que interesaba estudiar si existen diferencias significativas en el valor de la variable de respuesta y entre los distintos valores que puede adoptar la variable explicativa de tipo categórico. Los modelos de tipo ANOVA estudian la influencia que tienen distintos niveles o categorías de una variable independiente sobre una variable dependiente.

En esta Tesis los modelos de tipo ANOVA han sido utilizados en el capítulo 4 para determinar la influencia de dos tipos de tratamiento (luz y exclusión de lluvia, cada uno con dos niveles) sobre el contenido en agua del suelo en la plantación bajo cubierta arbórea en una masa mixta.

1.9. Objetivos y organización general de la Tesis

El objetivo principal de la presente Tesis Doctoral es profundizar en el conocimiento de los procesos de dinámica, crecimiento y regeneración de las distintas especies que componen las masas mixtas con presencia dominante de *Pinus pinea* en los páramos calizos de la Meseta Norte de España.

Para alcanzar este objetivo general, la Tesis se organiza a través de tres capítulos principales donde se presentan de manera independiente y en formato de artículo científico los resultados de tres experimentos centrados en el estudio de la dinámica en este tipo de masas mixtas. La Tesis se complementa con un capítulo de Introducción, un capítulo de Discusión General y un capítulo de Conclusiones.

Los objetivos generales de cada uno de los capítulos principales son:

Capítulo 2.

- Evaluar el efecto de composición y la competencia en el crecimiento secundario interanual de *P. pinea* en masas mixtas y monoespecíficas en series de 15 años con condiciones climáticas contrastadas.

Capítulo 3.

- Determinar mediante modelos de árbol individual los factores climáticos y de competencia intra e interespecífica que controlan la dinámica del crecimiento secundario intraanual en tres especies arbóreas mediterráneas que coexisten en masas mixtas de la Meseta Norte: *P. pinea, Q. ilex* subsp. *ballota,* y *J. thurifera*.

Capítulo 4.

- Estudiar el patrón espacio-temporal de supervivencia de plántulas de *P. pinea, Q. ilex* subsp. *ballota,* y *J. thurifera* de una savia plantadas a lo largo de un gradiente de luz y considerando dos regímenes de precipitación (control y exclusión).

Estos objetivos generales de cada capítulo se han alcanzado gracias a los siguientes objetivos específicos:

Capítulo 2.

- Comparar la respuesta a la competencia intraespecífica e interespecífica en el patrón de crecimiento de *P. pinea* ajustando modelos dependientes de distancia a nivel de árbol individual.
- Evaluar el patrón de variabilidad interanual en la competencia intraespecífica e interespecífica que está asociado a las fluctuaciones climáticas.

Capítulo 3.

- Determinar los factores de competencia que determinan el crecimiento secundario potencial diario a nivel de árbol.
- Dilucidar los factores climáticos que limitan el incremento radial potencial diario para cada una de las especies arbóreas que coexisten en masas mixtas de piñonero.

Capítulo 4.

- Identificar respuestas específicas en la supervivencia de plántulas de una savia de las tres especies de estudio, a lo largo de un gradiente de disponibilidad de luz.
- Examinar si una reducción de la precipitación del 30%, que es el escenario de cambio climático más probable para la cuenca mediterránea, puede alterar la respuesta específica a la irradiación en términos de supervivencia.
- Evaluar el efecto diario de la temperatura y la precipitación en la supervivencia.

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Chapter 2

Interannual variability in competitive effects in mixed and monospecific forests of Mediterranean stone pine.

Based on: de-Dios-García, J., Pardos, M., Calama, R., 2015. Interannual variability in competitive effects in mixed and monospecific forests of Mediterranean stone pine. For. Ecol. Manage. 358, 230–239. https://doi.org/10.1016/j.foreco.2015.09.014

Specific objectives:

- To compare the growth pattern response of *P. pinea* to intra and interspecific competition by fitting individual distance dependent tree models.
- To assess the pattern of interannual variability in competition within and between species associated with climatic fluctuations.

Data:

- Radial increment data from the period 1997-2011 from 372 trees (*Pinus pinea*, *Quercus ilex* subsp. *ballota*, *Juniperus thurifera* and *Quercus faginea*) grown in mixed and monospecific stands.

Methodology:

- Several distance dependent competition indices were calculated and compared through linear mixed models to understand the effect of stand composition and competition on annual growth

Main findings:

- We obtained competitive reduction and tree growth amelioration in mixed *vs*. monospecific stands of *P. pinea* indicating a spatial and temporal niche separation between species and size-symmetric effects for interspecific competition.
- Competition within pines was size-asymmetric.
- Growth was enhanced in mixed *vs*. monospecific stands in water stressed years.

Resumen

La gestión de la composición y de la competencia son dos opciones propuestas desde la gestión forestal para adaptar las masas forestales a los esperados impactos negativos que el cambio climático tendrá sobre el crecimiento de los bosques en la cuenca mediterránea. La mezcla de especies puede mejorar la resistencia y la resiliencia de los ecosistemas forestales para afrontar el cambio global. Sin embargo, es probable que el cambio global modifique la dinámica de las masas mixtas. Por tanto, estudiar las relaciones entre árboles a una escala anual es clave para comprender la dinámica de los ecosistemas en esta región. El objetivo de este trabajo fue evaluar los efectos de la composición de especies arbóreas y la competencia en el crecimiento secundario anual de *Pinus pinea* en masas mixtas y monoespecíficas a lo largo de un periodo de 15 años, bajo condiciones climáticas contrastadas. Se obtuvieron datos de crecimiento, expresados en área basimétrica, a partir de la lectura de anillos de crecimiento de canutillos y secciones transversales de 372 árboles de las especies *Pinus pinea* L., *Juniperus thurifera* L., *Quercus ilex* subsp. *ballota* (Desf.)) Samp. y *Quercus faginea* Lam., en la meseta norte. Aproximadamente la mitad de estos árboles estaban en masas puras y la otra mitad en masas mixtas. Se analizó el efecto de la competencia intra e interespecífica sobre el crecimiento secundario de *P. pinea* comparando distintos índices de competencia dependientes de distancia mediante modelos lineales mixtos. Estos índices de competencia se calcularon para todos los árboles de cada parcela para cada uno de los años de estudio. Los resultados mostraron una reducción competitiva y una mejora del crecimiento en masas mixtas frente a puras indicando una separación espacio-temporal de nichos entre especies y efectos simétricos en la competencia interespecífica. Se observó que la competencia entre pinos es asimétrica lo cual indica que los individuos de mayor tamaño obtienen la mayoría de los recursos limitando el crecimiento de los pinos vecinos más pequeños. Las interacciones intraespecíficas fueron más negativas que las interespecíficas. Por último, se muestran evidencias de mejores crecimientos en masas mixtas frente a puras en años de mayor estrés hídrico, lo cual indica que la promoción de las masas mixtas es una herramienta de gestión adecuada para mitigar los efectos del cambio climático en la región.

Palabras clave

Masas mixtas; *Pinus pinea*; reconstrucción; índices de competencia dependientes de distancia; modelos lineales mixtos; complementariedad de nichos.

Abstract

The management of species composition and competition are two of the main adaptive options that forest managers propose to cope with the expected negative impacts of climate change on forest growth in the Mediterranean basin. Species mixture can improve the resistance and resilience of forest ecosystems to face up global change. However, it seems likely that global change will modify mixed stands dynamics. Thus, studying inter-tree relationships on an annual basis is key to understanding ecosystem dynamics in the region. The aim of this paper was to evaluate the effects of tree species composition and competition on *P. pinea* annual secondary growth in mixed vs. monospecific stands over a period of 15 years with contrasting climatic conditions. We obtained basal area growth data from tree ring measurement on cores and cross section slices from 372 trees of *Pinus pinea* L., *Juniperus thurifera* L., *Quercus ilex* subsp. *ballota* (Desf.)) Samp. and *Quercus faginea* Lam., in the Spanish Northern plateau, approximately half of which were in monospecific stands and half in mixed stands. We analysed the effect of intra and interspecific competition on *Pinus pinea* secondary growth comparing the performance of several distance dependent competition indexes through linear mixed models. These competition indices were calculated for all trees within each plot for each year of study. The results showed competitive reduction and tree growth amelioration in mixed vs. monospecific stands of *Pinus pinea* indicating a spatial and temporal niche separation between species and size-symmetric effects for interspecific competition. Size-asymmetric results obtained for competition within pines indicated that the largest individuals obtain the majority of the contested resources suppressing the growth of their smaller pine neighbours. Intraspecific interactions were more negative than interspecific interactions. And we finally provide evidence of a growth enhancement in mixed vs. monospecific stands in water stressed years indicating that the promotion of mixtures in *Pinus pinea* stands is a powerful management tool to buffer the effects of climate change in the region.

Keywords

Mixed stands; *Pinus pinea*; backdating; distance dependent competition indices; linear mixed models; niche complementarity.

2.1. Introduction

The management of species composition and competition are two of the main adaptive options that forest managers can propose in the face of expected negative effects of global change on forest dynamics (Lindner and Calama, 2013). While competition is one of the main factors that limit tree growth in forest ecosystems, numerous studies point out that the effects of competition on growth are different in mixed and monospecific stands (e.g. Pretzsch et al., 2013; Río et al., 2014b). Studies in different bioclimatic regions have reported benefits in growth and productivity from interspecific interactions in mixed stands compared to monospecific stands (Forrester, 2014; Perot and Picard, 2012). Advantages from different tree associations may include: increases in resource supply due to increased leaf nutrient content and leaf litter decomposition (Jonard et al., 2008); improved soil nutrient mineralization and better use of available water due to root stratification, soil chemistry and mycorrhiza (Brown, 1992; Rincón et al., 1999); or between species facilitation through hydraulic lift (Dawson, 1993).

Recent publications comparing growth or productivity in mixed vs. monospecific stands have also found that within species competition is stronger than between species competition (Forrester et al., 2011; Perot and Picard, 2012). This confirms that tree diversity may enhance growth and guarantee stability through species complementarity (Loreau et al., 2001; McCann, 2000). Positive interactions between species or inter-specific differences in the requirement and use of the resources are two of the possible mechanisms leading to this niche complementarity. The spatio-temporal variability of resource availability and other environmental conditions results in dynamic relationships within and between species (Forrester et al., 2011). These relationships are likely to change with life stage and plant age due to the dynamic nature of nutrient, water and carbon cycles, and light availability during stand development (Forrester et al., 2011);

and may also change on an annual basis with complementary effects predominating in low-growth years and competition in high-growth years (Río et al., 2014b).

It is widely accepted that species mixture can improve resistance and resilience of some forest ecosystems (Landeau and Landmann, 2008; Legay et al., 2008) but not others (Grossiord et al., 2014). However, it seems likely that global change will modify mixed stands dynamics; thus, studying the different growth responses of tree species that grow together to different levels of stocking, degree of mixture and climate conditions remains a challenge. Different approaches have been proposed to analyse and compare growth in monospecific and mixed stands, including “replacement” experiments, where the proportion of each species varies while total density remains constant (Garber and Maguire, 2004), data from large-scale forest inventories (Río and Sterba, 2009) and modelling approaches. Single-tree growth models are a powerful tool to evaluate competition processes and have been previously used to explore the interactions between forest tree species (Perot and Picard, 2012; Río et al., 2014a). Among the different type of single tree models, empirical distance dependent models, including distance dependent competition indices as fixed effects (Contreras et al., 2011; Ledermann and Stage, 2001), have proved to accurately describe between and within species competition processes and to be good predictors of tree growth (Radtke et al., 2003).

Climate in the Mediterranean basin is characterized by a great interannual variability (Pugnaire et al., 2000) that conditions vegetation growth and diversity. Mediterranean forests have higher diversity levels than temperate European forests due to a higher species richness in the understory (Legay et al., 2008). Despite the importance of Mediterranean mixed forests as hotspots of specific diversity, the dynamics, production and management of these mixed forests are scarcely known. In addition, the Mediterranean basin is considered one of the most vulnerable regions under climate change scenarios, and evidence of processes of growth decline, tree decay and dieback, species shift and replacement, and changes in phenology have already been detected as a response to severe drought induced stresses (Peñuelas and Filella, 2001; Sánchez-Salguero et al., 2012).

Pinus pinea L. (Mediterranean stone pine) is a widespread tree species in European Mediterranean forests occurring across an area of 400,000 ha in Spain (Montero et al., 2008). Its management plays an important role in the local economy for the production of pine nuts and wood (Calama et al., 2012). Although it is well adapted to the current Mediterranean environmental conditions, the climate in the Mediterranean basin is expected to get hotter and drier, especially in the summer season (Lindner and Calama, 2013), inducing a decline in growth in Mediterranean forests (Peñuelas et al., 2001; Sánchez-Salguero et al., 2012) which may severely affect *P. pinea*'s distribution in the Iberian Peninsula (Benito Garzón et al., 2008).

The aim of the present study was to evaluate the effects of tree species composition and competition on *P. pinea* secondary growth in monospecific and in mixed stands in a series of 15 years with contrasting climatic conditions. The specific objectives of this analysis were to (a) compare the growth pattern response of *P. pinea* to intra and interspecific competition by fitting individual distance dependent tree models; (b) assess the pattern of interannual variability in competition within and between species associated with climatic fluctuations. Our first hypothesis is that the effect of competition on growth is different in monospecific vs. mixed *P. pinea* stands as shown in other studies (Pretzsch et al., 2013; Río et al., 2014b). In accordance with the principle of "niche complementarity" we further expect to find differences in competition between and within species (Loreau et al., 2001). Based on the same principle, our third hypothesis is that intra-specific interactions will be more competitive than inter-specific interactions

(Forrester, 2014; Pretzsch, 2014) due to inter-specific differences in crown and root architecture and intra-specific differences due to inter-specific interactions. Finally, we expect that the effects of competition in dry and wet years will not be the same in monospecific and mixed stands with a growth enhancement in mixed vs. monospecific stands on driest years (Pugnaire et al., 2000).

2.2. Material and methods

2.2.1. Data collection and processing

2.2.1.1. Study area

The study area is located in the limestone plain areas in the east of the province of Valladolid (Spain), within the geographical region of the Spanish Northern Plateau, defined by the river Duero basin. “Limestone areas” is a specific natural unit within the existing general ecological stratification of the region, based on soil, climate, rock and orographic attributes (Gordo, 2004). Altitude ranges from 800 to 890 m, the average annual precipitation is highly variable (between 220-630 mm) and the mean annual temperature is 11ºC. The area has a Mediterranean continental climate with a characteristic dry summer period during which mean monthly precipitation is 21 mm. The main types of soils found in the area are alfisols, entisols and inceptisols, with an average water holding capacity (WHC) of 248 mm/m.

2.2.1.2. Composition

In the province of Valladolid, *P. pinea* occupies 74,000 ha (29,000 ha are monospecific stands, 33,000 are mixed stands with other conifers and 12,000 ha are mixed stands with hardwoods). Mixed stands with hardwoods represent the most diverse and complex forest systems in the region and are mainly located in limestone plain areas.

In these stands *Pinus pinea* grows with *Quercus ilex* subsp. *ballota* (Desf.)) Samp. and *Quercus faginea* subsp. *faginea* Lam., *Juniperus thurifera* L. and *Pinus pinaster* Aiton. The present study will focus on these more complex admixtures, which are considered to reach the maximum level of specific diversity within the region (Madrigal, 2014).

2.2.1.3. Stand management

From the end of the 19th century to mid-1970s the management of *P. pinea* forests in the Spanish Northern Plateau tried to maximize timber production while maintaining a secondary pine nut production. To attain this aim, *P. pinea* stands were transformed into monospecific even-aged high stocking stands by applying clearcuts by strips followed by direct seeding (Gordo, 1999; Montero et al., 2008). Other codominant species, like *Quercus* species, were either removed from these stands, or intensively coppiced for fuelwood. This type of silviculture was carried out in public forests until the 1980s, when high prices of edible pine nuts in the international markets set nut production as the main management objective. When nut production is the main objective, thinnings must aim for low densities to encourage crown development, avoid crown overlapping and promote individual cone production (Calama et al. 2008). Traditional nut oriented management focuses on these low density stands, proposing high intensity thinnings and shelterwood system regeneration methods. These practices have resulted in large open gaps where *P. pinea* has regeneration problems (Manso et al., 2012), but where other species are nowadays naturally recruited.

Land ownership has played a critical role in the maintenance of *P. pinea* admixtures with *Quercus* and *Juniperus.* Currently most of these complex mixed stands grow in lands that were privately owned until the 1980s. The lack of investments from private owners and the absence of management plans and previously described practices contributed to the preservation of these mixtures. Most of these lands were sold to the regional government in the 1980's. At this time selective cuttings began to be carried out to favour all tree species in mixed stands. Current management focuses on a tree selection system, promoting growth and regeneration of individuals of all the species. Conservation of biodiversity is the main management objective in these forests, together with other ecosystem services such as cone and nut production, timber and biomass, mushrooms and recreational uses.

2.2.1.4. Experimental design – data set

Data for this study were collected in publically owned forests within the limestone areas in the Northern Plateau. Data were collected in two types of forests according to species composition: monospecific even aged *P. pinea* forests and heterogeneous mixed forests where *P. pinea* grows mixed with hardwood species. Attributes of the stands are shown in Table 2.1.

Homogeneity in site conditions between monospecific and mixed stands was tested by comparing soil attributes obtained through soil analysis carried out in three mixed and six monospecific plots selected among the analysed plots. Comparisons revealed non-significant differences among the soil attributes analysed: water holding capacity (p-value = 0.9216); % organic matter (p-value = 0.6622); % nitrogen in superficial layers (p-value = 0.6279); pH (p-value = 0.4364); clay content (p-value = 0.6656) and sand content (p-value = 0.1788).

Table 2.1. Attributes of the stands, estimated using trees with diameter at breast height ≥5cm. N: stand density; G: basal area; Dg: quadratic mean diameter; H: mean total height; min: minimum; av: average; max: maximum. Blank cells indicate the species was not present.

		Monospecific stands			Mixed stands		
		min	av	max	min	av	max
N (stem/ha)	Total	38	211	884	173	394	943
	P. pinea	38	211	884	73	191	497
	Q. ilex or *Q. faginea*				27	85	163
	J. thurifera				30	109	253
G (m^2/ha)	Total	4.66	14.39	31.42	9.26	12.62	18.82
	P. pinea	4.66	14.39	31.42	7.25	11.20	16.77
	Q. ilex or *Q. faginea*				0.07	0.42	0.88
	J. thurifera				0.25	1.00	1.54
Dg (cm)	*P. pinea*	16.32	33.27	65.81	20.73	30.98	36.32
	Q. ilex or *Q. faginea*				5.02	7.30	10.11
	J. thurifera				6.67	11.56	17.50
H (m)	*P. pinea*	6.30	9.99	16.03	7.18	8.37	9.16
	Q. ilex or *Q. faginea*				3.71	4.33	4.66
	J. thurifera				4.09	5.33	6.05

2.2.1.5. Even aged monospecific stands

Thirty-three circular plots of variable area were installed in monospecific even aged stands of *P. pinea* L (Fig. 2.1). These plots are part of a network of permanent plots for monitoring growth and cone production established by INIA-CIFOR in 1995. Each of these plots comprised 20 trees with dbh > 5 cm. The design used to select the plots tried to include a balanced representation of the age range, density and site index available. Around each plot, a buffer area with similar conditions was defined. During plot installation, different measurements were made in all the trees within the plot: tree coordinates, diameter at breast height (dbh), stump diameter, total height, height to crown base, and four perpendicular crown radii measured in cardinal directions. Plots were remeasured in 2001 and 2008. During the period of study some trees were felled due to common thinning practices, but years of cut were recorded. In fall 2011 the 5 trees closest to the centre of each plot were cored in two perpendicular directions at 1.30 m above ground using a Pressler increment borer in order to obtain the tree ring growth series. Cores were dried at 35ºC for one week, mounted on wooden slides and polished using sand paper of different grain sizes. After being processed, samples were scanned and visually dated with Lignovision 1.37 software (Rinntech, Heidelberg, Germany).

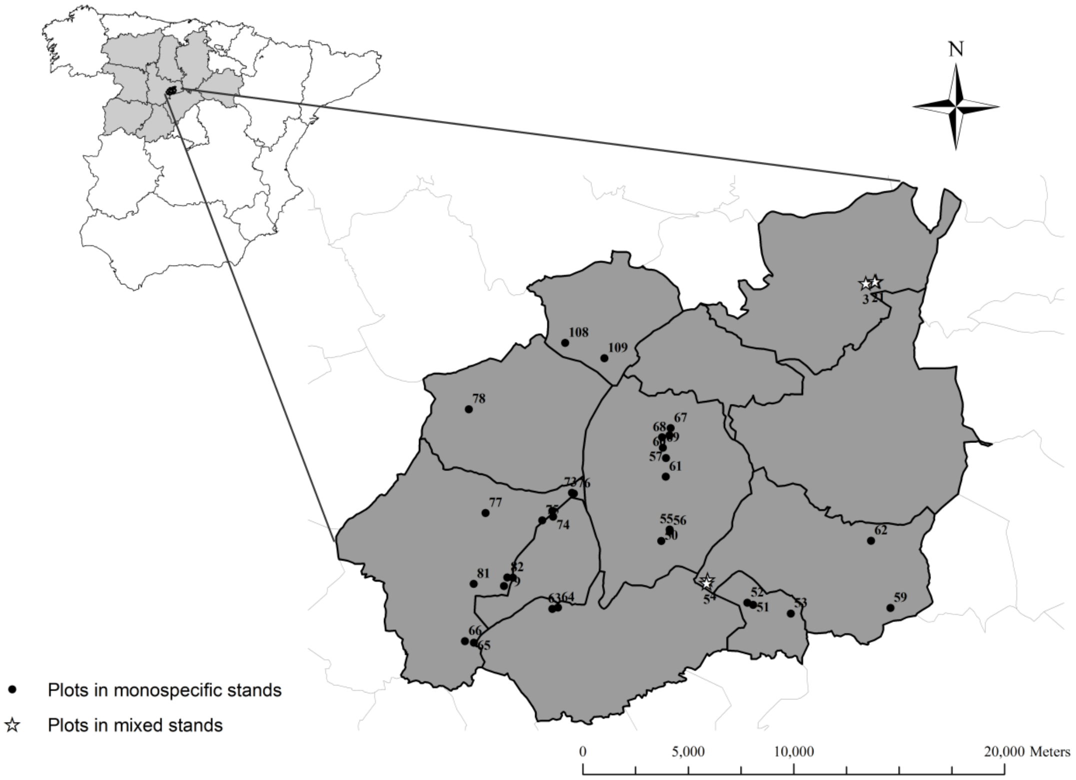


Fig. 2.1. Location of the study area and the experimental plots.

2.2.1.6. Mixed stands

Five rectangular plots (50m x 60m) were installed in mixed heterogeneous stands of *P. Pinea* during the summer of 2011 (Fig. 2.1). The selection of these stands tried to cover the different typologies of mixtures of *Pinus pinea-Quercus-Juniperus* identified in the area. Within each plot, the (x, y) coordinates for trees over 1.30m high were recorded. Position and diameter of all the stumps remaining from earlier cuttings were also recorded. In the trees taller than 1.30m we measured dbh, stump diameter, total height, height to crown base, and four perpendicular crown radii measured in cardinal directions. In order to study radial growth a representative sample of trees was selected covering the whole range of diameters identified in the study area. Radial increment measurements were obtained from 23-30 *P. pinea* trees per plot, 10 *J. thurifera* trees per plot, 10 *Q. faginea* trees per plot and 3-4 *Q. ilex* per plot. *P. pinea* radial increment cores were obtained as the average growth from two perpendicular measurements taken at 1.30 m above ground using a Pressler increment borer. Considering that the study area is flat and that most *J. thurifera* and *Q. faginea* trees were young individuals, with dbh less than 5cm, it was assumed that cross sections of these two species were circular, and so only one core per tree was extracted for these two species. Due to the difficulty for extracting cores in *Q. ilex,* the radial increment for the species was obtained from cross section slices taken at breast height in felled trees. Cores were dried, mounted and sanded. Cross section slices were dried at 40ºC for 15 days and polished. *P. pinea* samples were scanned and ring width measurements were visually dated with Lignovision 1.37 software. For *Q. faginea*, *Q. ilex* and *J. thurifera* –where rings are not so easily visible as in *Pinus* species-samples ring width was measured with a resolution of 0.01mm using LINTAB measurement equipment fitted with a stereoscope and analysed with TSAP software

(Frank Rinn, Heidelberg, Germany). Cross dating was performed visually using standard methods.

2.2.2. Data analysis and statistical methods

2.2.2.1. Modelling approach

In order to attain the specific objectives we propose a modelling approach. Annual basal area increment of the *P. pinea* cored tree *i* within plot *s* attained during year *t* (BAI_{ist}), covering the period 1997-2011, was used as the dependent variable in the models. Basal area increment of subject tree *i*, from plot *s*, in the year *t* was obtained from radial increment data (RI_{ist}), computed by averaging the measured ring widths from radial increment cores obtained at tree breast height (1,30 m), and tree dbh at the beginning of the year *t*.

The choice of BAI instead of radial increment (RI) or diameter increment (DI) as a response variable in growth models has been widely discussed in the literature. BAI is generally preferred as it is less dependent on age than DI, correcting the trend of decreasing ring width with increasing tree size (Biondi and Qeadan, 2008) while preserving low frequency variability (Martin-Benito et al., 2010).

To attain normal distribution of the residuals, reduce heterocedasticity and linearize the relationship between the dependent variable and the variables used as predictors, a natural logarithmic transformation of the basal area increment was performed (log (BAI_{ist})).

Dependence among the log-transformed annual basal area increment and several distance dependent competition indices (AOI, see below) were evaluated by means of linear models. In the complete version of the model, competition was divided into within-species (AOI_w, competition assessed by *P. pinea* trees) and between-species (AOI_b, competition assessed by other species) competition. Moreover, in the case of within species competition we differentiated among the competition exerted in monospecific (AOI_{wm}) and mixed (AOI_{wx}) stands. Apart from competition indices, tree section at the beginning of each year (g_{ist}) was included in the model (Pesonen et al., 2009). Finally, in order to account for the effect of climate on growth in year *t*, we tested the inclusion of mean annual precipitation by year (pp_t).

The data had a spatially hierarchical structure: individual trees which grow within plots and plots that are located in different stands. Also plots were neither installed nor measured in the same year, indicating that there is also a level of variability associated with the period of measurement. Since data from the same tree, plot and period tend to resemble each other to a more than average extent, the observations could be largely correlated. A random parameter modelling approach was therefore adopted, using mixed models (Henttonen et al., 2009; Pesonen et al., 2009). Mixed models are composed of a fixed part, common to the complete population, and random components acting at each sampling level. In the complete model, AOI_{wm}, AOI_{wx}, AOI_b, g and pp were included as fixed effects. Random intercepts at tree (u_i), plot (v_s) and year (w_t) level were included in the model. Apart from this, year specific random parameters (p_t, x_t, k_t) affecting competition indices were also included. Thus, a general expression for our evaluated model is:

$$\log\ (BAI_{ist}) = a + u_i + v_s + w_t + bg_{ist} + jpp_t + [c + p_t]AOI_{wm} + [d + x_t]AOI_{wx} + [f + k_t]AOI_b + e \quad (1)$$

2.2.2.2. Distance dependent competition indices

The competition indices used in this study are distance dependent competition indices developed by Bella (1971) and later modified by Tomé and Burkhart (1989). They are area overlap indices (AOI) which calculate a tree size related influence zone around each tree (eq. 2).

$$AOI_i = \sum_{j=1}^{n} \frac{ZO_{ij}}{ZA_i} \times \left(\frac{dbh_j}{dbh_i}\right)^k \qquad (2)$$

These competition indices sum over *n* (the number of tree competitors whose zone intersects that of the subject tree i) the proportion of the influence zone of the subject tree (ZA_i) that is included in the influence zone of each competitor (ZO_{ij}) (Fig. 2.2). These proportions are weighed by the term $\left(\frac{dbh_j}{dbh_i}\right)^k$. where dbh_i and dbh_j are diameter at breast height of the subject tree i and of the competitor tree j respectively; and k is a power factor. This family of indices has been applied effectively in prior studies in uneven-aged *P. pinea* stands (e.g. Calama et al., 2008). These indices were calculated only for *P. pinea* cored trees for each one of the 15 years of study. Edge effect was corrected using Martin et al. method (1977).

Evaluated alternatives were all possible combinations between k = 0 and 1 and radius of influence zone area equal to R = 10, 15, 20, 25, 30 and 40 times the diameter at breast height, resulting in 12 potential combinations. We assumed that the area of influence for pine trees will be the same whether they are growing in monospecific or in mixed stands, but the area of influence for other species could be different. Thus the total number of combinations of competition indices in model (1) is 12 x 12 = 144. Selection of the most adequate values for the radius of influence of pines and other species, as well for the weighting factor k was carried out by fitting the 144 mixed models and comparing them in terms of the Akaike’s Information Criterion (AIC).

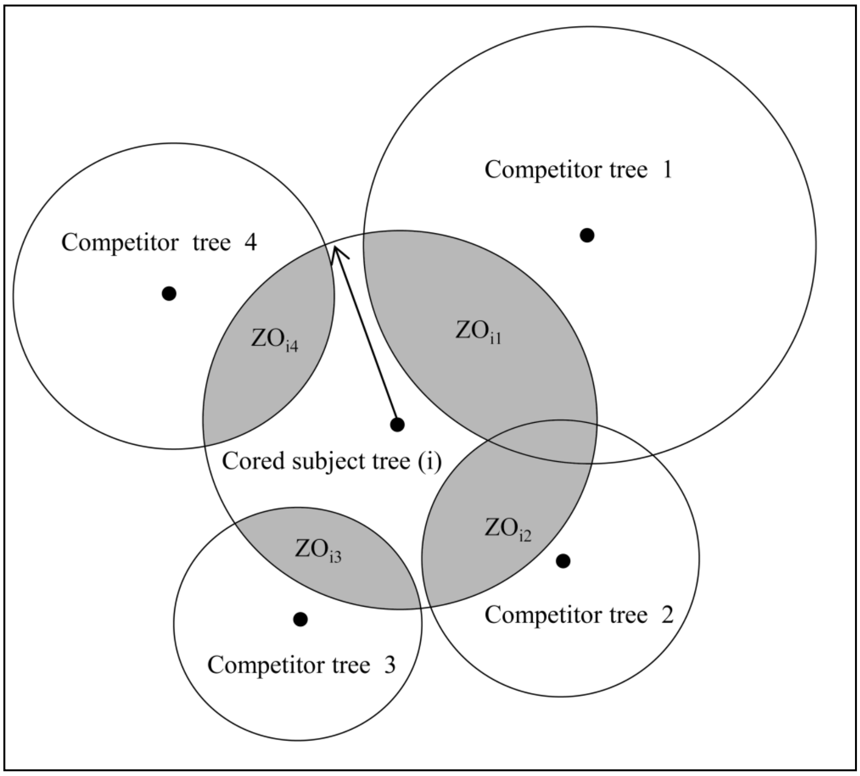


Fig. 2.2. Influence zone area of a cored subject tree (i) and areas of zone overlap between the subject tree and four competitor trees (ZO$_{ij}$).

2.2.2.3. Backdating

The individual tree basal area increment models were constructed for a growth period of 15 years (1997-2011) which meant that data on both dbh and annual basal area increments of each year of the series 1997-2011 were needed for each tree to be modelled. Apart from this, data on annual dbh for all the trees from all the species within the plot are required in order to calculate the AOI competition indices for each tree and year. The aim of the backdating was to reconstruct the state of the plots in each year of the series of study. We knew the diameters at breast height for all trees at the time of plot installation (dbh$_{is1997}$ in the case of monospecific plots, dbh$_{is2011}$ in the mixed plots) and the individual annual radial increment for the subsample of trees cored of each plot (RI$_{ist}$). In the cored trees, dbh$_{ist}$ at the beginning of a given year *t* was obtained by either adding (monospecific plots) or subtracting (mixed plots) twice the annual radial increment (average from the two observed radial increments). In order to reconstruct the state of the rest of the trees that had not been cored, the diameter increment for a given year "DI_{ist}" was estimated by fitting simple linear regression models by plot for each tree of each species and year:

$$DI_{ist} = a_{st} + b_{st}\left(dbh_{ist\_2011}\ \right) \quad (3)$$

We used the data of stump diameter and dbh from standing trees in order to fit simple linear models which allow to determine dbh for felled trees in the year previous to felling. From this estimated value, we used the latter model to reconstruct the diameter of the felled tree for each year between 1997 and the year when the tree was felled.

2.2.2.4. Hypothesis testing

To contrast our hypotheses we compared model (1), from now on defined as the *complete model*, with *reduced models* where some assumptions are considered. We also compared the different *reduced models*. Apart from between model comparison, we evaluated the absolute values and sign of the parameter estimates associated with competition indices in order to identify differences in between and within species competition patterns.

Hypothesis (i) states that the effect of competition on growth is different in monospecific than in mixed *P. pinea* stands. For this purpose we fitted model (4) and model (5) (eq. 4 and 5). Model (4) considers that competition is the same in monospecific and in mixed stands no matter what species are competing and growing on the stand; hence a single competition index is required (AOI_{all}). Model (5) considers that the pattern of competition is different depending on stand composition. In this case, $AOI_{monospecific}$, for monospecific stands, equals AOI_{wm}; while AOI for mixed stands, AOI_{mixed}, is the sum of the competition exerted by pines (AOI_{wx}) and by the other species (AOI_{b}), regardless of the species considered. To contrast hypothesis (i) we compared models (4) and (5).

$$\log\left(BAI_{ist}\right) = \left(a + u_i + v_s + w_t\right) + bg_{ist} + jpp_t + \left(c + p_t\right)AOI_{all} + \varepsilon \qquad (4)$$

$$\log\left(BAI_{ist}\right) = \left(a + u_i + v_s + w_t\right) + bg_{ist} + jpp_t + \left(c + p_t\right)AOI_{monospecific} + (d + x_t)AOI_{mixed} + \varepsilon \qquad (5)$$

For testing Hypothesis (i) we compared the best alternative – in terms of AIC – for eq. 4, among the 12 potential AOI evaluated, with the best alternative for eq. 5, where in this case 144 combinations were evaluated. Comparisons between the best models for (4) and (5) where carried out by means of weighted AIC (see below).

Hypothesis (ii) postulates that there are differences in competition between and within species. To contrast Hypothesis (ii), we compared model (4) with the reduced model in eq. 6, which considers that the effect of within species competition among pine trees on pine growth is the same in monospecific and in mixed stands (AOI_w, which equals AOI_{wm} in monospecific stands and AOI_{wx} in mixed stands), but different from competition done by other species (AOI_b).

$$\log\left(BAI_{ist}\right) = \left(a + u_i + v_s + w_t\right) + bg_{ist} + jpp_t + \left(c + p_t\right)AOI_w + \left(d + x_t\right)AOI_b + \varepsilon \qquad (6)$$

Hypothesis (iii) is formulated to elucidate if intra-specific interactions are more competitive than inter-specific interactions and to identify differences in intra-specific due to inter-specific interactions. To test this hypothesis we compared model (6) with the complete model (1), where we assume different effect of within species competition in monospecific than in mixed stands.

Trees considered for the computation of the different AOI used in models (1), (4), (5) and (6) are shown in Table 2.2.

Hypothesis (iv) postulates that the effect of competition in dry and wet years is not constant in monospecific and mixed stands; thus, we expect that growth response in drier years will be better in mixed than in monospecific stands. To test Hypothesis (iv) year random parameters affecting competition indices (p_t, f_t and k_t from model (1)) and mean annual precipitation were plotted for the whole period of study (1997-2011).

Table 2.2. Trees considered for each AOI computation. *x*: trees that are considered for AOI computation; 0: trees that are not considered for AOI computation. AOI_{all}: Competition index common to all species, irrespective of the type of stand; AOI_{mixed}: Competition index common to all species in mixed stands; $AOI_{monospecific}$: Competition index in monospecific stands; AOI_{wm}: Competition index for within species competition in monospecific stands; AOI_w: Competition index for within species competition irrespective of the type of stand; AOI_{wx}: Competition index for within species competition in mixed stands; AOI_b: Competition index for between species competition irrespective of the type of stand.

		Monospecific stands	Mixed stands	
	Model	*P. pinea*	*P. pinea*	Other species
AOI_{all}	(4)	*x*	*x*	*x*
AOI_{mixed}	(5)	0	*x*	*x*
$AOI_{monospecific} = AOI_{wm}$	(1) , (5)	*x*	0	0
AOI_w	(6)	*x*	*x*	0
AOI_{wx}	(1)	0	*x*	0
AOI_b	(1) , (6)	0	0	*X*

2.2.2.5. Model fitting, evaluation and comparison

Analyses were carried out using the MIXED procedure in SAS 9.2 (SAS Institute Inc., 2009).The linear mixed models (1), (4), (5) and (6) were fitted through maximum likelihood, comparing all the possible combinations of distance dependent competition indices, and selecting for each model the combination that minimized AIC. It was also checked through the t-test that all the fixed regression parameters were significant at the level P = 0.05. The significance of random effects was tested with the Wald test. Temporal autocorrelation among observations coming from the same tree was tackled by including a first-order autorregressive term AR(1) in the variance-covariance matrix for the residuals.

Once the best combination of AOI indices was selected for each model, a test of contrast of the hypothesis between models was carried out by means of weighted AIC for model *i* -W_i(AIC)- which is a measure of the relative likelihood of the model:

$$\mathrm{W_i(AIC)} = \frac{\exp\left\{-\frac{1}{2}[\mathrm{AIC_i} - \mathrm{AIC_{min}}]\right\}}{\sum_{k=1}^{n} \exp\left\{-\frac{1}{2}[\mathrm{AIC_k} - \mathrm{AIC_{min}}]\right\}} \tag{7}$$

where $\mathrm{AIC_{min}}$ is the minimum value of AIC among the compared *n* models. W_i(AIC) can be interpreted as the probability that model *i* is the best model (in the AIC sense, that minimizes the Kullback–Leibler discrepancy), given the data and the set of candidate models (Wagenmakers and Farrell, 2004). Thus, for carrying out pairwise comparisons between models, we used the normalized probability $p\ i_j$ of model i explaining better than model j, defined ratio among weighted AIC corresponding to model i and the sum of weighted AICs for models i and j:

$$p\ i_j = \frac{W_i(AIC)}{W_i(AIC) + W_j(AIC)} \tag{8}$$

2.3. Results

Table 2.3 shows the best combination of competition indices resulting in lower AIC for each fitted model, as well as the parameter estimates for the fixed effects and the random variance components. Best AOI always resulted in a radius of influence R of 30 times dbh for all the indices where *P. pinea* competitors were considered. For the indices where only other species apart from *Pinus* are considered ($\mathrm{AOI_b}$), the radius of influence was larger, resulting in 40 times dbh. Concerning the weighting factor, for those indices where *P. pinea* is considered, best results were obtained with k = 1, indicating asymmetry on competition, i.e., that the competition of a large tree over a smaller tree was larger than the contrary. On the other hand, between species competition indices (AOI_b) presented a weighting factor $k = 0$, indicating symmetric effects.

Once the best combination of AOI indices was selected for each model, pairwise comparisons between the models help to contrast the main hypotheses.

Table 2.3. Parameter estimates for the best AOI combination for models (1), (4), (5) and (6). R: radius of influence (times dbh), k: weighting factor. * p-value <0.05, ** p-value <0.01, *** p-value <0.001. Blank cells indicate that the effect was not considered in the model. AOI_{all}: competition index common to all species, irrespective of the type of stand; $\text{AOI}_{\text{monospecific}}$: competition in monospecific stands; AOI_{wm}: competition index for within species competition in monospecific stands; $\text{AOI}_{\text{mixed}}$: competition index common to all species in mixed stands; AOI_{w}: competition index for within species competition_irrespective of the type of stand; AOI_{wx}: competition index for within species competition in mixed stands; AOI_{b}: competition index for between species competition irrespective of the type of stand; g: tree section (cm^2); pp: mean annual precipitation (mm/year); σ^2: Random parameter variance; AR(1): First-order autorregressive parameter; AIC: Akaike information criterion.

Effect		Complete (1)	(4)	(5)	(6)
AOI_{all}	R		30		
	k		1		
	Estimate		-0.0962***		
$\text{AOI}_{\text{monospecific}}$ = AOI_{wm}	R	30		30	
	k	1		1	
	Estimate	-0.0808***		-0.1093***	
$\text{AOI}_{\text{mixed}}$	R			30	
	k			1	
	Estimate			-0.0822***	
AOI_{w}	R				30
	k				1
	Estimate				-0.0951***
AOI_{wx}	R	30			
	k	1			
	Estimate	-0.1100***			
AOI_{b}	R	40			40
	k	0			0
	Estimate	0.0891*			0.1108*
G	Estimate	0.0005***	0.0005***	0.0005***	0.0005***
Pp	Estimate	0.0018***	0.0018***	0.0018***	0.0018***
Intercept	Estimate	1.7276***	1.7667***	1.7454***	1.7462***
σ_u^2 (tree)	Estimate	0.0645***	0.0596***	0.0658***	0.0593***
σ_v^2 (plot)	Estimate	0.1047***	0.1102***	0.1041***	0.1155***
σ_w^2 (year)	Estimate	0.0279**	0.0206**	0.0285***	0.0204***
σ_p^2 (year x AOI)	Estimate	0.0006*	0.0001*	0.0008*	0.0001*
σ_k^2 (year x AOI)	Estimate	0.0026*			0.103*
σ_x^2 (year x AOI)	Estimate	0.0001*		0.0001*	
AR(1)	Estimate	0.5767***	0.5850***	0.5762***	0.5778***
AIC		403.0	635.3	419.0	514.9
Number of evaluated models		144	12	144	144

As shown in Table 2.4, with a probability over 0.9997, the complete model explains our observed data better than the other models. Concerning pairwise comparisons to contrast hypothesis, for Hypothesis (i), model (5), assuming differential response in growth to competition in monospecific vs. mixed stands, shows a normalized probability over 0.9999 of explaining better than model (4), which assumes common response to competition in monospecific and mixed stands, providing a strong evidence for supporting Hypothesis (i).

Table 2.4. Pairwise comparisons between models (1), (4), (5) and (6). AIC: Akaike information criterion; AIC_{min}: Minimal AIC of all models considered; $W_i(AIC)$: Weighted AIC for model i; P_{iq}: Pairwise comparison between model i and model q.

Model	AIC	AIC-AIC_{min}	$W_i(AIC)$	Pi4	Pi5	Pi6	Pi1
(4)	653.3	250.3	4.445E-55		<0.0001	<0.0001	<0.0001
(5)	419.0	16.0	3.354E-04	>0.9999		>0.9999	0.0004
(6)	519.9	116.9	4.124E-26	>0.9999	<0.0001		<0.0001
Complete (1)	403.0	0	0.9997	>0.9999	0.9997	>0.9999	

For Hypothesis (ii), superiority of model (6) over model (4) (probability >0.9999) indicates that there is a differential effect of between and within species competition over growth. In this case, as $c < 0$ and $d > 0$, our results indicate that the presence of other species exerts a positive influence on *P. pinea* growth, at least in the degree of mixture found within the region.

Hypothesis (iii) assumes that apart from between species competition, there exists a differential pattern of within species competition in *P. pinea* between monospecific and mixed stands. Superiority of the complete model, with a probability over or equal to 0.9997 of explaining our observed data better than the other models, confirms this hypothesis. In this case, $|c| < |d|$, with $c<0$ and $d<0$, which indicates that the same level of within species competition results in higher growth of *P. pinea* trees in a monospecific stand than in a mixed one. Apart from this, parameter $f>0$, which indicates that the presence of other species facilitates growth of pine trees in mixed stands.

Hypothesis (iv) postulates that the pattern of *P. pinea* growth response to within species competition exerted by pine trees in monospecific and mixed stands and between species in mixed stands is specific for each year, showing different response in dry and humid years. The significant year x AOI effect for the three competition components in the complete model supports this hypothesis. Fig. 2.3 shows the annual random parameter affecting within species competition index in monospecific and mixed stands, plotted against annual precipitation. Positive values of the random effect indicate that for that year growth is greater than the expected, given the current level of competition.

According to Fig. 2.3, the most interesting finding was that after 2002, the second driest year within the series, random year effect affecting within *Pinus* competition index in monospecific stands show a declining trend, aggravated after 2005 drought. On the other hand, neither the random year effect affecting within species competition in mixed stands nor the effect associated with between species competition show this declining effect, presenting a prompt recovery after this severe drought episode. This indicates that, given the same level of competition, the growth of *P. pinea* in monospecific stands following drought years (2002 and 2005) has been lower than that expected on a mixed stand, showing a delayed effect of this severe drought extended up to five years. This trend is also supported by Fig. 2.4, showing relative values of basal area increment (BAI/g) for monospecific and mixed stands, where increments are larger in monospecific stands up to 2002, while from that year up to the end of study – coinciding with a drier and warmer period - *Pinus pinea* in mixed stands attained larger increments.

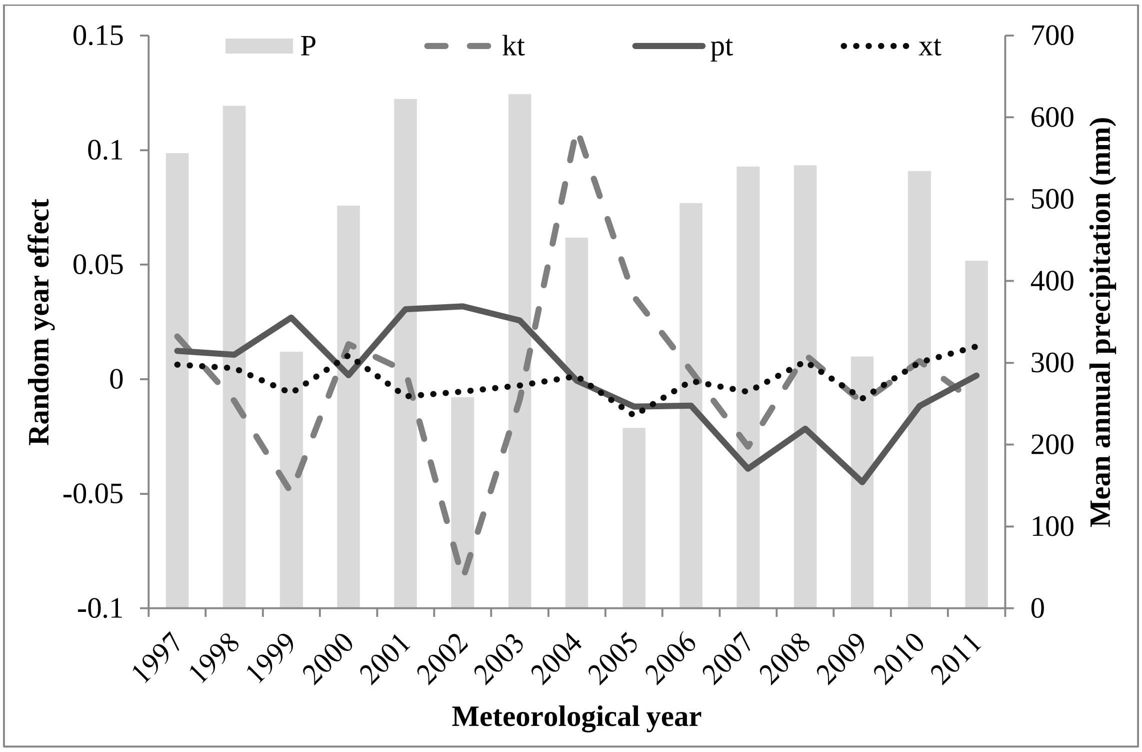


Fig. 2.3. Random year effects (RYE) associated to each competition term in model (1) plotted against mean annual precipitation. Mean annual precipitation (P, mm); RYE associated to between species competition in mixtures (k_t); RYE associated to within species competition in monospecific stands (p_t); RYE associated to within species competition in mixed stands (x_t) for the period 1997-2011 (Valladolid meteorological station).

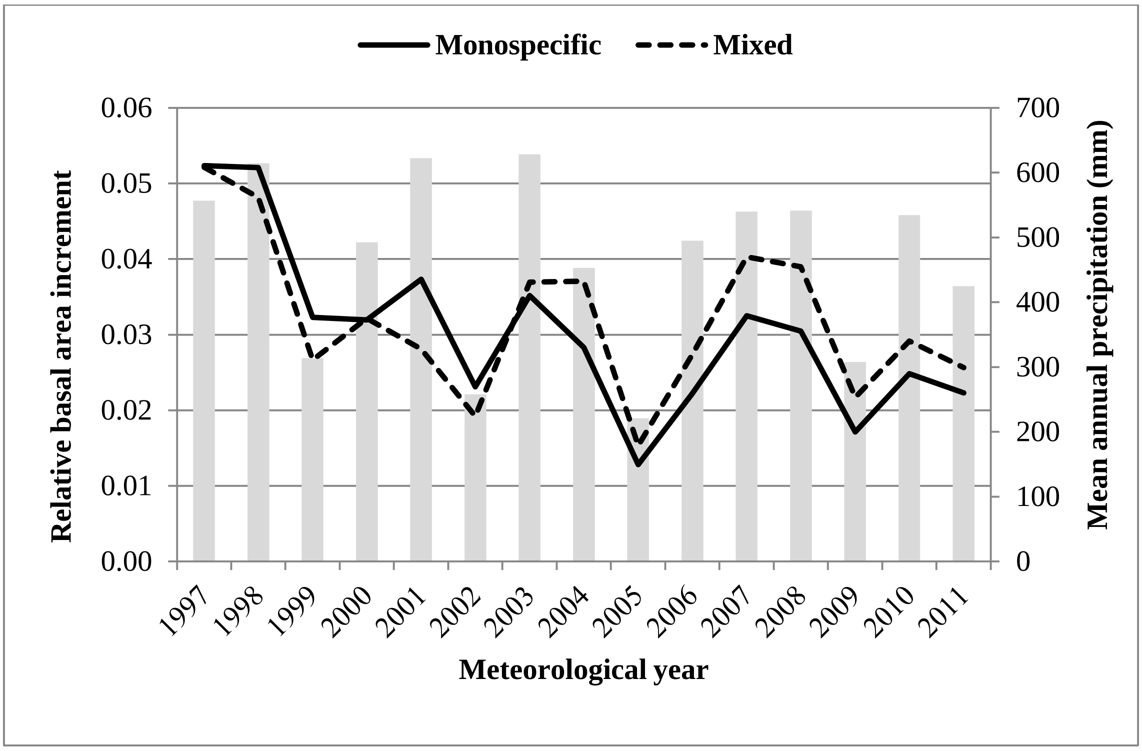
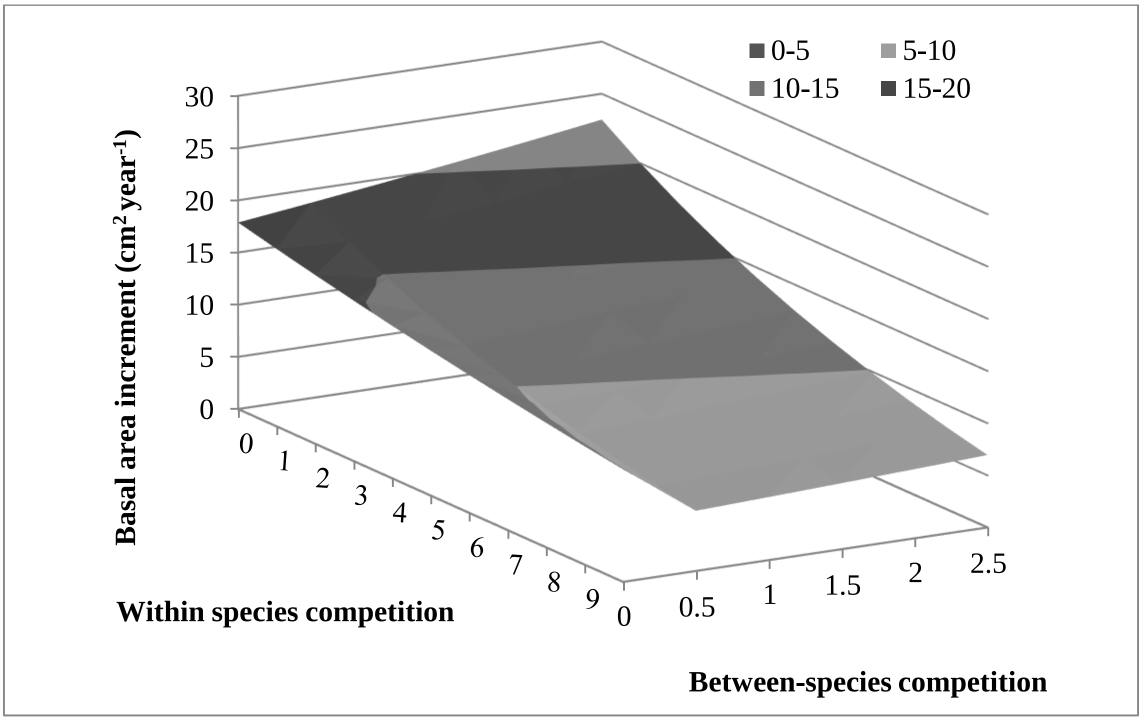


Fig. 2.4. Relative basal area increment in mixed and monospecific stands obtained from model (1) plotted against mean annual precipitation (mm).

Fig. 2.5 shows the model predictions from complete model [1] for annual basal area increment in an average *P. pinea* tree (25 cm dbh) growing in a mixed stand, for the years 2001 and 2005, as a function of between and within species competition. Year 2001 was a very humid year (total precipitation 630 mm), located just after a favorable period (extending from 1996) while 2005 is the driest year of the series (total precipitation 230 mm). As can be seen, we obtained a positive effect of the presence of other species, at least up to the level of between-species competition shown in these stands. This effect was steeper in the absence of within species competition (Ao031<1). Under a high degree of within species competition (Ao031 > 8), we observed that in a humid year there was not a positive effect of mixture, thus indicating total use of resources by the dominant species. However, in a dry year, as 2005 (and all the years afterwards), between-species competition exerted a positive effect over growth, even under the highest levels of within-species competition.



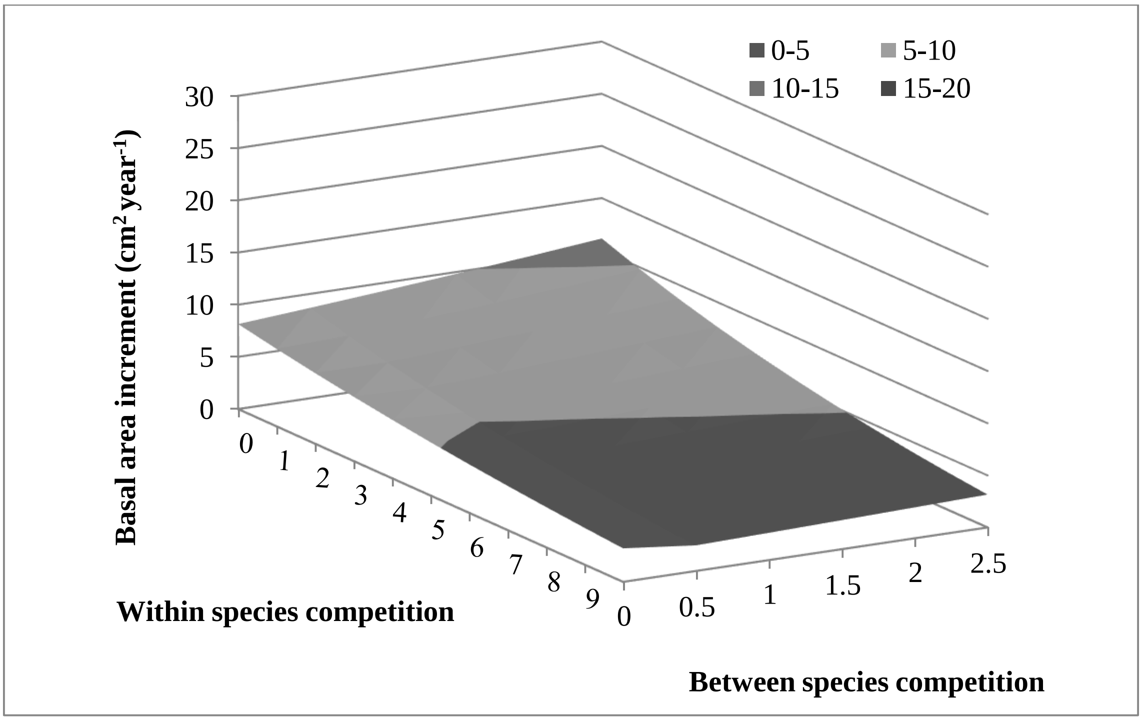


Fig. 2.5. Effect of within and between species competition over annual basal area increment for a tree with dbh = 25 cm, in a humid year (2001, above) and a dry year (2005, below).

2.4. Discussion

2.4.1. Competitive reduction and enhanced tree growth in mixed vs. monospecific stands

Our results agree with the niche complimentarity theory (Loreau et al., 2001), showing an enhanced growth in pine trees growing in mixed stands compared with those growing in monospecific stands. Pairwise comparisons between basal area growth models of pines growing in monospecific and mixed stands highlight the importance of plant interactions in determining the growth response of trees to environmental changes. The lower effect of competition on growth, for equal density levels, in mixed versus monospecific stands could be due to niche complementarity and/or owing to a direct support effect of the species coexisting in mixed stands (Garber and Maguire, 2004).

Resource uptake might be higher in mixed stands than in monospecific stands due to a temporal and spatial niche separation of the tree species present in mixed stands (Brown, 1992; Perot and Picard, 2012). Pugnaire et al. (2000) indicate that niche partitioning may occur through many aboveground and belowground mechanisms. From an aboveground perspective, species can stratify within the canopy if they have contrasting traits for light interception or different water use strategies. Recent studies in mixed *P. pinea* stands in the Spanish Central Range indicate that *P. pinea* and *Q. ilex* have different water regulation strategies (Mayoral et al., 2015; Pardos et al., 2014). Perot and Picard (2012) studied a conifer-broadleaf forest with species having very contrasting traits for light interception as well as different root distribution patterns (Brown, 1992). Light interception by the pine foliage was lower than the light interception by the oak foliage (Balandier et al., 2006; Sonohat et al., 2004) and indicated that the complementarity of the two species for the use of light, as well as for nutrient and water use, is a strong hypothesis to explain a productivity increase in these mixed stands.

Possible causes of niche complementarity can be inferred relating within and between species competition with the mode of competition (size-symmetric vs. size-asymmetric) (Río et al., 2014a). We obtained size-symmetric effects for competition between species. Completely size-symmetric competition or two-sided competition occurs where resource uptake among competitors is independent of their relative sizes and tends to be a belowground competition (Río et al., 2014a; Schwinning and Weiner, 1998). Following the same idea, our results suggest that in the mixed stands, *Q. ilex*, *Q. faginea* and *J. thurifera* are competing with *P. pinea* mainly for belowground resources. Moreover, the complementarity detected in interspecific interactions compared to intraspecific interactions could be due to root stratification. These results are consistent with the multistratified root system of *P. pinea* whose primary taproot aborts early but forms numerous secondary roots that grow far beyond their canopy projection sending vertical tertiary roots to deeper ground layers (Mutke et al., 2012). Mediterranean oaks have taproots more often when growing in drier environments than in mesic sites and have the capacity to send roots quite deep in the soil substrate when the soil can be penetrated (Canadell et al., 1996). Conversely, the root system of *Juniper* species is shallower and cannot access deep soil water (e.g. Gimeno et al., 2012).

Size-asymmetric results obtained for within species competition reflect that *P. pinea* trees are not equally affected by the scarcity of resources (Pugnaire et al., 2000) in a way that largest individuals obtain the majority of the contested resources (Schwinning and Weiner, 1998) suppressing the growth of their smaller pine neighbours. Although there is not a general relationship between the degree of size asymmetry and the particular growth limiting resource (Río et al., 2014a), many studies (Weiner et al., 1990; Wichmann, 2001) point to an association between size-asymmetric effects and above-ground competition for light. So despite water rather than light is the main factor limiting growth in sandy flatlands and dunes, where many *P. pinea* stands grow in the Spanish Northern Plateau (Mutke et al., 2012), our results indicate that intraspecific competition in limestone plain areas may also be controlled by light. Finally, the observed differences in the response to intraspecific competition in monospecific and mixed stands is in agreement with previous studies that indicate that the interspecific environment may foster differential patterns of crown and/or root expansion, with respect to their behaviour in monospecific stands (Dieler and Pretzsch, 2013). These differences could result in intraspecific differences in crown morphology, architecture and allometric relationships which can influence aspects as the absorbed photosyntetically active radiation, and subsequently, net primary productivity and tree growth (Pretzsch, 2014).

2.4.2. Differential secondary growth response of mixed vs. monospecific stands to drought events

Secondary growth decay in monospecific stands after 2002 drought event is in agreement with past studies that stated that the effect of drought may persist after the episode (Sánchez-Salguero et al., 2012). Both in dry years and on xeric sites less drought resistant trees, like *P. pinea*, may favour root growth at the expense of shoot growth (e.g. Comeau and Kimmins, 1989) in order to improve access to water and nutrients. Low growth in drought periods may be induced by scarce nutrient availability and capture due to reduced organic matter breakdown and mineralization, which are both dependent on moisture (Canadell et al., 1996; Pugnaire et al., 2000).

Our results suggest a positive effect of mixture on *P. pinea* basal area growth in water-stressed years. Other studies have reported similar growth benefits from interspecific interactions in mixed stands compared to monospecific stands in low growth years (Río et al., 2014b), when competition for belowground resources are expected to be even higher than in high growth years. Pretzsch et al. (2013) provide evidence of drought stress release through species mixing in mixed stands of European tree species. Hydraulic lift has been proposed as an atractive mechanism that could be implied in this growth enhancement in dry years (Zapater et al., 2011). This mechanism has already been described for *Q. ilex* and another pine species in the Iberian peninsula during the summer drought (David et al., 2007; Peñuelas and Filella, 2003). But the direct use of uplifted water by neighbour tree species has not yet been described in the Mediterranean basin. We believe that this topic deserves further investigation.

2.4.3. Management of composition and competition as a tool for adaptation to global change

Natural processes alone are too slow to withstand the expected environmental changes in the Mediterranean basin. In order to improve resistance and resilience in Mediterranean forests in Europe, planned adaptation measures must deal with drought stress in the region (Lindner and Calama, 2013). At drought prone sites, species mixing may improve forest resilience buffering the effect of inter-annual climate variation through shifts between competition in years with high resource availability and facilitation in high stress years (Río et al., 2014b). In the case of *P. pinea* forests, promotion of mixtures can be done by direct planting of *Quercus* and *Juniperus* seedlings under pine canopy, or by releasing advanced regeneration of complimentary species naturally installed after thinnings. Thinnings also enhance individual vigour of remaining trees of all the co-occurring species, and may play an important role in mitigating the extended drought events as they reduce natural mortality of standing trees, control competition, increase resilience to low soil moisture and improve the recovery in subsequent years after the dry periods (Garber and Maguire, 2004; Martin-Benito et al., 2010).

This work contributes to a better understanding of mixed forest performance, narrowing the knowledge gap in mixed stands management in the Mediterranean basin and helping to promote species coexistence as a tool to buffer the effects of climate change in the region.

Acknowledgements

We are grateful to the Forest Service of Castilla y León administration for permission and support to carry out the field experiment. We also wish to thank Mar Conde for her help in the data collection; Enrique Garriga for core mounting and sand processing; and Guillermo Madrigal for data collection and Fig. 2.1 elaboration. This study was financed by the projects AGL-2010-15521, RTA-2013-00011-C02-01 and AT-2013-004. And we also wish to thank Miren del Río for her feedback on a previous draft of this paper as well as an anonymous reviewer who provided constructive comments to improve this manuscript.

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Chapter 3

A new multifactorial approach for studying intra-annual secondary growth dynamics in Mediterranean mixed forests

Based on: de-Dios-García, J., Manso, R., Calama, R., Fortin, M., Pardos, M., 2018. A new multifactorial approach for studying intra-annual secondary growth dynamics in mediterranean mixed forests: Integrating biotic and abiotic interactions. Can. J. For. Res. 48. https://doi.org/10.1139/cjfr-2017-0139

Specific objectives:

- To determine the competition factors that define the daily potential secondary growth of the subject tree.
- To elucidate the main climatic factors that limit the daily potential girth increment for each tree species coexisting in *P. pinea* mixed stands.

Data:

- We obtained girth increment data from band dendrometers installed on 58 trees (*Pinus pinea* L., *Juniperus thurifera* L., and *Quercus ilex* subsp. *ballota* (Desf.) Samp.) from May 2012 to April 2015 in two stocking densities.

Methodology:

- Nonlinear multifactorial model considering daily and cumulative climatic effects together with inter- and intra-specific competition indices.

Main findings:

- Spatio-temporal niche separation between species.
- *Q. ilex* has a wider thermal amplitude, higher optimum temperatures for growth and a milder effect of drought.
- Secondary growth reduction for *P. pinea* and growth enhancement for *Q. ilex* in a future climate in these Mediterranean mixtures.

Resumen

El estudio de la dinámica de crecimiento intraanual mediante modelos matemáticos ha demostrado ser útil para caracterizar las diferencias en la fenología de la madera entre especies, así como las desviaciones en los crecimientos esperados como consecuencia del cambio climático. El objetivo de este trabajo fue determinar los factores climáticos y los rasgos de competencia inter e intraespecífica que dirigen la dinámica del crecimiento secundario intraanual en tres especies mediterráneas que coexisten de forma natural en la meseta norte española (*Pinus pinea*, *Juniperus thurifera* and *Quercus ilex*). Con este propósito obtuvimos datos de crecimiento en circunferencia de dendrómetros de banda instalados en 58 árboles entre mayo de 2012 y abril de 2015. La mitad se colocaron en una parcela de alta densidad y la otra mitad en una parcela de baja densidad. Estos datos fueron analizados a través de un modelo no lineal multifactorial considerando efectos climáticos diarios y acumulativos junto con índices de competencia inter e intraespecíficos. Nuestros resultados proporcionan evidencia de una separación espacio-temporal de nichos entre especies. Comparado con otras especies *Q. ilex* mostró una mayor amplitud térmica, una mayor temperatura óptima de crecimiento y un efecto más leve de la sequía en su crecimiento secundario. Según las proyecciones climáticas actuales las simulaciones hechas con nuestro modelo predicen una reducción del crecimiento secundario en *P. pinea* y una mejora del crecimiento de *Q. ilex* en estas masas mixtas mediterráneas.

Palabras clave

Dendrómetros; masas mixtas; cambio climático; modelos mixtos no lineales; especies mediterráneas.

Abstract

Studying intraannual growth dynamics through a modelling approach has proved useful for characterizing differences in wood phenology between species and deviations from the expected tree growth due to climate change. The aim of this paper was to determine the climatic factors and the inter- and intraspecific competition traits that drive intraannual secondary growth dynamics in three Mediterranean tree species that naturally coexist in the Spanish Northern plateau (*Pinus pinea*, *Juniperus thurifera* and *Quercus ilex*). For this purpose we obtained girth increment data from band dendrometers installed on 58 trees from May 2012 to April 2015. Half of them were located in a high-density plot and half in a low-density plot. These data were analysed through a non-linear multifactorial model considering daily and cumulative climatic effects together with inter- and intraspecific competition indices. Our results provide evidence of a spatio-temporal niche separation between species. Compared to other species, *Q. ilex* showed a wider thermal amplitude, a higher mean optimum temperature for growth and a milder effect of drought on its secondary growth. Under current climate change projections, simulations based on our model predict a secondary growth reduction for *P. pinea* and a growth enhancement for *Q. ilex* in these Mediterranean mixtures.

Keywords

Dendrometers; Mixed stands; Climate change; Non-linear mixed models; Mediterranean species.

3.1. Introduction

Mixed-species forests have gained significant attention in recent years as many studies have shown that tree species richness is a key feature for most forest functions and services (Río et al., 2016). Some studies have stressed the role of certain mixtures in the improvement of individual tree resistance and resilience (e.g. Lebourgeois et al., 2013). These benefits are not observed neither in all forest types, nor for all tree species (Grossiord et al., 2014; Merlin et al., 2015) but they are expected to be more frequent in drought-prone sites (Pretzsch et al., 2013) like Mediterranean forests. However it remains unclear how global change will modify mixed forests dynamics in the Mediterranean basin.

Global warming is known to alter plant phenology (Cleland et al., 2007) leading to decreases in tree radial growth in some cases (Lebourgeois et al., 2010; Natalini et al., 2015). The analysis of intraannual growth dynamics through a modelling approach has proved useful for characterizing differences in wood phenology between species and deviations from the expected tree growth due to climate change (Michelot et al., 2012). Although height growth patterns tend to be similar between coexisting tree species, this does not apply to diameter growth. Carbon assimilated by trees through photosynthesis is firstly assigned to build new photosynthetic tissues (Gea-Izquierdo et al., 2009) and primary growth, and only remaining carbohydrates are allocated to girth increment. During the growing season the timing, duration and rate of radial growth can change among species (Rossi et al., 2006) and may also change through species interactions and with varying climatic conditions.

The role of competition restraining individual tree growth has been widely discussed in the forestry literature, mainly by the use of competition indices. Recent studies have addressed this issue studying the role of inter- and intraspecific interactions on interannual growth (de-Dios-García et al., 2015; Manso et al., 2015). However understanding how these inter- and intraspecific interactions affect seasonal or daily tree growth in mixtures remains a challenge.

Studies on intraannual growth dynamics have been performed using manual band dendrometers (Martín et al., 2014), automatic band dendrometers (Urban et al., 2013), electronic point dendrometers (Zweifel et al., 2006) and core (Delpierre et al., 2016) or microcore extraction (Rossi et al., 2006). In spite of their low resolution on a daily basis, advantages from manual band dendrometers are related to their low cost of installation and maintenance (McMahon and Parker, 2015) which allows to carry out measurements over a larger sample of trees and during longer time spans. These methods are more accurate for analysing the radial growth of the whole stem than invasive techniques like core or microcore extraction and electronic point dendrometers, which can be affected by local changes in the xylem or the bark (Gutiérrez et al., 2011).

Despite the widespread use of band dendrometers for assessing intraannual growth patterns, most studies have focussed on defining patterns of seasonal dynamics and growth phenology (Urban et al., 2013), with only a few studies aiming to gain insight into the factors driving differences in intraannual growth between trees, sites and species (McMahon and Parker, 2015).

The effect of climatic factors on intraannual growth has usually been evaluated by means of univariate analysis, such as Pearson's correlation coefficient (Grogan and Schulze, 2012) or univariate regression models, which focus on an assumed linear relation among the studied effect and a single factor at each time. However, understanding the effect of multiple factors as well as their complex interactions on growth should be approached through more complex multivariate and non-linear models (Paine et al., 2012).

Our aim was to determine the climatic factors and the inter- and intraspecific competition traits that drive intraannual secondary growth dynamics in three Mediterranean tree species, *Pinus pinea* L., *Quercus ilex* subsp. *ballota* (Desf.) Samp., and *Juniperus thurifera* L., co-occurring in mixed forests in the Spanish Northern Plateau, by means of a modelling approach.

The specific objectives of this analysis were (a) to determine the competition factors that define the daily potential secondary growth of the subject tree; (b) to elucidate the main climatic factors that limit the daily potential girth increment for each tree species coexisting in *P. pinea* mixed stands. Our first hypothesis was that the effect of inter- and intraspecific competition on potential growth would be different for each species, *P. pinea* being more competitive than *J. thurifera* and *Q. ilex* subsp. *ballota* both with conspecific trees and with the other tree species (de-Dios-García et al., 2015). In line with other studies (Mayoral et al., 2015) our second hypothesis was that *Q. ilex* subsp. *ballota* (hereafter *Q. ilex*) would reach its optimum growth conditions at higher temperatures than *P. pinea* and *J. thurifera*. Our third hypothesis was that *Q. ilex* would be more tolerant to summer drought than the other tree species (Mayoral et al., 2015), achieving higher girth increments in relative terms than *P. pinea* and *J. thurifera* during the dry season.

3.2. Material and methods

3.2.1. Data collection

3.2.1.1. Study area

The study area is located in the Carrascal state forest (41º36’N, 4º19’W), in a flat zone within the limestone plain areas in the east of the province of Valladolid, in the Spanish Northern Plateau. The elevation is around 885 m, the average annual precipitation is highly variable ranging from 220 to 630 mm and it mainly falls during autumn and spring. The mean annual temperature is 11ºC, reaching maximum average values of 37ºC in the warmest months (July and August) and minimum average values of -5ºC in the coldest ones (December and January), according to historical data (1975-2010) from Valladolid meteorological station (www.aemet.com). The area has a Mediterranean continental climate with a characteristic hot and dry summer period during which mean monthly precipitation is 21 mm. The main types of soils are inceptisols with an average water holding capacity of 176 mm/m.

In the province of Valladolid, *P. pinea* occupies 74,000 ha (29,000 ha are pure stands, 33 000 are mixed stands with other conifers and 12,000 ha are mixed stands with hardwoods). Mixed stands with hardwoods represent the most diverse and complex forest systems in the region and are mainly located in limestone plain areas. The present study focused on these more complex admixtures, where *Pinus pinea* grows with *Quercus ilex* and *Juniperus thurifera*.

Land ownership has played a critical role in the maintenance of mixed broadleaf-conifer forests in the Spanish Northern Plateau, where *P. pinea, P. pinaster, Q. ilex, Q. faginea* and *J. thurifera* naturally coexist. Nowadays most of these structurally complex admixtures are found on land that was privately owned until the 1980s. The lack of investments from private owners and the absence of management plans contributed to the preservation of these mixtures. Most of this land was sold to the regional government in the 1980s. At that time, management in mixtures began to focus on a tree selection system, promoting growth and regeneration of all tree species. Conservation of biodiversity is the main management objective in these forests, together with other ecosystem services such as cone and nut production, timber and biomass, mushrooms and recreational uses.

3.2.1.2. Experimental design – dendrometer measurements

Data were collected from two adjacent 50 m x 60 m plots placed in two contrasting stocking densities: A high density plot (basal area G = 18.8 m^2/ha), which is located in a wildlife corridor that has not been managed since the 1970s and a low density plot (basal area G = 9.6 m^2/ha), where the last forest management intervention was carried out in 2002. Within each plot, the coordinates of all trees with height greater than 1.30 m were recorded during the summer of

2011. During that measurement as well as in the subsequent measurements, diameter at breast height (dbh), stump diameter, total height, height to crown base, and four perpendicular crown radii measured in cardinal directions were recorded for each tree. Stand attributes are shown in Table 3.1.

Table 3.1. Stand attributes, estimated using trees with diameter at breast height ≥5cm. N: stand density; G: basal area; Dg: quadratic mean diameter; H: mean total height; LDP: low density plot; HDP: high density plot.

		LDP	HDP
N (stem/ha)	Total	383	943
	P. pinea	83	497
	Q. ilex	163	147
	J. thurifera	137	253
G (m^2/ha)	Total	9.6	18.8
	P. pinea	7.2	16.8
	Q. ilex	0.9	0.5
	J. thurifera	1.4	1.5
Dg (cm)	*P. pinea*	33.3	20.7
	Q. ilex	5.0	6.7
	J. thurifera	10.2	8.8
H (m)	*P. pinea*	9.1	7.2
	Q. ilex	4.5	4.2
	J. thurifera	5.4	5.3

Intraannual girth increment was measured by means of band dendrometers (Dendrometer Increment Sensor DB20 EMS Brno, (www.emsbrno.cz), which were mounted at breast height (1.30 m) on 58 trees (dbh > 5cm) after leveling off the bark with a rasp. In order to have a balanced design the dendrometers were split half and half between the high density plot (HDP) and the low density plot (LDP). We selected a balanced representation of the whole range of tree diameters observed in the study area for each tree species. We monitored the secondary growth of 21 *P. pinea* trees (12 in the HDP and 9 in the LDP), 13 *Q. ilex* trees (5 in the HDP and 8 in the LDP) and 24 *J. thurifera* trees (12 in the HDP and 12 in the LDP). The dendrometer bands were revisited on 59 occasions on a regular basis (average period 17 ± 6 days) from May 2012 to April 2015 and the girth of each tree was measured with a precision of 0.1 mm. To avoid diurnal biases due to changes in tree water status (Baker et al., 2002), all measurements were taken at around 11 am. Details on the characteristics of the selected trees are listed in Table 3.2.

Table 3.2. Characteristics of the 58 trees with band dendrometers. Diameter classes correspond to: II = 5cm≤D<10cm, III = 10cm≤D<15cm, IV = 15cm≤D<25cm, V = 25cm≤D<35.

Species	Site	Diameter class	Number of trees	Range of tree heights (m)	Range of dbh (cm)
Pinus pinea	High density	III	4	6.2-7.1	12.65-14.95
		IV	4	7.5-9.3	23.2-24.8
		V	4	9.6-10.4	25.5-34.35
	Low density	III	1	4.7-4.7	12.25-12.25
		IV	4	5.6-8.2	18.05-24.25
		V	4	8.5-10.8	28.45-34.3
Quercus ilex	High density	II	4	3.7-5.4	7.5-9.15
		III	1	6-6	10.85-10.85
	Low density	II	5	3.4-4.7	5.6-9
		III	3	4.9-5.3	10.05-10.9
Juniperus thurifera	High density	II	4	5.3-7.8	8.8-9.65
		III	6	5.6-8.7	11.1-14.85
		IV	2	8.5-9	17.7-20.6
	Low density	II	4	3.7-6.1	6.75-9.6
		III	4	5.6-7.1	11.35-14.35
		IV	4	7.2-8.8	16.9-24.8

Daily climatic variables including mean, maximum and minimum temperatures, daily precipitation, days without precipitation and days with frost were gathered from a meteorological station located in the area of study (41º34'N, 4º20'W, 2.5 km from the study site) and managed by the local forest service. 5.9% of absent data were estimated using data from Valbuena de Duero meteorological station (41º38'N, 4º17'W, 6 km from the study site), which are available from www.inforiego.org.

3.2.2. Data analysis and statistical methods

3.2.2.1. Modelling approach

Due to the hierarchical structure of the data, three indices were defined, *i*, *j* and *s*, which represent the tree, the time interval between measurements and the species, respectively. We chose the girth increment (mm) as the response variable (gi_{ijs}). It was defined as the difference between the girth observations in two consecutive measurements. Since our objective was to study the effects involved in wood expansion at breast height, we smoothed our original dendrometer series (Delpierre et al., 2016) by specifying that no shrinkage in girth increment was allowed, thus negative values for gi_{ijs} were set to zero. A logarithmic transformation was applied to comply with the assumption of normality and homogeneous variances:

$$y_{ijs} = Log\left[\left(gi_{ijs} \cdot 10\right) + 1\right] \tag{1}$$

We assumed there were some daily potential effects acting at tree level that define a theoretical daily maximum secondary growth and climate covariates that limit this potential growth. The daily potential effects (PE_{is}) represent the expected growth when the other factors are at optimal values. Thus, the sum of the daily effects over the time interval *j* can be used to predict the total secondary growth during this interval.

Among the PE_{is} , we included tree-level covariates: inter- and intraspecific competition indices ($AOI_{inter,is}$, $AOI_{intra,is}$), dbh_i and a species effect (see eq. 2). We used the area overlap distance dependent competition indices (AOI) developed by Bella (1971) and later modified by Tomé and Burhart (1989) to define inter- and intraspecific interactions between the trees of the area of study. Further details on the description and use of these indices are annexed to this paper (See Appendix).

Given the hierarchical structure of the data, it could be suspected that there would be a violation of the assumption of independence. In order to account for this assumption, a tree random effect (u_i) was included on the intercept. We assumed that the differences in stand density among both two plots were accounted for by the inter- and intraspecific competition indices. Additionally, since both plots were adjacent, we did not consider the inclusion of a random plot effect accounting for unobservable effects due to differences in site conditions.

$$PE_{is} = \alpha_s + (\beta_s \cdot AOI_{inter,is}) + (\gamma_s \cdot AOI_{intra,is}) + (\theta_s \cdot dbh_i) + u_i \qquad (2)$$

where the terms α, β, γ, θ are estimable, in some cases species-specific, parameters, $AOI_{inter,is}$ and $AOI_{intra,is}$ stand for inter- and intraspecific competition, respectively, for tree *i* of species *s*, dbh_i is the diameter at breast height of tree *i* and u_i is a tree random effect, so that $\mathbf{u} \sim N(0, \sigma^2_u)$, σ^2_u being the variance of the tree random effects.

For climate predictors, we considered thermal covariates such as the days since the last frost event, daily mean and maximum temperatures (Tav_m, $Tmax_m$ in ºC) and water availability-related variables based on daily precipitation and on days since the last precipitation event. Climate variables were grouped into a temperature effect, a frost effect and a drought effect (see eq. 3). Thereby the cumulative effects CE_{ijs} affecting girth increment of tree *i* of species *s* over interval *j* were defined as:

$$CE_{ijs} = PE_{is} \sum_m TE_{ms} \cdot FE_{ms} \cdot DE_{ms} \qquad (3)$$

where m extends from the first day to the last day of the increment period j, PE_{is} represents the potential effects as defined in eq. 2 and TE_{ms}, FE_{ms} and DE_{ms} represent the temperature, frost and drought effects at the day m on species s, respectively. These three effects were expressed as non-linear functions of climatic variables.

The functions were designed to range from 0 (total inhibition of potential growth) to 1 (growth reaches all its potential). Stem growth response to temperature can adopt different shapes depending on the species and can even vary between subspecies of the same genus (Lempereur et al., 2015; Mayoral et al., 2015). We chose a Gaussian function for the temperature effect since it had been found adequate in other modelling approaches for *Q. ilex* subsp. *ballota* and *P. pinea* in mixed and monospecific *P. pinea* forests in the Iberian peninsula (Manso et al., 2013; Mayoral et al., 2015) under similar climatic conditions as in our study site. The function can be expressed as follows:

$$TE_{ms} = exp\left[-\frac{(T_m - \mu_s)^2}{\sigma_s^2}\right] \tag{4}$$

where T_m is either daily average temperature ($T_{av,m}$) or daily maximum temperature ($T_{max,m}$), μ_s stands for optimum daily average temperature ($\mu_{av,s}$) or optimum daily maximum temperature ($\mu_{max,s}$) for species s, σ_s^2 represents the variance of the normally distributed response of secondary growth to T_m for species s.

In the case of frost and drought, we assumed they would have a long lasting effect on secondary growth. Freezing was thought to inhibit girth increment as a function of the number of days since the last frost, with the maximum growth reduction on the very day the frost event occurred. Hence, it was parametrised as:

$$FE_{ms} = 1 - exp\,(\varphi_s \cdot DF) \tag{5}$$

where φ_s is the parameter associated to the frost effect on species *s*, which was expected to adopt negative values; DF stands for days since the last frost.

In regard of drought effects, two approaches were tested (eq. 6.1 and eq. 6.2.1):

$$DE_{ms}\,1 = exp(\lambda_s \cdot DP) \tag{6.1}$$

$$DE_{ms}\,2 = 1 - exp\,(\delta_s \cdot WR_m) \tag{6.2.1}$$

$$WR_m = (P_m + WR_{m-1})\,exp\,(\lambda \cdot DP) \tag{6.2.2}$$

where DE_{ms} is the drought effect on species *s* on day *m*, DP are the days since the last precipitation event. For the second approach, WR_m is a proxy for the daily water reserve on day *m*, and is iteratively computed considering precipitation on day *m*, P_m, the value of WR_m in the previous day *m-1*, and DP. λ_s and δ_s are two specific parameters approaching how soil water content diminishes as days without precipitation increase, thus they should adopt negative values.

The combination of the climatic effects and the daily potential, as shown in eq. 3, yields the cumulative effects CE_{ijs} that we tried to use as a predictor of gi_{ijs}. After preliminary checks of the residuals, we found out that a log-transformation of CE_{ijs} was needed, the resulting model being as follows:

$$Log\left[(gi_{ijs} \cdot 10) + 1\right] = Log\left(CE_{ijs} + 1\right) + \epsilon_{ijs} \tag{7}$$

where ε_{ijs} is the error term such that $\varepsilon_{ijs} \sim N(0, \sigma^2)$, with σ^2 the residual variance.

3.2.2.2. Model fitting

The model was fitted using a maximum likelihood estimator. We followed a sequential procedure to select the effects entering the model: (i) competition and size factors determining daily potential growth, (ii) thermal effects, (iii) drought related effects, (iv) random effects, (v) species specific climatic responses. Preliminary models attained at each step of the model construction were compared in terms of bias (standardized residuals plotted against time), level of significance of the parameter estimates included and three different criteria for model comparison (Akaike information criterion, Bayesian information criterion and minus twice the maximum log-likelihood). At each step, the residuals were checked to identify heteroscedastic patterns. All calculations were carried out using PROC NLMIXED in SAS 9.2. (SAS Institute Inc., 2009).

3.2.2.3. Model evaluation

The model evaluation was primarily carried out by computing goodness-of-fit statistics such as mean error (E), root mean square error (RMSE) and modelling efficiency (MEF), computed over the residuals in real scale. The model was evaluated at different scales: whole data-set, per species, per plot and per combination of species and plot. A second evaluation was based on visual comparison of the girth increment trajectories between observed and predicted values. Finally, the accuracy of the model in predicting cumulative girth increment at tree level for the whole period was also tested at different scales by means of E, RMSE and MEF. We performed a t-test on the mean error under the null hypothesis that the model was correct, i.e. E was equal to 0. Consequently, any significant probability could be interpreted as a lack of fit. Evaluation of the model was carried out over raw, non-transformed values, thus antilogarithmic back-transformation of predicted values was carried out by multiplying the exponential of the predicted value per 0.5 times the variance of the error terms (Duan, 1983).

3.2.2.4. Model validation

We did a model validation over a set of trees from the two plots included in the assay. The growth increment data used for the validation was obtained from cores and cross section slices extracted in 2011, thereby corresponding to different years than the ones considered to study girth increment (2012-2015). These cores and cross section slices were obtained from a representative sample of trees covering the whole range of diameters identified in the area of study. Total number of trees used in the validation were 48 *P. pinea* (24 per plot), 15 *J. thurifera* (7 from the low density plot, 8 from the high density plot) and 4 *Q. ilex* (2 per plot). *Q. ilex* trees used for the validation had to be felled, which explains the lower amount of *Q. ilex* trees used for the validation compared to the other species. Model validation was based on computing the Pearson's correlation coefficient between the observed values of the annual radial increment (taken from increment cores and cross section slices) and the predicted annual girth increment obtained from our model. Temporal extent of the validation covered from 1997 to 2011 (15 years). Correlation coefficients were thus computed using the 15 observed-predicted annual values for each tree. We did not convert annual girth increment data into annual radial increment since girth measurements take into account bark growth but core increments do not.

3.2.2.5. Growth projections under current and forecasted climate scenarios

The final model was used to predict annual girth increment for the three species comparing current climate data with simulated climate data from IPCC RCP 8.5 climate scenario for 2075. Daily climate data were obtained from AEMET projections using climate model ACCESS 1-0 (http://www.aemet.es/es/serviciosclimaticos/cambio_climat/datos_diarios), resulting in a 4.5ºC increase of the average temperature, and a 30% decrease in annual rainfall. For this simulation competition was not considered.

3.3. Results

3.3.1. Definition of secondary growth function

The sequential process of construction of the models for the secondary growth is shown in Table 3.3. At each step of the model construction a new factor was included and compared in terms of -2LL, AIC and BIC with the same model without this effect. Among the main constant factors determining the daily potential growth tree dbh was discarded as it was only significant for *J. thurifera* and it did not improve the performance of the model either (models [1] and [2]). Hence, daily potential girth increment was defined by a species effect in the intercept and inter- and intraspecific competition indices. With respect to thermal effects, mean daily temperature resulted in a best fit than maximum temperature (models [3] and [4]). Integrating the frost effect did not improve the model significantly, consequently the frost effect was removed in the process of model construction (models [4] and [5]). However both drought approaches tested were significant. Drought effect 2 was chosen in preference to drought effect 1 since it improved the model fit in terms of AIC, BIC and -2LL when compared with the same model with drought effect 1 (models [6]-[7]). The inclusion of a tree random effect resulted in a significant improvement in terms of AIC, BIC and -2LL (models [7] and [8]). We finally tested the different alternatives of inclusion of specific interactions on the climatic effects (models [9]-[15]). The fit of the complete model [15] could not be attained due to convergence problems. Comparison among models [9]-[14] resulted in very minor differences. We finally opted to select the model [12], including specific parameters for thermal amplitude and drought effect and a common parameter for drought occurrence, as it can be considered a good compromise between goodness of fit and parsimony in the number of parameters entering the model. Table 3.4 presents the parameter estimates of the preferred model.

3.3.2. *Factors affecting intraannual growth patterns*

The final girth increment model produced a hyperplane, depending on biotic and abiotic interactions from which we could infer contrasting growth responses by species for the different factors. Growth patterns were characterized by a succession of sharp increases followed by plateaus, which corresponded to growth increments during spring and fall periods and growth cessation in summer and winter times, respectively (Fig. 3.1).

Table 3.3. Comparison of fitting statistics and sequential procedure for model construction. Intrasp.: Intraspecific; Intersp.: Interspecific; dbh_i: diameter at breast height of the target tree *i*; T_{max}: daily maximum temperature; T_{av} : daily average temperature; α_s is the intercept for species *s*; β_s: parameter associated to interspecific competition for species *s*; γ_s: parameter associated to intraspecific competition for species *s*; θ_s: parameter associated to diameter at breast height of the target tree of species *s*; μ_s: optimum daily temperature for species *s*; λ: parameter related to drought occurrence; λ_s: parameter related to drought occurrence for species *s*; δ: parameter linked to the drought effect; δ_s: parameter linked to the drought effect on species *s*; σ^2: variance of the scaled normally distributed response of secondary growth to daily temperature; σ^2_s: variance of the scaled normally distributed response of secondary growth to daily temperature for species *s*; σ^2_{ui}: variance linked to the tree random effect; -2LL: -2 log likelihood; AIC: Akaike information criterion; BIC: Bayesian information criterion.

Modelling step	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Intercept	α_s	α_s	α_s	α_s	α_s	α_s	α_s	α_s	α_s	α_s	α_s	α_s	α_s	α_s	α_s
Intersp. competition	β_s	β_s	β_s	β_s	β_s	β_s	β_s	β_s	β_s	β_s	β_s	β_s	β_s	β_s	β_s
Intrasp. competition	γ_s	γ_s	γ_s	γ_s	γ_s	γ_s	γ_s	γ_s	γ_s	γ_s	γ_s	γ_s	γ_s	γ_s	γ_s
dbh_i	θ_s	-	-	-	-	-	-	-	-	-	-	-	-	-	-
T_{max}	-	-	μ_s	-	-	-	-	-	-	-	-	-	-	-	-
T_{av}	-	-	-	μ_s	μ_s	μ_s	μ_s	μ_s	μ_s	μ_s	μ_s	μ_s	μ_s	μ_s	μ_s
Frost effect	-	-	-	-	φ	-	-	-	-	-	-	-	-	-	-
Drought occurrence	-	-	-	-	-	Λ	λ	λ	λ	λ	λ_s	λ	λ_s	λ_s	λ_s
Drought effect	-	-	-	-	-	-	δ	δ	δ	δ_s	δ	δ_s	δ	δ_s	δ_s
Thermal amplitude	-	-	σ^2	σ^2	σ^2	σ^2	σ^2	σ^2	σ^2_s	σ^2	σ^2	σ^2_s	σ^2_s	σ^2	σ^2_s
Random tree effect	-	-	-	-	-	-	-	σ^2_{ui}	σ^2_{ui}	σ^2_{ui}	σ^2_{ui}	σ^2_{ui}	σ^2_{ui}	σ^2_{ui}	σ^2_{ui}
-2LL	10,124	10,134	9,570	9,500	9,489	8,942	8,718	8,668	8,656	8,663	8,661	8,650	8,647	8,660	-
AIC	10,150	10,154	9,598	9,528	9,519	8,972	8,750	8,702	8,694	8,701	8,699	8,692	8,689	8,702	-
BIC	10,230	10,215	9,684	9,614	9,611	9,063	8,848	8,737	8,733	8,741	8,738	8,735	8,733	8,745	-

Table 3.4. Summary of parameter estimates for the definitive model [12], where subscripts: 1 = *P. pinea*, 2 = *Q. ilex*, 3 = *J. thurifera*. α is the intercept for species 1, 2, 3; β is the parameter associated to interspecific competition for species 1, 2, 3; γ is the parameter associated to intraspecific competition for species 1, 2, 3; δ is the parameter linked to the drought effect on species 1, 2, 3; λ is the parameter related to drought occurrence; μ represents the optimum daily average temperature for species 1, 2, 3; σ^2 stands for the variance of the scaled normally distributed response of secondary growth to daily average temperature for species 1, 2, 3; σ^2_{ui} is the variance linked to the tree random effect.

Parameter	Estimate	Stand. error	Df	t-value	p-value
α_1	3.5498	0.5647	57	6.29	<0.001
α_2	2.0815	0.6622	57	3.14	0.003
α_3	1.9852	0.3492	57	5.69	<0.001
β_1	-0.0989	0.1555	57	-0.64	0.527
β_2	-0.0960	0.0442	57	-2.17	0.034
β_3	-0.0545	0.0278	57	-1.96	0.055
γ_1	-0.1692	0.0343	57	-4.94	<0.001
γ_2	0.1000	0.1201	57	0.83	0.409
γ_3	-0.3425	0.1281	57	-2.67	0.010
δ_1	-0.1382	0.0256	57	-5.40	<0.001
δ_2	-0.2559	0.0871	57	-2.94	0.005
δ_3	-0.1123	0.0215	57	-5.22	<0.001
λ	-0.6390	0.1136	57	-5.62	<0.001
μ_1	16.3750	0.3871	57	42.30	<0.001
μ_2	31.9969	4.3007	57	7.44	<0.001
μ_3	17.7550	0.5837	57	30.42	<0.001
σ^2_1	64.7046	7.5925	57	8.52	<0.001
σ^2_2	210.3400	64.1181	57	3.28	0.002
σ^2_3	67.4487	9.8537	57	6.84	<0.001
σ^2_{ui}	0.1731	0.0666	57	2.60	0.012

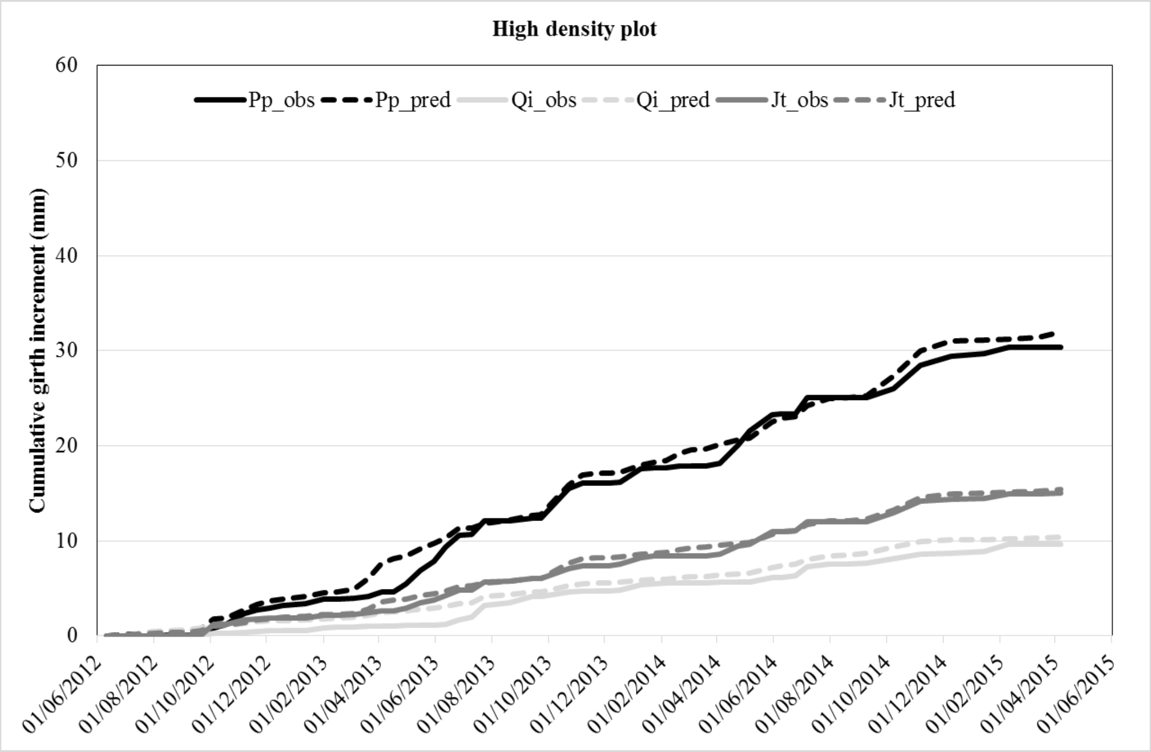

Fig. 3.1a.

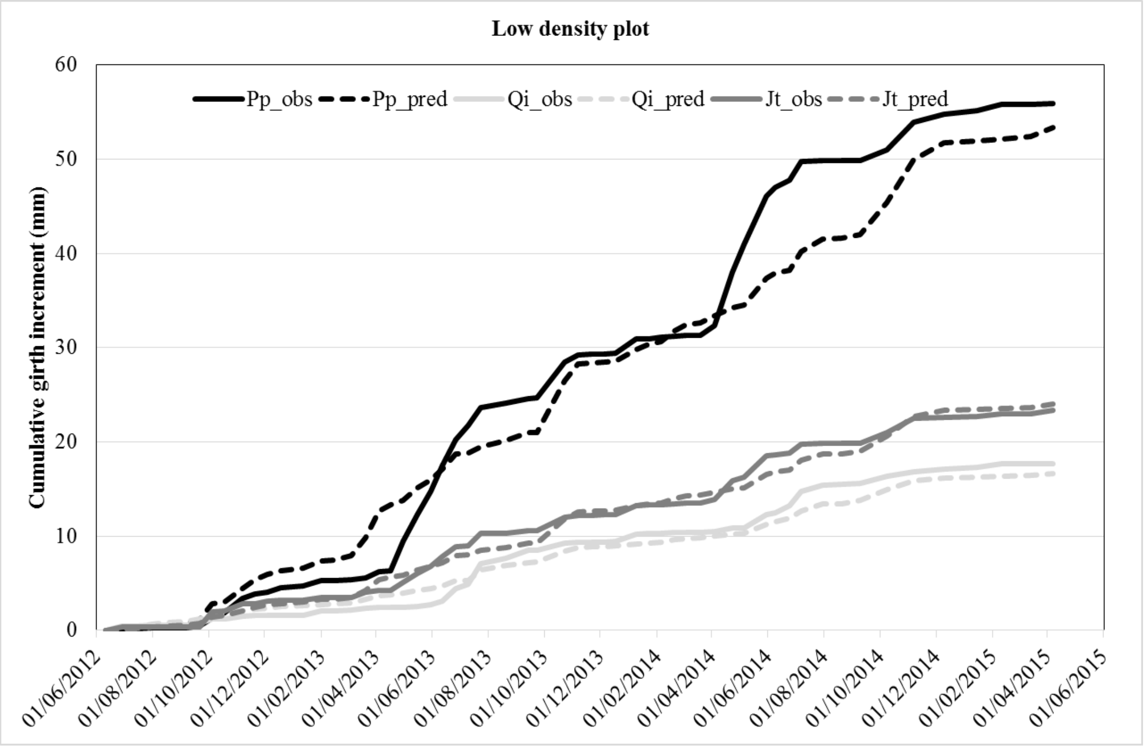

Fig. 3.1b.

Fig. 3.1. Average trajectories for the observed (solid lines) and predicted (dashed lines) girth increment values for the three species involved (Pp – *P. pinea*, Qi – *Q. ilex*, Jt – *J. thurifera*). a) High density plot b) Low density plot.

3.3.2.1. Daily potential effects

The species effect on the intercept (α_s) was significant for the three species implying different average girth increments for each of them. The effect was greater for *P. pinea* ($\hat{\alpha}_1$ = 3.5498), followed by *Q. ilex* ($\hat{\alpha}_2$ = 2.0815) and *J. thurifera* ($\hat{\alpha}_3$ = 1.9852). Concerning interspecific competition, significant values were observed for *Q. ilex* (p-value = 0.034) and close to significant for *J. thurifera* (p-value = 0.055), being growth inhibition larger for *Q. ilex* ($\hat{\beta}_2$ = -0.09597) than for *J. thurifera* ($\hat{\beta}_3$ = -0.05453). Interspecific competition effect was not significant for *P. pinea* (p-value = 0.527). With respect to intraspecific competition we obtained a significant inhibition of the potential girth increment for *P. pinea* (p-value = <0.001) and *J. thurifera* (p-value = 0.010), being more than two times lower for *P. pinea* ($\hat{\gamma}_1$ = -0.1692) than for *J. thurifera* ($\hat{\gamma}_3$ = -0.3425). The effect of intraspecific competition was non-significant for *Q. ilex* (p-value = 0.409).

3.3.2.2. Climate covariates

For temperature effect, optimum daily average temperatures for secondary growth were 16.4ºC for *P. pinea* ($\hat{\mu}_1$), 32.0ºC for *Q. ilex* ($\hat{\mu}_2$) and 17.8ºC for *J. thurifera* ($\hat{\mu}_3$). The scaled normally distributed response of girth increment to daily average temperature differed between species, being three times greater for *Q. ilex* ($\hat{\sigma}_2^2$ = 210.3400) than for *J. thurifera* ($\hat{\sigma}_3^2$ = 67.4487) and *P. pinea* ($\hat{\sigma}_1^2$ = 64.7046) pointing to a wider thermal amplitude for *Q. ilex* than for the other tree species. The symmetric thermal intervals, together with the optimum average temperatures and different thermal amplitudes by species, can be seen in Fig. 3.2a. With respect to the drought effect on girth increment, it differed across the species, being more limiting for the intraannual secondary growth of *P. pinea* ($\hat{\delta}_1$ = -0.1382) and *J. thurifera* ($\hat{\delta}_3$ = -0.1123) than for *Q. ilex* ($\hat{\delta}_2$ = -0.2559). To facilitate the interpretation of the drought effect, we ran a simulation considering initial water reserve values of 0 and a single episode of precipitation of 5 mm on the first day of the simulation (Fig. 3.2b). Lower values obtained for the drought effect for *P. pinea* (0.4989) and *J. thurifera* (0.4297) than for *Q. ilex* (0.7218), the first day of the simulation imply that *Q. ilex* makes better use of water than the other two species after an isolated rainfall event when soil water reserves are scarce.

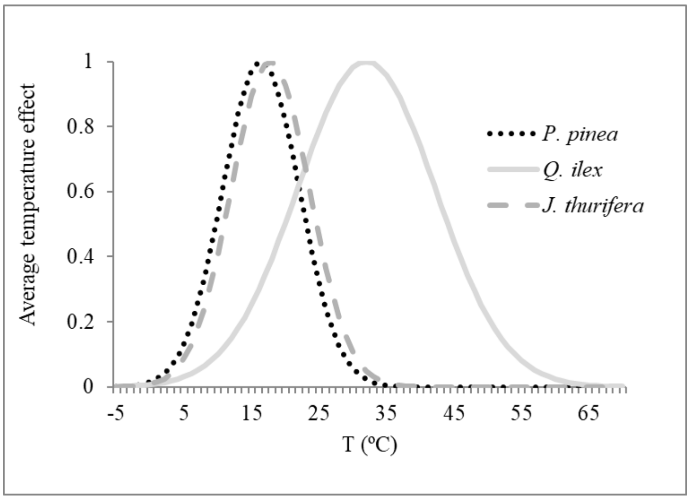

Fig. 3.2a.

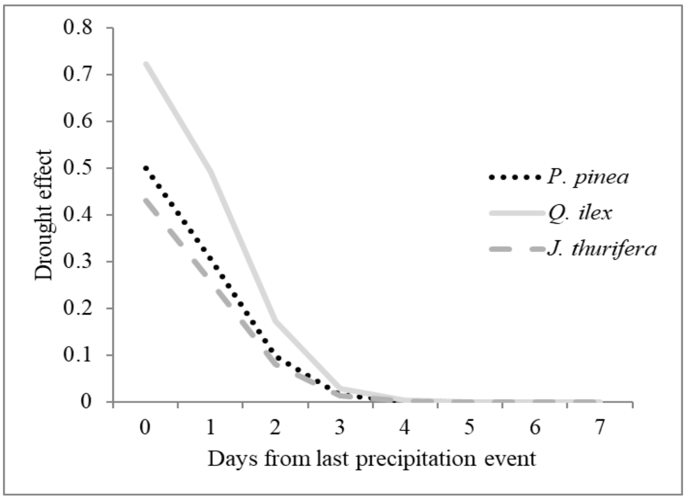

Fig. 3.2b.

Fig. 3.2. Effects on secondary growth of the different covariates included in the definitive model. a) Optimum daily average temperature with different thermal amplitudes by species. b) Drought effect simulation considering initial water reserve (WR_0) = 0 and a single precipitation event on the first day of the simulation, where P_1 = 5mm.

3.3.3. Model evaluation

Accuracy of the model was first evaluated by means of common statistics as mean error, root mean square error and modelling efficiency, for the whole data set, and separately for each plot, species and each combination of plot and species (Table 3.5). Non-significant p-values under the null hypothesis that the mean error (E) = 0 imply that the difference between observed and predicted values is non-significant and thereby there is no systematic bias in the predictions. Model predictions of girth increment were unbiased for all levels of grouping. At global scale, RMSE reached 0.694 mm, with MEF over 33.4%. We obtained more accurate predictions for the HDP than for the LDP, especially for *Q. ilex*, and *J. thurifera*. The main part of the observed bias was associated with *P. pinea* girth increment in the LDP. This result is mainly due to the unexpected larger summer growth in 2014 observed in three pines in the LDP.

Table 3.5. Goodness-of-fit statistics calculated for different levels of grouping. $\hat{E}$: estimated mean error; p-values calculated under the null hypothesis H_0: E = 0; $\widehat{RMSE}$: estimated root mean square error; $\widehat{MEF}$: estimated modelling efficiency; n: Amount of girth increment observations by level of grouping; Pp: *P. pinea;* Qi: *Q. ilex* subsp. *ballota*; Jt: *J. thurifera*; LDP: low density plot; HDP: high density plot. Period evaluated May 2012 to April 2015.

Scale	Level of grouping	$\hat{E}$	p-value	$\widehat{RMSE}$	$\widehat{MEF}$	n
Whole	-	0.0092	0.445	0.694	33.4%	3,306
Species	Pp	0.0320	0.267	0.997	25.1%	1,197
	Qi	0.0023	0.865	0.363	39.2%	741
	Jt	-0.0069	0.588	0.473	37.5%	1,368
Plot	LDP	0.0341	0.114	0.876	25.6%	1,653
	HDP	-0.0156	0.153	0.444	49.8%	1,653
Plot x Species	Pp – LDP	0.1128	0.064	1.379	11.7%	513
	Qi – LDP	0.0083	0.668	0.414	38.6%	456
	Jt – LDP	-0.0078	0.715	0.559	30.7%	684
	Pp – HDP	-0.0286	0.181	0.559	47.4%	684
	Qi – HDP	-0.0074	0.633	0.262	35.4%	285
	Jt – HDP	-0.0060	0.668	0.368	47.0%	684

The visual agreement between average observed and predicted increment trajectories through the whole cycle (Fig. 3.1), perfectly mimicking the bimodal growth patterns, again points to a better performance of the model in the HDP than in the LDP, particularly for predicting the secondary growth of *Q. ilex* and *J. thurifera*.

We finally tested the ability of the model to predict the cumulative girth increment of the 58 trees evaluated along the whole period of study (1,062 days). Unbiased predictions were obtained for all scales evaluated (Table 3.6, Fig. 3.3). The combinations of plot and species could not be tested due to the small number of trees involved in some combinations. The accuracy of the model was greater in predicting the girth increment in the HDP, than in the

LDP, especially for *J. thurifera*. Once more, higher RMSE values for *P. pinea* are due to the unexpected summer growth of three dominant trees (Fig. 3.3). However, MEF reached values over 86% and RMSE below 5.6 mm for all the scales studied, showing a high agreement between observed and predicted values, and a notable long-term model accuracy.

Table 3.6. Goodness-of-fit statistics over the cumulative girth increment for the 58 trees studied. $\hat{E}$: estimated mean error; p-value calculated under the null hypothesis H_0: E = 0; $\widehat{RMSE}$: estimated root mean square error; $\widehat{MEF}$: estimated modelling efficiency; n: number of trees. Period evaluated May 2012 to April 2015.

Scale	Level	$\hat{E}$	p-value	$\widehat{RMSE}$	$\widehat{MEF}$	n
Whole		0.5351	0.386	4.653	92.6%	58
Species	*P. pinea*	1.8369	0.183	6.235	85.5%	21
	Q. ilex	0.1356	0.770	1.575	93.8%	13
	J. thurifera	-0.3876	0.655	4.119	96.2%	24
Plot	Low density	1.9529	0.076	5.929	90.8%	29
	High density	-0.8827	0.096	2.853	93.3%	29

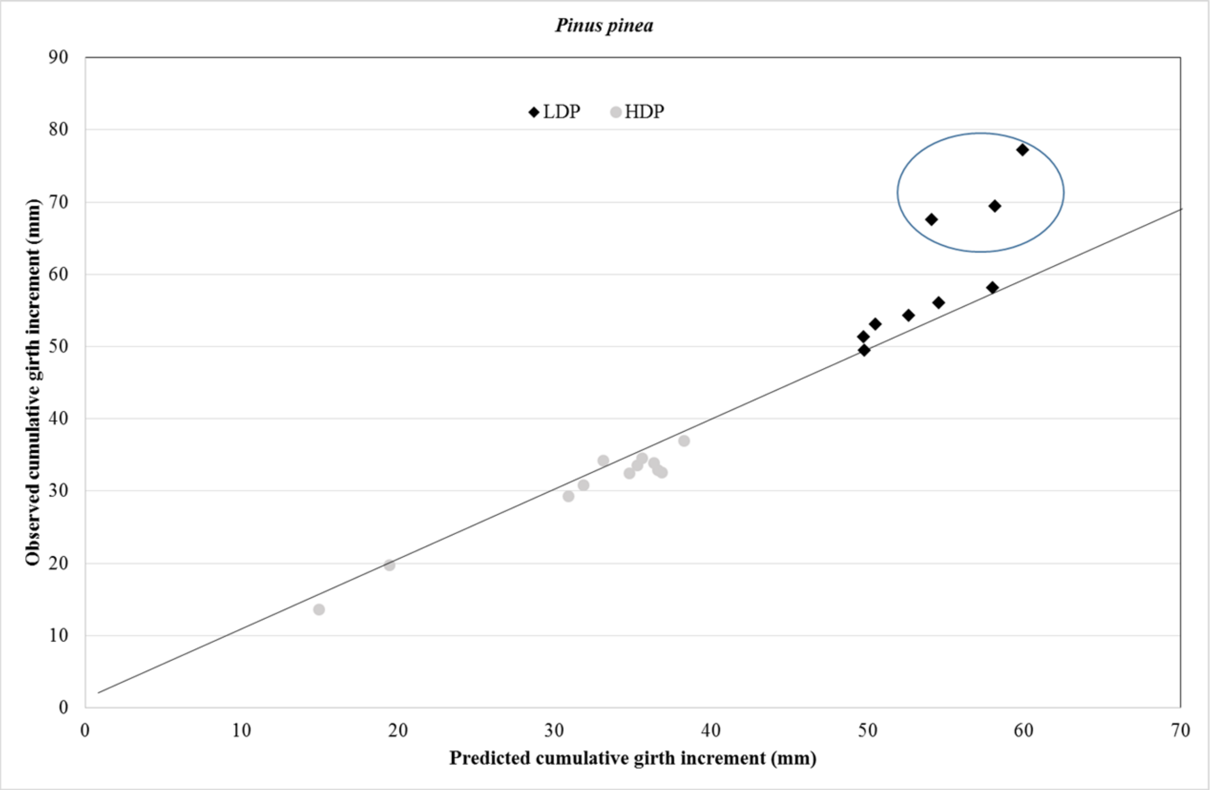

Fig. 3.3a.

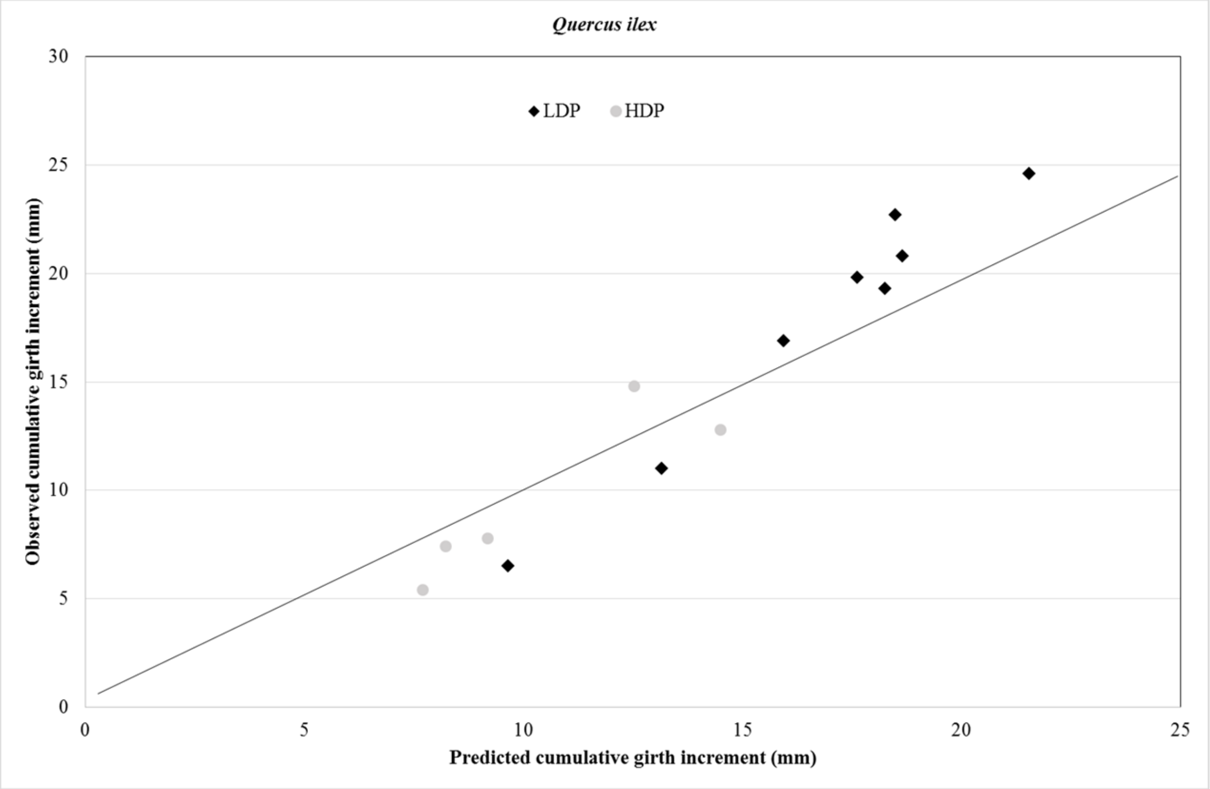

Fig. 3.3b.

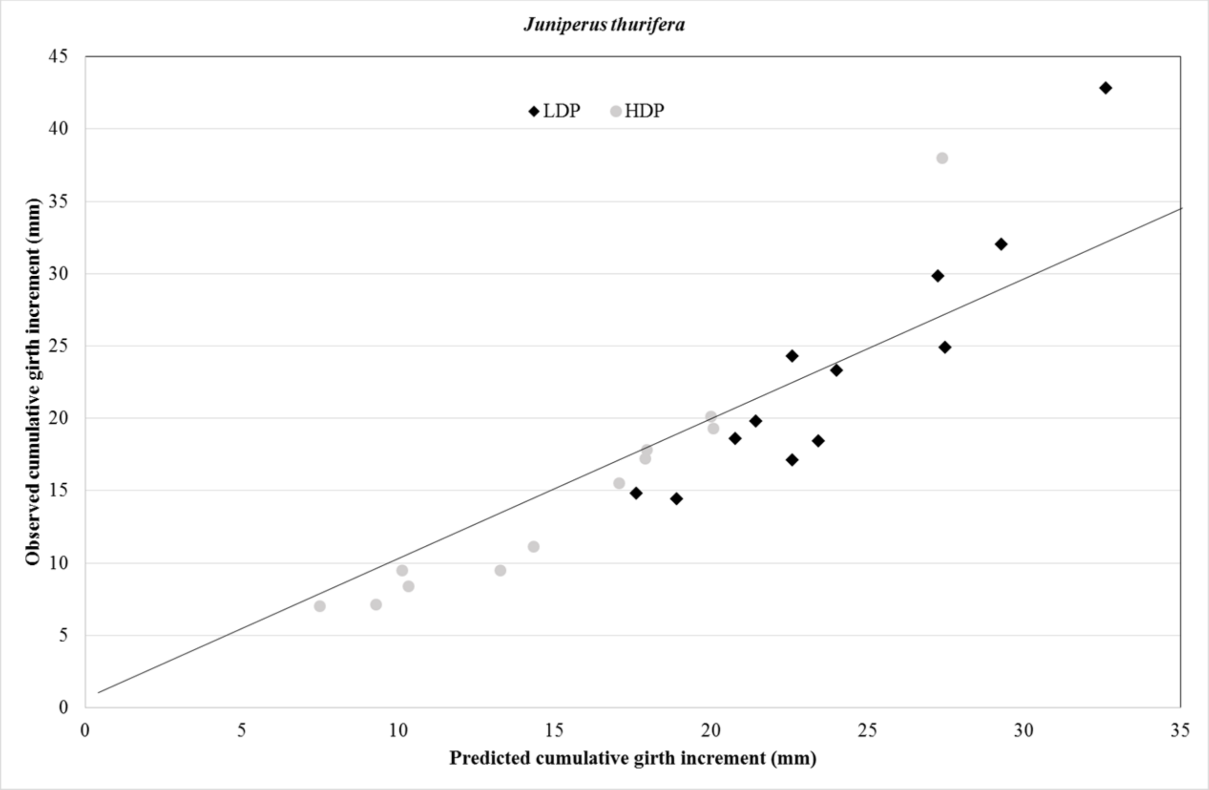

Fig. 3.3c.

Fig. 3.3. Observed vs. predicted cumulative girth increment values of individual trees shown by species at the end of the study period (1,062 days). a) *P. pinea*. b) *Q. ilex*. c) *J. thurifera*. Solid lines refer to the 1:1 line. Remarked are those P. pinea trees responsible for the bias in the low density plot. LDP: low density plot; HDP: high density plot.

3.3.4. Model validation

Model validation showed a clear agreement between observed annual increment data obtained from cores and cross section slices and the values of annual girth increment predicted using the model (Table 3.7). The main part of the tree-level correlations (63 out of 67) between observed radial increment and predicted girth increment were positive and statistically significant. Average correlation values ranged from 0.40 – 0.55 for all the species and plots, with maximum values of 0.57 – 0.75 depending on the species. Models for *P. pinea* and *Q. ilex* performed better in the high-density plot, while models for *J. thurifera* performed better in the low-density plot.

Table 3.7. Summary of model validation with annual radial increment data. n: number of trees sampled for the validation, n-sig: number of trees with a significant positive correlation between observed annual radial increment (obtained from cores and cross section slices) and predicted annual girth increment (obtained through the model); Ave-r: average value of the Pearson's correlation coefficient for the observed significant correlation; Max-r: maximum value of the Pearson's correlation coefficient. Validation time period: 1997-2011.

Species	Low density plot				High density plot			
	n	n-sig	Ave-r	Max-r	n	n-sig	Ave-r	Max-r
P. pinea	24	23	0.4007	0.6262	24	22	0.4761	0.6721
Q. ilex	2	1	0.4111	0.4111	2	2	0.4000	0.5736
J. thurifera	7	7	0.5497	0.7474	8	8	0.4248	0.6827

The model mimicked the pattern of interannual variability in radial increment (Fig. 3.4), especially in the last years of the simulation (2005-2011). However, the model was not able to match perfectly the effect of the 2002 thinning carried out in the low density plot, since we predicted a 2-year delayed response with respect to the real observed values (Fig. 3.4a, 3.4b and 3.4c).

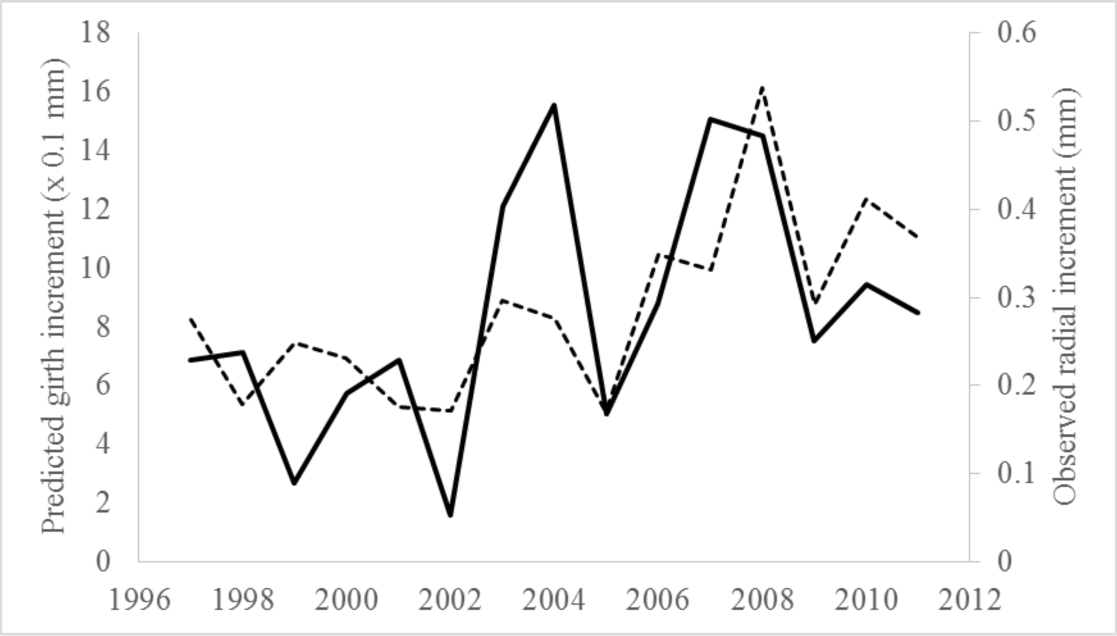

Fig. 3.4a.

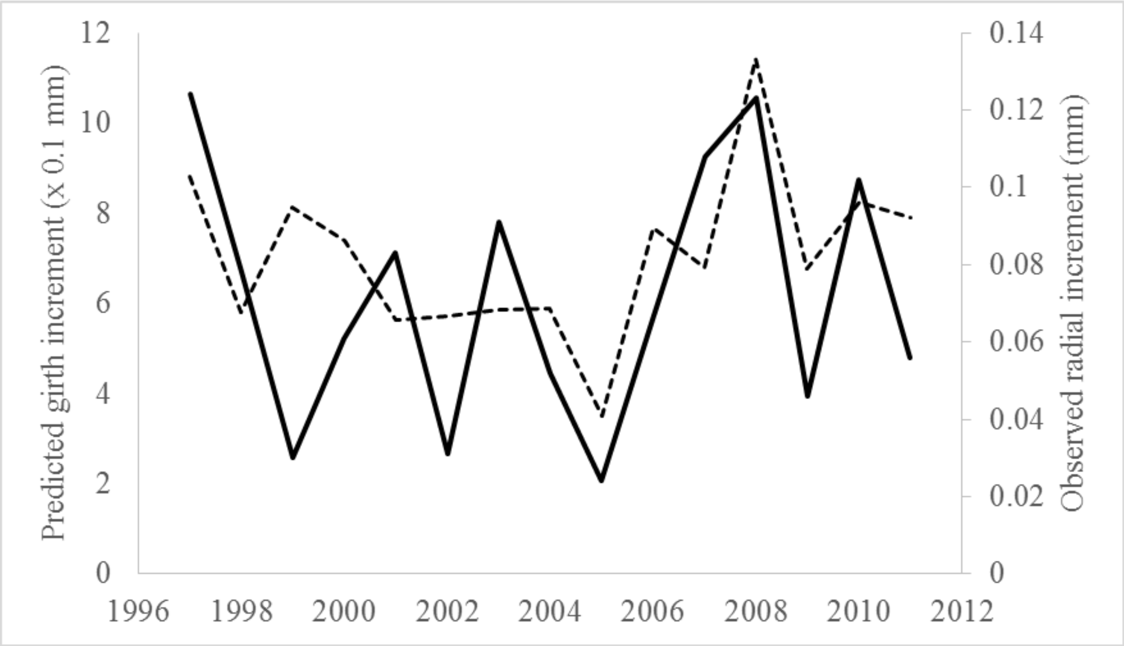

Fig. 3.4b.

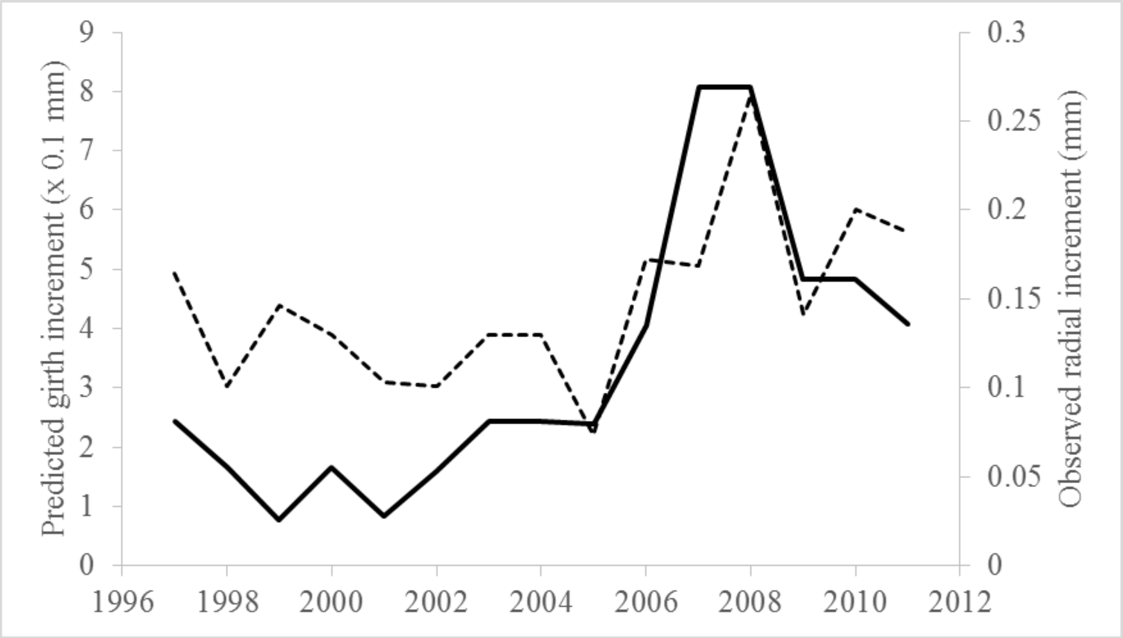

Fig. 3.4c.

Fig. 3.4. Observed values of annual radial increment (solid lines) vs predicted values of girth increment (dashed lines) for the randomly selected a) tree 1018 (*P. pinea*, low density plot), b) tree 1813 (*Q. ilex*, high density plot) and c) tree 1115 (*J. thurifera*, low density plot).

3.3.5. Growth projections under changing climate scenarios

The results from our simulations under current climate and RCP 8.5. climate scenario indicate secondary growth reductions of 19.1 % for *P. pinea* and 6.5 % for *J. thurifera* and a growth increase of 61.6 % for *Quercus ilex* under these simulated climate projections (Fig. 3.5). We would like to stress that competition was not considered for this simulation as the definitive model [12] only had slightly lower values in terms of minus twice the maximum log-likelihood (-2LL = 8650) when compared with the same model without competition (-2LL = 8689). Including competition at tree level also implied solving many technical problems when running the simulations. Thereby these growth projections are referred to open grown trees and must be treated with caution.

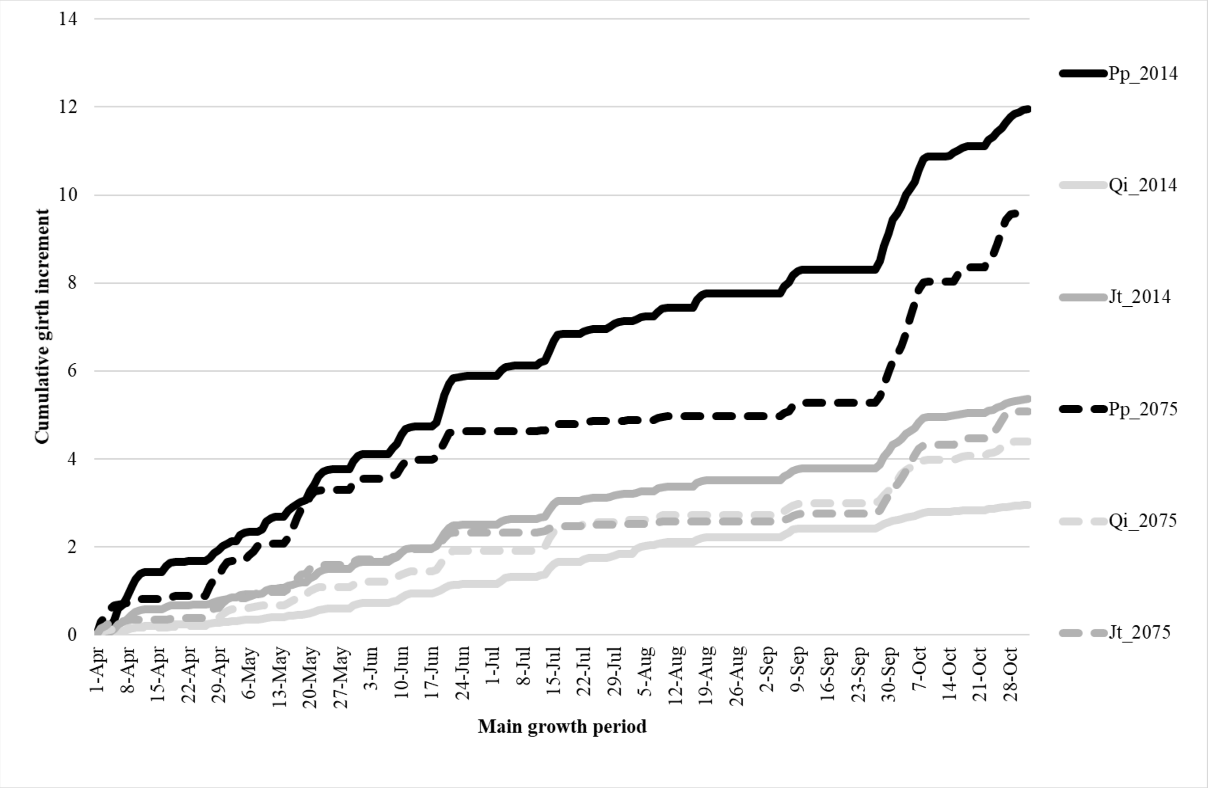

Fig. 3.5. Cumulative girth increment by species during the main growth period under current climate conditions (2014) and future climate forecasts (2075). 2075 growth projections calculated with an increment of 4.5ºC on average temperature, and a decrement of 30% in annual rainfall (climate model ACCESS 1-0).

3.4. Discussion

3.4.1. Advantages from a multifactorial non-linear approach for intraannual tree growth studies

Linear correlations between growth estimates and different climatic variables (Camarero et al., 2010; Michelot et al., 2012) and linear mixed models (e.g. Martín et al., 2015) have been used to study intraannual growth dynamics. However many climate-growth interactions are known to be non-linear. Previous studies have also highlighted the need of integrating both competition and climatic data for intraannual tree growth studies (Gutiérrez et al., 2011). In the Mediterranean areas many climatic factors like high temperatures, elevated transpiration and soil water depletion intervene simultaneously constraining intraannual girth increment. We thereby propose a non-linear multifactorial approach that can cope with all this limitations allowing us to understand the ecological needs of different species at one time.

3.4.2. Intraannual growth patterns

Many studies have found different growth dynamics in pine and oak species during the growing season concerning the date of budburst, leaf unfolding, radial growth onset and cessation, secondary growth rates or contrasting patterns of carbon allocation (e.g. Michelot et al., 2012; Zweifel et al., 2006). Girth increment data obtained from band dendrometers have limitations to identify some phenological events due to the reversible stem shrinking and swelling. However, we believe our model represents a good alternative to study girth increment based on daily and cumulative climatic effects as it only considers stem growth with stem shrinkage set to values of zero. Model predictions for cumulative girth increment were unbiased and show a notable long-term model accuracy. The general growth rates of the three tree species we studied (Ruiz de la Torre, 2006) indicate that *P. pinea* has the highest potential girth increments followed by *J. thurifera* and *Q. ilex* which is consistent with the intercept values we obtained. Previous studies in the Iberian peninsula (Camarero et al., 2010; Campelo et al., 2007b; Martín et al., 2014) have reported bimodal growth patterns for the three species over the year, characterized by a succession of sharp growth increases followed by plateaus, which is in line with our results. Diameter growth increased mainly during spring and autumn, coinciding periods of higher precipitation, increased soil water reserves and milder temperatures for growth (Pinto et al., 2011). Girth increment was repressed in summer, which is in agreement with a growth inhibition by high average temperatures and soil water deficit during the summer (Campelo et al., 2009). Secondary growth also stopped in winter, probably due to cambial dormancy caused by low average temperatures (Gea-Izquierdo et al., 2009; Liphschitz et al., 1984) and photoperiod shortening (Cherubini et al., 2003).

3.4.3. Size effects and intraannual competition differences between and within species

We obtained significant growth restrains by interspecific competition for *J. thurifera* and *Q. ilex*. Interspecific competition was also size-symmetric (de-Dios-García et al., 2015), implying that resource uptake is independent of target tree sizes and takes place mainly for belowground resources (Schwinning and Weiner, 1998). However interspecific competition was not significant for *P. pinea* on a daily basis. Juniper trees seem to develop shallower root systems in drought stressed sites than co-occurring pine species (Willson et al., 2008) while Mediterranean oaks tend to develop large taproots reaching deeper soil layers when growing in drought-prone environments (Canadell et al., 1996). We further obtained competitive reduction for *J. thurifera*, interspecific interactions being less intense than intraspecific interactions, which is another proof of niche partitioning and interspecific differentiation in resource use (Forrester, 2014).

Intraspecific competition was significant for *J. thurifera* and *P. pinea* having in both cases a negative impact on secondary growth. Intraspecific interactions, as defined by the competition index (de-Dios-García et al., 2015), were also size-asymmetric, indicating that larger trees benefit from a larger part of the resources, which limits the growth of their smaller conspecific neighbours (Schwinning and Weiner, 1998). However and contrary to our third hypothesis, the effect of intraspecific competition on girth increment was two fold in *J. thurifera* compared to *P. pinea.* Low levels of intraspecific competition imply complete growth cessation for *J. thurifera*, but not for *P. pinea.* The more limiting effect of intraspecific competition on *J. thurifera* secondary growth could be due to their clumped spatial pattern (unpublished data) found in the field around bigger *P. pinea* trees. In the case of the evergreen oak *Q. ilex* intraspecific competition indices were not significant. A large scale study on the 15 most important tree species in the Iberian peninsula indicated that Mediterranean evergreen broadleaved species were the least sensitive to competition in terms of growth (Gómez-

Aparicio et al., 2011). Another explanation for this result might be the low diameters found for *Q. ilex* in these forests that were intensively coppiced for fuelwood and charcoal production until 1950s, constituting nowadays mainly a coppice forest.

3.4.4. Secondary growth responses to climate are species dependent

Previous studies state that the main climatic effects constraining intrannual secondary growth of *Q. ilex* are temperature at short time scales (Gutiérrez et al., 2011) and water availability (Corcuera et al., 2004; Martín et al., 2014), which were both significant in our study. *J. thurifera* is also known to have a pronounced phenological activity, with a strong cambium dormancy in xeric sites during summer and a radial growth resumption due to cambium reactivation following late-summer and autumn rainfalls (Camarero et al., 2010). We obtained higher autumn girth increments for *J. thurifera* than for *Q. ilex*. Autumn precipitation events are known to moisten only the most superficial soil layers in Mediterranean continental areas (Camarero et al., 2010). Since *J. thurifera* roots are mainly developed in the upper soil profile, this may provide them a competitive advantage, allowing them to invest more resources on diameter growth than co-occurring pines and oaks during the autumn season. As regards *P. pinea,* latewood formation, which occurs during the summer, is limited by drought stress and extreme temperatures (Campelo et al., 2007b).

Recent studies on mixed *P. pinea* stands in the Spanish central range have identified higher optimum temperatures for photosynthesis for *Q. ilex* than for *P. pinea* and other *Juniper* species (Mayoral et al., 2015), which are consistent with the optimum temperatures for growth that we obtained for each of these species. These results are also in accordance with a more thermophilic and light demanding strategy for *Q. ilex* than for *P. pinea* and *J. thurifera* trees. However, studies on intraannual growth in other *Pinus* and *Quercus* species indicate that the carbon fixed through photosynthesis is not directly used for radial growth in above-ground wood, evidencing that the early phase of radial growth completely depends on internal C-stores (Zweifel et al., 2006).

The wider thermal amplitude obtained for *Q. ilex*, compared with *J. thurifera* and *P. pinea* confirms the eurythermic character of this species, as it had been previously outlined in the literature (Ruiz de la Torre, 2006), capable of maintaining secondary growth along a wide thermal range. Gea-Izquierdo et al. (2009) found a negative correlation between high temperatures and growth for *Q. ilex*. Our results indicate that considering only elevated temperatures is not sufficient to explain this growth suppression. A combined effect of high temperatures, elevated evapotranspiration and soil water stress could cause the secondary growth inhibition, as observed in this study.

Drought effect was significant and inhibited growth for all species. However it was less limiting for *Q. ilex* than for *J. thurifera* and *P. pinea*. Other studies have found different growth responses to drought events between pine and oak species, oaks being more resistant to summer droughts and pine species being more resistant to spring droughts (e.g. Morán-López et al., 2014). Pine trees are known to unfold their needles during the summer and can attain one fourth of the total annual radial growth by the time their leaves reach full expansion (Zweifel et al., 2006). However summer droughts, which were the main drought events that occurred during the period of study, can strongly affect the secondary growth of pines since they hamper needle formation and cell enlargement reducing their radial increment (Merlin et al., 2015). Furthermore, both *Q. ilex* and *J. thurifera* are known to profit from isolated summer rainfalls (Camarero et al., 2010; Corcuera et al., 2004; Gutiérrez et al., 2011) activating xylogenesis and expanding their radial growth forming double rings (Campelo et al., 2007a). As opposed to this, *P. pinea* cannot benefit from this water supply during the driest months of the year (Campelo et al., 2007b). This behaviour in *Q. ilex* is particularly interesting in trees living in a

Mediterranean continental area. Diameter growth during the summer has been observed in *Q. ilex* trees living in more mesic locations (Cherubini et al., 2003). However, studies from open *Q. ilex* woodlands in continental sites in the Iberian peninsula, with similar precipitation regimes and lower stand densities obtain opposite growth tendencies with respect to late-summer precipitations (Gea-Izquierdo et al., 2009). We hypothesize that similar precipitation regimes in Mediterranean continental sites may be more favourable in mixed forests, due to niche complementarity, leading to less water-stressed conditions in the summer for evergreen broadleaf trees.

3.4.5. Model validation and growth projections

There is a marked recent tendency towards drier and hotter summer seasons in the region of study according to historical data (1975-2010) from Valladolid meteorological station (www.aemet.com). The model was constructed with data from 2012-2015, therefore considering more similar climate conditions to the ones found in the last period of the validation (2005-2011). The low density plot was also subjected to thinning practices to reduce stand density in 2002. The effect of thinning on the secondary growth of remaining trees was not considered in the model, which was constructed with girth increment data from 2012-2015, ten years after the thinning treatment was applied. We believe this may explain the poorer model performance in the first years of the validation and the more accurate growth predictions three years after the thinning treatments were applied.

According to our model projections for 2075 the 4.5ºC increase on average temperature and 30% decrease in annual rainfall expected in the region of study will negatively affect the secondary growth of *P. pinea*. If competition were included in these projections, intraspecific competition may even be translated in lower secondary growths for *P. pinea*. *Q. ilex* will be favoured maybe due to its wider thermal amplitude; however reduced growth could be expected if interspecific competition were considered. *J. thurifera* will remain practically unaffected but may have slight growth reductions including inter- and intraspecific competition.

3.5. Conclusions

Forest managers should be cautious to extrapolate these results at a forest management scale due to the low explained growth variance, particularly for *P. pinea* growing in mixed stands in low densities. However our predictions for cumulative girth increment show a notable long-term model accuracy. We thereby believe that this model is a useful tool to describe the effect of inter- and intraspecific competition and different climate change scenarios on secondary growth and may help orientate forest management decisions. Current management practices in the Spanish Northern Plateau have favoured *P. pinea* over *Q. ilex*. Based on all the previous findings and in accordance with the simulations carried out with the model for future climate scenarios, forest managers may wish to modify their management schedules lowering *P. pinea* stand densities and promoting species like *Q. ilex* in mixtures, with a higher plasticity in response to climatic conditions during the growing season (Gutiérrez et al., 2011). In line with other authors (Gea-Izquierdo et al., 2009), we believe this would be a more balanced stand combination in sclerophyllous oak-conifer mixtures, better adapted to the expected change in climatic conditions.

Acknowledgements

We are grateful to the Forest Service of Castilla y León administration for permission and support to carry out the field experiment. We also wish to thank Mar Conde, Enrique Garriga and Guillermo Madrigal for their help in the data collection. This work was supported by the Spanish Ministry of Economy and Competitiveness (MINECO) [grant FPI BES-2011-050760 to J.D.G., projects AGL-2010-15521 and RTA-2013-00011-C02-01]; by the National Institute for Agricultural and Food Research and Technology from Spain (INIA) [AT-2013-004]; and by the agreement between ITACyL-Diputación de Valladolid-INIA [CC-16-095-PROPINEA]. The UMR 1092 LERFoB is supported by a grant overseen by the French National Research Agency (ANR) as part of the "Investissements d’Avenir programme" [ANR-11-LABX-0002-01, Lab of Excellence ARBRE].

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Appendix. Distance dependent competition indices

We used the distance dependent competition indices developed by Bella (1971) and later modified by Tomé and Burhart (1989) to define intraspecific and interspecific interactions between the trees of the area of study. They are area overlap indices (AOI) which calculate an influence zone around each subject tree (ZA_i), where ZA_i dimension is related to tree size:

$$AOI_i = \sum_{j=1}^{n} \frac{ZO_{iq}}{ZA_i} \cdot \left(\frac{dbh_q}{dbh_i}\right)^k \tag{8}$$

These competition indices sum over all tree contestants for a subject tree i (n, being the number of tree competitors whose area of influence intersects that of the subject tree i) the proportion of ZA_i that is included in the influence zone of each competitor (ZO_{iq}). These proportions are weighed by the term $\left(\frac{dbh_q}{dbh_i}\right)^k$, where dbh_i and dbh_q are diameter at breast height of the subject tree *i* and of the competitor tree q respectively; k is a power factor. Among the different possible combinations between k and radius of influence zone area for each species, R, we selected R equal to 30 times dbh for intraspecific competition and 40 times dbh for interspecific competition. Concerning the weighting factor k, we set k = 1 for intraspecific interactions, indicating asymmetry on competition, and k = 0 for interspecific interactions, pointing to symmetric effects between species. This AOI combination has already proved to accurately describe the effect of competition on growth in these *Pinus pinea* admixtures in previous studies of the group. For more information on the use of this family of indices in mixtures see de-Dios-García et al. (2015).

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Chapter 4

Increased drought and high maximum temperatures alter recruitment patterns in Mediterranean forests: Linking climate, canopy cover and seedling survival in three co-occurring tree species

Based on: de-Dios-García, J., Pardos, M., Madrigal, G., Garriga, E., Conde, M., Kobe, R., Calama, R. Increased drought and high maximum temperatures alter recruitment patterns in Mediterranean forests: Linking climate, canopy cover and seedling survival in three co-occurring tree species (Submission pending).

Specific objectives:

- To identify species-specific responses in seedling survival along a light availability gradient.
- To examine how a 30% of rainfall reduction, which is the most probable climate change scenario predicted for the Mediterranean basin, influences seedling survival responses to irradiance.
- To assess the effect of temperature and precipitation variability on species specific seedling survival.
- To model species specific seedling survival probability along a light availability gradient considering two climatic scenarios for 2100.

Data:

- We used 3.5 years of seedling survival data from a plantation of 864 initial plants of *P. pinea*, *Q. ilex* and *J. thurifera* installed under an adult canopy of the three species.

Methodology:

- Lifetime analysis techniques considering daily and cumulative climatic data, three levels of light availability and two precipitation regimes (control and exclusion).

Main findings:

- Facilitation from adult trees has proved to be fundamental in early stages of tree species development. Optimal regeneration niche for *P. pinea* and *Q. ilex* seedlings under current and future climatic conditions (RCP8.5 scenario) is found in microsites where canopy cover intercepts between 50-75% of total incident light.

- Benefits from the canopy cover in these Mediterranean mixtures are not more humid soil conditions but rather lowered radiation levels and milder soil temperature conditions.
- Daily maximum temperatures over 25ºC exert a negative effect on *P. pinea* and *Q. ilex* seedling survival under all light treatments considering average values of precipitation for the area of study. However, *J. thurifera* seedlings remain practically unaffected under these climatic conditions.
- *P. pinea* and *J. thurifera* seedlings had a lower sensitivity to water scarcity than *Q. ilex* under all light treatments considering daily average maximum temperatures for the area of study.
- *Q. ilex* regeneration will rely on its ability to resprout, being its seedlings survival severely compromised. *J. thurifera* will undoubtedly keep colonising these Mediterranean mixtures, being less affected by extreme climatic factors in all levels of light availability that we evaluated.

Resumen

Está ampliamente aceptado que los principales factores limitantes para el establecimiento de las plántulas en ecosistemas mediterráneos es la escasez de agua junto con las temperaturas elevadas y la irradiación intensa. Las plántulas en la cuenca mediterránea están sometidas a muchos factores de estrés que actúan de forma simultánea y cuyas interacciones son aún poco conocidas. Estudios previos han analizado el efecto de la sequía sobre la supervivencia en condiciones naturales en la Península Ibérica construyendo canalones de exclusión de lluvia. Este tema es de gran relevancia dado que las condiciones climáticas se están volviendo más cálidas y secas debido al cambio climático y pueden afectar a la dinámica de regeneración natural. Sin embargo, la dinámica de la regeneración natural en masas mixtas de *Pinus pinea* en los páramos calizos de la Meseta Norte aún es poco conocida. En estas masas *P. pinea, Quercus ilex* subsp. *ballota* y *Juniperus thurifera* comparten hábitat. Con motivo de identificar el nicho óptimo de regeneración de estas especies diseñamos un experimento factorial a lo largo de un gradiente de luz y considerando dos escenarios climáticos para la precipitación (control y exclusión). Hemos utilizado datos de supervivencia de 3.5 años de una plantación de 864 plántulas de las tres especies de estudio, instalada bajo cubierta de las tres especies. Empleamos técnicas de análisis de vida para modelizar la supervivencia e identificar el ambiente óptimo de luz y los factores climáticos más determinantes para garantizar una regeneración natural exitosa en estas masas mixtas. El nicho óptimo de regeneración para las plántulas de *P. pinea* y *Q. ilex* tanto en las condiciones climáticas actuales como en las futuras (escenario RCP 8.5) se da en ambientes en los que la cobertura arbórea intercepta entre un 50-75% de la luz incidente total. La cobertura arbórea no aporta mayor humedad al suelo sino niveles de irradiación más bajos y temperaturas más suaves en el suelo. El efecto de las temperaturas máximas y de las precipitaciones acumuladas varía entre especies, viéndose la supervivencia de las plántulas de *Q. ilex* seriamente comprometida. *J. thurifera* continuará indudablemente colonizando estas masas mixtas mediterráneas, viéndose menos afectada por factores climáticos extremos en todos los niveles de luz que hemos evaluado.

Palabras clave

Bosque mixto; *Pinus pinea*; *Juniperus thurifera*; *Quercus ilex*; condiciones naturales; exclusión de lluvia; plantación.

Abstract

It is widely accepted that the main limiting factors during plant establishment in Mediterranean ecosystems are water shortage, together with high temperatures and intense irradiance. Seedlings in the Mediterranean basin are thereby subjected to multiple co-occurring stresses whose interactions are still poorly understood. Previous studies have analysed the effect of drought on seedling survival, in field conditions in the Iberian Peninsula building rain exclusion shelters. This topic is highly relevant since climatic conditions are becoming hotter and drier due to climate change and may affect forest regeneration dynamics. However, knowledge of natural regeneration dynamics in mixed *P. pinea* forests growing in limestone plain areas in the Spanish Northern Plateau is still scarce. In these forests *P. pinea*, *Quercus ilex* subsp. *ballota* and *Juniperus thurifera* share the habitat. In order to identify the optimal regeneration niche for these species, we designed a factorial experiment along a light availability gradient considering two climatic scenarios for precipitation (control and exclusion). We used 3.5 years of seedling survival data from 864 seedlings of all the species of study installed under an adult canopy of the three species. Lifetime analysis techniques were employed to model seedling survival to identify the key climatic factors and optimal light environment to guarantee a successful natural regeneration in these mixtures. The optimal regeneration niche for *P. pinea* and *Q. ilex* seedlings under current and future climatic conditions (RCP 8.5 scenario) is found in microsites where canopy cover intercepts between 50-75% of total incident light. Benefits from the canopy cover in these Mediterranean mixtures are not more humid soil conditions but rather lowered radiation levels and milder soil temperature conditions. The effect of daily maximum temperatures and cumulated precipitation differed between species, seedling survival being severely compromised for *Q. ilex*. *J. thurifera* will undoubtedly keep colonising these Mediterranean mixtures, being less affected by extreme climatic factors in all levels of light availability that we evaluated.

Keywords

Mixed forest; *Pinus pinea*; *Juniperus thurifera*; *Quercus ilex*; field conditions; rainfall exclusion; seedling plantation.

4.1. Introduction

It is widely accepted that the main limiting factors during plant establishment in Mediterranean ecosystems are water shortage, together with high temperatures and intense irradiance (e.g. Granda et al., 2012). Rainfall in the Mediterranean basin is particularly scant during the summer, reducing soil water availability for plants. High summer temperatures also cause large carbon losses through respiration (Reichstein et al., 2002). In addition, heat and high radiation co-occur in Mediterranean summers increasing the evaporative demand, altering plant water balance and its photosynthetic status and leading to high rates of seedling mortality (Calama et al., 2015; Gómez-Aparicio et al., 2006). Moreover, intense radiation and summer drought trigger photoinhibition, reduce plant carbon gains (Valladares et al., 2005), and cause a deficit in carbon assimilation (Reichstein et al., 2002). Seedlings in the Mediterranean basin are thereby subjected to multiple co-occurring stresses whose interactions are still poorly understood. This topic is highly relevant since climatic conditions are becoming hotter and drier due to climate change and may affect forest regeneration dynamics.

Species mixing has proved to have buffering effects to resist fluctuating environmental conditions in woody saplings (Van de Peer et al., 2016). This is particularly relevant in the Mediterranean basin, which is characterized by a great interannual variability in terms of precipitation. However, some species are better adapted than others to higher average temperatures and more intense droughts (Peñuelas et al., 2001). Similarly, high light and shade tolerance is species-specific, varies with life-stage and depends on a complex combination of morphological and physiological plant traits. However, shade tolerance can be significantly modified by water availability (Sánchez-Gómez et al., 2006b, 2006a). It is therefore crucial to unveil how water shortage may modify seedlings species-specific light preference to guarantee the persistence of Mediterranean forests in a changing climate.

Light availability is a key environmental factor to define the regeneration niche of Mediterranean woody species, since climatic and ecological characteristics make light a stress factor in Mediterranean ecosystems (Gómez-Aparicio et al., 2006). Several studies have found interspecific differences in seedling survival along light availability gradients (Sack, 2004; Sánchez-Gómez et al., 2006b, 2006a). However, very few studies have analysed this problem under field conditions in the Mediterranean Basin (Granda et al., 2014, 2012). Likewise, many authors point to water shortage as the main factor determining seedling mortality in Mediterranean ecosystems (e.g. Gómez-Aparicio et al., 2004) causing a stronger impact on ecosystem functioning than other global change drivers like warming or elevated CO_2 (e.g.Beier et al., 2012). Previous studies have analysed the effect of drought on survival, and growth in field conditions in the Iberian Peninsula building rain exclusion shelters (Cotillas et al., 2009; Matías et al., 2012). However, while progress has been made in identifying the abiotic drivers of seedling mortality (e.g. Granda et al., 2014) more field studies under natural and simulated conditions are needed to broaden our knowledge of regeneration dynamics.

Natural regeneration dynamics in mixed *P. pinea* forests has been studied on the sandy continental soils of the North West of the Iberian Peninsula (Ledo et al., 2014; Moreno-Fernández et al., 2018), but knowledge of the dynamics on the limestone plain areas is still scarce. In these mixtures *P. pinea*, *P. pinaster*, *Q. ilex* subsp. *ballota* (hereafter *Q. ilex*), *Q. faginea*, and *J. thurifera*, share the habitat under different degrees of mixture, but species composition varies between stands. Adult-seedling relationships in *P. pinea* mixtures have been analysed through spatial point pattern analysis (Ledo et al., 2014) and through logistic additive models (Moreno-Fernández et al., 2018). Optimal light environments for regeneration in mixed stands have been explored through photosynthetic process models (Mayoral et al., 2015). In this context, the role of climate change possibly altering microclimatic conditions in these forests due to reduced precipitation remains uncertain.

Natural regeneration in managed *Pinus pinea* stands in the Spanish Northern Plateau is known to suffer from high failure rates in monospecific forests due to its masting habit (Calama et al., 2011), seed dispersal limitations (Barbeito et al., 2008) and seed predation (Manso et al., 2014). Temperatures may reach -15ºC in winter in the Spanish Northern Plateau (Calama et al., 2015), however the main bottleneck for tree seedlings growing in this area is surviving to severe drought and heat summer conditions (Pardos et al., 2005).

Quercus ilex forms mostly coppice forests in the Western Mediterranean basin. Its high ability to resprout from stumps after coppicing or to regrow from pre-existing trees made the study of seedling recruitment largely overlooked for years in areas subjected to long-term regular management (Espelta et al., 1995). However widespread mortality of *Quercus ilex* in open woodlands (Natalini et al., 2016) has set the alarm again on fostering its sexual reproduction and the need to identify its optimal regeneration niche.

Little is known about the regeneration niche of *Juniperus thurifera*. Its recent expansion has been attributed to changes in land use, with crop abandonment in many rural areas, and a successful community of seed dispersers by thrushes and carnivores (Escribano-Ávila et al., 2012). It has been suggested that it recruits preferentially under canopied microhabitats (Escribano-Ávila et al., 2013) with a gender biased self-facilitation in some sites (Montesinos et al., 2007) but not in others (Granda et al., 2014). Behind this outstanding recruitment performance in a changing climate could be its good physiological adaptation to the cold and to hydric stress (Jiménez et al., 2005), low growth seedling rates as seen in other Mediterranean Junipers (Mayoral et al., 2016) and its capacity to develop secondary growth tissues following summer rains (Camarero et al., 2010). However, the influence of simultaneous climatic stresses on its ability to survive or die at a seedling stage remain unknown.

Seedling survival and mortality along light gradients in Mediterranean conditions has been approached through linear and non-linear regressions (Valladares et al., 2005), and comparisons between species have been carried out through analysis of variance (Gómez-Aparicio et al., 2006). However, these models lack an integration of daily and cumulative climatic effects that could be clear to ascertain the combination of climatic effects that make plants die or survive in the field at critical periods of time. To overcome this problem we used lifetime analysis techniques (Calama et al., 2015; Manso et al., 2013), that define the probability of a mortality event on a day *t* as a function of light availability, daily temperatures and cumulative precipitation.

In this study we used 3.5 years of seedling survival data from a plantation of *P. pinea*, *Q. ilex* and *J. thurifera* installed under an adult canopy of the three species. Our aim was to study the spatiotemporal pattern of seedling survival along a light availability gradient considering two precipitation regimes (control and exclusion). The specific objectives were: i) to identify species-specific responses in seedling survival along a light availability gradient, ii) to examine how a 30% of rainfall reduction, which is the most probable scenario of rainfall reduction during the summer predicted for the Mediterranean basin, influences seedling survival responses to irradiance, iii) to assess the effect of air temperature and precipitation variability on species specific seedling survival, iv) to model seedling survival through lifetime analysis techniques. Our first hypothesis was that seedlings survival response to similar shade and climatic conditions is species-specific (Granda et al., 2012). The second hypothesis was that higher levels of canopy closure would lower radiation levels creating microclimatic conditions more favourable for seedling survival (Barbeito et al., 2008). Our last hypothesis was that precipitation reduction would endanger seedling survival (Matías et al., 2012).

4.2. Material and methods

4.2.1. Study area

This study was carried out in a 1,108 ha mixed forest in the limestone plain areas in the east of the province of Valladolid (Spain), within the geographical region of the Spanish Northern Plateau and integrated in "El Carrascal" Site of Community Importance of the Natura 2000 network (41º35'N, 4º19'W). Mean altitude is 885 m. The area has a Mediterranean continental climate with a highly variable annual rainfall (between 220-630 mm) and a characteristic summer drought during which mean monthly rainfall (July-September) is 21 mm and temperatures can reach 42ºC. Soils in the area of study are inceptisols with a water holding capacity of 176 mm·m^{-1}.

4.2.2. Composition

Oak-conifer mixed stands represent the most diverse and complex forest systems in the province of Valladolid and are mainly located in limestone plain areas. In these stands *P. pinea* grows with two oak species: holm oak (*Quercus ilex* subsp. *ballota*) and portuguese oak (*Quercus faginea* subsp. *faginea*), the Spanish juniper (*Juniperus thurifera*) and *Pinus pinaster*. Grazing by wild herbivores such as wild boar (*Sus scrofa*) and roe deer (*Capreolus capreolus*) are common in the area. And the Iberian wolf (*Canis lupus* subsp. *signatus*) inhabits and breeds in these forests too.

The present study is a plantation experiment under field conditions that will focus on these more complex admixtures, which are considered to reach the maximum level of specific diversity within the territory (Madrigal, 2014).

4.2.3. Stand management

Land ownership in the Spanish Northern Plateau has played a critical role in the maintenance of mixed *Pinus pinea* stands with *Quercus* and *Juniperus.* Currently most of these complex sclerophyllous mixtures grow in lands that were privately owned until the 80s, some of them by important local vineyard landlords. The lack of investments from private owners contributed significantly to the conservation of these mixed stands. In the 1980's most of these lands were sold to the regional government. At this time selective cuttings began to be carried out to favour tree species diversity in these mixtures. Current management focuses on a tree selection system, promoting growth and regeneration of all tree species. Rotation period between selective cuttings within a given block is approximately 25 years. Sustainable management is the main objective in these forests, trying to obtain a profitable cone production in *P. pinea* compatible with a successful natural regeneration, together with timber and biomass extraction, mushroom harvesting and other recreational uses.

4.2.4. Site selection and experimental design

This study was conducted in a mixed public owned forest within the flat limestone area of the Spanish Northern Plateau. In this forest *Pinus pinea* grows mixed with *Quercus ilex* and *Juniperus thurifera*, which will be the target species for this study. Within this forest we established twelve 45 m^2 (5 x 9 m^2) experimental plots trying to cover the whole range of light and microenvironmental soil conditions. To test the effect of canopy cover and water availability on seedling survival we performed a factorial field experiment. In order to capture the widest range of light availability in the site we estimated the Global Site Factor (GSF) in 21 potential places before plot installation. GSF is the proportion of global solar radiation (direct plus diffuse) under a plant canopy relative to that in the open, ranging from 0 (completely closed canopy) to 1 (completely open canopy). GSF was calculated from two hemispheric photographs at each of these potential places using Hemiview 2.1 software (Delta-T Devices, Ltd, Cambridge, UK). We established 3 levels of canopy cover (hereafter light treatments) based on the GSF values of the 21 potential places for plot instalation: High, medium and low light availability corresponding to average GSF values of 0.75, 0.45 and 0.26 respectively (Table 4.1). Four plots were installed by light treatment, resulting in the final number of twelve plots.

Table 4.1. Global Site Factor by plot and light availability. HLA: high light availability; MLA: medium light availability; LLA: low light availability; GSF: Global site Factor; SD: Standard deviation. Plots with * include 1 subplot with rainfall exclusion.

Light availability	Plot	GSF	SD
HLA	1*	0.749	0.020
	2*	0.773	0.010
	3	0.769	0.098
	4	0.698	0.025
MLA	5*	0.456	0.064
	6	0.584	0.018
	7	0.454	0.016
	8*	0.314	0.123
LLA	9	0.264	0.044
	10*	0.261	0.085
	11*	0.223	0.041
	12	0.273	0.013

Every plot (Fig 4.1a) was divided into two subplots (4 m x 4 m), and within each subplot we defined 4 blocks (2 m x 2 m) where in December 2011 we planted nine one year old seedlings, three seedlings per species (Fig. 4.1b). The total number of planted seedlings was 864 (12 plots x 2 subplots/plot x 4 blocks/subplot x 9 plants/block). Seedlings were obtained from the Nursery of the Forest Service of Castilla y León. Plots were surrounded with a 1.8 m height wire fence to exclude herbivory (Fig. 4.1a).

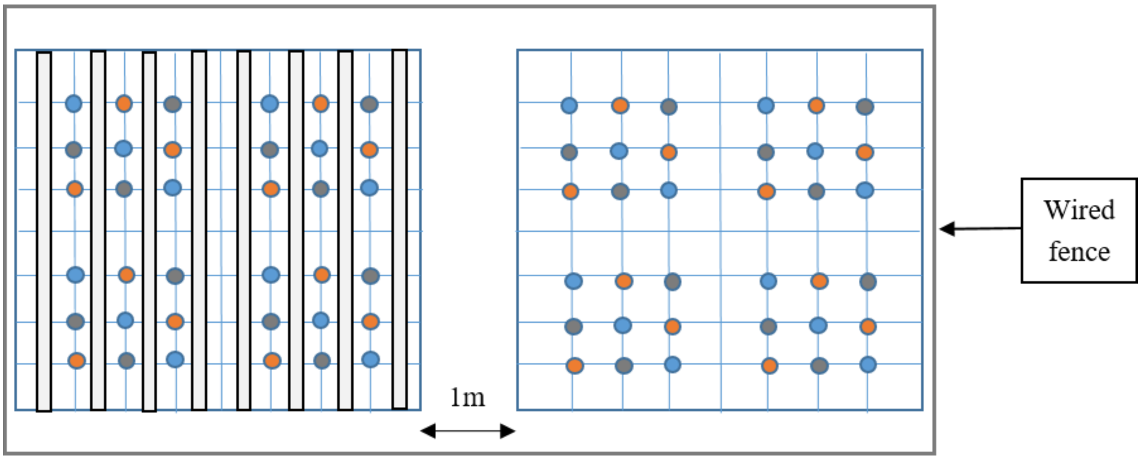

Fig. 4.1a. Schematic representation of a plot consistent of two subplots. The subplot on the left shows longitudinal stripes representing a rain exclusion shelter.

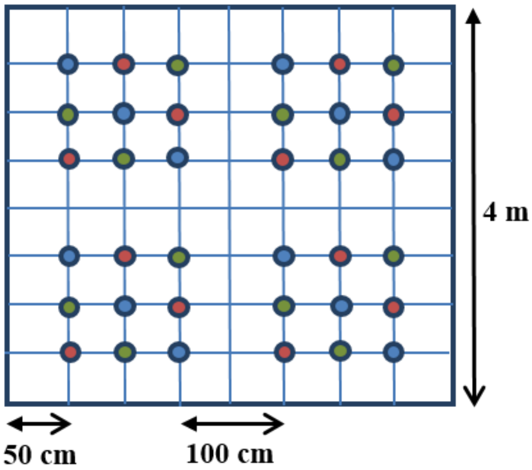

Fig. 4.1b. Diagram of a subplot without a rain exclusion shelter. Each color circle stands for tree seedlings of one species (Blue: *P. pinea*; Red: *Q. ilex*; Green: *J. thurifera*).

With respect to the water availability we selected two levels based on (1) current climate conditions; and (2) 30% of rainfall reduction predicted for Mediterranean areas during the summer. Hereafter these levels of water availability will be referred to as *control* and *exclusion* treatment. The rainfall reduction is based on the RCP 8.5 scenario by Intergovernmental Panel on Climate Change (IPCC, 2013). For this purpose we built rain exclusion shelters (Matías et al., 2012) formed by a 1.5 m × 3 m metal frame supprorting V-shaped clear methacrylate bands without UV filter (Barlocast®; Faberplast

S.L., Madrid), covering 30 % of the surface, and intercepting the same percentage of natural water supply by rain. Rainfall shelters were installed in one of the subplots on six out of the twelve plots (Table 1, Fig. 4.1a) in March 2013, covering two subplots by light treatment (Fig. 4.2).

Fig. 4.2. Rain exclusion shelters formed by a metal frame supporting V-shaped clear methacrylate bands without UV filter.

Daily climatic variables, such as the minimum, mean and maximum temperatures and daily precipitation, were gathered from a nearby meteorological station (41º34’N, 4º20’W) located 2.5 km from the study site. Soil moisture (20 cm depth) was continuously monitored every 10-min in the rainfall excluded and non-excluded subplots from April 12 2013 until October 8 2014, within two contrasting light level plots (high light availability and low light availability), using two HOBO micro-weather stations (Micro-HWS, ONSET, Massachusetts, USA). Air temperature and lux intensity (20 cm aboveground) were also continuosly monitored on each plot at 10 min intervals with a combined light-temperature sensor and data logger, HOBO Pendant®.

4.2.5. Dead plants replacement

Climatic conditions during 2012 were drier and hotter than usual, which forced postponing the installation of the rain exclusion shelters. To cope with this exceptional lack of precipitation we supplied additional water to try to prevent a massive seedling death. We watered plants in mid-July and mid-September 2012, providing 12.7 l/m^2 of water by plot each time, trying to simulate the average rainfall conditions of the area of study of this period. Plants were watered with the help of a water pump coupled with a valve to regulate water flow. Despite irrigation, a great number of plant deaths was recorded (19.21% by July 2012, 39.21% by September 2012 and 47.69% by February 2013). Thus in February 2013 412 dead plants were replaced.

4.2.6. Survival measurements

The experiment started on December 1, 2011 and ended in May 12, 2015. During this period the plantation was revisited regularly (average period = 47 days ± 18) on 19 occasions to evaluate seedling survival. Plants were considered dead when they had lost all their aerial biomass, lacked any photosynthetically active leaves and had lost flexibility in the upper third portion of their aerial structures (Sánchez-Gómez et al., 2006a).

4.2.7. Data analysis

4.2.7.1. Efficiency of rainfall exclusion

In order to check the real effect of light availability, rainfall exclusion and their interaction on the volumetric soil water content (VWC), we used a two-way analysis of variance (ANOVA) by season. This approach allowed comparing the effect of rainfall reduction on VWC while accounting for the light availability treatment. When applicable we employed Tukey multiple comparison tests with a p-level of 0.05 to identify significant differences between treatments. ANOVA and Tukey analysis were performed with procedure GLM in SAS®.

4.2.7.2. Survival analysis

The probability of seedling survival was modelled from the survival assessment dataset using survival analysis techniques (Lawless, 2003). Survival analysis is based on defining a random variable τ as the time (in days) elapsed since the beginning of the experiment (December 1 2011) and the date of seedling mortality. For the replaced seedlings beginning of the experiment was February 1 2013. Thereby, each seedling is considered by the model from the moment it was planted until it dies or until the end of the experiment. This consideration allows to account for seedling age.

For the sake of simplicity, we assumed an exponential distribution of τ (as in Calama et al., 2015). The cumulative density probability of τ at time t is the probability that plant *i* dies at or before day *t*, i.e. $F_i(t) = P_i(\tau \leq t)$. The survival function $S_i(t)$ is then defined as the probability for plant *i* to remain alive after day *t*, i.e. $S_i(t) = 1- F_i(t)$. $S_i(t)$ is modelled through the hazard function $h_i(t, x)$, which represents the instantaneous mortality rate for seedling *i* during day *t*, conditioned to seedling survival up to that date. The hazard can be a function of a set of covariates *x*. The hazard function is related to the survival function as follows:

$$S_i(t) = \exp\left[-\sum_{m=1}^{t} h_i(m)\right] \qquad (1)$$

The survival function (eq. 1) implies that the probability of a seedling *i* remaining alive at date *t* is a decreasing function of the sum of all hazards prior to time *t*. In the present study we tested different time-independent and time-dependent (daily varying) covariates as potential predictors for daily hazard. As time-independent covariates we evaluated: a) Species (*P. pinea, Q. ilex, J. thurifera),* b) light availability (high, medium, low), c) rainfall exclusion (yes / no). In addition, we included first order interactions between these factors. As time-dependent covariates we tested: a) Daily climatic variables: minimum, mean and maximum temperatures (T_{min}, T_{mean} and T_{max} in ºC) and daily precipitation (P_t in mm), b) cumulative precipitation for the last 30 days ($Pcum_t$ in mm).

Under the exponential distribution of τ, the complete version of the hazard function can be formulated as follows:

$$h_{it} = exp\big(\alpha_s + (\beta_{ls}LA) + (\gamma_s RE) + \big(\delta_{ls}(LA \cdot RE)\big) + (\ \theta_s\, T_t) + (\mu_s P_t) + (\rho_s\ Pcum_t\big) \qquad (2)$$

where subindex s indicates that the parameter is species specific; α is the intercept term for species; LA is a categorical dummy variable that stands for light availability and has three levels, corresponding to high light availability (LA_0), medium light availability (LA_1) and low light availability (LA_2); LA value is 1 if the plant is included in the light availability treatment LA_0, LA_1, LA_2, respectively and 0 if not. RE is a dummy variable that stands for rainfall exclusion and equals 1 when the seedling *i* is in the rainfall exclusion treatment and 0 when it is not. T_t refers to the minimum, mean and maximum temperature of day *t*, P_t is the precipitation of day t, $Pcum_t$ is the cumulated precipitation from day *t*-30 to day *t*.

4.2.8. Model fitting, evaluation and comparison.

In order to determine if seedlings response in terms of survival is species specific we firstly constructed a simple model only including the species effect in the hazard function (eq. 3).

$$h_{it} = exp\left(\alpha_p PP + \alpha_q QI + \alpha_J JT\right) \tag{3}$$

where *PP*, *QI* and *JT* are dummy variables whose value is 1 if the plant is a *P. pinea, Q. ilex* or *J. thurifera* respectively, and 0 otherwise.

If we detect a significant effect of the species, and in order to avoid convergence problems due to overparameterization and complex interactions, we would fit model (2) separately for each species. Entrance of the covariates into the model was evaluated by means of a sequential procedure, starting by the time independent covariates (light availability, rainfall exclusion and their interaction), and then the time dependent covariates (minimum, mean and maximum daily temperature, daily rainfall and cumulative rainfall during the last 30 days). In the last step the inclusion of a random plot effect into the model was evaluated.

Model comparison between sequential steps was performed in terms of the Bayesian Information Criterion (BIC). BIC was preferred over other criteria, as AIC or –2LL, since it penalizes the entrance of extra parameters on the model. A variable was retained if its entrance resulted in a significant improvement of the model for at least one of the species. Models were fitted through maximum likelihood methods using SAS® procedure

NLMIXED. Comparison between species was done through the hazard function of each species.

4.2.9. Hazard function projections under current and predicted climate conditions

The hazard function from the complete model by species was used to compare the seedlings risk of mortality under current climate conditions (2015) and forecasted climate conditions for 2100 considering climate change scenario RCP 8.5 from Intergovernmental Panel on Climate Change (IPCC). We considered average temperature and precipitation values for 2015. Daily climate projections for the area of study where obtained from the AdapteCCa platform (www.adaptecca.es), resulting in a 4.5ºC increase in temperature and a 15% reduction in annual rainfall for 2100.

4.3. Results

4.3.1. Exploratory analysis

The mean values of the rate of survival at the end of first summer (October 2012 or October 2013 for initial or replanted) and at the end of the experiment (May 2015) by species, treatment and instant of plantation (Table 4.2) show some particularities:

- The main part of the mortality in plants, for all the species, treatments and instant of plantation, occurs during the first summer after plantation.
- Higher rates of survival after the first summer and total survival are found for *J. thurifera* irrespective of the light availability, rainfall exclusion treatment and date of plantation. *J. thurifera* shows values of final survival of 47%, 70% and 89% for HLA, MLA and LLA respectively, without considering exclusion.
- *P. pinea* shows the second higher survival rates after the first summer and the total survival for the set of initial plants (total survival between 28% – 40%), while lower values for final survival were shown in the replanted plants, especially in HLA and MLA environments.
- *Q. ilex* showed the lowest rates of survival in the case of the initial set of plants (between 11%-21% depending on light environment), while it showed much higher rates of survival for the replanted plants, especially in MLA and LLA environments.
- All the species showed the highest rates of survival under low light availability (shaded environments), followed by medium light availability, while higher rates of mortality were attained on fully exposed high light environments.
- There is no evident pattern associated with the effect of rainfall exclusion, probably being affected by the experimental imbalance (exclusion affecting six out of twelve plots).

Table 4.2. Rates of seedling survival at the end of the first summer (October 2012 for the initial set of plants, October 2013 for the plants replanted on February 2013) as a function of the species, light availability, rainfall exclusion and date of plantation.

			Survival at the end of 1st summer			Survival at the end of experiment		
Origin	Light	Exclusion	PP	QI	JT	PP	QI	JT
Initial: planted on January 2012 (n=864)	HLA	NON	29.2%	19.4%	68.1%	23.6%	9.7%	47.2%
		EX	50.0%*	54.2%*	62.5%*	41.7%	16.7%	45.8%
		Ave	34.4%	28.1%	66.7%	28.1%	11.5%	46.9%
	MLA	NON	54.2%	37.0%	81.7%	36.1%	19.2%	69.0%
		EX	62.5%*	29.2%*	87.5%*	45.8%	16.7%	75.0%
		Ave	56.3%	35.1%	83.2%	38.5%	18.6%	70.5%
	LLA	NON	61.3%	42.5%	91.2%	36.0%	20.5%	89.7%
		EX	79.2%*	41.7%*	100.0%*	50.0%	25.0%	87.5%
		Ave	65.7%	42.3%	93.5%	39.4%	21.6%	89.1%
	Average		52.2%	35.2%	80.9%	35.4%	17.2%	68.6%
Replanted on February 2013 (n=412)	HLA	NON	17.3%	23.5%	69.7%	11.5%	7.8%	45.5%
		EX	28.6%	41.2%	55.6%	28.6%	29.4%	55.6%
		Ave	19.7%	27.9%	66.7%	15.2%	13.2%	47.6%
	MLA	NON	29.4%	56.0%	87.5%	20.6%	40.0%	75.0%
		EX	40.0%	64.7%	66.7%	30.0%	58.8%	66.7%
		Ave	31.8%	58.2%	84.2%	22.7%	44.8%	73.7%
	LLA	NON	86.2%	84.4%	88.9%	69.0%	68.9%	88.9%
		EX	57.1%	93.8%	NO	57.1%	75.0%	NO
		Ave	80.6%	86.9%	88.9%	66.7%	70.5%	88.9%
	Average		38.4%	56.6%	74.3%	30.1%	41.8%	60.0%

*where HLA, MLA and LLA: high, medium and low light availability environments; NON and EX refer to non-excluded and rainfall excluded plants; Ave indicated the mean value for the same light environment, Average the mean value for the species. *Rainfall exclusion experiment was not installed until February 2013; thus these plants are not affected by exclusion at all.*

4.3.2. Efficiency of water exclusion experiment

Data obtained from the micro-weather stations (Table 4.3) indicates that intercepting 30% of annual rainfall in the subplots with rainfall exclusion resulted in an average 14.8% reduction of the volumetric soil water content (VWC) when compared with the non-excluded subplots (average value of VWC for the whole period of study in non-excluded plots was 0.197 vs 0.168 m^3 water · m^{-3} soil in excluded plots). ANOVA showed that the effect of the exclusion is less evident in the drier seasons (summer 2013 & 2014, fall 2014) than in the humid seasons. Another interesting finding is the significant effect of light availability on VWC, with higher values in the HLA than in the LLA for all seasons evaluated except for winter 2014 (Fig. 4.3, Table 4.3).

Table 4.3. Mean values per treatment and two-way ANOVA summary table for the volumetric soil water content (VWC) by season. NON and EX refer to non-excluded and rainfall excluded plants; Ave refers to mean value for both LA environments; LA, light availability; RE, rainfall exclusion; LA·RE, interaction; *$P \leq 0.05$; **$P \leq 0.001$; ***$P \leq 0.0001$; NS, nonsignificant.

Exclusion	LA	Spring13	Summer13	Fall13	Winter14	Spring14	Summer14	Fall14	Total
NON	Average	0.261	0.139	0.215	0.290	0.188	0.128	0.122	0.197
	HLA	0.265	0.178	0.247	0.288	0.219	0.170	0.172	0.223
	LLA	0.257	0.099	0.182	0.292	0.157	0.085	0.072	0.170
EX	Average	0.191	0.126	0.183	0.266	0.152	0.112	0.097	0.168
	HLA	0.210	0.145	0.195	0.267	0.186	0.145	0.166	0.189
	LLA	0.172	0.107	0.170	0.265	0.118	0.079	0.028	0.146
ANOVA	LA	***	***	***	NS	***	***	***	
	RE	***	*	***	***	***	**	NS	
	LA·RE	*	**	**	NS	NS	*	NS	

Comparable VWC values for the HLA and LLA, and daily average precipitation from April 16 2013 until October 8 2014 is shown in Fig. 4.3. VWC increased in the HLA and LLA plots following the precipitation events and soil water content decreased as the time elapsed since the last precipitation event increased, being this decrement more evident in LLA. In addition, differences between exclusion and non-exclusion treatment tend to be larger in HLA than in LLA.

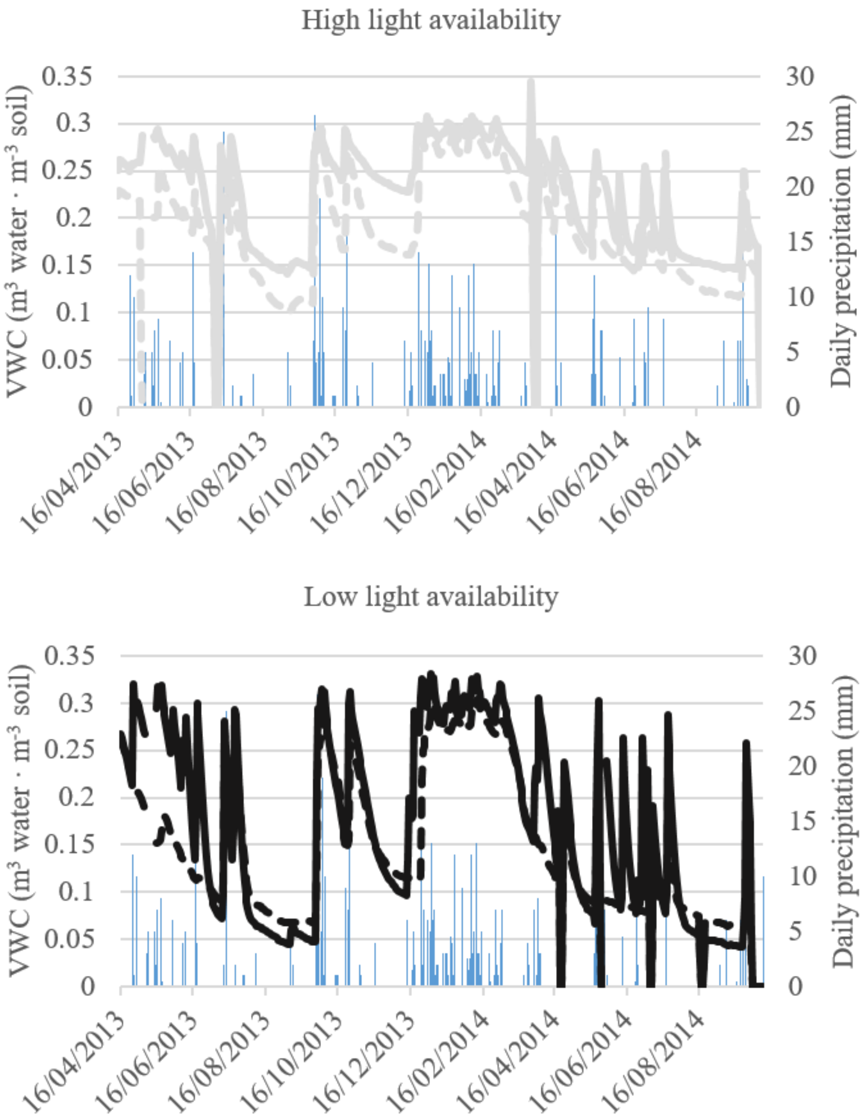

Fig. 4.3. Daily average volumetric soil water content (VWC) and precipitation trends in a high light availability plot (above) and a low light availability plot (below) under two levels of water availability [control (continuous lines) and exclusion (dashed lines)]. Blue columns indicate daily average values of precipitation.

4.3.3. Simple model

To test our first hypothesis, we constructed a basic model considering only a species effect in the hazard function (Table 4.4).

Table 4.4. Summary of estimates of parameter α for the basic model.

Species	Estimate	SE	Df	t value	p-value
P. pinea (α_1)	-6.7682	0.05863	1,319	-115.43	<0.001
Q. ilex (α_2)	-6.4237	0.05113	1,319	-125.64	<0.001
J. thurifera (α_3)	-7.9215	0.09245	1,319	-85.68	<0.001

Convergence was attained for the basic model (-2LL = 6157, AIC = 6163, BIC = 6179) resulting in an intermediate risk of mortality for *P. pinea* (α_1 = -6.7682), higher for *Q. ilex* (α_2 = -6.4237) and lower risk for *J. thurifera* (α_3 = -7.9215). This confirms our first hypothesis that seedlings survival response is species specific.

4.3.4. Hazard function definition

Due to convergence problems we constructed species specific models to test the inclusion of the rest of the covariates. The sequential procedure for model construction was the same for the three species and it is shown in Table 4.5.

Table 4.5. Comparison of fitting statistics and sequential procedure for model construction. LA, light availability; RE, rainfall exclusion; LA·RE, interaction; T_{min}, minimum daily temperature; T_{mean}, mean daily temperature; T_{max}, maximum daily temperature; P_t, precipitation on day *t*; $Pcum_t$, cumulated precipitation for the period *t*-30 to *t*; α_s is the intercept for species *s*; β_l, parameter associated with light availability; γ, parameter associated with rainfall exclusion; δ_l, parameter associated with a first order interaction between light availability and rainfall exclusion; σ, parameter associated with minimum daily temperature; τ, parameter associated with mean daily temperature; θ, parameter associated with maximum daily temperature; μ, parameter associated with daily precipitation; ρ, parameter associated with the cumulated precipitation for the period *t*-30 to *t*; σ_u^2 variance for the plot random effect BIC, Bayesian information criterion.

	Modelling step									
	0	1	2	3	4	5	6	7	8	9
Intercept	α_s	α_s	α_s	α_s	α_s	α_s	α_s	α_s	α_s	α_s
LA	-	β_l	β_l	β_l	β_l	β_l	β_l	β_l	β_l	β_l
RE	-	-	γ	γ	γ	γ	γ	γ	γ	γ
LA·RE	-	-	-	δ_l	-	-	-	-	-	-
T_{min}	-	-	-	-	σ	-	-	-	-	-
T_{mean}	-	-	-	-	-	τ	-	-	-	-
T_{max}	-	-	-	-	-	-	θ	θ	θ	θ
P_t	-	-	-	-	-	-	-	μ	-	-
$Pcum_t$	-	-	-	-	-	-	-	-	ρ	ρ
Plot random	-	-	-	-	-	-	-	-	-	σ_u^2
BIC *P. pinea*	2291	2268	2267	2282	1905	1840	1813	1799	1813	1702
BIC *Q. ilex*	2699	2650	2633	2651	2327	2289	2276	2281	2263	2187
BIC *J. thurifera*	1185	1141	1146	1162	1074	1059	1052	1067	1049	1003

Among the time independent covariates defining the hazard functions the inclusion of light availability (LA) improved the performance of the models (model 1) over the simple model only including the specific intercept. The inclusion of the rainfall exclusion (RE) resulted in improvement for *Quercus ilex* and – to a lesser extent – in *P. pinea,* with no improvement in *J. thurifera* (model 2), while their interaction did not result in fitting improvement (model 3), so only LA and RE were included. As regards the daily climatic effects T_{max} provided lower values of BIC for all species than T_{min} and T_{mean} (models 4-6), therefore T_{max} was selected. The inclusion of daily precipitation (model 7) was significant only for *P. pinea*, while the inclusion of the cumulated precipitation ($Pcum_t$) improved the model for *Q. ilex* and *J. thurifera*, so the latter was preferred due to its easier biological interpretation (model 8). Therefore, the parameters finally included in the hazard functions of all species were: Intercept, light availability, rainfall exclusion, T_{max} and $Pcum_t$. To take into account the inherent correlation due to repeated observations from the same plot, as well as the potential imbalance associated with the rainfall experiment, a plot random effect was also included into the definitive model (9). Parameter estimates for the definitive models by species are shown in Table 4.6.

Table 4.6. Summary of parameter estimates for the definitive model 9 by species. α_s is the intercept for species *s*; β_0, parameter associated with high light availability; β_1, parameter associated with medium light availability; β_2, parameter associated with low light availability; γ, parameter associated with rainfall exclusion; θ, parameter associated with daily maximum temperature; ρ, parameter associated with the cumulated precipitation for the period *t*-30 to *t*; −2LL, −2 log likelihood; AIC, Akaike information criterion; BIC, Bayesian information criterion. P-values for all parameters of the three definitive models were <0.0001. Notice that lower values of the parameter indicate a lower risk of daily mortality.

	P. pinea		*Q. ilex*		*J. thurifera*	
	Estimate	p-value	Estimate	p-value	Estimate	p-value
α_s	-4.5877	<0.0001	-2.5056	<0.0001	-3.6027	<0.0001
β_0	-6.2714	<0.0001	-5.5579	<0.0001	-5.5738	<0.0001
β_1	-6.8684	<0.0001	-6.2343	<0.0001	-6.3409	<0.0001
β_2	-7.3206	<0.0001	-6.7103	<0.0001	-7.5960	<0.0001
γ	-0.2505	0.2681	-0.6709	0.0054	-0.0533	0.8627
θ	0.1807	<0.0001	0.1125	<0.0001	0.0944	0.0001
ρ	-0.0107	0.0261	-0.0157	0.0015	-0.0202	0.0219
σ_u^2	0.4473	0.0525	0.1863	0.0626	0.3643	0.1149
-2LL	1682	-	2167	-	983	-
AIC	1698	-	2183	-	999	-
BIC	1702	-	2187	-	1003	-

4.3.5. Light availability effect

We obtained a highly significant effect of light availability on plant risk of mortality, being higher for the three species growing under high light availability (HLA), followed by medium (MLA) and low light availability (LLA) (Fig. 4.4). Among the three species *Q. ilex* has the highest risk of mortality under the three light treatments, followed by *P. pinea* and *J. thurifera*.

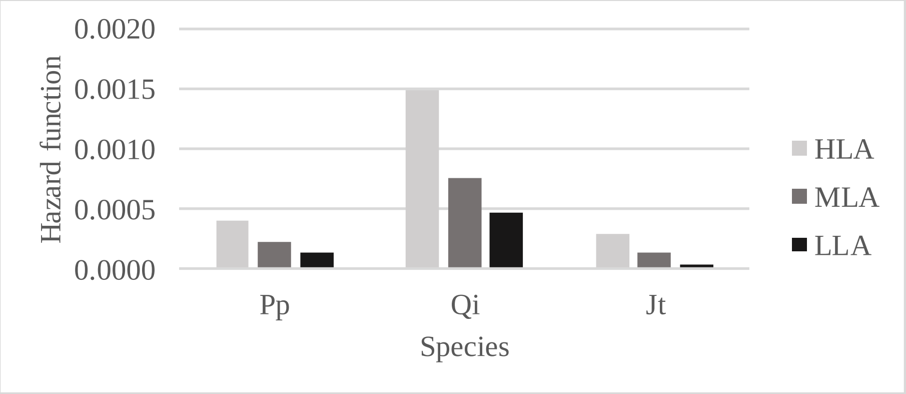

Fig. 4.4. Hazard function by species and light availability from the complete model considering average maximum temperature and average cumulated precipitation of the last 30 days of the period of study (T_{max} = 19ºC and $Pcum_t$ = 37 mm). Pp: *P. pinea*; Qi: *Q. ilex*; Jt: *J. thurifera*; HLA: high light availability; MLA: medium light availability; LLA: low light availability. Results of the simulation refer to non-excluded plots.

4.3.6. Rainfall exclusion effect

The effect of the rainfall exclusion treatment on daily hazard of mortality (Table 4.6) was nonsignificant for *Pinus pinea* (p-value 0.2681) and *Juniperus thurifera* (p-value = 0.8627), while for *Quercus ilex* we observe a significant effect (p-value = 0.0054), though pointing to a lower risk of mortality for plants grown under a 30% of rainfall exclusion, obtaining a negative value for the parameter (-0.6709). As this effect is observed only in *Q. ilex*, and given the additive character of the term into the model and the lack of a significant interaction, in the next simulations we will only present the results for the non-excluded (natural) conditions.

4.3.7. Daily maximum temperature modulates species specific risk of seedling mortality

Daily maximum temperatures exert a larger influence on risk of mortality than minimum or mean daily temperatures. Increasing air temperatures augmented the values of the hazard function for all species, though this effect is much more evident for *P. pinea* (θ = 0.1807) than for *Q. ilex* (θ = 0.1125) or *J. thurifera* (θ = 0.0945).

To understand the joint effect of light availability and air temperature on the hazard function we carried out a simulation fixing the effect of $Pcum_t$ at an average value for the period of study ($Pcum_t$ = 37mm) (Fig. 4.5). While the three species show similar hazard values for maximum temperatures below 25ºC, the risk of mortality is accelerated for all the species when daily maximum temperatures are over 33-35ºC, especially under HLA environments. In this range of temperatures, the risk of mortality is approximately 3 times higher in HLA than in the LLA and 1.6 times in MLA than in LLA for *P. pinea* and *Q. ilex*, and 7.6 times and 3.5 times higher for *J. thurifera*. If comparing between species, *Q. ilex* showed the highest hazard until temperatures are over 37ºC, where hazard of mortality for *P. pinea* is 1 – 1.5 times the value obtained for *Q. ilex*, depending on the light treatment. Also, *P. pinea* and *Q. ilex* showed hazard of mortality between 7-8 times higher than *J. thurifera* for HLA, values than can be 18-20 times higher for LLA, always in the range of temperatures over 37 ºC. In this sense, it is noteworthy to mention that temperatures over 37ºC were surpassed in 22% of the days in July and August of the period evaluated in the area of study.

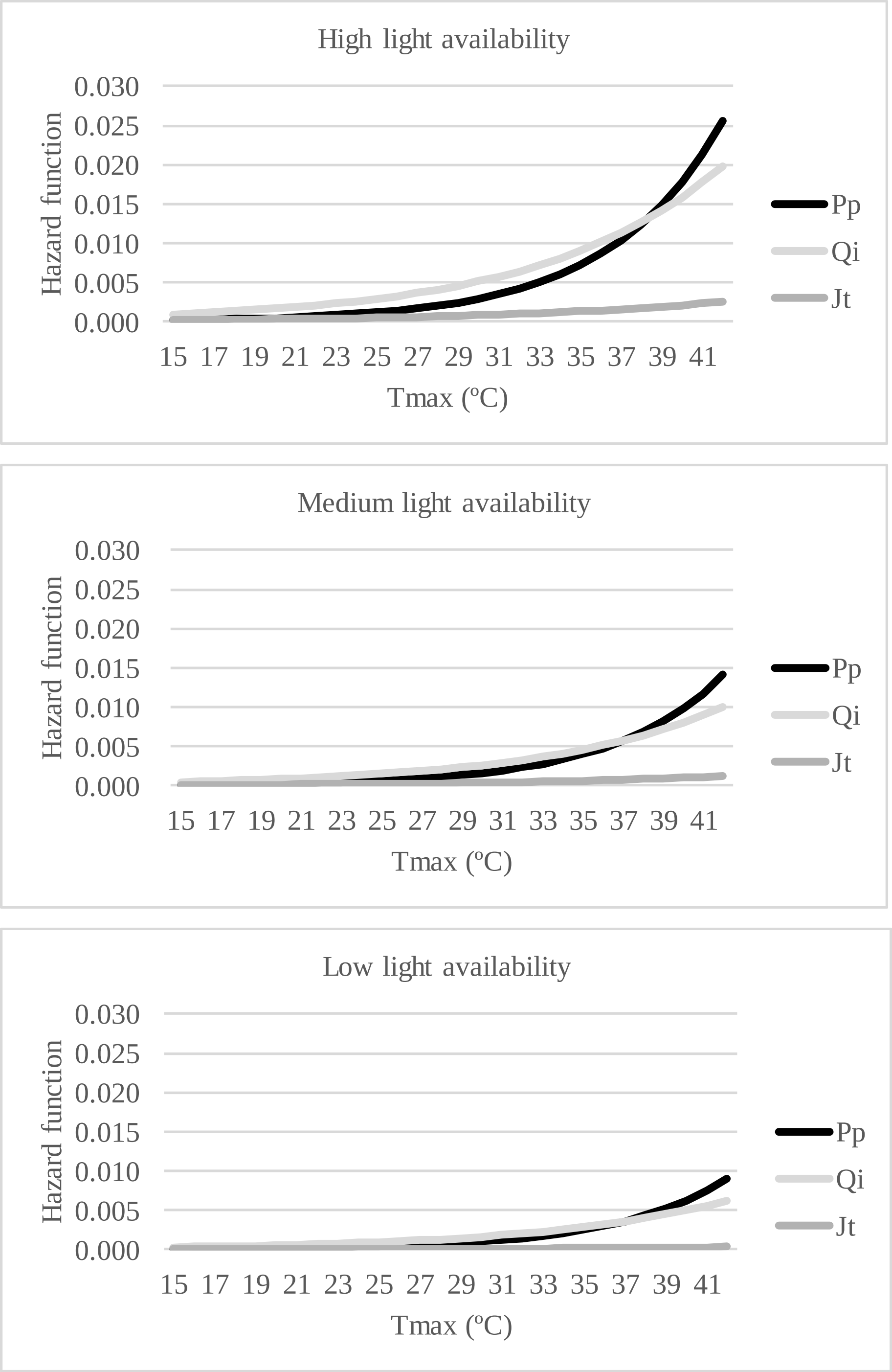

Fig. 4.5. Hazard function by species and light treatment from the complete models as a function of maximum observed temperatures considering the average cumulated precipitation of the period of study ($Pcum_t$ = 37 mm). HLA: high light availability; MLA: medium light availability; LLA: low light availability. Results of the simulation refer to non-excluded plots.

4.3.8. Low precipitation maximizes species specific differences in the risk of mortality.

The three species showed significant reduction in mortality hazard associated with increasing water reserves (defined by the cumulative precipitation in the last 30 days), although the least sensitive is *J. thurifera* ($\rho = -0.0202$) if compared to *Q. ilex* ($\rho = -0.0157$) or *P. pinea* ($\rho = -0.0107$). To understand the joint effect of the light environment and the cumulated precipitation of the last 30 days ($Pcum_t$) on the hazard function we fixed the effect of $Tmax_t$ at the average daily value of the period of the study of 19ºC (Fig. 4.6). $Pcum_t$ values below the average of 37mm were registered on 59% of the days of the period of study. In this range of $Pcum_t$ ($0 \leq Pcum_t < 37$mm) the hazard function values for *P. pinea* and *J. thurifera* are quite similar, and show values of hazard 4-5 times lower than those simulated for *Q. ilex* in all light treatments.

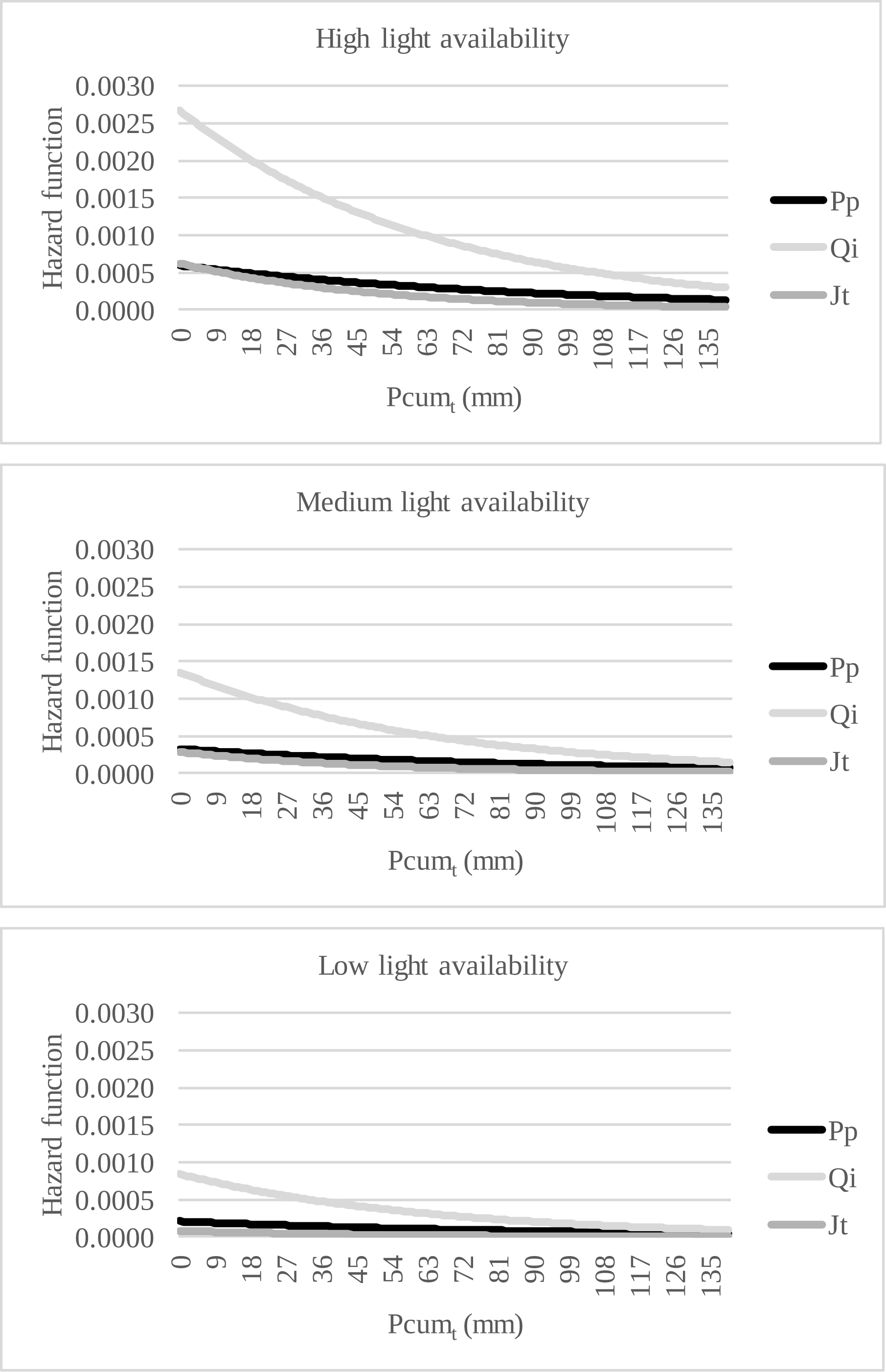

Fig. 4.6. Hazard function by species and light treatment from the complete models as a function of the cumulated precipitation of the last 30 days (Pcum$_t$) considering the average maximum temperature of the period of study (Tmax = 19ºC). HLA: high light availability; MLA: medium light availability; LLA: low light availability. Results of the simulation refer to non-excluded plots.

4.3.9. Hazard projections under climate change

The results from our simulation under current and IPCC's climate scenario RCP 8.5 indicate an increase in risk of seedling mortality for all species in 2100 (Fig. 4.7), though this increment is not constant for all the species. We expect an increased risk of mortality in 2100 with respect to 2015 2.39 times higher for *P. pinea*, 1.81 times higher for *Q. ilex* and 1.71 times for *J. thurifera*. Comparisons between species indicate that while under current 2015 conditions the risk of mortality is between 1.4 - 3.6 times higher for *P. pinea* than for *J. thurifera*, with higher risk at increasing light, it shifts to 1.9 - 5.0 times under 2100 conditions. As regards *Q. ilex* its risk of mortality was 5 – 12 times higher for *Q. ilex* compared to *J. thurifera* under actual climate, we only expect a slight shift to 5.4 – 12.8 times higher under forecasted climate conditions for 2100.

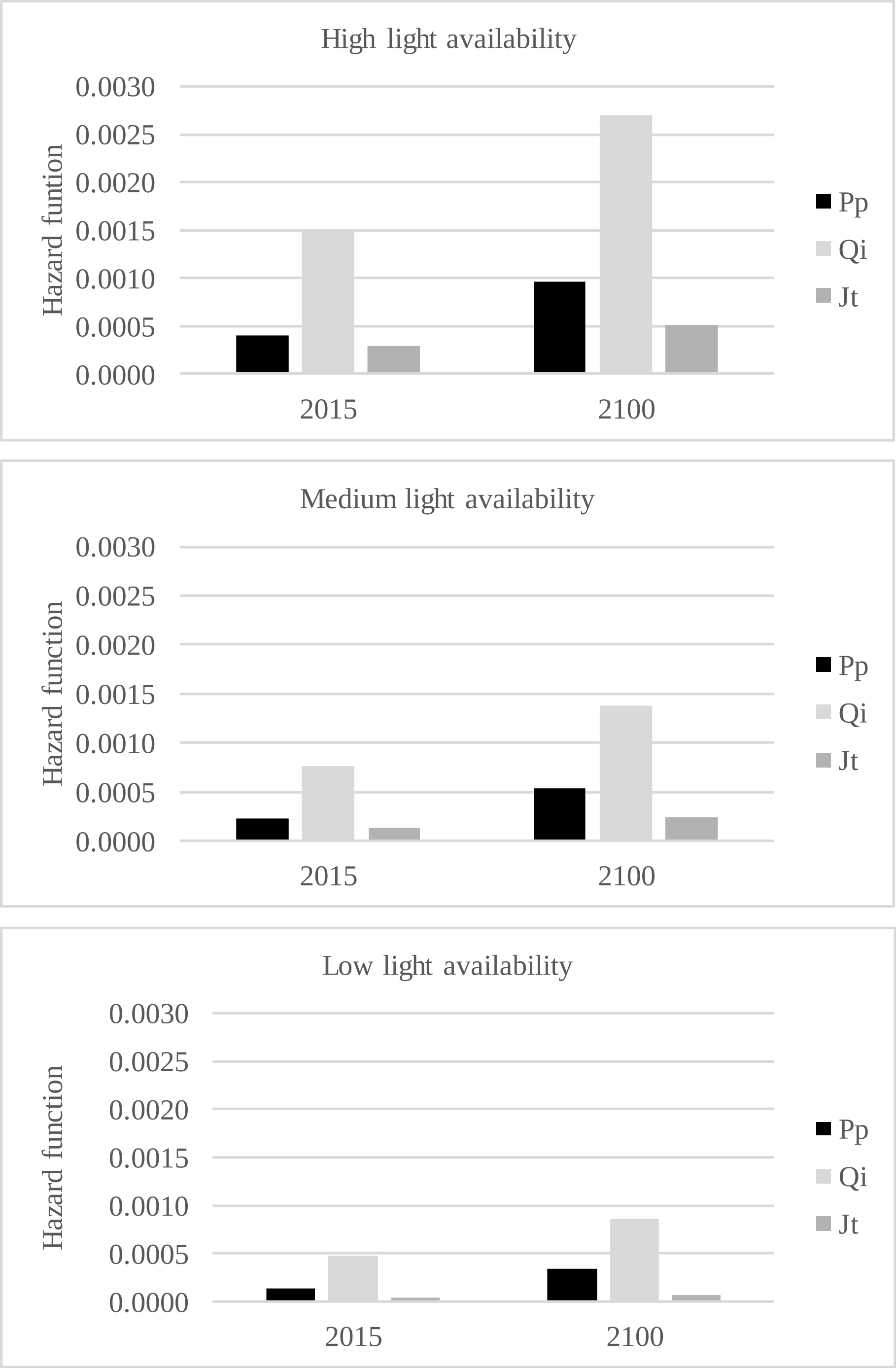

Fig. 4.7. Hazard function by species and light treatment from the complete models considering current climate conditions (2015) and future conditions under climate change scenario RCP 8.5 (2100). We considered average values for maximum temperature (Tmax) and the cumulated precipitation of the last 30 days ($Pcum_t$) of the period of study for 2015 and temperature increases of 4.5ºC and 15% of rainfall reduction for 2100. Results of the simulation refer to non-excluded plots.

4.4. Discussion

The use of lifetime analysis techniques has proved useful to model seedling survival, identifying the key climatic factors and optimal light environment to guarantee a successful natural regeneration in the limestone plains of the Spanish Northern Plateau. We found that high radiation, daily maximum temperatures and water scarcity can severely hamper seedling survival, as suggested in previous studies (Corcobado et al., 2014; Taeger et al., 2015). We identified a specificity in the risk of mortality inherent to the species studied. *Q. ilex* seems to be the most vulnerable of the three species under a forecasted warmer climate with more recurrent and longer droughts that will endanger its survival at the seedling stage (e.g. Corcobado et al., 2014).

4.4.1. Light availability effect

Facilitation from adult trees has proved to be fundamental in early stages of tree species development, moreover in drought prone sites (Ledo et al., 2014) where facilitative plant-plant interactions are generally more important and intense than in more mesic sites (Bertness and Callaway, 1994; Lortie and Callaway, 2006). However, our results suggest that benefits for early seedling establishment from a closer canopy (GSF = 0.25) in these Mediterranean mixtures are not more humid soil conditions but rather lowered radiation levels and milder soil temperature conditions. Lower radiation levels promoted by overstory trees provide shade that is not limiting for seedling survival and growth and avoids damages by excessive radiation (Gómez, 2004; Retana et al., 1999). Lower soil temperature under the canopy may diminish seedlings evaporative demand, reducing evapotranspiration and alleviating hydric stress despite the lower soil water availability (Valladares et al., 2005; Zamora et al., 2008) favouring seedling survival (Gómez-Aparicio et al., 2006).

4.4.2. Light preference is not species specific

Low survival values obtained for *P. pinea* in the high light treatment are probably related to the high temperatures attained on the bare soil in forest gaps, which cause high seedling death (Ledo et al., 2014; Pardos et al., 2014). Optimal regeneration niche for *P. pinea* and *Q. ilex* seedlings is found in medium and low light availability plots, which coincides with the results obtained in other sites for naturally regenerated *P. pinea* seedlings (Calama et al., 2015) and studies using facilitative nurse shrubs (Gómez-Aparicio et al., 2004). Valladares et al. (2005), obtained higher percentages of seedling survival in shade than in sun phenotypes of *Q. ilex* subjected to an experimental drought cycle. This may imply that *Q. ilex* seedlings grown in the shade develop morpho-functional adaptation traits that allow them to resist better Mediterranean summers than seedlings grown in full sunlight. Gómez-Aparicio et al. (2006) obtained that seedlings grown in shade invest more resources in aerial growth at the expense of a reduced root biomass. However, water absorption could be maximized developing longer roots with a higher area/biomass relationship. Light capture could be optimized by increasing leaf surface area, assigning more N to chlorophyll and allocating more chlorophyll to light harvesting complexes richer in Chlb (Gómez-Aparicio et al., 2006; Osunkoya et al., 1994). Growth and ecophysiological fitness should be evaluated in future studies.

Canopy cover by the crowns of *P. pinea* adult trees are known to act as a facilitation agent for conspecific and heterospecific seedlings (Vergarechea et al., 2019). Previous studies have also suggested that the milder environmental conditions under canopy closure promote seedling performance in *Q. ilex* in terms of germination and seedling survival (Bran et al., 1990). *Q. ilex* is considered a shade tolerant species since it is able to persist in the understorey without significant net growth underneath a closed canopy. But its performance largely depends on seedlings life stage and on the development of the crown of the upper adult trees. Previous studies have observed increased survival rates in older *Q. ilex* seedlings under some degree of canopy closure, obtaining higher seedling densities just before complete canopy closure and reduced seedling survival when radiation levels are lower than 10% (Espelta et al., 1995).

Seedling mortality of *J. thurifera* was significantly higher under high light than under low light availability. Previous studies obtained higher rates of survival for *J. thurifera* than for *Q. ilex* and other pine species in the Alto Tajo Natural Park in *J. thurifera* forests with a low tree cover (Granda et al., 2014) which is consistent with our results under all light treatments and consistent with the water stress tolerance of these and similar species (Flexas et al., 2014).

4.4.3. Rainfall exclusion effect

Our results point to a limited effect of the rain exclusion shelters on water availability limitation for seedling survival. Generally, VWC reduction was more important in seasons with high values of soil moisture (spring 2013 and 2014 and fall 2013) and less evident in drier seasons (summer 2013 and 2014). This may indicate that our experimental design is underestimating the effects of increased drought under the climate change scenario considered (Cotillas et al., 2009). The VWC reduction observed may not be sufficient to explain our seedling mortality data, at least for *P. pinea* and *J. thurifera*. However, drought has been related to altered biomass partitioning between above and belowground structures in seedlings of eleven Mediterranean woody species (Mayoral et al., 2016; Olmo et al., 2014); more biomass being assigned to develop roots reaching deeper soil levels and very fine roots involved in the acquisition of the most limited resource. As regards *Q. ilex*, we can only speculate that *Q. ilex* seedlings subjected to induced drought may have invested more resources on root biomass than on shoot biomass as seen in previous studies (Corcobado et al., 2014; Olmo et al., 2014) benefitting from water not available to not induced plants.

4.4.4. Daily maximum temperature effect

Daily maximum temperatures over 25ºC exert a negative effect on *P. pinea* and *Q. ilex* seedling survival under all light treatments considering average values of precipitation for the area of study. However, *J. thurifera* seedlings remain practically unaffected under these climatic conditions. Previous studies have indicated that elevated maximum temperatures as the ones attained in August were the main climatic variable associated with seedling mortality in *P. pinea* mixtures of the Spanish Northern Plateau (Moreno-Fernández et al., 2018). Higher rates of seedling mortality of *Q. ilex* in the high light treatment compared to *P. pinea* and *J. thurifera* in the range of maximum temperatures 19-39ºC may seem contradictory due to the stronger capacity of acclimation of *Q. ilex* to high temperatures, and the wider thermal amplitude at which root sprouts and adults of *Quercus ilex* grow compared to *P. pinea* and other junipers (De-Dios-García et al., 2018; Mayoral et al., 2015). But *Q. ilex* seedlings may be behaving differently to maximum temperatures than its root sprouts as seen for drought stress in previous studies (Lloret et al., 2004; Pardos et al., 2014). However, this tendency changes for temperatures over 39 ºC where *P. pinea* could be suffering from its higher vulnerabilty to xylem embolism than *Q. ilex* and *J. thurifera* seedlings (Calama et al., 2015).

4.4.5. Specific drought resistance

Many studies confirm that the consequences of drought on woody seedlings can be assessed more reliably in terms of survival rather than on seedling growth under field conditions (e.g. Engelbrecht et al., 2007). However seedlings differ widely in the way they cope with drought (Pardos et al., 2005). *P. pinea* and *J. thurifera* seedlings had a lower sensitivity to water scarcity than *Q. ilex* under all light treatments considering daily average maximum temperatures for the area of study. Juveniles of *Q. ilex* have been classified as water-savers in their response to drought based on their stomatal control of transpiration (Valladares et al., 2005) following Vilagrosa's definition (Vilagrosa et al., 2003). However, seedlings and root sprouts differ in the way they cope with drought (Corcobado et al., 2014; Mayoral et al., 2015). *Q. ilex* root sprouts benefit from the root system and storage of the parent plant (Pardos et al., 2005) that could confer them a higher resistance to water shortage increasing their survival with respect to seedlings (Lloret et al., 2004). But, *Q. ilex* seedlings in our experiment did not benefit from this water saving strategy and had the highest mortality rates in all light treatments of all species. Some authors have pointed to carbon starvation induced by drought in temperate climates as a possible explanation to this high mortality rates under drought (Maguire and Kobe, 2015). However, we believe that hydraulic failure, not studied in this analysis, could be a better explanation to this high mortality rates induced by drought in a Mediterranean context and should be further assessed.

4.4.6. Future climate forecasts

P. pinea and *Q. ilex* seedlings will probably be relegated under future climatic conditions to microsites where canopy shelter intercepts between 50-75% of total incident light. If these predictions are met and in accordance to previous results in the study area (de-Dios-García et al., 2018, 2015), these Mediterranean mixtures will very likely be transformed into a *Q. ilex* coppice forest with sparse *P. pinea* trees and a wider abundance of *J. thurifera*; *Q. ilex* regeneration will rely on its ability to resprout, being its seedlings survival severely compromised. *J. thurifera* will undoubtedly keep colonising these Mediterranean mixtures, being less affected by extreme climatic factors in all levels of light availability that we evaluated.

Acknowledgements

We are grateful to the Forest Service of Castilla y León administration for permission and support to carry out the field experiment. We also wish to thank Mar Conde, Enrique Garriga and Guillermo Madrigal for their help in the data collection. This study was financed by the projects AGL-2010-15521, RTA-2013-00011-C02-01 and AT-2013-004.

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Chapter 5

General discussion

5.1. Patrones de crecimiento intraanual

Muchos estudios han encontrado dinámicas de crecimiento intraanual diferentes entre especies de los géneros *Quercus* y *Pinus* durante el periodo vegetativo en lo que respecta al momento de apertura de las yemas, el despliegue de las hojas, el comienzo y cese del crecimiento radial, tasas distintas de crecimiento secundario y patrones contrastados en la movilización de carbono (e.g. Michelot et al., 2012; Zweifel et al., 2006). Los datos de crecimiento en circunferencia que hemos obtenido mediante dendrómetros de banda tienen limitaciones para identificar algunos eventos fenológicos debido a los cambios reversibles de contracción y dilatación que se producen en la madera. Sin embargo, consideramos que el modelo de crecimiento desarrollado en el marco de la presente Tesis Doctoral para analizar el crecimiento intraanual es una buena alternativa para estudiar el crecimiento en circunferencia basado en la competencia intra e interespecífica y en efectos climáticos diarios y acumulados (de-Dios-García et al., 2018). Las predicciones acumuladas del modelo han sido insesgadas y muestran una eficacia notable del modelo a largo plazo. Las tasas generales de crecimiento de las tres especies de estudio indican que *P. pinea* tiene el mayor potencial de crecimiento seguido de *Q. ilex* y *J. thurifera* lo cual concuerda con las estimaciones obtenidas. Estudios previos en la Península Ibérica han identificado patrones de crecimiento bimodales para las tres especies a lo largo del año (Camarero et al., 2010; Campelo et al., 2007b; Martín et al., 2014), con dos claros periodos de crecimiento seguidos por periodos de reducción o cese del crecimiento, lo cual coincide con nuestros resultados. El crecimiento en diámetro se produce principalmente durante la primavera y el otoño, coincidiendo con los periodos de precipitación más elevada, mayores reservas de agua en el suelo y temperaturas más suaves para el crecimiento (Pinto et al., 2011). El crecimiento en circunferencia se vio limitado en verano lo cual concuerda con una inhibición del crecimiento asociada a temperaturas medias elevadas, elevada evapotranspiración potencial y a un déficit de agua en el suelo durante el verano (Campelo et al., 2009). El crecimiento secundario también se detuvo en invierno, probablemente por una dormancia en el cámbium provocada por bajas temperaturas medias (Gea-Izquierdo et al., 2009; Liphschitz et al., 1984) y un acortamiento del fotoperiodo (Cherubini et al., 2003).

5.2. Interacciones entre especies arbóreas

Las interacciones entre especies arbóreas modulan la respuesta en términos de crecimiento y supervivencia de los árboles a los factores ambientales (capítulos 2, 3 y 4). En los siguientes apartados se engloban y discuten las interacciones de competencia, reducción competitiva y facilitación analizadas en los capítulos 2, 3 y 4.

5.2.1. Competencia

En la presente Tesis se ha identificado que la competencia intraespecífica en *P. pinea* es asimétrica (capítulos 2 y 3), lo cual indica que los individuos más grandes obtienen la mayor parte de los recursos disponibles, limitando el crecimiento de los pinos más pequeños de manera que la escasez de recursos no afecta a todos por igual (Pugnaire et al., 2000; Schwinning and Weiner, 1998). Pese a no haber un consenso general entre el grado de simetría en la competencia y un recurso particular limitante para el crecimiento (Río et al., 2014a), diversos estudios (e.g. Weiner et al., 1990; Wichmann, 2001) coinciden en relacionar los efectos de la competencia asimétrica, dependiente del tamaño del árbol sujeto, con la competencia por la luz. En consonancia con estos trabajos, pese a que en una fase inicial de desarrollo las plántulas de *P. pinea* se ven favorecidas por una cubierta arbórea (capítulo 4), en fases posteriores el arbolado adulto inhibe el desarrollo de los individuos de menor tamaño instalados bajo su copa limitando su acceso a la luz (capítulos 2 y 3).

En lo que respecta al modelo de crecimiento intraanual la competencia intraespecífica resultó ser significativa para *J. thurifera* y para *P. pinea*, teniendo en ambos casos un impacto negativo sobre el crecimiento secundario. Sin embargo y en contra de lo esperado el efecto de la competencia intraespecífica sobre el crecimiento en circunferencia fue dos veces mayor para *J. thurifera* que para *P. pinea*. Altos niveles de competencia intraespecífica implican un cese completo del crecimiento para *J. thurifera,* pero no para *P. pinea*. El efecto más limitante de la competencia intraespecífica sobre el crecimiento de *J. thurifera* podría deberse a su disposición espacial agregada (datos no publicados) en torno a árboles de *P. pinea* de gran tamaño. En el caso de *Q. ilex* la competencia intraespecífica no fue significativa. Un estudio a gran escala de las 15 especies arbóreas más importantes de la Península Ibérica indicaba que los esclerófilos mediterráneos, como *Q. ilex,* eran los menos sensibles a la competencia en términos de crecimiento (Gómez-Aparicio et al., 2011). Otra posible explicación de este resultado podrían ser los pequeños diámetros de *Q. ilex* en esta masa que fueron intensamente explotados para la obtención de leña y la producción de carbón hasta los años 1950 formando ahora un monte bajo. Además, este monte bajo crece principalmente a partir de cepas, que podrían estar atenuando el efecto de la competencia dentro de la propia cepa y entre cepas contiguas.

Tanto en el modelo de crecimiento en área basimétrica de *P. pinea* (capítulo 2) como en el modelo de crecimiento intraanual (capítulo 3) hemos obtenido que la competencia interespecífica es simétrica. La competencia totalmente simétrica se da cuando la captación de recursos es independiente del tamaño relativo de los árboles competidores y tiende a ser una competencia por los recursos del suelo (Río et al., 2014a; Schwinning and Weiner, 1998).

Por otra parte, el declive observado en el crecimiento secundario interanual del arbolado adulto tras la sequía de 2002, más acentuado en masas puras, es indicativo de que la escasez de recursos hídricos puede hacer prevalecer las relaciones competitivas en estas masas. Asimismo concuerda con otros estudios que muestran que el efecto de una sequía prolongada sobre el crecimiento puede perdurar en el tiempo (Sánchez-Salguero et al., 2012). Tanto en años secos como en sitios xéricos los árboles menos resistentes a la sequía, como *P. pinea*, pueden priorizar el crecimiento radical frente al crecimiento primario o secundario para mejorar el acceso al agua y nutrientes (Comeau and Kimmins, 1989). Los bajos crecimientos en periodos de sequía pueden deberse a una escasez en la disponibilidad y la captación de nutrientes debido a menores tasas de descomposición de la materia orgánica y de la mineralización del suelo, ambos dependientes de la humedad del suelo (Canadell et al., 1996; Pugnaire et al., 2000).

5.2.2. Reducción competitiva

Los resultados del modelo de crecimiento en área basimétrica de *P. pinea* (capítulo 2) muestran que, en condiciones similares de espesura, el efecto de la competencia sobre el crecimiento anual es menor en masas mixtas que en puras (de-Dios-García et al., 2015). Estos resultados pueden verse avalados bien por la teoría de complementariedad de nichos (Loreau et al., 2001) o por un apoyo mutuo directo entre las especies que coexisten en la masa mixta (Garber and Maguire, 2004). La captación de recursos puede ser mayor en masas mixtas que en puras debido a una complementariedad de nichos espacio-temporal de las especies arbóreas en masas mixtas (Brown, 1992; Perot and Picard, 2012). Pugnaire et al. (2000) indicaron que la compartimentación de nichos puede darse por muchos mecanismos que afectan tanto a la parte aérea de las plantas como a la subterránea. Entre los mecanismos que afectan a la parte aérea, están la estratificación interespecífica a nivel de copa si cada especie tiene rasgos contrastados para la captación de luz o estrategias distintas del uso del agua. Estudios recientes en el Sistema Central de la Península Ibérica indican que *P. pinea* y *Q. ilex* tienen distintas estrategias del uso del agua, al menos en el estado de plántula y de regenerado incipiente y avanzado (Mayoral et al., 2015; Pardos et al., 2014). Perot y Picard (2012) estudiaron una masa de coníferas y planifolios cuyas especies presentaban caracteres muy diferentes para interceptar la luz y patrones contrastados en la disposición de sus raíces (Brown, 1992). La captación de luz que observaron en las acículas de los pinos era inferior a la de las hojas de los robles (Balandier et al., 2006; Sonohat et al., 2004) e indicaron que la complementariedad entre ambas especies por la captación de luz y por el uso de agua y nutrientes permitían explicar los incrementos en la productividad observados en esas masas mixtas.

Podemos inferir las posibles causas de la complementariedad de nichos relacionando la competencia intraespecífica e interespecífica con el grado de simetría de esta competencia (competencia simétrica vs. competencia asimétrica) (Río et al., 2014a). Siguiendo esta idea nuestros resultados sugieren que en una masa mixta *Q. ilex*, *Q. faginea* y *J. thurifera* compiten con *P. pinea* principalmente por los recursos subterráneos (de-Dios-García et al., 2015). *Q. ilex* y *J. thurifera* ven limitado su crecimiento intraanual de forma significativa por la competencia interespecífica. Sin embargo, la competencia interespecífica no es significativa a escala intraanual para *P. pinea* (de-Dios-García et al., 2018).

Por otra parte, la complementariedad detectada en las relaciones interespecíficas comparada con las intraespecíficas, que son de mayor intensidad para *P. pinea* a escala interanual (capítulo 2) y para *J. thurifera* a escala intraanual (capítulo 3) puede deberse a una estratificación de las raíces. Estos resultados se ven avalados por el sistema radical de *P. pinea* cuya raíz pivotante inhibe enseguida su crecimiento pero forma numerosas raíces secundarias que se extienden mucho más allá de la proyección de sus copas y que a su vez envían raíces terciarias a capas profundas del suelo (Mutke et al., 2012). Los *Quercus* mediterráneos desarrollan raíces pivotantes más a menudo cuando crecen en ambientes secos que cuando crecen en ambientes más mésicos y tienen la capacidad de dirigir sus raíces a las capas más profundas del suelo cuando este lo permite (Canadell et al., 1996). Por el contrario, el sistema radical de especies del género *Juniperus* es más somero y superficial y no puede acceder al agua de las capas más profundas (e.g. Gimeno et al., 2012).

Por último, las diferencias observadas en la respuesta a la competencia intraespecífica entre masas mixtas y puras coincide con estudios previos que indican que la mezcla puede fomentar la aparición de patrones contrastados en la disposición de las raíces y en las copas con respecto a los que aparecen en una masa pura (Dieler and Pretzsch, 2013). Estas diferencias podrían deberse a diferencias intraespecíficas en la morfología y arquitectura de las copas o a cambios en las relaciones alométricas que podrían influir sobre aspectos como la absorción de radiación fotosintéticamente activa y por extensión la producción primaria neta y el crecimiento del árbol (Pretzsch, 2014).

5.2.3. Facilitación

5.2.3.1. Facilitación entre arbolado adulto

Los resultados del modelo en crecimiento en área basimétrica (capítulo 2) sugieren un efecto positivo de la mezcla para *P. pinea* en años de estrés hídrico (de-Dios-García et al., 2015). Otros estudios han obtenido mayores crecimientos debidos a interacciones interespecíficas en masas mixtas respecto a masas puras en años de bajos crecimientos (Río et al., 2014b) en los que se esperaría que la competencia por los recursos subterráneos fuese de mayor intensidad que en los años de crecimientos mayores.

Pretzsch et al. (2013) aportaron evidencias de una atenuación del estrés por sequía debida a la mezcla de especies arbóreas en masas mixtas europeas. Se ha propuesto que el bombeo de agua de las capas profundas del suelo hacia horizontes más superficiales que hacen determinadas especies, podría ser un mecanismo implicado en esta mejora del crecimiento en años secos (Zapater et al., 2011). Este mecanismo ha sido descrito en *Q. ilex* y en otras especies de pinos de la Península Ibérica durante la sequía estival (David et al., 2007; Peñuelas and Filella, 2003). Sin embargo, no hemos encontrado referencias bibliográficas que demuestren un uso directo de esta agua bombeada por otras especies arbóreas vecinas en la cuenca mediterránea. Pensamos que este es un aspecto que merece ser explorado en investigaciones futuras.

5.2.3.2. Facilitación arbolado adulto-plántula

La facilitación por parte del arbolado adulto ha demostrado ser fundamental para las etapas iniciales de desarrollo del arbolado, más aún en sitios proclives a la sequía (Ledo et al., 2014), en los que las interacciones facilitadoras planta-planta son en líneas generales de mayor relevancia que en los sitios más mésicos (Bertness and Callaway, 1994; Lortie and Callaway, 2006). Asimismo, los resultados de esta Tesis (capítulo 4) sugieren que los beneficios de una mayor cobertura arbórea (GSF = 0.25) para el establecimiento de las plántulas en estas masas mixtas mediterráneas no se asocian tanto con un mayor contenido de agua en el suelo durante los meses de verano sino con unos niveles de irradiación más bajos y temperaturas más suaves en el suelo. Niveles más bajos de irradiación debidos a la cobertura arbórea proporcionan sombra que no es limitante para la supervivencia y crecimiento de las plántulas y evita los daños por irradiación excesiva (Gómez, 2004; Retana et al., 1999). Temperaturas más bajas bajo cubierta disminuyen la demanda evaporativa de las plántulas, reduciendo la evapotranspiración y aliviando el estrés hídrico pese a que haya menor disponibilidad de agua en el suelo (Valladares et al., 2005; Zamora et al., 2008). Estas condiciones favorecen la supervivencia del regenerado (Gómez-Aparicio et al., 2006).

Los valores bajos de supervivencia de *P. pinea* obtenidos en el tratamiento de luz elevada, HLA (capítulo 4), están probablemente relacionados con las altas temperaturas que se alcanzan en el suelo en zonas desprovistas de arbolado, y que causan una elevada mortalidad a nivel de plántula (Ledo et al., 2014; Pardos et al., 2014). El nicho de regeneración óptimo para plántulas de *P. pinea* y *Q. ilex* está en las parcelas con niveles de disponibilidad de luz baja y media, coincidiendo con los resultados de regeneración natural obtenidos en otros sitios en estado de plántula (Calama et al., 2015) y con estudios que han utilizado la facilitación de arbustos como plantas nodriza (Gómez-Aparicio et al., 2004). Valladares et al. (2005), obtuvo porcentajes elevados de supervivencia en fenotipos de sombra de *Q. ilex* sometidos a sequía inducida. Esto podría implicar que las plántulas de *Q. ilex* que crecen a la sombra desarrollan rasgos morfo-funcionales adaptativos que les permiten resistir mejor los veranos mediterráneos que a las plántulas que creen sin limitación de luz. Gómez-Aparicio et al. (2006) obtuvieron que las plántulas que crecían a la sombra invertían más recursos en el crecimiento aéreo a expensas de una biomasa más reducida a nivel radical. Sin embargo, la absorción de agua podría verse incrementada desarrollando raíces más largas con una relación área/biomasa más elevada. La captación de luz podría optimizarse incrementando la superficie del área foliar, asignando más nitrógeno a la formación de clorofilas y movilizándola a las estructuras captadoras de luz que son ricas en Chlb (Gómez-Aparicio et al., 2006; Osunkoya et al., 1994). Pensamos que este estudio debería complementarse en investigaciones futuras con estudios fisiológicos y de crecimiento a nivel de plántula.

La cobertura arbórea por parte de las copas del arbolado adulto de *P. pinea* facilita la instalación de plántulas conespecíficas y heteroespecíficas (Vergarechea et al., 2019). Estudios previos han sugerido que las condiciones ambientales menos adversas bajo copa mejoran el comportamiento de *Q. ilex* en términos de germinación y de supervivencia de las plántulas (Bran et al., 1990). *Q. ilex* es considerada una especie tolerante a la sombra debido a su capacidad de persistencia bajo cubierta, aunque no tenga un crecimiento significativo en condiciones de umbría. Sin embargo, su comportamiento depende ampliamente del estado de desarrollo a nivel de plántula y del desarrollo de las copas del arbolado bajo el que crece. Estudios previos han observado tasas elevadas de supervivencia en plántulas de edad más avanzada bajo cobertura arbórea, obteniendo densidades de plántulas más elevadas antes del cierre completo de las copas y tasas de supervivencia más bajas cuando los niveles de irradiación están por debajo del 10% (Espelta et al., 1995).

Los resultados del capítulo 4 indican que la supervivencia de plántulas de *J. thurifera* fue significativamente más elevada en el tratamiento de baja disponibilidad de luz (LLA) que en el de alta disponibilidad de luz (HLA). Estudios previos han obtenido tasas de supervivencia más elevadas en *J. thurifera* que en *Q. ilex* y otra especie del género *Pinus* en el Parque Natural del Alto Tajo en sabinares de *J. thurifera* con baja cobertura arbórea (Granda et al., 2014) lo cual coincide con nuestros resultados en todos los niveles de luz y con la mayor tolerancia al estrés hídrico de esta especie y de otras similares (Flexas et al., 2014).

5.3. Respuesta al clima

5.3.1. Efecto del clima sobre el arbolado adulto

Estudios previos han establecido que los principales factores climáticos limitantes del crecimiento secundario intraanual en *Q. ilex* son la temperatura a escalas de tiempo cortas (Gutiérrez et al., 2011) y la disponibilidad de agua (Corcuera et al., 2004; Martín et al., 2014), factores que resultaron ser significativos en nuestro estudio (capítulo 3). *J. thurifera* tiene también una actividad fenológica característica, con dormancia en el cámbium en sitios xéricos durante el verano y una reanudación del crecimiento radial debida a una reactivación del cámbium tras las lluvias tardías de verano y del otoño (Camarero et al., 2010). Hemos obtenido mayores incrementos en el crecimiento en circunferencia en otoño en *J. thurifera* que en *Q. ilex*. Las lluvias de otoño humedecen solo las capas más superficiales del suelo en áreas mediterráneas continentales (Camarero et al., 2010). Y dado que las raíces de *J. thurifera* se desarrollan principalmente en el perfil superior del suelo, esto puede proporcionarles una ventaja competitiva permitiéndoles asignar más recursos al crecimiento en diámetro que los pinos y los *Quercus* durante el otoño. En lo que respecta a *P. pinea*, la formación de la madera tardía, que se forma durante el verano, se ve limitada por el estrés hídrico y temperaturas extremas (Campelo et al., 2007b).

Estudios recientes en masas mixtas de *P. pinea* en el Sistema Central han identificado temperaturas óptimas para la fotosíntesis más elevadas en *Q. ilex* que en *P. pinea* y otras especies de *Juniperus* (Mayoral et al., 2015). Estos resultados concuerdan con las temperaturas óptimas de crecimiento que hemos obtenido para estas especies (de-Dios-García et al., 2018). Asimismo, estos resultados coinciden con el comportamiento más termófilo y de mayor demanda de luz del arbolado adulto de *Q. ilex* que de *P. pinea* y *J. thurifera*. Sin embargo, otros trabajos de crecimiento intraanual en otras especies de *Pinus* y *Quercus* indican que el carbono fijado a través de la fotosíntesis no se invierte directamente en el crecimiento secundario de estructuras aéreas, lo que implicaría que la primera fase del crecimiento radial depende completamente de las reservas internas de carbono (Zweifel et al., 2006).

La mayor amplitud térmica obtenida para *Q. ilex*, comparado con *J. thurifera* y *P. pinea* confirma el carácter euritérmico de la especie que había sido apuntado previamente en la literatura forestal (Ruiz de la Torre, 2006), capaz de mantener el crecimiento secundario a lo largo de un rango amplio de temperaturas. Gea-Izquierdo et al. (2009) encontraron una correlación negativa entre temperaturas elevadas y crecimiento en *Q. ilex*. Nuestros resultados indican que considerar únicamente las altas temperaturas no es suficiente para explicar esta caída del crecimiento. Sin embargo, el efecto combinado de temperaturas altas, elevada evapotranspiración y estrés hídrico en el suelo podrían ser los causantes de esta inhibición del crecimiento secundario (de-Dios-García et al., 2018).

El efecto de la sequía ha sido significativo e inhibió el crecimiento de todas las especies. Sin embargo fue menos limitante para *Q. ilex* que para *P. pinea* y *J. thurifera*. Otros estudios han encontrado respuestas distintas a la sequía en términos de crecimiento entre especies de los géneros *Pinus* y *Quercus*, siendo los *Quercus* más resistentes a la sequía estival y los pinos más resistentes a la sequía de primavera (e.g. Morán-López et al., 2014). Es conocido que los pinos desarrollan sus acículas en verano y pueden alcanzar un cuarto de su crecimiento radial total para el momento en que las hojas alcanzan toda su expansión (Zweifel et al., 2006). Sin embargo, la sequía estival, que fue la principal durante el periodo de estudio, puede afectar al crecimiento secundario de los pinos limitando el desarrollo de las acículas y el alargamiento celular reduciendo su incremento radial (Merlin et al., 2015). Por otra parte, *Q. ilex* y *J. thurifera* pueden aprovechar episodios aislados de lluvia en verano (Camarero et al., 2010; Corcuera et al., 2004;

Gutiérrez et al., 2011) activando la xilogénesis y reanudando su crecimiento radial formando anillos dobles (Campelo et al., 2007a). En contraposición *P. pinea* no puede beneficiarse de este aporte de agua en los meses más secos del año (Campelo et al., 2007b). Este comportamiento en *Q. ilex* es particularmente interesante en áreas mediterráneas continentales. Se han observado crecimientos en verano en *Q. ilex* en ambientes más mésicos (Cherubini et al., 2003). Sin embargo, estudios en dehesas continentales de *Q. ilex*, con bajas densidades, han obtenido tendencias opuestas en lo que se refiere a las precipitaciones estivales (Gea-Izquierdo et al., 2009). Esto nos lleva a hipotetizar que régimenes de precipitación similares en medios mediterráneos continentales pueden ser más favorables en masas mixtas, debido a una complementariedad de nichos. Esto implicaría que la mezcla puede aliviar el estrés hídrico en verano para las especies esclerófilas.

5.3.2. Impacto del clima sobre la supervivencia del regenerado

5.3.2.1. Efecto de la temperatura máxima diaria

Tomando como referencia valores medios de precipitación del área de estudio, temperaturas máximas diarias por encima de los 25ºC tienen un impacto negativo sobre la supervivencia de *P. pinea* y *Q. ilex* en todos los niveles de luz considerados (capítulo 4). Sin embargo, las plántulas de *J. thurifera* prácticamente no se ven afectadas en estas condiciones climáticas. Estudios previos han indicado que temperaturas máximas como las alcanzadas en agosto son la principal causa de muerte en estado de plántula en masas mixtas de *P. pinea* de la Meseta Norte (Moreno-Fernández et al., 2018). Tasas más altas de mortalidad en *Q. ilex* en el tratamiento de mayor irradiación (HLA) comparado con *P. pinea* y *J. thurifera* en el rango de temperaturas máximas entre 19 y 39ºC podría parecer contradictorio debido a la elevada capacidad de aclimatación de *Q. ilex* a temperaturas elevadas y a la mayor amplitud térmica a la que crecen los rebrotes de cepa e individuos adultos de *Q. ilex* comparado con *Q. ilex* y otros *Juniperus* (de-Dios-García et al., 2018; Mayoral et al., 2015). Sin embargo, las plántulas de *Q. ilex* procedentes de semilla – que son las estudiadas en esta Tesis - parecen tener una respuesta distinta a las temperaturas máximas que los rebrotes de cepa, de manera similar a lo que sucede con la respuesta a estrés por sequía (Lloret et al., 2004; Pardos et al., 2014). Esta tendencia cambia a temperaturas superiores a 39ºC, a las que *P. pinea* podría estar sufriendo por su mayor vulnerabilidad a la embolia en el xilema que las plántulas de *Q. ilex* y *J. thurifera* (Calama et al., 2015).

5.3.2.2. Resistencia específica a la sequía

Muchos estudios confirman que las consecuencias de la sequía en plántulas leñosas pueden evaluarse de manera más fiable en términos de supervivencia que en términos de crecimiento en condiciones naturales (e.g. Engelbrecht et al., 2007). Sin embargo, cada especie difiere en la forma en que hace frente a la sequía (Pardos et al., 2005). *P. pinea* y *J. thurifera* mostraron una menor sensibilidad a la escasez de agua que *Q. ilex* en todos los tratamientos de luz, considerando temperaturas máximas promedio del área de estudio. Siguiendo la definición de Vilagrosa (Vilagrosa et al., 2003) los juveniles de *Q. ilex* se han clasificado como ahorradores de agua en función de su control estomático de la transpiración (Valladares et al., 2005). Sin embargo, las plántulas y los rebrotes de cepa confrontan la sequía de manera distinta (Corcobado et al., 2014; Mayoral et al., 2015). Los rebrotes de cepa de *Q. ilex* se benefician del sistema radical de la planta madre (Pardos et al., 2005) que puede conferirles una mayor resistencia a la escasez de agua incrementando su supervivencia con respecto a las plántulas (Lloret et al., 2004). Sin embargo, en nuestro experimento las plántulas de *Q. ilex* no obtuvieron un beneficio de esta estrategia y tuvieron las tasas más altas de mortalidad en todos los tratamientos de luz de entre todas las especies estudiadas. En climas templados algunos autores inciden en que el agotamiento de las reservas de carbono inducido por sequía podría ser una de las causas de muerte en condiciones de estrés hídrico (Maguire and Kobe, 2015). Sin embargo, pensamos que un fallo hidráulico, no estudiado en este trabajo, podría ser una mejor explicación a estas elevadas tasas de mortalidad en condiciones de agua limitantes en un contexto mediterráneo que sería interesante evaluar en investigaciones futuras.

5.4. Proyecciones climáticas y vulnerabilidad al cambio climático

De acuerdo a los datos observados en las estaciones meteorológicas AEMET existentes en la región de estudio (ww.aemet.es/es/portada) existe una marcada tendencia actual hacia condiciones más secas y cálidas en la Meseta Norte, tendencia que puede verse agravada en las próximas décadas, y que va a afectar de forma distinta a cada etapa del desarrollo del arbolado de cada una de las especies de la zona de estudio.

Hemos elaborado unas proyecciones de crecimiento intraanual del arbolado adulto en masas mixtas contemplando un escenario de altas emisiones de CO_2 con incrementos en la temperatura media de 4.5ºC en la temperatura media y un 30% de disminución en la precipitación anual (escenario RCP 8.5 del IPCC, capítulo 3). Las proyecciones de este modelo para 2075, en ausencia de competencia, predicen que el crecimiento potencial de *P. pinea* se vería reducido respecto a las condiciones actuales. Estos crecimientos previsiblemente serían más reducidos de incluirse la competencia intraespecífica en las proyecciones. *Q. ilex* se vería favorecido debido a su mayor amplitud térmica. Sin embargo, su crecimiento podría verse algo reducido de considerarse la competencia interespecífica, principalmente de *P. pinea*. *J. thurifera* prácticamente no vería afectado su crecimiento potencial, aunque este podría verse ligeramente reducido de considerarse la competencia inter- e intraespecífica.

Basándonos en el mismo escenario climático considerado para el modelo de crecimiento intraanual hemos hecho unas proyecciones de supervivencia para plántulas de las 3 especies de estudio en masas mixtas para el año 2100. Estas proyecciones apuntan a que las plántulas de *P. pinea* y *Q. ilex* se verán relegadas a micrositios en los que la cubierta arbórea intercepte entre un 50-75% de la irradiación incidente total. De cumplirse estas predicciones en el área de estudio y de acuerdo a nuestros resultados (de-Dios-García et al., 2018, 2015) estas masas mixtas, en ausencia de gestión o favorecidas por ella, muy probablemente se transformarán en un monte bajo de *Q. ilex*, con pies más aislados de *P. pinea* y una mayor abundancia de *J. thurifera*. La regeneración de *Q. ilex* quedará ligada a sus rebrotes de cepa, viéndose la supervivencia de sus plántulas seriamente comprometida. *J. thurifera* indudablemente continuará colonizando estas masas mixtas dado que se ve menos afectada por factores climáticos extremos en todos los niveles de luz que hemos evaluado.

5.5. Utilidad de las herramientas estadísticas

En el estudio del crecimiento anual en área basimétrica (capítulo 2) se ha utilizado una base de datos con múltiples niveles de dependencia, al tratarse de observaciones anuales del crecimiento procedente de series dendrométricas obtenidas en árboles, que a su vez se encontraban ubicados en parcelas permanentes. La violación del supuesto de independencia asociado a estos niveles de dependencia entre árboles, parcelas, años y sus interacciones, se aborda mediante el uso de modelos mixtos lineales multinivel, de manera similar a lo expuesto en otros trabajos (Calama et al., 2019).

El estudio de la dinámica de crecimiento secundario intraanual (capítulo 3) hasta ahora se había abordado bien mediante correlaciones lineales entre estimaciones del crecimiento y las variables climáticas (Camarero et al., 2010; Michelot et al., 2012), bien mediante modelos lineales mixtos (e.g. Martín et al., 2015). Sin embargo, muchas interacciones entre variables climáticas y crecimiento no son lineales. Estudios previos han destacado la necesidad de integrar la competencia y los datos climáticos en los estudios de crecimiento intraanual (Gutiérrez et al., 2011). En las regiones con clima mediterráneo hay muchos factores climáticos que limitan el crecimiento en circunferencia y que intervienen simultáneamente. Entre ellos están las altas temperaturas, la elevada evapotranspiración y las limitadas reservas de agua en el suelo. La aproximación no lineal y multifactorial que hemos hecho permite abordar estas limitaciones ayudándonos a comprender los requerimientos ecológicos de cada especie (de-Dios-García et al., 2018).

Por otra parte, la utilización de técnicas de análisis de vida (capítulo 4) ha demostrado ser útil para modelizar la supervivencia en el estado de plántula identificando los principales factores climáticos y el ambiente de luz óptimo para garantizar una regeneración natural exitosa en los páramos calizos de la Meseta Norte.

5.6. Implicaciones para la gestión en masas de *P. pinea* en los páramos calizos de la Meseta Norte

Los procesos naturales por sí mismos son muy lentos para poder hacer frente al cambio climático, que puede ser especialmente notable en la cuenca mediterránea. Para poder mejorar la resistencia y la resiliencia en las masas mediterráneas se deben planificar medidas de adaptación que alivien el estrés por sequía (Lindner and Calama, 2013) y el aumento de la evapotranspiración debido al incremento de las temperaturas. En sitios proclives a la sequía, como la región mediterránea, fomentar una mezcla adecuada de especies puede contribuir a mejorar la resiliencia de las masas. La mezcla de especies puede tamponar el efecto de la variación climática interanual modulando sus interacciones entre mayor competencia en años en los que hay mayor disponibilidad de recursos hídricos y relaciones de complementariedad en años más secos (Río et al., 2014b).

En el caso de las masas de *P. pinea* de los páramos de la Meseta Norte, la mezcla podría promoverse en los rodales de masas puras más vulnerables a las nuevas condiciones climáticas abriendo espacios para el regenerado avanzado de especies complementarias que ya esté instalado de forma natural y que presente una mayor plasticidad en respuesta a las condiciones climáticas durante el periodo de crecimiento (de-Dios-García et al., 2018, 2015; Gutiérrez et al., 2011). Entre estas especies más plásticas están *Q. ilex* subsp. *ballota*, *Q. faginea* o *Juniperus thurifera*. Otra opción para favorecer la mezcla es la siembra o plantación directa de plántulas de estas especies o de otros *Quercus* y *Juniperus* nativos de esta región, y con comportamiento ecológico similar, bajo cubierta de copas de *P. pinea* (de-Dios-García et al., 2015). Para garantizar la supervivencia inicial y el desarrollo de este regenerado sería recomendable que el dosel interceptase entre un 50-75% de la radiación incidente total. Esta mezcla de especies se ha sugerido que puede ser una mezcla de especies balanceada para el clima mediterráneo continental en un contexto de cambio global (Gea-Izquierdo et al., 2009).

Una forma compatible con la promoción de especies complementarias para aliviar el estrés por sequía tanto en masas puras como en masas mixtas es la reducción de la densidad. Esta reducción de la densidad permite mejorar el vigor individual de los pies remanentes de todas las especies y puede jugar un papel importante para hacer frente a sequías más prolongadas. El papel de las claras puede ser decisivo para reducir la mortalidad de los individuos en pie, controlar la competencia e incrementar la resiliencia ante la baja humedad del suelo mejorando la recuperación tras los periodos más secos (Garber and Maguire, 2004; Martin-Benito et al., 2010). Asimismo, las claras pueden utilizarse para modificar la composición del estrato arbóreo. En cualquier caso, estas claras deben orientarse a mantener las proporciones actuales de mezcla, o a aumentar ligeramente la proporción de *Quercus* sp. y *Juniperus thurifera*, pero siempre manteniendo la dominancia de *Pinus pinea*.

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Chapter 6

Conclusions

Conclusiones generales

I. A igualdad de densidad de masa el efecto de la competencia sobre el crecimiento de *P. pinea* es menor en masas mixtas que en puras, efecto que se ve acentuado en los años secos. Este resultado es acorde con lo expuesto por la teoría de complementariedad de nichos y con la hipótesis del gradiente de estrés (capítulo 2).

II. La competencia intraespecífica es asimétrica, mientras que la interespecífica es simétrica (capítulos 2 y 3). Esto indica que los individuos más grandes de *P. pinea* y de *J. thurifera* obtienen la mayor parte de los recursos disponibles suprimiendo el crecimiento de los individuos conespecíficos más pequeños, siendo esta competencia intraespecífica principalmente por luz. Sin embargo, la competencia interespecífica es independiente del tamaño relativo de los árboles competidores siendo esta competencia interespecífica principalmente por los recursos del suelo.

III. La competencia intraespecífica en *P. pinea* y en *J. thurifera* tiene un mayor efecto sobre la reducción del crecimiento que la interespecífica en masas mixtas (capítulos 2 y 3).

IV. El empleo de una aproximación no lineal y multifactorial es útil para describir el efecto de la competencia intra- e interespecífica y de distintos escenarios de cambio climático sobre el crecimiento secundario intraanual y tiene una eficacia notable en el largo plazo (capítulo 3).

V. De cumplirse las predicciones de un escenario climático futuro de altas emisiones de CO_2 (escenario RCP 8.5 del IPCC) el crecimiento secundario del arbolado adulto de *Q. ilex* puede verse favorecido debido a su mayor amplitud térmica, en las masas mixtas objeto de estudio, frente a *P. pinea* y *J. thurifera*.

VI. En consonancia con estudios previos y de acuerdo con las simulaciones llevadas a cabo con el modelo de crecimiento intraanual para escenarios climáticos futuros se sugiere a los gestores forestales que modifiquen los esquemas de gestión en masas mixtas de *P. pinea*. Se plantea como alternativa de gestión disminuir las densidades y promover especies con una respuesta más plástica a las condiciones climáticas durante la estación de crecimiento como *Q. ilex* en las mezclas (capítulo 3).

VII. La facilitación por parte del arbolado adulto es fundamental para las etapas iniciales de desarrollo del arbolado. El nicho de regeneración óptimo para plántulas de *P. pinea* y *Q. ilex* en las condiciones climáticas actuales y futuras (escenario RCP 8.5 del IPCC) está en micrositios en los que la cubierta arbórea intercepte entre un 50-75% de la irradiación incidente total. Los beneficios de una mayor cobertura arbórea para el establecimiento de estas especies en estas masas mixtas mediterráneas no se asocian tanto con un mayor contenido de agua en el suelo durante los meses de verano sino con unos niveles de irradiación más bajos y temperaturas más suaves en el suelo (capítulo 4).

VIII. Temperaturas máximas diarias por encima de los 25ºC tienen un impacto negativo sobre la supervivencia de *P. pinea* y *Q. ilex* en todos los niveles de luz considerados. Sin embargo, las plántulas de *J. thurifera* prácticamente no se ven afectadas en estas condiciones climáticas (capítulo 4).

IX. Las plántulas de *P. pinea* y *J. thurifera* muestran una menor sensibilidad a la baja disponibilidad de agua que *Q. ilex* en todos los tratamientos de luz, considerando temperaturas máximas promedio del área de estudio (capítulo 4).

X. En rodales de masas puras de *P. pinea* más vulnerables a las nuevas condiciones climáticas se plantea promover la mezcla abriendo espacios para el regenerado avanzado de especies complementarias que ya esté instalado de forma natural y que presente una mayor plasticidad en respuesta a las condiciones climáticas durante el periodo de crecimiento. En el caso de que estas especies no estén instaladas se plantea recurrir a la siembra directa. Entre estas especies más plásticas están *Q. ilex* subsp. *ballota*, *Q. faginea* o *Juniperus thurifera* (capítulos 2, 3, 4 y 5).

XI. En ausencia de gestión o favorecida por ella, las masas mixtas objeto de estudio se transformarán muy probablemente a largo plazo en un monte bajo de *Q. ilex*, con pies aislados de *P. pinea* y una mayor abundancia de *J. thurifera*. La regeneración de *Q. ilex* quedará ligada a sus rebrotes de cepa, viéndose la supervivencia de sus plántulas procedentes de bellota seriamente comprometida. *J. thurifera* indudablemente continuará colonizando estas masas mixtas dado que se ve menos afectada por factores climáticos extremos en todos los niveles de luz que hemos evaluado (capítulos 2, 3 y 4).

General conclusions

I. At equal density levels competition effects on growth are reduced in *P. pinea* mixtures vs. monocultures. This effect is more evident in dry years and is in agreement with the niche complementarity theory and the stress gradient hypothesis (chapter 2).

II. Intraspecific competition is size-asymmetric, whereas interspecific competition is size-symmetric (chapters 2 and 3). This indicates that the largest *P. pinea* and *J. thurifera* trees obtain the majority of the contested resources suppressing the growth of their smaller conspecific neighbours, intraspecific competition being mainly for light. However, interspecific competition is independent of the relative size of the competitor trees, being mainly a competition for belowground resources.

III. Intraspecific competition has a more negative effect on growth than interspecific competittion for *P. pinea* and *J. thurifera* in mixed stands (chapters 2 and 3).

IV. The use of a non-linear multifactorial approach is a powerful tool to describe the effects of intra- and interspecific competition and different climate change scenarios on intraanual secondary growth and has notable long-term accuracy (chapter 3).

V. If the high CO_2 emissions scenario is accomplished (RCP 8.5 scenario, IPCC) the secondary growth of adult *Q. ilex* trees will be favoured due to its wider thermal amplitude, in the mixed stands studied, over *P. pinea* and *J. thurifera*.

VI. Based on all of the previous findings and in accordance with the simulations carried out with the intraanual growth model for future climate scenarios, forest managers may wish to modify their management schedules in mixed stands, lowering *P. pinea* stand densities and promoting species such as *Q. ilex* in mixtures with a higher plasticity in response to climatic conditions during the growing season (chapter 3).

VII. Facilitation from adult trees has proved to be fundamental in early stages of tree species development. Optimal regeneration niche for *P. pinea* and *Q. ilex* seedlings under current and future climatic conditions (RCP 8.5 scenario, IPCC) is found in microsites where canopy cover intercepts between 50-75% of total incident light. Benefits from higher canopy cover in these Mediterranean mixtures are not more humid soil conditions but rather lowered radiation levels and milder soil temperature conditions (chapter 4).

VIII. Daily maximum temperatures over 25ºC exert a negative effect on *P. pinea* and *Q. ilex* seedling survival under all light treatments considering average values of precipitation for the area of study. However, *J. thurifera* seedlings remain practically unaffected under these climatic conditions (chapter 4).

IX. *P. pinea* and *J. thurifera* seedlings had a lower sensitivity to water scarcity than *Q. ilex* under all light treatments considering daily average maximum temperatures for the area of study (chapter 4).

X. Promoting mixture is a useful adaptive management tool for *Pinus pinea* monocultures. In the most vulnerable stands, mixture can be promoted liberating space for naturally installed advanced regeneration of complementary species with a higher plasticity in response to the new climatic conditions during the growing season. If complementary species are not already present direct seeding can be applied. Among these more plastic species are *Q. ilex* subsp. *ballota*, *Q. faginea* and *Juniperus thurifera* (chapters 2, 3, 4 y 5).

XI. In absence of management or favoured by it, these Mediterranean mixtures will very likely be transformed into a *Q. ilex* coppice forest with sparse *P. pinea* trees and a wider abundance of *J. thurifera*; *Q. ilex* regeneration will rely on its ability to resprout, being its seedlings survival severely compromised. *J. thurifera* will undoubtedly keep colonising these Mediterranean mixtures, being less affected by extreme climatic factors in all levels of light availability that we evaluated (chapters 2, 3 y 4).