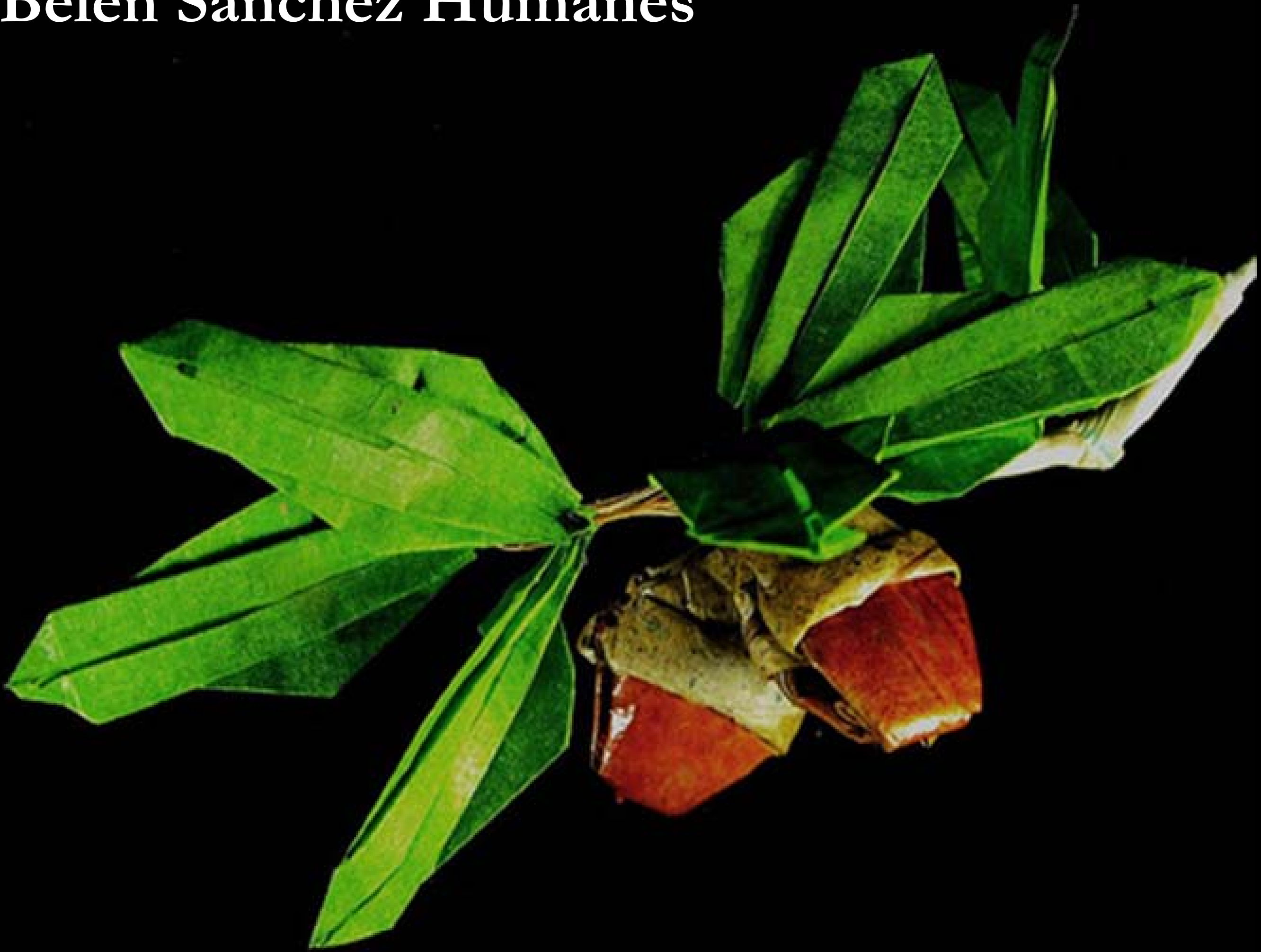
Acorn production and growth in Mediterranean oaks: Trade-offs and the role of climate, modular organization and phenology

Belén Sánchez Humanes



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Acorn production and growth in Mediterranean oaks: Trade-offs and the role of climate, modular organization and phenology

Memoria presentada por:

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para optar al grado de Doctora

Con la aprobación de:

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¿No nos creemos (...) que la Naturaleza nos habla? ¿Y no nos parece percibir un sentido en sus voces misteriosas, una respuesta, según nuestros deseos, a las anhelantes preguntas que le dirigimos? Y lo más probable es que la Naturaleza, en su grandeza infinita, no tenga ni la más remota idea de nosotros ni de nuestra vana ilusión.

El difunto Matías Pascal (Luigi Pirandello)

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PRÓLOGO (o Libro del Génesis de mi tesis)

En el principio era Tete. Todos los papeles de la beca por él fueron firmados, y sin él nada de lo que ha sido hecho, fue hecho.

Al principio mi tesis era algo informe, las tinieblas cubrían el abismo, y el soplo de la incertidumbre aleteaba sobre las aguas.

Entonces Tete dijo: “Que la niña acompañe a José Luis al campo”. Y yo le acompañé. Y vi que salir al campo era bueno (a veces), y separé el campo del despacho. Y llamé al campo Muestrear y al despacho Analizar. Muestreamos todos los árboles del paraíso quemado del Bages y el Berguedà. Este fue el primer año.

Dijo Tete: “Que la niña se vaya a Zaragoza para que aprenda cosas nuevas”. Y así sucedió. Visité a Chechu y aprendí a medir anillos de árboles. Y Chechu lo llamó Dendrocronología. Este fue el segundo año.

Tete dijo: “Que la niña vaya donde le apetezca”. Y me fui a California y conocí a Victoria, el surf, las patinadoras en bikini y los robles centenarios. Y vi que todo esto era bueno. Y llamé a los robles *Oaks* y a las bellotas *Acorns*. Este fue el tercer año.

Entonces Tete dijo: “Que la niña sigua muestreando, que analice los datos y escriba cuatro capítulos”. Y así sucedió…más o menos.

Y al final del cuarto año dijo Tete: “pues va a ser que no la terminas en cuatro años”. Y razón tenía. Llamé a los días Escribir y a las noches Escribir (licencia literaria). Y vi que ir acabando sería bueno.

Y un día del décimo mes del quinto año, concluí la obra que había emprendido. Guardé cambios, cerré el Word y me fui a comer un helado de chocolate y plátano. Y entonces…entonces descansé.

Este fue el origen de mi tesis.

Capítulo 1

Introducción General [1]

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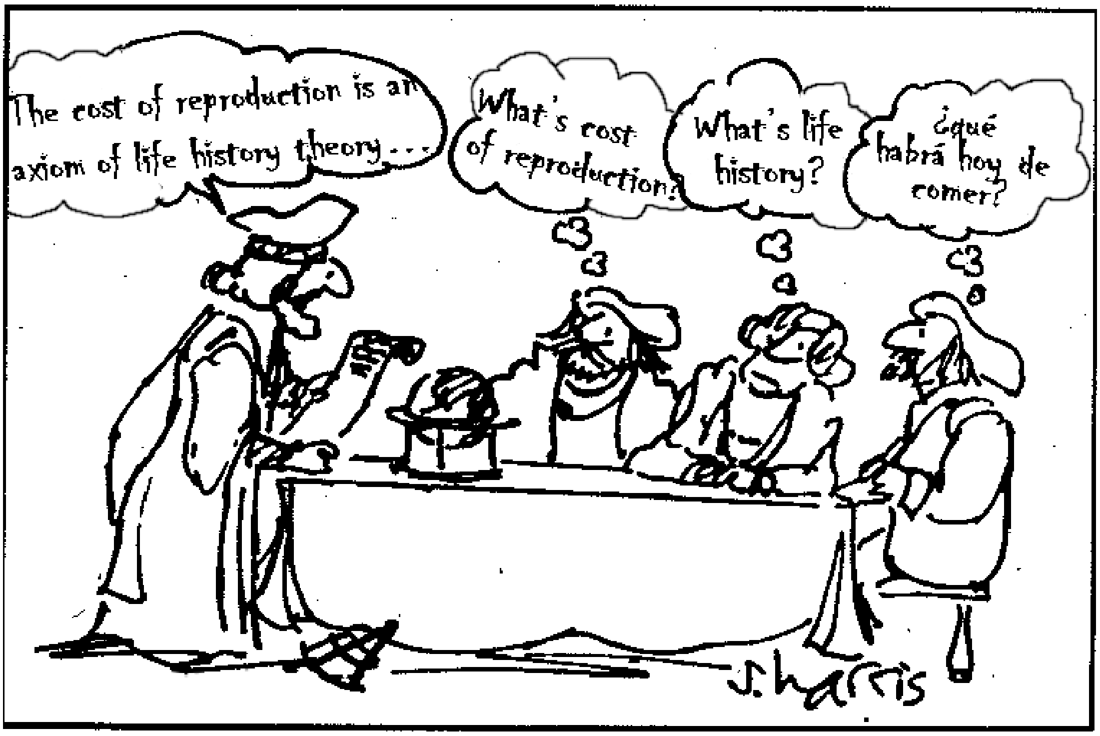
[1] This chapter is written in Spanish.
For the English version, please, contact me at belen.sanchez@creaf.uab.es

1. El por qué de una introducción



Lo primero es lo primero, y lo segundo va después (Sánchez Alonso 1999). Y en este caso lo primero es sentar las bases y el contexto de esta tesis. Hay muchos conceptos, términos y teorías que nombro y cito en los diferentes capítulos de mi tesis, y que me gustaría explicar sucintamente a un lector no especializado. Hay todo un marco histórico y científico que envuelve las preguntas que me hice, mi forma de abordarlas, y las repuestas que les dí.

Lo segundo son los capítulos que siguen, y donde explico los trabajos que llevé a cabo durante estos años, mis hipótesis, mis diseños experimentales, mis resultados y mis ideas al respecto.

Empecemos por lo primero:

2. La historia vital y la competencia por los recursos

La historia vital es el conjunto de todas las características de un individuo que determinan su capacidad para sobrevivir y dejar descendencia fértil. Entre estas características podemos encontrar el crecimiento, la frecuencia de la reproducción, el número de crías o semillas o la inversión de recursos en cada evento reproductivo (Reznick *et al.* 2000).

Un concepto casi tan antiguo como el de historia vital es el de la competencia por recursos entre diferentes características de la historia vital. Todas las actividades de un organismo requieren del empleo de energía, que es un recurso limitado, por lo que inversiones en una actividad conllevan pérdidas en las potenciales inversiones en otra actividad (Obeso 2002). A esto se le llama el Principio de Asignación (Levins 1968). Las teorías de la evolución de la historia vital se basan en esta asignación competitiva de recursos al crecimiento, a la manutención y a la reproducción. Podemos generar una imagen muy intuitiva de esta competencia si pensamos en la historia vital como algo similar a una tarta dividida en porciones. Cada porción está destinada a una función diferente (crecimiento, mantenimiento, acumulación, reproducción). Como se asume que la tarta tiene un tamaño fijo (aunque discutiremos esto más adelante), incrementar el tamaño de una de las porciones implica que tengamos que disminuir el tamaño de otra/s porción/es (Reznick *et al.* 2000). A esta relación inversa entre la energía invertida en una función y la invertida en otra le llamamos *trade-off*. El término *trade-off* no tiene una traducción muy precisa en español. Podría traducirse por *compromiso* o *trueque* pero utilizaré la palabra en inglés para evitar confusiones con las otras acepciones no científicas de estas traducciones.

Usando una frase hecha (igual de intuitiva que la imagen de la tarta, pero mucho más castiza) podríamos describir un *trade-off* como aquello de "no se puede estar en misa y repicando", es decir, que invertir esfuerzos en una función es incompatible con invertirlos en otra. En ausencia de otros factores que incidan sobre el *trade-off*, éste se puede medir como correlaciones negativas entre dos características vitales (Roff & Fairbairn 2007). Sin embargo, a pesar de que hay un fuerte marco teórico que sitúa a los *trade-offs* como pilar de la teoría de las historias de vida (Williams 1966, Roff 1992), falta mucho para comprender los mecanismos subyacentes a estos *trade-offs*.

3. Los costes de reproducción

Los costes de reproducción son un ejemplo de *trade-offs* entre distintas características de la historia vital de un organismo. Se manifiestan en una reducción medible de alguna característica de la historia vital, causada por la asignación de recursos a la reproducción (Reznick *et al.* 2000). En último término, los costes de reproducción representan pérdidas en el éxito de potenciales futuras reproducciones causadas por inversiones en la reproducción actual (Jonsson 2000). Por ejemplo, un incremento en la energía destinada a la producción de frutos puede causar un descenso en la probabilidad de supervivencia del individuo (Reznick 1985, Roff 1992) o una menor capacidad de reproducirse en el futuro (Sork *et al.* 1993). **En esta tesis me he centrado en los costes que puede tener la producción de frutos sobre el crecimiento vegetativo en plantas**. Este tema es aún objeto de debate en ecología (Obeso 2002) a pesar de que fue planteado por primera vez hace ya algunos años (Aristóteles 350 a. C.): *Muchos árboles, si han producido una excesiva cantidad de fruto, se debilitan una vez que el fruto ha desaparecido, porque no les queda alimento para ellos mismos.*

¿Cómo y dónde medir los costes de reproducción en plantas? A pesar de que la hipótesis de los costes de reproducción es muy intuitiva, el tema ha resultado más complejo de lo que parecía cuando estos costes se han intentado evaluar experimentalmente (Reznick 1992). Los trabajos realizados hasta ahora, con experimentos realizados en campo y laboratorio, arrojan resultados ambiguos y a veces contradictorios en cuanto a la existencia de costes asociados a la reproducción (Obeso 2002, Roff & Fairbairn 2007). Se han encontrado diversas dificultades a la hora de estudiar los costes de reproducción, como el método para medirlos (Reznick 1992), la ausencia de costes en años con alta disponibilidad de recursos (Horvitz & Schemske 1988), la variabilidad de los costes en distintos ambientes (Sgro & Hoffmann 2004), el efecto confusor del clima sobre los patrones de reproducción y crecimiento (Knops *et al.* 2007), la variación inter-individual (Reznick *et al.* 2000) o la naturaleza modular de las plantas (Lovett Doust & Lovett Doust 1988). Las plantas leñosas son organismos modulares con un patrón jerárquico de organización: están compuestas por un tronco, que da lugar a ramas, y estas a brotes. Al estar una planta dividida en estas subunidades semiautónomas, el coste de la reproducción puede ser local, en lugar de afectar a la planta entera (ej. Hasegawa *et al.* 2003). Por eso es necesario definir en qué nivel modular se tienen que evaluar los costes de reproducción (Lovett Doust & Lovett Doust 1988, Obeso 1997). **En esta tesis he abordado varias de estas complicaciones con la intención de arrojar luz sobre el tema. Por ejemplo, he pretendiendo aislar y determinar cuál es el papel que juega el clima en la relación reproducción-crecimiento, y he estudiado si diferentes condiciones climáticas locales pueden conducir a diferentes relaciones reproducción-crecimiento incluso para una misma especie (Capítulo 2). Por otra parte, he hecho hincapié en la importancia de las variaciones entre individuos, estudiando estos fenómenos no sólo a partir de datos**

poblacionales, sino mediante datos individuales (Capítulos 2, 3, 4 y 5). En el Capítulo 3 explorado en qué lugar de la planta pueden ocurrir los costes.

4. Un caso especial: las plantas veceras

Las plantas veceras pueden ofrecer un ejemplo extremo de los costes de reproducción porque realizan producciones de fruto masivas de forma esporádica, lo que puede trastocar las relaciones reproducción-crecimiento. La vecería o *masting* es un patrón reproductivo que consiste en una producción de semillas muy variable entre años, que ocurre de forma sincrónica y a intervalos irregulares en una población de plantas (Norton & Kelly 1988). Esto implica que gran parte de los años la producción de semillas es muy baja o nula, pero algunos años casi todos los individuos de la población realizan una producción masiva de semillas. Al año siguiente de esta reproducción masiva, los niveles de producción de semilla vuelven a ser nulos o casi nulos. Los periodos entre producciones masivas son de una duración irregular.

Hay diversas hipótesis que pretenden explicar el origen del *masting*. Las dos principales son el *resource matching* y la economía de escala. El r*esource matching* es la hipótesis más parsimoniosa, y dice que la producción variable de semillas es función de condiciones climáticas variables (Norton & Kelly 1988, Sork 1993, Kelly 1994, Houle 1999). Según esta hipótesis, las plantas simplemente ajustan su producción de semillas cada año a la cantidad de recursos disponibles (Monks & Kelly 2006). En un ambiente muy variable, esto conduciría a una producción de semillas también muy variable entre años, sin que tengan que existir presiones selectivas que favorezcan esa enorme variación. La hipótesis de la economía de escala, en cambio, sostiene que grandes esfuerzos reproductivos son más eficientes en términos de éxito de reproducción (Janzen 1978, Norton & Kelly 1988), y atribuye a este patrón reproductivo altamente irregular un valor adaptativo (Herrera *et al.* 1998). Se han expuesto varios procesos que se verían beneficiados de una economía de escala, como la eficiencia de la polinización (Norton & Kelly 1988, Smith *et al.* 1990), la eficacia de la dispersión (Norton & Kelly 1988) y la tolerancia a la depredación (Janzen 1969). La hipótesis más consistentemente demostrada es la tolerancia a la depredación, que sostiene que este patrón de altas y bajas producciones de semillas sincronizadas entre individuos resulta en menores tasas de depredación, y por eso es seleccionado (Janzen 1971). De esta forma, durante el año de producción masiva de frutos se produce un saciado de las poblaciones de depredadores, sin que éstos acaben con todas las semillas, mientras que los años de de escasa producción se provoca su inanición. La combinación errática de estos eventos favorece el control del tamaño de la población de depredadores y favorece la disponibilidad de semillas para germinar.

Pero, ¿qué dicen estas hipótesis sobre los costes de reproducción? En el caso del *resource matching* no se espera un *trade-off* entre crecimiento vegetativo y producción de semillas. Si esta hipótesis es cierta, las plantas veceras deberían hacer más de todo (crecer y reproducirse) en años buenos, y menos de todo en años malos (Monks & Kelly 2006), de forma que la relación entre reproducción y crecimiento estaría mediada por el clima (Knops *et al.* 2007). Sin embargo, la hipótesis de la economía de escala propone que el *masting* ocurre o bien porque la planta invierte en reproducción los recursos que otros años estaban destinados al crecimiento (hipótesis del *switching*) (Norton & Kelly 1988), o bien porque acumula recursos durante los años previos al año de *masting* (hipótesis de la acumulación de recursos) (Sork *et al.* 1993). Bajo la hipótesis del *switching* se espera una correlación negativa entre los recursos destinados a reproducción y los recursos destinados al crecimiento (Monks & Kelly 2006). Es decir, la planta puede asignar recursos bien al crecimiento, o bien a la reproducción, pero no a ambas a la vez. Según la hipótesis del *switching*, la planta tendría que desviar sus recursos hacia la reproducción en algunos años, y hacia otras funciones que no son la reproducción durante otros años. En cambio la hipótesis de la acumulación de recursos no predice *trade-offs* reproducción-crecimiento debido al almacenamiento de recursos previo al año de *masting*, pero sí predice que tras la reproducción masiva habrá un agotamiento de esos recursos acumulados, lo que repercutirá negativamente en la reproducción del año/s siguiente/s (Sork *et al.* 1993).

A pesar de los numerosos estudios que han contribuido a generar este marco teórico, las evidencias empíricas no son concluyentes. Muchos trabajos han encontrado evidencias de *switching* en diferentes especies veceras, tanto gimnospermas como angiospermas, en diferentes climas (ej. Eis *et al.* 1965, Norton & Kelly 1988, Koenig & Knops 1998), aunque otros muchos trabajos no han encontrado evidencias de esta relación negativa entre reproducción y crecimiento (ej. Nienstaedt 1985, Cremer 1992, Despland & Houle 1997, Yasumura 2006). Los trabajos publicados hasta el momento sobre el tema, apoyan de forma experimental o bien la hipótesis del *resource matching* (Despland & Houle 1997), o bien la del *switching* (Monks & Kelly 2006) o bien la de la acumulación de recursos (Sork *et al.* 1993). Pero puede que adscribirse a una sola de las tres hipótesis resulte un tanto simplista. **En esta tesis pretendo evaluar experimentalmente estas hipótesis en distintos árboles veceros, en distintos lugares del árbol y en diferentes ambientes, que conforman un marco para entender los potenciales *trade-offs* (Capítulos 2 y 3).**

5. *Masting* y costes de reproducción en el clima Mediterráneo

El clima Mediterráneo nos plantea un interesante escenario donde estudiar patrones de reproducción, crecimiento, y sus relaciones, porque es un clima donde la limitación estacional de recursos afecta en gran manera a estos procesos. Se caracteriza por sus inviernos fríos y sus veranos calurosos y secos. En general, las precipitaciones son escasas, con gran variabilidad interanual (Aschmann 1973). Este patrón climático hace que las plantas hayan tenido que hacer frente a dos tipos de estrés climático: el frío invernal y la sequía estival (Mitrakos 1980), que constriñen en gran medida sus patrones de crecimiento y reproducción (Terradas & Save 1992). Años con gran escasez de precipitación pueden llegar a limitar el crecimiento y a inhibir la producción de semillas por falta de recursos, afectando a los patrones de *masting* (Espelta *et al.* 2008) y a las relaciones entre reproducción y crecimiento. Debido a estos factores de estrés climático, el crecimiento de las plantas mediterráneas suele estar restringido a los meses de primavera, en que las precipitaciones son más abundantes y las temperaturas moderadas (Montserrat-Martí *et al.* 2008). El otoño puede suponer también una época favorable para el crecimiento, porque aumentan las precipitaciones cuando las temperaturas aún no son muy bajas. Por eso es frecuente que algunas especies reanuden durante el otoño su crecimiento interrumpido por la sequía estival, tanto en tronco como con nuevas brotaciones de ramas (Castro-Díez & Montserrat-Martí 1998). La posibilidad de crecer en otoño cuando, usualmente, los frutos ya han sido dispersados, puede relajar potenciales fenómenos de *trade-offs* entre crecimiento y reproducción (Milla *et al.* 2006). **En esta tesis abordo este tema mediante el estudio de la duración de la estación de crecimiento, tanto del tronco (Capítulo 2), como de las ramas (Capítulo 4) durante el otoño y discuto sus implicaciones para el resto de procesos del árbol (crecimiento y reproducción).**

6. ¿Cómo afectará el cambio climático a estos procesos?

Una pregunta casi obligada en los trabajos que estudian procesos afectados por el clima es la cuestión de cómo influirá en ellos el cambio climático. Para la Cuenca Mediterránea los modelos atmosféricos predicen un aumento de las temperaturas y una disminución de las precipitaciones, con aumento de la estacionalidad, que conducirán a un incremento en la frecuencia y severidad de los episodios de sequía (IPCC 2007). En resumen, nuestros veranos serán aún más calurosos y secos. Este incremento de la temperatura y de las sequías durante las próximas décadas afectará a la fisiología, fenología, crecimiento, reproducción, establecimiento y, finalmente, a la distribución de los seres vivos, y por tanto, a la estructura y funcionamiento de los ecosistemas (Peñuelas & Filella 2001). Para abordar el tema del efecto de estos cambios sobre los patrones de crecimiento y reproducción de los árboles mediterráneos, hay dos cuestiones que hemos de tener en cuenta: La primera es que esta mayor sequía tendrá efectos limitantes para los procesos reproductivos y vegetativos (Ogaya *et al.* 2003), lo que puede tener consecuencias muy importantes para el mantenimiento y la extensión de sus poblaciones. En el Mediterráneo se han comprobado experimentalmente descensos en la fotosíntesis (Epron & Dreyer 1993), en el crecimiento de ramas y tronco (Borghetti *et al.* 1998, Corcuera *et al.* 2004a, b) y en la reproducción (Ogaya & Peñuelas 2007a) como consecuencia de la sequía. La segunda cuestión que tener en cuenta es que la sequía estival y aumento de temperaturas promoverá aún más una extensión de la estación vegetativa hacia el otoño (Peñuelas *et al.* 2002), lo que provocará un alargamiento de de la estación de crecimiento y cambios en la fenología de las especies (tanto adelantamiento de la brotación y floración como retraso del fin del crecimiento) (Peñuelas & Filella 2001) pudiendo generar desacoplamientos entre los procesos fisiológicos individuales, pero también entre las interacciones a nivel poblacional y de comunidad.

Frente a estos cambios, la gestión forestal puede llegar a ser una herramienta clave para el mantenimiento de los bosques, porque ha demostrado tener un gran efecto tanto sobre el crecimiento de los árboles como sobre la producción de fruto (Lindner 2000). Entre las diferentes estrategias de gestión, sobre todo de bosques en regeneración tras alguna perturbación, destacan el aclareo, consistente en el control de la densidad mediante la corta (ej. Verkaik & Espelta 2006), y el resalveo (en el caso de especies rebrotadoras) y que consiste en la eliminación de los pies menos vigorosos de cada individuo, para favorecer el o los más desarrollado/s (Ducrey & Toth 1992). Estos modelos de gestión persiguen controlar la competencia por recursos (nutrientes, agua, luz…) para los árboles o pies que quedan en el bosque (Karlsson & Örlander 2002, Cañellas *et al.* 2004). Estudios desarrollados en bosques mediterráneos han demostrado que estos tipos de gestión incrementan el crecimiento primario y secundario de los árboles (Mayor & Rodà 1993, Ne'eman *et al.* 1995, Gracia *et al.* 1999), el número de pies reproductivos, la producción de semillas por árbol o por unidad de área y el peso de las semillas (Zulueta & Montero 1982, Serrada *et al.* 1992, Verkaik & Espelta 2006). Sin embargo, pese a que se ha sugerido que las prácticas silvícolas pueden modificar la respuesta de los bosques frente a diferentes escenarios climáticos (Sabaté *et al.* 2002), se ha investigado muy poco experimentalmente sobre si estas prácticas de gestión forestal pueden revertir o mitigar las consecuencias de un incremento de sequía sobre la estructura y funcionamiento del bosque, y en especial sobre la capacidad reproductiva. **En esta tesis he pretendido, por una parte, estudiar el efecto de un potencial incremento de sequía sobre las características reproductivas en un bosque mediterráneo en regeneración post-incendio, a la vez que**

he explorado la capacidad de las prácticas de resalveo para revertir los potenciales efectos negativos de la sequía (Capítulo 5).

7. *Quercus*, los protagonistas

Para estudiar los patrones reproductivos y de crecimiento, sus relaciones, su fenología y el potencial efecto del cambio climático, he elegido cuatro especies del género *Quercus*. Las especies que estudio son *Quercus ilex*, *Q. humilis*, *Q. faginea* y *Q. lobata* (Figura 1.1), todas del grupo de los *white oaks* (subgénero *Quercus*, sección *Leucobalanus*). Estas especies son especialmente interesantes para este estudio porque todos ellas son árboles típicamente mediterráneos (Quezel & Medail 2003) todas son especies veceras, con episodios de *masting* evidentes, y comparten características como el crecimiento estacional (Castro-Díez & Montserrat-Martí 1998), la capacidad de rebrotar (Bonfil *et al.* 2004) y la maduración de las bellotas en seis meses (Castro-Díez & Montserrat-Martí 1998, Pavlik *et al.* 1991), por lo que son fácilmente comparables. *Q. ilex* comparte hábitat con *Q. humilis* en el NE peninsular, sobre todo en las zonas más cercanas a la costa, y con *Q. faginea* más hacia el interior. *Q. lobata* es un roble endémico de California, que ocupa bosques húmedos y extensas sabanas.

***Quercus ilex* L.**

***Q. humilis* Mill.**

***Q. faginea* Lam.**

***Q. lobata* Née**

Figura 1.1. Porte del árbol y detalle de las bellotas para las cuatro especies estudiadas.

8. Objetivos y estructura de la tesis

Esta tesis pretende ahondar en el estudio de los patrones de crecimiento, reproducción y su relación, en una serie de *Quercus* mediterráneos. Por una parte, la comprensión de los procesos de crecimiento reproductivo y vegetativo, su fenología y sus relaciones, nos servirá para aportar alguna luz al actual debate sobre el origen del *masting* y los costes de reproducción, avanzando en la construcción de un marco teórico unificado. Por otro lado, el estudio de las repercusiones del cambio climático sobre estos procesos, y las implicaciones directas de estos resultados para la gestión de los bosques de quercíneas son de gran interés para la biología de la conservación.

Hay varias preguntas generales que me he hecho, y que pretendo responder con los trabajos de esta tesis:

1. ¿Existe una competencia entre producción de bellotas y crecimiento vegetativo? (Capítulos 2, 3 y 4)
2. ¿Varía esta competencia en diferentes climas locales (Capítulo 2), niveles modulares dentro de la copa, y con tamaños de cosecha diferentes (Capítulo 3)?
3. ¿A qué se debe la extensión del periodo de crecimiento en otoño? ¿Puede esta extensión tener algún efecto sobre el crecimiento vegetativo y la reproducción posteriores y sobre la relación entre ambos? (Capítulo 3 y 4)
4. ¿Cómo afectará la sequía a los procesos reproductivos en estas especies? ¿Puede el resalveo revertir los potenciales efectos negativos de la sequía? (Capítulo 5)

Estas preguntas se abordan en los objetivos específicos de cada capítulo:

Capítulo 2: Is timing the answer? Climate and phenology mediate in the apparent trade-off between growth and reproduction in Mediterranean oaks.

En este capítulo estudio si existen relaciones entre patrones de producción de bellotas y crecimiento radial, y si estas están mediadas por el clima, en *Q. ilex*, *Q. humilis* y *Q. faginea* y en dos ambientes mediterráneos, pero con climas locales diferentes. Además, estudio la fenología del crecimiento radial y de la producción de bellotas para determinar la extensión del periodo de crecimiento y de producción de semilla y su grado de solapamiento temporal y de competencia por recursos.

Capítulo 3: Costs of reproduction during a mast year occur at different hierarchical levels within the canopy and vary among high and low productive trees.

El objetivo es determinar a qué nivel (ramas o brotes) ocurren los costes de reproducción en un roble californiano, *Q. lobata* , y descubrir si hay diferencias en los costes de reproducción entre árboles con alta y baja producción de bellota durante un año de *masting*.

Capítulo 4: Extension of shoot growth in *Quercus ilex* during autumn: Are spring growth, phenology and reproductive effort causes or effects?

En este capítulo pretendo cuantificar el crecimiento de otoño en ramas de *Q. ilex*, y descubrir si el crecimiento de primavera en ramas y tronco, la fenología del crecimiento y la producción de bellotas previos están relacionados con el crecimiento de otoño. También estudio las consecuencias de crecer en otoño para la fenología y la magnitud de futuros eventos de crecimiento y reproducción.

Capítulo 5: Increased drought reduces acorn production in Mediterranean *Quercus ilex* coppices: traditional low selective thinning mitigates this effect but only in the short-term.

El objetivo es determinar los efectos de un incremento de sequía sobre la precocidad reproductiva de *Q. ilex*, su producción de flores y bellotas y la maduración de éstas, y comprobar si la gestión por resalveo puede revertir los potenciales efectos negativos de la sequía, en un contexto de cambio climático.

9. Información práctica

Los cuatro capítulos que vienen a continuación están redactados en formato de artículo científico, por lo que las descripciones de las especies y de algunas áreas de estudio sufren cierta redundancia inevitable. Sin embargo, he unificado las referencias bibliográficas de todos los capítulos al final de la tesis, para evitar repeticiones. Todos los capítulos son fruto de colaboraciones con Josep Maria Espelta (mi director de tesis) y con otras personas que aparecerán mencionadas el capítulo correspondiente. Finalmente, todos los capítulos están concebidos para ser enviados como artículos a revistas científicas de carácter internacional.

Capítulo 2

Is timing the answer? Climate and phenology mediate in the apparent trade-off between growth and reproduction in Mediterranean oaks

This chapter has been done in collaboration with J.M. Espelta, J.J. Camarero & G. Montserrat-Martí.

ABSTRACT

- The occurrence of trade-offs among functional traits is a fundamental tenet in life history theory. Therefore, why different studies report positive or negative relationships between radial growth and seed production in tree species is a challenging question. We suggest that climate can mediate in this relationship, which would disappear once the effect of climate is removed. However, this has been seldom explored and no reasonable hypotheses have been provided on how these two processes may become independent (do not compete) once climate influence is controlled. The investigation of this question would benefit from the comparison of growth and reproduction patterns of the same species in different climates, and a detailed analysis of the phenology and temporal overlap of these processes.

- We investigated the potential trade-off between radial growth and acorn production in three Mediterranean oaks, in two sites with different climate (Coastal, Inland). We monitored acorn production and measured radial growth for several years, and we intensively monitored their phenology and temporal overlap during one entire year.

- Raw radial growth and acorn production yearly values were either positive or negative related depending on local climate. However, once climatic effects were extracted, they became independent.

- The three oak species showed a longer extension of radial growth in comparison to acorn development: i.e. more than 80% of radial growth occurred before acorns started developing, and even some growth could well occur after acorn dispersal. Moreover, previous radial growth did not influence reproductive effort nor did reproductive effort constrain growth after acorn dispersal. The linkage of growth and reproductive effort (number of acorns x acorn weight) with precipitation events seems to be an important key to understand growth-reproduction relationships.

- Our results confirm that radial growth and reproduction may be positively or negatively related depending on local climate, but they are independent once this effect is controlled. The phenology of growth and reproduction in Mediterranean oaks suggests that an extended growing season may help to relax a growth vs. reproduction trade-off. This highlights the need to consider both climate and phenology when dealing with the potential trade-off between growth and reproduction in trees.

INTRODUCTION

One primary axiom of life history theory is the occurrence of trade-offs between reproductive and vegetative processes (Williams 1966, Reznick 1985; Begon *et al.* 1986, Roff 1992, Obeso 2002). Since resources are finite, it has been suggested that reproduction must occur at the expense of direct (resource allocation) or indirect (demographic) costs (Bañuelos & Obeso 2004). Although the hypothesis of the direct effects of the costs of reproduction for plant growth has been widely tested in many plant species (Obeso 2002 and references therein), no other case study has been expected to illustrate this trade-off more dramatically than “mast seeding” plants (Kelly 1994, Koenig & Knops 1998, Kelly & Sork 2002, Monks & Kelly 2006).

Mast seeding is the synchronous production of highly variable seed crops among years (Silvertown 1980, Norton & Kelly 1988, Sork *et al.* 1993, Kelly & Sork 2002). A large allocation of resources to reproduction during high crop years might occur at the expense of vegetative growth, and this potential trade-off (“switching”) has been regarded as one of the bases for considering masting as a reproductive strategy (Kelly & Sork 2002, Monks & Kelly 2006). However, when studying the correlation between growth and reproduction, contradictory results have arisen: either negative (Eis *et al.* 1965, Norton & Kelly 1988, Silvertown & Dodd 1999, Selas *et al*. 2002, Monks & Kelly 2006) or positive (Nienstaedt 1985, Despland & Houle 1997, Alley 1998, Yasumura 2006).

The analysis of the potential costs of reproduction on growth may not be easy to determine as the strength and the sign of this relationship can vary depending on the influence of external factors such as climate (Obeso 2002, Monks & Kelly 2006, Knops *et al.* 2007). The potential confounding effect of climate on both growth and reproduction events has long been discussed (Despland & Houle 1997, Selas *et al*. 2002, Corcuera *et al.* 2004a, b, Overgaard *et al.* 2007, Espelta *et al.* 2008). Nonetheless, the analysis of the relationship between growth and reproduction once the effect of climate has been extracted has been seldom explored. Recently, Knops *et al*. (2007) observed that the negative relationship between radial growth and reproduction in mast seeding oaks was dependent on climate, and rejected the existence of switching. Nevertheless, the reason why growth and reproduction become independent once the effects of climate are extracted remains still unexplained. The question is, how can plants sustain a high radial growth during or after years of extremely high fruit crops (mast years)? One explanation could be the across year accumulation of resources to sustain both reproduction and growth during a mast year (Sork *et al*. 1993). Alternatively, if we assume that current resources may be involved in seed production (Hasegawa *et al*. 2003, Hoch 2005) we should focus our attention to when each process occurs. Surprisingly, the role of the phenology of growth and reproduction and their influence for the existence of a growth/reproduction trade-off has been systematically ignored. If radial growth and fruit production show a different phenological extension and a reduced temporal overlap, then their potential competition for resources could be partially relaxed, and thus both processes could act as complementary resource sinks during the same year. Clearly, the exploration of this hypothesis would benefit from: (i) the comparison of the radial growth and fruit production patterns of similar species in different climates, and (ii) a detailed phenological analysis of the temporal overlap between these two processes.

We have assessed the existence of a trade-off between radial growth and acorn production in three Mediterranean oaks (*Quercus* sp.): the evergreen *Quercus ilex* L. and two closely related winter-deciduous oaks: *Q. faginea* Lam. and *Q. humilis* Mill. Temperate and tropical oaks have long been recognized as masting species (e.g. Sharp 1967, Sork 1993, Sork *et al*. 1993, Koenig *et al*. 1994b, Koenig & Knops 2002, Espelta *et al*. 2008) although scarce research has focused on the possible trade-off between radial growth and acorn production and the effect of climate in these two processes (but see Koenig 1997, Koenig & Knops 1998, Knops *et al*. 2007). Moreover, Mediterranean-type climate offers an interesting scenario to study the relationship between growth and reproduction. On the one hand, the existence of wet and temperate spring and autumn seasons (Terradas & Save 1992) may favour the initiation and the extension of vegetative growth far beyond the reproductive period which, mainly occurs during summer (Castro-Díez & Montserrat-Martí 1998), thus reducing the temporal overlap between the two processes. On the other hand, plants in a Mediterranean-type climate may be extremely affected by summer drought (Terradas & Save 1992), thus constraining the occurrence of reproductive events (Espelta *et al*. 2008) and reducing radial growth (Corcuera *et al*. 2004a, b, Campelo *et al*. 2007). We included both evergreen and winter-deciduous co-occurring oak species in our study because deciduous trees have been assumed to have a higher growth potential, yet a higher dependence on the availability of resources than evergreen ones (Aerts 1990, Reich *et al*. 1992).

In this study we address two main hypotheses. First, the relationship between radial growth and acorn production is mediated by climate. Thus, different local climates may lead to different relationships between radial growth and acorn production (either positive or negative), which will disappear after removing the effect of climate. Second, the competition for resources between radial growth and acorn production may be relaxed or even disappear if both phenological processes show a low temporal overlap. For instance, in a Mediterranean climate the temporal overlap between radial growth and acorn development might be relatively small due to the very early spring growth and the potential growth resumption in autumn after acorn ripening. We carried out this study in two different sites in NE Spain (with Coastal and Inland Mediterranean climate) where we monitored acorn production and radial growth for 7 to 10 years (1998-2007). We tested the relationship of acorn production vs. radial growth, including and excluding the effect of climate, at the population level in the two sites and also at the individual level (*per tree*) in the Coastal site. To determine the seasonality and the degree of overlap of radial growth and acorn production we intensively monitored radial growth and reproductive effort (number and weight of acorns) biweekly to monthly for one entire year.

MATERIAL AND METHODS

Species and study site

Quercus humilis, *Q. faginea* and *Q. ilex* are three Mediterranean oaks that frequently coexist in mixed forests. *Q. humilis* and *Q. faginea* are two deciduous oaks, historically outcrossed, while *Q. ilex* is an evergreen. In spite of their different leaf habit, the three species share most of their life traits, such as slow growth, resprouting ability after disturbances and similar regeneration niches (Espelta *et al*. 2005). They flower from March to May and acorns mature in summer and early autumn (Castro-Díez & Montserrat-Martí 1998).

Our study was conducted at two different sites in NE Spain, Collserola (thereafter, Coastal site) and Agüero (thereafter, Inland site), where mixed oak forest are frequent (Photo 2.1). The climate in both sites is Mediterranean, with high precipitation variability and severe summer droughts. Collserola (41º 24’ N, 2º 06’ E, 200 to 500 m asl) is a Natural Park, close to the Mediterranean coast, where mixed forests of *Q. humilis* and *Q. ilex* subsp. *ilex* are abundant. Soil is mainly developed on slates with scattered granitic outcrops. The mean annual precipitation was 556 mm for the study period (1998-2007) and mean monthly temperatures ranged between 12.2º C and 19.7º C. In the Agüero site (42° 18’ N, 0° 47’ W, 750 m asl), vegetation is an open tall scrub with scattered individuals of *Q.*

faginea and *Q. ilex* subsp. *ballota*. The soil in this area is a calcisol with a bed rock of calcareous sandstone. Mean annual precipitation was 564 mm, and mean monthly temperatures ranged between 4.3° C and 28.4° C during the 1998-2007 period.

Photo 2.1. Coastal (left) and Inland (right) study sites. Both are mixed forests dominated by *Q. ilex*, *Q. humilis* and *Pinus halepensis* in the Coastal site and *Q. ilex*, *Q. faginea* and *P. halepensis* in the Inland site.

Sampling design

A. Inter-annual patterns of acorn production and radial growth

Acorn production was measured yearly through a quantitative estimation of total acorn crop per individual in the Coastal site, during 8 consecutive years (1998-2005), and through a qualitative index of population acorn production in the Inland site, during 10 consecutive years (1998-2007). In the Coastal site, 38 *Q. humilis* and 14 *Q. ilex* individuals with similar diameter and height were randomly chosen for this study (see for details of the sampling design Espelta *et al.* 2008). In the Inland site, acorn production was visually estimated by using the semi-quantitative McDonald's method (McDonald 1992) in 25 *Q. faginea* and 25 *Q. ilex* individuals with similar diameter and height.

Radial growth was assessed using standard dendrochronological methods. The sampling was carried out in 2004 for *Q. ilex* and 2005 for *Q. humilis* at the Coastal site, and winter 2007 for the Inland site. Two radial cores were extracted from the main trunk of each tree using a Pressler increment borer. In the laboratory, after the cores were dried, they were sanded, visually cross-dated and measured with an accuracy of 0.01 mm using a LINTAB measuring device (Rinntech, Heidelberg, Germany). Cross-dating quality was checked using COFECHA (Holmes 1983). In every core we measured as many rings as possible, varying this number between 19 and 66. To correct radial growth for the effect of increasing tree size and age, the mean original ring-width series were transformed into indexed values by fitting simple linear functions. Tree-ring widths were then converted into indices by dividing the observed by the expected values estimated by the linear functions. Then, autoregressive modelling was performed to remove the first-order temporal autocorrelation. This process was carried out using ARSTAN (Cook 1985). The standardized series of indices have constant mean and variance.

B. Seasonal pattern of acorn production, acorn growth and radial growth

In February 2007 we installed 60 manual band dendrometers (Agriculture Electronics Corporation, Tucson, USA) at 1.3 m in the trunk of 15 *Q. ilex* individuals and 15 *Q. humilis / Q. faginea* in each study site. Bark was brushed off before installing the dendrometers. Radial growth was monitored every 15 days in the Coastal site and every 30 days in the Inland site with a precision of 0.1 mm from February 2007 until growth ceased in December 2007. To compare radial growth with acorn production and acorn development through time, we measured acorn abundance and acorn weight from acorn appearance until acorn dispersal in the same days that growth was recorded. The abundance of acorns was estimated for every tree as the proportion of the canopy bearing acorns, while the mean acorn dry weight was calculated after randomly collecting 10 sound acorns per tree. As the premature abortion of acorns during acorn maturation is considerable (Espelta *et al*. 2008), a compound index of reproductive effort (RE) was calculated for each tree and sampling date. This index summarizes the abundance of acorns and their weight at a date: RE= 1- exp (-(mean weight of acorns) x (proportion of the canopy bearing acorns)). RE may take values between 0 and 1.

Climate variables

We selected monthly mean temperature and monthly precipitation as the potential predictors of radial growth and mature acorn production based on previous studies (Despland & Houle 1997, Corcuera *et al*. 2004a, b, Monks & Kelly 2006). For the Coastal and Inland sites, precipitation and temperature data were obtained from the Observatory Fabra (41º 25’ N, 2º 07’ E, 415 m) and the Ayerbe meteorological station (42º 16’ N, 0º 41’ W, 585 m), respectively.

Data Analysis

A. Inter-annual patterns of acorn production and radial growth

The relationship between acorn production and radial growth was tested both with the raw data (hereafter, acorn production vs. radial growth) and after extracting the effect of climate in the two variables (hereafter, non-climatic acorn production vs. non-climatic radial growth) (see also Monks & Kelly 2006, Knops *et al*. 2007). For the analysis of acorn production vs. radial growth, we calculated Pearson or Spearman correlations (according to the type of the acorn production data) between yearly mature acorn production and yearly radial growth. Data were ln transformed when necessary to meet the assumptions of normality. For the analysis of non-climatic acorn production vs. non-climatic radial growth, we first removed the effect of climate on both variables before re-evaluating the relationship between them. To achieve this, we first tested the effect of precipitation and temperature on mean radial growth over the last 30 years and on mean mature acorn production during the sampling period, by means of Pearson or Spearman correlation analyses. The variables included in these correlation analyses were monthly precipitation and monthly mean temperature from May of the year previous to growth (*t*-1) up to November of the year of growth or reproduction (*t*), similarly to previous studies on climate-growth relationships (Tessier *et al.* 1994, Despland & Houle 1997, Corcuera *et al.* 2004a, b, Monks & Kelly 2006). Significant variables were used as predictors for stepwise lineal regressions of climate vs. radial growth, and residuals were used as non-climatic radial growth. For acorn production, only 7 to 10 years of data were available, thus, we avoided including a large set of variables as predictors of the lineal regression. Total precipitation in spring (March, April and May, spring mean temperature), summer drought (calculated as in Sork *et al.* 1993) and previous year summer drought were selected as the most influential variables in acorn production in Coastal site, and were used as predictors for the stepwise lineal regression. In the Inland site no climatic variable was significantly related to acorn production, so it was not necessary to extract a climatic effect from acorn production data. In order to determine the sign of the relationship between radial growth and acorn production at the tree basis, the same abovementioned analyses were carried out for each individual at the Coastal site.

To further check whether the potential trade-off between acorn production and radial growth could only emerge those years with extremely large acorn crop sizes we explored in detail the relationship between both variables during a masting event (2002) by means of a regression analysis. To make values from different trees comparable, relative radial growth and relative acorn production per individual tree was calculated as the relation between the value in year 2002 and the mean over the study period.

Finally, in order to test whether current acorn production could constrain the next reproductive event, temporal autocorrelation in acorn production was checked for both sites and species at 1-year time lags (Knops *et al*. 2007).

B. Seasonal pattern of acorn production, acorn growth and radial growth

In order to evaluate the overlap extent between radial growth and reproductive effort (abundance and weight of acorns) total radial growth in 2007 was divided into three different periods: (i) radial growth previous to acorn development, (ii) radial growth during acorn development and (iii) radial growth after acorn dispersal. To determine these three periods, reproductive effort (RE) values were first calculated (every 15 or 30 days for Coastal and Inland site respectively) for each tree. The period previous to acorn development covers all the time until RE begins the maximum increase. The period of acorn development ranges between RE maximum increase and acorn dispersal, and the third period correspond to the time after acorn dispersal. The percentage of total radial growth that occurred during every period was calculated for all species and for the two sites, and differences were tested by means of ANCOVA analyses. The proportion of radial growth performed during each of the three periods was introduced as dependent variables, while site (Coastal or Inland) and species (deciduous or evergreen) were independent variables. To control for the effect of the RE on the radial growth performed during and after acorn production (second and third period), maximum RE was introduced as a covariate.

The possibility that the radial growth performed before acorn development conditioned the maximum reproductive effort was analysed by means of an ANCOVA where RE was the dependent variable, and species, site and radial growth (covariate) were the independent variables.

RESULTS

In both sites and for the three studied species, acorn production was highly variable among years, with differences between high and low acorn crops more pronounced in the Coastal than in the Inland site (Figure 2.1). Interestingly, a masting episode occurred in 2002 for all species in the two sites. Mature acorn crop was usually higher for the evergreen oak (*Q. ilex*) than for the deciduous oaks (Figure 2.1). Similarly to acorn production patterns, radial growth was also extremely variable over the years in the two sites, with the larger variability observed in the Coastal site.

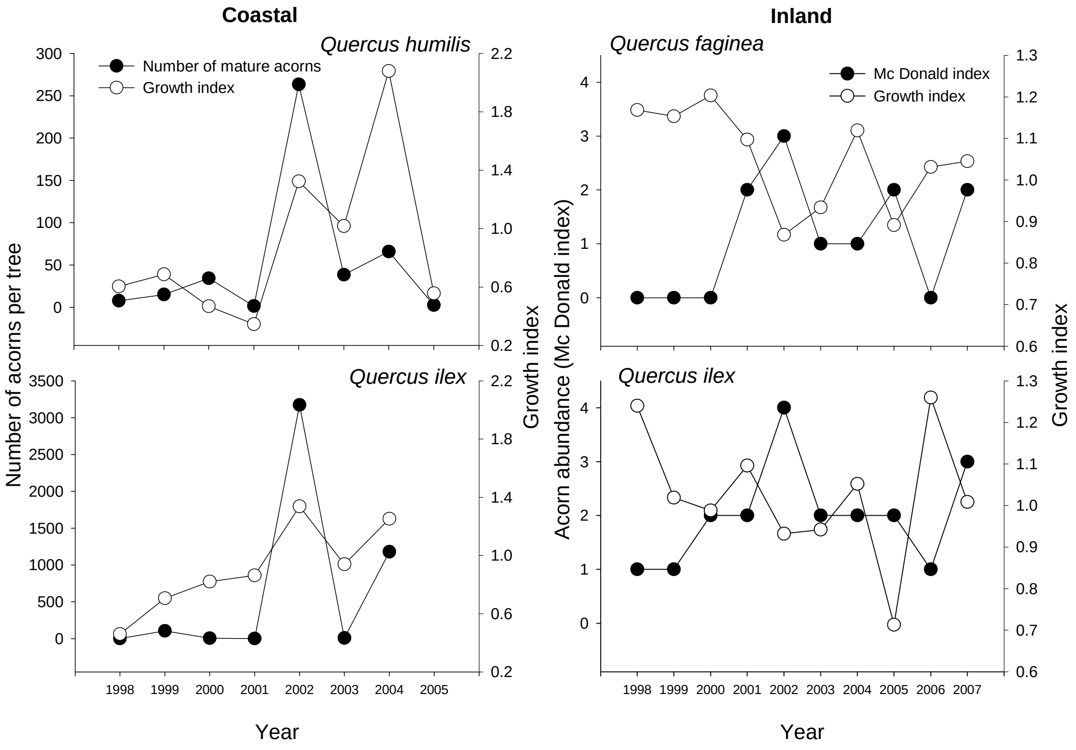


Figure 2.1. Mean annual acorn production (solid dots) and mean annual radial growth index (open dots) for *Q. humilis* and *Q. ilex* in the Coastal site and for *Q. faginea* and *Q. ilex* in the Inland site. In the Coastal site acorn production was measured as the number of mature acorns per tree while in the Inland site it was measured by means of a semi-quantitative index (McDonald's index).

A. Inter-annual patterns of acorn production and radial growth

The sign of the relationship between radial growth and acorn production was markedly different in each site. In the Coastal site the correlation analysis showed a significant positive relationship for *Q. humilis* (Pearson correlation, r=0.78, p=0.02) and marginally positive for *Q. ilex* (r=0.75, p=0.05), whereas in the Inland site, on the contrary, the relationship was clearly negative for the two species (Spearman correlation, r_s=-0.65, p=0.04; and r_s=-0.71, p=0.02, for *Q. ilex* and *Q. faginea* respectively). The correlation analyses between climate variables and radial growth revealed that growth was similarly influenced by climate in the two sites (Figure 2.2). High precipitation and cool temperatures during spring of the current year (March, April and May) enhanced radial growth in deciduous oaks while for *Q. ilex* growth was enhanced by July precipitation in the Coastal site. Acorn production was enhanced by similar climatic variables to those influencing radial growth in the Coastal site (plus precipitation in June, July and August), while no significant climatic influence on acorn production could be detected in the Inland site (Figure 2.3). Once the effect of climate on radial growth and acorn production (only for the Coastal site) was removed, the relationship between non-climatic radial growth and non-climatic acorn production became null for all species and sites (respectively, r=0.40, p=0.38, r=0.16, and p=0.55 for *Q. ilex* and *Q. humilis* in the Coastal site; r_s=-0.56, p=0.09, and r_s=0.00, p=1.00 for *Q. ilex* and *Q. faginea* in the Inland site).

Individual (*per tree*) analyses conducted at the Coastal site revealed that 39% of *Q. humilis* and 55% of *Q. ilex* trees presented a positive relationship between radial growth and acorn production, while the rest showed no significant relationship (Appendix 2.1). As previously detected at the population level, when the effect of climate was extracted from both radial growth and acorn production, most trees (83% of *Q. humilis* and 92% of *Q. ilex*) exhibited no relationship (Appendix 2.1). Interestingly, no negative relationships between radial growth and acorn production were found in any tree, either including or excluding the climatic effects. The lack of a negative relationship between radial growth and acorn production was also confirmed during the mast year (2002), either with the raw data or after excluding the climatic effects (linear regression, $p > 0.05$ in all cases). Concerning a potential relationship among successive reproductive events, no autocorrelation between acorn production at 1-year time lags was observed for any oak species, suggesting that current acorn production does not constrain future reproduction.

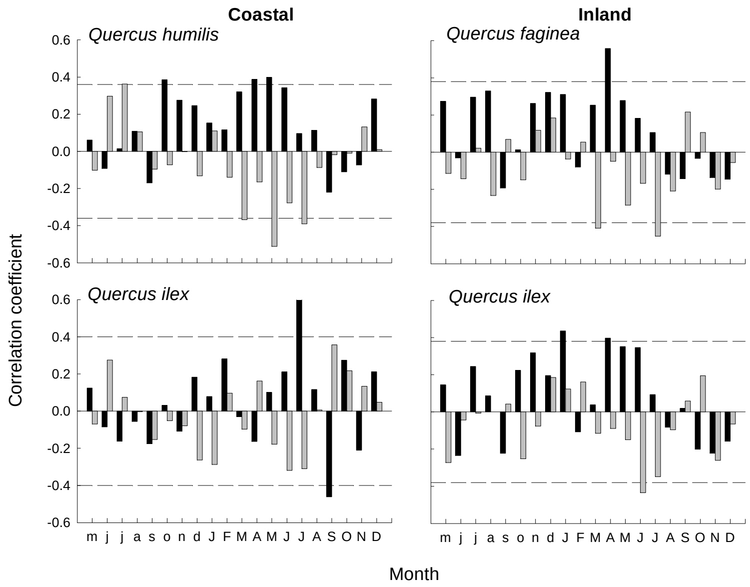


Figure 2.2. Climate-radial growth index relationships in *Q. ilex* and *Q. humilis*/*Q. faginea* based on the correlation between monthly meteorological data (total precipitation in black bars, mean temperature in grey bars) and the series of radial growth index (8 years for the Coastal site and 10 years for the Inland site). Radial growth index and climate were compared from May of the year previous to reproduction up to December of the current year. Upper- and lower-case letters indicate respectively current year and previous year months included in the analyses. The dotted horizontal lines are significance thresholds ($p < 0.05$).

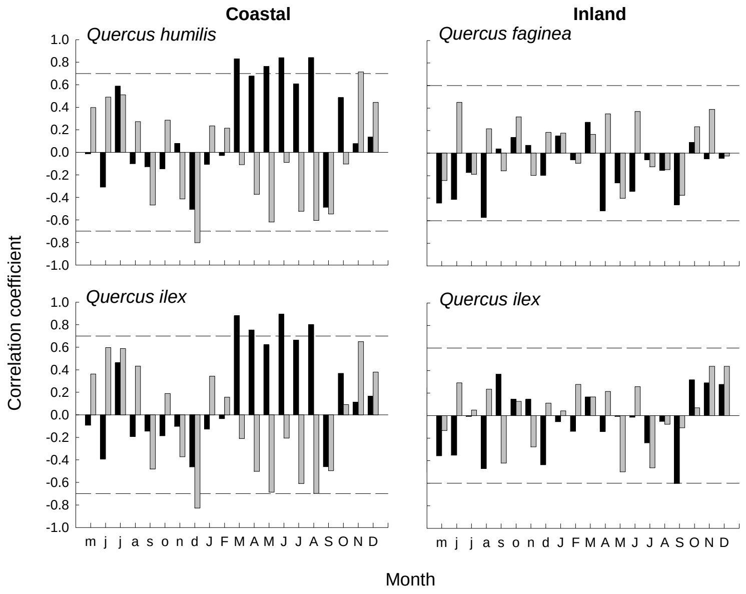


Figure 2.3. Climate-mature acorn production relationships in *Q. ilex* and *Q. humilis*/*Q. faginea* based on the correlation between monthly meteorological data (total precipitation in black bars, mean temperature in grey bars) and acorn production (mean number of acorns for the Coastal site and McDonald's index for the Inland site). Acorn production and climate were compared from May of the year previous to reproduction to December of the current year. Upper- and lower-case letters indicate respectively current year and previous year months included in the analyses. The dotted horizontal lines are significance thresholds ($p < 0.05$).

B. Seasonal patterns of acorn production, acorn growth and radial growth

The three oak species began radial growth in April, after the first precipitation events (Figure 2.4d and 2.4e). Notwithstanding this coincidence between the two sites, the rest of the radial growth pattern was different. The main peak of radial growth was observed in May in the Coastal and in June-July in the Inland site. Radial growth mostly ceased during summer (July in the Coastal site and August in the Inland site). Additionally, but to a lesser extent, radial growth peaks in late summer and autumn (August, October) were also found in both sites. In the Coastal site, late summer and autumn radial growth was closely connected to the occurrence of precipitation events, especially in the case of *Q. ilex* (compare Figure 2.4d and 2.4e). In *Q. humilis* / *Q. faginea*, 85 to 90 % of the annual radial growth was completed between April and July, whereas in *Q. ilex* it was 60 to 70%.

In both sites, female flowers appeared in April-May but acorns did not start to gain weight until June-July (Figure 2.4a, 2.4b). Acorns in deciduous oaks appeared 15 to 30 days earlier than in the evergreen oak in both sites (Figure 2.4a). In all oaks, once the maximum percentage of the canopy bearing acorns was reached, abortion started occurring. However, the reproductive effort stayed more or less constant during the entire season: i.e. the abortion of part of the acorn crop was compensated by the growth of the remaining acorns (Figure 2.4c). These two results suggest a local competence for resources among acorns in the same tree. Mature acorn weight was considerably lower in the Coastal than in the Inland site (1.03 ± 0.10 g vs. 1.52 ± 0.18 g and 0.64 ± 0.08 vs. 1.17 ± 0.14 g for *Q. humilis* / *Q. faginea* and *Q. ilex*, respectively).

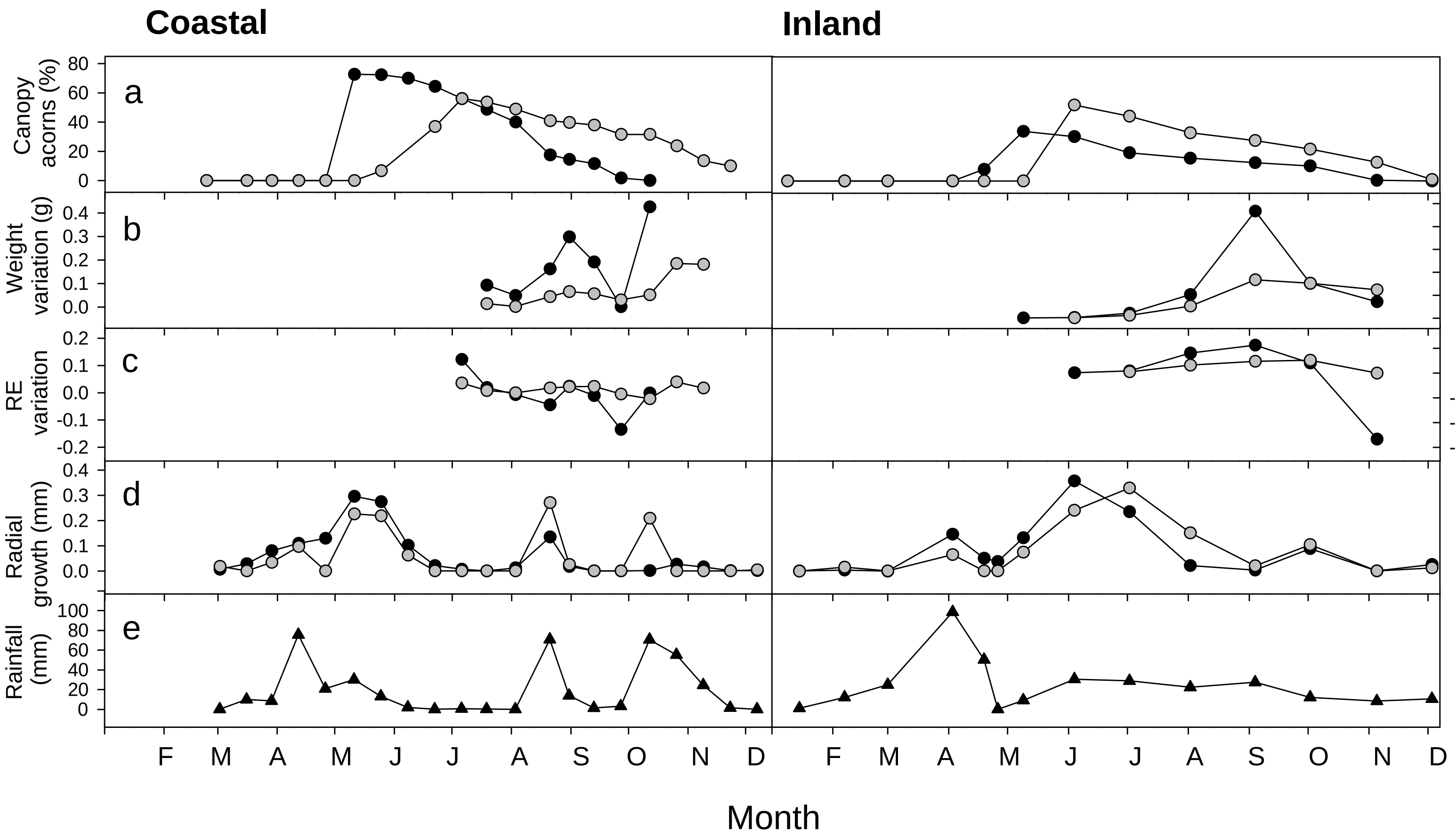


Figure 2. 4. Temporal variation of reproductive, vegetative and climatic variables during 2007 in *Q. humilis* / *Q. faginea* (black dots) and *Q. ilex* (grey dots) trees in the Coastal and Inland sites. a) Acorn abundance, b) Acorn weight variation, c) Reproductive effort index (RE) variation, d) Radial-growth and e) Precipitation.

In the two sites 80.23 ± 2.69 % of the total radial growth occurred before acorns began to gain weight (Figure 2.5), with no significant differences between sites or species (Table 2.1). Moreover, the amount of radial growth carried out before acorn development did not influence the subsequent reproductive effort (abundance x acorn weight) of the tree (ANCOVA, df=1, F=1.08, p=0.305). These results indicate that a great portion of radial growth does not overlap with the period when acorns are acquiring more resources and that this previous growth does not constrain resources to be invested in reproduction.

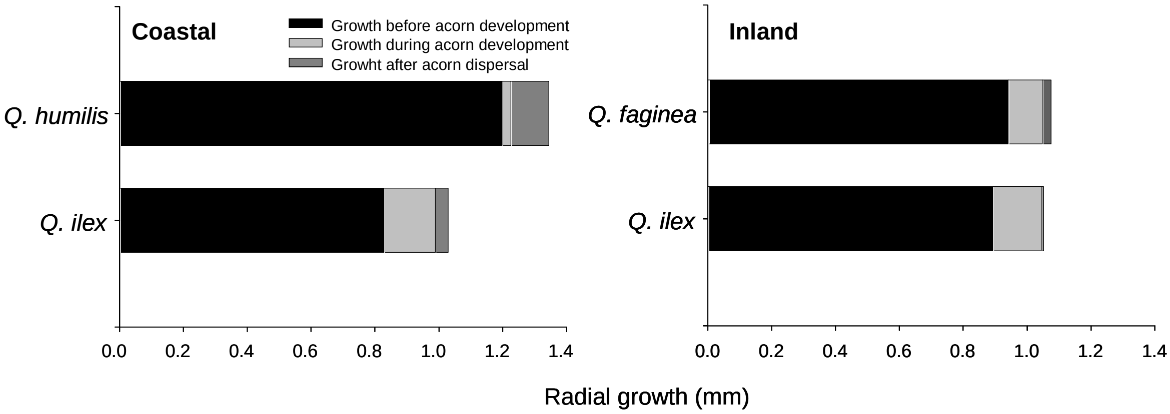


Figure 2.5. Radial growth performed before acorn development, during acorn development and after acorn dispersal in *Q. humilis / Q. faginea* and *Q. ilex* in the Coastal and Inland sites.

The amount of radial growth occurring during acorn development differed between the two sites and species (Table 2.1). Radial growth was much lower in the Coastal site (2.4 ± 3.3 % for *Q. humilis* and 14.2 ± 3.6 % for *Q. ilex*) than in the Inland site (24.8 ± 12.0 % for *Q. faginea* and 23.0 ± 7.6 % for *Q. ilex*). The amount of radial growth during acorn development was independent of the reproductive effort in the Coastal site but negatively influenced in the Inland site (interaction site x reproductive effort in Table 2.1). Interestingly, part of radial growth took place in autumn after acorn dispersal (up to November), differing significantly between sites (see Table 2.1): 8.0 ± 2.3 % in the Coastal site vs. 1.0 ± 1.1 % in the Inland site. This portion of autumn radial growth was not constrained by the magnitude of the previous reproductive effort (Table 2.1).

Table 2.1. Results of the ANOVA for the effects of site (Coastal, Inland), species (*Q. humilis* / *Q. faginea, Q. ilex*) and reproductive effort (RE) on the fraction of radial growth (RG) occurred before acorn development, during acorn development and after acorn dispersal. RG percentages were arcsin transformed. Significant results are shown in bold.

Effects		RG before acorn development		RG during acorn development		RG after acorn dispersal	
	df	F	p	F	p	F	p
Site (SI)	1	1.6	0.210	**18.2**	**< 0.001**	3.6	0.067
Species (SP)	1	0.4	0.552	0.1	0.706	0.2	0.683
Reproductive Effort (RE)	1			2.9	0.099	1.5	0.235
SI x SP	1	0.7	0.408	**4.5**	**0.044**	1.5	0.225
SI x RE	1			**6.4**	**0.017**	0.4	0.524
SP x RE	1			0.1	0.774	2.5	0.122
SI x SP x RE	1			0.9	0.348	2.6	0.119

DISCUSSION

This paper presents two contributions to understand the apparent trade-off between radial growth and reproduction in mast seeding oaks. First, we prove that the relationship between raw radial growth and fruit production may be either positive or negative in different local environments for the same species (Hypothesis 1). Thus, as suggested by Kelly & Sork (2002) climate strongly mediates this relationship, which finally disappears once the effects of climate are extracted (see also Despland & Houle 1997, Knops *et al.* 2007). Second, we demonstrate that at least for Mediterranean oaks, radial growth extends over a longer period than seed production (Hypothesis 2), beginning much earlier than acorn development and extending beyond acorn dispersal. This pattern, coupled with the fact that radial growth before acorn development does not constrain the extent of the reproductive effort, nor does this reproductive effort constrain the subsequent radial growth in autumn, suggests that a long vegetative season and a low degree of overlap between growth and reproduction might well contribute to escape a trade-off between these two processes.

The fact that radial growth and acorn production showed a positive relationship in the Coastal site whereas the association was negative in the Inland site supports the idea that local climatic variability can modify the extent of the correlations among functional traits, even for the same species (Stearns *et al.* 1991, Sgro & Hoffmann 2004, Gutteling *et al.* 2007). Interestingly, while radial growth of oaks was influenced by climate in a similar way in the two sites, acorn production was differently affected, indicating that the sign of the relationship between these two traits was mostly controlled by differences in the influence of local climate on reproduction. In the two sites, radial growth of oaks was mostly enhanced by rainy and cool spring and summer periods and by the precipitation amount in the previous autumn/winter, a pattern typical of Mediterranean areas with low water availability (Tessier *et al.* 1994, Corcuera *et al.* 2004a, b, Campelo *et al.* 2007). As high precipitation and cool temperatures in spring and early summer also favoured acorn production in the Coastal site (see also Sharp 1967, Sork 1993, Ogaya & Peñuelas 2007a), this resulted in a positive relationship among the two traits when raw data are used. For the Inland site, no effect of climate variables on acorn production was observed, and thus, it becomes difficult to explain the causes of a negative relationship among them. One explanation for this negative relationship among tree growth and reproduction is the positive effects of spring rainfall in tree growth but negative in pollination (Rodríguez-Rajo *et al.* 2005).

Local differences in the patterns of radial growth and reproduction among the Coastal and the Inland sites were also evidenced during the detailed monitoring of these two processes in summer 2007 (Figure 2.4). In the Coastal site radial growth and acorn growth were closely connected by the occurrence of episodic rain events (compare Figure 2.4b, 2.4d and 2.4e). This supports the positive relationship among these two traits observed in the previous inter-annual comparison and it coincides with other studies in the area, which have shown water availability during summer to be of paramount importance to sustain growth (Terradas & Save 1992, Campelo *et al.* 2007) and acorn production (Espelta *et al.* 2008). Conversely in the Inland site, radial growth and acorn development during the summer season did not coincide (compare Figure 2.4b and 2.4d), and both processes were even negatively related (interaction site x reproductive effort in Table 2.1). Interestingly in this area, rainfall was mostly concentrated in spring (from March to May in Figure 2.4e) and no episodic storms occurred during summer. This suggests a scenario where water availability becomes progressively scarce in summer which might partly explain the potential competition between growth and reproduction during the peak of summer (i.e. radial growth was almost stopped while acorns developed; compare Figure 2.4b and 2.4d, see also Montserrat-Martí *et al.* 2009).

Our results confirmed a longer extension of radial growth (April to November) in comparison to acorn development (June to October), and thus a low temporal overlap between them: i.e. more than 80% of radial growth occurred before acorns started to gain weight, and even some growth (8% in the Coastal site and 1% in the Inland site) could well occur after acorn dispersal, due to the mild and rainy conditions of the autumn season in a Mediterranean-type climate. To what extent such an extended growing season may also help to escape a potential trade-off among radial growth and reproduction is an exciting question to be further investigated.

Moreover, spring growth did not influence reproductive effort nor did reproductive effort constrain autumn growth after acorn dispersal. We hypothesize that such independence between radial growth and fruit production during a single season could be explained by three alternative mechanisms. First, in these Mediterranean oaks primary growth (shoots growth and leaf extension) is fully accomplished by the end of June when new leaves are totally functional (Castro-Díez & Montserrat-Martí 1998, Montserrat-Martí *et al.* 2009), and just before acorns start growing. Therefore, as suggested by other studies it may well be that acorn growth is mostly supported by the resources provided by the photosynthates of current-year leaves (Hasegawa *et al.* 2003, Hoch 2005). Second, an alternative hypothesis is resource accumulation during the previous years (Sork *et al.* 1993). In this case no trade-off is necessary within a mast year, although a depletion of resources must imply a negative autocorrelation in reproduction among successive years. Our results discard such a negative autocorrelation in seed production. Third, if some degree of autonomy of branches is assumed, potential trade-offs between growth and reproduction may be more likely to detect at lower levels in the canopy, such as branches or shoots (Obeso 1997, Chapter 3) but not at the trunk because vegetative branches might compensate the cost of reproduction of reproductive branches (Bañuelos & Obeso 2004).

Our results emphasize the need to consider the length of the vegetative season, the temporal occurrence of radial growth and fruit development and their overlap to analyse the relationship between growth and reproduction in mast seeding species, and suggest several questions to be further explored. First, it must be noticed that most studies that claimed a negative relationship between growth and reproduction have been carried out in species experiencing a greater overlap between radial growth and fruit production, either because a shorter vegetative season (e.g. boreal species in Nienstaedt 1985, Silvertown & Dodd 1999, Selas *et al*. 2002) or because fruit production occurs throughout the year (e.g. *Nothofagus truncata* in Monks & Kelly 2006). Thus, a comparison of the growth vs. reproductive patterns of similar species under a wide range of climatic conditions could help to elucidate the role of the overlap between these two processes in the sign of their relationship. Second, under a climate change scenario, the need to consider the length of the vegetative season and potential phenological shifts in its extension becomes crucial due to the constraining effect of an increased summer drought on vegetative and reproductive processes (Ogaya *et al*. 2003, Ogaya & Peñuelas 2007a, b) and the extension of the vegetative season during autumn (Peñuelas *et al.* 2002).

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Capítulo 3

Costs of reproduction during a mast year in a Californian oak: The influence of the hierarchical level within the canopy and tree crop size

This chapter has been done in collaboration with V.L. Sork & J.M. Espelta.

ABSTRACT

- The existence of trade-offs between reproduction and other fitness traits is a fundamental principle of life history theory. Costs of reproduction for vegetative growth have been expected to be especially dramatic in mast seeding trees because reproduction during mast episodes requires high investment of resources. However, it has been recently demonstrated that masting may not result in a reduction of secondary tree growth. Therefore, whether masting involves growth costs and at what level they occur, remains unresolved.

- In this study we tested the existence of the costs of reproduction in the California endemic *Quercus lobata* during a mast year by measuring the reproductive effort and the vegetative growth at two hierarchical levels within the canopy (branch,shoot) in trees with high and low acorn production.

- We found reduction of growth on vegetative shoots neighbouring reproductive shoots, indicating costs of reproduction due to local source/sink processes in both high and low acorn production trees. However, costs of reproduction at lower levels (branch) were found only in trees of low acorn production, and not on high acorn production trees. A path analysis indicated that a major factor determining acorn production was the amount of previous year growth on branches, probably a by-product of the resource availability of the tree.

- Together, these findings suggest that trees with large acorn crops had more available resources allowing the allocation of resources to both growth and acorn

production and the compensation for local costs of seed production. However, the fact that all the trees produced seeds despite the cost for vegetative growth suggests the existence of a strong synchronizing cue.

- It is important to locate the level at which costs of reproduction are acting. Costs of reproduction do not have to affect the whole tree, but can be detected at branches or shoots instead of the trunk. Our results indicate that the costs of reproduction vary among individuals of a population attending to their resource availability. Finally, we suggest that there must exist a synchronizing cue that triggers seed production regardless of the cost for vegetative growth in mast seeding trees.

INTRODUCTION

A fundamental tenet of life history theory is that reproduction comes at a cost, resulting in trade-offs with some other fitness trait (Williams 1966, Roff 1992, Obeso 2002). Studies across a range of plant species have documented trade-offs between reproduction and growth (Morris 1951, Gross 1972, Abrahamson 1975, El Kassaby & Barclay 1992, Obeso 1993). No phenomenon is likely to illustrate the potential costs of reproduction more dramatically than mast-seeding in woody plant species (Kelly 1994, Koenig & Knops 1998, Kelly & Sork 2002, Monks & Kelly 2006, Sork 1993, Sork & Bramble 1993, Yasumura 2006). Mast-seeding is a reproductive strategy that results in the synchronized production of large crops during some years and small or negligible crops during other years (Janzen 1971, Silvertown 1980, Norton & Kelly 1988, Sork *et al.* 1993, Kelly &

Sork 2002). It has been hypothesized that the production of large crops is possible because (i) plants match their reproductive output to the variable resources available (Monks & Kelly 2006), (ii) resources are accumulated since last mast episode (Sork *et al.* 1993), or (iii) resources are shifted from vegetative growth to reproduction via trade-offs (Norton & Kelly 1988).

To understand the proximate causes of masting, the first step is to look for the presence of trade-offs during a mast year. The trade-off hypothesis has also been referred to as the resource switching hypothesis because resources are differentially allocated to developing fruits at a cost to local vegetative growth (Norton & Kelly 1988, Kelly & Sork 2002, Obeso 2002, Monks & Kelly 2006). The trade-off hypothesis assumes that resources for mast crops come at a cost of vegetative growth within the same year. For example, many studies report an inverse relationship across years between increment growth measure in trunk rings and seed production (e.g. Eis *et al.* 1965, Norton & Kelly 1988, Koenig & Knops 1998, Monks & Kelly 2006). Yet, this evidence is not universal (Nienstaedt 1985, Dick *et al.* 1990, Cremer 1992, Despland & Houle 1997, Alley 1998, Snook *et al.* 2005, Yasumura 2006). Moreover, this correlation may be the indirect outcome of other factors affecting tree growth, rather than evidence for the cost of reproduction. For example, Knops *et al.* (2007) reanalyzed their previous data from several California oak species (Koenig & Knops 1998) and concluded that oscillations in tree ring growth correlate with rainfall and once this effect is removed, no trade-offs were evident in overall growth measured in the trunk. In fact, the cost of reproduction may not affect vegetative growth in the trunk, but in reproductive branches or shoots. Competition for local resources could be most intense between shoots or branches, which may be autonomous to some extent from other parts of the tree's canopy (Dick *et al.* 1990, Despland & Houle 1997, Obeso 1997, Yasumura 2006). Therefore, the trade-off between growth and reproduction may be more apparent within a shoot of a branch or among branches than in the trunk because the overall cost of reproductive modules could be compensated by the growth of vegetative ones elsewhere (Obeso 1997, Watson & Casper 1984). Thus, an alternative way to test the trade-off hypothesis would be to simultaneously document growth and reproduction at various levels within a tree (Henriksson & Ruohomaki 2000, Suzuki 2000, 2005, Hasegawa *et al.* 2003, Obeso 2004b, Kawamura & Takeda 2006). For this test, it is more likely to detect the trade-off between growth and seed production during a mast year, when investment in reproduction is very large, because trade-offs are more evident when resources are limiting (Tuomi *et al.* 1983).

The other resource-based hypotheses do not necessary lead to the expectation that trade-offs exist. They predict that (i) mast years are a reflection of year-to-year variation in the amount of resources produced as a consequence of environmental variation (resource matching hypothesis) (Kelly 1994, Kelly & Sork 2002); or (ii) mast years are possible when resources are previously accumulated. In the resource matching scenario, we might not necessarily see trade-offs between growth and reproduction because both processes are matched to resource availability (Despland & Houle 1997). Resource accumulation could avoid trade-offs if sufficient resources are available that both seed production and vegetative growth can occur. Thus, these two hypotheses could help explain the production of large acorn crops in absence of trade-offs.

To explore the trade-off hypothesis, it would be helpful to examine the evidence for trade-offs in trees with large and small crops because the cost of reproduction might vary among individuals with different levels of investment in acorn production (e.g. Isagi *et al.* 1997, Herrera *et al.* 1998, Sork *et al.* 1993). Do trees that produce large fruit crops do so because they allocate more of their resources to reproduction than to vegetative growth or because they have an overall high level of resource availability? In this paper, we will assess the trade-offs in vegetative growth and reproduction in a mast-seeding tree, *Quercus lobata* Née (California valley oak) during a mast year. Oaks are considered to be a classic masting species due to the phenomenon of periodic, synchronous acorn production in different populations and species (Sork *et al.* 1993, Koenig *et al.* 1994b, Kelly & Sork 2002 and references therein, Espelta *et al.* 2008), despite the fact that the magnitude varies tremendously across species. Here we focus on the proximate costs of reproduction on vegetative growth at tree, branch and shoot level as a basic step toward establishing evidence for trade-offs. Our main questions are, first, whether acorn production reduces growth on shoots and branches and whether this pattern changes within high production vs. low production trees, and second, which causal relationships link resource availability, and vegetative and reproductive investment? This investigation was done during a year of high acorn production for a population that had not produced widespread significantly large acorn crops in five years. The first part of paper examines the results of a factorial experimental design at tree, branch and shoot level to see whether there are trade-offs between growth and reproduction on (1) trees with high versus low acorn production, (2) reproductive branches versus vegetative branches and (3) shoots with acorns versus those without acorns on reproductive branches and vegetative branches. In the second part, we utilize a path analysis to interpret direct and indirect causal relationships among previous year biomass, shoot growth, and acorn production.

MATERIAL AND METHODS

Species and Study Site

Quercus lobata Née (California valley oak) is endemic to California, where it occurs in savanna oak communities on deep loamy soils, principally below 600 m of elevation in the Central Valley, surrounding valleys, and foothills (Pavlik *et al.* 1991). *Quercus lobata* is a diploid, wind-pollinated, monoecious, and predominantly outcrossing tree species (Sork *et al.* 2002). It flowers in March – April before leaves emerge and each female flower develops into an acorn over the summer, maturing in late September to early October of the year of pollination.

The study site is located at Sedgwick Reserve, which is administered by the University of California at Santa Barbara as part of the University of California Natural Reserve System. The 2380 ha reserve is 10 km northeast of Santa Ynez (Santa Barbara County, California, USA). The study trees sampled for this study are located in the valley along Figueroa Creek (34°42’N, 120°02’W) (Photo 3.1) twith elevations ranging from 300 to 400 m above sea level. Stem density averages about 1.19 adult trees/ha (Sork *et al.* 2002); adult trees have breast height diameters greater than 40 cm, and adult crown areas range from 64.5 – 581.9 m^2 with a mean 291.6 m^2 ± 129 SD (Pluess *et al.* 2009).

Photo 3.1. Study site, at Sedgwick Reserve. The photo was taken in the sampling period (October 2007).

Sampling design

To analyze the allocation of resources during a mast-fruiting year, we selected 10 pairs of valley oak adults located in the vicinity of each other: 1 tree with high acorn production and 1 tree with low acorn production. These trees were part of a separate phenology study of flower and acorn development for 100 trees, where we estimated acorn crop size during this same season (Lentz & Sork, unpublished data). For our study, high acorn-producing trees came from the top 20 percentile of this sample, and low acorn-producing trees, came from the low 20 percentile, based on their ranks for acorn production measured by visual counts of acorns on each tree (Koenig *et al.* 1994a).

During last week of October 2007, when both the vegetative and the reproductive growth seasons were finished, and the stems, leaves, and acorns were at their maximum size, we conducted the sampling for this study. Within each tree, we randomly selected five reproductive and five non-reproductive branches (Figure 3.1) from a band of the canopy 5 - 8 m from the ground located on the south side, where acorns were consistently most abundant. Using a large pruning pole, we cut each branch such that it included one stem developed during 2006 and all of its shoots with their leaves and acorns that developed during spring and summer 2007. Branches were tagged and kept in separate bags at 4ºC until measures were taken.

To quantify previous year growth (2006), we measured length, diameter and dry biomass of last year's stem. To measure current (2007) growth in reproductive and non-reproductive branches, we measured the number of reproductive and vegetative shoots, leaves, acorns, and cupules for each branch. In reproductive branches, shoots and their leaves were separated into two groups: shoots with and without acorns. We measured length, diameter, volume, number of leaves, and number of acorns found on the largest shoots with (if any) and without acorns for each branch, either reproductive or vegetative. To measure biomass for the various parts of the branches, we then dried all fractions in an oven at 70ºC for 96 hours and weighed to the nearest 0.001 g. Vegetative biomass of a branch was calculated as the sum of shoots and leaves biomass, and total biomass was the sum of shoots, leaves and acorns biomass.

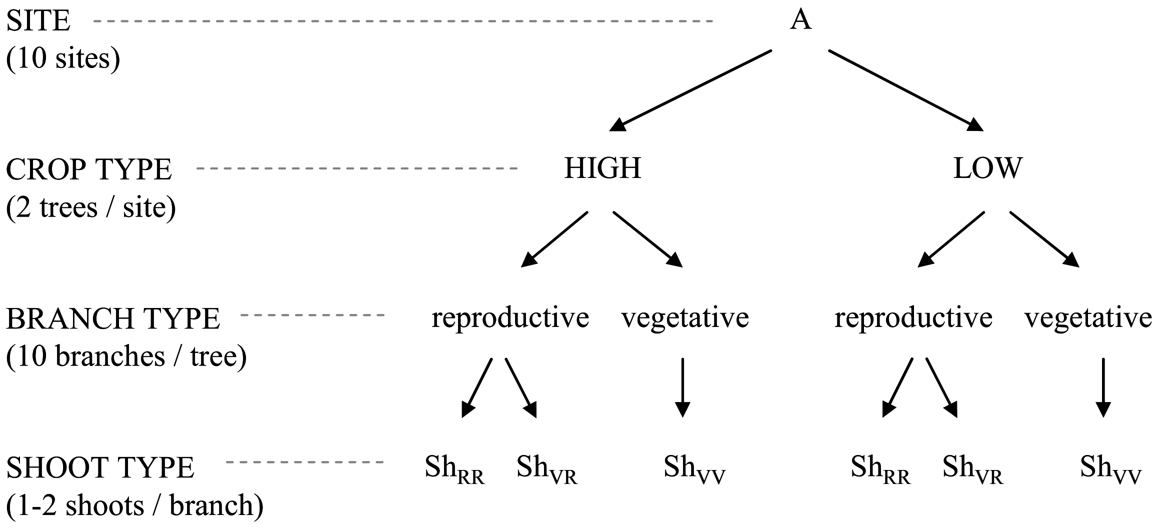

Figure 3.1. Sampling design: Two trees were chosen from 10 different sites (from A to J) within Figueroa valley. *A* designs the first site. One tree of the pair presented high acorn production and the other, low acorn production (Crop type: High and Low). Within each tree, we selected randomly five reproductive and five non-reproductive branches (Branch type: Reproductive and Vegetative). The longest shoot with and without acorns was registered for each branch (Shoot type: Sh_{RR} are shoots with acorns, Sh_{VR} are shoots without acorns from reproductive branches and Sh_{VV} are shoots from vegetative branches).

Some of the acorns were already dispersed at the time of sampling, which we ascertained because the cupules were still attached to the shoot. The diameter of the cupule was measured in these cases. We estimated the biomass of these acorns using a regression approach that linked diameter of the cupule and dry mass of the acorns, from a set of acorns randomly selected ($y = 0.4192x – 3.8158$, $r^2 = 0.70$, $n = 75$).

Data analysis

To identify the location of resource allocation from vegetative to reproductive growth, we analyzed growth in branches and shoots at three hierarchical levels of study (Figure 3.1): tree, branch, and shoot. At tree level, we compared trees with high and low acorn production. At branch level, we compared two branch types: reproductive branches vs. vegetative branches. At the shoot level, we compared three shoot types: Shoots with acorns (Sh_{RR} thereafter), shoots without acorns from reproductive branches (Sh_{VR} thereafter), and shoots from vegetative branches (Sh_{VV} shoots thereafter).

To test the effects of crop type, branch type and shoot type on vegetative growth, Mixed Lineal Models (also known as Hierarchical linear models) were performed so that we could test the effect of both fixed and random factors taking into account the hierarchical structure of the data (Shoots within Branches within Trees within Sites). We used two sets of model designs. The first one (which we will refer to as Branch models) tested the effect of branch type and crop type on the vegetative and reproductive growth of the branch. For the Branch models, dependent variables were total biomass, vegetative biomass, number and mass of shoots and leaves and leaf area of branches. Site (10 sites) and Tree (20 trees), nested within Site, were random factors. Crop type (high or low production) and branch type (reproductive or non reproductive branches) were fixed factors. In order to control for the effect of previous year growth on current year growth (Woollons & Norton 1990, Brienen *et al.* 2006), biomass of last year stem was introduced in the model as a covariate.

In the second set of models, we focused on the shoot level (referred to as Shoot models hereafter) and tested the effect of shoot type and crop type on the shoot growth variables.

We were not able to incorporate the shoot level into the previous hierarchical model because shoots with and without acorns could not be nested hierarchically into branches with and without acorns. Moreover, the type of measurements we made at the shoot level could not be made comparably to those conducted at the branch level. For the shoot models, dependent variables were length, diameter, volume and number of leaves of the largest shoot of the branch both without and with acorns (if present). Site, Tree, nested within Site, and Branch (10 branches per tree), nested within Tree, were random factors. Crop type and Shoot type (Sh_{RR}, Sh_{VR} and Sh_{VV} shoots) were fixed factors. Biomass of previous year stem was also considered as a covariate. For both sets of models, the variables were natural log or square-root transformed when necessary to meet the assumption of normality. The above mentioned analyses were performed with the SAS statistical software (SAS 9.1).

To examine direct and indirect relationships between previous year growth, current growth of reproductive and vegetative shoots, leaves and acorns, to eliminate spurious relationships and to construct a possible causal model among variables to be verified with the data, we conducted a path analysis (Wright 1921, Mitchell 1992). Path coefficients (standardized regression coefficients) quantify direct effects of an independent variable on a dependent one (Mitchell 1992). We assumed unidirectional relationships when the directionality was clear and otherwise used bidirectional relationships when cause and effect were not apparent. All the reproductive branches sampled have been included in the analysis (five branches per tree and 20 trees). Branches are nested within tree, providing each branch one observation. In our path model, growth of previous year, measured as the biomass of 2006 stem, was introduced as the exogenous variable (variable with no explicit causes). Biomasses of vegetative and reproductive shoots of the branch, vegetative leaves (those from vegetative shoots) and reproductive leaves (those from reproductive shoots), and acorns were introduced as endogenous variables (variables that participate in the model as dependent and/or independent), but leaves biomass, given its high correlation with shoots biomass, was dropped from the model to avoid collinearity. Our model takes into account that previous year biomass can directly affect biomass of reproductive and vegetative shoots, and that reproductive shoots may affect acorns biomass. Moreover, if resources are reallocated from vegetative to reproductive shoots in a branch, it would be indicated by negative paths between vegetative and reproductive shoots (Figure 3.2). Path analysis was performed with the Mplus statistical software (Mplus v. 5)

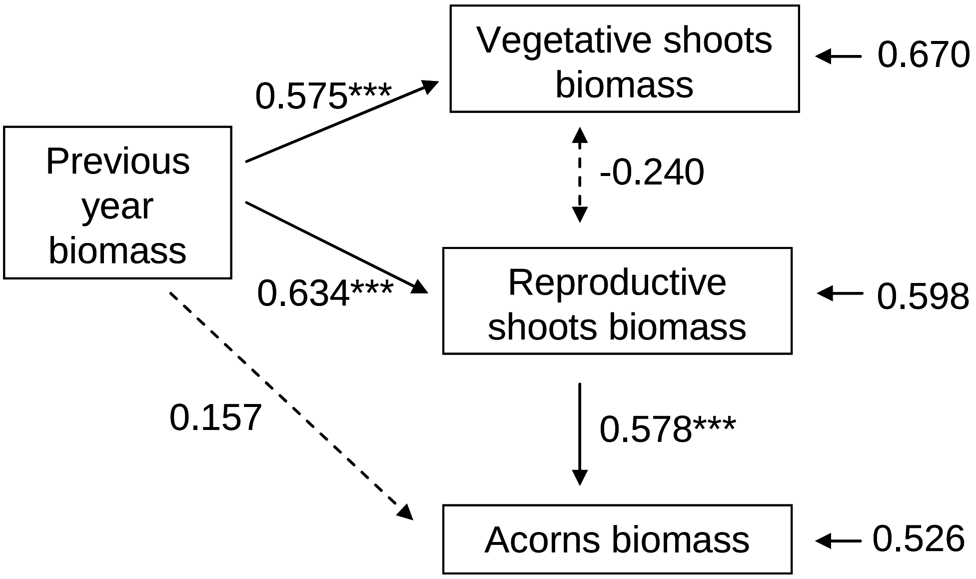

Figure 3.2. Path model showing the partial correlation coefficients between 2006 biomass of branches, 2007 biomass of vegetative shoots, 2007 biomass of reproductive shoots, and acorn biomass from reproductive branches (N=100). The estimate of r^2 for each endogenous variable is given. Variables are square root transformed to reach normality. Significance at $P < 0.05$ is indicated by *, for $P < 0.01$ by **, and $P < 0.001$ by ***.

RESULTS

For all growth parameters, the biomass of vegetative growth in 2006 significantly covaried with the dependent variables (Table 3.1a). In other words, for all the trees, their branch growth was positively correlated with how much the branch grew during the previous year. The model with total biomass showed no significant difference between type of tree, but it did show a dramatic difference between reproductive and non-reproductive branches, and leaf biomass showed a modest, but significant effect as well (Table 3.1a). During this mast year, reproductive branches produced more total biomass than vegetative branches (Figure 3.3). The main effects in these models did not show a consistently strong effect for the rest of growth variables. But, as seen in Figure 3.3 for vegetative branch biomass, the Mixed model results for all growth variables showed a highly significant interaction between crop type and branch type (Table 3.1a). In the high crop trees, the vegetative biomass did not differ between branches with and without acorns, but in low producing trees, the reproductive branches had lower vegetative biomass than the branches without acorns (Figure 3.3). Consistently across all growth variables, the branches with acorns on small crop trees always had adjusted mean values that are significantly less than the other tree types of branch (Table 3.1b). This result provides support for a trade-off between vegetative branch growth and acorn production exclusively for low crop trees.

Table 3.1a. F values of six growth variables measured at the level of a branch for separate Mixed Lineal Models, testing the effects of Branch type (BT: Reproductive versus Non-reproductive), Crop type (CT: high versus low acorn production), including their interactions, and biomass of 2006 as a covariate (N=200).

Effects	df	Total Biomass[1]	Vegetative biomass[2]	Shoots biomass[2]	Leaf biomass[2]	Number of shoots[1]	Number of leaves[1]
Branch type (BT)	1	391.50***	1.02	4.83	4.34*	0.02	0.79
Crop type (CT)	1	3.33	1.09	0.18	1.19	6.80*	7.34*
BT x CT	1	24.11***	10.57**	10.89**	8.24**	7.30**	10.94**
Biomass 2006	1	91.67***	174.18***	298.09***	104.63***	65.04***	94.61***

* $P < 0.05$, ** $P < 0.01$, ***$P < 0.001$

Table 3.1b. Adjusted means of the six growth variables per crop type and branch type.

Effects	n	Total Biomass[1]	Vegetative biomass[2]	Shoots biomass[2]	Leaf biomass[2]	Number of shoots[1]	Number of leaves[1]
High crop, Non-reproductive branch	50	1.64±0.12	2.44±0.14	1.10±0.07	2.16±0.13	1.63±0.08	3.43±0.10
High crop, reproductive branch	50	3.25±0.12	2.60±0.14	1.32±0.07	2.21±0.13	1.81±0.08	3.61±0.10
Low crop, Non-reproductive branch	50	1.72±0.12	2.53±0.14	1.20±0.07	2.22±0.13	1.63±0.08	3.45±0.10
Low crop, reproductive branch	50	2.69±0.12	2.22±0.14	1.16±0.07	1.89±0.13	1.42±0.09	3.13±0.10

[1] ln transformed, [2] Square root transformed

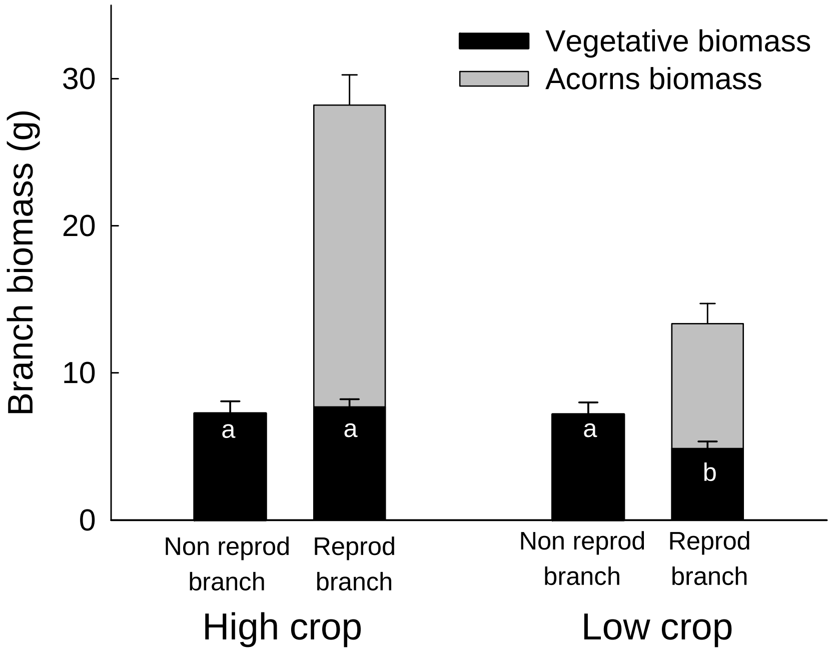

Figure 3.3. Mean total biomass (g) (and SE) produced in 2007 by reproductive and non reproductive branches in high and low acorn production trees (N=200). Total biomass is partitioned into vegetative (in black) and acorns biomass (in gray). Vegetative biomasses with same letters are not significantly different based on a *posteriori* tests of means at at P < 0.05.

When we examine the data at the shoot level, we observe a very different pattern, although these results also suggest costs of reproduction. We did not find significant differences in mean shoot size between small and large crop trees for the four shoot variables (Table 3.2). However, we found significant differences among shoot types (Table 3.2). The cause of these differences is that, first, shoots on vegetative branches were the longest and showed the higher number of leaves (Figure 3.4a,b), and second, shoots with acorns on reproductive branches showed higher diameter and volume than shoots without acorns or shoots on vegetative branches (Figure 3.4c,d). Interestingly, shoots without acorns on reproductive branches showed the lowest values for all the growth measures. Thus, the shoots that were close to shoots with acorns showed reduced growth, suggesting a local vegetative cost of the adjacent reproduction.

Table 3.2. Results for differences among four growth variables measured on shoots with acorns, shoots without acorns from reproductive branches and shoots from vegetative branches (Shoot type) in high and low acorn production trees (Crop type), for four separate Mixed Lineal Models, including biomass of 2006 as a covariate (N=300).

Effects	df	Length[1]	Diameter[1]	Volume[1]	Number of leaves[1]
Shoot type (ST)	2	13.39***	120.85***	43.76***	18.21***
Crop type (CT)	1	3.65	3.20	0.81	2.61
ST x CT	2	1.36	2.46	0.36	1.19
Biomass 2006	1	1.16	0.21	0.29	0.33

* $P < 0.05$, ** $P < 0.01$, ***$P < 0.001$, [1] Square root transformed

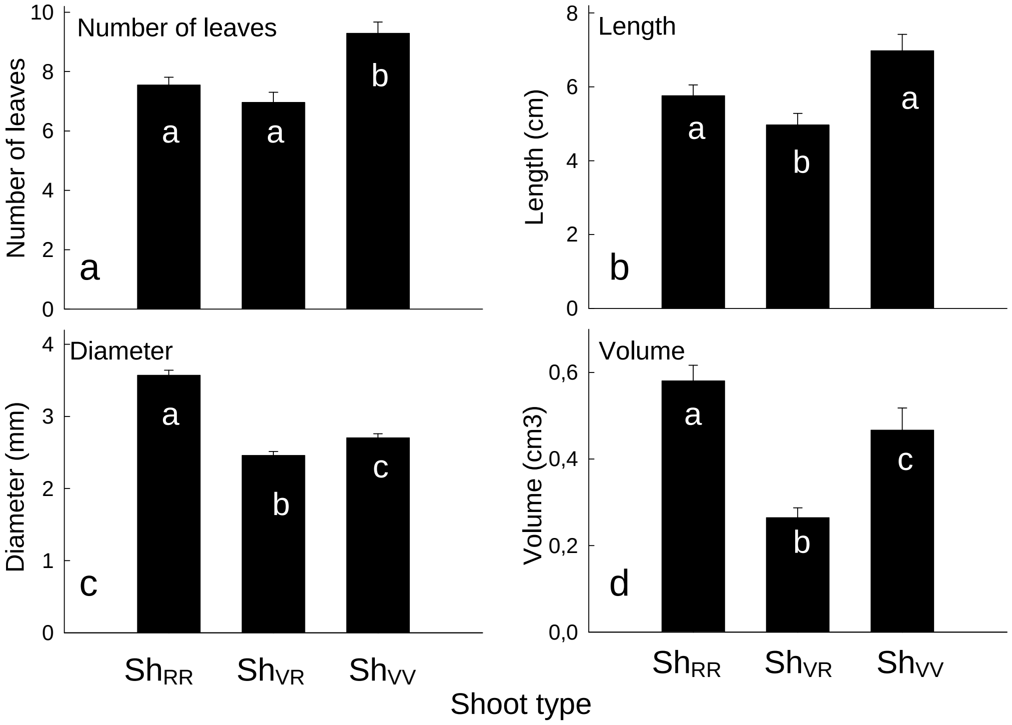

Figure 3.4. Mean (and SE) of number of leaves, length, diameter and volume of Sh_{RR} (Shoot with acorns from reproductive branches), Sh_{VR} (Shoot without acorns from reproductive branches) and Sh_{VV} (Shoots from vegetative branches) (N=300). Bars with same letters are not significantly different based on a *posteriori* tests of means at at $P < 0.05$.

To view the relationships among the vegetative growth and reproduction, we used a path model (Figure 3.2). The model explained 53% of the variation in acorn production. Previous year biomass had a strong positive effect on both reproductive and vegetative shoot biomass, as expected, and only a slight direct effect on acorns (Figure 3.2). However, acorn biomass is highly enhanced by reproductive shoots biomass, and indirectly by previous year biomass through its effect on reproductive shoots biomass. The slightly negative trend between the biomass of vegetative versus reproduction shoots ($p < 0.10$), suggest the existence of a cost of reproduction within branches that is consistent with the reduction in biomass shown by Sh_{VR} (shoots without acorns from reproductive branches) in the Mixed Model. Thus, the path model patterns indicate that the proximate mechanism for producing large acorn crops is to produce large numbers of reproductive shoots, and, overall, this increased production of many reproductive shoots comes at only a marginal cost to vegetative shoots.

DISCUSSION

This study provides three valuable insights about the trade-offs between growth and reproduction during a mast seeding year of *Quercus lobata*: (1) *hierarchy counts*: presence of costs differ at the different canopy levels (tree canopy, branch and shoot); (2) *costs of reproduction are not universal in a population*: costs may vary among trees with high vs. low seed production; (3) a strong *cue synchronizes tree reproduction* : in a mast year, trees increase seed production regardless of the growth costs involved.

At what hierarchical level do costs of reproduction occur? Our comparison of biomass allocation associated with growth and reproduction indicated different patterns for branch versus shoot level analysis. At the branch level, branches with acorns showed a reduction in allocation to vegetative growth only within low crop trees. Thus, it appears that the branch is an important level to observe trade-offs. Conversely, at the shoot level, no differences were noticeable between high and low crop trees, yet we did observe a difference in size between shoots with and without acorns in the two types of trees: shoots with acorns are not the longest but the biggest in diameter and volume. This difference in size may be a physiological constraint because thicker stems or larger volume might facilitate transport of resources (Zimmermann 1983) resulting in the presence of acorns on the bigger shoots. An alternative explanation is that shoots with acorns are bigger because they are sinks of resources from adjacent shoots or branches (Wardlaw 1990, Newell 1991, Obeso 2004a). We can distinguish between these two hypotheses by looking at the rankings of diameters and volumes across types of shoot. We found: *Shoots with acorns* > *Shoots from vegetative branches* > *Shoots without acorns from reproductive branches*. For the first hypotheses, we should not see any difference in size between shoots from vegetative branches and shoots without acorns on reproductive branches. The finding that shoots without acorns from reproductive branches are much smaller than shoots on vegetative branch provides evidence that shoots with acorns steal resources from their adjacent shoots without acorns (Hasegawa *et al.* 2003). Acorns seem to have high sink strength (Wardlaw 1990, Obeso 2002). Thus, allocation of resources to different kinds of shoots is likely to be the outcome of source/sink processes within branches.

Combining results derived from branch and shoot models, we verify that costs of reproduction differ at different hierarchical levels. At the shoot level, we see trade-offs between growth and reproduction in all type of trees. At the branch level, we see those trade-offs only for trees with limited resources, which in our study were the low acorn production trees. The fact that some studies do not observe trade-offs across years of high and low seed production on secondary growth (Knops *et al.* 2007) may be due to the fact that the impact of seed production is not experienced strongly at the scale of the whole tree. Moreover, secondary growth in Mediterranean-type oaks exhibits a wider temporal window than tree reproduction: growth can well occur before acorn development begins, and even after acorn dispersal (Chapter 2). Our study supports the suggestions of others that the costs of reproduction are more likely to be detected at lower levels (Lovett Doust & Lovett Doust 1988, Obeso 1997).

Why aren't the costs of reproduction universal? We found differential evidence for the costs of reproduction at branch level in high versus low acorn production trees. The lack of trade-off in high crop trees could be explained by a wealth of resources (Reznick *et al.* 2000, Sgro & Hoffmann 2004), either by current photosynthesis (Newell 1991, Hasegawa *et al.* 2003, Ichie *et al.* 2005) or/and stored resources (Newell 1991, Miyazaki *et al.* 2002, Yasumura 2006). Indeed, our study showed that a major determinant of current growth and acorn production is branch biomass from the previous year (Figure 3.2), what we interpret as an indicator of tree resource availability. The relationship between last year's and this year's growth has been shown by others (Woollons & Norton 1990, Fox *et al.* 2001, Brienen *et al.* 2006). The high acorn production trees apparently had sufficient growth during the prior year, so they could allocate resources to both growth and acorn production. What we cannot determine is whether they grow well because they are in good locations for growth, because they are in the stage of their life span for optimal growth (Bullock *et al.* 2004, Vieira *et al.* 2009), and/or they are genetically good seed producing trees (Reznick *et al.* 2000). On the contrary, low acorn production trees do show costs of reproduction in terms of local vegetative growth (Figure 3.3). Given the energy one would expect to be required for the maturation of acorns, we had anticipated that at the local scale allocation of resources to the developing acorns would involve a depletion of resources for growth in a mast year if resources are limiting. The finding that the costs of reproduction were not uniform across trees points to the importance of resource accumulation during the intervening years, but it also indicates that resource accumulation alone is not the causal mechanism.

Why do trees produce seeds at a cost for vegetative growth? All the trees produced acorns in spite of a cost to vegetative growth of shoots, and low trees showed even reduced growth in branches with acorns. This, added to the fact that the trees did not produce any single acorn in the last 4 years, suggest the existence of a strong cue for synchronicity that induce all trees to increase their seed production (Kelly & Sork 2002) regardless of the resource level of each individual tree and the cost for vegetative growth. The only thing we can infer about this cue is that resource levels alone are unlikely to be the primary triggering mechanism.

Implications for Masting Theories

The critical questions for the evolution of masting in tree populations are: How do trees produce large crops in some years and not others? And, how do they do so synchronously? Our work focuses on the first question, which requires an understanding of how resources are allocated to produce such annual fluctuations. Among the alternative scenarios defined by previous works for explaining the relationship between resource allocation and the production of large crops we discard the resource matching hypothesis (Kelly 1994, Kelly & Sork 2002) and the resource accumulation hypothesis (Sork *et al.* 1993) because trees produced acorns even at a cost to growth, especially low crop trees. However, we cannot dismiss certain role of resource accumulation since the last acorn crop year because there was a correlation between trees with lots of growth also showing greater ability to produce large acorn crops. Our findings support partially the switching hypothesis, because costs of reproduction are happening, not at tree level but at branch or shoot level. All trees showed a cost of reproduction in shoot growth when acorns were present, and the low acorn crop trees showed reduced growth in branches with acorns. However, the fact that even trees with low biomass production produced acorn acorns in this mast year suggests that all the trees must be responding to a cue that triggers synchronous production, regardless of the level of resources within an individual tree. Our single season data cannot address the depletion of resources because we would have to monitor future growth and acorn production to test it. However, under both scenarios (resource switching and accumulation), we might expect negative autocorrelation between a large acorn crop year and subsequent years because resources have been depleted, such as that reported in other studies (Sork *et al.* 1993, Kelly & Sork 2002, Buonaccorsi *et al.* 2003, Koenig *et al.* 2003, Liebhold *et al.* 2004, Knops *et al.* 2007).

In conclusion, we propose that trees are able to produce large acorn crops through trade-offs between reproductive or vegetative growth at the level of the branch or the shoot. Our data indicate that large acorn crops are not necessarily the result of matching seed production to current resource availability (e.g. Despland & Houle 1997, Snook *et al.* 2005), resource accumulation (e.g. Sork *et al.* 1993, Yasumura 2006), or trade-offs at the level of the whole tree (e.g. Eis *et al.* 1965, Koenig & Knops 1998, Monks & Kelly 2006). These findings demonstrate that some trees are able to produce large acorn crops with minimal cost to vegetative growth, while others definitely show trade-offs. Synchronized seed production must be triggered by a strong cue, resulting that trees with lots of resources are able to compensate for local costs of seed production, while trees with less resource availability show a higher cost of reproduction. This notion that the answer varies across trees adds a new consideration into the discussion of the mechanisms of masting.

ACKNOWLEDGEMENTS

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Capítulo 4

Extension of shoot growth in *Quercus ilex* during autumn: Are spring growth, phenology and reproductive effort causes or effects?

This chapter has been done in collaboration with J.M. Espelta.

ABSTRACT

- In Mediterranean-type climates, cold temperatures in winter and water stress in summer interrupt plant growth. Although plant growth takes place mainly during the spring, it has been widely observed that some woody species may resume and extend their growth during wet and mild autumns.

- Yet, even though the climatic drivers of autumn growth are roughly known, the individual (plant) characteristics that may determine the likelihood of this process have seldom been explored. The fact that this new growth event occurs after a previous period of growth (spring), and after seed production, could make it more variable among individuals, depending on their phenology, previous growth and reproductive effort.

- The main aims of this study were to explore, for two consecutive years (2007-2008), whether differences in phenology, spring growth and reproduction effort among *Q. ilex* trees could determine the occurrence and amount of autumn growth, and the consequences of this second growth effort for following-year phenology, growth and reproductive patterns. This was investigated at two hierarchical levels (tree and branches).

- All sampled individuals and branches experienced spring-shoot growth in 2007. A second bud break occurred in late summer 2007, following a precipitation event, but this was restricted to half of the sampled trees and not all branches. The trees with a higher mean spring-shoot biomass had a lower abundance of autumn shoots

in the canopy, which suggests that autumn growth might partially compensate low spring growth. Reproductive effort was positively related to autumn shoot biomass, indicating that there is no competition between autumn growth and seed production.

- The branch seems to be an important location for looking at resource allocation in autumn: The branches with autumn growth invested more resources in growth during the whole year (spring + autumn) than the branches without autumn growth. Moreover, autumn shoot growth was positively determined by the previous spring growth.

- An abundance of autumn-growth shoots had no significant effect on vegetative and reproductive growth of trees for the following year but trees with higher autumn-shoot growth had a more advanced growth phenology. This effect might intensify in a climate change scenario, if the magnitude of autumn growth increase due to the lengthening of the growing season.

INTRODUCTION

Trees cannot grow continuously in most type of climates. Except for the equatorial/tropical rainforest type, all other climates present at least one period or season which is favourable to growth and at least another one which is unfavourable, depending for the most part on the magnitude of precipitation and temperatures (Walter & Box 1976). In these seasonal climates, growth onset and extension is primarily driven by photoperiod and temperature (Partanen *et al*. 1998, Chuine & Cour 1999, Menzel & Fabian 1999, Borchert & Rivera 2001, Jolly *et al*. 2005), rainfall (Wielgolaski 2001, Peñuelas *et al*. 2004) and soil conditions (Wielgolaski 2001).

The Mediterranean-type climate is a temperate climate characterized by hot-dry summers and cool, mostly wet winters (Aschmann 1973). Water limitation is the largest constraint for plant growth and reproduction but so is cold temperature in winter (Terradas & Save 1992). This is known as "the double stress limitation" (*sensu*, Mitrakos 1980): tree growth is usually interrupted during winter because of low temperatures (Nilsson & Walfridsson 1995, Palacio & Montserrat-Martí 2006) and in summer because of water scarcity (Borchert 1994, de Fay *et al*. 2000). Secondary growth, bud break and the main growth of stems and leaves occur mainly in spring, when temperatures are mild and precipitations abundant (Di Castri & Mooney 1973). Bud break is followed by stem and leaf expansion and by the formation of new buds that will usually remain dormant until the following spring. This process involves such a high mobilization of resources and depletion of previous reserves that in most Mediterranean woody species growth is restricted to spring, when photosynthetic production is maximum (Montserrat-Martí *et al*. 2008). However, in the Mediterranean-type climate the occurrence of both secondary and primary growth in autumn may take place if precipitations occur when temperatures are still not too low (Chapter 2). This provides plants with the chance to resume their growth interrupted by summer drought. For example, a fraction of secondary growth of *Quercus ilex* and *Q. humilis* may take place in autumn after the summer pause (Chapter 2). Similarly, shoot growth, although beginning in spring and stopping during summer, can also be extended to autumn months (De Lillis & Fontanella 1992). Moreover, certain species can even initiate the development of their stems in autumn, moving forward with regard to the following spring (Montserrat-Martí *et al*. 2008), and thus present more than one period of bud break and growth over the same year (Collet *et al*. 1997, Ogaya & Peñuelas 2004, Negi 2006).

As a consequence of climate change, atmospheric models forecast that during the current century the Mediterranean Basin will see an increase in temperatures of 2.2 to 5.1ºC, the occurrence of severe summer drought episodes and an increase in rainfall seasonality (including the higher autumn precipitations) (IPCC 2007). The worsening of growth conditions during summer, and their improvement during autumn, may encourage changes in growth patterns, including a more severe recess in summer but a more intense resumption of growth during autumn months. Indeed, in recent decades, an extension of the growing season has been observed from several days to even a month in Mediterranean plant communities (Peñuelas & Filella 2001) because warmer temperatures have entailed an extension of the favourable season for growth, by advancing the beginning of growth in spring and extending growth in autumn (Menzel & Fabian 1999, Peñuelas *et al*. 2002). Changes in the phenology and extension of the growth season may have important consequences. From a functional point of view, the possibility of growth both before and after seed dispersal may relax the occurrence of trade-offs between these two processes (Milla *et al*. 2006, see also Chapter 2). In light of ecological processes, this new scenario may encourage the persistence and expansion of species that are able to adapt to longer growth seasons compared with those with no phenological plasticity (Bradley *et al*. 1999, Pop *et al*. 2000, Morin *et al*. 2009). Moreover, phenological changes in some species but not in others may decouple species interactions (Peñuelas & Filella 2001).

Although autumn growth in Mediterranean plants has been widely reported (Molinas *et al.* 1989, Castro-Díez & Montserrat-Martí 1998; De Lillis & Fontanella 1992; Ogaya & Peñuelas 2004, García-Mozo *et al.* 2007) and it may have an extraordinary importance in recently predicted climatic scenarios, this phenomenon has seldom been explored. Multiple events of bud break during the same growth season may depend not only on weather conditions but also on individual factors related to resource availability. Indeed, the second bud break occurring in late summer or early autumn takes place after a previous period of growth (spring) and probably during or after seed production. Thus, it could be hypothesised that autumn growth could be more variable than spring growth among individuals, depending on their phenology, previous growth or seed crop size (Quiring & McKinnon 1999). However, in Chapter 3 we showed that trade-offs on resource allocation occur on lower modular levels (branches) rather than at the individual (tree) level. Thus, we also wondered whether autumn growth could occur more frequently in certain branches than in others and if it is more dependent on previous branch growth than on overall tree growth.

The main aim of this study has been to explore which individual (tree and branch) factors can influence the occurrence of a second bud break after summer and the extent of autumn growth, and to determine the consequences of autumn growth for the the following growth seasons. For this purpose we have selected a sample of *Quercus ilex* L. oaks, a Mediterranean evergreen oak that usually flushes its new shoots and leaves in spring (Castro-Díez & Montserrat-Martí 1998), although it may present a second bud break episode later, in late summer/early autumn (Ogaya & Peñuelas 2004). Our first objective has been to explore which trees and branches present a second bud break. We have considered a couple of possibilities, either related with resource availability or with phenology: (i) Differences in autumn bud break among trees are a matter of differences in resource availability. This is based on the supposition that some trees can achieve a higher quantity of resources (Reznick *et al.* 2000) and thus perform well in terms of spring growth, reproductive growth (Chapter 3) and autumn growth. (ii) Differences in autumn bud break could respond on the other hand to differences in the phenology of trees. Trees with more advanced phenology will have time to finish their growth earlier in spring, to create new buds and to produce a second bud break in autumn if environmental conditions are favourable. Our second question explores the consequences that this second bud break may involve for future growth, reproduction or phenology. Autumn growth requires an investment in resources that, together with the previous investment in reproduction and radial growth, may cause a depletion of resources for growth or reproduction the following year.

Thus, our main objective is (i) to quantify second bud break and growth in a population of *Q. ilex*, (ii) to determine the effect of previous vegetative growth, reproductive effort and phenology on the presence, abundance and magnitude of autumn growth, both at the tree and branch level, and (iii) to establish the possible consequences of autumn growth and growth on subsequent vegetative growth, reproductive effort and phenology. To achieve these objectives, we measured branch and radial (trunk) growth, phenology, and acorn production in a population of Q. ilex during 2007 and 2008.

MATERIAL AND METHODS

Species and study site

The Mediterranean evergreen holm oak (*Q. ilex*) is a slow-growing tree that begins shoot and leaf expansion in approximately April and its shoot growth lasts until June (Castro-Díez & Montserrat-Martí 1998). However, sporadic additional growth events may well take place in autumn (Castro-Díez & Montserrat-Martí 1998, Ogaya & Peñuelas 2004). Female flowers emerge about one month later than leaves, and acorns develop over the summer, being dispersed from October to December (Castro-Díez & Montserrat-Martí 1998, Espelta *et al*. 2009a).

This study was conducted in Collserola Natural Park (41º 24’ N, 2º 06’ E, 200 to 500 m asl), a Mediterranean massif close to the coast, covered by mixed oak and pine forests with *Q. ilex* being the most abundant species: the park covers 8.5 km^2, of which *Q. ilex* is present in 95% of the forested area. The climate is Mediterranean, with severe summer droughts and mild winters. Precipitation is highly variable, and mainly concentrated in spring and autumn months. Soil is for the most part developed on slate with scattered granitic outcrops. The mean annual precipitation was 571±47 mm and mean monthly temperatures ranged between 12.3ºC and 19.7ºC over the last decade.

Sampling design

For the purposes of this study we used the same 15 *Q. ilex* trees monitored in Chapter 2 (see the design for the Inland site in the Material and Methods section, subsection B), taking advantage of the installation of trunk dendrometers from 2007 onwards. By "autumn growth", we refer to the primary growth occurring after the summer interruption and extending into the autumn season, independently of whether it actually started in the late-summer or in early-autumn season.

To find out whether growth, reproduction or phenological characteristics of trees influenced the occurrence of autumn growth in 2007, we measured the radial growth, mean growth of spring branches, reproductive effort and phenology of each individual in 2007. Furthermore, so as to also study the determinants of autumn growth at a lower hierarchical level than the individual level, we took growth measurements of branches with and without autumn shoots (when possible) in all trees.

We determined the abundance of autumn growth branches in each tree by selecting 30 random branches from the sun-exposed side of the mid-canopy and by counting how many of them showed autumn shoots. This quantification of autumn growth intensity was carried out in 2008, before spring bud break began, so as to easily distinguish between spring and autumn shoots grown in 2007.

Vegetative growth and reproductive effort measurement at the tree level

In order to verify whether the abundance and size of autumn growth shoots in a tree depended on its previous shoot growth in spring, in 2007 we measured the spring-shoot growth of every tree. The sampling was carried out in July 2007, after the spring extension of shoots and leaves had finished. We collected five three-year-old branches from the sun-exposed part of the canopy of every individual. The number of shoots and leaves per branch was counted and their dry weight measured.

Radial growth (trunk growth) was measured every fifteen days, by means of manual band dendrometers (Agriculture Electronics Corporation, Tucson, USA) installed in the trunk of every *Q. ilex* tree (see also Chapter 2, Material and Methods section, subsection B). We calculated "spring radial growth" as the growth accomplished before the occurrence of autumn bud break (from approximately March to August).

To link the reproductive effort made with autumn growth, we calculated an index of reproductive effort (RE) per tree, every fifteen days, based on the abundance of acorns and weight of mature acorns (for further details see Chapter 2). For the purposes of this study we selected the maximum value per tree in 2007 and 2008.

The phenology of bud break and shoot extension might also be a key factor affecting autumn growth. Thus, we registered the phenology of each tree every fifteen days, from February 2007 to December 2008. We considered 4 phenophases: (I) bud swell, (II) bud break, (III) stem and leaf extension, (IV) stem lignification. For each tree and date, we assigned a visual estimation of the percentage of the canopy in each of the four phenophases. At the end of the year, according to Montserrat-Martí (personal communication), we selected the date of the highest variability between trees and calculated a phenology index (PI) for this date (PI = 0.5 x I + II + 1.5 x III + 2 x IV). The coefficients applied to each phenophase aim to give higher weights to more advanced phenophases in order for trees with more advanced phenology to exhibit higher values of

PI. Moreover, we registered, for each tree, the dates when bud break, branch and radial growth and acorn development took place in 2007 and 2008.

Vegetative growth measurement at the branch level

In order to find out whether the occurrence and the magnitude of autumn-shoot growth in a branch depended on how much the branch grew during spring, we randomly collected 6 current-year branches with spring but not autumn shoots on all trees and up to 6 branches with both spring and autumn shoots on the trees where autumn growth was detected. In the first case, each branch included the shoot developed during spring 2007 and its leaves, and in the second case, the spring shoot and leaves plus the shoot and leaves developed in autumn 2007. To measure both spring and autumn-shoot growth, the branches were separated into these two fractions (spring and autumn shoots and leaves), and we measured the dry weight of each fraction and the length and diameter of the shoots. In order to ascertain whether annual shoot growth was greater in the branches growing in spring and autumn than those growing only in spring, we calculated the total annual shoot growth as the sum of the biomass of spring and autumn shoots (if any).

Climate variables

The occurrence of autumn growth might be closely related to precipitation events (see Chapter 2). To establish the potential link of precipitation events with the occurrence of autumn growth, we obtained daily precipitation data from the Fabra Observatory (41º 25' N, 2º 07' E, 415 m) for 2007 and 2008 and we calculated the accumulated precipitation on a biweekly basis, coinciding with the dates of collection of measurements of radial growth, phenology and reproductive effort.

Data analysis

We performed Pearson correlation analyses between all the measures of vegetative branch growth (shoot length, shoot diameter, shoot biomass, number of leaves and leaves biomass) separately for spring and autumn shoots. All of these measures proved to be highly correlated (data not shown). Shoot biomass was the one with the best correlation with all of the others (Pearson coefficient > 0.5 and highly significant). Thus, in order to avoid collinearity in the statistical analyses, we used only shoot biomass as the measure of branch growth. In the statistical analyses, biomass of spring or autumn shoots were ln(x) transformed, when necessary, to achieve normality.

Differences in autumn bud break were analyzed using a hierarchical approach: (i) between trees, and (ii) between branches on trees.

For the between-tree analyses, we analyzed how vegetative growth, reproductive effort and phenology in 2007 conditioned the occurrence of autumn growth. For this purpose we tested the effects of tree size (DBH), mean spring-shoot biomass, spring radial growth, maximum reproductive effort (RE) and phenology index (PI) on the proportion of branches of the canopy with autumn growth. We performed a Generalized Lineal Model with a Poisson error distribution and a log link function, where the dependent variable was the number of branches with autumn growth. We avoided over-dispersion in this model by using the variance as the scaling parameter. We made all possible models including from one to all of the independent variables and we selected the best-fitting model (the one with the lowest AIC value). Furthermore, on the 9 trees showing autumn growth, we explored whether branch growth, radial growth, reproductive effort or phenology could affect the magnitude of autumn-shoot growth. To do this, we performed a stepwise regression, where the mean autumn-shoot biomass per tree was the dependent variable and the branch shoot biomass, spring radial growth, RE and PI during 2007 were the independent variables.

For the between-branches analysis, in the trees that showed autumn growth, we compared the spring and total annual growth of the branches with autumn growth vs. branches without autumn growth. For this purpose we performed a General Lineal Mixed Model in order to see the effect of the occurrence of autumn growth (yes, no) on spring-shoot biomass and on the total-annual shoot biomass (spring + autumn biomass) of the up to 12 branches sampled per tree in 2008. The tree was introduced into the analysis as a random factor. In order to see how spring-shoot growth affected the magnitude of autumn-shoot growth, we performed a General Lineal Mixed Model with the branches showing autumn growth. In this analysis we used spring-shoot biomass as the independent variable, tree as a random factor and autumn-shoot biomass as the dependent variable.

The second main purpose of our study was to investigate the consequences of autumn growth on vegetative growth, reproductive effort and phenology during the the following year. First we checked the relationship between the previous year's and current year's spring radial growth (Woollons & Norton 1990, Brienen *et al.* 2006), phenology (Wesolowski & Rowinski 2006) and reproductive effort (Sork *et al.* 1993, Knops *et al.* 2007) by means of Pearson correlation analyses between spring radial growth, RE and PI of 2007 and 2008. We proved that each of them was positively autocorrelated between years, but that there was no significant correlation among the different variables in 2007 and 2008 (data not shown). After this, we tested the consequences of autumn growth on the following year's radial growth, RE and PI by means of stepwise regressions, where the independent variable was the proportion of branches with autumn growth, and previous year radial growth, RE, and PI respectively (to control their effect on the following year performance). On the 9 trees showing autumn growth, we also explored how the mean autumn-shoot biomass affected radial growth, RE and phenology, also by means of similar stepwise analyses.

RESULTS

All of the sampled branches of every tree experienced spring-shoot growth in 2007. Spring bud break began in mid-late April, within a period of 13 days of difference between early and late trees (from 13th to 26th April approx.) and all trees finished their shoot expansion by the end of May or beginning of June (Figure 4.1). A second bud break event occurred within a range of 15 days in late August 2007 (from 14th to 31st August), preceded by a precipitation event and the resumption of radial growth (see Figure 4.1). This second shoot growth (hereinafter, autumn growth) did not occur in all trees and branches. Only 9 out of the 15 trees monitored presented a perceptible abundance of autumn growth in their branches (at least 1 of the 30 sampled branches per tree). With respect to the abundance of autumn shoots, we found a high variability among trees: 70% of the branches of one tree presented autumn shoots, while the other eight trees ranged from 3 to 27%. In 2008, spring growth began later than in 2007, coinciding with the high precipitations in early May, and no autumn growth was detected in any tree. Interestingly scarce precipitations were registered in late summer of that year. Nonetheless, these scarce precipitations coincided with a resumption of radial growth (Figure 4.1).

Trees with a higher mean spring-shoot biomass in 2007 had a lower abundance of autumn shoots in the canopy (Chi square= 7.32, B=-12.6, p<0.01) (N=15) while DBH, radial growth, reproductive effort or phenology had no effects. However, in the trees that presented autumn growth, reproductive effort was positively related with the biomass of autumn shoots (Figure 4.2).

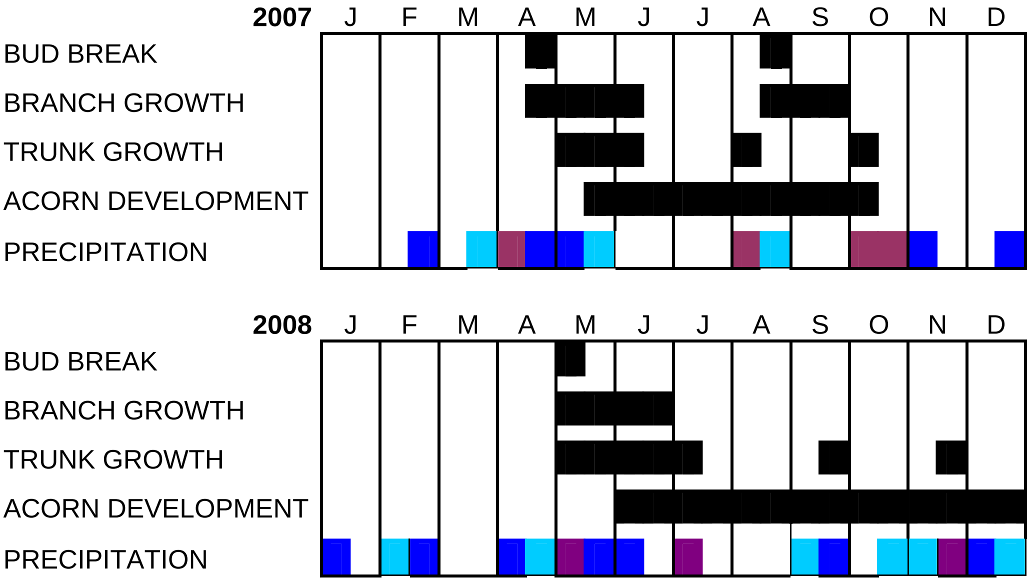

Figure 4.1. Diagram of the phenology of growth and acorn production in *Q. ilex* during 2007 and 2008. The colour black indicates the period when each process (bud break, branch growth, trunk growth or acorn development) took place. The amount of accumulated precipitation in each 15-day period is shown by means of different colours: White indicates under 10 mm; light blue: 10 to 19 mm; dark blue: 20 to 50 mm; and purple: over 50 mm.

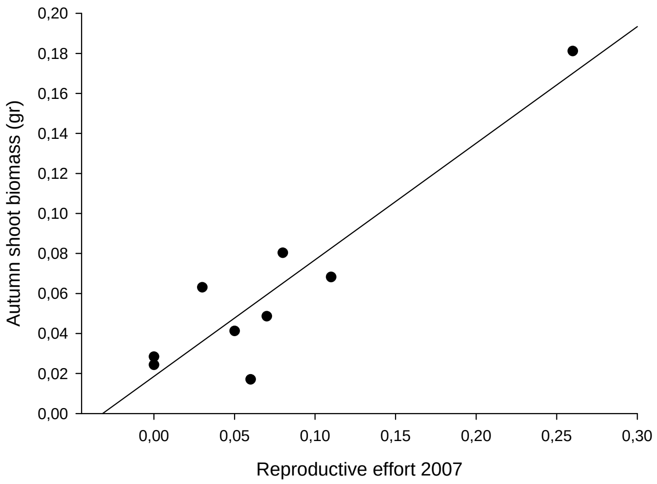

Figure 4.2. Relationship between the maximum reproductive effort in 2007 and the mean biomass of autumn shoots. The best linear fit line is highly significant (r^2= 0.84, p < 0.001). However, this relationship is highly determined by the tree with the greatest autumn-shoot biomass. N = 9.

In the 9 trees with autumn growth, branches bearing both spring and autumn shoots did not differ in spring-shoot biomass compared with the branches that did not experience autumn growth (F=1.67, p=0.200) (Figure 4.3). Yet the biomass invested over the whole vegetative season (spring + autumn) was higher for the branches having both spring and autumn growth than for the others (F=23.55, p<0.001) (Figure 4.3). Interestingly, spring and autumn shoot biomass were positively related: the more a branch grew in spring, the more it grew in autumn (F=12.43, B=0.55, p<0.001). The three analyses revealed a high variability among trees, as shown by the estimate of the parameter of covariance (0.12±0.08; 0.13±0.08 and 0.26±0.17 respectively).

The autumn growth did not have any significant effect either on spring radial growth or reproductive effort of trees in the following year, but trees with a higher amount of autumn-shoot biomass had a more advanced growth phenology (Figure 4.4). Moreover, we detected that, over the two years of study, trees were consistently early or late phenologically (r^2=0.47, B=0.69, p=0.005). The same occurred with regard to reproductive effort: 2007 and 2008 values were positively related (r^2=0.29, B=0.553, p=0.040).

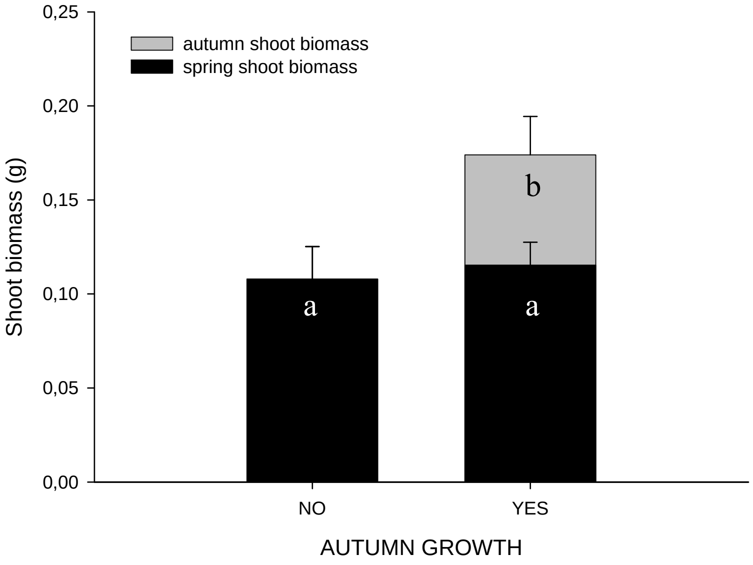

Figure 4.3. Mean annual biomass (g) (and SE) of shoots produced in 2007 by branches with and without autumn growth (N=102). Annual biomass is partitioned into spring (black column) and autumn biomass (grey column). Different letters indicate significant differences in the biomass of the different fractions (α=0.05).

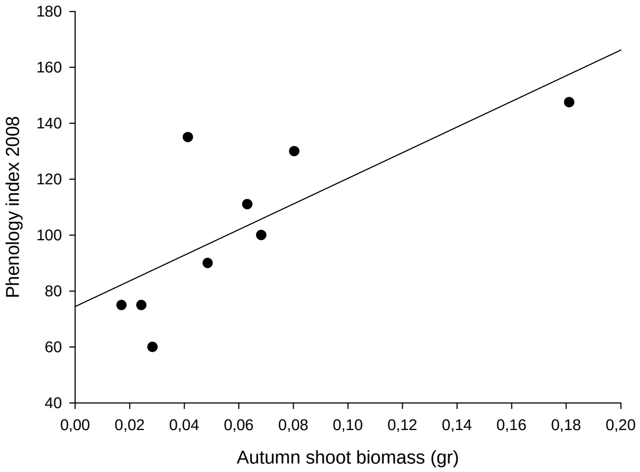

Figure 4.4. Relationship between the mean autumn growth biomass experienced in 2007 and the phenology index of the following year, based on the 9 trees that experienced autumn growth (r^2=0.65, p=0.009). However, this relationship is highly conditioned by the tree with the greatest autumn shoot biomass.

DISCUSSION

We have quantified autumn branch growth in *Q. ilex* trees for the first time: We have observed that autumn growth happens frequently, but (i) not in all years, (ii) not in all trees, and (iii) not in all branches. We propose an explanation to this within-years, within-trees and within-branches variability based on the potential linkage of autumn growth to precipitation events and on its relationship with spring growth at the tree and branch level, reproductive effort and phenology.

More than half of the sampled trees experienced autumn growth in 2007. However, we observed that in *Q. ilex* autumn growth occurred in 2007 but not in 2008. We propose that a combination of late phenology and unfavourable weather conditions may prevent a second bud break in *Q. ilex*, as happened in 2008. We have noticed that radial growth followed precipitation events very closely during both years even though those precipitation events were moderated (as in late September 2008). Nonetheless, bud break seemed to take place only after high precipitations (see also de Fay *et al.* 2000), as in early August 2007 (see Figure 4.1). One of these high precipitation events took place in early July 2008, but the buds were probably not mature enough to generate a new bud break due to a later phenology in that year compared to 2007 (presumably caused by a later spring precipitation). Although day length and temperature have been considered as the main drivers of bud break (Jolly *et al.* 2005, Cleland *et al.* 2007), the importance of precipitation has also been reported (de Fay *et al.* 2000, Wielgolaski 2001, Peñuelas *et al.* 2004). We suggest that the stressful drought conditions of Mediterranean climate make all growing events depend especially on precipitation (Terradas & Savé 1992). However, the fact that not all trees experienced autumn growth indicates that optimum weather conditions alone do not guarantee the occurrence of autumn growth unless other individual conditions are also favourable.

We hypothesised that either (i) good spring-growing trees or (ii) trees with more advanced phenology would be those that grew better in autumn. Neither of the two hypotheses explained the abundance of autumn growth shoots. Conversely to our predictions, autumn growth was not affected by tree phenology and it took place preferably in poor spring- rather than in good spring-growing trees. This result suggests that growing in autumn could partially compensate the low spring growth in poor- growing trees. This process could be somewhat similar to the overcompensation of shoot biomass observed in plants exposed to the damage caused by herbivory (McNaughton 1983). In those plants, tissue damage activates dormant lateral buds, allowing a new shoot growth event which can even exceed the quantity of lost biomass (Aarssen 1995, Gadd *et al.* 2001, Hawkes & Sullivan 2001, Thomson *et al.* 2003). In our case, we cannot determine what makes some buds preformed in late spring to become active in autumn. Indeed, a more accurate study of the resource and hormonal balance in those branches with low spring growth would be necessary.

When studying the process at a lower modular level (the level of branch, instead of the whole tree) we found that the branches with autumn growth invested more resources in total annual growth than the other branches (Figure 4.3). This could mean that autumn shoots act as a sink for resources coming from other locations of the canopy (Wardlaw 1990), or from stored reserves (Chapin *et al.* 1990) or that the branches with autumn shoots are those with more resource availability. This might be expressed in larger spring shoots. Although we could not detect differences in spring-shoot biomass among the branches with and without autumn growth, branches with autumn growth showed bigger diameters than the other branches (data not shown). This is especially noteworthy because large diameters are of paramount importance in the conduction of resources (Zimmermann 1983, Chapter 3) as they allow a higher influx of resources through them. If this is true, larger spring shoots should generate larger autumn shoots, as we certainly observed. A positive relationship between current and following-year growth has been previously shown in trees (Fox *et al*. 2001, Brienen *et al*. 2006, Chapter 3), and, according to our results, it also holds for spring and autumn growth events. All of these results suggest that the branch is the most relevant hierarchical level for studying resource availability and allocation in relation to autumn growth (see also Chapter 3). However, whether a branch carries out autumn growth due to higher resource availability or to other phenological or physiological causes is a matter we cannot totally settle with our data. To solve this accurately we should also investigate branch phenology, bud size and development (Montserrat-Martí *et al.* 2009) and branch position (Harmer *et al.* 1991).

We want to put a special emphasis on the fact that the reproductive effort of trees was positively related to their autumn-shoot growth, even when some trees presented up to 70% of their canopy bearing acorns by the time autumn-shoot elongation was performed (see Chapter 2). We have to treat this result carefully, because the statistical relationship between reproductive effort and autumn growth is highly conditioned by a single tree with the highest reproductive effort (which in time is the one with the highest autumn-shoot growth) (Figure 4.2). And yet, this result may indicate that trees can at the same time sustain the swelling of the acorns and the autumn branch growth. This contradicts the results of other works reporting a cost of reproduction for the vegetative growth of shoots in mast seeding trees (Newell 1991, Henriksson & Ruohomaki 2000). Nevertheless, it tallies with our previous results which showed that: (i) radial growth is possible during acorn development (Chapter 2, Montserrat-Martí 2009,) and (ii) the potential cost of reproduction may depend on the resource availability of trees (Chapter 3).

Autumn growth had no effect on the performance of trees in the following year, neither in radial growth nor in reproductive effort. Do these results mean that autumn growth has no importance? The only effect we detected was that autumn-shoot biomass was related to a more advanced phenology in the following year. We do not know to what extent this may be determined by the time when buds are formed, but an important difference may exist in the development of a bud formed either in spring or in autumn. The question of whether differences in the histology and physiology of autumn buds determine this advanced phenology deserves further research.

Our work was performed in the current climate conditions, yet we have reasons to believe that both the magnitude of autumn growth and its effects on the trees performance will increase in a climate change scenario (Myneni *et al.* 1997, Peñuelas *et al.* 2004, Cleland *et al.* 2007, Bronson *et al.* 2009). In summary, this study is a modest but pioneer insight into autumn branch growth in a Mediterranean tree, but above all it is a call to focus further efforts on elucidating all of the potential changes that climate change may cause on Mediterranean ecosystems.

AKNOWLEDGEMENTS

We thank E. Pérez, N. Reguant, R. Solé and J. Pujantell for their helpful field and laboratory assistance and the Can Balasc biological station for their collaboration. This research has been funded by the projects MCIIN (CGL2008-04847-C02-02), Consolider-Ingenio Montes (CSD2008-00040), and the Consorci del Parc de Collserola.

Capítulo 5

Increased drought reduces acorn production in Mediterranean *Quercus ilex* coppices: traditional low selective thinning mitigates this effect but only in the short-term

This chapter has been done in collaboration with J.M. Espelta.

ABSTRACT

- Mediterranean areas are one of the most vulnerable biomes to global climate change, because they represent a transition zone between arid and humid regions. In the Mediterranean Basin, general circulation atmospheric models forecast an increase in temperature and an overall decline in precipitation in the next few decades. In order to explore the effects of climate change on Mediterranean forests and to mitigate its consequences, it is necessary to determine species-specific responses to increased drought and to identify appropriate forestry practices to maintain the resilience of forest ecosystems. Many experimental and modelling studies explore physiological and functional effects of drought in Mediterranean forests, and yet demographic consequences are seldom analyzed. In particular, few studies consider the effects on reproductive traits, even though seed production is the first step required for the maintenance of plant populations.

- The main aim of this study was to experimentally assess, over a 4-year period (2005-2008), the effects of increased drought, mediated by a 15% reduction in annual rainfall, on the reproductive attributes of *Quercus ilex* L. and, to assess whether traditional low selective thinning (selection of one to a few stems per stump) could mitigate the consequences of increased drought in oak coppices.

- Soil moisture was higher in thinned-plots and lower in increased-drought plots, although as expected under a Mediterranean-type climate, yearly values and the effects of experimental factors showed a high inter-annual variability. Increased drought reduced the number of reproductive trees, mean number of female flowers

produced, and acorn crop size, although most of these effects appeared only in the last two years of the experiment. In a different way, selective thinning enhanced all reproductive attributes, but its main effects were transient and covered only one or two years after the experiment onset (2005, 2006).

- In comparison to previous studies that showed no effects of increased drought in mortality or growth in *Q. ilex* coppices, our results indicate that a moderate reduction in rainfall (15%) reduces the reproductive ability of *Q. ilex*. This may have long-term negative consequences for recruitment as well as for the fauna feeding on acorns.

- Traditional low selective thinning enhances reproduction ability and it may mitigate the consequences of increased drought, but it has a remarkably short-term effect. This highlights the need to re-examine traditional forestry practices as potential adaptive strategies for coping with climate change in Mediterranean forest.

INTRODUCTION

Climate change means new challenges for forest conservation (Chapin *et al*. 2001). Over the last century, temperatures in the Mediterranean Basin already showed an overall trend towards warming, while precipitation showed a remarkable decrease, thus leading to increased evapotranspiration (Piñol *et al*. 1998, De Luis *et al*. 2001). As a consequence of climate change, atmospheric models forecast for the Mediterranean Basin during the current century, a general rise in mean temperature of between 2.2 to 5.1ºC and a potential decline of 4-27% of rainfall with increasing frequency and severity of drought episodes (Douville *et al*. 2002, Wang 2005, IPCC 2007). Since summer drought is already one of the main factors limiting plant distribution and growth in Mediterranean-type climates (Mooney 1983, Terradas & Save 1992), if climatic conditions become even drier, Mediterranean ecosystems will be particularly affected. Whether forests will be able to adapt to such conditions is a matter of concern (Scarascia-Mugnozza *et al*. 2000, Sabaté *et al.* 2002). However, many authors have highlighted the priority of identifying appropriate management procedures in order to maintain or enhance the resilience of forest ecosystems to the projected impacts of climate change (Lindner 2000, Resco *et al*. 2007, Cotillas *et al*. 2009).

The negative consequences of increasing drought for Mediterranean-type forests have been thoroughly documented with regard to several aspects of their structure and dynamics: e.g. recurrence of tree mortality episodes (Martínez-Vilalta & Piñol 2002, Lloret *et al*. 2004), and reduction of primary and secondary growth (Corcuera *et al.* 2004b, a, Cotillas *et al*. 2009). In comparison, its potential effects on tree reproduction have been much less explored. A shortage in water availability may constrain seed production, by reducing flowering (Ogaya & Peñuelas 2007a) and/or increasing seed abortion (Ogaya & Peñuelas 2007a, Espelta *et al.* 2008). Drought may affect not only the magnitude of the final seed crop size produced, but many other parameters related with reproduction as well, such as: (i) delaying the reproductive onset of trees (Moya *et al*. 2008), (ii) altering the phenology of seed production (Peñuelas *et al.* 2002) (3), decreasing seed size (Long & Jones 1996), and iv) increasing interannual variability in seed crop size (Kelly & Sork, Espelta *et al*. 2008). These changes may trigger negative effects on tree recruitment either reducing seed supply (Espelta *et al*. 2008, Espelta *et al*. 2009b) or limiting seedling establishment (Lloret *et al*. 2004).

The evergreen *Quercus ilex* L. (holm oak) is one of the most widespread tree species in the Mediterranean Basin, present over a large area extending 6000 km x 1500 km, from Portugal to Syria and from Morocco and Algeria to France (Quezel & Medail 2003). Due to a long history of repeated disturbances (e.g. wildfires, clear-cutting, livestock grazing) most Mediterranean *Q. ilex* forests are “coppices” characterised by high-density stands of multi-stemmed stumps with slow growth rates (Terradas 1999). Difficulties in the sexual regeneration of Mediterranean oak coppices have been thoroughly documented (Espelta *et al*. 1995, Gracia *et al*. 2001, Cañellas *et al*. 2004), and this has been envisaged as a potential constraint for their long-term maintenance (Ducrey & Toth 1992, Retana *et al*. 1999). This situation may become even worse if increasing drought conditions tend to decrease acorn production. Traditionally, in order to ameliorate the structure of oak coppices, their mid-term gradual conversion into “stored coppices” (i.e. coppices in which only one or two stems are left per stump) and in the long term to "high forests" has been suggested, through the selective thinning of the weakest resprouts (Serrada *et al*. 1996). Reduction in stand density may increase the availability of resources such as water and nutrients for the remaining stems by reducing competition (Cañellas *et al*. 2004, Moreno *et al*. 2007) and thus result in an increase in tree growth and survival (Retana *et al*. 1992, Espelta *et al*. 2003, Rodríguez-Calcerrada *et al*. 2008).

Despite the importance of seed supply for long-term maintenance of plant populations, the consequences of increased drought on the reproductive patterns of holm oak forests have seldom been explored (however see Ogaya & Peñuelas 2007a). Moreover, whether or not traditional selective thinning might be able to mitigate these potential negative effects remains elusive. Therefore, the main aims of this study have been: (i) to analyze the effect of increased drought on several reproductive traits of *Q. ilex* (onset of reproduction, flowering intensity, seed crop size, size of acorns) and (ii) to assess whether traditional forest management (low selective thinning) conducted in these oak coppices can reduce the potential negative effects of increased drought. Furthermore, we wonder whether the effects of drought and thinning may vary with time, as very few experiments study their influence at mid-term (Hanson *et al.* 2001; Ogaya *et al.* 2003). To achieve these objectives, we performed an experiment during 4 consecutive years (from 2005 to 2008) in a *Q. ilex* coppice, where we factorially combined two experimental treatments: drought (increased vs. natural drought) and thinning (thinning vs. no thinning). We expect the results obtained may improve our knowledge about the reproductive response of Mediterranean oaks to rainfall decline, as well as help us to develop management guidelines for forest conservation in light of climate change.

MATERIAL AND METHODS

Study site and species

This study was conducted in the region of Bages, Catalonia, NE of Spain (41º 44'N, 1º39'E) from January 2005 to November 2008. Mean elevation in the study area is 800 m asl, with 10% of slope and facing south. According to the data provided by the nearest Meteorological Station (8 km) the mean annual temperature is 12ºC and mean precipitation is 600 ± 135 mm, characterized by an irregular seasonal distribution and a high year-to-year variability. Climate in the area is dry-subhumid Mediterranean according to the

Thornwaite index. The geological substrate is predominantly calcareous and soil has a mean depth c.a. 25-50 cm with a high surface rockiness. Forest structure corresponds to a 7-year-old oak coppice with multi-stemmed oak stumps regenerated by resprouting after a large wildfire in 1998 (Espelta *et al*. 2002). *Quercus ilex* is the dominant tree species accompanied by the winter-deciduous *Q. cerrioides* and some scattered pines (*Pinus halepensis*). *Q. ilex* is a Mediterranean evergreen oak that flowers from April to May, and matures acorns during the summer, being dispersed from September to December of the same year (Espelta *et al*. 2009a).

Experimental design and sampling protocol

In order to test for the effects of drought and thinning on the reproductive patterns of *Q. ilex* trees, two levels of drought (natural drought vs. increased drought) and thinning (thinning vs. no thinning) were factorially combined in four treatments with three replicates (plots). The 12 plots (circa 15m x 20m) were randomly distributed in the sampling area (10.8 ha) with at least a 10- m buffer surrounding each plot. Increased drought simulation was done through the installation of parallel drainage channels suspended at ca. 50 cm above the soil and covering 15% of the ground surface on the selected plots (Figure 5.1, for further details see Cotillas *et al*. 2009). This device intercepted around 15% of rainfall, which, according to the IPCC (2007), is a reasonable predicted decline in precipitation for the western rim of the Mediterranean Basin in the near future (Borghetti *et al.* 1998; Ogaya & Peñuelas 2004). Selective low-thinning was applied following the traditional criteria applied in young Mediterranean oak coppices (Retana *et al*. 1992, Espelta *et al*. 1999): i.e. a reduction in 20-30% of total stump basal area per plot by leaving from one to three dominant stems per stump.

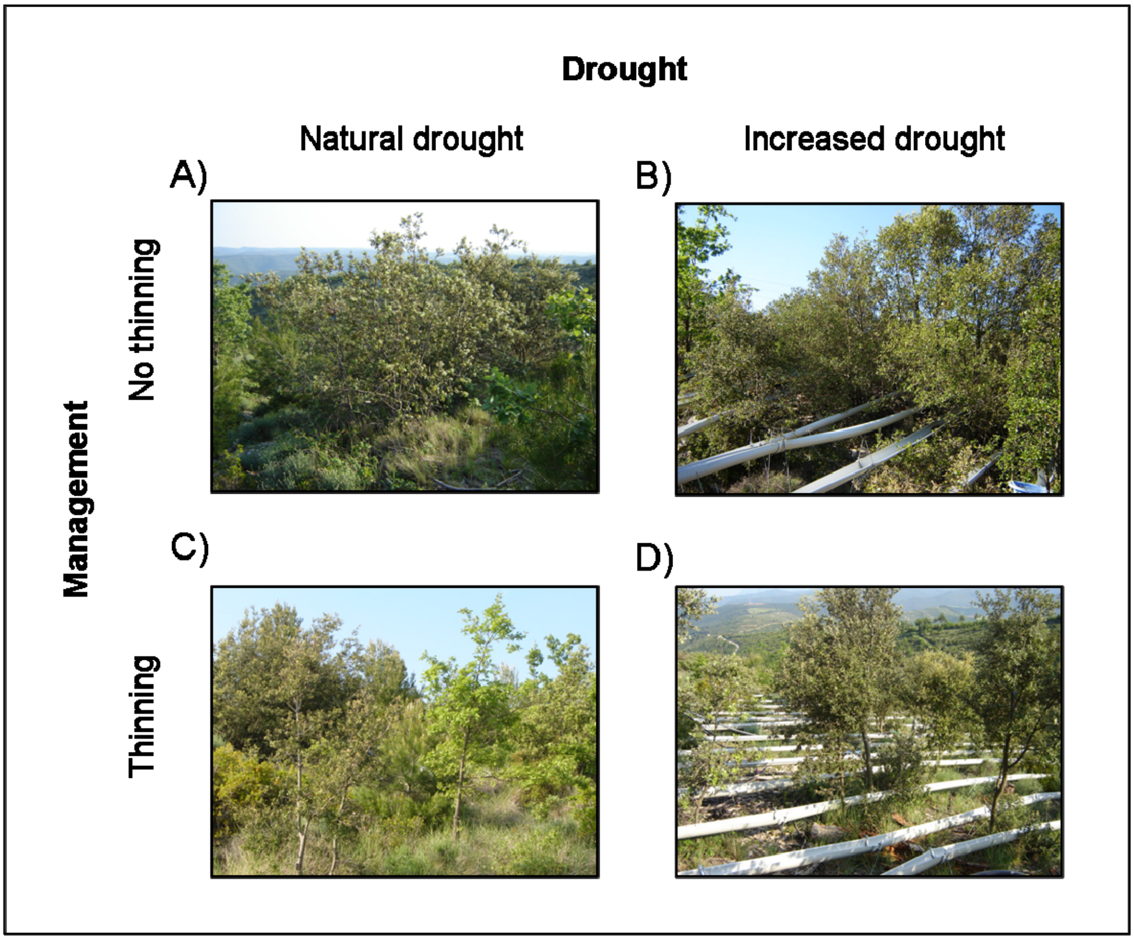

Figure 5.1. General view of the plots where the experimental treatments were combined: A) no-thinning and natural drought, B) no thinning and increased drought, C) thinning and natural drought and D) thinning and increased drought. Photographs are courtesy of M. Cotillas and S. Sabaté.

To check for the effects of rainfall level and thinning on soil moisture, we monitored it regularly throughout the entire experiment (weekly or biweekly) by means of ten Time Domain Reflectometer (TDR) probes per plot, permanently installed in the same place. To summarize the large amount of data obtained, values of soil moisture per plot were seasonally averaged (the mean values in winter, spring, summer and autumn of the different years monitored are presented in Cotillas *et al.* 2009). For the purposes of the present study we only retained and used the mean soil moisture values in spring and summer, as the environmental conditions during these two seasons are the most important in determining reproductive success in Mediterranean oaks: i.e. spring conditions for flowering and summer water stress for acorn maturation (Chapter 2, Espelta *et al*. 2008).

After the experimental treatments were applied, we censed and permanently tagged all *Q. ilex* individuals (multi-stemmed stumps) present in the plots and in order to characterize changes in forest structure during the experiment, the following variables were measured every year (February) before the onset of vegetative growth: density of trees per plot and basal diameter of all stems per stump. The sum of the basal area of all stems per stump (stump basal area) was calculated as an overall measure of tree size (Cotillas *et al*. 2009). The main structural characteristics of the experimental plots assigned to the different rainfall and thinning levels at the onset of the experiment are shown in Appendix 5.1.

The reproductive response of *Q. ilex* trees to the experimental treatments was assessed by measuring every year in all oaks per plot: (i) production of female flowers, (ii) production of fertilized acorns (number of acorns in the middle of summer, after non-fertilized flowers have dropped) and (iii) production of mature acorns (number of fully mature acorns, before acorn dispersal). Because of the small size of the oaks, we were able to make absolute counts of the abovementioned variables for every oak. To test the effects of the experimental treatments on the size of acorns, up to 30 sound mature acorns were randomly collected every year from each plot. The acorns' length and width were measured with the aid of a digital calliper, and their volume was calculated. The acorns were dried (70ºC, 96 hours) and weighed to the nearest 0.001 g. Due to the low acorn production in some of the experimental treatments and the occurrence of lean years (see the Results section), mean acorn volume and dry weight were calculated on a per plot basis.

Data analysis

The effects of the drought and management treatments on spring and summer soil moisture were analyzed through two separate repeated measures ANOVA models. In these models, management and drought treatments were the independent variables, “plot” was the subject variable, and “year” was the intra-subject variable. We conducted two separate analyses (spring and summer), because the moderate number of replicates (3 plots) for each combination of drought and thinning levels did not allow us to conduct a more detailed analysis including both “season” and “spring” as intra-subject (two repeated) variables.

The effect of the experimental treatments on the yearly proportion of flowering trees (i.e. trees that flowered, independently of whether female flowers became mature acorns or not) and fruiting trees (i.e. trees that produced mature acorns) was analyzed by means of a repeated measures Generalized Lineal Model with a binomial error and a logit link function. In these analyses “plot” was the subject variable and “year” the intra-subject variable. To control for the effect of differences on tree density among the experimental plots (Appendix 5.1, see also Cotillas *et al*. 2009) we introduced it as a covariate. In a similar way, the effects of the experimental treatments on the number of female flowers and mature acorns produced per tree, was analyzed by means of a repeated measures Generalized Lineal Mixed Model with a Poisson error and a log link function, where “tree” was the subject variable and “year” was the intra-subject variable. In these analyses we included “plot” as a random factor and “basal area” of each individual as a covariate to control for differences in tree size.

To assess whether the effects of drought and thinning might have a different influence in pollination-fertilization (proportion of female flowers that became fertilized acorns) and acorn development (proportion of fertilized acorns that reached maturity), we conducted a repeated measures Generalized Lineal Mixed Model analysis with a Poisson error and a log link function. In this analysis the dependent variables were the number of fertilized and mature acorns per tree and the offset variables were, respectively, the number of flowers and the number of fertilized acorns (both transformed to their logarithmic form). The independent variables in this analysis were management, drought, year and stage of acorn development (fertilized acorns, mature acorns). In the model, “tree x year” was the subject variable and “stage” was the intra-subject variable.

The influence of the experimental factors and year in mean acorn size per plot was analyzed by means of a repeated measures ANOVA.

To evaluate whether the effects of increased drought and thinning on a per tree basis, resulted in general differences among forest plots, we carried out a Generalized Lineal Model of the effects of the experimental factors and year on the total number of mature acorns produced per plot (acorns ha^{-1}). To control for differences in forest structure among plots, we included oak density as a covariate in this analysis.

RESULTS

As expected in a Mediterranean-type climate, soil moisture in spring and summer showed a high inter-annual variability (factor Year in Table 5.1): soil moisture values in spring were lower in 2005 (10.2±0.3%) and 2006 (9.7±0.3%) than in 2007 (17.9±0.5%) and 2008

(16.4±0.7), while values in summer were higher in 2005 (11.1±0.3%) in comparison to the rest of the years (9.0±0.4 in 2006, 8.9±0.5 in 2007, 8.5±0.2 in 2008). Throughout the 4 years monitored, the mean soil moisture in spring was higher in natural- than in increased-drought plots (respectively, 14.3±0.4 % vs. 12.8±0.4%) while the interaction Management x Year (Table 2) revealed higher values in thinned than in non-thinned plots only in the first two years after the experimental treatment was applied (2005 and 2006 in Figure 5.2A). Soil moisture values in summer were not influenced by thinning but they changed according to the interaction Drought x Year (Table 5.1): no differences were found among natural- and induced- drought plots in 2005 and 2006 but higher values of soil moisture were observed in plots subjected to natural-drought in 2007 and 2008 (Figure 5.2B).

Table 5.1. Results of the repeated measures ANOVA for the effects of drought (natural vs. increased), forest thinning (thinning vs. no thinning) and year (2005, 2006, 2007, 2008) on mean soil moisture values in spring and summer in the experimental plots. Significant coefficients at $\alpha = 0.05$ are indicated in bold. N= 48.

Effects		Soil moisture in spring		Soil moisture in summer	
	df	F	p	F	p
Drought (D)	1	**6.2**	**0.038**	3.5	0.099
Management (M)	1	**8.4**	**0.020**	0.2	0.694
D x M	1	0.6	0.476	1.5	0.254
Year (Y)	3	**94.5**	**<0.001**	**25.5**	**<0.001**
Y x D	3	1.1	0.375	**4.1**	**0.017**
Y x M	3	**3.5**	**0.030**	0.2	0.918
Y x D x M	3	2.7	0.067	1.7	0.189

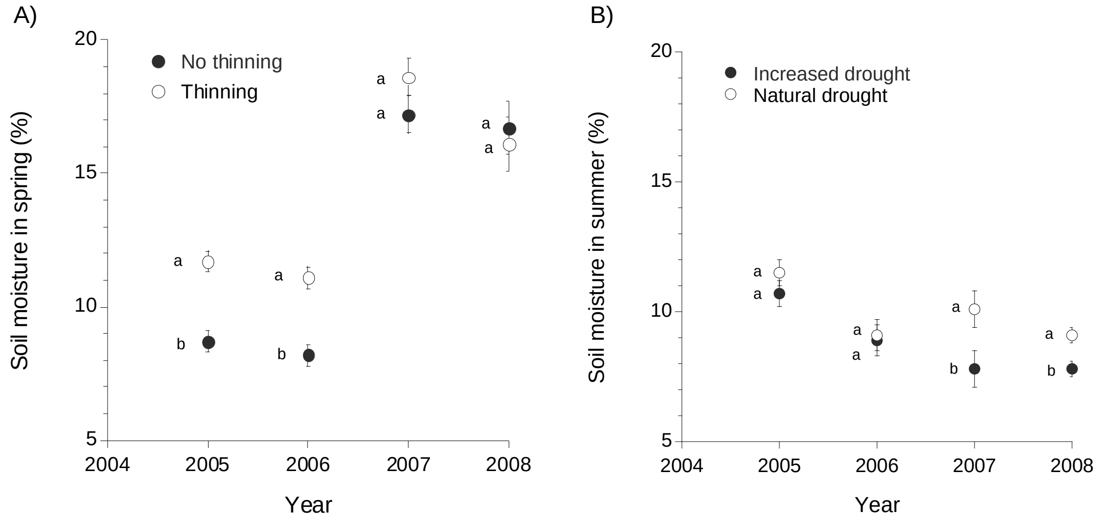

Figure 5.2. Mean±SE Soil moisture values in spring (A) and summer (B) in thinned and no thinned plots during the 4 years monitored in this experiment (2005, 2006, 2007, 2008). Different letters indicate significant differences among thinned and no thinned plots per year according to the LS means test. N= 48.

Only 31 % of oaks flowered at least one of the 4 years of study, while this percentage decreased to 23 % as regards fruiting trees. The mean size (basal area) of flowering and fruiting trees was higher than for non-reproductive ones (respectively, 3915 ±216 cm^2 vs. 1021 ±93 cm^2 and 4308 ±269 cm^2 vs. 1418±108 cm^2). Concerning the two experimental factors, most reproductive characteristics of oaks significantly differed according to the drought and thinning treatments applied (Table 5.2 and Table 5.3), although the sign and the strength of these differences varied with time (interactions with the Year effect in Table 5.2 and Table 5.3). Interestingly, an interaction between the two experimental factors was observed for the proportion of flowering trees and the mean number of female flowers produced per tree, yet for neither the proportion of fruiting trees nor their mean acorn crop size. As shown in Figure 5.3A, the combined effects of thinning and drought on the proportion of flowering trees differed over the 4 years of study, with three remarkable results: (i) no differences throughout the experiment were observed among non-thinned plots subjected either to natural or to increased drought, (ii) thinning enhanced the proportion of flowering trees both in natural and increased drought conditions in comparison to non-thinned plots, only the first year after the experiment onset (2005), (iii) significant differences among the two most negative and positive situations in the hypothetical gradient of resource availability (non-thinned plots subjected to increased drought vs. thinned plots subjected to natural drought) were observed in 3 out of the 4 years (2005, 2006 and 2007). A similar effect of the interaction between drought and thinning was observed for the mean number of female flowers produced per tree (Figure 5.3B): i.e. (i) thinning enhanced the mean number of flowers produced per tree (both in natural- and increased-drought conditions) only the first year after the experiment onset (2005) and (ii) the positive effects of thinning decreased with time, especially in thinned plots subjected to increased drought.

Table 5.2. Results of the repeated measures Generalized Lineal Model for the effects of drought (natural vs. increased), forest thinning (thinning vs. no thinning), year (2005, 2006, 2007, 2008) and tree density on the proportion of flowering and fruiting trees per plot. Significant coefficients at α = 0.05 are indicated in bold. N=48.

Effects	Flowering trees			Fruiting trees	
	df	Chi	p	Chi	p
Drought (D)	1	0.5	0.482	0.1	0.796
Management (M)	1	**4.5**	**0.033**	**5.5**	**0.019**
D x M	1	0.1	0.898	0.1	0.742
Year (Y)	3	**259.2**	**0.000**	7.0	0.073
Y x D	3	**28.0**	**0.000**	**12.5**	**0.006**
Y x M	3	**11.7**	**0.009**	**51.7**	**0.000**
Y x D x M	3	**60.4**	**0.000**	2.8	0.417
Tree density	1	0.7	0.389	1.5	0.228

Table 5.3. Results of the repeated measures Generalized Lineal Mixed Model for the effects of drought (natural vs. increased), forest thinning (thinning vs. no thinning), year (2005, 2006, 2007, 2008), plot and tree size (basal area) on the number of female flowers and mature acorns produced per tree. For female flowers the analysis was restricted to 2005, 2007 and 2008. Significant coefficients at α = 0.05 are indicated in bold. N= 1008 and 732 respectively.

Effects	Female flowers			Mature acorns		
	df	Chi	p	df	Chi	p
Drought (D)	1	**10.7**	**0.001**	1	**7.6**	**0.006**
Management (M)	1	**14.7**	**<0.001**	1	**9.3**	**0.002**
D x M	1	1.2	0.267	1	0.1	0.724
Year (Y)	2	**50.5**	**<0.001**	3	**92.0**	**<0.001**
Y x D	2	2.6	0.274	3	**11.0**	**0.012**
Y x M	2	**17.9**	**<0.001**	3	**43.4**	**<0.001**
Y x D x M	2	**8.4**	**0.015**	3	4.4	0.225
Plot	8	14.5	0.069	8	**33.7**	**<0.001**
Tree size	1	**75.5**	**<0.001**	1	**14.8**	**<0.001**

In addition to the reported effects on flowering, thinning and drought also significantly influenced the proportion of fruiting trees as well as the number of acorns produced, although the two experimental factors did not interact (Table 5.2 and Table 5.3). As previously shown for flowering (see above), thinning enhanced the proportion of fruiting trees and their mean acorn crop size but with a transient and short term effect: i.e. according to the interaction Management x Year (Table 5.2 and Table 5.3) differences between thinned and non-thinned plots were only observed in 2005 (Figure 5.4A, 5.4B). Whereas differences due to thinning were only observed at the beginning of the experiment (2005), differences between the two drought levels appeared mostly in 2007 and 2008 (interaction Drought x Year in Tables 5.2 and 5.3): i.e. in plots subjected to increased drought the proportion of fruiting trees was lower both in 2007 and 2008 (Figure 5.5A) and so was their mean acorn crop size (Figure 5.5B).

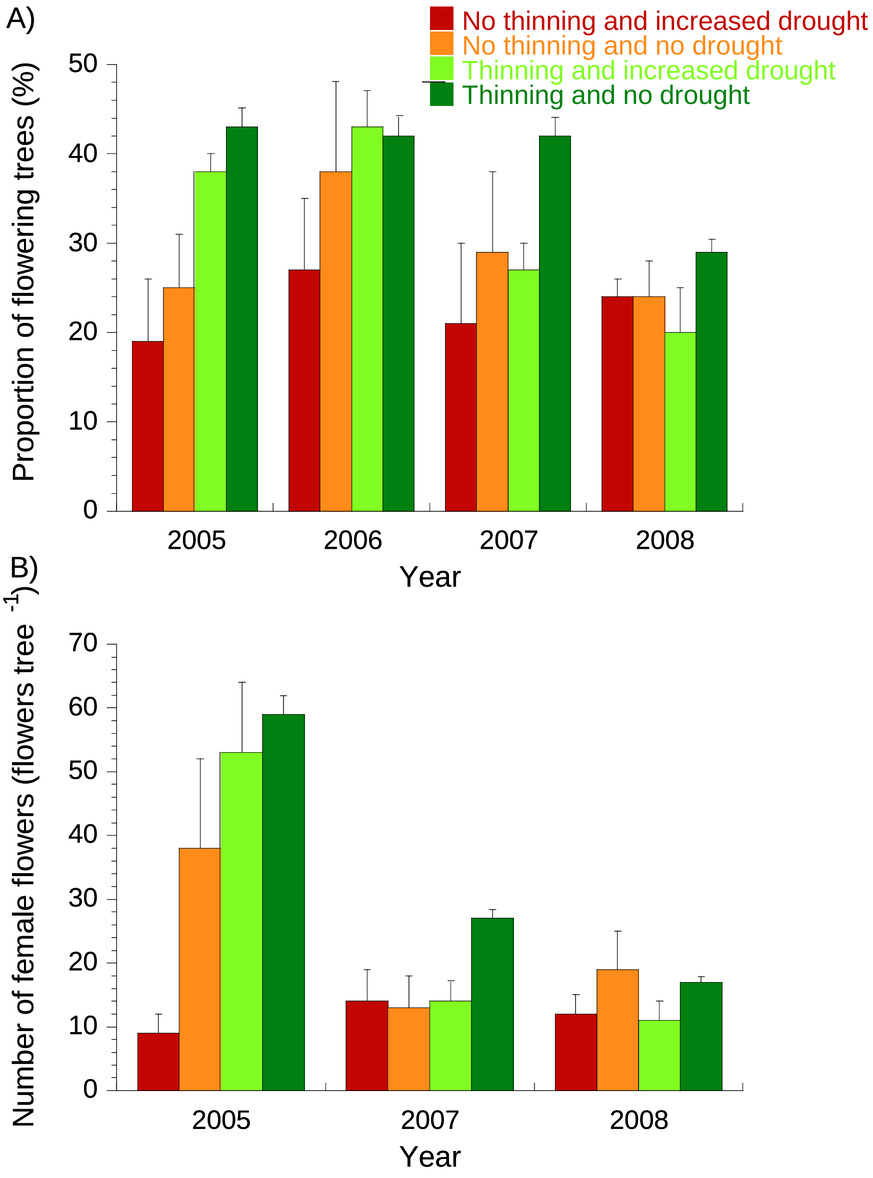

Figure 5.3. Mean±SE proportion of flowering trees (A) and number of female flowers produced per tree (B) in thinned and no thinned plots subjected to natural or increased during the 4 years experiment. N= 48.

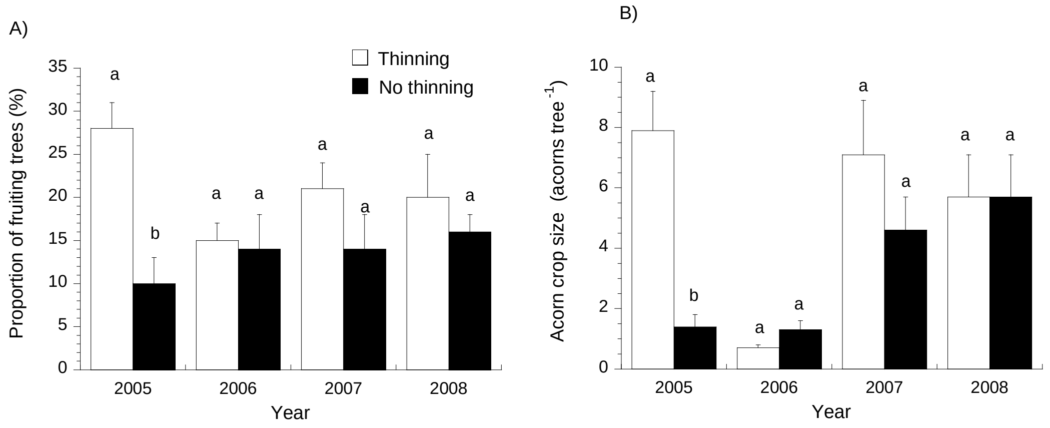

Figure 5.4. Mean±SE proportion of fruiting trees (A) and number of acorns produced per tree (B) in thinned and no thinned plots during the 4 years experiment. Different letters indicate significant differences among the two thinning levels per year according to the LS means test. N= 48.

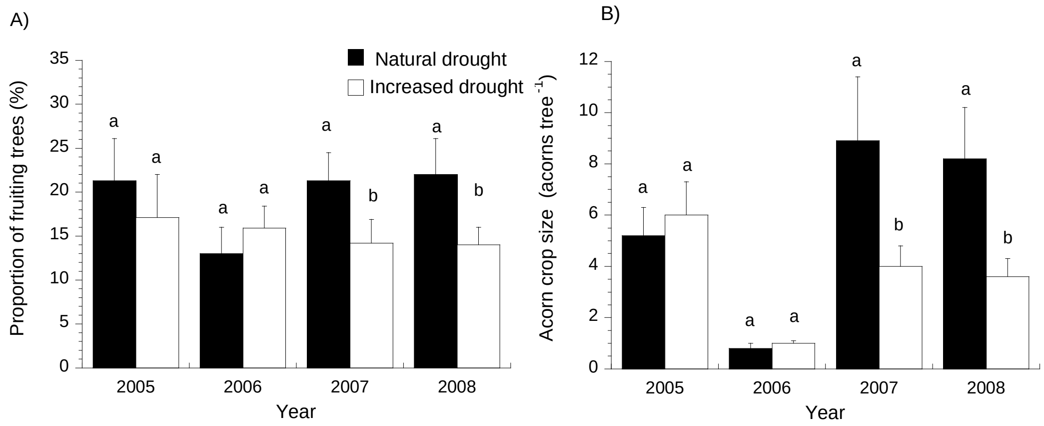

Figure 5.5. Mean±SE proportion of fruiting trees (A) and number of acorns produced per tree (B) in plots subjected to natural or increased drought during the 4 years experiment. Different letters indicate significant differences among the two drought levels per year according to the LS means test. N= 48.

The results of the detailed analysis of drought and thinning effects on the likelihood of success during the two stages involved in acorn development (from female flowers to fertilized acorns and from fertilized to mature acorns) are shown in Table 5.4. Differences in success were mostly due to the development stage, drought, and thinning level (see the significance of the main effects and their interactions in Table 5.4). The developmental stage had a paramount influence on the overall success of acorn production: roughly, 66.7±0.2% of female flowers became fertilized acorns, yet only 30.1±0.2% of fertilized acorns reached maturity. However, differences in the relevance of these two processes were found between years (interaction Year x Stage in Table 5.4): differences were much larger in 2007 in comparison to 2005 and 2008 (Figure 5.6). On the contrary, the effects of drought and management did not vary over the 4 years. The interaction Management x Stage indicates that the effect of thinning on increasing mature acorn crop size was due, not to an effect on the number of flowers fertilized (68±2% in managed vs. 65±3% in non-managed plots), but rather for the most part to an increase in the number of fertilized acorns that reached maturity (33±2% in managed plots vs. 25±3% in non managed plots). In a different way, the significance of the drought effect (Table 5.3), yet the lack of any interaction with the factor stage, indicates that increased drought reduced the size of the mature acorn crop due both to a decrease in the proportion of fertilized flowers and the proportion of acorns that reached maturity (accounting for both processes together, 51±3% of flowers became mature acorns in plots under natural-drought conditions vs. 34.1±3% in plots subjected to increased drought).

Differences among plots on the total number of acorns produced paralleled those reported on a per tree basis: i.e. acorn production decreased with drought and increased with thinning, although there was a high year to year variability (respectively, $\chi^2 = 180.2$ $p < 0.001$ and $\chi^2 = 17.4$ $p < 0.001$). As shown in Figure 5.7, acorn crop size was higher in 2005 and 2007 in thinned plots, while acorn production was higher in natural- than in increased drought plots in 2007 and 2008.

Acorn size was barely influenced by any of the experimental treatments applied, and the only significant differences were found between years (repeated measures ANOVA, df=3, F=36.2, p <0.0001): mean acorn size was larger in 2005 (1.9±0.2 cm ^{3}) than in 2006, 2007 and 2008 (respectively, 0.8±0.2 cm^{3}, 0.5±0.1 cm^{3}, 0.8±0.3 cm^{3}).

Table 5.4. Results of the repeated measures Generalized Lineal Mixed Model for the effects of drought (natural vs. increased), forest thinning (thinning vs. no thinning), year (2005, 2007, 2008), stage of acorn development (fertilized, mature) plot and tree size (basal area) on the likelihood of survival during acorn development (from female flowers to fertilized acorns and from this stage to mature acorns). Significant coefficients at α = 0.05 are indicated in bold. N= 3024.

Effects	Survival during acorn development		
	df	Chi	p
Drought (D)	1	**13.4**	**<0.001**
Management (M)	1	**15.7**	**<0.001**
Stage (S)	1	**251.2**	**<0.001**
D x M	1	0.3	0.603
D x S	1	0.1	0.770
M x S	1	**4.7**	**0.030**
D x M x S	1	**3.9**	**0.048**
Year (Y)	2	5.2	0.074
Y x D	2	3.9	0.143
Y x M	2	3.7	0.154
Y x S	2	**12.6**	**0.002**
Y x D x M	2	3.16	0.206
Y x D x S	2	2.20	0.332
Y x M x S	2	1.86	0.394
Plot	8	**31.8**	**<0.001**
Tree size	1	**11.0**	**0.001**

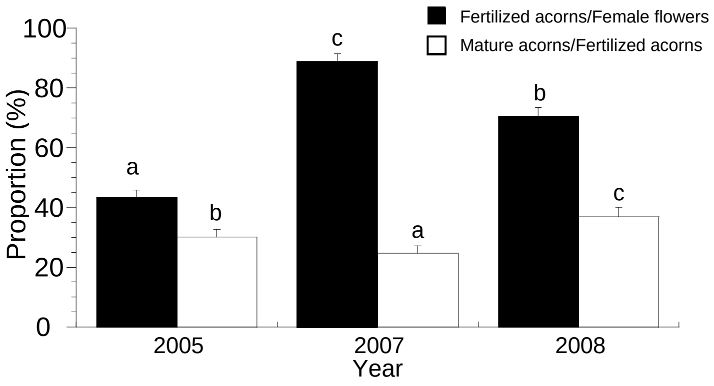

Figure 5.6. Mean±SE proportion of fertilized acorns out of female flowers produced (black columns) and mature acorns out of fertilized acorns (white columns). Different letters indicate significant differences among years in each of the two stages of acorn development according to the LS means test. N= 3024.

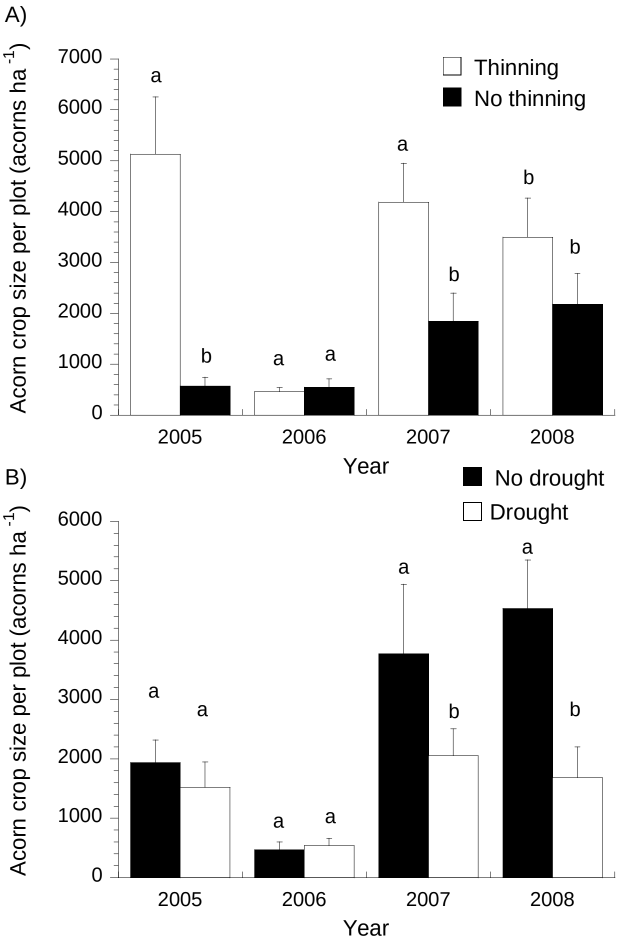

Figure 5.7. Mean±SE production of mature acorns per plot in thinned and no thinned plots (A), and in plots subjected to natural or increased drought (B) during the 4 years experiment. Different letters indicate significant differences among the experimental levels per year according to the LS means test. N = 48.

DISCUSSION

This study presents two main contributions to understanding the effects of a new climatic scenario (increased drought) on *Q. ilex* coppices in the Mediterranean Basin. First, increased drought, mediated by a small reduction in rainfall (15%), may not cause immediate changes in mortality or growth (see the results of Cotillas *et al*. 2009 for the same study area) yet it may reduce the reproductive ability of *Q. ilex*. This may have long-term negative consequences for the maintenance of these oak forests as well as for the fauna feeding on acorns. Second, low selective thinning enhances reproduction ability and it may mitigate some of the negative consequences of increased drought, yet it has a remarkable short term effect. This highlights the need to re-examine the consideration of traditional forest management practices as potential adaptive strategies for coping with the consequences of climate change for forest ecosystems (Lindner 2000, see also Cotillas *et al*. 2009).

Although we could well simulate a decrease in soil moisture mediated by a reduction in rainfall, the negative consequences of increased drought observed in this study may be partly underestimated when compared with those occurring under the forecasted climate change scenario in the Mediterranean Basin. In fact, our design incorporated neither the raising of temperatures predicted, nor the occurrence of extreme drought episodes in summer (IPCC 2007). Inclusion of these factors could even make the positive impact of thinning on increasing reproductive ability more transient.

It is a well-known fact that plants need to achieve a certain size before they start reproducing, because previous accumulation of resources is necessary (for oaks, see Goodrum *et al.* 1971, Abrahamson & Layne 2002a, b). Interestingly, although traditionally viewed as a species that bases its resilience to fire on a successful resprouting strategy, *Q. ilex* began to produce acorns at least at a post- fire regeneration age of 7 years (similar to the results of Abrahamson & Layne 2002a for oak species in xeric and fire-prone environments in Florida). Clearly, the mean acorn crop size in these young trees was extremely low in comparison to the values reported for more mature oak woodlands or forests, but the high density of trees in these coppices (c.a. 1500 stumps ha^{-1}, see Appendix 5.1) may render a large crop size on a population basis (see Figure 5.7). Such a reproductive precocity in *Q. ilex* could grant this species the chance to expand its distribution soon after the fire event (Ostertag & Menges 1994), at least in contrast to heterospecifics with a later reproductive onset (e.g. *Q. cerrioides* in our study area). Clearly, future research should be aimed at assessing whether these early acorn crops may encounter suitable micro sites for germination and establishment and the potential role played by acorn dispersers (e.g *Apodemus sylvaticus*, *Mus spretus*, *Garrulus glandarius* in our study area) in the likelihood of colonization of surrounding areas.

Increased drought reduced the number of flowering and fruiting trees and, on a per tree basis, the production of female flowers and mature acorns. Although *Q. ilex* is recognized as a drought-tolerant species (Terradas 1999), seeding may be highly dependent on water availability (Siscart *et al.* 1999, Ogaya & Peñuelas 2007a). Interestingly, our results indicate that drought not only during summer but also during spring diminished the acorn crop size, by decreasing the production of female flowers and the proportion of those that were fertilized. This result partly contrasts with previous studies that have ascribed to the process of acorn maturation a preeminent role in determining acorn crop size, by considering flowering and fertilization to be two less resource-demanding processes, and thus less affected by resource shortage (see Sork 1993, Espelta *et al*. 2008). Although soil moisture during summer was in a similar range of values during this 4-year experiment (see Figure 5.3), the negative consequences of increased drought for acorn production became more evident over the last two years (Figure 5.6). This suggests the potential existence of cumulative negative effects of sustained drought, either in the soil compartment (e.g. a progressive lowering of moisture in the entire soil profile) or at the plant level (e.g. a progressive exhaustion of resources needed for seed production). Unfortunately, up to now, there have been very few studies including long-term experiments to test the effect of sustained drought (but see Ogaya & Peñuelas 2007a, b), and they have not yet identified the ultimate cause of these potentially accumulative effects.

Selective low thinning of the weakest resprouts had a positive effect on the reproductive ability of *Q. ilex* trees. Thinned plots had a proportion of flowering and fruiting trees 1.3 and 1.4 times higher than non-thinned ones, and both flowering and acorn production increased in trees in the former plots. Numerous studies conducted in Mediterranean oak coppices have stressed the benefits of thinning to reduce intra-individual competition between stems, and thus increase resource availability (light, water and nutrients) for the remaining stems (Espelta *et al*. 2003 and references therein). From a functional point of view, thinning involves the sudden rupture in the established partition of biomass among above- and belowground ground compartments, thus leading to an extraordinary increase in the root to shoot ratio (Canadell & López Soria 1998, Riba 1998). Moreover, this practice has a beneficial effect on ventilation and irradiation due to the overture of the canopy layer (Mayor & Rodà 1993), which may indirectly enhance seed production by facilitating pollination (see for the effects of thinning in pine forests Barnett & Haugen 1995, Grayson *et al*. 2004, Verkaik & Espelta 2006). Therefore, the benefits of selective thinning in oak coppices have been extensively reported for tree growth (Ducrey & Toth 1992, Retana *et al*. 1992, Gracia *et al*. 1999), and to a lesser extent for tree reproduction (Zulueta & Montero 1982). However, very often, these studies have also highlighted the short and transient effects of selective low thinning (Cutter *et al*. 1991, Mayor & Rodà 1993, Healy *et al*. 1999, Espelta *et al*. 2003). In our study the effect of thinning on reproduction mostly disappeared only one to two years after the treatment was applied (Figures 4 and 5). Two main processes could be responsible for making the increase in resource availability quickly disappear and return to the previous situation of above- and belowground biomass partitioning: a quick expansion of the canopy in the retained stems (Gracia *et al*. 1999, M. Cotillas, unpublished results) and, primarily, the vigorous production of a new wave of resprouts from the stump (Cotillas *et al*. 2009, see also Espelta *et al*. 2003). In fact, among thinned plots, the benefits of thinning for acorn production disappeared earlier in plots subjected to increased drought (see Figure 5.4A), where the production of a new wave of resprouts was more intense (Cotillas *et al*. 2009).

Our results draw attention to the importance of drought and thinning levels for *Q. ilex* reproduction. Intriguingly, in spite of their relevance, the two experimental factors applied did not interact or interacted weakly (except for the proportion of flowering trees). Is this a consequence of the different timing they have in their effects? As our results suggest, stronger and immediate effects of thinning suppress those of increased drought but once this transient effect has disappeared, differences mediated by drought may arise. Clearly, a longer series of data, as well as new experiments combining a wider range of drought and thinning levels, would help to answer this question and to fine-tune appropriate forestry practices to help Mediterranean forests cope with climate change. In addition, further research should be conducted on the demographic consequences of a lower acorn production (recruitment and establishment of *Q. ilex* seedlings) as well as its potential consequences for the trophic cascades based on this resource.

AKNOWLEDGEMENTS

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Capítulo 6

Discusión General [1]

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[1] This chapter is written in Spanish.
For the English version, please, contact me at belen.sanchez@creaf.uab.es

En la Introducción General planteé cuatro preguntas básicas que pretendía resolver con mi tesis. Combinando los resultados de los cuatro capítulos anteriores, procuraré ofrecer cuatro respuestas acompañadas de una breve discusión de cada una.

1. ¿Existe una competencia entre producción de bellotas y crecimiento vegetativo?

La respuesta es… depende. En *Quercus ilex*, *Q. humilis* y *Q. faginea* no encontré ninguna competencia de la producción de bellotas con el crecimiento anual y estacional del tronco una vez controlados los efectos del clima, ni con la reproducción futura (Capítulo 2), ni tampoco con el crecimiento de otoño en ramas de *Q. ilex* (Capítulo 4). En cambio, en *Q. lobata*, aunque no encontré costes de reproducción en el crecimiento de las ramas de árboles con una alta producción de bellotas, sí los hubo para los árboles con baja producción durante un año de *masting*; y en el caso de los brotes, los costes fueron generalizados para todos los tipos de árboles (Capítulo 3). En resumen, he encontrado *trade-offs* en los brotes, sin embargo, estos son evitados a nivel de rama por los árboles con más recursos, y en el crecimiento tronco, es decir, a nivel del individuo, no se observan en ningún caso.

Pero esto… ¿qué quiere decir en términos de las hipótesis del masting? Las principales hipótesis que tratan de explicar el *masting* (*resource matching* y economía de escala) hacen diversas predicciones en cuanto a lo que cabría esperar de los potenciales *trade-offs* reproducción-crecimiento en especies veceras ¿Con cuál nos quedamos? En la tabla 6.1 se resumen las predicciones de cada hipótesis en cuanto a los costes de reproducción y la concordancia o no de mis hallazgos con estas predicciones. Asumiendo el riesgo de simplificar excesivamente, esta tabla nos puede dar una imagen rápida de lo esperado y encontrado.

Tabla 6.1. Expectativas de encontrar trade-offs entre reproducción y crecimiento en especies veceras, según cada una de las hipótesis del masting. Los símbolos de la columna "¿qué encuentro en *Quercus*?" responden a la concordancia (✓) o no (✗) de lo observado en mi trabajo de tesis con las expectativas de estas hipótesis, para cuatro especies mediterráneas del género *Quercus (Q. ilex, Q. humilis, Q. faginea, Q. lobata).*

Hipótesis	**Expectativas Trade-off reproducción vs. crecimiento**	**¿Qué encuentro en *Quercus*?**			
Resource matching	NO	✗			
Switching (economía de escala)	SÍ	✓	Sólo en brotes	✗	No a nivel de individuo
Acumulación de recursos (economía de escala)	NO (pero sí reproducción actual-reproducción futura)	✓	Pero no suficiente	✗	No hay coste en reproducción futura

¿Qué quiere decir esto? (i) Que existe *switching*, pero limitado a un solo estrato del árbol (el brote), y no al individuo entero, (ii) que debe de existir cierta acumulación de recursos que permite que los árboles que más han acumulado puedan compensar estos costes, pero no los que han acumulado pocos recursos (Speer 2001), y (iii) que debe de existir un mecanismo desencadenante del masting para que los árboles se sincronicen para producir bellotas a pesar de presentar costes en sus ramas o brotes (Kelly & Sork 2002). Con esto descartamos la hipótesis del *resource matching*, y aceptamos una variación de la hipótesis de *switching*, modulada por la acumulación de recursos y matizada por una fuerte variabilidad individual.

2. ¿Varía la competencia reproducción-crecimiento en diferentes climas locales, niveles modulares dentro de la copa, y con tamaños de cosecha diferentes?

Si la respuesta a la primera pregunta era “Depende”, esta segunda pregunta pretende ahondar en el “¿de qué depende?”. Los procesos de crecimiento y reproducción y la relación entre ambos están afectados por elementos como el clima, la parte del árbol donde se estudian los *trade-offs* (brote, rama o tronco), la variabilidad individual, y la fenología, que complican el estudio de los costes de reproducción. A pesar de que estos elementos han sido ignorados en muchos de los trabajos que se han dedicado al estudio de los *trade-offs*, he confirmado que tienen una gran importancia, lo que hace que sea imprescindible tenerlos en cuenta si queremos descubrir la existencia de *trade-offs* subyacentes a ellos.

(i) Efecto del clima

En el Capítulo 2 hemos visto que el clima tiene un gran efecto sobre la relación reproducción-crecimiento, de forma que esta relación puede ser positiva o negativa bajo diferentes climas locales, incluso para las mismas especies. Al extraer los efectos del clima tanto sobre el crecimiento como sobre la reproducción, la relación entre ambos (cualquiera que fuera su signo) se pierde, lo que indica que es el clima quien controla esta relación. El hecho de que tanto el crecimiento como la reproducción estén influenciados por el clima es algo que se sabe hace tiempo (Despland & Houle 1997, Selas *et al.* 2002, Corcuera *et al.* 2004a, b, Overgaard *et al.* 2007, Espelta *et al.* 2008). En cuanto a la relación entre ambos procesos, Despland y Houle (1997) constataron en *Pinus banksiana* que no había *trade-offs* aparentes entre crecimiento y reproducción porque ambos procesos variaban de forma similar a lo largo del tiempo, al compás de las fluctuaciones del clima. Sin embargo, desde entonces ha habido cierta controversia al respecto. Monks y Kelly (2006) obtuvieron una relación negativa entre crecimiento y reproducción en *Nothofagus truncata* después de extraer el efecto del clima (pero sólo del crecimiento anual, y no de la producción de semilla). Más tarde Knops *et al.* (2007) demostraron que las correlaciones entre crecimiento radial y producción de fruto en varios *Quercus* mediterráneos no eran causales, sino una consecuencia de la dependencia del crecimiento y la reproducción de las condiciones ambientales, por lo que rechazaron, al igual que Despland y Houle (1997), el *switching*, arguyendo que en sus especies el crecimiento radial y la reproducción son independientes uno de la otra. Mis datos apoyan esta idea probando además que diferentes climas locales pueden incluso cambiar el signo de la relación (Capítulo 2, ver también Stearns *et al.* 1991, Sgrò & Hoffmann 2004, Gutteling *et al.* 2007). Además, con mi trabajo propongo dar un paso más, es decir, no sólo constato la independencia de reproducción y crecimiento radial, sino que perfilo el por qué de esta independencia: una de las posibles respuestas es que sí existan costes, pero no se den a nivel de tronco, sino a otros niveles del árbol (e.g. Capítulo 2, 3, Obeso 2002, Hasegawa *et al.* 2003, Bañuelos & Obeso 2004, Hoch 2005). Una segunda posibilidad es que la acumulación de recursos durante años previos al año de producción masiva permita que esta reproducción se lleve a cabo sin tener que acarrear costes para el crecimiento vegetativo (Capítulo 3, Sork *et al.* 1993). La tercera es que la competencia pueda ser evitada si los periodos en que crecimiento y reproducción están precisando de recursos no coinciden en el tiempo (Capítulo 2, Milla *et al.* 2006). Estas tres posibilidades no tienen por qué ser excluyentes, lo cual complica el asunto, pero también hace que la expectativa de encontrar costes de reproducción sea más flexible, dependiendo de las características de la especie de estudio y las circunstancias en que se hallan sus poblaciones, e incluso sus individuos, lo cual se ajusta mejor a los múltiples resultados aparentemente contradictorios que se obtienen en cuanto a los costes.

(ii) Efecto del nivel modular

Mis resultados muestran que no hay un coste de la reproducción a nivel de individuo (en el tronco) (Capítulo 2), que lo hay a nivel de rama pero sólo para los individuos con menos recursos, y que este coste es generalizado para todos los individuos a nivel de brote (Capítulo 3). Este patrón nos aporta información sobre el nivel de integración que tienen los módulos en el roble. Bañuelos y Obeso (2004) afirmaban que si las ramas son autónomas, los costes podrían detectarse a niveles modulares bajos (brotes, ramas) pero ser compensados a nivel de individuo por las ramas no reproductivas, como parece que es el caso de las especies de *Quercus* estudiadas. En cambio, si no fueran autónomas, las ramas reproductivas podrían fácilmente atraer recursos desde otras ramas, de forma que el coste no sería perceptible a nivel de rama, sino que se detectaría sólo al nivel de la planta entera. Probablemente, esta cuestión no es un asunto de blanco o negro, sino que las ramas son autónomas para algunos recursos y son dependientes de otras ramas para otros (Sprugel *et al.* 1991). En todo caso, mi trabajo pone de manifiesto la importancia de considerar el nivel modular cuando se pretenden establecer los costes de reproducción (ej. Louvett Doust & Louvett Doust 1988, Hoch 2005). Además, he observado que el nivel modular es importante también a la hora de estudiar otros procesos del árbol, como la brotación y crecimiento de otoño (Capítulo 4). Por último, el hallazgo de costes al nivel de rama sólo para los árboles con menos bellotas sugiere que la ocurrencia de costes, además se depender del nivel modular, es dependiente de la cantidad de recursos de un árbol, es decir, que existe gran variabilidad individual en cuanto a los costes de reproducción, incluso dentro de una misma población.

(iii) Efecto de la variabilidad individual

Por un lado, he mostrado en *Q. lobata* que árboles que producen muchas bellotas no presentan costes de reproducción en sus ramas, pero árboles que producen pocas bellotas sí que los presentan (Capítulo 3). Por otro lado, hemos visto en *Q. ilex* que sólo algunos árboles son capaces de brotar en otoño, y que lo hacen con diversas intensidades, dependiendo de su crecimiento de primavera (Capítulo 4). El por qué hay árboles que parecen hacer todo bien (crecer, reproducirse), y otros que flojean en todo (y estos son precisamente los que sufren más los costes de la reproducción), es un asunto que no está del todo claro. Una respuesta muy atractiva la encontramos en la historia vital de las especies. Siguiendo con la analogía de la tarta (en que aumentar el tamaño de una porción disminuye el de las otras), Reznick *et al.* (2000) propusieron que la tarta no tiene por qué tener un tamaño fijo, y que algunos individuos poseen tartas más grandes que otros. Estos individuos parecen poder emplear muchos recursos en todas sus funciones sin tener que sufrir *trade-offs* (Van Noordwijk & de Jong 1986) porque tienen una mayor capacidad "genética" de adquirir recursos (aunque resulte que esta mayor capacidad también tenga sus costes) (Reznick *et al.* 2000). Sin embargo, entre los árboles que he estudiado en esta tesis, no puedo distinguir si los que parecen tener más recursos para todo los tienen por este motivo, es decir, que es una cuestión de genética, o porque están situados en mejores sitios o porque están en la edad más óptima para crecer y reproducirse (Bullock *et al.* 2004, Vieira *et al.* 2009). Monks y Kelly (2006) insistieron con gran énfasis en la importancia de estudiar estos procesos mediante datos individuales y no poblacionales, aunque todavía es una asignatura pendiente en muchos estudios sobre *trade-offs*. En esta tesis he tratado con datos individuales y he demostrado que existe una alta variabilidad individual tanto en crecimiento como en reproducción, y que esta variabilidad influye de forma contundente en las relaciones entre ambos.

Además del clima, el nivel modular y la variabilidad individual, la fenología del crecimiento y la reproducción es otro elemento que puede modificar las relaciones entre estos dos procesos. A este punto está dedicada la tercera pregunta.

3. ¿A qué se debe la extensión del periodo de crecimiento en otoño? ¿Puede esta extensión tener algún efecto sobre el crecimiento vegetativo y la reproducción y sobre la relación entre ambos?

Para explicar por qué los *Quercus* que he estudiado no sufren costes de la reproducción en el crecimiento radial, considero que la fenología de estos procesos puede ser un punto clave (además de la naturaleza modular o la acumulación de recursos) para evitar una competencia directa por los recursos. Los robles que he estudiado realizan más del 80% de su crecimiento anual antes de que las bellotas empiecen a ganar peso, crecen algo (aunque poco) mientras las bellotas se desarrollan, y siguen creciendo tras la dispersión (Capítulo 2). Sin embargo, en especies donde la fenología de ambos procesos está ampliamente solapada, debido a estaciones vegetativas muy cortas como en coníferas boreales (Nienstaedt 1985, Silvertown & Dodd 1999, Selas *et al.* 2002) o a la producción de fruto durante la mayor parte del año (ej. *Nothofagus truncata* en Monks & Kelly 2006) es mucho más probable encontrar competencia entre reproducción y crecimiento. Esto nos sugiere que una estación larga de crecimiento puede relajar la competencia entre ambos procesos

(Milla *et al.* 2006), y pone de manifiesto la importancia de considerar la fenología de crecimiento y reproducción a la hora de estudiar la relación entre ambos. En los árboles mediterráneos, una estación larga de crecimiento, además de implicar una reanudación del crecimiento del tronco, puede conllevar segundas brotaciones, con nuevo crecimiento de brotes en otoño. Apenas hay información sobre las causas y consecuencias de este proceso (De Lillis & Fontanella 1992, Castro-Díez & Montserrat-Martí 1998), por lo que mi trabajo, aunque modesto, es casi pionero en el tema. En *Q. ilex*, he podido observar que el crecimiento de otoño está relacionado con incrementos del esfuerzo reproductivo y con fenologías más avanzadas, y que sucede más frecuentemente en árboles con escaso crecimiento de sus ramas en primavera (Capítulo 4), lo que sugiere que largas estaciones de crecimiento pueden ser una ocasión para compensar en otoño crecimientos fallidos o limitados durante la primavera. Las consecuencias de la laga extensión de la estación de crecimiento (mitigación de la competencia con la producción de semilla, compensación de pobres crecimientos en primavera, e influencia sobre la fenología de años sucesivos) ponen de manifiesto la necesidad de estudiar más a fondo la fenología del crecimiento y la reproducción y sus implicaciones, especialmente en un contexto de cambio climático en que las expectativas generales apuntan a una aún mayor extensión del crecimiento, con un avance del inicio del crecimiento y un retraso del final en otoño (Peñuelas & Filella 2001).

4. ¿Cómo afectará la sequía a los procesos reproductivos en estas especies? ¿Puede el resalveo revertir los potenciales efectos negativos de la sequía?

Mi trabajo describe efectos claros de la sequía sobre la capacidad reproductiva de *Q. ilex*, disminuyendo su precocidad reproductiva, la cantidad de flores y bellotas e influyendo negativamente en el proceso de maduración de las bellotas (Capítulo 5). Aunque Ogaya y

Peñuelas (2007) ya habían descrito descensos en la producción de fruto de diferentes especies mediterráneas, son muy pocos los trabajos que, como el mío, han estudiado si hay forma de revertir estos efectos negativos mediante gestión forestal. A pesar de la falta de información, las prácticas tradicionales de gestión forestal han sido a menudo subvencionadas porque supuestamente aumentan la resiliencia de los bosques mediterráneos frente al cambio climático (Scarascia-Mugnozza *et al*. 2000). Sin embargo, según mis resultados, no podemos hacernos vanas ilusiones en cuanto al resalveo tradicional como estrategia mitigadora de los potenciales efectos de la sequía: su efecto es intenso, pero fugaz. El resalveo resulta una buena herramienta a corto plazo: su efecto es contario al de la sequía (aumentan el número de árboles con flor y fruto y la cantidad de flores y bellotas maduras). Sin embargo, al cabo de uno o dos años de haber sido aplicado el tratamiento, pierde todo su efecto, posiblemente por la gran rebrotada (Espelta *et al.* 2003, Cotillas *et al.* 2009) o por el crecimiento de copas (Gracia *et al.* 1999). Mi estudio pone de manifiesto la necesidad de cuestionar si las prácticas tradicionales de gestión forestal son las adecuadas para enfrentarse a las consecuencias del cambio climático en ecosistemas forestales, no ya sólo en el ámbito de la producción de semilla, sino en el de otras funciones ecológicas o servicios del bosque (Cotillas *et al.* 2009, Mayor & Rodà 1993).

Sería muy interesante ir un paso más allá en el estudio de las respuestas al cambio climático, e investigar cómo un efecto combinado de altas temperaturas (que implican la extensión de las estaciones de crecimiento vegetativo y reproductivo) y mayores sequías (que implican el descenso en estos mismos procesos) afectará a los patrones reproductivos de poblaciones maduras de *Quercus* (ver Llorens *et al.* 2004 y Sebastià 2007 para estudios en otras especies) y qué efecto tendría sobre las relaciones reproducción-crecimiento. Sin embargo, la aplicación experimentos de simulación de altas temperaturas y sequía es complicada a nivel de bosque, y todavía estamos en los primeros pasos, intentando comprender los efectos directos de ambos parámetros sobre el crecimiento (ej. Hanson *et al.* 2001, Cotillas *et al.* 2009, Ogaya & Peñuelas 2007b) y la reproducción (Ogaya & Peñuelas 2007a).

CONCLUSIONES POR CAPÍTULOS

Capítulo 2: Is timing the answer? Climate and phenology mediate in the apparent trade-off between growth and reproduction in Mediterranean oaks.

Para las tres especies *Q. ilex*, *Q. humilis* y *Q. faginea*:

- La relación entre crecimiento radial y producción de fruto es positiva en un ambiente mediterráneo de tipo costero pero negativa en uno mediterráneo de tipo continental: en el primer caso los años de gran producción de bellotas se corresponden con años de gran crecimiento, pero ocurre lo contrario en el segundo caso.

- El clima tiene gran efecto sobre el crecimiento y, en el ambiente costero, sobre la producción de semilla. Si se extrae el efecto del clima sobre ambos procesos, la relación entre ellos desaparece en los dos ambientes, y reproducción y crecimiento resultan independientes.

- En un año de gran producción de bellotas (2002), no existe relación entre el crecimiento del tronco y el tamaño de la cosecha. Asimismo, tampoco se observa ningún tipo de autocorrelación entre la cantidad de bellotas producidas en años consecutivos.

- El periodo de crecimiento del tronco (de abril a noviembre) es más largo que el periodo de engrose de las bellotas (de julio a noviembre) Más del 80% del crecimiento radial ocurre antes de que las bellotas comiencen a aumentar de peso, y hasta un 10% ocurre después de la dispersión, lo que puede relajar la competencia directa por recursos entre crecimiento y reproducción.

- El crecimiento radial realizado antes del engrose de las bellotas no limita al posterior esfuerzo reproductivo, ni éste al crecimiento radial que se produce tras la dispersión de las bellotas.

Capítulo 3: Costs of reproduction during a mast year occur at different hierarchical levels within the canopy and vary among high and low productive trees.

En *Q. lobata*:

- La presencia de costes de reproducción difiere en los diferentes niveles jerárquicos del árbol (rama, brote): mientras que a nivel de brote todos los árboles muestran costes de reproducción, a nivel de rama sólo presentan costes algunos árboles (los de menor producción).

- Los costes de reproducción varían entre árboles con alta y baja producción de bellotas: los árboles con baja producción de bellota sufren una reducción en el crecimiento de las ramas reproductivas, cosa que no ocurre en los árboles con alta producción.

- La biomasa vegetativa del año previo, que se puede considerar como un indicador de la disponibilidad de recursos, es uno de los mayores determinantes del crecimiento vegetativo de los brotes, y éste de la producción de bellotas.

- El hecho de que todos los árboles produzcan semillas a pesar del coste para el crecimiento vegetativo sugiere la existencia de un factor que sincroniza de forma contundente la producción de bellotas entre individuos.

Capítulo 4: **Extension of shoot growth in *Q. ilex* during autumn: Are spring growth, phenology and reproductive effort causes or effects?**

- Todos los árboles y ramas estudiados crecieron en primavera. Una segunda brotación tuvo lugar a finales de verano de 2007, tras intensas precipitaciones. Esta brotación sólo se dio en la mitad de los árboles muestreados y no en todas las ramas. Sin embargo, en 2008, año de escasas precipitaciones a final de verano, no se detectó crecimiento de otoño en ningún árbol.

- Los árboles que produjeron más brotes de otoño son aquellos que presentan menores crecimientos en sus ramas durante la primavera. Sin embargo, las ramas que crecieron en otoño presentan un mayor crecimiento anual (primavera + otoño) que el resto de ramas. Además, el crecimiento de la primavera está fuertemente correlacionado con el crecimiento de otoño: cuanto mayor es la biomasa del brote de primavera, mayor es el brote de otoño que genera.

- Esfuerzos reproductivos mayores aparecen ligados a mayores crecimientos de otoño, lo que sugiere que es compatible el engrose de las bellotas con el crecimiento de otoño sin que exista una competencia entre ambos procesos.

- El crecimiento de otoño no tiene ningún efecto en el crecimiento radial ni en el esfuerzo reproductivo del año siguiente, pero los árboles con mayores brotes de otoño presentan fenologías más avanzadas durante 2008. Este efecto podría intensificarse si se incrementan los eventos de crecimiento otoñal debido a la extensión de la estación de crecimiento por causa del cambio climático.

Capítulo 5: Increased drought reduces acorn production in Mediterranean *Q. ilex* coppices: traditional low selective thinning mitigates this effect but only in the short-term.

- Durante el experimento, la humedad del suelo es mayor en las parcelas sometidas a resalveo y menor en las sometidas a un incremento de sequía; si bien, como corresponde a un clima mediterráneo, se observa una gran variabilidad interanual.

- El incremento experimental de la sequía reduce el número de árboles reproductivos, la producción de flores y de bellotas maduras. Los efectos negativos del incremento de sequía se producen tanto en el proceso de fertilización de las flores como en el de maduración de las semillas. Este efecto es más evidente durante los dos últimos años del estudio (2007 y 2008).

- El resalveo de baja intensidad incrementa el número de árboles reproductivos y de flores y bellotas producidas por árbol. Sus efectos positivos se producen principalmente durante la maduración de las bellotas más que durante la fertilización. Los efectos positivos del resalveo para la reproducción son muy limitados en el tiempo (1 o 2 años tras la aplicación del tratamiento).

- Pese a las diferencias estructurales y de densidad entre parcelas, los efectos de los tratamientos experimentales observados a nivel de árbol, se traducen en una mayor producción total de bellotas en las parcelas que experimentaron niveles naturales de sequía y en las que se aplicó el resalveo.

- Los resultados obtenidos en este estudio muestran que los efectos del resalveo son intensos e inmediatos tras la aplicación del tratamiento y suprimen los efectos de la sequía, pero al ser tan efímeros, una vez desaparece su influencia, el efecto de la sequía se hace patente.

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APÉNDICE

Appendix 2.1. Regression coefficients between individual values of radial growth – acorn production and non-climatic growth – non-climatic acorn production for *Q. humilis* (a) and *Q. ilex* (b) in the Coastal site. Logarithmic transformations have been applied to acorn production data. Significant results are shown in bold. The symbol (-) means no acorn production during the 7-8 year series, thus regression analysis was not possible.

2.1 a)

Individual	Growth – Acorn production		Non-climatic growth – Non-climatic acorn production	
	r	p	r	p
1	0.69	0.061	-0.02	0.955
2	0.21	0.626	-0.31	0.463
3	-	-	-	-
4	-0.08	0.849	-0.31	0.460
5	0.01	0.976	0.46	0.252
6	0.21	0.614	-0.19	0.660
7	**0.85**	**0.008**	0.46	0.247
8	-0.34	0.406	-0.50	0.205
9	0.56	0.154	0.20	0.632
10	-	-	-	-
11	0.21	0.615	0.00	1.000
12	**0.91**	**0.002**	**0.81**	**0.015**
13	0.47	0.240	-0.23	0.582
14	0.05	0.906	-0.23	0.582
15	0.13	0.758	0.08	0.843
16	-0.21	0.619	-0.04	0.935
17	0.46	0.254	0.32	0.440
18	0.38	0.355	0.04	0.923
19	-0.07	0.876	-0.13	0.758
20	**0.80**	**0.018**	0.35	0.390
21	0.55	0.155	0.27	0.512
22	0.40	0.321	0.47	0.245
23	-	-	-	-
24	0.68	0.063	0.69	0.058
25	0.52	0.186	0.17	0.696
26	0.28	0.507	0.18	0.669
27	0.29	0.488	-0.08	0.856
28	0.41	0.317	0.27	0.515
29	**0.77**	**0.025**	**0.77**	**0.025**
30	0.66	0.076	0.36	0.377
31	-	-	-	-
32	0.16	0.703	0.06	0.886
33	-	-	-	-
34	0.65	0.082	**0.84**	**0.009**
35	0.37	0.367	0.58	0.131
36	-	-	-	-
37	**0.82**	**0.013**	-0.28	0.500
38	-	-	-	-

2.1 b)

Individual	Growth – Acorn production		Non-climatic growth – Non-climatic acorn production	
	r	p	r	P
1	0.28	0.550	-0.44	0.329
2	0.70	0.080	0.21	0.648
3	0.58	0.175	0.24	0.603
4	0.68	0.096	0.62	0.135
5	**0.89**	**0.008**	-0.42	0.354
6	0.37	0.420	0.75	0.051
7	**0.79**	**0.036**	-0.07	0.877
8	0.16	0.729	-0.31	0.500
9	0.37	0.372	-0.28	0.496
10	0.09	0.834	-0.38	0.356
11	0.17	0.749	-0.24	0.653
12	0.69	0.060	-0.24	0.575
13	0.60	0.119	0.02	0.966
14	0.50	0.203	-0.06	0.896

Appendix 5.1. Main structural characteristics of *Q. ilex* in the experimental plots assigned to the two drought and thinning treatments at the onset of the experiment.

Plot	Drought	Thinning	Stem density (i ha^{-1})	Stump density (i ha^{-1})	Mean stump basal area (cm^2)	Mean stem height (cm)
1	Natural drought	No thinning	6630	2127	18.9	108
2	Natural drought	No thinning	4307	1335	32.5	138
3	Natural drought	No thinning	5661	1506	41.1	156
4	Natural drought	Thinning	3176	2175	23.3	164
5	Natural drought	Thinning	3746	2087	31.2	182
6	Natural drought	Thinning	2622	1766	19.5	141
7	Increased drought	No thinning	7597	2377	34.2	138
8	Increased drought	No thinning	5383	1630	26.2	125
9	Increased drought	No thinning	3188	1204	23.6	111
10	Increased drought	Thinning	2499	1781	18.9	139
11	Increased drought	Thinning	4197	2912	15.8	151
12	Increased drought	Thinning	2436	1638	22.4	160

AGRADECIMIENTOS

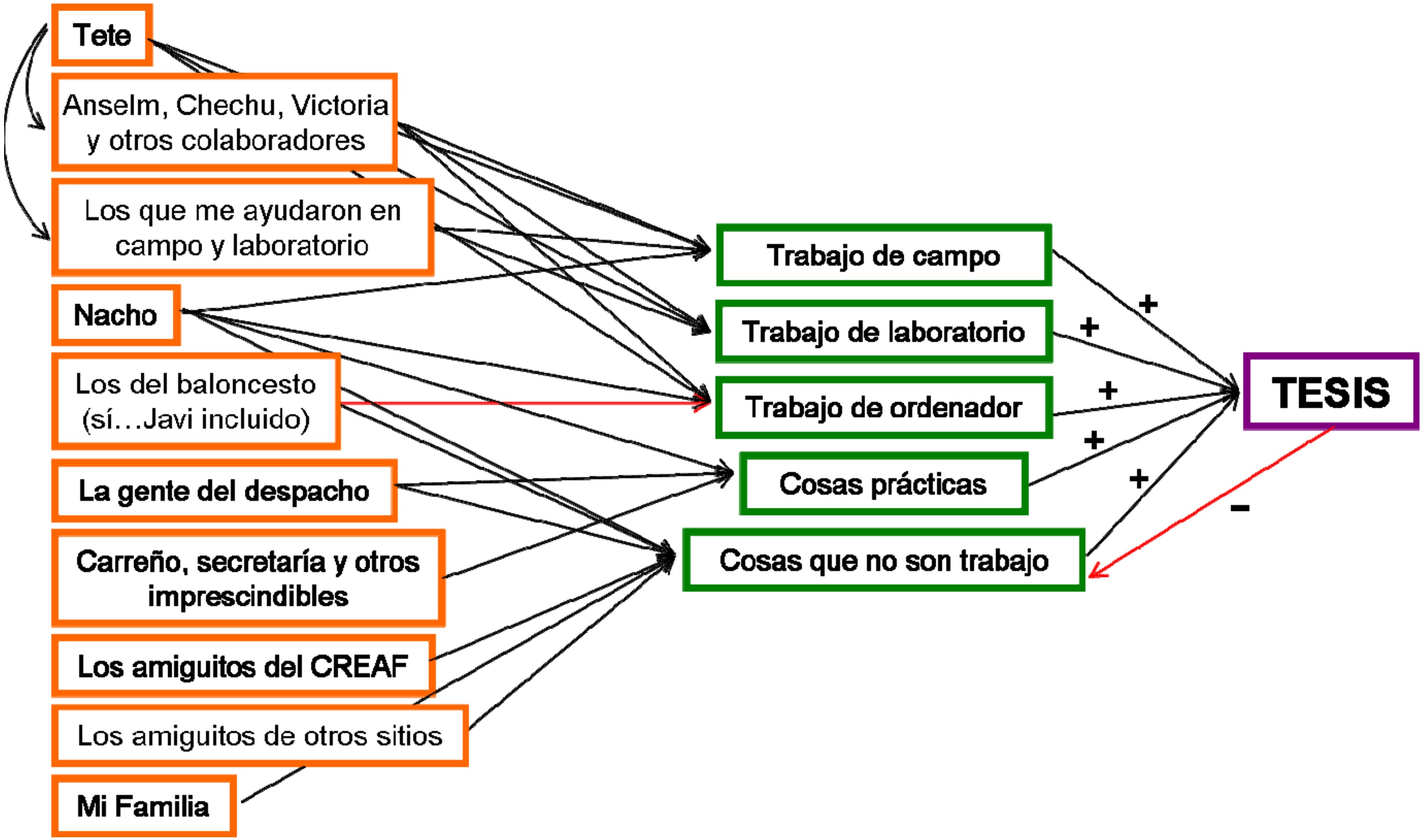

Figura a.1. Diagrama de *path* análisis donde se muestra la relación entre variables causales (cajas naranjas), variables endógenas intermedias (cajas verdes) y variable endógena dependiente (caja morada). Las flechas en color negro representan relaciones positivas y las flechas en color rojo relaciones negativas. Todas las flechas corresponden a coeficientes de path altamente significativos ($p < 0.05$).

* Este *path* análisis ha sido financiado por el Ministerio de Ciencia e Innovación mediante una beca FPU.

¿Qué tienes tú, negra encina
campesina,
con tus ramas sin color
en el campo sin verdor;
con tu tronco ceniciento
sin esbeltez ni altiveza,
con tu vigor sin tormento,
y tu humildad que es firmeza?
En tu copa ancha y redonda
nada brilla,
ni tu verdioscura fronda
ni tu flor verdiamarilla.
Nada es lindo ni arrogante
en tu porte, ni guerrero,
nada fiero
que aderece su talante.
Brotas derecha o torcida
con esa humildad que cede
sólo a la ley de la vida,
que es vivir como se puede.
El campo mismo se hizo
árbol en ti, parda encina.
Ya bajo el sol que calcina,
ya contra el hielo invernizo,
el bochorno y la borrasca,
el agosto y el enero,
los copos de la nevasca,
los hilos del aguacero,
siempre firme, siempre igual,
impasible, casta y buena,
¡oh tú, robusta y serena,
eterna encina rural!

Antonio Machado (Las encinas)