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MODELOS SILVOPASCÍCOLAS EN SISTEMAS ADEHESADOS DEL OESTE DE LA PENÍNSULA IBÉRICA

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EL PRESIDENTE LOS VOCALES

EL SECRETARIO

A mis padres,

con todo mi amor y gratitud

O sabe naturaleza
más que supo en otro tiempo,
o tantos que nacen sabios
es porque lo dicen ellos.

(Lope de Vega; La Dorotea, s. XVII)

“The natural ecosystems of the Earth are not just there for us to take as farmland; they are there to sustain the climate and the chemistry of the planet.”

(James Lovelock, The Revenge of Gaia; 2006)

“[…] y tuvo razón, porque la verdad adelgaza y no quiebra, y siempre anda sobre la mentira como el aceite sobre el agua; y así, prosiguiendo su historia, dice que así como Don Quijote se emboscó en la floresta, *encinar* o selva junto al gran Toboso, mandó a Sancho volver a la ciudad […]”

(Miguel de Cervantes, s. XVII)

Agradecimientos

De igual manera que los trabajos científicos utilizan modelos matemáticos simplificando la realidad con la confianza de que su utilidad excuse sus defectos, las palabras son modelos simplificados de sentimientos e ideas, y por lo tanto rara vez logran expresar en su totalidad lo que se pretende. Por esta razón, hacer justicia por escrito en este apartado se me antoja una empresa del todo imposible, y por eso espero que los justamente agradecidos (e incluso los que se sientan desagradecidos) sean indulgentes tras revisar estas líneas.

La verdad es que al analizar los últimos años adquiero plena consciencia de que un porcentaje de la tesis no es directamente atribuible al que la firma. Como en cualquier otro suceso, han sido diversas las circunstancias y personas que se han tenido que conjugar para que, de las muchas combinaciones posibles, resultara la consecución de otra tesis doctoral, en este caso la mía. En primer lugar quería expresar mi más profundo agradecimiento a mi directora Isabel Cañellas, sin cuya confianza, apoyo constante, paciencia, psicología y amistad hubiera sido totalmente imposible llevar a buen término este trabajo. Agradezco a Gregorio Montero el que me ofreciera la posibilidad de realizar la tesis al concederne la beca predoctoral, es un verdadero privilegio que te paguen para estudiar la naturaleza y aprender lo poco que sabemos de ella. Creo necesario también agradecer a mi codirectora Barbara Allen-Díaz, así como a James W. Bartolome y Lynn Huntsinger, cuyo ayuda tanto económica como profesional en EEUU me permitieron no sólo sobrevivir, si no finalizar con éxito una experiencia absolutamente enriquecedora en todos los aspectos, la cual forma parte también de este escrito. No hubiera completado la tesis sin su imprescindible participación. Además han resultado fundamentales el apoyo, consejos y amistad de Alfonso San Miguel. Muchas gracias por ofrecer siempre una sonrisa y una palabra correcta.

Sobra decir que sin la ayuda de muchos de mis compañeros del INIA tampoco sería posible estar escribiendo estas líneas. No voy a dar una lista completa con los nombres por ser extensa (muchos están ya en los anexos y comunicaciones de congresos, ya en agradecimientos ya como coautores), pero muchas gracias a todos los que me han ayudado estos años en los muestreos (ya fuera la ‘halterofilia’ con las encinas o los dichosos pastos) y procesado de muestras o los que han respondido pacientemente a mis muchas preguntas y otros devaneos pseudo-científico-filosóficos. No puedo olvidarme de agradecer a Quique por procesar las improcesables encinas. Agradecimientos especiales he de dar a mi amigo y compañero Darío, sin cuya discusión, compañía y apoyo nada hubiera sido igual, sobre todo estos dos últimos años, esperemos conservar la ilusión que tantas satisfacciones proporciona. Gracias a Pablo, por tantos y tan buenos ratos echados filosofando gratuitamente sobre trabajo y lo que no lo es tanto. También agradecer a Nacho por compartir las tardes y mucho más, y al resto de los habitantes de la caverna 214, han sido muchas horas juntos. Gracias a todos los que se han leído la memoria en español mejorándola cuando yo sólo veía ya palabras inconexas: gracias Rafa C., D., A. y familia; y por supuesto agradecer a Mariola su ayuda, particularmente en los últimos momentos de pánico al maquetar.

Quería agradecer al Dehesón del Encinar y a Celia López Carrasco por facilitarme las tareas de muestreo y al Instituto Arbitral Agroalimentario por analizar las muestras del año 2004. A la gente de la cátedra de pascicultura en la ETSI Montes por ayudarme a identificar muchas de las especies inventariadas, así como a Jesús Fernández por determinar un buen número de ellas. Muchas gracias a todas las personas que hicieron posible la aparentemente imposible tarea de conseguir muestras de encina. Gracias Lourdes, Marta y Ángel de PyG por la amabilidad, realmente nos dieron la oportunidad de analizar un tesoro maravilloso. Al INIA agradezco que me haya albergado estos años y el Instituto Nacional de Metorología cedió amable y gratuitamente los datos de clima, los cuales esperemos que den más frutos en un futuro no muy lejano.

Quiero recordar a las muchas personas, la mayoría anónimas, que han hecho y hacen posible que desde personas como yo, en la humildad de mis contribuciones, hasta grandes científicos y otras personas apasionadas cualquiera que sea la labor que desempeñen, puedan mantener la ilusión en una tierra en ocasiones tan ingrata como la nuestra para depende qué cosas. Tristemente algunos nos han abandonado en los últimos meses.

Finalmente agradecer de todo corazón a mi familia, la cual es responsable directa de todo lo bueno, y es mucho, que me ha sucedido en la vida. No hay palabras, así que no las busco. Sé que resulta duro soportar mi humor y particular ‘cosmovisión’, especialmente los últimos tiempos predoctorales. Gracias. Y por supuesto incluyo en la familia a mis pocos pero tantos amigos, y a Carolina, posiblemente la persona que más paciente e intensamente ha sufrido el temible (y ridículo) síndrome predoctoral. Y, finalmente, por si no lo había dicho, muchas gracias a todos.

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RESUMEN

La dehesa de encinas (*Quercus ilex* L.) del Oeste peninsular es una sistema agrosilvopastoral de origen antrópico el cual, pese a poseer un gran interés ecológico y económico, aún encierra múltiples interrogantes. La sociedad actual exige que la gestión de los espacios naturales se realice de modo sostenible, para lo cual es necesario adquirir un amplio conocimiento sobre el funcionamiento de los sistemas y las interacciones entre sus componentes. En este sentido los modelos selvícolas son una herramienta fundamental que nos permite simular diferentes escenarios y predecir las consecuencias que nuestras actuaciones producirán sobre el ecosistema. La falta de conocimiento de muchos de los procesos que componen el sistema dehesa desaconsejó la implementación de un modelo global. Por eso, en el presente trabajo estudiamos por separado tres elementos fundamentales de la dehesa como son el crecimiento del árbol y su respuesta al clima, la producción de fruto y la interacción entre el árbol y las comunidades herbáceas, con el fin último de avanzar en el estudio de los diferentes factores que componen la dehesa que nos permitan abordar en un futuro próximo la consecución de un modelo sistémico múltiple.

Presentamos en primer lugar la primera serie dendrocronológica para la encina en las dehesas, mediante la cual validamos los modelos de crecimiento a partir de lecturas de anillos que ajustamos posteriormente. Los rodales estudiados están respondiendo al calentamiento climático extendiendo su período de crecimiento en otoño y mostrando síntomas de mayor estrés hídrico en verano. Además, reflejaron una señal climática común a determinadas series procedentes de toda la región mediterránea.

En segundo lugar se proponen las primeras ecuaciones en diferencias de crecimiento en diámetro para la especie, y se compararon modelos dependientes e independientes de la edad. Los modelos en diferencias dependientes de la edad presentaron un error en predicción entre el 7 y el 10% en las clases diamétricas más abundantes en las dehesas. Las ecuaciones en diferencias independientes de la edad, pese a aumentar ligeramente este error (≈15%), pueden resultar muy útiles por no requerir la estimación de la edad.

Además, se ajustaron ecuaciones de incremento en diámetro, donde se compararon también formulaciones dependientes e independientes de la edad, y se discutió el efecto de la competencia en rodales de baja densidad como los de las dehesas. La selección de la densidad en los modelos de incremento en diámetro nos indica la existencia de competencia en los rodales, la cual posiblemente se produce entre sistemas radicales. La competencia por luz es reducida o ausente, razón por la cual el crecimiento está directamente relacionado con la edad y en su ausencia el diámetro como sustitutivo de la edad. Los modelos lineales generalizados con distribución de error Gamma mejoraron los modelos lineales normales transformados, resultando formulaciones más sencillas.

A continuación se analizó el estado de conocimientos de la producción de fruto. Después de un profundo análisis de la bibliografía existente de esta producción en el sistema, y a pesar de la importancia que posee, se concluyó que no existen trabajos suficientemente detallados que permitan comprender este fenómeno por lo que modelizar el proceso con el nivel de conocimientos actual es inviable.

Finalmente, se estudió el efecto que produce la presencia del estrato arbóreo sobre el pasto herbáceo subyacente, discutiendo la variabilidad espacial y temporal de un fenómeno que tradicionalmente se ha considerado estático y constante. Pese a que como media el árbol tiende a incrementar la producción de pasto en los suelos más pobres, el efecto del árbol sobre la comunidad herbácea es un fenómeno variable en tiempo y espacio, cambiando el sentido de la interacción el año más seco estudiado. El aumento en nutrientes en el suelo bajo la copa dirigió este incremento en la producción. Sin embargo, no varió la concentración de nutrientes en los tejidos vegetales, excepto en el caso del K y en menor medida el Ca, aunque existen otros estudios en la bibliografía que obtienen resultados diferentes. Las modificaciones que la presencia del árbol produce en el pasto subyacente, particularmente en su calidad, parecen ser muy reducidas comparadas con la variación temporal relacionada con la climatología cambiante del área de estudio.

Estos modelos suponen un avance en la modelización de las dehesas, pero aún existen elementos sin estudiar en detalle, tales como la producción de fruto o el efecto de distintos tratamientos selvícolas sobre el crecimiento, que impiden implementar un modelo completo del sistema.

ABSTRACT

The holm oak (*Quercus ilex* L.) dehesa from the West Iberian Peninsula is a manmade agrosilvopastroal system. Despite its high ecological and economical importance, there are still many unsolved questions in the ecosystem. Today, the society demands sustainability in natural resources management, and to achieve sustainable management it is necessary to fully understand ecosystem functionining an interactions among its components. Silvicultural models are an important tool to predict forest response to different scenarios. The lack of knowledge on many of the processes that compose the dehesa system made impossible the implementation of a global systemic model. For this reason, in this dissertation we studied sepparately three different fundamental elements of the dehesa, namely tree growth and its response to climate, fruit production and tree-grass interactions, to increase knowledge on the different elements of the system with the final aim of implementing a systemic model in the next future.

We started building the first dendrochronology for the holm oak in dehesas, validating the use of annual growth estimation from crossections to fit growth models. The stands studied are responding to climate warming by expanding the growth period in fall and showing greater symptoms of water stress in summer. In addition, they shared a climatic signal with certain tree chronologies from the Mediterranean Region.

After building the chronology we fitted dinamic diameter growth models for the holm oak, comparing age dependent and age independent formulations. Dynamic age dependent models yielded predictions errors between 7 and 10% in the most abundant diameter classes within the system. Age independent models slightly increased the error (≈15%) compared to age dependent formulations but they can be very useful since age it is not necessary to be estimated.

Diameter increment models were estimated to study competition in open stands like those encountered in dehesas, also comparing age dependent and age independent formulations. The models selected density as one of the significant covariates, hence there was competiton between trees, which most probably was symmetric competition between radical systems. Competition for light is reduced or absent in the system, and this was the reason explaining that age, or DBH as a substitute in age independent models, were the covariates explaining more variability. Gamma generalized linear models outcompeted log-transformed gaussian models, resulting in more parsimonious models.

We followed analyzing the state of the art in acorn production, and concluded that despite the great importance of fruit production of the system, there are no detailed studies able to explain this complex phenomenon, hence making system modeling today impossible.

Finally we studied the effect of the tree upon the understory, discussing the spatial and temporal variability of an interaction traditionaly believed to be static and constant. In average, grass production was higher below the canopy in the poorest soils. However, tree-grass interaction was variable in time and space, changing the interaction when abiotic water stressed increased in the drought year. Nutrient increase below canopy drove the increase in production, however and in spite of other authors reporting opposite results, it did not increase grass tissue nutrient concentration, with the exception of K and to a lower extent Ca. Modifications by trees in the understory, particularly pasture quality, seem to be most related to year variability, hence spatial variability induced by trees seems to be very reduced compared to variability driven by climate.

These models will help to model the system, but there are still unresolved questions, like fruit production or the effect of different silvicultural practices upon growth, that make still not possible to implement a complete systemic model.

PRÓLOGO

La presente tesis doctoral ha sido realizada gracias a una beca de formación predoctoral, incluida dentro del proyecto ‘Técnicas silvopascícolas para la gestión sostenible de las dehesas españolas y de los ranchos californianos’ financiado por el Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria (INIA).

Los resultados de esta tesis se han plasmado en seis artículos de los cuales dos están ya publicados, tres se encuentran en fase de revisión en revistas científicas incluidas en el Science Citation Index (SCI) y uno se presenta como manuscrito previo a su envío para su publicación en una revista científica. Estos seis trabajos se incluyen como anexos, y en ellos pueden encontrarse más extendidos los contenidos y métodos de la tesis, los cuales han sido resumidos en la memoria para facilitar su lectura y comprensión. Los artículos incluidos en los anexos, los cuales se corresponden con los capítulos, son los siguientes:

- **Anexo I**: Gea-Izquierdo G, Martín-Benito D, Cañellas I. Climate-growth variability in *Quercus ilex* L.: is there a climatic signal shared by tree species along the Mediterranean? En revisión.

- **Anexo II**: Gea-Izquierdo G, Cañellas I, Montero G. 2008. Site index in agroforestry systems: age-dependent an age-independent dynamic diameter growth models for *Quercus ilex* in Iberian open oak woodlands. Canadian Journal of Forest Research 38, 101-113.

- **Anexo III**: Gea-Izquierdo G, Cañellas I. Analysis of holm oak intraspecific competition using Gamma regression. En revisión.

- **Anexo IV**: Gea-Izquierdo G, Cañellas I, Montero G. 2006. Acorn production in Spanish holm oak woodlands. Investigación Agraria, Sistemas y Recursos Forestales 15(3), 339-354.

- **Anexo V**: Gea-Izquierdo G, Montero G, Cañellas I. Changes in limiting resources determine spatio-temporal variability in tree-grass interactions. En revisión.

- **Anexo VI**: Gea-Izquierdo G, Allen-Díaz B, San Miguel A, Cañellas I. Tree influence upon mediterranean annual grassland nutrient variability. Manuscrito.

1.

Introducción:

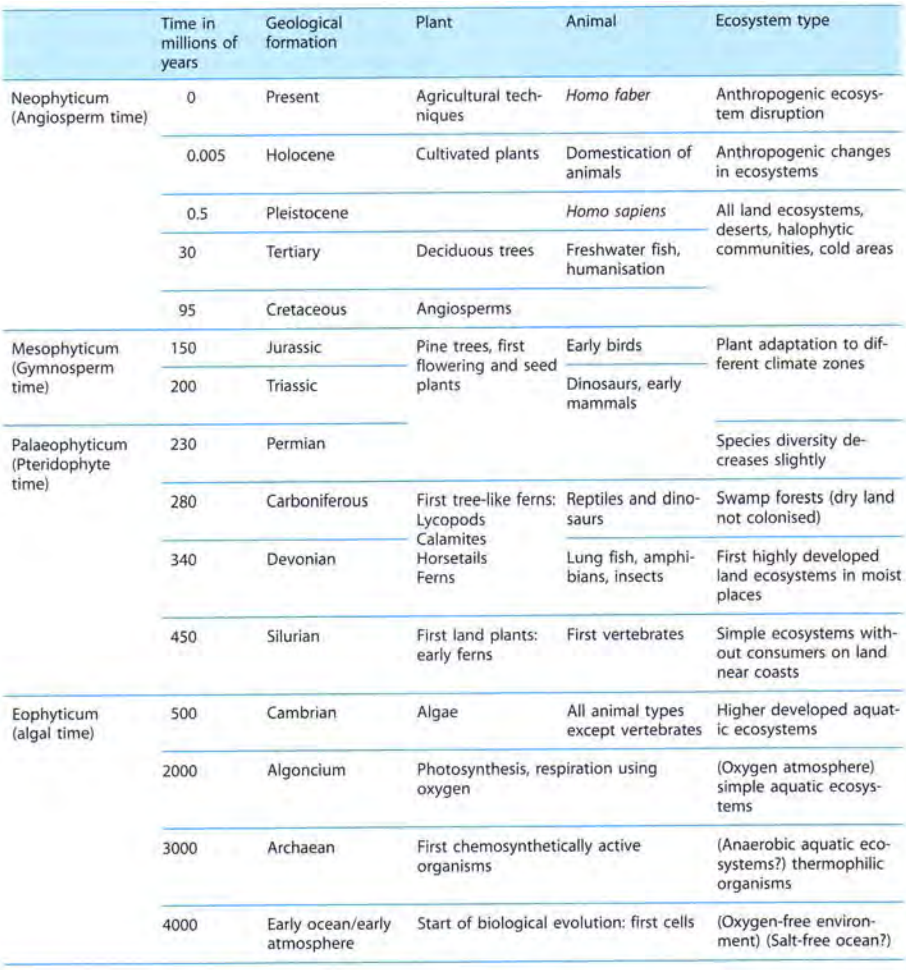
La dehesa y la gestión forestal

1. INTRODUCCIÓN

El medio natural y su correcta gestión gozan cada día de un mayor reconocimiento en las políticas nacionales e internacionales, y en la sociedad en general. La gestión sostenible de los recursos naturales requiere de técnicas y conocimientos objetivos basados en estudios científicos contrastados. Para desarrollarlos es necesario conocer tanto la ecología de los ecosistemas como su historia e interrelaciones. Por este motivo, en primer lugar presentamos una breve introducción a la historia y ecología del ecosistema y la especie motivos de estudio en este trabajo, es decir, la encina (*Quercus ilex* L.) en las dehesas del oeste y suroeste de la Península Ibérica. En segundo lugar se desarrollan seis capítulos en los cuales se estudian diferentes elementos que componen el sistema, en particular el crecimiento en diámetro de la encina, el efecto de la competencia sobre el crecimiento en diámetro, la producción de fruto y el efecto del árbol sobre la producción, composición y calidad del pasto herbáceo. Estos estudios aislados deberían formar parte, en un futuro no muy lejano, de un modelo de sistema global que permita gestionar adecuadamente el ecosistema que se estudia. Los contenidos que se desarrollan a continuación están complementados en los siete anexos con que se concluye este trabajo.

1.1 Breve historia de la dehesa

La dehesa es un sistema agrosilvopastoral localizado en el Oeste de la Península Ibérica y por tanto en el occidente de la región Mediterránea. Además de la historia, las características del clima y el sustrato geológico sobre el que se encuentra, su existencia, al igual que la de todos los ecosistemas forestales de esta región, no puede entenderse sin analizar el papel desempeñado por el hombre como factor transformador primordial del paisaje a lo largo de la Historia (Scarasccia-Mugnozza, 2000; García Gómez *et al.*, 2003). La tierra posee una edad estimada de unos 4600 millones de años, mientras que se piensa que el primer homínido (*Australopithecus afarensis*) que caminó por primera vez erguido lo hizo hace sólo alrededor de 3,2 millones de años en el Plioceno (Meléndez Hevia, 2004; Arsuaga y Martínez, 1998), aunque esta fecha acaba de ser revisada por algunos autores hasta 6 millones de años (Richmond y Jungers, 2008). Se considera que esto coincidió con cambios en el clima de algunas regiones (Arsuaga y Martínez, 1998) que en África Oriental dieron lugar a la transformación del bosque tropical en sabanas abiertas permitiendo el fin de la vida arborícola de algunos homínidos. A su vez, estos cambios coincidieron en la región Mediterránea con el inicio de la sequía estival (Suc, 1984) y por tanto del clima Mediterráneo que caracteriza y determina el área de estudio donde se engloba esta tesis doctoral. Hoy se cree que el primer homínido conocido en Europa y en la Península Ibérica llegó hace al menos 1,2 millones de años (Carbonell *et* *al*., 2008), aunque constantemente se están realizando nuevos hallazgos que en breve podrían modificar estas fechas y teorías. Estas comunidades paleolíticas eran cazadores-recolectores (Arsuaga y Martínez, 1998) y de igual manera que los homínidos precedentes, es muy probable que no provocaran un gran impacto sobre los bosques. El verdadero impacto del hombre en los bosques es por tanto muy reciente (Figura 1), comenzando con el inicio de la agricultura (Kimmins, 2004) en el Neolítico, es decir, alrededor del 9000 a.C. en Mesopotamia, y no llegando a la Península Ibérica posiblemente hasta alrededor del 5000 a.C. (Maroto, 1998).



	Time in millions of years	Geological formation	Plant	Animal	Ecosystem type
Neophyticum (Angiosperm time)	0	Present	Agricultural techniques	*Homo faber*	Anthropogenic ecosystem disruption
	0.005	Holocene	Cultivated plants	Domestication of animals	Anthropogenic changes in ecosystems
	0.5	Pleistocene		*Homo sapiens*	All land ecosystems, deserts, halophytic communities, cold areas
	30	Tertiary	Deciduous trees	Freshwater fish, humanisation	
	95	Cretaceous	Angiosperms		
Mesophyticum (Gymnosperm time)	150	Jurassic	Pine trees, first flowering and seed plants	Early birds	Plant adaptation to different climate zones
	200	Triassic		Dinosaurs, early mammals	
Palaeophyticum (Pteridophyte time)	230	Permian			Species diversity decreases slightly
	280	Carboniferous	First tree-like ferns: Lycopods Calamites Horsetails Ferns	Reptiles and dinosaurs	Swamp forests (dry land not colonised)
	340	Devonian		Lung fish, amphibians, insects	First highly developed land ecosystems in moist places
	450	Silurian	First land plants: early ferns	First vertebrates	Simple ecosystems without consumers on land near coasts
Eophyticum (algal time)	500	Cambrian	Algae	All animal types except vertebrates	Higher developed aquatic ecosystems
	2000	Algoncium	Photosynthesis, respiration using oxygen		(Oxygen atmosphere) simple aquatic ecosystems
	3000	Archaean	First chemosynthetically active organisms		(Anaerobic aquatic ecosystems?) thermophilic organisms
	4000	Early ocean/early atmosphere	Start of biological evolution: first cells		(Oxygen-free environment) (Salt-free ocean?)

Figura 1. Cuadro cronológico mostrando la evolución de las diferentes formas de vida en la Historia de la Tierra (tomado de Schulze *et al*., 2002; pág. 469).

Muchas zonas forestales fueron transformadas para usos agrícolas desde épocas anteriores a la dominación romana. De igual manera, muchos montes españoles fueron aprovechados desde antiguo, habiendo tenido un gran impacto sobre ellos, entre otros, su uso como fuente de energía y materia prima directamente en los hogares o en industrias como la minería y el sector naval (Manuel y Gil, 1999; Costa *et al*., 2005). El término dehesa proviene del término latino "*deffesa*", que describe terrenos acotados o protegidos del libre pastoreo y reservados para el ganado de labor. Este término aparece por primera vez en el Fuero Juzgo en el siglo VII (Joffre *et al*., 1999) pero cobró especial importancia en el s. XIII, con la fundación del Honrado Concejo de la Mesta en 1273 (el cual duró hasta 1836) y la necesidad de proteger ciertos montes a la entrada de sus rebaños (San Miguel, 1994; Costa *et al*., 2005; Ezquerra y Gil, en prensa). Sin embargo, algunos autores consideran que la existencia de una estructura adehesada parecida a la que hoy encontramos podría haber existido en determinadas zonas del SO de la Península ya anteriormente al año 2000 a.C., coincidiendo con los primeros impulsos de la industria de la vid en la región (Stevenson y Harrison, 1992). En cualquier caso, e independientemente de la influencia que los antiguos pobladores pudieron ejercer sobre el medio con anterioridad a la Edad Media, la estructura actual de las zonas de dehesa del Oeste Peninsular tiene su origen fundamental en los procesos de Reconquista cristiana y posteriores repoblaciones humanas de las zonas situadas al sur del río Duero. Hay referencias a dehesas desde la Baja Edad Media (San Miguel, 1994; Linares y Zapata, 2003) y como se ha comentado, además de la Reconquista hay que reseñar la importancia de la Mesta desde el s. XIII en la distribución y aprovechamiento de los sistemas forestales y pastos de toda España, incluidas las zonas hoy ocupadas por dehesas, las cuales tradicionalmente formaban parte de los pastos de invierno del ganado trashumante en el Oeste peninsular.

La influencia del hombre ha sido fundamental en la selección de especies y composición de las masas forestales. En este sentido, la encina ha sido favorecida tradicionalmente frente a otras especies en las dehesas (Ezquerra y Gil, en prensa). El arbolado de las dehesas fue protegido en múltiples lugares por los beneficios que proporcionaba (leña, cobijo, ramón y sobre todo bellotas [García Gómez *et al*., 2002]), pero esta protección se centró en el arbolado adulto, por lo que muchas dehesas desaparecieron por falta de regeneración (Ezquerra y Gil, en prensa). Además, grandes superficies arboladas se perdieron en Extremadura en la edad moderna debido a los incendios causados por los pastores trashumantes y por roturaciones periódicas (DGB, 1999; Ezquerra y Gil, en prensa). A pesar de todo, es muy probable que grandes áreas del Oeste Peninsular se mantuvieran arboladas al menos hasta el s. XIX. Los montes huecos a los que hacen referencia algunos autores en la Edad Media (Linares y Zapata, 2003) posiblemente se limitaran a las zonas más fértiles y cercanas a los núcleos habitados, que probablemente fueron deforestadas antes incluso de la Reconquista (Manuel y Gil, 1999). Posiblemente algunas dehesas tengan su origen en los comienzos de la Edad Moderna o incluso en la Edad Media y hayan sido mantenidas hasta nuestros días mediante siembras, exclusiones rotacionales al pastoreo y/o porque las cargas y usos fueran menos intensivos (Gallego Fernández y García Novo, 1997). Sin embargo, muy probablemente muchas de esas primeras dehesas estén hoy desarboladas, habiéndose transformado ya en baldíos o en zonas de matorral. La baja población de muchas de las áreas del Oeste Peninsular hasta el s. XIX y los cambios socioeconómicos derivados de este aumento poblacional, así como de los procesos desamortizadores y grandes roturaciones que se produjeron en ese siglo, hacen pensar que la mayoría de las dehesas sean mucho más jóvenes. De este modo, es muy probable que muchas hayan sido creadas principalmente por actuaciones antrópicas sobre terrenos incluidos en las Desamortizaciones de Madoz y Mendizábal en el s. XIX y sobre bosques que previamente no habían sido objeto de aprovechamiento constante o directo como dehesas (Gallego Fernández y García Novo, 1997; Martín Vicente y Fernández Alés, 2006; Ezquerra y Gil, en prensa). Este hecho es de suma importancia ya que, de ser esto cierto, el arbolado de la mayoría de las dehesas que hoy encontramos estaría en su primer “turno” de aprovechamiento. Finalmente, parece ser que la estructura de las dehesas se ha mantenido relativamente constante desde mediados del s. XX (García del Barrio *et al*., 2004), a lo que contribuye la falta de regeneración del arbolado en el sistema (Pulido *et al*., 2001; Pulido y Díaz, 2005).

1.2 El clima de la Península Ibérica y su influencia en la distribución de los bosques

Son muchos los cambios climáticos que ha sufrido el planeta a lo largo de su Historia, habiendo sido algunos de ellos la causa más probable de grandes extinciones de animales y plantas (Meléndez Hevia, 2005). Acabamos de situar el origen de la agricultura como punto de partida para entender la ecología de muchos ecosistemas. La razón por lo que el hombre comenzó la agricultura es incierta (Maroto, 1998) pero posiblemente no fue una casualidad que comenzara en el Próximo Oriente y después de la última glaciación. Más bien se considera que podría ser una consecuencia de ella, y de los ajustes ecológicos que provocó el deshielo (Maroto, 1998). Por ello un cambio de clima pudo dar origen a la civilización humana actual y a la vegetación que la ha sustentado. Actualmente el mundo científico es casi unánime en considerar el calentamiento global sufrido las últimas décadas como una consecuencia de las actividades antrópicas (IPCC, 2001; Raupach *et al*., 2007). Las repercusiones del cambio climático, como se ve, pueden ser beneficiosas o perjudiciales dependiendo de la región y de la época. En cualquier caso, los cambios climáticos son un hecho que la gestión forestal debe tener en cuenta, ya que las consecuencias sobre la población pueden ser muy graves si el calentamiento sigue acelerándose como viene ocurriendo durante las últimas 4-5 décadas.

En la Figura 1 se muestra la cronología evolutiva de los distintos grupos de organismos vegetales. Las angiospermas surgieron a finales del Mesozoico, habiéndose extendido, diversificado y dominado en muchas zonas (como en las ocupadas por las dehesas) en el Cenozoico (Meléndez Hevia, 2005; Schulze *et al*., 2005). Para comprender la fitogeografía ibérica actual hay varios hechos necesariamente reseñables. El clima del período terciario se considera a grandes rasgos como húmedo y cálido, lo cual permitía el desarrollo de vegetación semejante a la macaronésica, al menos en muchas zonas del litoral y valles interiores. La crisis del Messiniense (último piso del Mioceno Superior), hace 6,5 millones de años, cuando retrocedió la línea de costas en el Mediterráneo y se conectaron África y Europa a través del Estrecho de Gibraltar, permitió grandes migraciones de muchos táxones no presentes antes en Iberia, la cual acababa de convertirse en Península (Costa *et al*., 2005; Meléndez Hevia, 2005). Además, independientemente de que en el período Terciario haya habido oscilaciones climáticas, como se ha comentado, se cree que no fue hasta hace 3,2 millones de años cuando se comenzó a formar el clima mediterráneo, con su característica sequía estival (Suc, 1984). En el Holoceno, parece que la mediterraneidad del clima se ha ido acentuando y extendiendo hacia el norte, con los consiguientes reajustes de la vegetación (Jalut *et al*., 2000), y este fenómeno podría estar aún sucediendo. A su vez, la distribución de las Cordilleras ha limitado la migración de especies en el eje Norte-Sur europeo, lo cual ha motivado que la riqueza en especies arbóreas de la Península Ibérica, con cadenas montañosas en dirección E-O, sea reducida en comparación con la de latitudes homólogas de América o Asia (Costa *et al*., 2005), donde estas cadenas están distribuidas en dirección N-S. Además, el hombre ha simplificado en muchos casos la estructura del bosque, seleccionando determinadas especies, por lo que la ya de por sí baja diversidad en especies arbóreas se ve aún más reducida (Ezquerra y Gil, en prensa).

La Península Ibérica se puede dividir en dos grandes zonas climáticas, matizadas en las zonas de montaña: (i) la Iberia templada o atlántica, al Norte de la Cordillera Cantábrica; (ii) la Iberia Mediterránea, en el resto. Aunque la geografía diversifica los tipos climáticos, genéricamente uno y otro se diferenciarían por la ausencia (templado) o presencia (mediterráneo) de una sequía estival acusada (Rivas Martínez, 1987; Rivas Martínez y Loidi, 1999; Costa *et al*., 2005). Las dehesas se sitúan bajo clima mediterráneo típico, con inviernos más fríos cuanto más al norte y mayor distancia al Océano Atlántico.

El género *Quercus* es posiblemente el más importante entre las frondosas en el hemisferio Norte, y su abundancia se ha visto incrementada tras el fin de la última glaciación hace más de 10.000 años. A excepción del óptimo templado alrededor del

5000 a.C. (Carrión, 2002; Schulze *et al*., 2004) donde tal vez pudo haber una mayor expansión de especies submediterráneas y eurosiberianas, se puede considerar que la mayoría de las áreas del Oeste y Suroeste peninsulares ocupadas por dehesas hoy en día (Figura 2) han sido durante el Holoceno zonas óptimas para las especies de *Quercus* perennifolios, particularmente *Quercus ilex* L. (encina) y *Quercus suber* L. (alcornoque). La dehesa es una transformación/simplificación del bosque primigenio. Independientemente de que pudieran existir claros formados/usados por el ganado en zonas aclaradas por la dinámica natural del bosque (fuegos principalmente), si el bosque no llegaba a ser mixto, sí al menos debió de estar formado por rodales de diferentes especies en mosaico a escala de paisaje, incluyendo pinos como *Pinus pinea* L. o *Pinus pinaster* Ait., encinas, alcornoques, robles submediterráneos como rebollos (*Quercus pyrenaica* Willd.) o quejigos (*Quercus faginea* Lam.) y fresnos (*Fraxinus angustifolia* Vahl.), entre otras especies. Esta masa ocuparía casi toda la extensión que hoy constituyen las zonas de dehesa desde Salamanca hasta Sevilla-Huelva (Ezquerra y Gil, en prensa).

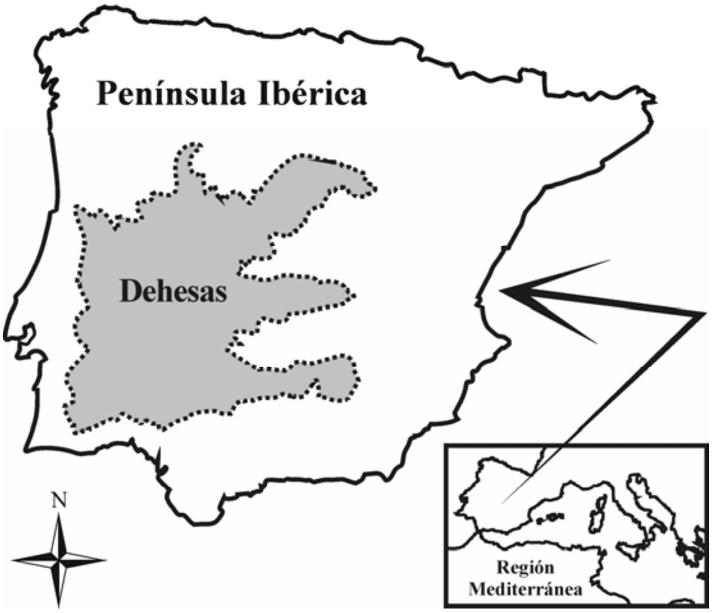


Figura 2. Distribución genérica de la dehesa de *Quercus* en la Península Ibérica.

Existen, por otro lado, dos períodos climáticos claramente diferenciados entre los descritos en la bibliografía a lo largo de la Historia reciente: uno cálido en la Edad Media y uno frío posterior, denominado Pequeña Edad del Hielo (LIA) que se extiende desde el s. XIV hasta mediados del s. XIX (Guiot *et al*., 2005; Luterbacher *et al*., 2006). La importancia que estos ciclos hayan podido tener en la dinámica de regeneración y establecimiento de las dehesas es algo que no se conoce, aunque como se ve, estos dos episodios climáticos son susceptibles de haber influido en la historia de la práctica totalidad de las dehesas que nos encontramos hoy en día, máxime cuando éstas llevan décadas donde la regeneración es muy reducida o nula (García del Barrio *et al*., 2004; Pulido *et al*., 2001; Pulido y Díaz, 2005).

El estudio del paleoclima y sus efectos sobre la flora y la vegetación es complejo. El aumento global de temperaturas detectado y en gran medida atribuido a la masiva emisión de gases de efecto invernadero (GHG) también afecta a la Península Ibérica (Guiot *et al*., 2005; Luterbacher *et al*., 2006; Raupach *et al*., 2007) y por tanto a las dehesas. Existen muestras de cambios abruptos en el clima en el pasado (Martrat *et al*., 2004; Overpeck y Cole, 2006), que ponen sobre aviso de cómo podrían producirse en cualquier momento cambios climáticos mucho más rápido de lo que se espera, lo cual supone un gran peligro potencial. Las tendencias en las precipitaciones no son tan claras como en el caso del aumento global de temperatura (Sumner *et al*., 2003; Luterbacher *et al*., 2006; Zhang *et al*., 2007). En algunas zonas del Este de la Península Ibérica se ha detectado una disminución de las precipitaciones y un aumento de su variabilidad (González-Hidalgo *et al*., 2001; Sumner *et al*., 2001), mientras en el Oeste de la Península Ibérica se ha detectado una disminución general de las precipitaciones, aunque esta reducción no es significativa en todas las zonas ocupadas por dehesas (Esteban Parra *et al*., 1998; Rodrigo y Trigo, 2007). En cualquier caso, el aumento de las temperaturas hace suponer que aumentará la evapotranspiración potencial (ETP), y por lo tanto las situaciones de estrés hídrico en un clima como el mediterráneo previsiblemente se incrementarán, con el consiguiente efecto sobre las especies vegetales. En este sentido, es probable que se produzcan reajustes en la distribución de muchas especies, que podrán desaparecer en algunas zonas y modificar su crecimiento en otras. El aumento en la temperatura y los niveles de GHGs previsiblemente no tendrá la misma repercusión ni en todos los lugares ni en todas las especies. En la región mediterránea, podría esperarse un aumento en el estrés hídrico como consecuencia del calentamiento en las masas más termófilas, lo cual podría ser negativo, pero a su vez podría producirse un efecto de fertilización por el aumento del CO_2 e incluso el aumento de la temperatura y alargamiento del período vegetativo podrían mejorar las condiciones de crecimiento en las masas más frías de montaña (Tognetti *et al*., 2000; Carrer y Urbinati, 2006; Soulé y Knapp, 2006; Andreu *et al*., 2007).

1.3 El suelo y el clima de la dehesa

La Península Ibérica actual no se formó hasta bien entrado el Cenozoico, al término de la Orogenia Alpina en el Mioceno (Costa *et al*., 2005; Meléndez Hevia, 2005). La zona objeto de estudio ocupada por la dehesa (Figura 2) se sitúa en el Oeste peninsular principalmente sobre materiales pertenecientes a las unidades geológicas del: (i) Macizo

Ibérico (también conocido como Varisco, Hespérico o Herciniano), particularmente las zonas Centroibérica, de Ossa Morena y Surportuguesa; (ii) cadenas sin cobertera plegadas en la Orogenia Alpina del Antepaís Ibérico (y por tanto incluidos en el basamento Varisco); (iii) cuencas cenozoicas del Antepaís Ibérico (Vera, 2004; Meléndez Hevia, 2005). La dehesas están asentadas bien sobre materiales paleozoicos influidos por los plegamientos cenozoicos de la Orogenia Alpina (cuencas de Antepaís) o bien sobre cuencas cenozoicas rellenadas con los materiales paleozoicos (principalmente procedentes de pizarras, esquistos, cuarcitas, gneises, granitos) erosionados. En la cuenca del Guadalquivir además de materiales variscos también se localizan otros más modernos (sobre todo mesozoicos) provenientes de las cordilleras Béticas (Vera, 2004; Meléndez Hevia, 2005). Las dehesas, por tanto, se extienden por los terrenos no aptos para la agricultura generalmente proterozoicos o paleozoicos del piedemonte del Sistema Central, de Sierra Morena y de los Montes de Toledo y penillanuras variscas del occidente ibérico, así como los cenozoicos de los valles del Tajo, Guadiana y Guadalquivir (Vera, 2004; Meléndez Hevia, 2005).

Los sustratos son generalmente arenosos, de pH ácido, con poca fertilidad y malas condiciones físicas, de ahí su escasa o nula aptitud agrícola, encontrándose desde suelos con un desarrollo muy escaso, como leptosoles y regosoles, hasta otros más desarrollados como cambisoles y luvisoles, donde ya aparecen horizontes de acumulación (Gómez Gutiérrez, 1992; Brady y Weil, 2002; Jones *et al*., 2005; DGB, 1999). En estas condiciones de baja fertilidad posee gran importancia la redistribución de nutrientes por la morfología ondulada, generándose un mosaico de comunidades vegetales que siguen los patrones de suelos con diferente fertilidad según se encuentren en el fondo de las vaguadas (suelos enriquecidos y con compensación hídrica), en las laderas o en las crestas (Montserrat, 1975; Puerto y Rico, 1992; San Miguel, 1994, 2001).

El clima en las dehesas es típicamente mediterráneo, lo que implica una marcada sequía estival entre junio y septiembre que condiciona el desarrollo de la vegetación y los aprovechamientos. La variabilidad en el clima es la norma, encontrándose generalmente los valores anuales medios de precipitación alrededor de 500-600 mm. La precipitación es muy variable tanto entre años como dentro del mismo año, con los máximos pluviométricos concentradas en otoño y primavera. Las temperaturas son variables, presentándose grandes oscilaciones entre máximas y mínimas y haciéndose más continentales cuanto más alejadas se encuentran las dehesas de la costa atlántica. La mayoría de las dehesas están localizadas en ombrotipos que van de secos a húmedos, siendo los termotipos mesomediterráneos y supramediterráneos (sobre todo inferior) los más habituales (Rivas Martínez, 1987). Las dehesas están localizadas en la provincia

Mediterránea Iberoatlántica, en particular en la subprovincia Luso-Extremadurense y sur de la subprovincia Carpetano-Leonesa (Rivas Martínez y Loidi, 1999).

1.4 Ecología de la dehesa

La ecología de la dehesa está condicionada por las características del clima y el suelo, brevemente descritas en el apartado anterior. El sistema está compuesto por un mosaico de diferentes teselas de vegetación. En general, el matorral y formaciones de monte bajo ocupan las zonas de más pendiente, mientras en las zonas más llanas la vegetación está compuesta por árboles en baja densidad con cultivos intercalados en los mejores suelos y pastizales naturales en los suelos no cultivados o en descanso entre cultivos (posíos). A su vez, y cómo las especies responden a los patrones ecológicos (Eviner y Chapin III, 2003) existen diversas comunidades de pastizales como se explica brevemente a continuación (San Miguel, 1994; Costa *et al*., 2005).

El carácter silvopastoral del sistema hace que el árbol y la vegetación subyacente interaccionen entre sí, además de con la fauna y el ganado. Esta interacción entre estratos vegetales se ha considerado tradicionalmente como beneficiosa para la vegetación subyacente al árbol (Montoya 1982a). Sin embargo, se ha demostrado que la interacción no tiene porqué ser siempre positiva, ni que sea más positiva al aumentar el estrés abiótico, es decir, cuanto más seco sea el clima o más pobre el suelo (Maestre *et al*., 2005; Brooker *et al*. 2008). El árbol genera una heterogeneidad edáfica y microclimática que provoca una diferenciación de las comunidades vegetales que se desarrollan bajo su copa respecto a las del exterior, aumentándose la biodiversidad a escala de ecosistema (González-Bernáldez *et al*., 1969; Marañón, 1986). Por tanto, a la heterogeneidad espacial creada por la topografía ondulada hay que añadir la heterogeneidad ambiental generada por el árbol. El árbol aumenta la fertilidad bajo su copa directamente como consecuencia del aporte de hojarasca y deposición de minerales por el agua de lluvia y la deposición seca (Escudero *et al*., 1985; Rhoades, 1997; Rodá *et al*., 1999) e indirectamente mediante la atracción que produce sobre los animales. Además, las temperaturas se suavizan bajo la copa, y se produce una redistribución del agua de lluvia (Montoya, 1982a; Joffre *et al*., 1988; San Miguel, 1994; Rhoades, 1997).

Las dehesas fueron creadas básicamente con una finalidad pastoral. Por tanto, el ganado y los animales silvestres poseen una gran importancia en la ecología del sistema, tanto en la redistribución de nutrientes y transformación de pastos (majadales) como a través de su influencia en la regeneración (o la ausencia de ella) (Gómez Sal *et al*., 1992; Malo *et al*., 2000; Pulido *et al*., 2001; Pulido y Díaz, 2005). La vegetación leñosa ha sido controlada tradicionalmente mediante rozas y quemas que posteriormente han de ser complementadas con pastoreo para que el matorral no vuelva a recolonizar. La vegetación que hoy encontramos en las dehesas está caracterizada por un estrato arbóreo del género *Quercus,* fundamentalmente encinas y alcornoques, pero también otros *Quercus* como melojos o quejigos, y un estrato de matorral que incluye diversas especies como jaras (*Cistus* sp.), brezos (*Erica* sp.), retamas (*Retama* sp.) y escobas (*Cytisus* sp.) o menos frecuentemente madroños (*Arbutus unedo* L.) y labiérnagos (*Phyllirea* sp.), entre otras (Gómez-Gutiérrez, 1992; Fernandes Lousa *et al*., 1999; Ladero y Amor, 1999; Costa *et al*., 2005). El estrato herbáceo es muy diverso como consecuencia de la acción del ganado, la topografía y el estrato arbóreo (Marañón, 1986; Puerto y Rico, 1992; Peco *et al*., 2006). Entre los principales grupos de herbáceas (excluyendo los cultivos), destacan los siguientes grupos, con diferente ecología y aprovechamiento (San Miguel 1994; 2001). En aras de la brevedad, en cada grupo se cita tan sólo la especie más destacada o característica, lo cual no significa que sea ni exclusiva de esa comunidad (aceptamos el término comunidad sin entrar en discusiones filosófico-ecológicas) ni la más abundante, ni la única especie característica:

(i) Pastos xero-mesofíticos de especies anuales y vivaces:

- Vallicares: localizados en suelos con compensación hídrica y caracterizados por *Agrostis castellana* Boiss. & Reut.;
- Majadales: comunidades de especies anuales-vivaces perpetuadas por el ganado, particularmente ovino, caracterizadas por *Poa bulbosa* L. y *Trifolium subterraneaum* L.;
- Berciales: caracterizados por *Stipa gigantea* Link.;

(ii) Pastos terofíticos dominados por especies anuales:

- Comunidades de especies anuales sobre suelos ácidos caracterizadas por *Xolantha guttata* (L.) Raf.;
- En suelos con gran contenido de arena los pastos de anuales están caracterizados por *Malcomia* sp.;
- Bonales: caracterizados por *Agrostis pourretii* Willd. en suelos con freatismo temporal pero de menor entidad que en vallicares;
- Posíos, o comunidades de herbáceas anuales nitrófilas que colonizan barbechos temporales (se cultiva cada 3-5 años) y están caracterizadas por gramíneas (géneros *Bromus, Avena* y otros*),* crucíferas, compuestas y otras familias, con muy amplia representación en las dehesas.

Es común en muchas dehesas cultivar los mejores suelos, generalmente con especies forrajeras como veza-avena, trébol-centeno o praderas de leguminosas, pero también últimamente con trigo y otros cultivos subvencionados por la Política Agraria Común (PAC). Finalmente, a su riqueza botánica hay que añadir en muchas zonas de dehesa la existencia de una gran riqueza faunística, que incluye especies tan amenazadas y emblemáticas como el águila imperial (*Aquila adalberti* Brehm) o el lince ibérico (*Lynx pardinus* Temminck), lo que les confiere un valor ecológico añadido.

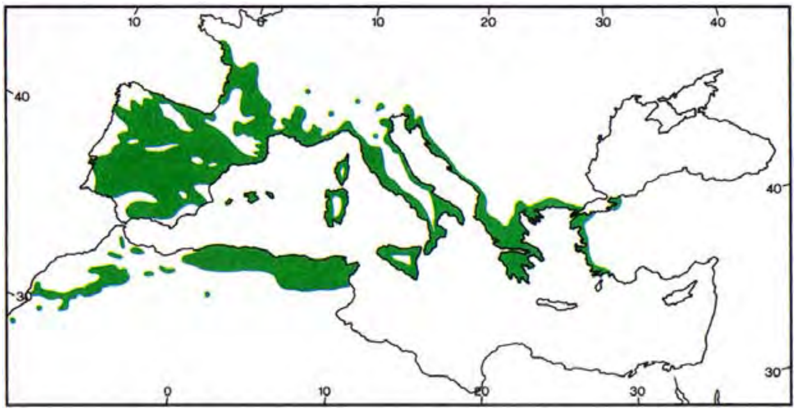


Figura 3. Distribución de la encina (*sensu lato*) en la región mediterránea (mapa extraído de Costa *et al*. 2005; pág.275).

1.5 La encina

La encina (*Quercus ilex* subsp. *ballota* (Desf.) Samp. = *Q. rotundifolia* Lam. = *Q. ilex* subsp. *rotundifolia* (Lam.) O. Schwarz ex Tab. Mor.) es la especie leñosa más extendida en las dehesas, además de por su gran amplitud ecológica y adaptación a las características edafoclimáticas de la zona ocupada por estas formaciones, por el hecho de haber sido favorecidas históricamente por el hombre. En la Figura 3 se muestra su distribución actual. La especie se adapta tanto a sustratos ácidos como básicos, y a una gran variedad de climas dentro del Mediterráneo, con termotipos desde termomediterráneos a submediterráneos y ombrotipos secos a hiperhúmedos, llegando por encima de los 2500 m en el Atlas marroquí y siendo capaz de aguantar las variantes más continentales mediterráneas en la Península Ibérica (Barbero *et al*., 1992; Costa *et al*., 2005). Es un taxon terciario dividido en dos morfotipos generalmente considerados subespecies: (i) *Quercus ilex* ssp. *ballota,* de zonas subcontinentales, que ocupa la práctica totalidad de la Península Ibérica y el Magreb, la cual es la subespecie incluida en las áreas de dehesas del Oeste peninsular; (ii) *Quercus ilex* ssp. *ilex*, más exigente en humedad y menos tolerante a la continentalidad, que ocupa el litoral mediterráneo desde Italia hasta Cataluña, así como diferentes enclaves cantábricos (Do Amaral, 1990; Barbero *et al*., 1992; Costa *et al*., 2005; López de Heredia, 2006).

La encina es una especie de hoja perenne, y aunque es monoica, tiende a la dioecia, presentando pocos ejemplares con muchas flores femeninas (y por tanto, frutos) y otros con más flores masculinas en forma de amentos colgantes (Ruiz de la Torre, 1979). Los frutos poseen una maduración anual. Generalmente la subespecie *ballota* no supera los 12-15 metros de altura (Do Amaral, 1990), siendo habituales en dehesas ejemplares que no superan los 10 metros como consecuencia de las podas. Se reproduce tanto por semilla como vegetativamente, por lo que se ha utilizado como combustible, razón por la que muchas masas se presentan en formación de monte bajo. Presenta un sistema radical extendido tanto horizontal como verticalmente (Canadell *et al*., 1996; Moreno *et al*., 2005). Se considera que puede alcanzar edades muy avanzadas aunque la estimación de estas edades no es un proceso sencillo por la anatomía y dureza de su madera, por lo que los valores proporcionados en la bibliografía suelen ser estimaciones subjetivas (Gené *et al*., 1993; Cherubini *et al*., 2003). La ecología ha sido muy estudiada principalmente en la subespecie *ilex* (Rodá *et al*., 1999) aunque también existen múltiples estudios en la subespecie *ballota* (Villar-Salvador *et al*., 1997; Corcuera *et al*., 2004). La encina es un taxon de evolución premediterránea, es decir pre-pliocena. En este sentido se ha puesto de manifiesto lo importante que resulta la facilitación por otras especies leñosas para el desarrollo de sus plántulas (Pulido y Díaz, 2005) lo cual coincidiría con tesis recientemente propuestas sobre la necesidad de facilitación de táxones terciarios por los cuaternarios para poder desarrollarse en las condiciones climáticas actuales (Valiente-Banuet, 2006). Al haber tenido una evolución terciaria, se considera una especie que tolera la sequía por medio de un sistema radical profundo que ocupa todos los perfiles edáficos (Rodá *et al*., 1999; Moreno *et al*., 2005). De este modo es capaz de extraer agua a bajo potencial hídrico, lo que le permite no necesitar un control estomático excesivo comparado con otras especies leñosas mediterráneas que se adaptan practicando un mayor ahorro de agua o llegando incluso a ser caducifolias facultativas (Peñuelas *et al*., 2000; Peñuelas *et al*., 2001; Ferrio *et al*., 2003).

1.6 La modelización forestal en la dehesa

Los modelos ecológicos se pueden dividir en dos grandes grupos: modelos empíricos y modelos mecanísticos (Peng, 2000; Porté y Bartelink, 2002). Los dos tipos tienen ventajas e inconvenientes, aunque los más complejos modelos mecanísticos expliquen con más detalle ciertos procesos biológicos, los empíricos son más susceptibles de ser usados en gestión y, en cualquier caso, todos los modelos tienen una parte de empirismo ya que deben ser contrastados con datos reales. Como la utilidad de los modelos dentro de unos límites aceptable de exactitud es lo que delimita lo apropiado o no de su uso, y ante la inexistencia de modelos de gestión del encinar en dehesas, hemos optado en este trabajo por utilizar modelos empíricos.

No existen hasta la fecha modelos de crecimiento de la encina que puedan ser utilizados en los planes de ordenación silvopascícola. Por ello es necesario desarrollar alguno que permita comprender el papel del arbolado en el sistema para poder gestionarlo. Estimar los crecimientos anuales en secciones de encina no es sencillo, pero sí posible como muestran varios estudios dendroecológicos (Zhang y Romane, 1991; Gené *et al*., 1993; Nabais *et al*., 1998-99; Cherubini *et al*., 2003; Campelo *et al*., 2007a). La dendroecología es una rama de la Dendrocronología, ciencia que estableció sus fundamentos a finales del s. XIX y que ha sido muy utilizada para diversos fines, entre ellos estudiar relaciones entre el crecimiento de especies leñosas y el clima, así como para datar muestras de madera e individuos o reconstruir la historia ecológica de los rodales (Fritts, 1976; Cook y Kairiukstis, 1990).

Conceptos típicamente forestales como, por ejemplo el índice de calidad de estación o las ecuaciones de crecimiento en altura (Vanclay, 1994, 1995; Prodan *et al*., 1997; Kiviste *et al*., 2002; Madrigal, 2003) no pueden ser directamente aplicados en las dehesas por las características del arbolado (baja densidad y podas). Sí pueden analizarse otras variables utilizadas típicamente en modelos forestales, como por ejemplo el crecimiento en diámetro, aunque con criterios distintos a los utilizados en montes maderables, ya que en un sistema silvopastoral la madera no es un producto prioritario. La edad es una covariable de máxima importancia en los modelos biológicos. Por esta razón la mayoría de los modelos forestales, bien en forma diferencial, en diferencias o integral la incluyen (Vanclay, 1994). Sin embargo, en especies como la encina donde la estimación de las edades es difícil, resulta interesante proponer modelos independientes de la edad siempre que el incremento en el error sea aceptable para facilitar su uso por gestores e investigadores. Las ecuaciones en diferencias algebraicas se han usado en los últimos años para implementar ecuaciones dinámicas de crecimiento en altura y diámetro, ya que reducen sensiblemente el error de predicción en comparación con las ecuaciones en forma integral, entre otras características deseables (Cieszewski y Bailey, 2000). Normalmente las ecuaciones en diferencias que se usan en la bibliografía están definidas en función del tiempo y dependen directamente de la edad en su formulación. En este sentido, recientemente se han propuesto modelos dinámicos independientes de la edad que, pese a sus mayores limitaciones, pueden resultar muy atractivos para modelizar especies como la encina o masas donde sea problemático estimar la edad (Tomé *et al*., 2006).

Por otro lado, la competencia y su influencia en el crecimiento es algo que debe estudiarse para modelizar el sistema. Se han utilizado múltiples índices para estudiar la competencia en sistemas forestales, incluyendo formulaciones dependientes e independientes de la distancia, las cuales incluyen distintas covariables susceptibles de influir en la competencia, tales como dimensiones de la copa, diámetros, alturas o densidad del rodal (Tomé y Burkhart, 1989; Biging y Dobbertin, 1995; Larocque, 2002). En dehesas, es común suponer que los árboles siguen un crecimiento libre (Hasenauer, 1997) porque el concepto de dominancia y crecimiento libre está particularmente ligado a la competencia asimétrica por luz entre copas. Ésta debería ser nula o casi nula en la mayoría de las dehesas y muy reducida en rodales con arbolado más denso (que formarían un estrato de copas dominante-codominante) comparado con los bosques típicamente estudiados en ecosistemas forestales. Sin embargo, si la extensión de los sistemas radicales es la que suponen ciertos estudios (Moreno *et al.*, 2005), es de esperar que exista competencia radical, al menos en los rodales de mayor densidad. Por tanto, también resulta necesario estudiar el efecto de la competencia en los modelos de crecimiento, lo cual suele realizarse ajustando ecuaciones de incremento en diámetro, en las cuales sí suele resultar más sencillo derivar formulaciones independientes de la edad.

1.7 Selvicultura y gestión sostenible de la dehesa

Desde casi el inicio de las prácticas selvícolas por los ingenieros de montes en el s. XIX, se reconocieron las peculiaridades de las masas mediterráneas y la necesidad de un aprovechamiento agrosilvopastoral en contraposición al meramente maderero de muchos montes altos europeos (Linares, 2007). Las dehesas no son susceptibles de aprovechamiento forestal o agrícola clásico, por las condiciones ya descritas de suelo y clima descritas. La dehesa es un sistema formado a través de la agro-silvo-pascicultura, es decir, mediante cultivo eventual, aclareos, entresacas, resalveos, fuegos pastorales, siembras y rozas con una finalidad pastoral. Como se ha comentado, no se puede entender el sistema sin la participación del hombre, y en este sentido nos encontramos con un difícil reto: proponer modelos de gestión sostenible adecuados para la situación socioeconómica de las zonas de dehesa en el s. XXI. Para ello será necesario decidir qué quiere la sociedad y si es viable mantener estos ecosistemas mediante la gestión humana. Hasta el día de hoy la gestión de las dehesas se ha realizado fundamentalmente por medio de conocimientos empíricos tradicionales, con escasa participación técnica. Por ello, surge la pregunta: ¿cómo adaptar los modelos de gestión forestales de montes maderables al arbolado de las dehesas?, ¿es ello posible?, ¿tiene interés?

En la dehesa la madera es un producto secundario en comparación con el pasto (tanto herbáceo como de frutos). Pese a que existen diversos escritos que describen cómo debería ordenarse una dehesa (San Miguel, 1994; Madrigal, 2003) no es habitual que estos espacios cuenten con planes de ordenación. Generalmente las extensiones y sobre todo la titularidad privada de las fincas dificultan su gestión por técnicos especializados. En este trabajo nos centramos en las dehesas de encina, para las cuales, como se ha mencionado, no existen modelos que puedan usarse para gestionar el estrato arbóreo. Las masas de alcornoque, como consecuencia del interés que desde principios del siglo XIX posee el corcho, sí son objeto de una selvicultura específica, la cual ha sido estudiada y desarrollada en mayor medida que en las masas de encina. Sin embargo, estos estudios han sido principalmente desarrollados en monte alcornocal y sólo en menor medida en dehesas de alcornoque (Montero y Cañellas, 2003; Montero *et al*., 2003; Sánchez-González, 2005). En general, las actuaciones selvícolas en encinares no han respondido a un esquema organizado, incluyendo rozas, quemas y aclareos para favorecer la estructura abierta del arbolado, pero también como se ha mencionado, una activa selección de la especie por parte del hombre, ya mediante empobrecimiento del bosque anterior o mediante siembras (Montoya, 1982b; Gómez-Gutiérrez, 1992; San Miguel, 1994; Étienne, 1996). Además hasta los años 60 del siglo pasado la leña poseía gran importancia económica, una de las razones por las que se han efectuado podas sistemáticamente. Actualmente está prohibido cortar encinas, práctica que fue común hasta mediados del siglo XX, por lo que no se realizan prácticas selvícolas reseñables, más allá de podas y cortas según un turno biológico, es decir, cuando mueren las encinas de forma natural. En los últimos años se han realizado numerosas reforestaciones en el Oeste español con el objetivo de recuperar y rejuvenecer superficies agrícolas abandonadas y dehesas degradadas.

El ganado es un componente fundamental de las dehesa. El sistema sustenta a diversas especies de ganado, como cerdo ibérico, vacas, ovejas y cabras, que aprovechan los pastos complementariamente. Entre ellas es particularmente valioso desde el punto de vista económico (y gastronómico) el cerdo ibérico que aprovecha la montanera durante los tres últimos meses de vida. La actitud pastoral del sistema hace que las actuaciones sobre los pastos hayan sido mucho más investigadas que las actuaciones sobre los árboles, incluyendo fertilizaciones (fósforo y nitrógeno, principalmente), siembras, introducción de especies pastoralmente interesantes, formación de majadales o cultivos de especies forrajeras, entre otras (Olea *et al*., 1990-91; Martín Polo, 2003a, b; Olea y San Miguel, 2006). Actualmente está cobrando mucha importancia la gestión de las especies cinegéticas, por lo que las actividades de mejoras pastorales se están encaminando en múltiples ocasiones a mejorar su alimentación, siendo la caza actualmente la actividad más lucrativa en los montes españoles (San Miguel *et al*., 1996). Por tanto, si se decide desarrollar modelos sistémicos en la dehesa, éstos deben incluir todos los productos, incluyendo la producción de fruto, de leñas, la producción de madera al final del turno, la influencia del arbolado sobre el pasto herbáceo subyacente, la dinámica de la regeneración y los productos indirectos ambientales, entre otros (San Miguel, 1994). En este sentido, hoy en día existen bienes y servicios ambientales que se unen a los tradicionales intereses agrosilvopastorales del sistema y que confieren un valor añadido cuantificable que cada día cobra mayor importancia (Campos *et al*., 2001).

1.8 ¿Es la dehesa un ecosistema en extinción?

Antes de abordar aspectos de carácter estrictamente científico, parece conveniente plantear ciertas cuestiones de carácter más básico o fundamental, pero no por ello menos trascendentes, como: ¿tiene sentido construir y proponer nuevos modelos de gestión basados en estudios científicos o es, por el contrario, suficiente continuar con la gestión tradicional?, ¿es viable socioeconómicamente mantener el sistema dehesa desde una perspectiva socio-económica? Si los motivos ecológicos no fueran suficientes (el sistema dehesa es un hábitat protegido por la Directiva Europea Hábitats, y por consiguiente es obligado mantenerlo en un estado de conservación favorable), actividades como el aprovechamiento del cerdo ibérico en montanera parecen por sí mismas suficientes para convencer a intereses meramente productivos sobre la necesidad de conservar el sistema. Sin embargo, reconociendo las incertidumbres que encierra la historia de muchas de las dehesas lo cierto es que hoy éstas se encuentran en grave peligro de extinción en muchas zonas y en otras el sistema se encuentra en transformación. ¿Cuál es el futuro de las dehesas? Existen suficientes conocimientos hoy en día para realizar un análisis racional del sistema, sin caer en falsos conceptos idílicos y localistas sobre su realidad e importancia. La dehesa se suele ponderar como un ecosistema modélico desde el punto de vista del aprovechamiento sostenible, pero, ¿es esto verdad? La realidad es que no, los aprovechamientos en las dehesas no son sostenibles hoy en día por diversos motivos y cambios con respecto a la época en que la estructura actual se creó. Entre ellos es necesario destacar la ausencia de regeneración de muchos rodales (Santos y Tellería, 1987; Pulido *et al*., 2001; Pulido y Díaz, 2005); el abandono del campo y cambios en los usos agrícolas; el fin de las prácticas trashumantes; las cargas ganaderas y de especies cinegéticas excesivas como consecuencia de las políticas agrarias y la importancia de la caza en la socioeconomía actual (Fernández Alés *et al*., 1992); o las enfermedades y decaimiento del arbolado (Brasier, 1992, 1996; Rodríguez Molina *et al*., 2002; Navarro Cerrillo *et al*., 2004).

Las causas que dificultan la regeneración son varias. Pese a que en algunas zonas es posible que la falta de regeneración sólo sea debida a unas cargas animales excesivas o actividades como laboreos superficiales, en otras masas es muy probable que la actual degradación del suelo por usos abusivos sobre terrenos muy poco productivos bajo unas condiciones climáticas cada vez más estresantes (aumento de la temperatura, aumento de la ETP con el consiguiente estrés hídrico para las plántulas) sean las responsables de la ausencia de regeneración. Esta segunda razón debe ser monitorizada, ya que se considera que cuando se establecieron las dehesas actuales el clima era diferente, posiblemente más frío (Luterbacher *et al*., 2006). Por tanto esta falta de regeneración y la degradación del medio en muchas zonas (Pulido y Díaz, 2005), hace que este sistema forestal diste mucho de ser el paradigma de sostenibilidad que habitualmente se pondera. Sí es cierto que la existencia de un estrato arbolado y su estructura en mosaico encierran una gran riqueza ecológica que confiere a las dehesas un gran atractivo, sobre todo comparadas con eriales, matorrales degradados o cultivos circundantes, pero estas razones no deben ocultar su situación de degradación en muchos casos. Es de esperar que, ya por motivos climáticos (inducidos o no por el hombre) ya por la excesiva expansión que hoy en día deben tener los encinares como consecuencia de la actuación humana en la Historia, la regeneración natural pueda presentar dificultades o incluso no ser posible en los peores suelos o en las variantes más secas del clima. El decaimiento del arbolado también es un tema complejo donde seguramente serán responsables varios agentes. Además de patógenos como *Phytophthora cinnamomi* Rands entre otros, se ha señalado que los pies situados en las variantes más secas del clima sobre los peores suelos podrían ser los más afectadas por el decaimiento (Navarro Cerrillo *et al*., 2004). Estos temas deben ser monitorizados y analizados correctamente, pues no sólo las consecuencias ecológicas, sino también económicas que pueden conllevar, son muy graves.

Por tanto, la sociedad deberá preguntarse si quiere conservar el ecosistema, y qué precio se está dispuesto a pagar para conseguirlo. La definición de qué es una dehesa y cuál es su estructura y composición es problemática (San Miguel, 1994). Sin embargo, no pretendemos entrar en esa discusión ya que consideramos que no posee mayor relevancia para el presente trabajo. Lo verdaderamente importante es la comprensión de la ecología del medio y qué podemos hacer para mejorarlo y aprovecharlo racionalmente. El ámbito de esta tesis se sitúa en un ecosistema bajo clima mediterráneo sobre sustratos ácidos y pobres desde el punto de vista agronómico, los cuales han sufrido un fuerte impacto antrópico a los largo de miles de años de Historia. Dentro del amplio conjunto de sistemas agroforestales que hay en España (San Miguel *et al*., 2002), nosotros estudiamos el ejemplo de dehesa más típico y extendido, esto es, los sistemas adehesados del Centro, Oeste y Suroeste peninsulares, y en especial los dominados por *Quercus ilex* L. Por tanto los resultados y conclusiones de este trabajo se refieren exclusivamente a este sistema agrosilvopastoral ibérico, denominado dehesa en España y “montado” en Portugal (Pinto-Correia, 1993), independientemente de que localmente se denominen dehesas a múltiples sistemas agroforestales y bosques abiertos con vocación pastoral (San Miguel *et al*., 2002).

2.

Objetivos

2. Objetivos

El principal objetivo de la tesis es avanzar en el desarrollo de modelos de gestión silvopastoral sostenible en dehesas de encina. A lo largo de los seis capítulos siguientes se estudian el crecimiento e influencia del árbol y la densidad del rodal sobre el resto de productos cuantificables del sistema, de modo que estos modelos puedan ser integrados en un futuro modelo sistémico agrosilvopastoral. Los objetivos concretos por capítulos son:

(1) Estudiar el potencial de la encina en las dehesas para realizar estudios dendroecológicos. Se analizará en primer lugar si forma anillos de crecimiento anuales que puedan ser usados en los modelos de crecimiento. Además se estudiará qué variables climáticas resultan más influyentes en el crecimiento y si la respuesta al clima ha variado en las últimas décadas coincidiendo con el calentamiento global. Finalmente se compara la respuesta climática de la encina en la zona de estudio con la de otras especies en la Región Mediterránea.

(2) Obtener ecuaciones en diferencias algebraicas que permitan estimar el crecimiento en diámetro y la producción de madera. Ante las dificultades que los gestores tendrían para estimar con precisión la edad de las encinas, se compararán ecuaciones dependientes e independientes de la edad, y se discutirá el sentido y posible utilización de un índice de calidad de estación calculado según el crecimiento en diámetro potencial.

(3) Analizar el efecto de la densidad del rodal en el crecimiento en diámetro de encinares adehesados. Se comparan diferentes índices de competencia y ecuaciones que incluyen la edad como covariable y que no la incluyen, para poder utilizar estas últimas en gestión.

(4) Discutir y analizar el estado de conocimientos de la producción de bellota en las dehesas de encina, para detectar y proponer líneas de mejora en áreas deficitarias de conocimiento.

(5) Estudiar cómo la influencia del árbol, al modificar la fertilidad y el microclima, modifica la producción en biomasa y composición de comunidades herbáceas de ecología distinta y bajo escenarios de precipitación variables.

(6) Analizar la influencia del árbol sobre la calidad pastoral y el ciclo de nutrientes de comunidades herbáceas anuales en dehesas, comparando con los resultados obtenidos en otras comunidades herbáceas de ecología diferente.

3.

Dendroecología y variabilidad del crecimiento en respuesta al clima de la encina en dehesas

Basado en:
Gea-Izquierdo G, Martín-Benito D, Cañellas I. Climate-growth variability in *Quercus ilex* L.: is there a climatic signal shared by tree species along the Mediterranean? En revisión.

(Anexo I)

3.1 Introducción

Como paso previo a la construcción de modelos de crecimiento a partir de mediciones en secciones es necesario asegurarse mediante técnicas dendrocronológicas que la especie a estudiar forma anillos anuales distinguibles. Actualmente, como consecuencia del calentamiento global y sus posibles impactos en el crecimiento y distribución de los bosques, es necesario estudiar la influencia del clima y su variabilidad en el crecimiento y distribución de las especies. Por estos motivos, en este capítulo se pretende construir una serie maestra dendrocronológica de encina para asegurarnos que los patrones de crecimiento anuales son distinguibles en las secciones. Además se estudia la respuesta de la especie al clima en las dehesas y sus posibilidades para realizar estudios dendroecológicos.

En la región mediterránea existen muchos más estudios dendrocronológicos en zonas de montaña que en zonas de baja altitud. Sin embargo es importante estudiar la dendroecología de todas las masas forestales, ya que previsiblemente un incremento de la temperatura y la ETP podrían afectar más a las formaciones vegetales situadas bajo termotipos más cálidos. Por ello, finalmente se discute la respuesta climática de la serie elaborada con la de otras especies y localidades de la región Mediterránea, la mayoría de zonas de montaña.

3.2 Material y métodos

Sitio de estudio

La muestra fue tomada en un ecosistema de dehesa típico aprovechando la ampliación de la carretera N-620 entre Ciudad Rodrigo y Fuentes de Oñoro (N-620), en el Sur de Salamanca, al Norte del Sistema Central (40º 37’ N, 6º 40’ W, 700 m). La precipitación media en la zona es de 609 mm, la temperatura media anual de 13,2ºC, la temperatura máxima media mensual de 25,3ºC y la temperatura mínima media mensual de 1,8ºC. Este régimen de temperaturas corresponde al límite entre el mesomediterráneo superior y el supramediterráneo inferior (Rivas-Martínez, 1987).

Diseño experimental

Se cortaron secciones en la base y a 1,30 m (DAP) de 125 encinas procedentes de 25 parcelas (ver Capítulo 4) situadas en una franja de 9 km de ancho y 50 m de ancho medio. Las secciones se secaron al aire y luego se cepillaron y lijaron con granos #60 a #1200. Se midió la anchura de todos los anillos de crecimiento con una precisión de 0,01 mm mediante una mesa de medición LINTAB acoplada a un ordenador con el programa TSAP (Rinntech, 2003). Una vez hechas las mediciones se comprobó la coincidencia de los crecimientos anuales entre todas las rodajas (sincronización). A continuación se seleccionaron sólo aquellas muestras basales que claramente sincronizaban entre ellas y se construyó una serie maestra dendrocronológica, es decir, una serie de crecimientos en la que se identifica perfectamente el crecimiento de cada año concreto, con el objetivo de identificar posteriormente aquellas muestras que presenten alguna dificultad de datación. Seleccionar “a posteriori” las muestras que mejor sincronizan es una práctica común en dendrocronología, ya que el interés radica en localizar aquellos individuos que mejor reflejen la señal común de interés, generalmente una señal climática (Fritts, 1976; Cooks y Kairiukstis, 1991).

Una vez obtenida la serie maestra, se seleccionaron 109 cronologías del International Tree Ring Data Bank (ITRDB: http://www.ncdc.noaa.gov/paleo/treering.html), procedentes de diferentes localizaciones en Europa, Magreb, Turquía y Oriente Medio. En la Península Ibérica se seleccionaron series de crecimiento procedentes del Sistema Central (Gredos y Guadarrama), Pirineos, Sistema Ibérico (Noroeste, alrededor de Urbión; Sur y Oeste, Sierra de Gúdar y Cuenca; Este, Sierra de Albarracín) así como del Sistema Penibético (Cazorla y Sierras de Cádiz-Málaga).

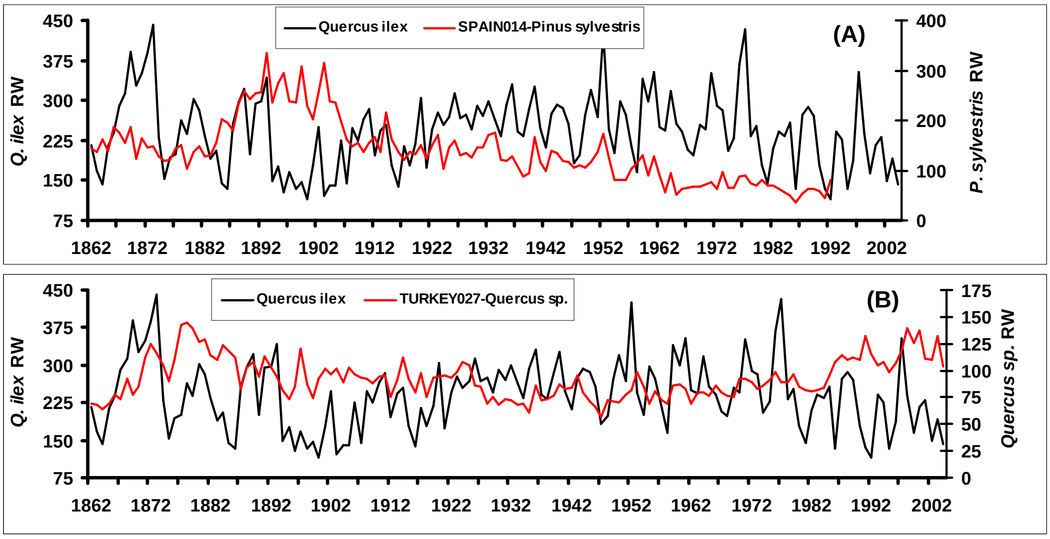


Figura 1. Cronología maestra elaborada para la encina (SALAM001) y: (A) la cronología con más alta sincronización (SPAIN014); (B) la cronología más alejada entre las que sincronizan en el Mediterráneo (TURKEY027). RW = ancho de anillo (0.01 mm). (ver Anexo I para nomenclaturas y más detalle de las cronologías).

Análisis estadísticos

En primer lugar las mediciones fueron sincronizadas visualmente y posteriormente se validó la sincronización visual utilizando el *Gleichläufigkeit* (Glk) y el *crossdate index* (CDI) en TSAP (Rinntech, 2003). Las series individuales se estandarizaron utilizando ARSTAN (Cook y Holmes, 1994): (i) para las de encina se utilizaron splines con una frecuencia de respuesta al 50% de 32 años; (ii) para el resto de las series, funciones de menor frecuencia como la *Hugershoff* o la exponencial negativa para retener la variabilidad común en períodos de tiempo más amplios. Para la encina se seleccionaron funciones con una frecuencia más alta para poder eliminar la influencia de la gestión intensiva (podas sobre todo), sacrificando la variabilidad temporal en intervalos mayores de 32 años (Cooks y Kairiukstis, 1990; Briffa *et al*., 2002).

Una vez estandarizadas las series temporales se calcularon índices dividiendo el crecimiento observado entre el ajustado en la estandarización (Fritts, 1976; Cook y Kairiukstis, 1990). La relación del índice de crecimiento con el clima se estudió utilizando correlaciones de Pearson y funciones respuesta utilizando DENDROCLIM2002 (Biondi y Waikul, 2004). Además, para analizar la relación clima-crecimiento en la serie maestra de encina se calcularon también la sensibilidad media (Fritts, 1976) para la serie total y para ventanas móviles de intervalo 30 años, así como se calcularon correlaciones móviles de Pearson entre el crecimiento y diferentes parámetros climáticos en ventanas móviles de 10 años (Sarris *et al*., 2007). Finalmente, la señal poblacional media (*expressed population signal*, EPS) fue calculada para evaluar la fiabilidad de la señal climática de las series en el período donde se analizó la relación crecimiento-clima (Andreu *et al*., 2007).

La serie de *Q. ilex* y las 109 de otras especies del ITRDB (ver Anexo I para más detalles) se compararon usando los estadísticos de sincronización previamente comentados. Además se realizaron análisis de componentes principales (PCA. [Mardia *et al*., 1979; McCune y Mefford, 1999]) sobre los índices estandarizados de las 110 cronologías para el período común 1923-1975 (matriz 110x58). A continuación, se realizaron análisis PCA sucesivos a subgrupos sugeridos por las ordenaciones precedentes. Las especies se agruparon en: (i) 'boreales' (=templadas y alpinas): *Abies* sp. (excepto *A. pinsapo* Boiss.), *Larix* sp., *Picea* sp. y *Q. robur* L.; (ii) mediterráneas, el resto.

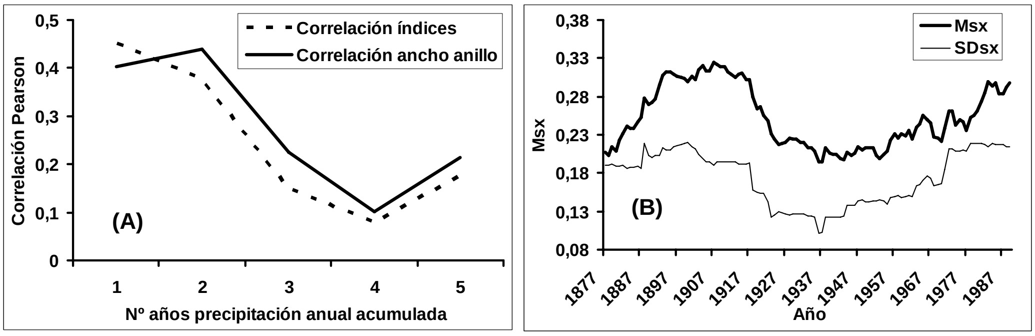


Figura 2. (A) Coeficiente de correlación de Pearson entre la precipitación anual acumulada (1945-2004), el índice calculado (línea discontinua) y el ancho de anillo (línea continua); (B) sensibilidad media en ventana móvil de 30 años de intervalo. Msx=sensibilidad media; SDsx=desviación estándar sensibilidad.

3.3 Resultados

Dendroecología y variabilidad del crecimiento en respuesta al clima de Quercus ilex

La serie maestra final comprendió el período 1862-2004 (longitud 143 años) y fue construida con 18 individuos y 35 radios (Figura 1). Su sensibilidad media fue de 0,252, la correlación media de las series estandarizadas fue 0,505 y el EPS mayor de 0,85 para el período usado para las relaciones clima-crecimiento. La respuesta del crecimiento fue máxima a la precipitación del año y el anterior acumulado (Figura 2A). La sensibilidad ha aumentado en las últimas décadas (Figura 2B), aunque este aumento es similar al que se observa en la misma muestra en la segunda mitad del siglo XIX. El crecimiento está muy influido por la precipitación y por las altas temperaturas (Figura 3). Precipitaciones altas en primavera y verano (particularmente junio-julio) y temperaturas mínimas altas en otoño del año precedente resultaron beneficiosas para el crecimiento, mientras temperaturas altas en verano tanto del año de crecimiento como el anterior resultaron muy negativas para el crecimiento.

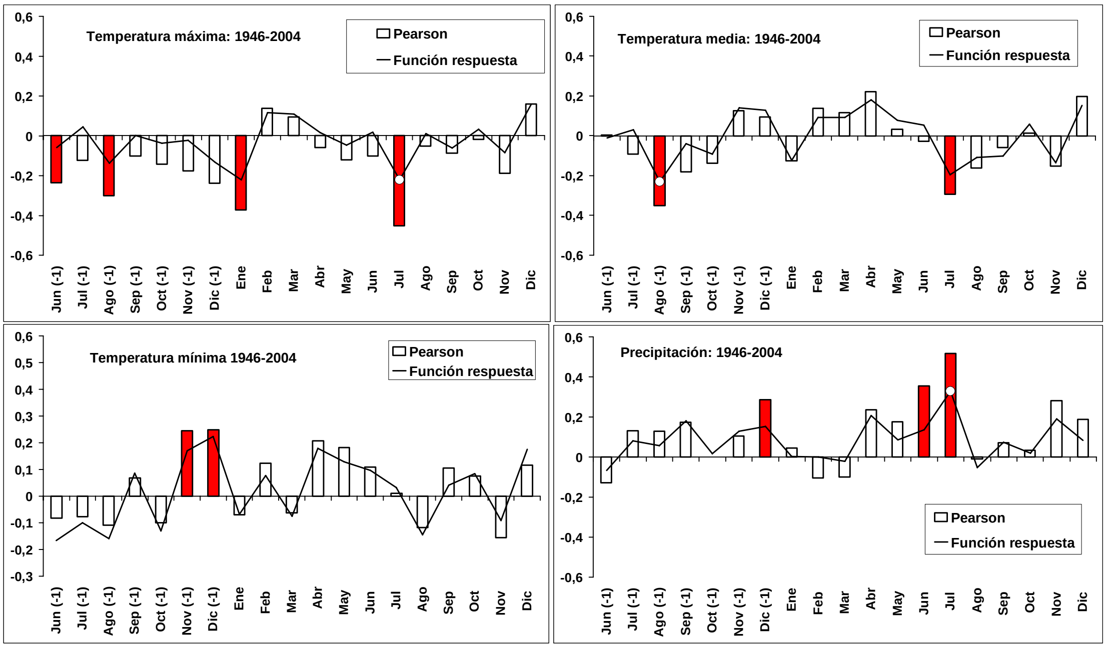


Figure 3. Coeficientes de correlación *bootstrap* (barras) y función respuesta (líneas) entre los índices de crecimiento y los datos climáticos mensuales desde junio del año precedente a diciembre del año de crecimiento. Barras rojas y círculos blancos denotan correlaciones significativas de Pearson y de la función respuesta respectivamente (α=0,05).

Hemos podido constatar cómo la respuesta del crecimiento al clima ha ido variando a lo largo del tiempo (Figura 4). La dependencia del crecimiento en la precipitación anual se ha visto incrementada en las últimas décadas (Figura 4A). El incremento observado en la influencia de la temperatura del mes de octubre del año en curso parece indicar que el período vegetativo puede estar alargándose en otoño. Las encinas analizadas han sufrido un incremento en el estrés estival en las últimas décadas (Figura 2B; 4C, 4D).

Comparación de la respuesta climática de Quercus ilex con otras especies de la región mediterránea

La cronología de encina estudiada sincronizaba claramente con diversas especies de *Pinus* sp. del Sistema Central, lo cual muestra que responden a cierta señal climática común, lo que nos permite afirmar que las mediciones de crecimiento realizadas son anuales. Además se detectó esta sincronización en una franja latitudinal Mediterránea hasta Turquía con diversas especies, como *Abies alba* Mill.*,* *Pinus nigra* Arn.*,* *Pinus uncinata* Mill. ex Mirb. o *Quercus frainetto* Ten. (Figura 1A; Figura 5), que exhibían cierta señal climática común con la serie maestra de encina. Esta sincronización pareció ser particularmente evidente al combinarse condiciones similares de latitud-altitud y posiblemente orientación (ver Anexo I).

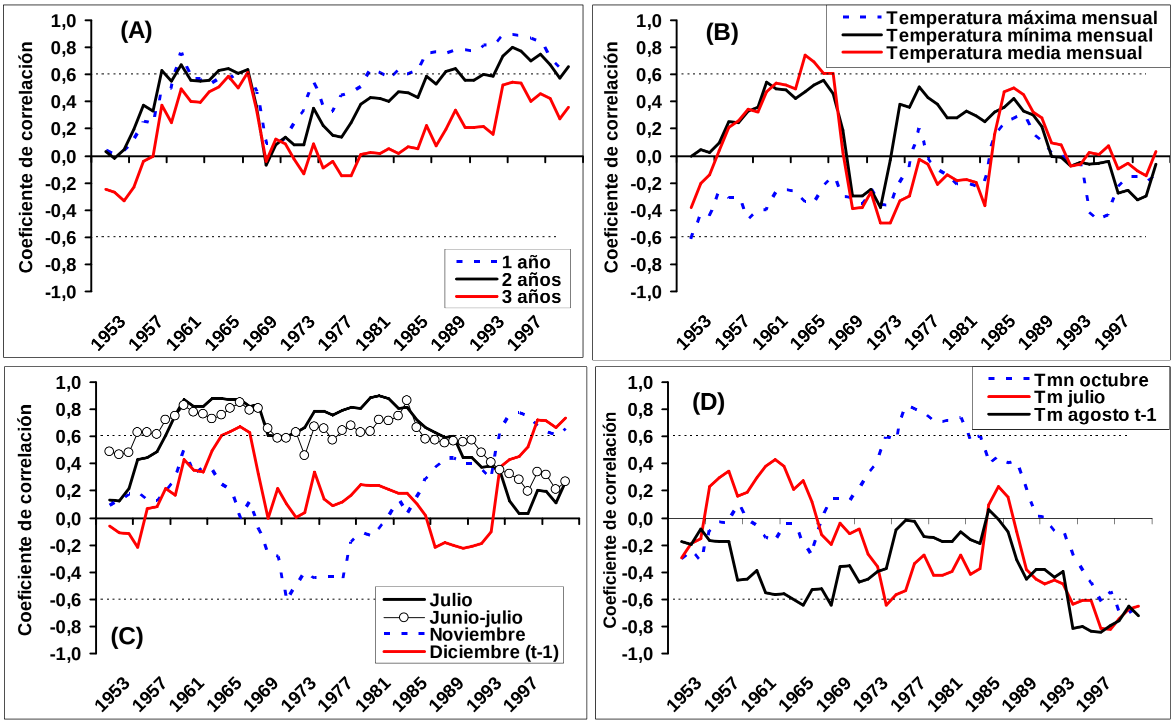


Figura 4. Correlaciones medias móviles (intervalo 10 años) entre el ancho de anillo y la precipitación anual acumulada (año, año+año-1, etc.) y las temperaturas medias, mínimas y máximas del año de crecimiento. (A) y (C) corresponden a datos de precipitación; (B) y (D) a datos de temperatura. (t-1)=datos climáticos del año precedente; el resto de resultados corresponden al año de crecimiento en curso. Tm=temperatura media mensual; Tmn=temperatura mínima mensual.

3.4 Discusión

Los estudios dendrocronológicos, particularmente en masas situadas a baja altitud, son mucho menos numerosos en la región mediterránea que en el dominio del bosque eurosiberiano. En este capítulo hemos obtenido la primera serie dendrocronológica para una de las especies mediterráneas más extendidas, *Quercus ilex,* y una de las primeras series procedentes de zonas de baja altitud del Oeste del Mediterráneo (Campelo *et al*., 2007b). La relación del crecimiento con el clima ha variado con los cambios experimentados por el clima durante las últimas décadas. La sensibilidad del crecimiento

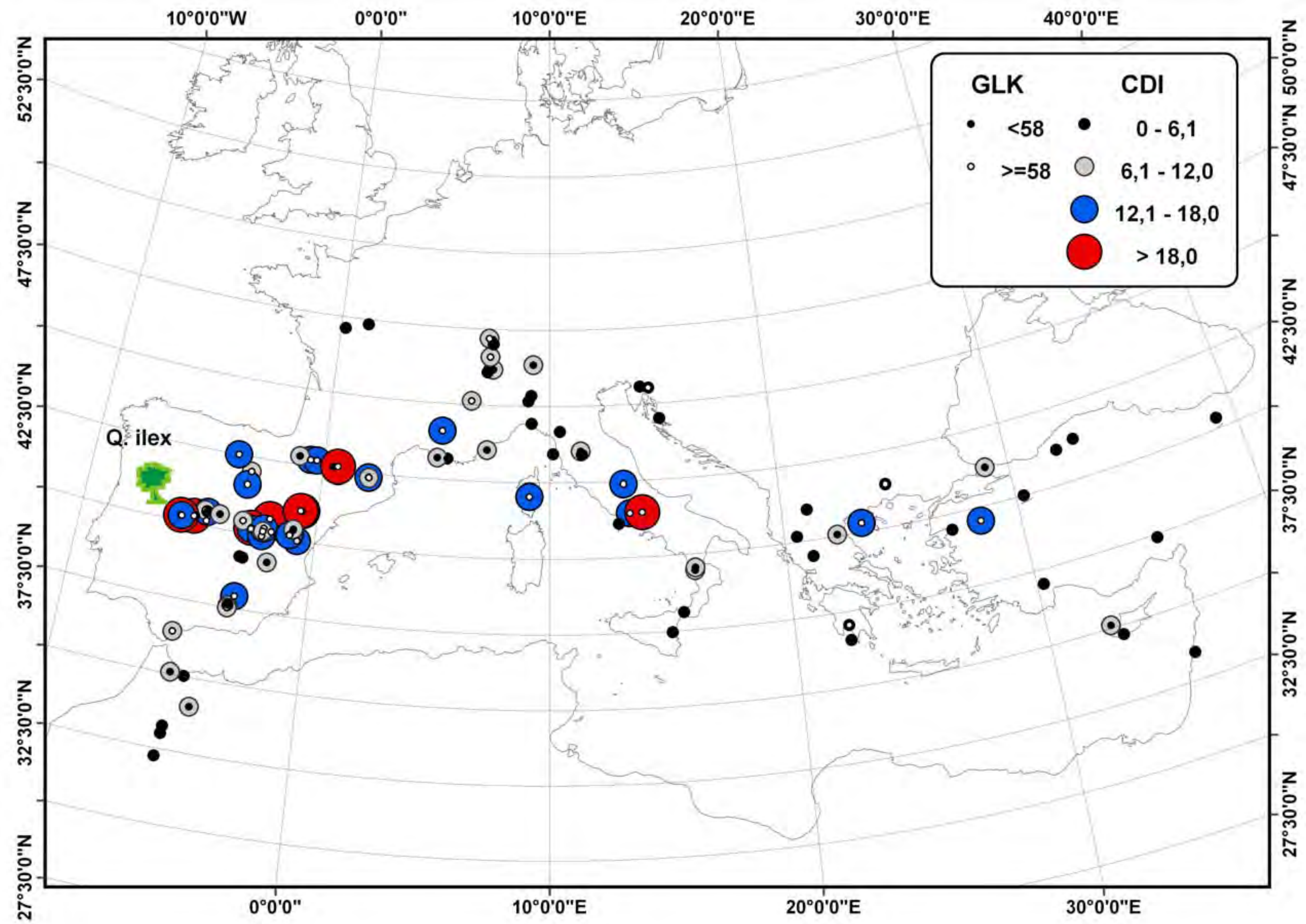


Figura 5: Localización de las cronologías del ITRDB utilizadas: se muestra el CDI y *Glk* de cada serie del ITRDB enfrentada a la serie maestra elaborada de encina.

de los árboles al clima está aumentando y el período de crecimiento se está alargando en otoño, de modo similar a como está ocurriendo en especies eurosiberianas en Europa y varias especies de pinos en las montañas de la Península Ibérica (Carrer y Urbinati, 2006; Andreu *et al*., 2007). Por tanto, el aumento de la sensibilidad generado por el ascenso de las temperaturas en las últimas décadas se puede extrapolar a masas. mediterráneas de zonas no montañosas, al menos en la región estudiada, siendo posible que sea éste un fenómeno general en muchos bosques europeos y mediterráneos.

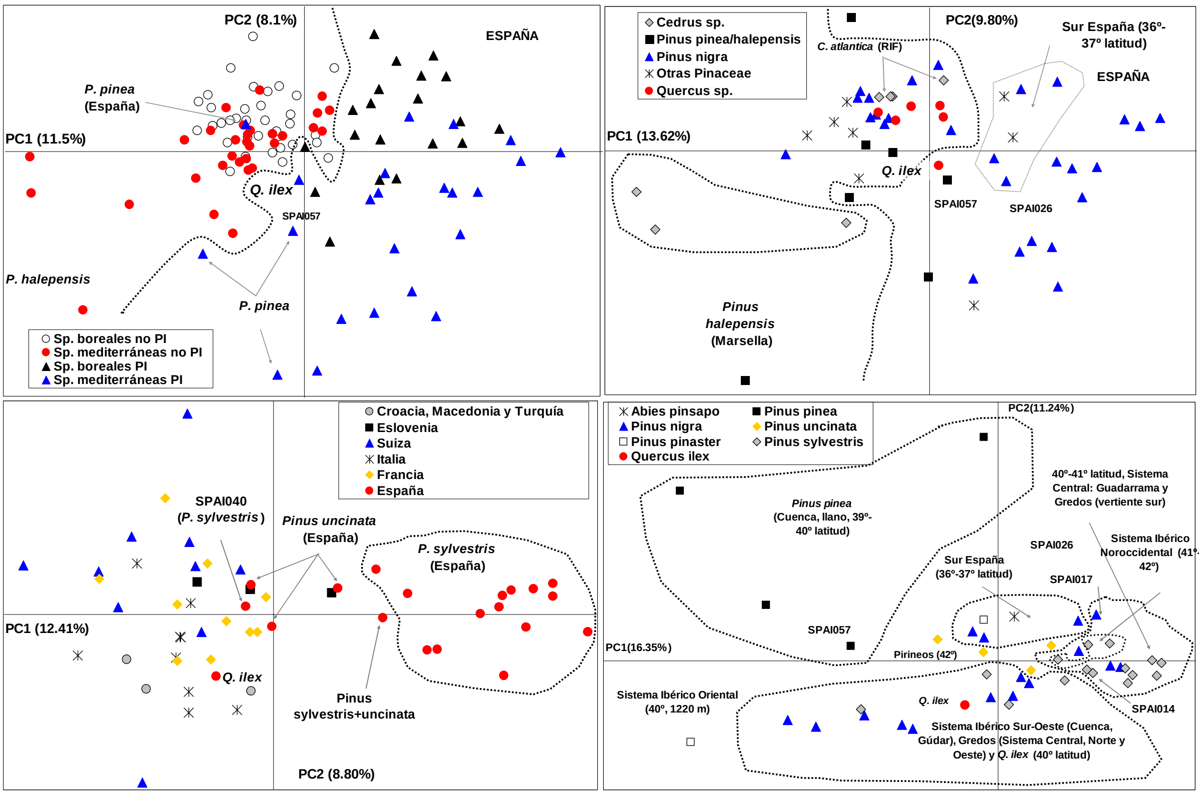


Figura 6: Resultados de las ordenaciones PCA: (A) usando todas las cronologías; (B) usando sólo táxones mediterráneos; (C) usando sólo táxones boreales; (D) usando sólo series españolas. Sp.=especie; PI=Península Ibérica.

Mediante la elaboración de la serie dendrocronológica se demuestra que el patrón de crecimiento de la especie en el Oeste Peninsular es similar a especies que crecen bajo clima templado, con una parada invernal y formación anual de anillos de crecimiento. Por tanto el análisis de secciones es una técnica correcta tanto para estimar edades como para usar las estimaciones de crecimiento en la elaboración de modelos estadísticos. En localizaciones más térmicas es posible que la construcción de series dendrocronológicas en la especie sea más compleja (Cherubini *et al*., 2003), aunque parece que la parada invernal es común en la encina en masas situadas en el sur peninsular (Huelva) a una latitud alrededor de 37º N (Vázquez, com. pers.). La existencia de crecimiento en verano es una constante en los trabajos consultados en la especie (Zhang y Romane, 1991;

Cherubini *et al.,* 2003; Corcuera *et al*., 2004). Sin embargo, y al igual que en nuestros resultados, las técnicas empleadas impiden garantizar la ausencia de una parada estival. Así, en las citadas localidades más meridionales (donde no existen estudios en la bilbliografía) la especie parece sufrir una segunda parada en verano, confirmada a través de mediciones con dendrómetros (Vázquez, com. pers.).

Como cabía esperar, las variables climáticas más influyentes en el crecimiento de la encina fueron la precipitación en primavera y al principio del verano (significativamente positivas para el crecimiento), y las temperaturas estivales, particularmente en agosto, tanto del año en curso como del anterior (que afectan negativamente). Como para cualquier otra especie, condiciones de alto estrés hídrico (temperatura y ETP) son negativas para el crecimiento. La correlación negativa con condiciones climáticas estresantes el año anterior pone de manifiesto la influencia sobre el crecimiento del año en curso de las reservas acumuladas o de la formación de las yemas de crecimiento el año anterior. El crecimiento muestra una máxima correlación con la precipitación del año en curso, a diferencia de los resultados de estudios en el Mediterráneo oriental que muestran como algunas especies están aumentando su dependencia de la precipitación a un mayor período acumulado como consecuencia del descenso en las precipitaciones de los últimos años (Sarris *et al*., 2007).

El patrón de crecimiento discutido es muy similar al descrito en la bibliografía para *Quercus suber* L. (Costa *et al.,* 2001; 2003). Ambas especies de *Quercus* dominan grandes extensiones en el Oeste de la Península Ibérica y comparten ecosistemas parecidos bajo climas similares (variantes más húmedas en el caso del alcornoque), parece que poseerían una respuesta al clima muy similar en la zona. De modo análogo a como se aprecia en nuestros resultados y en un escenario de calentamiento global como el que ahora estamos atravesando, el factor limitante para el crecimiento en ecosistemas mediterráneos sin compensación hídrica en el suelo (exceptuando quizá las zonas de alta montaña) podría ser el estrés hídrico. También en el escenario actual, existen por el contrario otros factores, como el incremento del CO_2 (Raupach *et al*., 2007), que podrían resultar beneficiosos para el crecimiento de las especies leñosas. Sin embargo, no todos los autores coinciden en considerar un efecto fertilizante sobre el crecimiento asociado a este incremento en dióxido carbono (Tognetti *et al*., 2000; Soulé y Knapp, 2006). Además, las especies que crecen en el área del mediterráneo en zonas de baja altitud (por tanto más cálidas) en el área del Mediterráneo podrían ser susceptibles de verse más afectadas por un aumento de la aridez. Estas dos últimas hipótesis deberán demostrarse en futuros estudios.

Las masas de encina estudiadas (límite entre el termotipo mesomediterráneo y el supramediterráneo [Rivas-Martínez, 1987]) parecen compartir cierta señal climática común con determinadas cronologías de especies localizadas en latitudes norte entre 39º y 42º. Por supuesto, esta señal común no explica toda la variabilidad del crecimiento, y como es habitual la sincronización es mayor cuanto mayor es la proximidad entre cronologías (Richter *et al*., 1991). Consideramos que esta señal obedece a una mezcla de latitud, altitud y orientación que determina la temperatura acumulada recibida. El crecimiento de las series situadas a más altitud está limitado principalmente por temperatura mientras las de baja altitud precipitación, que es un fenómeno climático más local que la temperatura (Briffa *et al.,* 2002). Esto se aprecia en nuestros resultados, particularmente al analizar el comportamiento de las series de *Pinus pinea*, las cuales se separan claramente del resto de las series analizadas en la Península (todas de zonas más altas). Entre las series de *P. pinea* tan sólo sincronizó con nuestra serie de encina la situada a mayor altitud (1055 m. SPAI057), mientras que las masas situadas a menor altitud mostraban una respuesta climática diferente al patrón común observado. Estos resultados sugeridos por los índices de sincronización fueron confirmados por las ordenaciones multivariantes.

Los resultados de la ordenación multivariante mostraron una clara diferenciación entre especies mediterráneas y ‘boreales’ en primer lugar, y en segundo lugar separaron las series mediterráneas occidentales españolas del resto de Europa (Richter *et al*., 1991; Briffa *et al*., 2002), mostrando un patrón mediterráneo común pero también una diferencia entre el mediterráneo oriental y occidental. Las ordenaciones detectaron principalmente patrones regionales a diferencia de los estadísticos de sincronización previamente discutidos, que como se ha comentado parecían responder a señales climáticas de mayor escala. Estos resultados podrían ser de gran importancia a la hora de analizar posibles bandas climáticas móviles de aridez parecidas a las detectadas durante el Holoceno en el Mediterráneo occidental (Jalut *et al*., 2000), un patrón que aún podría estar evolucionando.

4.

Modelos dinámicos de crecimiento en diámetro dependientes e independientes de la edad para la encina en dehesas

Basado en:
Gea-Izquierdo G, Cañellas I, Montero G. 2008. Site index in agroforestry systems: age-dependent and age-independent dynamic diameter growth models for *Quercus ilex* in Iberian open oak woodlands. Canadian Journal of Forest Research 38, 101-113.

(Anexo II)

4.1 Introducción.

Dentro del objetivo global de trabajar en la consecución de submodelos que puedan ser empleados en un modelo de sistema y tras constatar que no existen ecuaciones de crecimiento para la encina en el Oeste de la Península Ibérica, en este capítulo se elaboran modelos dinámicos de crecimiento en diámetro para la encina en dehesas. Ante la dificultad de estimar la edad en la especie, se discute el empleo de modelos en diferencias dependientes e independientes de la edad. Además se analiza el concepto de dominancia y se propone un índice de calidad de sitio basado en crecimiento en diámetro, así como la posibilidad de emplear una sola ecuación para estimar el crecimiento en diámetro de cualquier árbol del sistema, independientemente de la densidad del rodal y la condición social del individuo.

4.2 Material y métodos

Diseño experimental

El sitio de ensayo es el descrito en el apartado 3.1. Se replantearon 25 parcelas de radio variable en la franja de 9 km de largo por 50 m de ancho. Las parcelas se seleccionaron de modo que incluyeran el máximo rango de densidades posibles, resultando un rango de 39,2 a 210,4 pies/ha, con una densidad media de (media±desviación estándar) 129,9±37,9 pies/ha y área basimétrica media de 9,5±3,9 m^2/ha. En cada parcela se midieron las distancias y rumbos de los 10 árboles más cercanos al centro y se caracterizaron dasométricamente midiendo dos DAP perpendiculares, la altura del fuste y total del árbol y dos diámetros de copa perpendiculares. A continuación se apearon los 5 árboles centrales de cada parcela.

Las muestras fueron procesadas como se describe en 3.1 y los crecimientos diametrales anuales estimados. De las 125 encinas apeadas, sólo 115 mostraron al menos un radio completo medible, por lo que los modelos generales se construyeron con observaciones procedentes de 115 pies. La relación entre la edad en la base y la edad a 1,30 fue: Edadbasal=11,82+1,01·EdadDAP; R^2=0,93; Error medio cuadrático (RMSE)=7,67 años. Todos los análisis desarrollados en los capítulos 4 y 5 se refieren a crecimientos sin corteza (grosor corteza [mm]=0,02·DAP[cm]-0,39; R^2=0,55; RMSE=0,24 cm).

Al estar los árboles podados y ser las masas abiertas, no es posible definir en campo la posible dominancia (si existe) de los pies. Por ello, para ajustar curvas de crecimiento potencial y estudiar la diferencia de estos modelos con modelos ajustados para cualquier árbol del sistema (suponiendo codominancia), de los 5 pies apeados por parcela se eliminaron aquellos que presentaban gráficamente un crecimiento sensiblemente inferior al resto, aceptando que era por haber estado suprimidos. Los 88 pies restantes se promediaron por parcela, resultando 25 series medias de crecimiento en diámetro potencial (dominante) que fueron comparadas con curvas generales (tanto dependientes como independientes de la edad) ajustadas a los 115 pies suponiendo que en dehesas todos los pies son dominantes-codominantes.

Modelos y análisis estadístico

Se seleccionaron 4 modelos integrales entre los más usados en la bibliografía como ecuaciones de crecimiento biológico y se compararon ecuaciones en diferencias dependientes de la edad (Kiviste *et al*., 2002) con independientes de la edad (Tomé *et al*., 2006). Todos los modelos eran diferenciables y poseían las características deseables en una ecuación de calidad de estación (Cieszewski y Bailey, 2000): (i) polimorfismo; (ii) punto de inflexión; (iii) asíntota horizontal como límite al crecimiento; (iv) comportamiento lógico y biológico; (v) sencillez. A lo largo de este capítulo los modelos dependientes de la edad se denominan como E(i) mientras los independientes de la edad como T(i).

Para los modelos dinámicos dependientes de la edad se utilizó la formulación de ecuaciones en diferencias algebraicas generalizadas (GADA, generalized algebraic difference approach) (Cieszewski y Bailey, 2000; Cieszewski, 2004), la cual es una generalización de la aproximación en diferencias algebraicas (ADA) propuesta por Bailey y Clutter (1974). Por tanto, E1, E2, E4, E7, E10 y E11 son equivalentes a ADA polimórficos (Tabla 1); E3 es un GADA anamórfico y el resto (E5, E6, E8, E9) son GADA polimórficos con asíntotas variables. Algunos de estos modelos han sido ya previamente utilizados en otros estudios (Cieszewski *et al*., 2002; Barrio-Anta *et al*., 2006; Cieszewski *et al*., 2006; Diéguez-Aranda *et al*., 2006; Tomé *et al*., 2006). Los GADA fueron ajustados mediante el método del '*dummy approach*' (Cieszewski *et a*l., 2000; Cieszewski, 2003) para asegurar que los modelos fueran invariantes en cuanto a la edad base.

Los modelos dinámicos utilizados generalmente en la bibliografía requieren la estimación de la edad, ya que la definición de cualquier curva de crecimiento biológico la incluye (Zeide, 1993). Sin embargo, para especies como la encina estimar la edad resulta problemática para los gestores e investigadores, resulta interesante proponer modelos que sean independientes de la edad, siempre que el incremento del error no sea excesivo y pese a que estimar crecimiento sin incluir la edad en su predicción pueda resultar heterodoxo. En este sentido, en la formulación dinámica independiente de la edad recientemente propuesta por Tomé *et al*. (2006), se resuelve la ecuación en t_1 y luego se sustituye en t_2 expresada como $t_2=t_{1+dif}$, siendo 'dif' la longitud del intervalo de proyección.

Tabla 1. Ecuaciones base y ecuaciones en diferencias consideradas para desarrollar las ecuaciones dependientes de la edad.

Ecuación integral	Parámetro relacionado con el sitio	Solución para X	Ecuación dinámica	Id
Hosfeld IV (1822) Citado en Peschel (1938): $y = \frac{t^c}{b + at^c}$	b = X	$X_0 = t_1^c \cdot \left(\frac{1}{y_1} - a\right)$	$y_2 = \frac{t_2^c}{X_0 + a \cdot t_2^c}$	(E1)
	c = X	$X_0 = \frac{\ln\left(\frac{y_1 b}{1 - y_1 a}\right)}{\ln t_1}$	$y_2 = \frac{t_2^{X_0}}{b + at_2^{X_0}}$	(E2)
	a = X b = b_1X	$X_0 = \frac{t_1^c / y_1}{b_1 + t_1^c}$	$y_2 = \frac{t_2^c}{X_0 \cdot (b_1 + t_2^c)}$	(E3)
Korf (1939) Citado en Lundqvist (1957) $y = a \cdot \exp(-b \cdot t^{-c})$	b = X	$X_0 = \frac{-\ln(y_1 / a)}{t_1^{-c}}$	$y_2 = a \cdot \left(\frac{y_1}{a}\right)^{(t_1/t_2)^c}$	(E4)
	a = exp(X) b = b_1+(b_2/X)	$X_0 = 0.5 \cdot (b_1 t_1^{-c} + \ln(y_1) + F_0)$; $F_0 = \sqrt{((b_1 t_1^{-c} + \ln(y_1))^2 + 4b_2 t_1^{-c}})$	$y_2 = \exp(X_0) \cdot \exp(-(b_1 + (b_2 / X_0)) \cdot t_2^{-c})$	(E5)
	a = exp(a_2X) b = X	$X_0 = \frac{\ln(y_1)}{a_2 - t_1^{-c}}$;	$y_2 = \exp(a_2 X_0) \cdot \exp(-X_0 t_2^{-c})$	(E6)
von Bertalanffy (1957)- Richards (1959): $y = a \cdot (1 - \exp(-b \cdot t))^c$	b = X	$X_0 = -\frac{\ln(1 - \sqrt[c]{y_1 / a})}{t_1}$	$y_2 = a \cdot \left(1 - \left(1 - \sqrt[c]{\left(\frac{y_1}{a}\right)}\right)^{\frac{t_2}{t_1}}\right)^c$	(E7)
	a = exp(X) c = c_1+(1/X)	$X_0 = 0.5 \cdot (\ln(y_1) - c_1 F_0 + \sqrt{(c_1 F_0 - \ln(y_1))^2 - 4F_0}$; $F_0 = \ln(1 - \exp(-bt_1))$	$y_2 = \exp(X_0) \cdot (1 - \exp(-bt_2))^{(c_1 + (1/X_0))}$	(E8)
	a = exp(a_2X) c = X	$X_0 = \frac{\ln(y_1)}{a_2 + F_0}$; $F_0 = \ln(1 - \exp(-bt_1))$	$y_2 = \exp(a_2 X_0) \cdot (1 - \exp(-bt_2))^{(X_0)}$	(E9)
Weibull (1951)- Yang *et al*. (1978) $y = a \cdot (1 - \exp(-b \cdot t^c))$	b = X	$X_0 = -\frac{\ln(1 - (y_1 / a))}{t_1^c}$	$y_2 = a \cdot \left(1 - \left(1 - \frac{y_1}{a}\right)^{\left(\frac{t_2}{t_1}\right)^c}\right)$	(E10)
	c = X	$X_0 = \frac{\ln\left(-\frac{\ln\left(1 - \left(\frac{y_1}{a}\right)\right)}{b}\right)}{\ln t_1}$	$y_2 = a \cdot (1 - \exp(-b \cdot t_2^{X_0}))$	(E11)

Finalmente para generar una familia de curvas es necesario expandir uno de los parámetros por alguna covariable del sistema. Nosotros comparamos modelos dinámicos independientes de la edad expandidos por: (i) densidad; (ii) por el índice de sitio propuesto previamente; (iii) por densidad e índice de calidad de estación. La correlación serial de las series individuales de crecimiento en diámetro fue eliminada mediante una estructura autoregresiva de segundo orden (AR(2)). La heterocedasticidad en los residuos fue analizada gráficamente y los modelos que la presentaban ajustados mediante mínimos cuadrados generalizados ponderados por 1/Var(ε_i), siendo Var(ε_i) la función de varianza estimada para los residuos del modelo heterocedástico. Todos los cálculos se programaron en PROC MODEL de SAS 9.1 (SAS Institute Inc., 2004).

Por tanto, se compararon tres tipos de modelos dinámicos de crecimiento en diámetro:

(i) Modelos potenciales dependientes de la edad, ajustados a las 25 series (Tabla 1, Modelos E1 a E11).

(ii) Modelos generales dependientes de la edad, ajustados a los 115 individuos. Para probar la hipótesis de dominancia-codominancia y competencia ausente o reducida se ajustaron modelos con parámetros expandidos por densidad y sin expandir, formulados también como en Tabla 1 pero añadiendo el sufijo ‘d’ en aquellos que se expandían por densidad.

(iii) Modelos generales independientes de la edad:

a. Modelos Hossfeld IV, incluyendo T1, T2, T4s y T5s, expandidos a partir de la expresión genérica:

$$y_2 = \frac{\left(\sqrt[c]{\frac{y_1 \cdot b}{(1-a \cdot y_1)}} + \text{dif}\right)^c}{b + a \cdot \left(\sqrt[c]{\frac{y_1 \cdot b}{(1-a \cdot y_1)}} + \text{dif}\right)^c};$$

a, b y c son: en T1, b=(b_1·densidad); en T2 a=(a_1/densidad) y b=(b_1·densidad); en T4s, b=(b_{S1}/IS) y a=(a_{S1}·IS); y en T5s b=((b_{S1}/IS)+b_{d1}·densidad) y a=((a_{S1}·IS)+(a_{d1}/densidad)). a_{S1}, a_{d1} b_{S1} y b_{d1} son parámetros a estimar. El intervalo de proyección (‘*dif*’) es el número de años entre el diámetro conocido y el diámetro a predecir. El índice de sitio IS (en cm) se define a partir de las ecuaciones potenciales.

b. Ecuaciones basadas en la ecuación de Korf:

$$y_2 = a \cdot \exp\left(-b \cdot \frac{1}{\left(\left(\frac{-b}{\log(y_1/a)} \right)^{1/c} + dif \right)^c} \right);$$

utilizada en el modelo T3, con b=(b_1·densidad).

Los modelos fueron comparados mediante los estadísticos RMSE, R^2, sesgo y criterio de Akaike en diferencias (AICd) (más detalle en Anexo II). Al no poseerse una muestra independiente se realizó una autovalidación *Jackknife* (Myers, 1990).

4.3 Resultados

El DAP medio con corteza de la muestra fue de 30,8±13,0 cm, la edad 89,0±28,6 años (máximo 175 años), la altura total media de 6,3±1,8 m y el crecimiento medio anual radial de 0,175 cm.

Tabla 2. Estadísticos de ajuste (fases de estimación y validación) de los mejores modelos dinámicos potenciales dependientes de la edad (25 series) entre los mostrados en Tabla 1 (más detalle en Anexo II). $DAPsc_{350}$=DAP sin corteza predicho para la edad de 350 años en la clase de sitio I. RMSE=error medio cuadrático residual; AICd=criterio de información de Akaike en diferencias; EF=efficiencia; Adj. R^2= R^2 ajustado.

Id	Estimación			Validación (jack-knife)					
	RMSE (cm)	R^2	AICd	Sesgo (cm)	RMSE (cm)	EF	AICd	$DAPsc_{350}$ (IS=I; cm)	Asíntota (IS=I; cm)
E2	0,7646	0,9969	0,0	0,1899	2,4496	0,9679	8,5	81,2	95,6
E3	0,7703	0,9968	7,6	0,0716	2,7467	0,9596	124,8	105,9	133,3
E4	0,7901	0,9967	33,3	0,4147	2,6169	0,9634	75,7	128,0	1679,9
E5	0,7687	0,9968	6,4	0,1189	2,6005	0,9639	68,2	141,5	1564,7
E8	0,7745	0,9968	13,1	0,1082	2,7793	0,9586	139,9	96,2	98,8
E9	0,7773	0,9968	16,7	0,1129	3,2070	0,9450	282,2	104,2	107,4
E11	0,7666	0,9969	2,6	0,2468	2,4291	0,9685	0,0	67,1	67,1

Modelos dinámicos de crecimiento en diámetro potencial dependientes de la edad

En la Tabla 2 se muestran los resultados de los mejores modelos entre los ajustados (Tabla 1). En la fase de estimación casi todos los modelos tuvieron un comportamiento muy similar. Sin embargo, en la fase de validación el modelo con mejor comportamiento entre los que predicen un DAP realista a los 350 años fue E5 (Tabla 2), presentando las formulaciones GADA mejores ajustes de ajuste que las ADA. La expresión final del modelo (intervalos de confianza de los parámetros en Anexo II):

$$DAP_2 = \exp(X_0)\cdot\exp(-(14{,}77073+(\text{-}37{,}6516/X_0))\cdot t_2^{-0{,}237368}),$$
$$\text{donde } X_0 = 0{,}5\cdot(14{,}77073\cdot t_1^{-0{,}237368}+\ln(DAP_1)+F_0), \qquad (1)$$

$$\text{y } F_0 = \sqrt{((14{,}77073\cdot t_1^{-0{,}237368}+\ln(DAP_1))^2+4\cdot(\text{-}37{,}6516)\cdot t_1^{-0{,}237368}}).$$

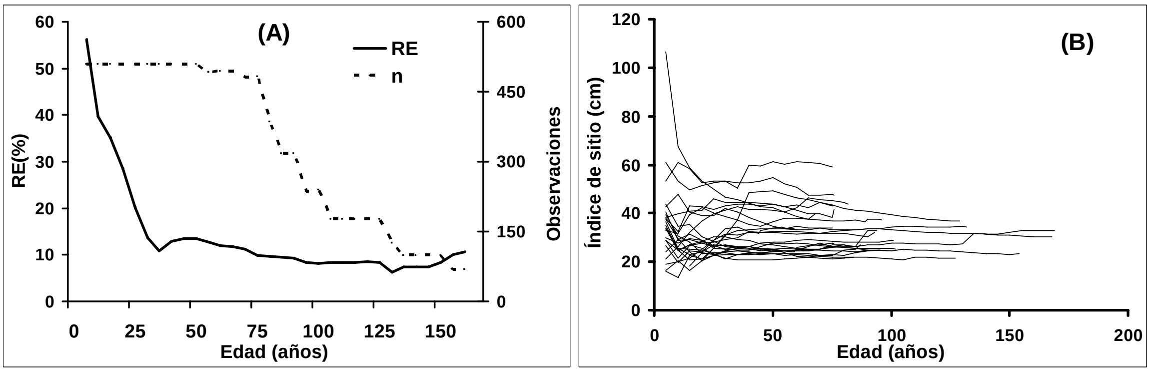


Figura 1. (A) Error medio cuadrático relativo (RE) en predicción y tamaño muestral (n=número de observaciones) según diferentes elecciones de edades de referencia para E5 por clases de edad de 5 años; (B) Predicción del índice de sitio en función de la edad para E5 construido con las 25 series potenciales.

A partir de (1) definimos un índice de sitio basado en crecimiento en diámetro potencial a una edad de referencia de 80 años. Se seleccionó esta edad por ser la mayor dentro del rango óptimo del número de observaciones y el error relativo en nuestra muestra (Figura 1A) y para facilitar la comparación con masas de *Quercus suber* (Sánchez-González *et al*., 2005). Los cuatro índices de sitio corresponden a los diámetros 50 cm (clase I), 41 cm (clase II), 32 cm (clase III) y 23 cm (clase IV). Los crecimientos originales y las curvas simuladas con los índices de sitio se muestran en la Figura 2A. El error medio en predicción potencial se situó alrededor del 7% en árboles dominantes entre 10 y 45 cm (Figura 3). El error de predicción fue menor del 15% para intervalos por debajo de 45 años, y sólo del 3,5 % para 5 años (Figura 4).

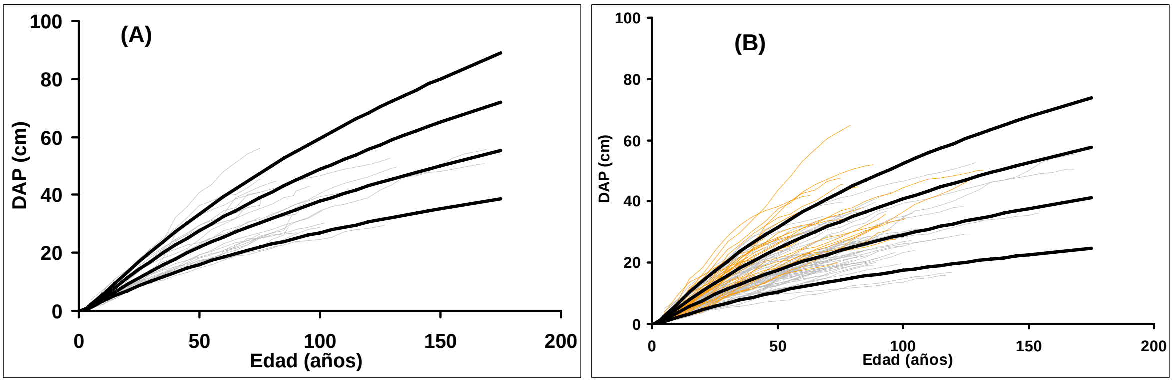


Figura 2: Modelos dinámicos dependientes de la edad: (A) curvas potenciales utilizando E5 para índices de sitio 50, 41, 32 y 23 cm a una edad de referencia de 80 años. (B) curvas de los modelos generales de crecimiento en diámetro (E5$_2$, para 115 árboles); las curvas se forzaron a pasar por DAP 45, 35, 25 y 15 cm a la edad base de 80 años; en (B) las líneas naranja delgadas corresponden a árboles creciendo en densidad≤100 pies/ha, mientras las líneas grises delgadas corresponden a pies creciendo en densidad>100 pies/ha.

Modelos dinámicos de crecimiento en diámetro generales dependientes de la edad

Al ajustar los modelos a las 115 series de crecimiento, los residuos fueron heterocedásticos (ver Anexo II para más detalle), por lo que se incluyó un factor de peso para ponderar el ajuste. De nuevo la mejor expresión correspondió al modelo $E5_2$, deducido a partir de la ecuación base de Korf. El modelo expandido por densidad ($E5_{2d}$) no mejoró el modelo general ($E5_2$) sin expandir (Tabla 3). La expresión del modelo final ($E5_2$, válido para cualquier árbol independientemente de la densidad) fue:

$$DAP_2 = \exp(X_0)\cdot\exp(-(8.310178 + (1/X_0))\cdot t_2^{-0.264597}),\ \text{donde}$$
$$X_0 = 0.5\cdot(8.310178\cdot t_1^{-0.264597} + \ln(DAP_1) + F_0)\ \text{y}$$
$$F_0 = \sqrt{((8.31017\cdot t_1^{-0.264597} + \ln(DAP_1))^2 + 4\cdot t_1^{-0.264597})} \qquad (2)$$

Aunque el error aumentó respecto a (1), éste fue aún aceptable, alrededor del 10% para árboles con 10 cm<DAP<50 cm (Figuras 3B y 4).

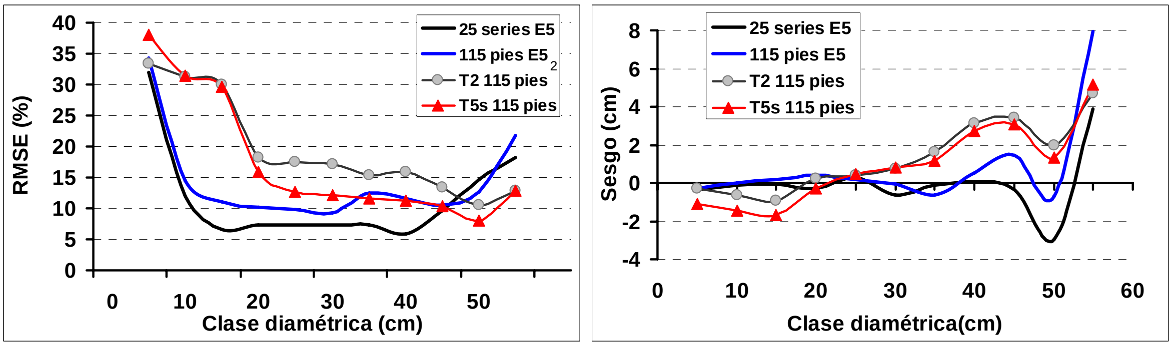


Figure 3. Error medio cuadrático relativo y sesgo en predicción de diámetro por clase diamétrica para E5 (línea continua) y $E5_2$ (línea discontinua), T2 (círculos) y T5s (triángulos).

Modelos dinámicos de crecimiento en diámetro independientes de la edad

De igual modo que para el caso anterior, los modelos fueron ajustados usando un factor de peso. El mejor modelo expandido sólo por densidad fue T2 (más detalle en intervalos de confianza y estimación de parámetros en Anexo II):

$$DAP_2 = \frac{(F + dif)^{1{,}007868}}{(0{,}23114\cdot densidad) + \left(\frac{0{,}465367}{densidad}\right)\cdot(F + dif)^{1{,}007868}},\ \text{con} \qquad (3)$$

$$F = t_1 = \sqrt[1{,}007868]{\frac{DAP_1\cdot(0{,}023114\cdot densidad)}{(1-\left(\frac{0{,}465367}{densidad}\right)\cdot DAP_1)}},\ \text{y dif=intervalo de proyección } (t_2\text{-}t_1).$$

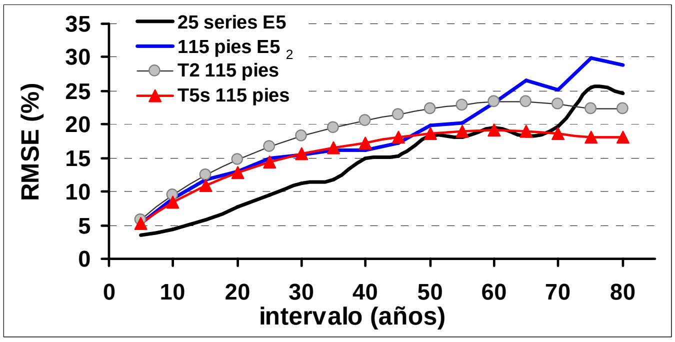


Figure 4. Error medio cuadrático relativo (RMSE, %) por intervalo de predicción para E5 (línea continua) y $E5_2$ (línea discontinua), T2 (círculos) y T5s (triángulos).

Tabla 3. Estadísticos de ajuste para los modelos generales dependientes de la edad (expandidos, E_{xd}, y no, Ex, por densidad) e independientes de la edad expandidos por densidad (Tx) y/o por índice de sitio y densidad (Txs). En E3d: $b=(b_1+b_d \cdot Densidad) \cdot X$; en E5d: $b=(b_1+b_d \cdot Densidad)+(1/X)$.

Id	Estimación			Validación (jack-knife)			
	RMSE (cm)	R^2	AICd	Sesgo (cm)	RMSE (cm)	EF	AICd
$E3_2$	0,7234	0,9926	8,5	0,0670	2,6532	0,9508	89,2
$E5_2$	0,7217	0,9927	0,0	-0,0492	2,5887	0,9532	0,0
$E9_2$	0,7327	0,9924	54,4	0,0827	3,0584	0,9347	603,3
E3d	0,7234	0,9926	10,3	0,0767	2,6787	0,9499	122,7
E5d	0,7217	0,9927	1,7	-0,0386	2,6031	0,9527	19,1
T1	0,6762	0,9927	900,0	-0,4007	4,7340	0,8333	6240,8
T2	0,6781	0,9927	981,2	-0,5587	4,6274	0,8407	5549,2
T3	0,6856	0,9925	1317,7	-0,4495	4,7475	0,8323	6327,3
T4s	0,6632	0,9930	307,7	-0,0742	4,0366	0,8788	1400,5
T5s	0,6565	0,9931	0,0	-0,1413	3,8545	0,8895	0,0

Aunque el error se incrementó al no incluir la edad como covariable, el error continuó siendo aceptable, menor del 15% para intervalos menores de 20 años (Figuras 4 y 5). Al expandir por índice de sitio además de por densidad el error se redujo en un 17% y el sesgo en un 75%. Estos modelos son “pseudos-independientes” de la edad, ya que se necesitaría estimar el índice de sitio. La expresión de T5s, el modelo que mejores estadísticos de validación y ajuste mostró, (Tabla 3) fue:

$$DAP_2 = \frac{(F + dif)^{0,859611}}{(0,002797 \cdot densidad + 31,4296 / IS) + \left(\left(\frac{-0,06588}{densidad}\right) + 0,000123 \cdot IS\right) \cdot (F + dif)^{0,859611}} \text{, con}$$

$$F = \sqrt[0,859611]{\frac{DAP_1 \cdot (0,002797 \cdot densidad + 31,4296 / IS)}{(1 - \left(\left(\frac{-0,06588}{densidad}\right) + 0,000123 \cdot IS\right) \cdot DAP_1)}} \qquad (4)$$

dif=intervalo de proyección, IS= índice de sitio en cm. En la Figura 5 se simulan las ecuaciones (3) y (4) para distintas densidades y clases de sitio. Estos modelos son también polimórficos y con diferentes asíntotas, igual que (1) y (2). Sin embargo, su tendencia asintótica podría no ser muy ortodoxa en ciertos casos: en las clases mayores de edad, fuera del rango de datos usados para el ajuste, en alguno de los casos simulados las curvas se cruzaron (Figura 5).

4.4 Discusión

En este trabajo proponemos las primeras ecuaciones de crecimiento en diámetro para *Q. ilex* ssp. *ballota*. Como consecuencia de la anatomía de la madera y particularidades de su gestión, modelizar el crecimiento de la especie no es tarea fácil comparado con otras especies incluso dentro del mismo género (Cherubini *et al.*, 2003). La especie es considerada de crecimiento lento, sin embargo en la muestra analizada el crecimiento no fue mucho más lento que el que presentan otros *Quercus* mediterráneos (Sánchez-González *et al*., 2005; Tomé *et al*., 2006; Adame *et al*., 2008), posiblemente por tratarse de una buena estación (límite supramediterráneo, precipitación por encima de 600 mm) y de menores densidades que los estudios en otros *Quercus*. Las edades obtenidas en este trabajo y las estimadas por otros autores (Plieninger *et al*., 2003) apoyarían la hipótesis que sitúa el origen de muchas dehesas a partir de la segunda mitad del siglo XIX, y el hecho de que se encuentren en su primer turno (Manuel y Gil, 1999; Pulido *et al.*, 2001; Martín Vicente y Fernández Alés, 2006).

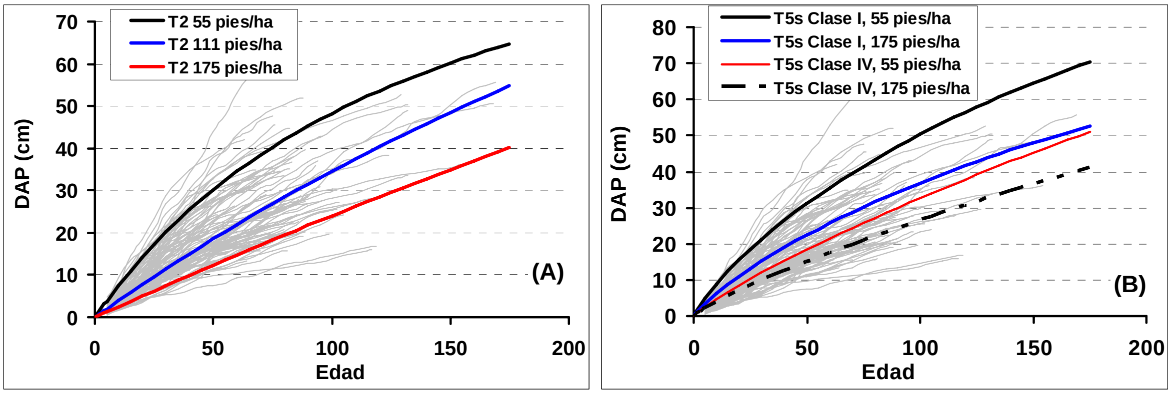


Figura 5. Modelos independientes de la edad: (A) T2 para densidades 55, 111 y 175 pies/ha; (B) T5s para clase de sitio 50 (Clase I) y 23 (Clase IV), y densidades 55 y 175 pies/ha.

Los modelos presentaron unos errores similares a otros estudios de crecimiento en especies forestales (Diéguez-Aranda *et al.,* 2005; Barrio-Anta *et al.*, 2006), siendo los menores errores los que se localizan en las clases diamétricas centrales, que son las más abundantes en la dehesa (Pulido *et al*., 2001). A su vez, los errores del modelo ajustado a todos los árboles de la parcela son muy similares a los del crecimiento potencial ajustados a las series por parcela, por lo que se puede usar un único modelo independientemente de la densidad y de la categoría social del árbol, con las ventajas que ello conlleva para los usuarios al no tener que discriminar "*a priori*" ninguna característica del árbol. Un árbol medio alcanzaría unos 15 cm de diámetro a los 30 años, lo cual coincide con la edad aproximada de exclusión al pastoreo de ganado vacuno sugerida en la bibliografía para la regeneración de los rodales (San Miguel, 1994).

Pese a que la ecuación (2) puede usarse para cualquier árbol del sistema, la dificultad de estimar la edad del individuo confiere a los modelos independientes de la edad un potencial de uso mucho mayor. Los modelos expandidos sólo por densidad, a pesar de presentar un pequeño sesgo y presentar unos estadísticos y comportamiento peor, ofrecen un error suficientemente pequeño como para recomendar su uso. El error se redujo al introducir el índice de sitio definido. Por ello, estas ecuaciones podrían mejorar si se poseyera una muestra procedente de un rango geográfico más amplio y datos de suelo y clima (Tomé *et al*., 2006), que se incorporaran al modelo y aportaran información sobre la calidad de estación.

5.

Análisis del efecto de la competencia sobre el crecimiento en diámetro de la encina en dehesas

Basado en:

Gea-Izquierdo G, Cañellas I. Analysis of holm oak intraspecific competition using Gamma regression. En revisión.

(Anexo III)

5.1 Introducción

El estudio del efecto de la competencia y la densidad en los rodales sobre el crecimiento es un requerimiento básico en los modelos selvícolas. Por ello, en este capítulo se estudia el efecto de la densidad y la competencia en el crecimiento en diámetro de la encina en las dehesas. En primer lugar la competencia es analizada y se evalúa el comportamiento de distintos índices habitualmente utilizados en la bibliografía. En segundo lugar, se modeliza el incremento en diámetro y se comparan modelos lineales gaussianos transformados logarítmicamente con modelos lineales generalizados con distribución Gamma y distintas funciones enlace. A continuación, se ajustan modelos que incluyen la edad como covariable y se comparan con modelos que no la incluyen, los cuales son más susceptibles de ser utilizados por la ventaja de no tener que estimar la edad. Finalmente se discuten las posibilidades del inventario forestal nacional (IFN) para modelizar el crecimiento en diámetro de la encina.

5.2 Material y métodos

Diseño experimental

Para analizar el efecto de la competencia en el incremento en diámetro de encina en dehesas se utilizaron 168 muestras procedentes de 37 parcelas de radio variable. Las 25 parcelas descritas en el apartado anterior, se completaron con datos de 12 parcelas procedentes de la provincia de Cáceres (39º 28’ N, 6º 11’ O, 393 m) replanteadas también en masas incluidas en el trazado de una autovía. Las parcelas se caracterizaron de modo idéntico a como se describió en el capítulo anterior.

La variable dependiente estudiada fue el incremento en diámetro en períodos de 10 años. El crecimiento se estimó como se describió en el capítulo 3. Las covariables analizadas fueron la edad a 1,30 m, las características dasométricas del pie, índices de competencia calculados como se detalla en la tabla 1 y el índice de sitio (IS) descrito en el capítulo 4. Entre las covariables estudiadas se incluyó el DAP^2, al ser el crecimiento biológico del árbol en diámetro un paraboloide con un punto de inflexión (Wykoff, 1990). Algunos de los índices de competencia que mejores resultados ofrecen en la bibliografía incluyen en su cálculo variables dependientes de la copa (Biging y Dobbertin, 1992; 1995). Sin embargo, la selvicultura aplicada a las dehesas (podas) invalida cualquier covariable que incluya características de copa en su formulación, por lo cual sólo probamos índices de competencia que no incluyeran ningún parámetro de copa (Tabla 1). Este hecho debería revestir menor trascendencia que en bosques cerrados ya que la competencia por luz (dependiente de las copas) debería ser mínima en sistemas abiertos como las dehesas, comparada al menos con la competencia subterránea entre sistemas radicales. Se estudió la competencia comparando 18 índices dependientes e independientes de la distancia. En los dependientes de la distancia se estudiaron diferentes radios de influencia (Tabla 1).

Tabla 1. Expresión de los índices de competencia consideradas. 'j' se refiere a un árbol competidor; dist_{ij}=distancia entre i y j; AB= área basimétrica parcela (m^2/ha); $\text{Dmc} = 2 \cdot \left(\sqrt{\text{AB} / \pi \cdot \text{Nn}}\right)$; n=número de pies en parcela k; r=radio de búsqueda

Índice	Nombre	Expresión	Referencia
Índices independientes de la distancia			
CII1	Densidad (Nn)	n/área parcela (en pies/ha)	
CII2	Área basimétrica parcela	$\sum_{i=1}^{n} \pi \cdot (\text{DAP}_i / 2)^2$	
CII3	Ddg	DAP_i/Dmc	
CII4	Glover	$\text{DAP}_i^2 / \overline{\text{DAP}}^2$	Glover y Hool (1979)
CII5	BAL	$\sum_{j=1}^{n-1} \pi \cdot (\text{DAP}_j / 2)^2$, cuando $\text{DAP}_j > \text{DAP}_i$	
CII6r	Número de competidores en r metros (N_r)		Moravie *et al*. (1999) citado en Paulo *et al*. (2002)
CII7r	Número de competidores en r metros si $\text{DAP}_j > \text{DAP}_i$		Moravie *et al*. (1999) citado en Paulo *et al*. (2002)
CII8r	Suma del DAP de los árboles en r metros	$\sum \text{DAP}_j$	Steneker y Jarvis (1963) citado en Paulo *et al*. (2002)
CII9r	Razón de tamaños	$\frac{\text{DAP}_i}{\sum_{i=1}^{n} \text{DAP}_i}$	Daniels *et al*. (1986) citado en Paulo *et al*. (2002)
Índices dependientes de la distancia			
CID10	Clark-Evans	$\left(\sum_{i=1}^{n} \min(\text{dist}_{ij}) / n\right) / \left(2 \cdot \sqrt{\text{Nn}}\right)$, (Nn en pies/$m^2$)	Clark y Evans (1954)
CID11	Distancia al vecino más próximo (NN)		Moravie *et al.*(1999) citado en Paulo *et al*. (2002)
CID12	Distancia al NN tal que $\text{DAP}_j > \text{DAP}_i$		Moravie *et al.*(1999) citado en Paulo *et al*. (2002)
CID13r	Razón de tamaños proporcional a la distancia	$\sum_{j=1}^{n} \frac{\text{DAP}_j}{\text{DAP}_i} \cdot \frac{1}{(\text{dist}_{ij} + 1)}$	Hegyi (1974) citado en Biging y Dobbertin (1995)
CID14r	Diferencia de tamaños proporcional a la distancia	$\sum_{j=1}^{n} \frac{\text{DAP}_j - \text{DAP}_i}{(\text{dist}_{ij} + 1)}$	Moravie *et al*. (1999) citado en Paulo *et al*. (2002)
CID15r	Razón de tamaños exponencial negativa	$\sum_{j=1}^{n} \frac{\text{DAP}_j}{\text{DAP}_i} \cdot \frac{1}{\exp(\text{dist}_{ij} + 1)}$	
CID16r	Razón de tamaños exponencial negativa con factor de pesos	$\sum_{j=1}^{n} \frac{\text{DAP}_j}{\text{DAP}_i} \cdot \exp[-(\text{dist}_{ij} + 1) / (\text{DAP}_i + \text{DAP}_j)]$	Martin and Ek (1984)
CID17r	Lorimer	$\sum_{j=1}^{n} \frac{\text{DAP}_j / \text{DAP}_i}{\sqrt{\text{Dist}_{ij} / r}}$	Lorimer (1983) citado en Mailly *et al*. (2003)
CID18r	'Crowding'	$\sum_{j=1}^{n-1} (\text{DAP}_j / \text{dist}_{ij})^{\gamma}$; con γ=1	Miina y Pukkala (2002); Stadt *et al*. (2007)

El inventario forestal español (IFN) está replanteado en una cuadrícula de 1 km UTM, en las cuales se miden diferentes parcelas circulares concéntricas en las que se incluyen determinadas clases diametrales (DGB, 1999). En este trabajo usamos sólo las dos circunferencias interiores (radio=10 m), por lo tanto se incluyeron sólo pies con DAP>12,5 cm de modo similar a otros estudios (Canham *et al.*, 2006), para reducir el sesgo de muestreo y la correlación entre datos. Como las características de la muestra obtenida y de los datos proporcionados por el IFN son muy diferentes, decidimos ajustar modelos separados para comparar su comportamiento. Para el desarrollo del modelo a partir del IFN, se seleccionaron parcelas de Salamanca, Cáceres y Badajoz (ver Anexo III para más detalle) monoespecíficas de encina, comparándose densidades diferentes (500, 250, 125 pies/ha) para evitar en lo posible formaciones de monte bajo arbustivas. De este modo se obtuvieron 2819 observaciones procedentes de 1566 parcelas. La variable dependiente fue la diferencia entre el DAP medido en el IFN2 y el medido en el IFN3. Además, se calcularon la densidad de parcela, área basimétrica, altura del árbol, coordenadas UTM, pendiente, datos meteorológicos (Sánchez-Palomares *et al.*, 1999), y cuenca hidrológica (las tres últimas covariables usando un GIS). No se pudieron calcular más índices de competencia ni otras covariables por las características de los inventarios realizados para la especie.

Tabla 2. Características de la muestra. AB= area basimétrica parcela (m^2/ha); Nn=Densidad en pies/ha; Edad=edad estimada en la base. *datos del IFN3: parcelas monoespecíficas de encina, radio parcela=10 m, DAP>12.5 cm, densidad<500 pies/ha.

	Ciudad Rodrigo				Cáceres				IFN*		
	DAP	Edad	Densidad	AB	DAP	Edad	Densidad	AB	DAP	Densidad	AB
Media	28,9	88	129,9	9,5	39,6	116	45,6	6,5	36,8	70,0	5,7
CV (%)	38,8	32,3	29,2	41,5	33,1	31,4	44,3	36,9	44,6	110,5	64,1
Mínimo	10,2	26	39,5	4,6	13,9	42	15,3	3,1	13,4	5,1	0,4
Máximo	68,4	175	210,4	18,0	96,8	212	87,3	10,6	108,2	489,6	31,4
n	115	110	25	25	53	46	12	12	2819	1566	1566

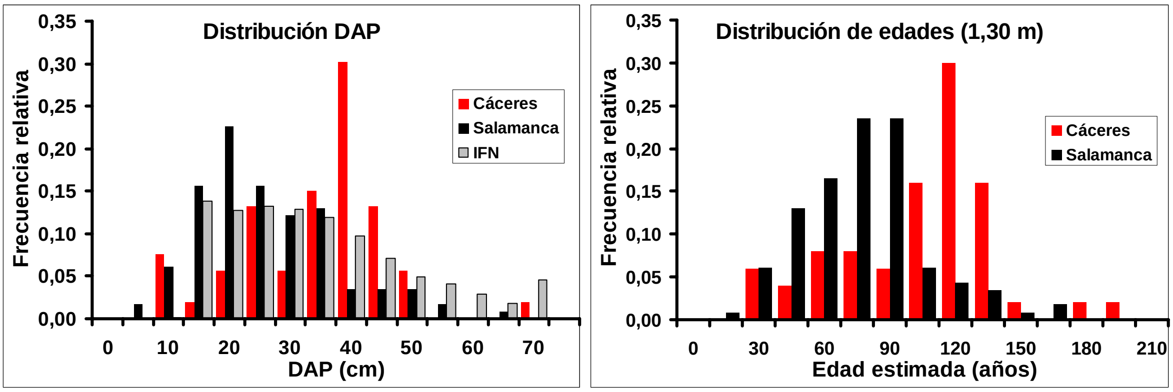


Figura 1. (A) Distribución diamétrica de las parcelas: (i) Barras rojas corresponden a Cáceres; (ii) barras negras a Salamanca; (iii) barras grises a parcelas del IFN. (B) Distribución de edades a 1.30 m.

Análisis estadístico

Se estudió el crecimiento en diámetro de los últimos 10 años comparando modelos empíricos (Porté y Bartelink, 2002) que incluyeron la edad como covariable y también sin incluirla. La transformación de variables en regresión lineal dificulta la interpretación de las ecuaciones finales, incluyendo sesgos en las estimaciones (Myers, 1990). Una solución a este problema es la utilización de modelos lineales generalizados (GLM), los cuales posibilitan una mayor flexibilidad en la distribución de los errores, incluyendo todas las distribuciones de probabilidad incluidas en la familia exponencial (McCullagh y Nelder, 1989; más detalle en Anexo III), es decir: $f_Y(y;\theta,\phi)=\exp\{(y\theta-b(\theta))/a(\phi)+c(y,\phi)\}$ donde θ y ϕ son los parámetros canónicos y de dispersión respectivamente.

Índice	**Completo**		**Densidad** **< 80 pies/ha**		**Densidad** **> 80 pies/ha**	
	EF (%)	ρ (p)	EF (%)	ρ (p)	EF (%)	ρ (p)
CII1	4,339	**-0,208**** **(0,0067)**	5,576	0,160 (0,1818)	7,782	**-0,231**** **(0,0230)**
CII2	2,898	**-0,171**** **(0,0269)**	3,679	0,064 (0,5932)	5,933	-0,186* (0,0677)
CII3	4,981	**-0,223**** **(0,0036)**	16,541	**0,371**** **(0,0015)**	3,236	-0,082 (0,4258)
CII4	2,706	**-0,170**** **(0,0274)**	9,744	**-0,266**** **(0,0252)**	3,103	-0,076 (0,4610)
CII5	1,865	0,032 (0,6767)	12,808	**0,315**** **(0,0074)**	2,137	-0,022 (0,8310)
CII6$_{20}$	0,718	-0,087 (0,2645)	6,803	**0,191**** **(0,1107)**	5,811	-0,183* (0,0732)
CII7$_{50}$	3,991	**0,200**** **(0,0094)**	11,653	**0,342**** **(0,0036)**	1,100	0,105 (0,3066)
CII8$_{50}$	1,676	0,130* (0,0930)	1,560	0,127 (0,2920)	0,310	-0,057 (0,5823)
CII9	0,261	-0,106 (0,1720)	15,181	**-0,352**** **(0,0026)**	2,610	-0,022 (0,8344)
CID10	3,178	-0,091 (0,2476)	10,322	0,111 (0,3691)	2,869	-0,053 (0,6068)
CID11	0,201	-0,064 (0,4110)	6,588	-0,187 (0,1175)	2,049	-0,040 (0,6970)
CID12	1,389	-0,118 (0,1267)	6,567	-0,185 (0,1231)	3,819	-0,113 (0,2710)
CID13$_{50}$	1,042	**0,202**** **(0,0088)**	15,022	**0,388**** **(0,0008)**	2,014	0,142 (0,1652)
CID14$_{20}$	5,678	**0,239**** **(0,0018)**	16,529	**0,371**** **(0,0015)**	3,712	0,107 (0,2968)
CID14$_{DBH2}$	6,499	**0,255**** **(0,0008)**	15,059	**0,350**** **(0,0028)**	5,578	0,176* (0,0850)
CID15$_{50}$	3,347	**0,187**** **(0,0151)**	6,453	0,183 (0,1264)	6,994	**0,218**** **(0,0322)**
CID16$_{50}$	6,668	**0,258**** **(0,0007)**	20,599	**0,423**** **(0,0002)**	3,313	0,086 (0,4028)
CID16$_{DBH7}$	6,401	**0,253**** **(0,0009)**	17,312	**0,416**** **(0,0003)**	0,794	0,090 (0,3834)
CID17$_{50}$	5,758	**0,240**** **(0,0017)**	9,122	**0,422**** **(0,0002)**	3,804	0,134 (0,1919)
CID18$_{50}$	1,889	**0,153**** **(0,0480)**	4,663	0,218* (0,0681)	1,838	0,161 (0,1162)

Tabla 3. Eficiencia para el modelo $Log(IncDAP_{10}+1)=\mu+\beta\cdot CI+b_i$ (b_i es el término aleatorio por parcela) y correlación de Pearson para: (i) datos completos; (ii) parcelas con densidad<80 pies/ha; (iii) parcelas con densidad >80 pies/ha. El subíndice 20/50 ó DBH2/DBH7 indica el radio de influencia ya sea fijo (20 o 50 m) o relativo al DAP [2·(0,2·DAP) o 7·(0,2·DAP) m]. **=significativo α=0,05; *=significativo α=0,10.

De este modo, se compararon modelos gaussianos transformados logarítmicamente con GLMs con estructuras de errores siguiendo una distribución normal (donde la varianza=$\phi=\sigma^2$) y Gamma (donde la varianza no es constante= $\mu^2\cdot\phi$) y diferentes funciones enlace (‘link functions’), como la identidad, logarítmica e inversa. Como la condición de independencia entre observaciones no se satisfizo con nuestro diseño muestral, para modelizar la correlación se utilizaron modelos lineales mixtos generalizados con efectos aleatorios y matriz residual de varianza no diagonal (GLMM.

Verbeke y Mohlenbergs, 2000; Diggle *et al*., 2002; Mohlenberghs y Verbeke, 2005). La expresión genérica de un GLMM es:

$f_i(y_{ij} \mid b_i, \beta, \phi) = \exp\{\phi^{-1}[y_{ij}\theta_{ij} - \psi(\theta_{ij})] + c(y_{ij}, \phi)\}$; donde $\mu_{ij} = E(Y_{ij} \mid b_i) = g^{-1}(x'_{ij}\beta + z'_{ij} b_i)$;

$g(\cdot)$ es la función enlace; x_{ij} y z_{ij} son las matrices de diseño de los efectos fijos y aleatorios respectivamente; β es un vector de efectos fijos de dimensión p, y b_i es un vector de efectos aleatorios de dimensión q tal que, $b_i \sim N(0,G)$. Y_{ij} son observaciones de cualquier distribución de la familia exponencial, con matriz de varianza-covarianza V, y donde ϕ es el parámetro de escala y θ el parámetro natural. Para estudiar la posible multicolinearidad entre las covariables se calculó el factor de inflación de la varianza (VIF. Myers, 1990) utilizando PROC REG. Para el resto de los ajustes estadísticos se usaron PROC MIXED, PROC GENMOD y PROC GLIMMIX (SAS Inc., 2004). Los modelos se autovalidaron de modo análogo al capítulo anterior, mediante una validación *Jackknife* (Myers, 1990) y se compararon usando estadísticos de bondad de ajuste habituales en regresión lineal (Anexo III).

Tabla 4. Selección de variables en modelo mixto normal transformado: (i) modelos dependientes de la edad; (ii) modelos independientes edad con datos propios; (iii) modelos independientes de la edad con datos IFN. p (χ^2)=test máxima verosimilitud, probabilidad asociada a la distribución χ^2. EF=eficiencia calculada para los residuos sin retransformar. Max VIF=máximo factor de inflado de la varianza correspondiente a la covariable x. Modelos ajustados usando estimación de máxima verosimilitud (ML). 'DumCac'=variable dummy para Cáceres; 'DumGuadi'=variable dummy para las parcelas incluidas en las cuencas del Guadiana y del Guadalquivir Tmin=media de las temperaturas mínimas del mes más frío. Modelo tipo: $\log(IncDAP_{10ij})=f(x)+b_i+\varepsilon_{ij}$; parcela i, árbol j, f(x) relación lineal de los efectos fijos, b_i es un efecto aleatorio por parcela correspondiente al término independiente.

Covariables	-2LL	p (χ^2)	EF (%)	Max. VIF
(i) Modelos dependientes edad [log(IncDAP$_{10}$)=f(x$_c$)]				
Edad	160,2	< 0,0001 (55,5)	33,19	1,00
Densidad (CII1)	151,1	0,0026 (9,1)	44,69	1,04
Ddg (CII3)	134,6	< 0,0001 (16,5)	50,01	1,61
(1/DAP)	126,6	0,0050 (8,0)	51,81	2,61
CID15$_{50}$	119,1	0,0062 (7,5)	53,09	2,61
(ii) Modelos independientes edad (datos propios) [log(IncDAP$_{10}$+1)=f(x$_c$)]				
(1/DAP)	79,1	< 0,0001 (24,0)	13,47	1,00
Densidad (CII1)	68,1	0,0009 (11,0)	21,57	1,04
DumCac	57,9	0,0014 (10,2)	26,98	1,83
CID15$_{50}$	50,9	0,0081 (7,0)	29,88	1,85
CII7$_{50}$	45,9	0,0253 (5,0)	30,98	2,00
DAP	41,7	0,0404 (4,20)	33,42	3,69
(iii) Modelos independientes edad (IFN) [log(IncDAP$_{10}$+1)=f(x$_c$)]				
Y UTM (km)	2643,2	< 0,0001 (29,7)	1,407	1,00
Pendiente	2611,9	< 0,0001 (31,3)	3,170	1,04
Densidad	2606,7	0,0226 (5,2)	3,649	1,07
DAP	2600,6	0,0135 (6,1)	3,763	1,23
Altura	2589,0	0,0066 (11,7)	4,306	1,72
Tmin	2583,8	0,0226 (5,2)	4,685	3,89
DumGuadi	2577,6	0,0128 (6,20)	4,906	4,04

5.3 Resultados

Los árboles se distribuyeron uniformemente en los rodales estudiados (Clark-Evans: 1,400±0,214). En la Tabla 2 se pueden ver las características de la muestra y en la Figura 1 la distribución de la variable dependiente, que como se aprecia se aleja de la distribución normal. Sorprendentemente, los índices de competencia que incluían el tamaño de los competidores en el numerador (DAP_j) o a los competidores de mayor DAP estaban todos positivamente relacionados con el crecimiento del árbol en cuestión (Tabla 3). Todos estos índices, con excepción de CID15, la densidad y el área basimétrica, estaban particularmente relacionados con el crecimiento diametral en los rodales de menor densidad (Tabla 3). En la Figura 2 se aprecia el comportamiento de los índices en función de la distancia de selección de los árboles competidores, pudiéndose apreciar que cada índice parece maximizar la correlación a distancias diferentes. Por este motivo se usaron distintas distancias de influencia para cada uno de ellos (Tabla 3).

Tabla 5. Comparación de comportamiento de modelos: (i) modelo lineal gaussiano transformado logarítmicamente (≈ GLM lognormal); (ii) GLM gaussiano con function link logarítmica; (iii) GLM Gamma con function link inversa (1/μ). Los estadísticos de ajuste del modelo lineal transformado se calculan usando las predicciones transformadas: $pred_{corr} = \hat{y} \cdot CF$; -2LL=-2 veces el logaritmo de la máxima verosimilitud.

Modelo		Estimación				Validación (*Jackknife*)		
		-2LL	Sesgo medio (cm)	RMSE (cm)	R^2_{SS} (R^2_D)	Sesgo medio (cm)	RMSE (cm)	EF (%)
Modelos dependientes de la edad	Transformado logarítmico normal	-	0,0244	1,0303	50,599	0,0145	1,0964	45,737
	GLM normal con log link	-236,5	0,0083	1,0176	51,787 (51,787)	-0,0105	1,1422	41,112
	GLM Gamma con log link	-203,95	0,0042	1,0261	50,977 (53,929)	-0,0035	1,0899	46,378
Modelos independientes de la edad	Transformado logarítmico normal	-	0,0000	1,2084	30,807	-0,0153	1,3021	22,059
	GLM normal con log link	-264,11	0,0216	1,1690	35,249 (35,249)	0,0252	1,2344	29,952
	GLM Gamma con log link	-241,81	0,0093	1,1965	32,163 (28,718)	-0,0049	1,2808	24,598

Nota: los modelos solo incluyen efectos fijos. Los modelos dependientes de la edad incluyen las cinco covariables seleccionadas en la Tabla 4, mientras los independientes de la edad incluyen las 6 covariables seleccionadas en la Tabla 4 excepto 1/DAP.

Competencia en modelos de incremento en diámetro dependientes de la edad

Las variables seleccionadas en los modelos gaussianos transformados se muestran en la Tabla 4. Posteriormente comparamos (Tabla 5) el modelo transformado con GLMs con distribuciones Gamma y normal con funciones enlace inversas ajustados con las mismas covariables seleccionadas en la Tabla 4. Se aprecia cómo los modelos Gamma mejoraron los resultados de los modelos mixtos normales transformados, con el beneficio añadido, respecto a los modelos gaussianos transformados, de no necesitar volver a transformar la variable en las predicciones (más detalle en la distribución de residuos en Anexo III). Finalmente, en la Tabla 6 se muestra cómo al utilizar la distribución Gamma para modelizar el crecimiento el número de covariables se redujo las que mostraban una relación más clara con la variable dependiente (ver Anexo III). El modelo final incluyó la densidad y la edad sólo como covariables, siendo éstas las únicas relaciones que resultaron evidentes en el análisis gráfico (intervalos de confianza y distribución de errores en Anexo III). El modelo Gamma finalmente ajustado fue:

$$\mathrm{Inc10}_i = \hat{\mu}_i = \frac{1}{0{,}05336 + 0{,}003095 \cdot \mathrm{Edad}_{\mathrm{DAP}} + 0{,}000889 \cdot \mathrm{Densidad}} + \varepsilon_i , \qquad (1)$$

con $\varepsilon_i \sim G(\mu, \mu^2/8{,}6817)$. En la Tabla 6 se muestran los estadísticos de ajuste y los detalles del modelo.

Competencia en modelos de incremento en diámetro independientes de la edad

En la tabla 5 se muestran los modelos ajustados con función enlace logarítmica para facilitar su comparación. Se aprecia (Tabla 5, Tabla 6) cómo los modelos con distribución Gamma son de nuevo los que mejor comportamiento tienen, seleccionando sólo tres variables y por tanto resultando modelos más parsimoniosos. El modelo final fue ajustado con función enlace inversa, ya que ésta minimizaba la función de máxima verosimilitud (ver Anexo III). La expresión resultante fue:

$$\mathrm{Inc10}_i = \hat{\mu}_i = \frac{1}{0{,}1068 \cdot \mathrm{DumCac} + 0{,}0056 \cdot \mathrm{DAP} + 0{,}0017 \cdot \mathrm{Densidad}} + \varepsilon_i ,$$

donde $\varepsilon_i \sim G(\mu, \mu^2/6{,}3218)$. En la Tabla 6 se muestran los estadísticos de ajuste y los detalles del modelo.

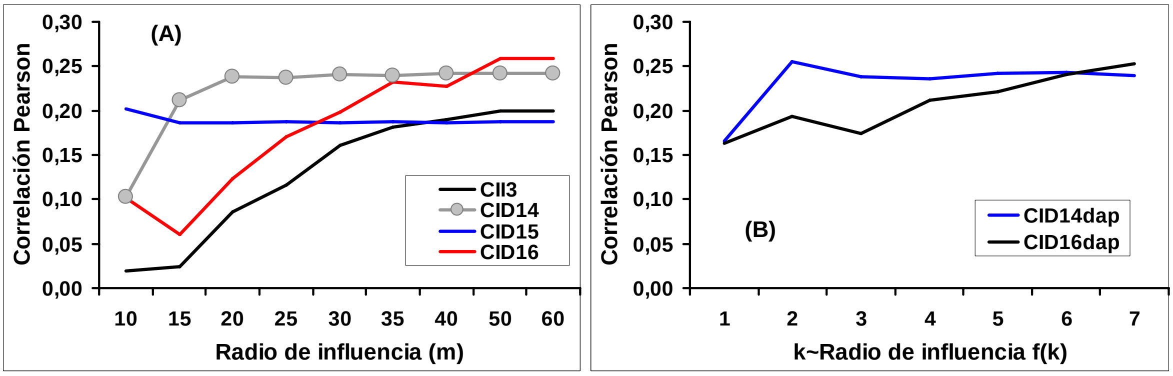


Figura 2. Resultado del coeficiente de correlación de Pearson calculado para los índices de competencia según distintos radios de radio de influencia. En (B) el radio de influencia=20·k·DAP en m.

¿Es factible el uso del IFN para modelizar el crecimiento en diámetro de las dehesas de encina?

En este caso utilizamos un modelo normal transformado logarítmicamente ya que la distribución de la variable dependiente era más próxima a una distribución normal (Figura 1) y para facilitar la discusión con otros trabajos de la bibliografía. Las covariables que más varianza explicaron fueron la pendiente y la latitud (coordenada Y UTM) (Tabla 3). La expresión final fue de:

$$\begin{aligned}\mathrm{Inc10} = \mathrm{CF}\cdot(\exp(-4{,}0376 + 0{,}001175\cdot\mathrm{YUTM} - 0{,}00448\cdot\mathrm{Pendiente} - 0{,}00038\cdot\mathrm{Densidad} - \\ - 0{,}00234\cdot\mathrm{DAP} + 0{,}02329\cdot\mathrm{Altura} + 0{,}02842\cdot\mathrm{Tmin} + 0{,}08161\cdot\mathrm{DumGuad} + b_i + \varepsilon_i) - 1)\end{aligned}$$

Con ε_i~N(0, 0,1032) y b_i~N(0, 0,05348); CF es el factor de corrección (1,11614 en nuestro caso), 'DumGuad' es una variable dummy para las cuencas del Guadiana y el Guadalquivir y Tmin es la media de las temperaturas mínimas del mes más frío. Los estadísticos de ajuste fueron: Sesgo=0,000, RMSE=1,548, y R^2=3,931.

5.4 Discusión

Competencia intra-específica en dehesas de encina

Los índices usados están diseñados para penalizar el tamaño y la cercanía de los árboles vecinos competidores. Sin embargo, en los resultados de los rodales de menor densidad muchos índices se comportaron contrarios a esta hipótesis: cuanto mayor era el tamaño de los vecinos, mayor fue la relación positiva con el crecimiento del árbol en cuestión (Tomé y Burkhart, 1989; Mailly *et al*., 2003). Esto sugiere que estos índices no estaban reflejando competencia, sino que están estimando la edad indirectamente a través del diámetro. En masas abiertas, al no haber competencia por luz, se expresa el crecimiento casi potencial, lo cual implica que las edades pueden ser estimadas a través de los diámetros con menor error que en bosques cerrados, y por tanto la probabilidad de que un árbol sea joven es directamente proporcional al número de competidores mayores que él. Los índices de competencia positivamente relacionados con el crecimiento se comportaron como estimadores indirectos de la edad. En este sentido, otros índices que no incluían el tamaño de los árboles competidores en el numerador sí estaban negativamente relacionados con el crecimiento, mostrando la existencia de competencia, al menos en los rodales de más de 80 pies/ha (Tabla 3). Sin embargo, la correlación entre estos índices que sí reflejan competencia y el crecimiento es baja (menor de 0,25; ver Anexo III), lo cual muestra la lógica menor competencia en estas masas abiertas en comparación con otros estudios en masas más cerradas (Biging y Dobbertin, 1995; Mailly *et al*., 2003). Por tanto, aunque existe competencia, la covariable que determina en mayor medida el crecimiento es la edad, ya que la competencia es reducida, sobre todo en los rodales en baja densidad, donde las copas tienden a formar un estrato-dominante codominante y por consiguiente, no compiten en exceso por luz. Por tanto la competencia también debe presentarse entre los sistemas radicales (competencia simétrica. [Schwinning y Weiner, 1998]), los cuales en la encina se considera que pueden extenderse más allá de las copas y penetrar a varios metros de profundidad (Rodá *et al.*, 1999; Moreno *et al.,* 2005).

Tabla 6. Estimadores de los parámetros e intervalos de confianza. Los valores de probabilidad ‘p’ se obtienen de los análisis de la devianza comparados a una distribución χ^2 (McCullagh and Nelder 1989). ϕ = parámetro de dispersion en GLM; SE=error estándar. σi^2 = estimador de la varianza del efecto aleatorio del término independiente en GLMM; entre paréntesis el error estándar de predicción. ** significativo α=0,05; * significativo α=0,10.

	Modelos dependientes edad			Modelos independientes edad			
	Normal transformado logarítmico	GLM Gamma con link inverso		GLM normal con link inverso		GLM Gamma con link inverso	
	Estimador (SE)	Estimador (SE)	p (valor χ^2)	Estimador (SE)	p (valor χ^2)	Estimador (SE)	p (valor χ^2)
Término independiente	1,2884 (0,1833)	0,05336 (0,0238)	0,0051** (7,84)	-0,2400 (0,0512)	< 0.0001** (21.51)	-	0.6737 (0.18)
Edad 1,30 m	-0,00989 (0,0011)	0,003095 (0,0003)	0,0001** (14,69)	-	-	-	-
Densidad	-0,00357 (0,0005)	0,000889 (0,0002)	0,0662* (3,38)	0,0020 (0,0002)	< 0.0001** (102.40)	0.0017 (0.0002)	< 0.0005** (29.05)
Ddg	0,6336 (0,1230)	-	0,1475 (2,10)	-	-	-	-
CID15$_{50}$	1,7446 (0,7970)	-	0,7667 (0,09)	-0,6319 (0,1184)	0.0006** (11.75)	-	0.3326 (0.94)
(1/DAP)	4,0504 (1,6200)	-	0,6512 (0,20)	-	0.8634 (0.03)	-	0.3945 (0.73)
CII7$_{50}$	-	-	-	0,0233 (0,0045)	< 0.0001** (27.92)	-	0.3792 (0.77)
DAP	-	-	-	0,0098 (0,0012)	< 0.0001** (73.07)	0.0056 (0.0007)	< 0.0001** (20.07)
Dummy Cáceres	-	-	-	0,1142 (0,0223)	< 0.0001** (36.59)	0.1068 (0.0260)	0.0863* (2.94)
ϕ	-	8,6817 (0,9380)		1,1154 (0,0609)		6,3218 (0,6723)	
Sesgo medio (cm)	0,0244	0,0000		0,0210		-0,0303	
RMSE (cm)	1,0303	1,0595		1,1188		1,2286	
R^2_{SS} (R^2_D)	50,599	48,697 (46,625)		40,692 (40,692)		29,340 (24,889)	
σ_i^2	0,01433 (0,01008)*	0,000 (-)		0,000 (-)		0,000 (-)	

Modelos de crecimiento en diámetro en dehesas de encina

Los modelos gaussianos seleccionaron demasiadas covariables, algunas superfluas, siendo máxima la verosimilitud al modelizar con la distribución Gamma. Los GLM Gamma fueron más sencillos, y seleccionaron sólo las covariables que mostraban una relación más clara con la variable dependiente. La edad y la densidad se relacionaron negativamente con el crecimiento en diámetro. Cuando se ajustaron con el mismo número de covariables, los GLM fueron mejores que los modelos transformados tanto en los modelos dependientes de la edad como en los independientes, además de poseer la ventaja de modelizar directamente la relación entre variables, evitando transformar (y por tanto la introducción de sesgo) o utilizar regresión ponderada (McCullagh y Nelder, 1989). Pese a que en la Tabla 6 se aprecia que el modelo transformado y el GLM gaussiano con función enlace (link) inverso aumentaban el coeficiente de determinación comparados con el modelo GLM Gamma, decidimos seleccionar los modelos Gamma ya que este inflado del R^2 es artificial y se produce al modelizar la variable dependiente con una función de probabilidad que no se adapta a sus características. En consecuencia, se selecciona un número excesivo de covariables que no mejoran la distribución del error, como se aprecia en que el sesgo y el error no se reducen prácticamente. Por ello consideramos que los mejores modelos fueron los GLM con distribución Gamma (los efectos aleatorios no resultaron significativos al ajustarlos como GLMM), tanto para los modelos dependientes como independientes de la edad.

En los modelos independientes de la edad resultó significativa una variable dummy para Cáceres que posiblemente esté reflejando la mayor edad de esta muestra, aunque también es posible que en esa procedencia (menor precipitación, mayor temperatura; datos no mostrados) el crecimiento sea menor. En estos modelos en vez de la edad se selecciona el DAP, que se comporta como un sustitutivo de aquella. Los modelos independientes de la edad explicaron menos variabilidad de la variable dependiente (>28%) que los dependientes de la edad (R^2=47,6), ya que al incluir la edad el comportamiento de los modelos mejoró sensiblemente, como se ha discutido. Los resultados de los dos tipos de modelos son similares a ecuaciones ajustadas a otras especies (Lessard *et al.*, 2001; Sánchez-González *et al*., 2005; Stadt *et al*., 2007). La estimación de la edad a partir del diámetro parece pues posible en este sistema, sobre todo en las masas abiertas. Pese a que se comete un error importante, éste podría ser aceptable en determinados estudios teniendo en cuenta la dificultad de estimar las edades ya comentadas en estas especies (Anexo III; Plieninger *et al*., 2003).

¿Es correcto usar datos del IFN para modelizar el crecimiento en diámetro de la encina?

Nuestros resultados no recomiendan usar el IFN para modelizar el crecimiento en diámetro en encinas, ya que los estadísticos de ajuste son muy pobres, incluso al compararlos con otros estudios que usan el IFN para estudiar el crecimiento en diámetro de otras especies (que habitualmente explican sólo alrededor del 20%; Lessard *et al*., 2001; Trasobares *et al*., 2004; Canham *et al*., 2006). Existen varias razones que apoyan esta afirmación: (i) la heterogeneidad de las masas de encina, incluyendo montes bajos, altos y medios; (ii) la dificultad de medir siempre en la misma posición en el tronco en muestreos repetidos en el IFN ya que los fustes son irregulares; (iii) la gestión de los rodales (en particular podas) dificulta la estimación del crecimiento; (iv) si se considera el error absoluto de muestreo como constante en un inventario independientemente de la especie que se esté muestreando, esto implica que las especies de crecimiento más lento (como la encina) incluirán un mayor error relativo, y por tanto se reducirá sensiblemente la precisión de los datos y su modelización. Los modelos lineales usados en este capítulo son los habitualmente utilizados en la bibliografía para ajustar ecuaciones de crecimiento en diámetro con datos de inventarios, y hay estudios que no han encontrado grandes mejoras usando métodos más complejos (Moisen y Frescino, 2002) por lo que consideramos nuestras conclusiones bien fundamentadas. Aunque estos modelos basados en el IFN no son útiles para predecir el crecimiento, sí podrían estar mostrando ciertas tendencias que sería interesante investigar en el futuro, particularmente la relación positiva del crecimiento con la latitud, que podría estar reflejando un mayor crecimiento o menor estrés hídrico en las masas situadas más al norte, como la analizada por nosotros en Salamanca.

6.

La producción de fruto en las dehesas de encina

Basado en:
Gea-Izquierdo G, Cañellas I, Montero G. 2006. Acorn production in Spanish holm oak woodlands. Investigación Agraria, Sistemas y Recursos Forestales 15(3), 339-354.

(Anexo IV)

6.1 Vecería y producción de fruto en *Quercus*

La variabilidad entre años y, en muchos casos entre individuos, es la norma en la producción de fruto en especies leñosas. Por vecería se entiende la existencia de grandes producciones de fruto sincronizadas determinados años, seguidas de períodos de escasa producción. Existen diversas teorías ecológicas que explican este fenómeno (Herrera *et al*., 1998; Kelly y Sork, 2002), sin embargo, aún no se comprenden todos los factores que lo determinan, y tampoco se ha demostrado (es posible que en parte por la dificultad de poseer series de tiempo suficientemente largas) que existan patrones cíclicos de producción en muchas especies como comúnmente se cree. Los patrones observados en determinadas especies pueden ser una combinación de factores ecológicos interaccionando con ciclos de reproducción intrínsecos de la especie (Herrera *et al*., 1998; Koenig y Knops, 2000). Estos ciclos en algunas especies de *Quercus* parecen coincidir con el período anual o bisanual de maduración de los frutos (Koenig y Knops, 2000; Kelly y Sork, 2002), aunque esto no ha sido demostrado en ninguna especie española.

Las especies del subgénero *Quercus*, sección *Quercus* (=*Lepidobalanus*) exhiben un patrón de maduración anual. Por tanto, el ciclo completo de formación del fruto dura dos años, desde que se forman los primordios el año anterior hasta que maduran los frutos en otoño del año siguiente. Este hecho tiene particular importancia a la hora de analizar la influencia del clima sobre la floración y fructificación. La producción de flores posee una alta correlación con la de fruto en varias especies del género aunque una alta producción flores no garantiza un gran número de frutos (Sork *et al*., 1993; Obeso, 2004). El crecimiento de los frutos se produce durante el verano, y los frutos maduran de octubre a febrero (Rodá *et al*., 1999). Las plántulas germinan la primavera siguiente, siendo importante la protección de otras leñosas (Pulido y Díaz, 2005).

Existen diferentes métodos de estimación de la producción de frutos de distinta precisión y esfuerzo. Destacan los muestreos visuales, incluyendo conteos totales o parciales en pie y métodos subjetivos de rangos, y los métodos que consisten en la recolección en trampas o en el suelo de todas o parte de las bellotas que caen. La elección del método depende mucho de los objetivos del estudio y deben ser estandarizados y validados en todos los casos para que posteriormente puedan ser debidamente utilizados y comparados.

6.2 Tamaño y morfología del fruto en encinas

Casi todos los trabajos realizados sobre la producción de fruto se centran más en cuantificar la producción que en caracterizar la misma. Existe una gran variación en el tamaño de los frutos tanto entre especies como dentro de cada especie. En algunos casos se ha detectado una correlación positiva del tamaño del fruto con la precipitación (Sork, 1993).

En la encina el tamaño del fruto es muy variable, en la bibliografía se encuentran desde bellotas de 1,2 g a más de 6,5 g (3,5 g/bellota; coeficiente de variación, CV>50%); que corresponden a un tamaño medio aproximado de 3,5 x 1,6 cm (CV≈10%), aunque el tamaño del fruto también es muy variable. Esta variabilidad parece explicarse por una combinación de características del árbol (genética), clima, suelo y características del rodal (Afzal-Rafii *et al.*, 1992). Existen aún muchas incógnitas sobre los factores que influyen en el tamaño de los frutos, entre ellos, el efecto de las podas o la densidad de rodal. La infestación por insectos reduce el peso de los frutos, produciendo además la caída prematura de muchos de ellos y una reducción de la tasa de germinación (Villagrán *et al.*, 2002).

6.3 Composición química del fruto

La composición química de las bellotas ha sido más estudiada que su producción, como consecuencia del interés que posee en la alimentación para el cerdo ibérico y la mayor sencillez de análisis por no requerir series de tiempo muy largas para obtener conclusiones válidas. La composición es variable también, sin embargo, las razones que explican esta variabilidad han sido poco estudiadas, no conciéndose cómo afecta la influencia del sitio o de la selvicultura (densidad, laboreos, etc.) en la calidad del fruto. En la Tabla 1 se muestran los resultados de algunos de los trabajos más reseñables que se pueden encontrar en la bibliografía.

Tabla 1. Composición química de bellotas de encina según diferentes autores. Se muestran entre paréntesis desviaciones estándar solamente cuando los autores las facilitan. Los datos de Afzal-Rafii *et* al. (1992) son medias de la localización "El Pardo".

Fuente	Afzal-Rafii *et al.* (1992)	Nieto *et al.* (2002)	Cañellas *et al.* (2003)	López- Carrasco *et al.* (2004)	Olea *et al.* (2004)
Pulpa (%)	-	80,8 (0,4)	-	-	71,5 (4,5)
Materia seca (%)	-	59,3 (0,05)	-	63,5	-
Proteína bruta (%)	4,9 (0,1)	4,8 (0,1)	5,0	5,6 (0,7)	4,7
Lípidos (%)	6,3 (1,4)	12,1 (0,2)	7,0	11,3 (2,8)	-
Fibra bruta (%)	-	-	3,2	0,9 (0,7)	-
Ceniza (%)	2,2 (0,2)	1,6 (0,1)	2,0	1,8 (0,2)	-
P (%)	0,15 (0,01)	-	0,08	-	0,22
Ca (%)	0,02 (0,01)	-	0,24	-	0,09
Mg (%)	0,04 (0,02)	-	0,07	-	-

6.4 Producción de fruto en la encina

La producción de fruto no ha sido suficientemente estudiada en ninguna de las especies arbóreas dominantes en las dehesas, y la poca bibliografía existente está recogida en publicaciones de ámbito local de difícil consulta. Estudiar la producción de fruto en especies leñosas es complejo, ya que a la gran variabilidad que presenta se une la necesidad de analizar series largas, de muy difícil obtención en campo. La producción de fruto en las dehesas de encina es muy variable tanto por árbol como entre años y rodales (Martín Vicente *et al*., 1998), lo cual es un fenómeno común en especies leñosas (Herrera *et al*., 1998; Koenig y Knops, 2000). Las características de la especie en estudio (clima mediterráneo, anemófila) sugerirían la existencia de vecería, la cual sería mayor en las estaciones más pobres (Sork *et al*., 1993; Herrera *et al*., 1998). Sin embargo, y pese a que se considera tradicionalmente vecera, no se ha demostrado con datos cuantitativos la existencia de vecería (entendida como ciclos sincrónicos de producción), entre otras cosas, porque las series de tiempo publicadas en la bibliografía son muy cortas. Sí se ha observado en series de 7 años, que podría existir sincronización en la producción en masas mixtas de *Quercus,* variable en distintos años según especies (Martín Vicente et al., 1998), lo cual es un fenómeno que se ha detectado en el mismo género en EEUU (Sork et al., 1993).

El modo en que se presentan los datos de producción de fruto es importante. Según nuestro criterio, el más objetivo es la producción por área de copa, sobre todo si luego se quieren comparar diferentes rodales y estudios. La variabilidad, como se ha dicho, es grande (Tabla 2), y es normal encontrar CV>100% en la bibliografía. Se han medido producciones de más de 300 kg en pies aislados, frente a otras especies que no producían nada y medias alrededor de 20-30 kg/árbol, que corresponden a producciones de rodal de 500-600 kg/ha (San Miguel, 1994).

6.4.1 Influencia de la poda en la producción de fruto

La poda es una actividad selvícola clásica en la dehesa. La encina ha sido posiblemente la especie más utilizada como combustible entre las especies españolas, sin embargo, con la introducción de los combustibles fósiles en los años 60 su importancia en este sentido ha disminuido notablemente. Tradicionalmente se considera que la poda mejora la producción de fruto (San Miguel, 1994), sin embargo, esto no ha sido demostrado y podría ser además un concepto erróneo, al menos en el caso de las podas más intensas (Cañelllas *et al*., 2007; Alejano *et al*., 2008). Las podas para mejorar la producción de fruto son comunes en diversas especies frutales. Existen diferentes tipos de podas, y el efecto de la poda es difícil de demostrar ya que se necesitarían series largas de producción de fruto tanto antes de podar como después. Por esta razón resulta difícil obtener conclusiones de los estudios existentes ya que todos son demasiado cortos y limitados y muchos no caracterizan suficientemente la masa estudiada. Aceptando estas limitaciones, la bibliografía sugiere que podas abusivas no sólo no son positivas para la producción de fruto si no que son negativas, lo cual parece lógico desde el punto de vista biológico (Cañellas *et al*., 2007; Alejano *et al*.,

Tabla 2. Producción de bellota en dehesas del oeste ibérico según diferentes autores. Los datos son medias de varios años y varios rodales. La poda no se tuvo en cuenta. Desviaciones estándar de las medias (SD) se muestran entre paréntesis como estimadores 'naïve' de dispersión;

Referencia	Procedencia	Método de estimación	Tamaño de muestra (Nº pies)	Muestra	Longitud estudio (años)	Densidad rodal (pies/ha)	Producción media		
							(g/ m^2 copa)	(kg/árbol)	(kg/ha)
Porras (1998)	Huelva	Recolección total	140	3 sitios x 2 tratamientos de poda/sitio	De 8 a 2	-	-	22,9 (10,8)	-
Álvarez *et al.* (2002)	Salamanca	Recolección total	-	3 x 2500 m^2 parcelas	1	25	-	19,0	475
Gómez *et al.* (1980)	Salamanca	Trampas	3	-	2	-	86,6	-	-
Escudero *et al*. (1985)	Salamanca	Trampas	-	-	3	-	120,1	-	-
Martín *et al*. (1998)	Sevilla	Trampas	-	2 x 1 ha parcelas;	7	23	285,8 (194,5)	25,3 (6,5)	-
						60	115,8 (83,2)	7,1 (1,9)	-
Carbonero *et al*. (2003)	Córdoba	Trampas	50	10 pies x 5 años tras poda	2	60-78	-	26,7 (5,1)	-
Torrent (1963)	España	-	2000	-	10	-	-	-	587
Medina (1963)	Extremadura	-	-	-	6	-	-	20,8	-
Olea *et al*. (2004)	Badajoz	Trampas	20	4 pies x 5 sitios	2	20-45	-	-	674,3 (120,4)

2008). Como hoy en día la importancia de la leña es mínima, se cree recomendable dejar de podar abusivamente el arbolado en la dehesa y las podas deberían limitarse a actuaciones ligeras o por causas sanitarias.

6.4.2 Producción por árbol y rodal

Efecto de la densidad y características dasométricas del rodal en la producción de fruto

La producción de bellota varía con la densidad de rodal. Aunque tampoco ha sido estudiado con suficiente detalle, los rodales de menor densidad producen menos por superficie pero más por árbol. Desde el punto de vista productivo, la variable que interesaría maximizar en los modelos es la producción por superficie, criterio que no tiene por qué ser común a optimizar la regeneración. En Martín Vicente *et al*. (1998) las máximas producciones por superficie se situaron en los rodales de densidades alrededor de 150 pies/ha, en los rodales localizados más al norte, por lo que se podría confundir con condiciones climáticas más beneficiosas. Otros trabajos muestran densidades menores para maximizar la producción (Vázquez *et al*., 1996) aunque estos estudios son demasiado limitados como para obtener conclusiones sobre densidades óptimas. En cualquier caso, un aumento en la luz recibida por los árboles en condiciones de mínima densidad y competencia, maximiza la producción por árbol en otros ecosistemas (Abrahamson y Layne, 2003).

Efecto de la calidad de sitio en la producción de bellota

La influencia de la calidad de sitio en la producción de fruto ha sido estudiada en otras especies, mostrando que una misma especie produce diferente en condiciones ecológicas distintas (Kelly y Sork, 2002; Abrahamson y Layne, 2003). En dehesas este fenómeno no ha sido muy estudiado aunque parece que suelos más fértiles y con más disponibilidad de agua producen más fruto (Rodá *et al*., 1999; Álvarez *et al*., 2002; Carbonero *et al*., 2004). Todas estas conclusiones son muy similares a las creencias tradicionales, sin embargo, es difícil encontrar trabajos que muestren relaciones claras con parámetros de suelo o clima específicos lo que dificulta su implementación en modelos de gestión basados en conocimientos contrastados.

Otros factores que afectan a la producción de fruto

La posición en la copa determina la fenología y producción de fruto (La Mantia *et al*., 2003). Algunos autores (Carbonero *et al*., 2002) han detectado un aumento no significativo de la producción en las zonas más soleadas de la copa (Sur y Suroeste). En este sentido, podría esperarse que rodales situados en orientaciones Sur y Suroeste produjeran más, hecho que ha sido observado en algunos bosques de *Quercus* norteamericanos (Liebhold *et al*., 2004). Las pérdidas anteriores y posteriores a la dispersión originadas por factores bióticos y abióticos pueden reducir en gran medida la producción anual (Pulido y Díaz, 2005). Así, las pérdidas por infestación de insectos, incluyendo las bellotas presentando ‘melazo’, pueden sobrepasar el 50% algunos años (Soria *et al*., 1996). Otros factores como el pastoreo, el laboreo o la fertilización podrían afectar a la producción de fruto. De igual modo, podría haber una componente genética determinando la producción de fruto, por lo que podría influir la selección realizada durante años sobre el arbolado en las dehesas. Sin embargo, no conocemos ningún estudio que haya tenido en cuenta ninguno de estos factores.

La importancia del método de estimación y sistematización de datos

Para finalizar, creemos importante resaltar la importancia que posee la correcta sistematización y presentación de los resultados. A la ya comentada falta de estudios con series temporales largas y completas hay que añadir el problema resultante de la mala caracterización de las zonas de estudio y sobre todo los rodales estudiados, como se habrá podido apreciar en algunos de los comentarios incluidos en los apartados anteriores de este capítulo. Al no especificar la mayoría de los estudios las características de los pies estudiados resulta difícil comparar con diferentes trabajos o realizar inferencias combinando distintos estudios presentes en la bibliografía, lo cual imposibilita actualmente la elaboración de modelos de gestión que se puedan defender con conocimientos objetivos.

7.

Variabilidad espacio-temporal de la biomasa y composición de pastizales de especies anuales en dehesas en relación con el estrato arbóreo

Basado en:

Gea-Izquierdo G, Montero G, Cañellas I. Changes in limiting resources determine spatio-temporal variability in tree-grass interactions. En revisión.

(Anexo V)

7.1 Introducción

Comprender la interacción entre el estrato arbóreo y el estrato herbáceo es fundamental en la modelización de sistemas agroforestales. En este capítulo se estudia la influencia del árbol en dehesas sobre la producción y composición del pasto herbáceo. Como en las dehesas el estrato herbáceo puede estar compuesto por diferentes comunidades de ecología distinta o por cultivos, la interacción con el árbol podría variar, presentándose desde facilitación hasta competencia (Brooker *et al*., 2008). Por esta razón estudiamos el efecto del árbol sobre una comunidad de especies anuales y discutimos con otro estudios de la bibliografía centrados en comunidades de anuales-vivaces y en cultivos.

7.2 Material y métodos

Sitio de estudio

Se seleccionaron 10 árboles en una dehesa situada en la finca “Dehesón del Encinar” (40ºN 5ºO) cerca de Torralba de Oropesa (Toledo). Los árboles se seleccionaron de tal manera que recibieran la mínima influencia de los circundantes. El DAP medio (desviación estándar, SD) fue de 63,5 (26,0) cm, la altura de 8,8 (1,6) m y el radio de copa medio 4,9 (1,8) m. La precipitación media anual en la zona es de 573 mm (septiembre-agosto). Durante el período de estudio (2004-2006) la precipitación fue (marzo-mayo entre paréntesis) de 782,3 (214,1), 343,9 (96,5) y 583,0 (205,3) mm, se puede apreciar que el año 2005 fue muy seco. La temperatura media es de 15ºC, siendo los suelos arenosos y ácidos (Tabla 1).

Tabla 1. Características del suelo (primeros 20 cm). SD=desviación estándar. MO=material orgánica; CIC=capacidad de intercambio catiónico; Ca, Mg y CIC están en meq/100 g.

	pH	MO (%)	N (%)	C:N	P (ppm)	K (ppm)	Ca	Mg	CIC	Arena (%)	Arcilla (%)	Densidad (g/cm^3)
Media	5,3	1,2	0,06	16,5	26,9	89,6	1,9	0,3	7,7	84,4	1,3	1,5
SD	0,5	0,4	0,03	7,6	15,1	42,3	1,1	0,1	2,6	4,2	0,3	0,2
Max	6,63	2,3	0,13	47,3	64,8	237,8	5,6	0,7	13,9	91,8	2,4	1,9
Min	4,49	0,4	0,01	8,3	0,0	41,5	0,5	0,1	2,3	70,1	0,8	1,1

El pastizal estaba dominado por especies herbáceas anuales, destacando, entre otras, por su abundancia, *Ornithopus compressus* L., *Vulpia myuros K* (L.) C.C.Gmel., *Bromus hordeaceous* L., *Xolantha guttata* (L.) Raf., *Tolpis barbata* Boiss. & Reu, *Rumex bucephalophorus* L., *Echium plantagineum* L., *Raphanus raphanistrum* L. y *Plantago lagopus* L. (ver Anexo VII para inventario florístico completo). Hoy en día el pastoreo se realiza fundamentalmente por especies cinegéticas, pero la zona ha sido pastoreada en el pasado con vacas y ovejas.

En este capítulo se analizaron las interacciones del árbol con la producción y composición del pasto subyacente (dividido en grupos funcionales). Se estudiaron dos factores para analizar la asimetría y extensión del efecto del árbol, los cuales son estimadores indirectos de diferencias en humedad, radiación, temperatura y fertilidad: (i) la orientación; (ii) la distancia al tronco. Se excluyó el pastoreo y se muestrearon 16 puntos por árbol, 8 en la orientación suroeste (SO) y 8 en la noreste (NE), replanteados a distancias proporcionales al radio de copa (de 0,25 veces el radio, 0,25R; a dos veces el radio, 2R) en cada orientación. El año 2006 se extendieron los puntos de muestreo a las distancias 2,25R y 2,5R, por lo tanto se muestrearon 200 puntos por fecha de muestreo Los muestreos fueron repetidos cada año en abril y mayo, excepto en 2004, donde sólo se realizó uno.

Para estimar la intercepción de la luz por la copa, se tomaron fotografías hemisféricas en los 200 puntos de muestreo, estimándose el porcentaje de luz transmitida mediante el software GLA 2.0 (Frazer *et al*., 1999). Se estimó la humedad del suelo mensualmente usando una sonda TDR (*Time Domain Reflectometry*) en 16 tubos de 0,5 m localizados a 6 distancias proporcionales en la orientación NE de 3 árboles. Además, se muestran datos de temperatura de suelo en un solo árbol considerando distintas profundidades en el período 1996-1999.

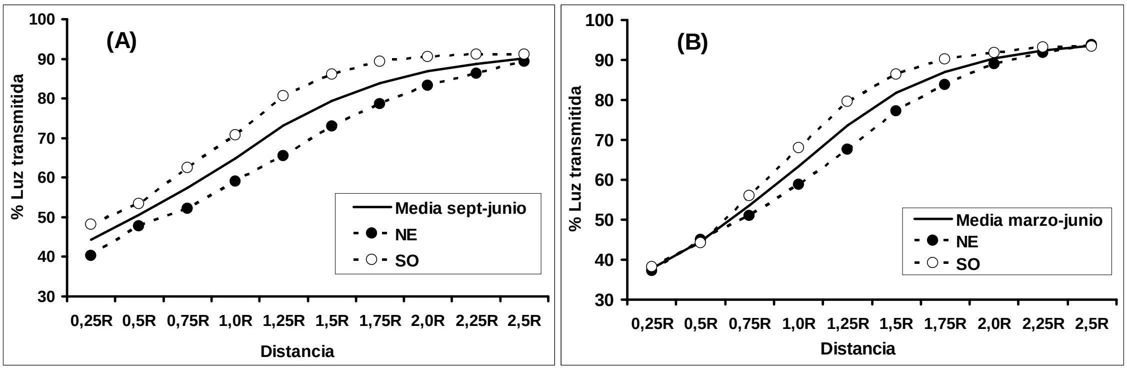


Figura 1. Porcentaje de luz transmitida en encinas aisladas según distancias proporcionales al radio para los períodos: (A) período fenológico completo del pastizal anual (21 de septiembre-21 de junio); (B) período máximo de crecimiento (1 de marzo-21 de junio).

Toma de datos

Se muestreó el pasto en cuadrículas de 20x50 cm en 2004 y 50x50 cm en 2005 y 2006, y posteriormente el pasto fue separado por grupos funcionales (gramíneas, leguminosas y resto de familias) y secado 48 horas a 60ºC (hasta peso constante) para proceder a pesarlas y estimar la producción en biomasa. En mayo de 2005 no se separó la muestra por estar prácticamente agostada por la fenología particular de ese año.

Análisis estadístico

Como las variables dependientes analizadas (producción y porcentaje de grupos) se pudieron aproximar a una distribución normal, se usaron modelos lineales mixtos con efectos aleatorios. La expresión del modelo genérico es $Y_u=X_u\cdot\beta+Z_u\cdot b_u+\varepsilon_u$; donde, X_u es la matriz de diseño de los efectos fijos asociada a esa observación; β es el vector que contiene los efectos fijos; Z_u es la matriz de diseño de los efectos aleatorios asociada; b_v es el vector que contiene los efectos aleatorios asociados y que se distribuye de acuerdo a una normal de media cero y matriz de varianza G; ε_u es un término aleatorio del error residual, distribuido según una normal de media 0 y matriz de varianza R. Esto implica que la variable Y se distribuye según una normal de media Xβ y varianza V=ZGZ'+R (Verbeke y Mohlenberghs, 2000).

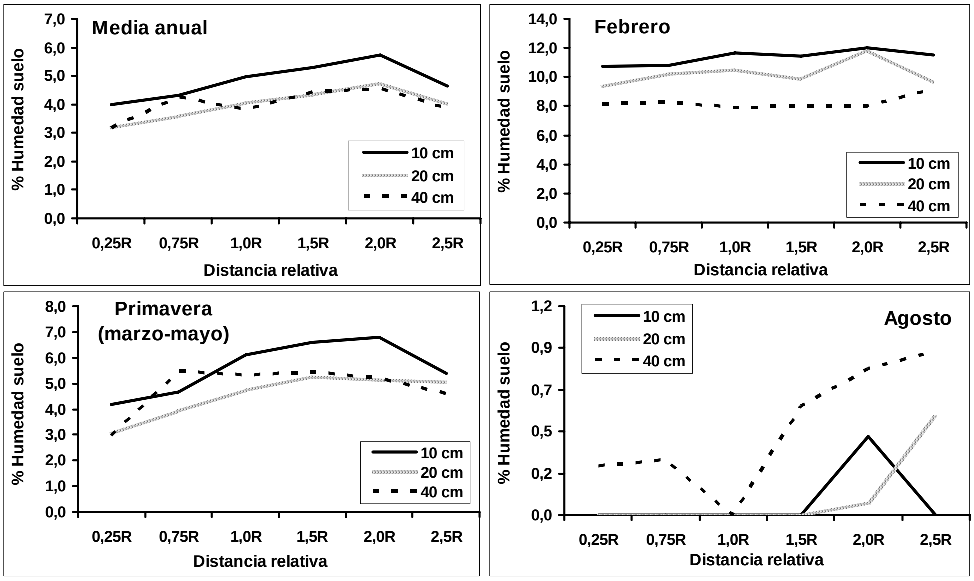


Figura 2. Contenido de agua en el suelo según distancias proporcionales al radio (media de mediciones de febrero de 2006 a junio de 2007): (1) media anual; (2) máximo (invierno, febrero); (3) primavera (marzo-mayo); (4) agosto (mínimo contenido anual de humedad).

Los factores distancia, orientación, año, mes y sus interacciones se analizaron como efectos fijos, y se incluyó un efecto aleatorio correspondiente a cada punto de muestreo, siendo la matriz de varianza residual modelizada mediante una estructura autoregresiva de primer orden (AR(1)), con submatrices correspondientes a cada árbol. Para estudiar diferencias dentro de los factores se comparó con la distribución F con grados de libertad calculados según Kenward y Roger (1997). Todos los test se valoran con un α = 0,05. Se calculó la eficiencia $\left(EF = 1 - \frac{\sum_{i=1}^{n}(est_i - obs_i)^2}{\sum_{i=1}^{n}(obs_i - \overline{obs})^2} \right)$ para cada factor significativo en los modelos finales y se ajustó una función no lineal a la distribución de la luz según la distancia al tronco utilizando los coeficientes de la distancia relativa (0,25, …, 2,25) como covariables. Todos los análisis se realizaron en SAS 9.1. (SAS Institute Inc., 2004).

La humedad en el suelo creció con la distancia al árbol, siendo máxima en los puntos más alejados (Figura 2). La temperatura fue de 14,5±5,8 ºC bajo la copa (temperatura media de las máximas mensuales 17,0ºC; temperatura media de las mínimas 12,8ºC) y 16,9±9,3ºC fuera de la copa (media de las máximas mensuales, 24,8ºC; media de las mínimas 11,9ºC).

La producción media de los 3 años (Tabla 2) fue mayor bajo la copa ($F_{1,415}$=71,42; p<0,0001) y en la orientación más soleada (SO; $F_{1,259}$=22,91; p<0,0001) tanto en abril como en mayo (Figura 3). Sin embargo, en el año 2005, el año más seco, el sentido de la interacción varió, siendo la producción mayor bajo la copa sólo en el NE ($F_{1,223}$=6,80; p=0,0097; Figura 3). El factor año (directamente relacionado con el clima) fue el más significativo, explicando el 49% de la eficiencia explicada por el modelo (EF=63%). El porcentaje de varianza explicado por el efecto aleatorio en el modelo de producción fue del 22,5%.

	MS	Gramíneas (%)	Leguminosas (%)	Otras (%)
Media	1901,8	43,1	15,3	41,6
SD	1122,6	27,6	18,9	24,7
Max	5777,0	100,0	95,1	100,0
Min	111,6	0,0	0,0	0,0

Tabla 2. Resultados de producción en biomasa y composición de la hierba. SD=desviación estándar; MS=materia seca (kg/ha-año) al final del período vegetativo (mayo).

Las gramíneas y resto de familias ('otras') constituyeron las fracciones más abundante del pastizal (Tabla 2), siendo en general las gramíneas dominantes bajo la copa ($F_{1,396}$=39,9; p<0,0001) y el resto de familias dominantes fuera de la misma ($F_{1,322}$=11,93; p=0,0006). Las leguminosas fueron el componente minoritario en el pastizal, aunque también fue la fracción que presentó mayor variabilidad tanto en tiempo como en espacio (Tabla 2; Figura 4). Se detectó una variación temporal en la composición dentro del año, así el grupo resto de familias resultó dominante al principio del período vegetativo, con el avance de la primavera las gramíneas y leguminosas cobraron más importancia. Las leguminosas fueron más abundantes fuera de la copa ($F_{1,347}$=10,59; p=0,0012) y en el SO ($F_{1,83}$=51,7; p<0,0001), mostrando su predilección por puntos con alta insolación.

La composición también varió entre años (Figura 4 y anexo V). En el 2005 se incrementó la presencia de gramíneas en el pastizal ($F_{1,74.7}$=40,9; p<0,0001), y fue menos evidente la diferencia en composición entre ambas localizaciones, sobre todo en el NE (Figura 4). La influencia de la copa en la composición (a través de la reducción de la incidencia lumínica) parece extenderse al menos hasta 2,5 veces el radio, ya que la proporción de gramíneas decrece uniformemente con la distancia al árbol en todo el rango estudiado y complementariamente la del resto de familias asciende (Figura 4). El año 2006 se produjo un gran aumento en la proporción de leguminosas ($F_{1,83}$=51,7; p<0,0001), incrementándose de una media de 3,8% en 2005 a 26,7% en 2006 (33,4% en mayo 2006, 40,1% al SO en mayo de 2006; 54,4% a 2,25R en el SO en mayo de 2006 [Figura 4]).

El porcentaje de varianza explicado por el efecto aleatorio fue de un 20,1% en el modelo con las gramíneas como variable dependiente, del 25,2% en leguminosas y 20,9% en el resto de familias. La eficiencia del modelo final en gramíneas fue de 44,2%, de los cuales 48,7% fueron explicadas por el efecto año. En leguminosas el año explicó el 75,4% de la variabilidad (de un total de 46,6% explicado por los cuatro factores) y 46,0% (de 22,7%) en el resto de familias, siendo este último modelo el que peor ajuste ofreció (más detalle en Anexo V).

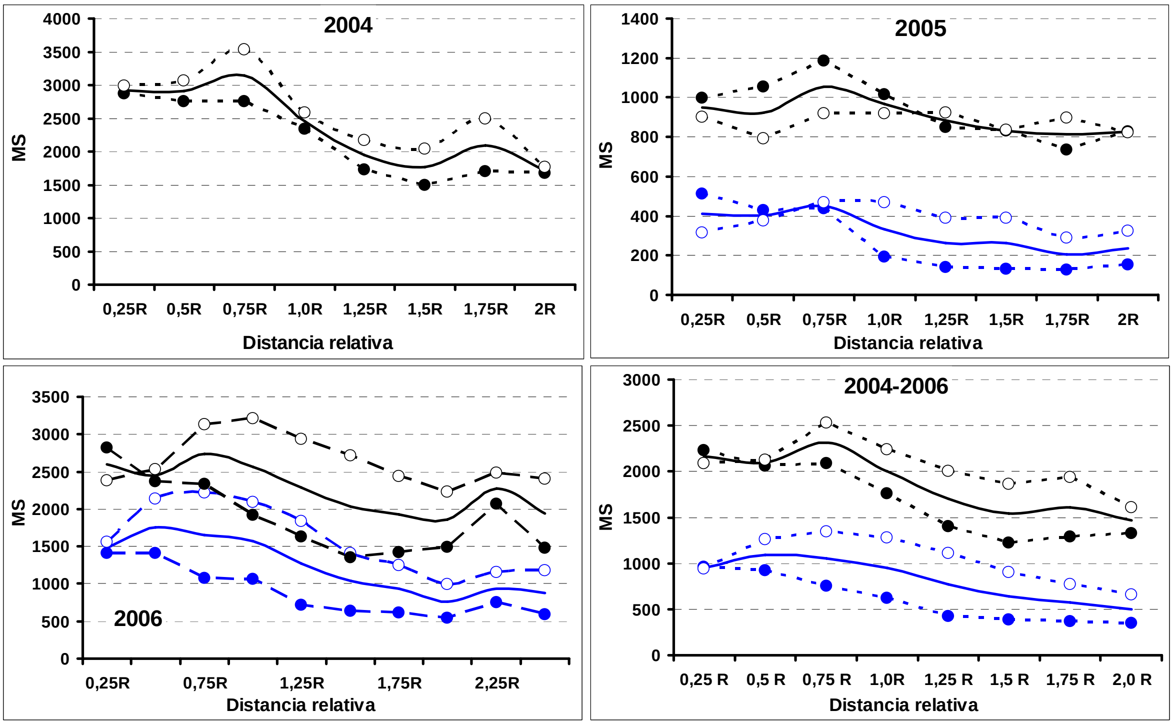


Figura 3. Producción de pasto por orientación y distancia los 3 años de estudio. MS=materia seca (kg/ha). En negro resultados de mayo, en azul resultado de producción de abril. La línea continua corresponde a la media entre orientaciones, mientras que líneas discontinuas con círculos blancos corresponde a la orientación SO mientras línea discontinua con círculos oscuros a la orientación NE.

7.4 Discusión

Competencia y facilitación coexisten en el mismo ecosistema y pueden alternarse dependiendo del factor ecológico que más limite el crecimiento (Belsky, 1994; Ludwig *et al.*, 2001; Brooker *et al.*, 2008). La Ley del Mínimo de Von Liebig (Von Liebig, 1840, citado en Koerselman y Meuleman, 1996) determina que la fertilidad de un sitio para plantas individuales se encuentra gobernada por la disponibilidad del nutriente más limitante. La variabilidad encontrada en la interacción planta-planta en la bibliografía (Brooker *et al*., 2008) podría significar la extensión de esta ley a cualquier otro factor que pueda ser limitante, no sólo nutricional, como la humedad o la luz (Ludwig *et al*., 2001).

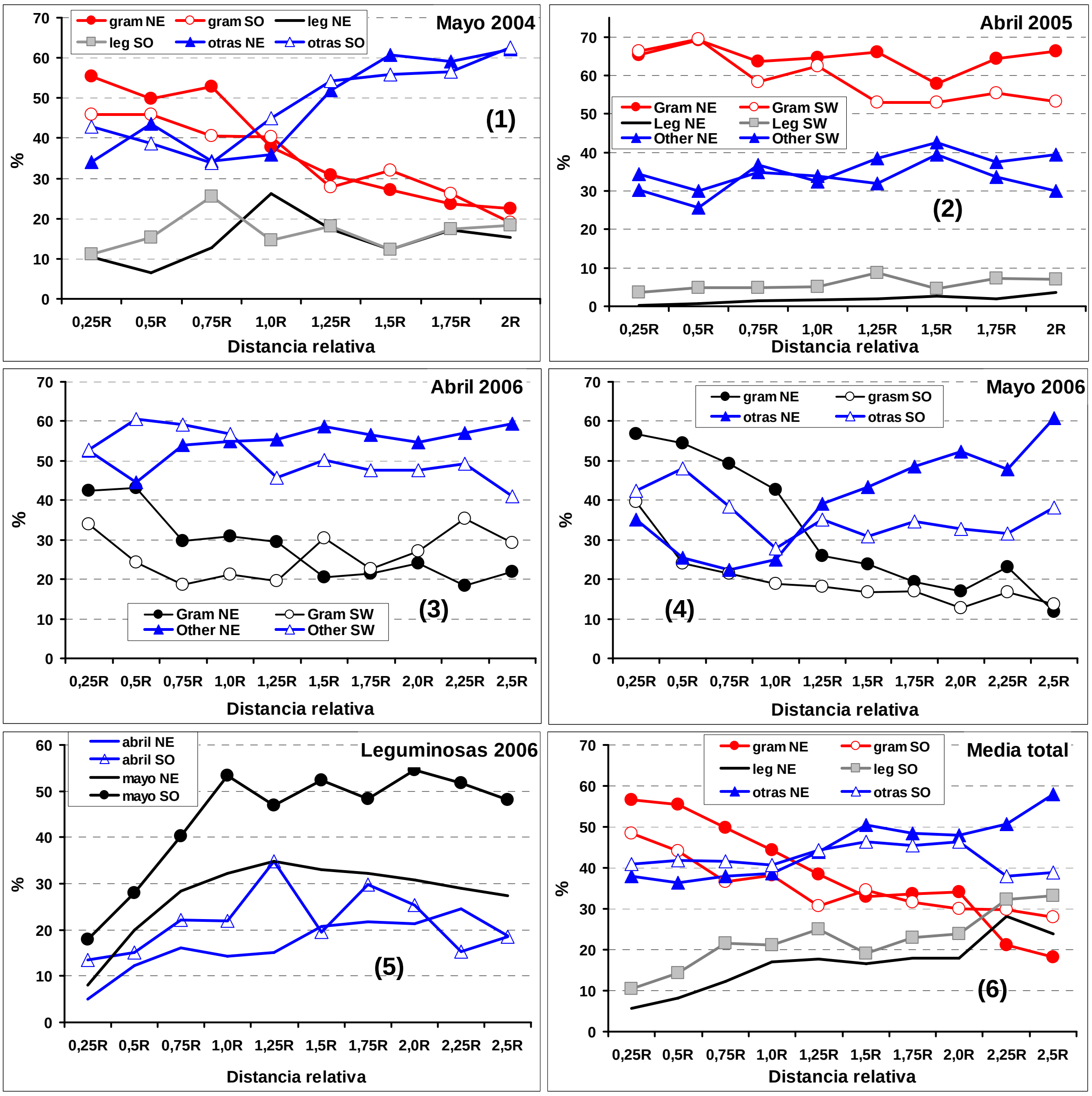


Figura 4. Composición media del pastizal según distancia y orientación en los tres años de estudio. El año 2006 las leguminosas se muestran en un gráfico independiente para facilitar su interpretación.

El efecto del árbol sobre la humedad del suelo varía dependiendo de varios factores (Vetaas, 1992; Belsky, 1994; Ludwig *et al*., 2004), por lo que no se debe generalizar que la presencia del árbol mejore la disponibilidad de agua bajo su copa en sistemas arbolados abiertos. En dehesas, nuestros resultados concuerdan con algunos estudios (Cubera y Moreno, 2007) pero no con otros (Joffre y Rambal, 1993), lo que podría explicarse por diferencias en textura del suelo o en precipitación. El descenso de la humedad en el suelo bajo la copa se explicaría por la intercepción del árbol y por la competencia radical (Rodá *et al*., 1999; Moreno *et al*., 2005).

La variabilidad espacial y temporal es la norma en la producción y composición en comunidades herbáceas Mediterráneas. La reducción de la radiación lumínica bajo la copa y la modificación de las temperaturas influyen en la producción del pasto (Vetaas, 1992). En promedio el pasto bajo la copa creció más (particularmente en el SO, aprovechando los suelos más soleados entre los más fértiles), seguramente mostrando la preponderancia de la facilitación por aumento de nutrientes en un suelo tan pobre como el de nuestro estudio (Tabla 1) frente a la intercepción de luz y la competencia radical. Sin embargo, en condiciones muy secas (como en el año 2005) posiblemente la disponibilidad y posibilidad de aprovechar el aumento de nutrientes bajo la copa se supeditó a la humedad, en ese caso el factor más limitante. En este sentido, también se ha visto en otros sistemas cómo el aumento de la fertilidad edáfica sólo puede ser aprovechado por las plantas si existe suficiente humedad y luz (Belsky, 1994; Rhoades, 1997; Maestre *et al*., 2005). El balance de la interacción entre el árbol y las comunidades herbáceas subyacentes puede resultar positivo, neutro o negativo, dependiendo de los condicionantes ecológicos (Somarriba, 1988; Belsky, 1994; Rhoades, 1997; Ludwig *et al*., 2004).

Por tanto, en dehesas parece que la facilitación podría ser más probable en los suelos más pobres, es decir, coincidiendo con las comunidades de anuales y sería negativo en los suelos más fértiles, como en los pastos fertilizados y fondos de valle ocupados por vallicares (Montalvo *et al*., 1980; Moreno, 2008). En el año más seco la interacción varió significativamente, produciéndose menos bajo la copa en la orientación SO y presentándose la mayor producción bajo la copa en el NE, lo cual posiblemente mostraba unas mejores condiciones de humedad ese año en la segunda orientación. Esto podría significar que en una primavera promedio la comunidad de anuales no sufre limitaciones de humedad en los pocos meses a los que se han adaptado para crecer, y por eso sus factores limitantes son la luz y, en el sistema estudiado, la fertilidad edáfica.

El contenido de leguminosas es muy importante tanto desde el punto de vista del suelo (contenido en nitrógeno) como el pastoral (Hauggaard-Nielsen y Jensen, 2005; Olea y San Miguel, 2006). Las leguminosas fueron más abundantes en las posiciones más soleadas. Las gramíneas fueron más abundantes en las posiciones más eutróficas lo que suele coincidir con un aumento en la producción, como suele reconocerse en la bibliografía (Marañón, 1986; San Miguel, 2001). A principio de la primavera parece que el resto de familias domina, mientras que al final de la primavera aumenta la importancia de gramíneas y leguminosas (Pérez Corona *et al*., 1998). El factor más importante tanto en la producción como en la composición fue el efecto del año, poniendo de manifiesto la importancia de las condiciones climáticas tanto del año en curso como del anterior, a través de la producción de semillas y su influencia en el banco del suelo.

Se ve que la interacción árbol-pasto es compleja y variable tanto en tiempo como en espacio. Existen varios factores, como la competencia entre sistemas radicales, que no se han considerado en este estudio pero que resultan muy importantes en el sentido de la interacción (Callaway *et al*.,1991; Ludwig *et al*., 2004; Moreno, 2008). En este trabajo nos hemos centrado en el análisis de grupos, sin embargo, si se estudiaran especies individuales es probable que algunas de estas especies mostraran un comportamiento distinto al de la media del grupo funcional al que pertenecen. Estas interacciones deben ser reflejadas en modelos silvopastorales de gestión, evitando caer en simplificaciones sobre el sentido de la interacción entre el árbol y las comunidades subyacentes.

8.

Influencia del estrato arbóreo en la variabilidad del contenido en nutrientes de pastizales de especies anuales en dehesas

Basado en:
Gea-Izquierdo G, Allen-Díaz B, San Miguel A, Cañellas I. Tree influence upon mediterranean annual grassland nutrient variability. Manuscrito.

(Anexo VI)

8.1 Introducción

Complementariamente al capítulo anterior analizamos la variabilidad espacio-temporal del efecto del árbol en dehesas sobre el contenido en nutrientes del pasto subyacente y sus consecuencias para la alimentación del ganado. Se discuten con la bibliografía las características de cada nutriente, así como la relación entre el aumento de la fertilidad en suelo generado por el árbol y la concentración de nutrientes en los tejidos de las plantas herbáceas que crecen en los diferentes ambientes originados.

Tabla 1. Datos de suelo en relación a la orientación y posición a la copa. Los estadísticos ‘bajo copa’ son medias de 0,375R y 0,75R. Los estadísticos ‘fuera de copa’ son medias de las distancias 2,0R y 2,5R.

		Bajo copa		**Fuera de copa**		**Media total**		
		NE	**SO**	**NE**	**SO**			
pH	Media	5,674	5,798	4,978	5,014	5,325	Max	6,630
	SD	0,420	0,483	0,312	0,269	0,499	Min	4,490
MO (%)	Media	1,467	1,631	0,744	0,941	1,165	Max	2,290
	SD	0,333	0,394	0,231	0,205	0,421	Min	0,350
N (%)	Media	0,072	0,078	0,036	0,048	0,056	Max	0,130
	SD	0,025	0,040	0,012	0,018	0,029	Min	0,010
C:N	Media	15,173	16,038	16,986	16,932	16,508	Max	47,270
	SD	2,463	10,416	5,748	10,216	7,635	Min	8,310
P (ppm)	Media	26,792	31,100	28,025	21,275	26,917	Max	64,800
	SD	17,040	15,595	15,293	12,601	15,056	Min	0,000
K (ppm)	Media	102,478	150,588	57,003	60,700	89,600	Max	237,780
	SD	34,784	40,323	10,205	10,707	42,300	Min	41,450
Ca (meq/100 g)	Media	2,572	3,251	0,804	1,348	1,859	Max	5,590
	SD	1,018	1,391	0,247	0,402	1,141	Min	0,460
Mg (meq/100 g)	Media	0,348	0,478	0,135	0,203	0,274	Max	0,720
	SD	0,116	0,142	0,042	0,073	0,146	Min	0,080
CIC (meq/100 g)	Media	8,685	9,663	6,703	6,849	7,678	Max	13,910
	SD	2,323	2,937	1,893	2,630	2,616	Min	2,340
Arena (%)	Media	85,020	84,412	86,192	82,496	84,386	Max	91,833
	SD	3,841	2,878	3,329	5,491	4,181	Min	70,085
Limo (%)	Media	12,564	14,619	12,667	16,063	14,340	Max	27,493
	SD	3,641	2,910	3,182	5,054	3,928	Min	7,214
Arcilla (%)	Media	1,224	1,362	1,141	1,440	1,274	Max	2,422
	SD	0,267	0,256	0,195	0,449	0,323	Min	0,785
Densidad (g/cm^3)	Media	1,396	1,378	1,664	1,559	1,501	Max	1,883
	SD	0,138	0,154	0,157	0,137	0,173	Min	1,082

8.2 Material y métodos

Sitio de estudio y diseño experimental

El sitio de ensayo y muestreo es el descrito en el capítulo anterior. Además, se muestreó la orientación NE en julio de 2006, para analizar la diferencia en la calidad del pasto en distintas posiciones respecto al árbol cuando el pasto ya se encuentra agostado. Se analizaron las 160 muestras recogidas en mayo de 2004 para estudiar la variabilidad espacial de la calidad del pasto. A su vez, para estudiar la variabilidad temporal se analizaron dos muestras compuestas según su localización: (i) 0,5R-0,75R, ‘bajo la copa’; (ii) 1,75R-2,0R, ‘fuera de la copa’; y según las dos orientaciones (por lo tanto cuatro muestras/árbol x 10 árboles) en cada corte realizado en 2005 y 2006.

Para estimar las características del suelo aprovechado por el pasto herbáceo se muestrearon los 20 cm superficiales en mayo de 2006 en 72 puntos replanteados alrededor de seis árboles a seis distancias proporcionales al radio de copa (0,375R a 2,5R) en las dos orientaciones (NE, SO). En las muestras de suelo se estimó el contenido en nitrógeno (N), fósforo (P), potasio (K), calcio (Ca), magnesio (Mg), capacidad de intercambio catiónico (CIC), pH, la relación carbono nitrógeno (C:N) y la textura (siguiendo los estándares USDA [Brady y Weil 2002]). En las muestras de pasto se estimaron el N, P, K, Ca, Mg y el cobre (Cu), todos los años; mientras el hierro (Fe) y el sodio (Na) sólo en 2005-06; la fibra neutro detergente (FND), fibra ácido detergente (FAD) y lignina en 2005-2006, y la fibra bruta en 2004. En el Anexo VI se pueden encontrar más detalles del análisis de las muestras de suelo y del pasto.

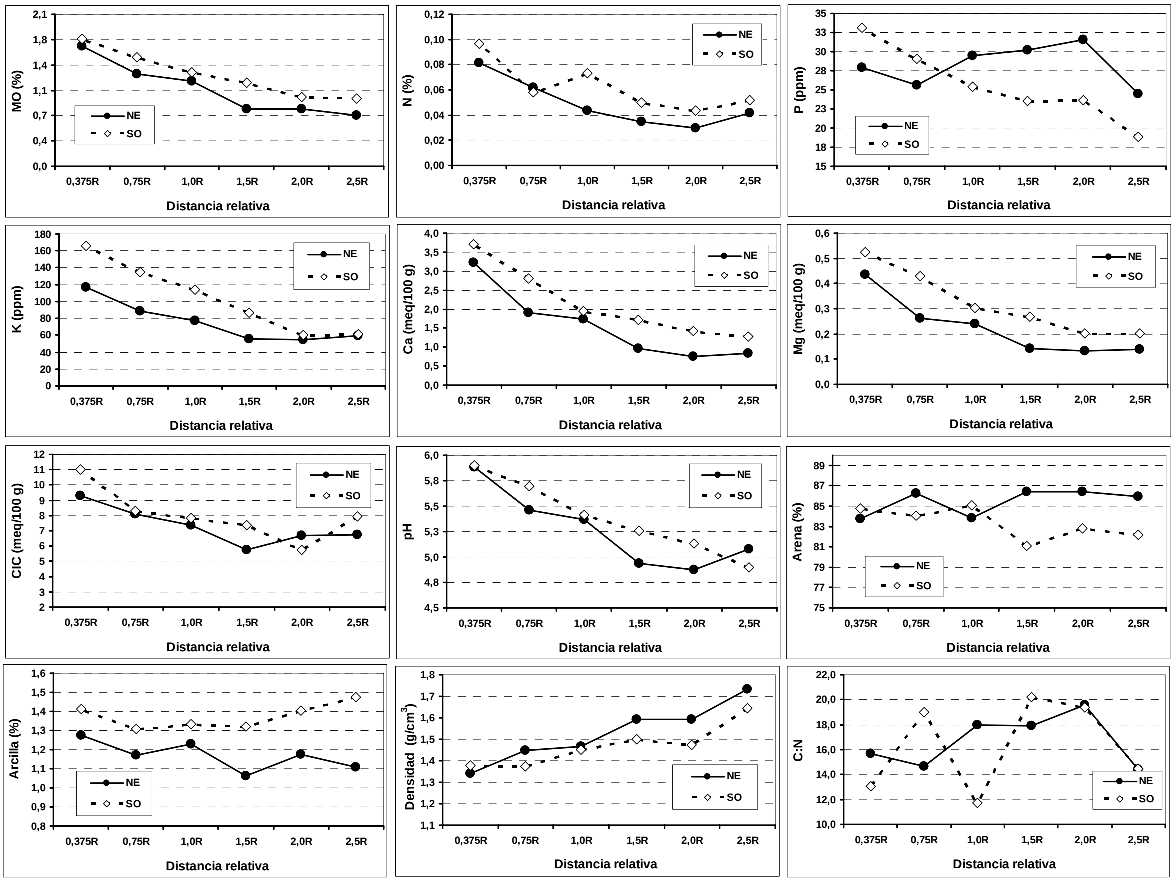


Figura1. Variables de suelo en función de la orientación y la distancia relativa a la base del árbol.

Tabla 2. Resultados de los modelos lineales mixtos con los macronutrientes como variables dependientes. DT=distancia a la base del árbol; OR=orientación. σ^2_i (b)= estimador de la varianza para término independiente. Toeplitz=valor para el test de la razón de máximas verosimilitudes (χ^2) testando los modelos con matriz de varianza residual con estructura tipo Toeplitz (Verbeke and Mohlenberghs, 2000) frente a los modelos al modelo con idénticos efectos fijos y aleatorios pero con matriz residual con estructura de varianza $I\cdot\sigma^2$. Los datos del mes de Julio no se incluyeron en los modelos para equilibrar los datos.

Parámetro	N (%)		P (%)		K (%)		Ca (%)		Mg (%)	
	F (gl)	p	F (gl)	p	F (gl)	p	F (gl)	p	F (gl)	p
DT	3,95 (1, 40)	0,0538*	1,40 (1,08)	0,3042	122,28 (1, 62)	<0,0001**	26,92 (1, 77)	<0,0001**	3,96 (1, 22)	0,0595*
OR	1,32 (1, 37)	0,2589	0,91 (1, 40)	0,3470	0,00 (1, 65)	0,9603	0,04 (1, 44)	0,8373	0,50 (1, 35)	0,4829
Año	2,29 (2, 76)	0,0801*	6,77 (2, 96)	0,0018**	3,21 (2, 28)	0,0553*	19,22 (2, 27)	< 0,0001**	28,36 (2, 30)	< 0,0001**
Mes	48,28 (1, 15)	< 0,0001**	66,65 (1, 95)	< 0,0001**	132,20 (1, 11)	<0,0001**	60,27 (1, 9)	< 0,0001**	108,13 (1, 14)	< 0,0001**
DT*OR	0,90 (1, 32)	0,3509	0,40 (1, 47)	0,4979	0,01 (1, 67)	0,9183	0,10 (1, 68)	0,7504	0,47 (1, 31)	0,4989
DT*Año	0,08 (2, 54)	0,9270	4,27 (2, 96)	0,0167**	4,17 (2, 69)	0,0196**	5,22 (2, 63)	0,0080**	0,80 (2, 79)	0,4544
DT*Mes	35,82 (1, 13)	< 0,0001**	16,19 (1, 95)	0,0001**	17,64 (1, 30)	0,0002**	6,68 (1,15)	0,0204**	3,03 (1, 22)	0,0962*
OR*Año	4,94 (2, 44)	0,0116**	3,89 (2, 96)	0,0238**	5,56 (2, 70)	0,0057**	1,79 (2, 45)	0,1794	2,29 (2, 56)	0,1106
OR*Mes	0,77 (1, 16)	0,3938	10,89 (1, 95)	0,0014**	2,49 (1, 28)	0,1261	3,39 (1, 37)	0,0738*	3,72 (1, 33)	0,0623*
DT*OR*Año	1,06 (2, 47)	0,3536	0,54 (2, 96)	0,5836	0,60 (2, 61)	0,5519	0,63 (2, 53)	0,5359	0,34 (2, 48)	0,7125
DT*OR*Mes	0,08 (1, 30)	0,7851	0,01 (1, 95)	0,9130	0,41 (1, 40)	0,5281	0,06 (1, 32)	0,8099	0,62 (1, 38)	0,4356
	Valor test	Valor-p	Valor test	Valor-p	Valor test	Valor-p	Valor test	Valor-p	Valor test	Valor-p
σ^2_i (b)	2,37	0,0090**	2,56	0,0052**	0,69	0,2442	0,51	0,3064	1,32	0,0933*
Toeplitz	13,90	0,05298*	10,40	0,1670	20,20	0,0051**	28,20	0,0002**	24,80	0,0008**

Análisis estadístico

De igual manera que en el capítulo anterior se usaron modelos mixtos lineales (Verbeke y Mohlenberghs, 2000). Como variables dependientes se consideraron los nutrientes estimados en los tejidos vegetales de las muestras compuestas (todo el pasto, sin separar por especies ni grupos funcionales). Las 160 observaciones de 2004 se analizaron testando los factores distancia, orientación y su interacción, modelizando la matriz de varianza residual mediante una estructura AR(1). La expresión del modelo sería: $y_{ij} = \beta_0 + OR_i + DT_j + OR_i * DT_j + \varepsilon_{ij}$. OR_i es la orientación (i=[1,2]), DT_j es la distancia a la base del árbol j (j=[1,8]), y_{ij} es la observación de la variable dependiente (N, P, K, Ca, Mg, etc.) correspondiente a la orientación i, distancia al árbol j y ε_{ij} es el error residual asociado a esa observación. En el análisis de los datos del período completo (2004-2006) se incluyeron también en el modelo como efectos fijos el año, el mes y las interacciones. Además, los modelos finales incluyeron en algunos casos un efecto aleatorio b_h en el término independiente, y la matriz de varianza residual fue del tipo Toeplitz(r) o $I \cdot \sigma^2$ según se especifica en resultados (Mohlenberghs y Verbeke, 2000).

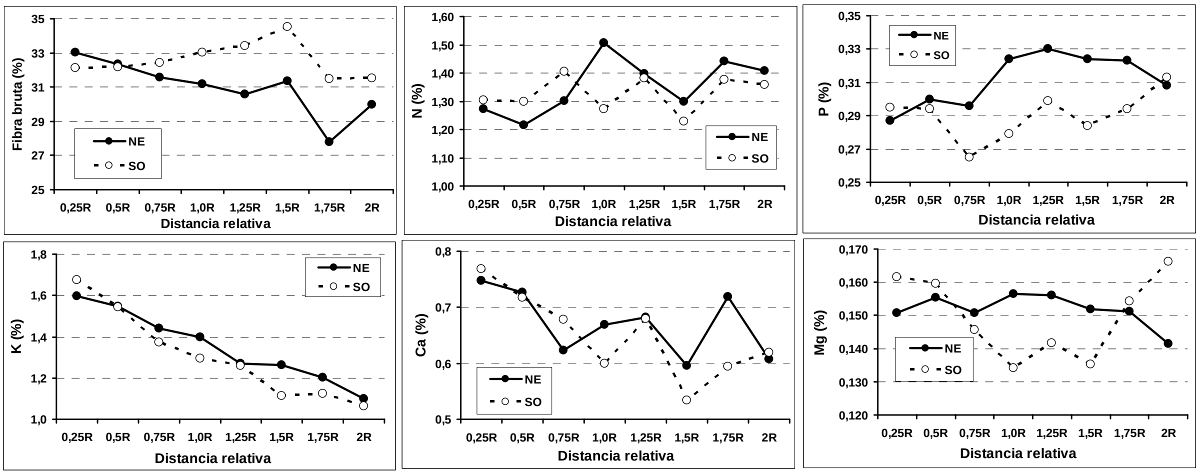


Figura 2. Variación espacial (según orientación y distancia) del contenido en nutrientes del material vegetal muestreado en mayo de 2004.

8.3 Resultados

Efectos del árbol aislado sobre la variabilidad espacial en la fertilidad edáfica

Los suelos donde se asienta la comunidad pascícola estudiada son muy pobres desde un punto de vista agronómico. Todos los nutrientes, excepto el fósforo, aumentaron bajo la copa (Tabla 1; Figura 1). La materia orgánica decreció con la distancia al árbol sólo bajo la copa (Figura 1. $F_{1,62}$=18,57; p<0,0001), y resulta homogénea fuera de la copa ($F_{1,62}$=1,44, p=0,2351). Lo mismo sucedió con los valores de N ($F_{1,62}$=13,51; p=0,0005), K ($F_{1,61}$=28,05; p<0,0001), Ca ($F_{1,62}$=60,43; p<0,0001), Mg

($F_{1,60}$=51,09; p<0,0001) y CIC ($F_{1,62}$=7,48; p=0,0081), decrecientes bajo la copa y homogéneos fuera de la proyección vertical de la misma. El pH también decreció con la distancia, presentando su máximo en el punto más cercano al árbol ($F_{1,62}$=42,46; p<0,0001). El fósforo no mostró diferencias significativas con la distancia ($F_{5,57}$=1,37; p=0,2478), siendo la variable edáfica que presentó mayor variabilidad. La densidad aparente se mostró complementaria a la MO y a la textura ($F_{1,46}$=29.20, p<0.0001), como cabía esperar (Brady y Weil, 2002).

Las diferencias en radiación recibida por el suelo (ver Capítulo 7) motivadas por la orientación, coincidieron con diferencias significativas en varios nutrientes edáficos. Se midieron contenidos de MO mayores en el SO que en el NE ($F_{1,24}$=6,79; p=0,0155), así como en todos los nutrientes dependientes de la materia orgánica, tales como el N ($F_{1,28}$=5,82; p=0,0226), K ($F_{1,22}$=10,03; p=0,0073), y Mg ($F_{1,22}$=9,47; p=0,0056); el Ca ($F_{1,22}$=3,13; p=0,0904) y la densidad ($F_{1,28}$=3,05; p=0,0918) resultaron significativos a un α=0,10. El P, pH y CIC no presentaron diferencias significativas entre orientaciones. Resulta destacable que la textura variara con la orientación, presentando las posiciones situadas al SO (más soleadas) niveles mayores de arcilla ($F_{1,27}$=5,11; p=0,0320).

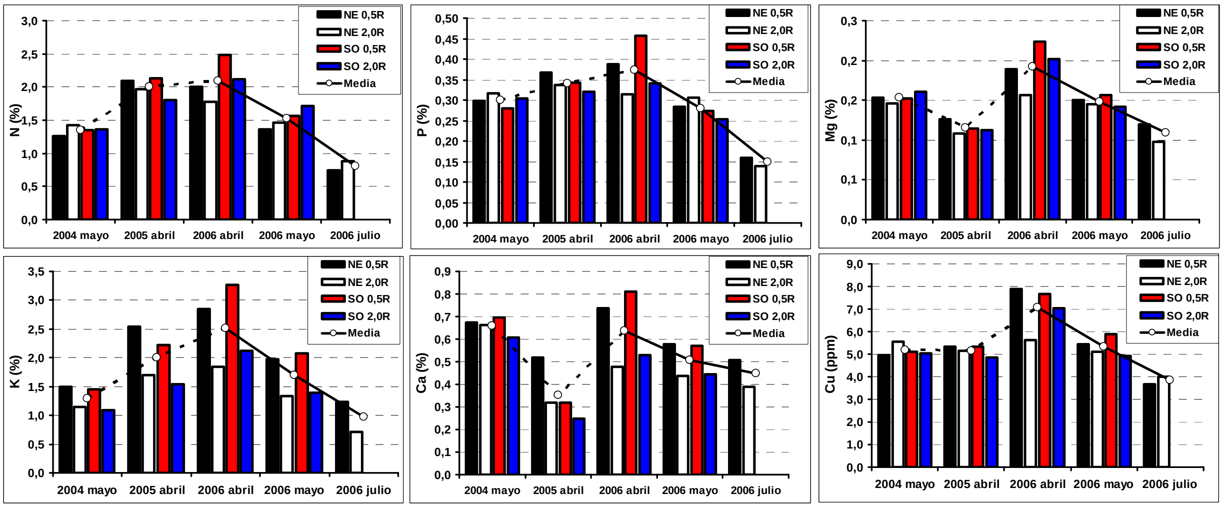


Figura 3. Variación temporal en la composición química del pasto (I) en macronutrientes y cobre. Las líneas continuas muestran la tendencia decreciente coincidente con el desarrollo de la comunidad herbácea dentro del ciclo anual en 2006. Las líneas discontinuas sirven como una referencia de valores medios en 2004 y 2005, años en los que sólo se analizó material proveniente de un muestreo.

Efecto del árbol sobre la variabilidad espacial del contenido en nutrientes de pastos anuales

Las diferencias entre orientaciones en los parámetros edáficos no se vieron reflejadas en los niveles de esos nutrientes en los tejidos de las plantas. El único nutriente que mostró una clara tendencia (decreciente) con la distancia fue el K ($F_{1,100}$=34,17; p<0,0001), aunque no presentó tampoco diferencias entre orientaciones ($F_{1,42}$=0,07;

p=0,7884). El nitrógeno mostró una tendencia creciente al 10% ($F_{7,119}$=1,80; p=0,0926), respondiendo a la proporción de leguminosas discutida en el capítulo anterior (Pearson ρ=0,872; p<0,001) más que a los factores estudiados (distancia y orientación). El contenido en Ca del pasto fue superior en los dos puntos más cercanos al árbol ($F_{1,106}$=5,21; p=0,0244), mientras ninguna de los otras variables estudiadas mostró diferencias significativas.

Efecto del árbol sobre la variabilidad temporal del contenido en nutrientes de pastos anuales

Como se esperaba, existe un gran descenso en el contenido de nutrientes con el avance del desarrollo (Figura 3), y este efecto fue claramente el más importante en la concentración de nutrientes presente en el pasto. En este sentido las pequeñas diferencias existentes entre orientaciones y distancias pueden ser en parte debidas a desfases en fenología entre orientaciones (provocadas indirectamente por el árbol) más que a diferencias reales provocadas por diferencias en suelo, humedad o sombra. Los resultados (Tabla 2; Figura 3) muestran que la interacción del árbol con el contenido en N de los tejidos vegetales varía con el desarrollo fenológico de la planta y según diferentes años. Los resultados sugieren que en abril el pasto posee más N bajo la copa ($F_{1,40}$=21,75; p<0,0001) mientras que en mayo y julio la relación se invierte, poseyendo más N el pasto situado fuera de la influencia de la copa, lo cual también podría sugerir una dependencia de las leguminosas (ver Capítulo 7). La orientación sólo fue significativa para el N en el 2006 ($F_{1,30}$=1,08; p=0,3019), lo cual coincidió con el año en que las leguminosas fueron particularmente abundantes en esa orientación (Capítulo 7).

No se obtuvieron resultados significativos para el P, más allá de la clara influencia del estado de desarrollo de las plantas (decreciente). El K fue el único nutriente claramente más abundante en las plantas creciendo bajo la copa (Tabla 2; Figura 3), diferencias que se fueron atenuando con el desarrollo fenológico pero que fueron significativas hasta en julio ($F_{1,68}$=11,16; p=0,0014). Las plantas que crecían bajo la copa presentaron significativamente mayores niveles de Ca (Figura 3; Tabla 2), aunque no en todas las fechas de muestreo, por ejemplo julio ($F_{1,39}$=0,64; p=0,4303). Los niveles de Ca ($F_{1,34}$=32,78; p<0,0001) y Mg ($F_{1,34}$=32,78; p<0,0001) fueron menores en 2005, de nuevo coincidiendo con el año de sequía.

Efecto del árbol sobre variables de interés pastoral

En 2004, en el análisis espacial detallado, la fibra bruta decreció con la distancia al árbol en la orientación NE ($F_{1,29}$=4,45; p=0,0452). La diferencia entre orientaciones seguramente vino motivada por diferencias en la fenología. También las variables de interés pastoral (Fe, Na, FND, FAD) mostraron el esperado descenso en la calidad del pasto con el avance del desarrollo fenológico. Los niveles de FND y FAD incrementaron notablemente al final de la primavera (Figura 4), mientras los niveles de Fe y Na no parecieron verse afectados por la orientación o distancia, estando fundamentalmente determinados por el estado de desarrollo del pasto (ver Anexo VI).

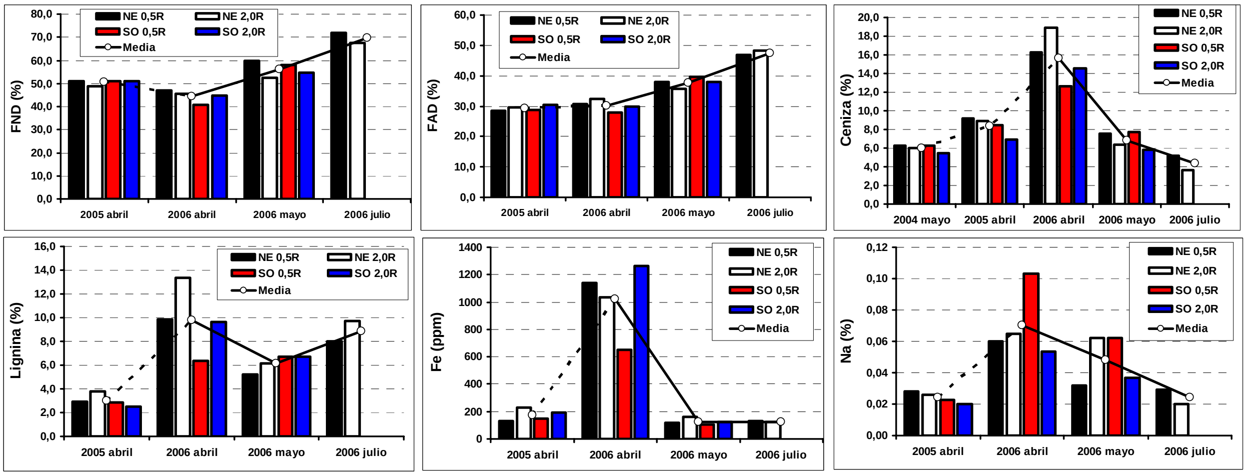


Figura 4. Variación temporal en la composición química del pasto (II): micronutrientes y variables de interés pastoral. Las líneas continuas muestran el declive anual en 2006. Las líneas discontinuas sirven como referencia de los valores medios en 2004 y 2005, donde sólo se analizó un muestreo.

8.4 Discusión

Efecto del árbol aislado sobre la variabilidad espacial en la fertilidad edáfica

La influencia del árbol sobre el suelo varía según la especie, el sustrato geológico y la gestión forestal (Augusto *et al*., 2002). La correlación negativa de la distancia al árbol con los contenidos del horizonte superficial de MO, N, K, Ca y Mg son una constante en la literatura, siendo la influencia del árbol máxima en ese horizonte (Puerto y Rico, 1988; Rhoades, 1997; Gallardo *et al*., 2000; Gallardo, 2003; Moreno *et al*., 2007). Además de indirectamente por la atracción de la sombra sobre los animales, este aumento de la fertilidad bajo la copa está originado fundamentalmente por la deposición de hojarasca y lavado de minerales por la lluvia (Escudero *et al*., 1985; Rodá *et al*., 1999), de modo diferencial según cada nutriente. Así por ejemplo el nitrógeno depende fundamentalmente de los aportes orgánicos, mientras el K es de todos los macronutrientes el que más se ve influido por el lavado de la lluvia (Brady y Weil, 2002; Barker y Pilbeam, 2007). La ausencia de tendencias encontradas en el P no está en consonancia con otros estudios que midieron un incremento de P bajo la copa (Joffre *et al*., 1988; Puerto y Rico, 1988; Moreno *et al*., 2007) aunque no todos los autores coinciden (Montoya, 1982a). El aumento en el pH encontrado es común a algunos estudios (González-Bernáldez *et al*., 1969; Puerto y Rico, 1988; Rhoades, 1997) pero no a otros (Montoya, 1982a; Gallardo *et* *al*., 2000; Moreno *et al*., 2007). Las plantas pueden aumentar o disminuir el pH del suelo, dependiendo de la materia orgánica que originan, del pH original y de la textura del suelo (Augusto *et al*., 2002; Brady y Weil, 2002). De este modo, quizá las encinas estén aumentando el pH sólo en los suelos más ácidos, aunque esto no sucede en todos los estudios discutidos (Moreno *et al*., 2007). La CIC también decreció con la distancia al árbol, mientras la densidad aumentó con la distancia en respuesta inversa al contenido en arcillas y la MO (Brady y Weil, 2002).

Además de a los aportes orgánicos e inorgánicos procedentes del árbol, los nutrientes del suelo respondieron a la radiación recibida. Los puntos localizados en el SO presentaron mayores niveles de macronutrientes, quizás por mostrar una mayor actividad bioquímica. Resaltar que el mayor contenido de arcillas podría estar relacionado con formación de arcillas “in situ” o mayores migraciones a horizontes más profundos en puntos que reciben más sombra. Este efecto del árbol sobre la textura coincide sólo con algunos estudios presentes en la bibliografía (Puerto y Rico, 1988; Moreno, 2008), aunque esto puede ser debido al mayor detalle que presenta nuestro diseño muestral.

Efecto del árbol sobre la variabilidad espacio-temporal del contenido en nutrientes de pastos anuales

El pasto respondió al aumento en la disponibilidad en nutrientes en suelo con el citado aumento en la producción media (Capítulo 7), pero no con un incremento en la concentración de esos mismos nutrientes en los tejidos de las plantas, que no reflejaron la disponibilidad de nutrientes en suelo, contrariamente a lo que se esperaba (Belsky, 1992; Ludwig *et al*., 2001; Barker y Pilbeam, 2007). Por tanto, a diferencia de otros estudios (Puerto y Rico, 1996), el pasto bajo la copa no contuvo significativamente mayor concentración de nutrientes que el pasto fuera de ella, salvo en el caso del K y en menor medida el Ca, los cuales sí respondieron a los niveles de estos elementos en el suelo. Sin embargo, como la biomasa aumenta bajo la copa, el contenido total por superficie de nutrientes en el estrato herbáceo es mayor. Las razones que puedan explicar esto son complejas y están fuera de los objetivos de este trabajo (Barker y Pilbeam, 2007). Además, un incremento mayor de la fertilidad podría derivar, por encima de cambios en el contenido mineral de las plantas o su producción, en una sustitución de especies (San Miguel, 2001).

El factor que más influyó en la concentración de minerales en los tejidos vegetales, por encima de la influencia del árbol, fue el estado fenológico y la madurez del pasto, al disminuir la calidad del pasto con el avance del estado de desarrollo (Montalvo *et al*., 1982; Olea *et al*., 1990-91; Pérez Corona *et al*., 1998). El árbol alarga el ciclo fenológico de las plantas que crecen bajo la copa (Montoya, 1982a), lo cual pudo explicar parte de las diferencias encontradas entre las diferentes posiciones y, por tanto, enmascarar verdaderas diferencias (si las hubiere) entre orientaciones y distancias. La disponibilidad de nutrientes en suelo y la respuesta del pasto a ellos se encuentran muy interrelacionados (Koerselman y Meuleman, 1996; Barker y Pilbeam, 2007). En este sentido, por ejemplo, un aumento en la fertilidad bajo copa podría favorecer una mayor abundancia de gramíneas, que suelen presentar menores concentraciones de nutrientes, en contraposición con las leguminosas (Montalvo *et al*., 1980; Puerto y Rico, 1996; García Ciudad *et al*., 1997; Pérez Corona *et al.*, 1998; Barker y Pilbeam, 2007). En este sentido, se considera que el aumento en nitrógeno podría ser co-responsable del aumento en gramíneas bajo la copa, sin embargo el contenido del pasto en N vendría más determinado por el contenido en leguminosas que, contrariamente, podría aumentar en posiciones que reciben más luz o en suelos con mayor contenido en P (Olea *et al*., 1990-91; San Miguel, 2001).

Implicaciones para la gestión silvopastoral

La calidad del pasto estudiado es muy pobre, incluso al compararlo con resultados obtenidos en otros pastos en dehesas (Olea *et al*., 1990-91; Olea y San Miguel, 2006). Además de básicos en la nutrición y distribución de las plantas, algunos de los nutrientes que se han discutido (N, P, K, Ca, Mg) son esenciales para la alimentación animal, por lo que las diferencias previamente comentadas son de interés a la hora de gestionar y desarrollar modelos silvopastorales, que deberán incluir la variabilidad espacial y temporal descrita. Otras variables de interés pastoral, como estimaciones de fibra (FAD, FND, lignina) o micronutrientes (Cu, Fe, Na) también determinan el tipo de pastoreo y gestión de los pastos (San Miguel, 2001). Debemos resaltar que el factor más determinante en la calidad del pasto fue el estado fenológico, lo cual simplificaría la gestión por las características de estas especies anuales. En primavera hay exceso de oferta, por lo que las leves diferencias encontradas (en calidad) con la presencia del árbol no supondrían a priori un factor muy importante, con la excepción quizá del K. Sí resulta interesante fomentar la calidad del pasto cuando éste es limitante, particularmente en el verano. En este sentido el mayor contenido en K bajo la copa, y aunque no significativo de Ca y Mg en verano podrían ser aprovechados en determinadas condiciones de pastoreo, y es un factor más a tener en cuenta.

9.

Conclusiones

9. Conclusiones

(1) Se ha elaborado la primera cronología de encina en dehesas, mediante la cual se demuestra que la especie sigue un patrón de crecimiento anual en la zona de estudio, por lo que es posible la utilización de secciones para implementar modelos de crecimiento.

(2) Las encinas estudiadas están respondiendo al calentamiento global mediante un aumento en la sensibilidad al clima. Las condiciones del verano parecen ser menos adecuadas para el crecimiento y se ha extendido el período vegetativo al menos en otoño. Esta variabilidad en la respuesta al clima detectada es similar a otras especies de termotipos más fríos de la Península Ibérica y Europa, en lo que podría ser un fenómeno común de respuesta al cambio climático en bosques europeos.

(3) Los rodales estudiados poseen una respuesta al clima común con otras especies y localidades mediterráneas en una banda latitudinal alrededor de 39-42º N. Esta sincronización en el crecimiento podría estar reflejando una combinación de latitud, altitud y orientación. Además, podría manifestar una limitación común por temperatura, frente a posibles limitaciones al crecimiento principalmente por precipitación en masas situadas en localidades de climas más cálidos.

(4) Las ecuaciones en diferencias algebraicas de crecimiento en diámetro potencial dependientes de las edad desarrolladas para la especie produjeron un error de predicción medio del 7%. Mientras, las ecuaciones de crecimiento en diámetro generales dependientes de la edad sólo incrementaron el error al 10%, por lo que en la muestra estudiada es correcto utilizar una sola ecuación para cualquier árbol.

(5) Las ecuaciones de crecimiento en diámetro en diferencias independientes de la edad, pese a proporcionar peores estimaciones que las ecuaciones dependientes de la edad, pueden resultar muy útiles para la modelización del sistema por la dificultad que encierra la correcta estimación de la edad en la especie estudiada. La inclusión del índice de sitio basado en crecimiento en diámetro potencial propuesto mejoró su comportamiento.

(6) La competencia al nivel de rodal limita el crecimiento en dehesas, lo cual se pone de manifiesto mediante la inclusión de la densidad en los modelos de incremento en diámetro. Al ser la competencia por luz reducida o nula, esta reducción en el

crecimiento es probable que se explique por competencia subterránea entre los sistemas radicales. La competencia detectada es en cualquier caso menor que en bosques cerrados y en este sentido la covariable que más explica el crecimiento es la edad o, en su ausencia, el DAP como sustitutivo.

(7) Los modelos de incremento en diámetro ajustados mediante modelos lineales generalizados con distribución Gamma redujeron el número de covariables seleccionadas, resultando modelos más sencillos sin incrementarse sensiblemente los errores, por lo que su uso es recomendable.

(8) Nuestros resultados sugieren que el IFN no debería ser utilizado para modelizar el crecimiento en diámetro de la encina, lo cual posiblemente podría ser extrapolado a otras especies de crecimiento lento o de características similares a la especie estudiada.

(9) No existen estudios en la bibliografía que analicen series de producción de bellota suficientemente largas para poder discriminar los distintos factores que intervienen en la producción. Por ello, los conocimientos que se manejan actualmente sobre la producción de fruto en dehesas proceden de conocimientos empíricos y, pese a su indudable valor, requieren ser validados. La importancia de este recurso hace que resulte urgente su estudio en detalle mediante series temporales de longitud suficiente.

(10) La interacción entre el árbol y la vegetación subyacente es un fenómeno complejo que puede resultar tanto en facilitación como en competencia. El efecto de la presencia del árbol sobre la producción de biomasa herbácea varía entre comunidades e incluso dentro de la misma comunidad en años climáticamente diferentes. En promedio, la presencia del árbol incrementa la producción en los suelos más pobres. Las gramíneas suelen ser el compontente mayoritario del pasto bajo la copa, mientras que las leguminosas son más abundantes en aquellos enclaves que reciben mayor radiación solar.

(11) A diferencia de otros estudios, el incremento en fertilidad edáfica provocado por la presencia del árbol no modificó la concentración de nutrientes en las plantas que crecían bajo la copa, con la excepción del potasio y en menor medida el calcio. Sin embargo, la mayor producción media bajo la copa hace que el flujo total de nutrientes

sea mayor en esas localizaciones. De modo análogo a como ocurrió con la biomasa y la composición, la variabilidad temporal relacionada con factores climáticos determina en mayor medida la calidad del pasto que la variabilidad espacial, lo cual posee implicaciones para los modelos silvopastorales.

10.

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ANEXO I

Gea-Izquierdo G, Martín-Benito D, Cañellas I. Climate-growth variability in *Quercus ilex* L.: is there a climatic signal shared by tree species along the Mediterranean? En revisión

CLIMATE-GROWTH VARIABILITY IN *Quercus ilex*: IS THERE A CLIMATIC SIGNAL SHARED BY TREE SPECIES ALONG THE MEDITERRANEAN?

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Abstract

It has been reported that some conifer species in certain locations are showing increasing sensitivity to climate as a consequence of rising temperatures and water stress. Dendrochronological studies from low elevations are scarce, especially in the Western Mediterranean. In this region, most studies have used long-lived coniferous species from high elevations. Here we present the first chronology (143 years) of *Quercus ilex* L., from a western Mediterranean continental site with oceanic influence. This chronology is compared with 110 European and Mediterranean chronologies from temperate, Alpine and Mediterranean locations. Our results suggest the existence of a temperature latitudinal climatic signal shared by *Q. ilex* with tree-ring chronologies from mid elevations as far as 3,000 km. The most influential climatic variables upon *Q. ilex* growth were early summer precipitation which enhanced growth; and high temperatures in the previous August and current July which reduced growth. A very similar summer response has previously been observed in *Quercus suber* L. and other species in the Mediterranean. Warming has increased holm oak sensitivity to climate and the expansion of the growing season in late fall; this has also been observed among trees from mountain areas in Europe. Additionally, the effects of summer stress on growth have increased and hence trees are likely to be more vulnerable to climatic changes. This increase in summer stress on tree growth has also been observed in high elevations in the Iberian Peninsula. The variation in the response of trees to changing climate reported in mountain areas in Western Europe can be applied to mid elevations in the Mediterranean. Chronologies of termophyllous species from low elevation seem to follow a distinct pattern, probably linked to local precipitation events. These changes are likely to impact on species distribution and future development of Mediterranean forests.

Keywords: holm oak; dendroecology; climate change; warming; dehesas; tree-rings.

INTRODUCTION

Mediterranean climates can be considered geographically and climatologically intermediate between temperate and subtropical climates. As Suc (1984) states ‘Mediterranean climatic conditions consist of a temperate climate characterized by dry summers, with rainfall concentrated during the other seasons and low temperatures in winter’. The summer drought and consequent water stress on plants is shared with subtropical dry ecosystems. Mediterranean species have been redistributing and adapting to a changing climate with summer drought for at least the past 3.2 M years (Suc 1984; Jalut *et al*. 2000). In the recent past, a general warming trend and global changes in precipitation since the 1960s have been reported (Zhang *et al*. 2007). Changes in climate are likely to occur in the future, as have happened in the past (Martrat *et al.* 2004) and this will have important consequences on species distribution, especially if human influence accelerates these climatic changes (Raupach *et al.* 2007).

The difficulties encountered in dendrochronological studies under climates where cambial stop in winter is not evident (such as the tropics and subtropics) are well known (Fritts 1976). Dendrochronological literature from Mediterranean species is less abundant than from temperate species. The majority are dendroclimatological studies that have focused on long lived coniferous species from high elevations, such as *Pinus* sp. (Serre-Bachet 1985). The concept of crossdating species from distant sites originates from the first dendrochronologists. Recently, some studies have demonstrated how climate-growth relationships change over the life of a tree (e.g. Carrer & Urbinati 2006; Macías *et al*.

2006; Andreu *et al*. 2007; d'Arrigo *et al*. In press). In addition, there has been an increase in the shared variance of trees from high elevations in the Iberian Peninsula as a consequence of warming (Andreu *et al*. 2007) and an increase in aridity in the East Mediterranean, with trees responding by uptaking water from deeper soil layers (Sarris *et al*. 2007).

Quercus sp. is a widespread genus in the Northern Hemisphere, and is the most important broadleaf genus in the Mediterranean. Unlike the Mediterranean *Quercus*, temperate *Quercus* species (such as *Q. robur* L.) have been widely used in dendrochronology. The most widespread *Quercus* species in the West Mediterranean is evergreen *Quercus ilex* L. Its distribution ranges from Southern France to the Anti-Atlas in Morocco, and from the sea level to elevations of over 2500 m a.s.l in the Atlas Mountains (Barbero *et al.* 1992; Rodá *et al.* 1999) which confers the species great potential for dendroecological studies. However, there are few dendrochronological studies that have used this species, and they have mostly focused on the more messic subspecies *Q. ilex* ssp. *ilex* in the Northern Mediterranean. The other subspecies, *Q. ilex* ssp. *ballota* is distributed in Western Iberia and North Africa (Rodá et al. 1999) where only one study could be found (Nabais *et al*. 1998-99). Some studies have shown the potential of the species for dendroecology, despite the presence of double and absent rings (e.g. Zhang & Romane 1991; Nabais *et al.* 1998-99). Nevertheless, the longest *Q. ilex* chronology in the literature is 65 years old (Cherubini *et al.* 2003). There is also a lack of dendrochronological studies in West Iberia (Campelo *et al*. 2006), where tree-ring series have been built using conifers from high elevations, often in refuges of boreal species such as *Pinus sylvestris* L. (Richter *et al*. 1991). Nevertheless, studying how low elevation stands respond to climate is essential to understand future shifts in species distributions. In the western Iberian Peninsula climate is influenced by Atlantic winds. The Atlantic influence reduces progressively towards the East, thus increasing continentality. In more continental sites, the winter cambial stop is likely to be more pronounced, and the formation of annual rings more obvious (Cherubini et al. 2003).

Understanding past tree growth-climate relationships is essential for future preservation of ecosystems and sustainable management. Our aim was to determine the relationship between the tree-ring growth of *Q. ilex* and climate, and to assess whether climate warming has increased the species sensitivity to climate or modified its vegetative growth period. We also compare our tree-ring chronology with those of other Mediterranean forests to discuss common growth patterns. We hypothesise that holm oak will be more sensitive to precipitation than the temperature-limited species in more Northern non-Mediterranean locations and high elevation conifers in the Mediterranean.

MATERIAL AND METHODS

Study site

The study site (40º 37' N, 6º 40' W, 700 m a.s.l.) is located on the North-West slope of the Central Mountain Range in Spain. The ecosystem is agrosilvopastoral *Quercus* sp. open woodland resulting from intense management of which probably originated from closed mixed forest, using a combination of thinning, coppicing and seeding. Tree density is generally low (scattered trees), permitting the existence of a layer of herbaceous species (grassland, mostly annuals), shrubs or crops, which interact with trees. Climate data from 'Salamanca-Matacán' station was used in the analyses rather than data from nearer stations (F. de Oñoro, C. Rodrigo) as the records dated back further and were more complete, while being highly correlated with records from closer stations (data not shown). Mean precipitation in the study area ('F. de Oñoro station': 1967-2005) was 609 mm, mean temperature ('C. Rodrigo station': period 1943-2005) 13.2ºC, maximum month temperature 25.3ºC and minimum month temperature 1.8ºC. Climatic data was provided by the Spanish National Meteorological Institute.

Sample characteristics

Although some authors have cored young holm oaks, with tree-like thick holm oaks it is necessary to analyze whole stem discs. Even in the exceptional case where there are very clear rings, the characteristic multiple thick parenchyma radii can interrupt the ring sequence (Cook & Kairiukstis 1990; Cherubini *et al*. 2003). In Spain, it is difficult to obtain samples from old trees as holm oaks are protected. Cross-sections were obtained from each tree at the base and at 1.30 m in summer 2005. We decided to use basal sections, as all of them presented only one centre and were generally less eccentric than sections at 1.30 m, and the rings were proportional at different stem heights (Zhang & Romane 1991).

Cross-sections were air-dried, sanded and polished (60 to 1200 grit). From the 125 trees sampled, only 115 holm oaks had at least one radius with visible rings. First, we selected a sub-sample of trees whose sections were clearly distinguishable (around 50), then this was reduced to the final 18 individuals (35 radii) used to construct the tree-ring chronology (Figure 2). Selecting only samples that clearly crossdate is a regular practice in dendrochronology (Fritts 1976; Cooks & Kairiukstis 1991). In this study, we performed such a strong selection as there are no previous studies on the species in this ecosystem and in order to build a master chronology to make sure that, despite the intense management and the climate, trees were forming annual rings. 80% of the final 18 trees came from stands with densities lower than 80 trees/ha, and these had the widest growth rings.

We compared the *Q. ilex* chronology with those obtained from the International Tree-Ring Data Bank (ITRDB: http://www.ncdc.noaa.gov/paleo/treering.html) to check for holm oak with series from the Iberian Central Mountain Range that could be used as master chronologies, and to look for climatic signal between this lowland series and series from different altitudes. Chronologies were built with the raw width data from 109 locations in Europe, Northern Africa and the Middle East. In the Iberian Peninsula we used data from the Iberian Central Range (Gredos and Guadarrama), the Pyrenees, Iberian range (North-West, around Urbión; West-South, Gúdar and Cuenca; East, Albarracín) and Andalusian ranges (Cazorla and Málaga-Cádiz).

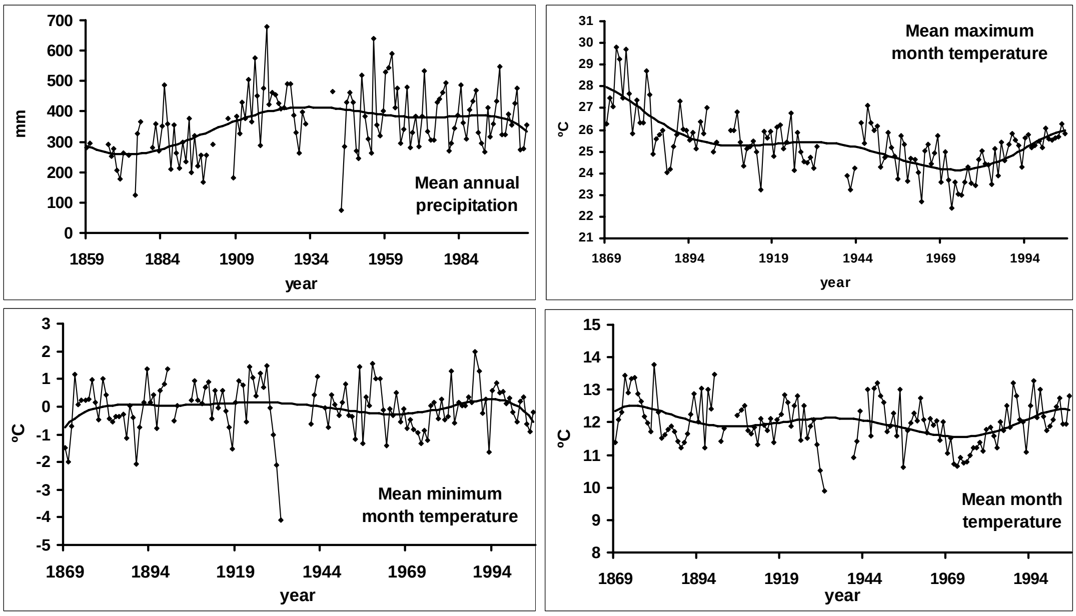

Figure 1. Climatic data from Salamanca city meteorological stations.

Analyses

Ring width was measured using LINTAB and TSAP software (Rinntech 2003). The raw ring width curves were first plotted and checked visually, then synchronized by the *Gleichläufigkeit* (Glk) and the crossdate index (CDI), which is a combination of the Glk and t-values (Rinntech 2003). Individual series were standardized and the autocorrelation removed using ARSTAN (Cook and Holmes 1994): (i) *Q. ilex* was detrended applying a spline function with a 50% frequency response of 32 years; (ii) series from the ITRDB were detrended using low frequency functions such as the Hugershoff or the negative exponential, except when these two yielded negative values. In this case we used more flexible splines with a 50% frequency response of 30 years. By using the Hugershoff and negative exponential functions we intended to keep the longest climatic signal. The *Q. ilex* curves were standardized with a higher frequency smoother as the stands are managed and abrupt growth changes are probably caused by pruning and thinning (Briffa et al. 2002; Macías et al. 2006).

Dimensionless ring width indexes (RWI) were computed by dividing the observed raw ring-width value by the value of the fitted spline. This index is normally distributed, hence we used Pearson correlation coefficients and response function to study the relationship with climate using DENDROCLIM2002 (Biondi and Waikul 2004) which uses bootstrapped calculations. The mean sensitivity was analyzed for the average *Q. ilex* chronology and for running windows of 30 years, as an indicator of the responsiveness of trees to environmental factors (Fritts 1976). The expressed population signal (EPS) was calculated to assess the reliability of the signal used in the climatic analyses. The climatic variables most correlated with growth were further analyzed using the Pearson correlation coefficients for running windows of 10 years (Sarris *et al*. 2007) to check whether the growth-climatic relationship is continuous in time or whether it responds to changing climate, particularly warming in the last decade.

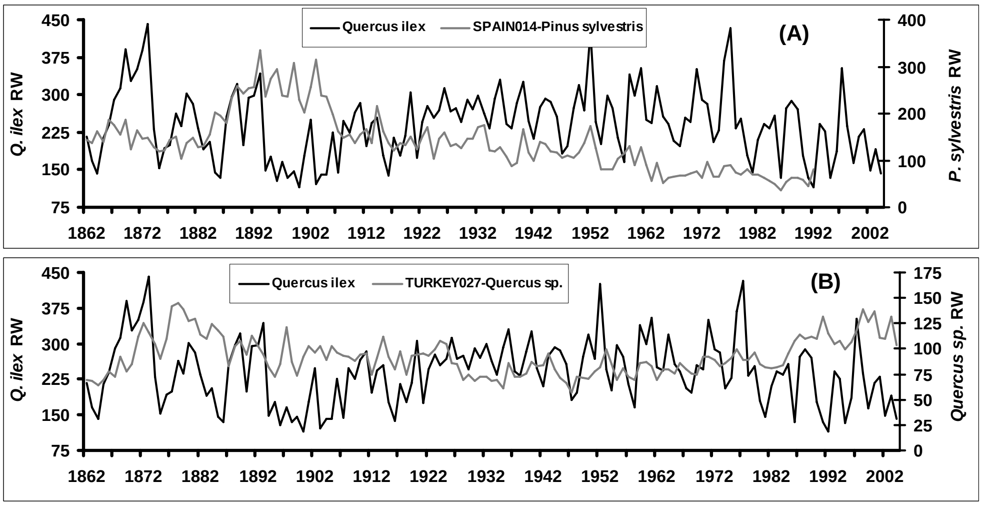

Figure 2. Mean tree ring chronologies of SALAM001 and: (A) the highest correlated chronology (SPAIN014); (B) the farthest crossdated chronology in the Eastern Mediterranean (TURKEY027). Only the overlapping period is showed for comparison purposes. RW=ring width (0.01 mm)

As well as analyzing growth synchrony between the *Q. ilex* chronology and those from ITRDB, we also performed principal component analysis (PCA) on the standardized indices of the 110 mean chronologies (Table 1) for the common period 1923-1975 (110x58 matrix). Then, PCA were run for subgroups suggested by different ordinations. For grouping purposes we considered boreal (=temperate and Alpine) taxa: *Abies* sp. (except *A. pinsapo* Boiss.), *Larix* sp., *Picea* sp., *Pinus sylvestris*, *P. uncinata* Mill ex Mirb., *Quercus petraea* (Mattuschka) Liebl and *Q. robur*. All other species were considered Mediterranean.

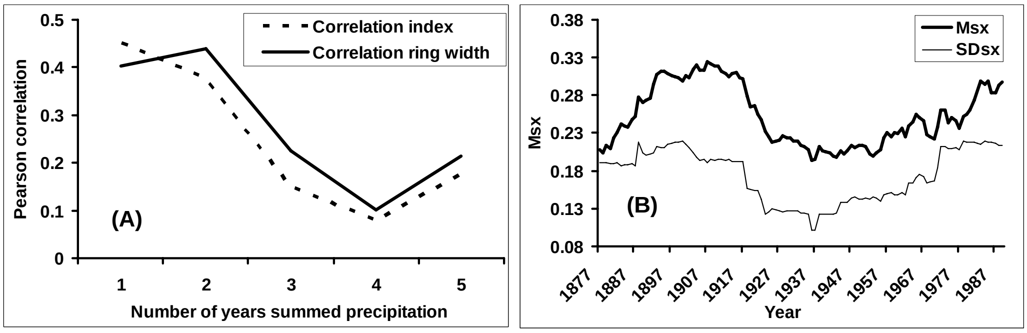

Figure 3. (A) Pearson correlation coefficients between cumulative annual precipitation (1945-2004) and between ring-width index (dotted line) and raw ring width (solid line); (B) 30 year-running mean sensitivity. Msx=mean sensitivity; SDsx=standard deviation sensitivity.

RESULTS

The months of maximum precipitation in the study area are May and November and the minimum in July and August. Summer precipitation showed the greatest variability; summer temperatures showed the least variability (data not shown). This was because there is an absence of rain some summers, but the summers are always hot. The annual mean precipitation, monthly mean temperature, mean minimum and maximum temperatures for series are shown in Figure 1. Although, only data from 1945 onwards was used in the analyses, we included data from the ‘Salamanca’ meteorological station. This showed that precipitation in the second half of the 19 century seemed to be lower than precipitation in the last decades of the 20th century, and temperature was higher. A clear increase in temperature and a slight decrease in precipitation since the 1960s could be observed in the region. This decrease in observed precipitation is not significant, but a consistent decrease in precipitation has been reported over the last few decades in West Iberia (Rodrigo & Trigo 2007).

Quercus ilex climate-growth relationships

The final chronology was built with 35 radii from 18 trees for the period 1862-2004 (Figure 2). The mean sensitivity (1862-2004) was 0.252. The EPS was greater than 0.85 after 1945, the period for which we had climatic data. Correlation with current annual precipitation was similar for ring width and indices, the maximum being 1-2 years and decreasing with longer integration periods (Figure 3A). The correlation between growth and precipitation was greater than the correlation with temperature (Figure 4), and this was particularly evident in early summer (June-July). July seemed to be the most important month for determining growth. Holm oak growth was negatively affected by July maximum temperatures; therefore evapotranspiration (ETP) and water stress are determinant. Additionally, previous December precipitation as well as high minimum temperatures in November and December of the previous year (hence absence of strong frost in late autumn) were beneficial to growth. Nevertheless, high maximum temperatures in January were significantly negative for tree growth. High temperatures, hence high water stress (ETP), in August of the previous year was strongly negative for the next year’s growth. Climate-growth relationships vary as the climate changes through the life of the holm oaks (Figure 5). The link between tree grow patterns and precipitation has become more pronounced since the 1960s (Figure 5A), and the growth season seems to be expanding into fall.

Table 1. Data series used and source. Glk and CDI calculatd between each series with SALAM001 for the corresponding overlapping period. Except in Gea-Izquierdo et al. and Martín-Benito et al., data are archived at the ITRDB. Part 1 :

Series name	Genus	Species	Latitude	Longitude	Altitude	Glk	CDI	Series length	Authors
ITALY010	*Abies*	*alba* Mill.	38.10	15.55	1850	55	4	1790-1980	Schweingruber,F.H.
ITALY011			39.45	16.12	1720	56	12	1800-1980	Schweingruber,F.H.
FRANCE038			42.05	9.12	1500	64**	16	1678-1980	Schweingruber,F.H.
FRANCE024			42.36	2.04	1700	64***	10	1742-1977	Schweingruber,F.H.
ITALY012			42.41	13.26	1700	62**	17	1654-1980	Schweingruber,F.H.
ITALY008			43.52	11.40	1450	54	8	1827-1980	Schweingruber,F.H.
FRANCE007			44.10	5.15	1775	65***	13	1653-1975	Serre-Bachet F.
SLOV002			45.52	14.58	950	54	2	1859-1994	Levanic, T.; Cufa, K.
SLOV003			45.52	14.58	600	58*	5	1890-1994	Levanic, T.; Cufa, K.
SLOV001			45.57	14.19	550	57*	5	1751-1992	Cufar, K.; Levanic, T.
SWITZER113			46.18	7.37	840	56	12	1822-1980	Schweingruber,F.H.
SWITZER158			46.59	7.21	597	63**	12	1887-1979	Schweingruber,F.H.
SWITZER156			47.02	7.24	560	66***	4	1877-1979	Schweingruber,F.H.
SWITZER155			47.02	7.24	560	56	5	1882-1979	Schweingruber,F.H.
SWITZER164			47.19	7.13	620	61*	7	1886-1982	Schweingruber,F.H.
SPAIN007		*pinsapo* Boiss.	36.40	-5.05	1650	58*	9	1728-1982	Schwreingruber, F.H:
ITALY022		sp.	43.40	11.46	1050	50	4	1539-1973	B. Becker
MOROC001	*Cedrus*	*atlantica* (Endl.) Manetti	32.25	-5.15	2200	46	5	1253-1983	Stockton, C.W.; Chbouki; N.; Meko, D.; Adams, R.; Harlan, T.; Glueck, M.
MOROC014			33.01	-5.04	2200	43	5	984-1984	Stockton, C.W.; Chbouki; N.; Meko, D.; Adams, R.; Harlan, T.; Glueck, M.
MOROC011			33.27	-5.02	1900	57	6	1253-1984	Chbouki,N.;Stockton,C.W.;Meko,D.;Harlan,T.P.;Adams,R.K
MOROC013			34.05	-4.11	1900	57*	9	1845-1984	Chbouki,N.;Stockton,C.W.;Meko,D.;Harlan,T.P.;Adams,R.K
MOROC002			35.02	-4.50	1700	56	5	1632-1984	Stockton, C.W.; Chbouki, N.; Harlan,T.; Meko, D.; Adams, R.; Glueck; M.F.
MOROC012			35.07	-5.06	1700	57*	10	1748-1984	Chbouki,N.;Stockton,C.W.;Meko,D.;Harlan,T.P.;Adams,R.K
LEBANON001		*libani* A. Rich.	33.41	35.41	1775	49	2	1829-2002	Touchan, R.; Hughes, M:
SWITZER183	*Larix*	*decidua* Mill.	46.35	9.24	2000	56	9	1807-2006	Bigler, C.; Tiri, R.
FRANCE018	*Picea*	*abies* (L.) H.Karst.	43.53	7.20	1700	55	12	1795-1975	Schweingruber,F.H.
CROATIA001			44.50	15.00	1550	53	1	1868-1981	Schweingruber,F.H.
FRANCE013			45.13	6.41	2100	58*	12	1740-1973	Schweingruber,F.H.
SWITZER157			47.02	7.24	560	55	3	1882-1979	Schweingruber,F.H.
CYPRUS010	*Pinus*	*brutia* Tenore	35.10	32.50	500	47	9	1857-1981	Schweingruber,F.H.
TURKEY032			37.02	30.28	700	57	6	1738-2001	Touchan, R.; Hughes, M:
FRANCE008		*halepensis* Mill.	43.21	5.00	738	57	8	1807-1973	Serre-Bachet F.
GREECE001		*leucodermis* Antoine	39.48	21.13	1750	52	6	1673-1981	Schweingruber,F.H.
ITALY015			39.54	16.14	2000	53	10	1441-1980	Schweingruber,F.H.
GREECE005			40.05	22.25	2250	54	9	1583-1981	Schweingruber,F.H.
CYPRUS001		*nigra* Arn.	34.70	32.90	-	47	1	1628-1980	Schweingruber,F.H.
GREECE009			36.55	22.21	1400	49	4	1657-1999	Kuniholm,P.I.;Groneman,C
GREECE002			37.05	22.20	1450	61**	4	1825-1981	Schweingruber,F.H.
TURKEY031			37.38	35.26	1500	53	0	1475-2001	Touchan, R.; Hughes, M:
ITALY013			37.47	15.03	1800	52	1	1773-1980	Schweingruber,F.H.
SPAIN026			37.49	-2.57	1800	63**	7	1585-1985	Richter, K.
SPAIN025			37.57	-2.56	1405	61**	10	1745-1985	Richter, K.
JAEN02			37.90	-3.00	1100	58*	15	1830-2005	Martín-Benito et al. (In press)
TURKEY010			39.48	27.08	1200	55	2	1556-2002	Kuniholm,P.I.; Groneman, C.
SPAIN031			40.00	-1.59	1225	61**	15	1728-1984	Richter, K.
TURKEY001			40.00	30.35	1400	51	4	1292-2001	Kuniholm,P.I.
SPAIN046			40.16	-1.56	1440	63**	10	1642-1985	Richter, K.
SPAIN041			40.17	-0.42	1475	64***	18	1681-1985	Richter, K.
GREECE007			40.18	20.54	1500	52	5	1676-1978	Kuniholm,P.I
SPAIN010			40.18	-2.08	1350	67***	17	1615-1988	Génova Fuster,M.;Fernández-Cancio,A.;Pérez Antelo,A
SPAIN039			40.18	-0.44	1450	62**	16	1681-1984	Richter, K.
SPAIN009			40.21	-2.08	1250	68***	25	1688-1988	Génova Fuster,M.;Fernández-Cancio,A.;Pérez Antelo,A
SPAIN017			40.26	-4.47	1350	56	10	1754-1991	Génova Fuster,M.; Fernández-Cancio, A.
SPAIN018			40.26	-4.56	1500	63**	24	1687-1989	Génova Fuster, M.
SPAIN032			40.26	-1.54	1440	61**	15	1794-1983	Richter, K.
SPAIN016			40.29	-4.47	1450	56	11	1667-1988	Génova Fuster,M.; Fernández-Cancio, A.
SPAIN043			40.38	-0.29	1500	56	12	1829-1985	Richter, K.
SPAIN019			40.47	-4.00	1600	65***	18	1523-1988	Génova Fuster,M.; Fernández-Cancio, A.
CUENCA06			40.60	-2.00	1100	69***	25	1890-2006	Martín-Benito (unpublished)
GREECE011			41.40	24.63	1320	60*	6	1706-1979	Kuniholm,P.I.;Latini,C.;Ashjian,C
ITALY001			41.46	13.49	1550	62**	17	1750-1987	F. Biondi
ITALY016			41.47	14.02	1550	62**	20	1844-1980	Schweingruber,F.H.
FRANCE027			42.04	9.12	1400	60*	11	1518-1980	Schweingruber,F.H.

(Continuation Table 1)

Series name	Genus	Species	Latitude	Longitude	Altitude	Glk	CDI	Series length	Authors
MACED001	*Pinus*	*peuce* Gris.	41.01	21.11	1900	48	4	1837-1981	Schweingruber,F.H.
SPAIN028		*pinaster* Aiton	37.58	-2.56	1380	57	1	1836-1985	Richter, K.
SPAIN022			40.18	-1.20	1225	58*	11	1821-1985	Richter, K.
SPAIN059		*pinea* L.	39.17	-1.21	705	51	7	1907-2001	Briongos, J.M.; Cerro Barja, A.
SPAIN056			39.20	-2.25	720	47	4	1882-1999	Briongos, J.M.; Cerro Barja, A.
SPAIN054			39.23	-2.38	700	48	1	1916-1999	Briongos, J.M.; Cerro Barja, A.
SPAIN057			40.40	-2.46	1055	67***	12	1874-2001	Briongos, J.M.; Cerro Barja, A.
ITALY002			41.12	13.00	0	54	1	1878-1988	Biondi F.
ITALY003			43.43	10.16	0	56	3	1861-1988	Biondi F.
SPAIN044		sp.	42.48	-0.42	1625	53	10	1605-1985	Richter, K.
ITALY017			44.17	10.48	800	51	4	1856-1989	Ori,G.G
SPAIN012		*sylvestris* L.	40.18	-4.00	1950	59*	6	1527-1988	Génova Fuster, M.; Fernández Cancio, A.
SPAIN040			40.18	-0.41	1650	61**	13	1859-1985	Richter, K.
SPAIN033			40.20	-5.10	1465	69***	21	1813-1985	Richter, K.
SPAIN034			40.20	-5.08	1470	66***	14	1769-1985	Richter, K.
SPAIN042			40.34	-0.29	1750	66***	12	1844-1985	Richter, K.
TURKEY004			40.34	39.17	1300	50	3	1717-1988	Kuniholm, P.I.
SPAIN037			40.47	-3.48	1950	54	7	1661-1985	Richter, K.
SPAIN002			40.48	-4.02	2050	59*	12	1663-1977	Schwreingruber, F.H:
SPAIN035			40.49	-4.03	1550	51	1	1726-1983	Richter, K.
SPAIN021			40.52	-4.12	1650	59*	12	1715-1988	Génova Fuster,M.; Fernández-Cancio, A.
SPAIN013			41.01	-0.04	1900	58*	14	1685-1992	Yuste Herederu, I; Fernández Cancio, A.
SPAIN014			41.01	-0.01	1620	67***	30	1791-1992	Yuster Herederu, I.
SPAIN015			41.01	-0.07	1525	59*	22	1787-1992	Yuster Herederu, I.
SPAIN047			41.59	-2.52	1750	62**	14	1567-1983	Richter, K.
SPAIN006			42.02	-2.42	1900	59*	11	1842-1977	Schwreingruber, F.H:
SPAIN052			42.50	-3.10	880	62**	15	1802-1985	Richter, K.
FRANCE006			43.19	5.44	750	57	2	1836-1982	Schweingruber,F.H.
SWITZER134			46.08	7.10	880	55	3	1843-1979	Schwreingruber, F.H:
SWITZER178			47.00	7.34	550	44	4	1714-1976	Schwreingruber, F.H:
SWITZER129			47.15	7.32	1220	50	4	1802-1982	Schwreingruber, F.H:
SPAIN053		*uncinata* Mill. ex Mirb	42.30	1.30	2000	65***	20	1811-1996	Paul Sheppard, Emilia Gutiérrez
FRANCE023			42.36	2.03	2100	60*	13	1769-1977	Schweingruber,F.H.
SPAIN001			42.40	0.07	1870	62**	14	1609-1977	Schwreingruber, F.H:
SPAIN004			42.41	0.34	1760	63**	13	1808-1977	Schwreingruber, F.H:
FRANCE021			42.58	0.44	1750	56	8	1659-1977	Schweingruber,F.H.
ITALY019	*Quercus*	*robur* L.	44.43	9.19	900	56	3	1779-1989	Nola,P
ITALY021			45.16	9.03	77	55	3	1888-1989	Nola,P
FRANCE002			47.14	0.22	140	49	5	1801-1979	Pilcher JR
FRANCE001			47.34	1.30	100	51	1	1732-1979	Pilcher JR
GREECE006		*frainetto* Ten.	40.29	23.35	600	60*	13	1740-1979	Kuniholm,P.I
SALAM001		***ilex* L.**	**40.37**	**-6.40**	**700**	**100*** **	**1000**	1862-2004	Gea-Izquierdo et al.
TURKEY028		*petraea* (Mattuschka) Liebl.	41.12	32.18	900	54	1	1699-2004	Petrucci,A.;Kuniholm,P.I.;Terrell,J.S.;Steele,L
TURKEY027		*sp.*	39.55	28.33	750	59*	15	1773-2004	Griggs, C.; Kuniholm, P.I.; Petrucci, A.
TURKEY007			41.20	29.00	150	57	9	1769-1985	Kuniholm,P.I.
TURKEY034			41.30	33.00	1050	54	3	1607-2001	Akkemik,U
ITALY018			45.34	9.17	190	54	2	1798-1990	Nola,P

Additionally, summer stress is becoming too high to permit growth, and therefore holm oaks are not able to utilise the scarce summer precipitation (Figure 5C). Summer temperatures are becoming more negatively correlated with growth as they get warmer (Figure 5D). As a consequence, tree sensitivity to climate has increased in the last few years (Figure 3B), although this sensitivity was still lower than in the second half of the 19th century, coinciding with the local minimum precipitation and maximum temperatures previously described.

Quercus ilex growth synchronicity with European and Mediterranean forests-growth

The Mediterranean and European chronologies compared are shown in Table 1. There seems to be a certain latitudinal (focused on 39-42º) synchronization between growth of *Q. ilex* from West Iberia and several species up to the Anatolian Peninsula, 3,000 km farther East (Figure 6). Among boreal European chronologies, *Abies alba* Mill.

had a similar growth response in many locations, some in peninsular Italy (ITA012), as well as *P. uncinata*, *P. sylvestris* and Mediterranean *Pinus nigra* Arn. that crossdated over many locations in Spain and Italy (Table 1).

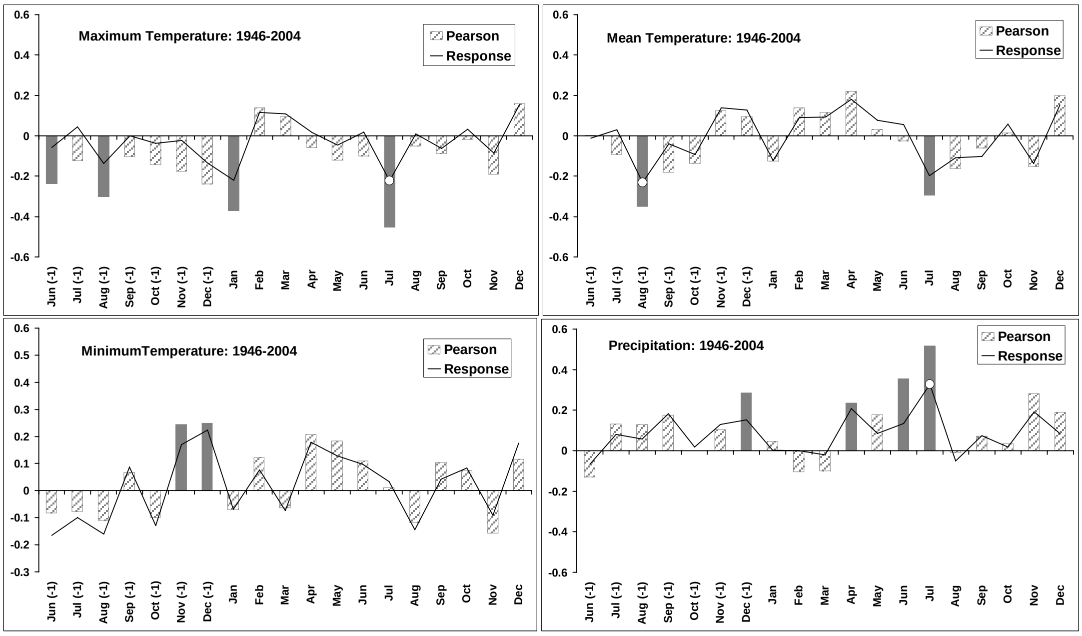

Figure 4. Bootstrapped correlation (bars) and response function (lines) coefficients between tree-ring indices and monthly climatic data from previous year June to current year December.. Dark grey bars and white circles are denote significant Pearson correlation and response function coefficients respectively (α=0.05).

Along with distance between chronologies (Richter et al. 1991), elevation to some extent also determines growth synchronicity. Table 1 suggests that chronologies crossdating with SALAM001 were located mostly in mid-high elevations. SALAM001 did not crossdate with any of the termophyllous chronologies of *Pinus pinea* L. (in this study there are no *P. pinea* stands from cold locations, e.g. from the North Iberian Plateau) or *Pinus halepensis* Mill. from the lowest elevations. The only *P. pinea* stand growing synchronously with SALAM001 was SPAI057, a stand growing in the highest elevation among *P. pinea* chronologies. In the Alps, *A. alba* chronologies from lowest altitudes showed the highest Glk and CDI (Table 1).

Aspect is also influencing growth synchrony as seen when analyzing chronologies from the Iberian Central Range: generally growth chronologies in the North-West aspect (e.g. SPAI014, SPAI015, SPAI033) crossdated very well with our chronologies (Figure 2A), whereas those from the East aspect (e.g. SPAI016, SPAI017) and/or in the highest (coldest) elevations (e.g. SPAI002, SPAI012, SPAI037), did not. The SPAI013, SPAI014 and SPAI015 chronologies (West aspect of the Central Range), obtained from the same forest were particularly interesting. The highest altitude chronology showed the lowest crossdating statistics with SALAM001 whereas those from mid-elevation chronologies were the highest.

Therefore, forest location (mostly as a combination of latitude, elevation and aspect) is determining the climatic synchronicity with SALAM001, whereas the influence of the species seemed to be of secondary importance. In accordance with this, GREECE006 and TURKEY027 (Table 1, Figure 2B), which are the most similar chronologies to SALAM001 in those countries (highest Glk and CDI), are both *Quercus* sp. chronologies growing in very similar altitude/latitude conditions as the *Q. ilex* series.

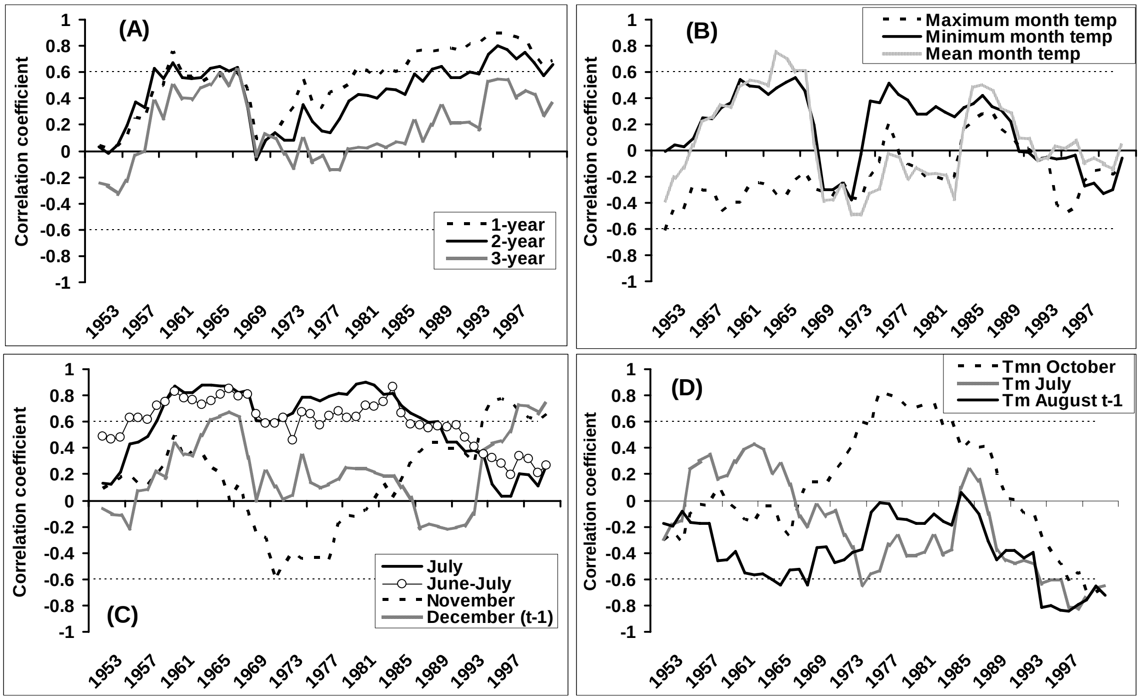

Figure 5. 10-year running average correlations between tree-ring index and cumulative annual precipitation (year, year+year$_{-1}$, year+year$_{-1}$+year$_{-2}$), and monthly maximum, minimum and mean temperatures (current year). (A) and (C) precipitation; (B) and (D) temperature data. (t-1) meaning climatic data from previous year, otherwise it is climatic data from current year.

The PCA results (Figure 7) showed a strong regionalized climatic pattern, although explained variability was low (<30%). First, there was a clear separation between boreal and Mediterranean taxa related to the first axes in Figure 7A, and another clear separation between Spanish chronologies and the rest. The Spanish series were clearly segregated from the rest when only Mediterranean taxa were compared (Figure 7B). Termophyllous pines (*P. pinea* and *P. halepensis*) showed an erratic disposal (similar to Figure 7A), far from other chronologies of different taxa. The southern most *Cedrus atlantica* (Endl.) Manetti chronologies from the Medium and High Atlas formed a distinct group. This group was separated from *C. atlantica* series from the Rif Mountains in Northern Morocco, which were integrated in the bulk of non-Spanish Mediterranean chronologies, very close to the Southern most chronologies from Spain (Andalusia). Boreal taxa (Figure 7C) clearly separated from most Spanish *P. sylvestris* chronologies, except SPAI040, which was situated together with *P. uncinata* between European boreal chronologies and Spanish ones. SPAI040 is located in the Gúdar Range, the Southern most natural location of *P. uncinata*. Finally, in Figure 7D the Spanish chronologies are clearly divided in two groups: the *P. pinea* chronologies and the rest. This second group was further divided in geographically and latitudinally related clusters, namely: (i) the Southern Spanish mountains of Andalusia; (ii) the Pyrenees; (iii) the North-Western Iberian ranges with Eastern and Southern slopes of the Central Range; (iv) the *Q. ilex* related to Western slopes of the Central Range (the closest geographical unit) and West aspects (Cuenca, Gúdar) from Eastern Spain Iberian range around 40º North. Other Mediterranean *Pinus* sp. such as *P. pinaster* had a growth response distinct from that of *Q. ilex*. In the Southern most location in the Andalusian mountains it is homogeneous with the other taxa in the area (*P. nigra*, *A. pinsapo*) and in the Eastern Iberian Range (Albarracín) it is included in the cluster of the South-West aspects of Iberian range (Cuenca, Gúdar) and West Central Range. This last chronology did not crossdate with *Q. ilex*, probably because it was located in the East side of the Iberian range, away from the influence of the Atlantic Ocean.

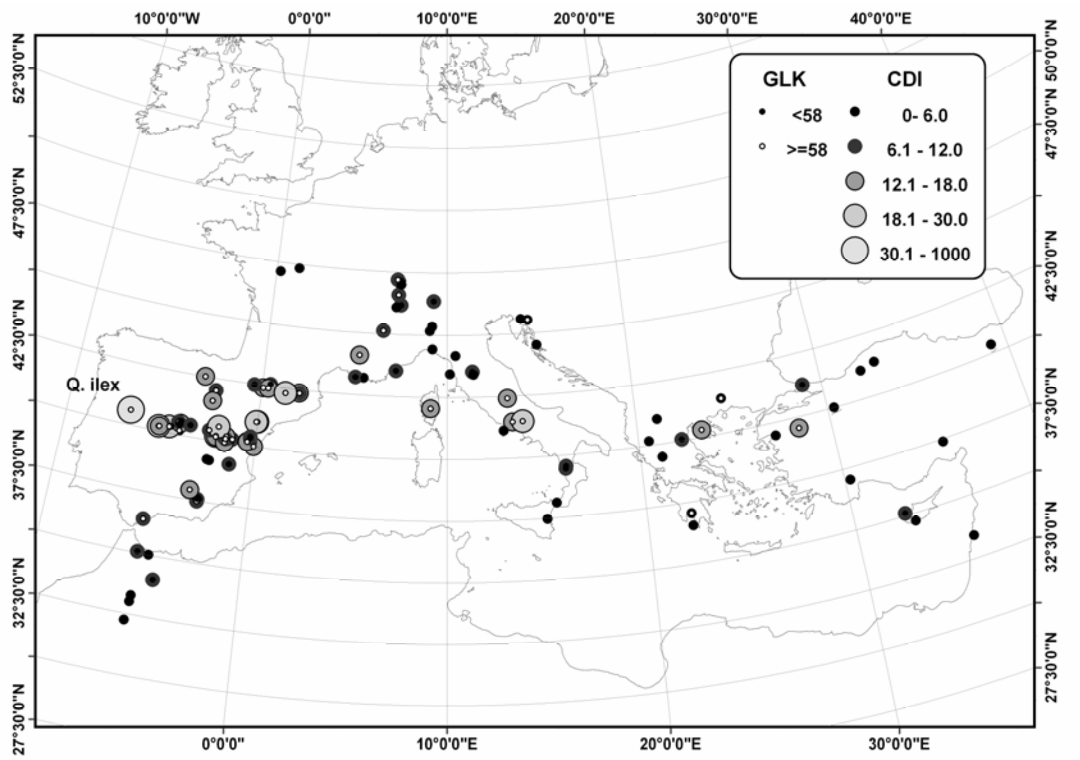

Figure 6: Geographical location of the mean chronologies analysed in this study. CDI and Glk were calculated against the *Q. ilex* chronology. The Q. ilex chronology is crossdated with itself for comparison pursposes (i.e. maximum Glk=100, CDI=1000).

DISCUSSION

Quercus ilex climate-growth relationships

In this study we build the first chronology for the species *Q. ilex.* The relationship between growth and climate has changed with changing climate over the life-span of the holm oaks, as has been detected in other species under temperate climates (e.g. Rozas 2005; Carrer and Urbinati 2006; Andreu et al. 2007). Coniferous species from Eastern Spain have modified their response and sensitivity to climate in the second half of the 20th century as a consequence of increased water stress (Andreu et al. 2007). Our results confirm that this increase in sensitivity to climate is also affecting broadleaf evergreen species at lower elevations and this finding could be extrapolated to include other Mediterranean sites. Holm oak growth is becoming more sensitive to annual precipitation as climate warms, and summer precipitation is becoming less important for annual growth.

The climatic records show that there has been an increase in temperature since the mid 20th century. This increase would be similar to that of 19th century and first half of the 20th century, which could be why maximum sensitivity is observed in the late 19th century (Figure 3B). This warmer period in the 19th century was totally unexpected (e.g. Luterbacher et al. 2006), and assuming that climatic data are accurate, it could be a local variation to general trends. In any case, we have observed that summer is becoming more limiting to growth and that the growing period is expanding into autumn, with trees also becoming increasingly sensitive to autumn temperatures. This reaction is similar to that of *Pinus* populations from mountain areas in eastern Spain (Andreu et al. 2007). In an average climatic year there will not be water stress in autumn, so an increase in annual temperature (and hence energy received by trees) is likely to lengthen the growing season (Figure 5), particularly in evergreen species. This suggests that the expansion of the growing season might be common to most of the Iberian Peninsula, probably excluding the dryer, more termophyllous non-continental sites.

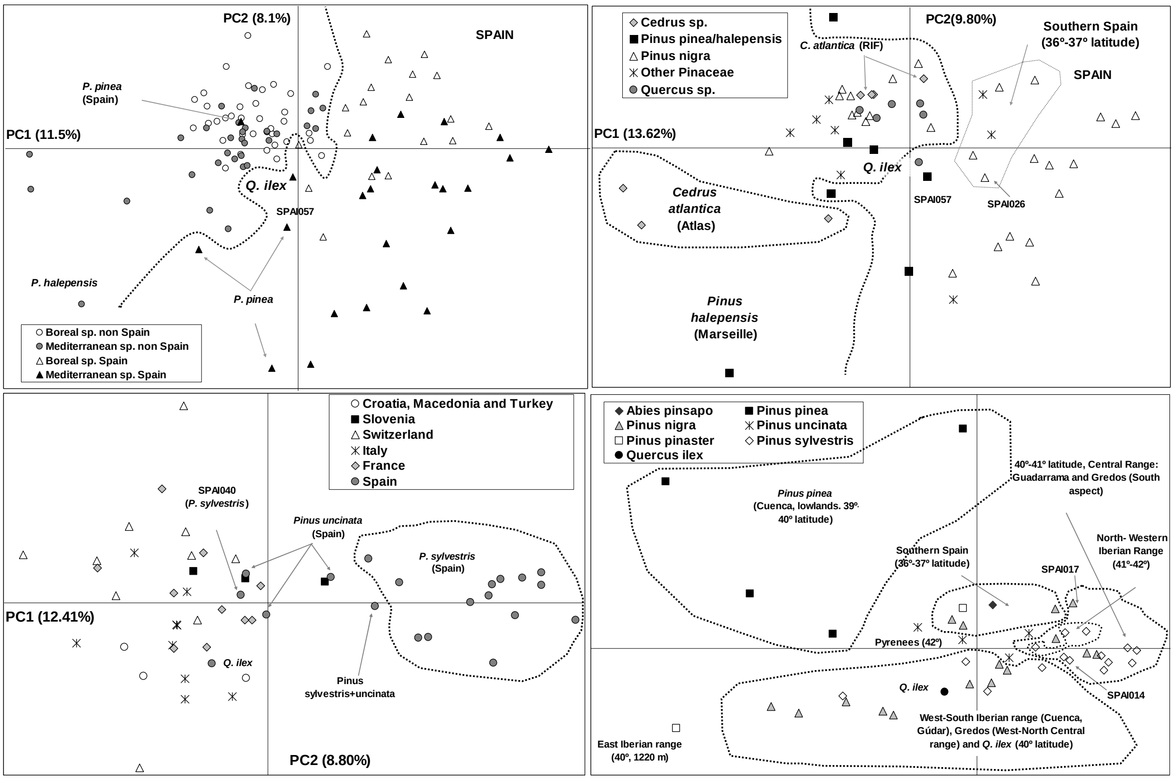

Figure 7: Results from four different PCA: (A) All chronologies; (B) Mediterranean taxa; (C) Boreal taxa; (D) Spain.

As it has been previously demonstrated for shorter growth series, it is possible to use *Q. ilex* for dendrochronology in Mediterranean continental locations. Our chronology begins in 1862, immediately after the end of the Little Ice Age (LIA) (e.g. Guiot *et al*. 2005; Luterbacher *et al.* 2006). The temperate species rhythm, namely cambial stop during winter, seems to be applicable to *Q. ilex*, at least in the locations studied (Zhang & Romane 1991; Cherubini *et al*. 2003). Although this has been shown to vary in other species in different distribution areas in the Mediterranean (summer cambial stop, winter-summer double stop), and in some species is likely to vary in different climatic years (Liphschitz & Lev-Yadum 1986; Cherubini *et al*. 2003). Hence dendrochronology could be more problematic in locations with mild winters and among Mediterranean perennial species rather than on deciduous ones (Cherubini *et al*. 2003).

The occurrence of summer growth in holm oak is a constant in studies under different Mediterranean climates (Zhang & Romane 1991; Cartan-Son *et al*. 1992; Nabais *et al*. 1998-99; Cherubini *et al.* 2003; Corcuera *et al*. 2004). Probably, rainy winters and springs coincide with rainy Julys (Pearson ρ=0.58) between spring precipitation and rain in July-August). In addition, or alternatively holm oaks may be able to use July storm water despite high ETP rates (Rodá *et al.* 1999), when there is no competition from dry understory annual plants. Shoot growth stops in May-June, although this can vary slightly with annual temperatures and at different latitudes/altitudes, (Castro-Díez & Montserrat-Martí 1998; La Mantia *et al.* 2003). This could mean that allocation of resources varies throughout the growing season (e.g. Mooney & Chu 1974): firstly, resources are used primarily to build the photosynthetic tissues, and then later diverted to xylem growth in order to increase water and nutrient uptake and transport, and tree structural resistance.

Mean tree-ring width (around 1.75 mm/year) was within the range of radial growth found in other studies (Cartan-Son *et al.* 1992; Zhang & Romane 1991), although those studies differ in the stand characteristics (density, age). Growth was most closely correlated with precipitation in the current and immediately previous years, contrary to recent results from the East Mediterranean (Sarris et al. 2007). As expected in Mediterranean ecosystems, spring precipitation is strongly correlated with growth, along with previous December rain (Figure 4). Nevertheless, in principle, there is no significant overall correlation of late summer-early fall precipitation with growth, in common with other continental sites and contrary to those in milder locations (Cherubini et al. 2003). July seems to be the key month for growth, presenting both the highest positive correlation with precipitation and greatest negative correlation with mean and maximum temperature. In addition, the negative correlation with mean and maximum temperature of the previous August was highly significant. Probably, when trees withstand high water stress (and excessive heat) during summer of the previous year, future growth is reduced by poor previous fall bud formation. The minimum temperatures in November and December of the previous year are positively correlated with growth. It may be that the absence of frosts permits holm oak growth in late fall, therefore extending the growing season or allowing trees to store carbohydrates for future growth (Miyazawa & Kikuzawa 2005). The negative correlation between growth and maximum temperatures in January could be related to competition with annual grasses.

In Western Iberia, evergreen oak woodlands of *Quercus suber* L. and/or *Q. ilex* are dominant in the landscape. In *Q. suber* trees in Portugal, there is generally a growth stop in December-February, with diameter (ring+bark) growth occurring all through the year (Costa et al. 2001, 2003), although this pattern might vary slightly between years and/or locations (Cartan-Son et al. 1992; Cherubini et al. 2003). *Q. suber* trees in West Iberia also generally reach optimum growth (wood and cork) in June-July and growth is negatively correlated with August temperature. At latitude 37º in Southern Spain, both *Q. suber* and *Q. ilex* also stop in winter, but not only, as they seem to have a summer cambial stop (J. Vázquez personal communication). Thus, it seems that perennial Western Mediterranean *Quercus* sp. (excluding thermophyllous *Q. coccifera* L.) generally grow all year except during the coldest months and do not suddenly stop with early Autumn cooler temperatures. These western Mediterranean evergreen formations would respond similarly to climate, generally with a winter stop, which may reflect their origin from ancient floras under more messic conditions in pre-glacial times (Liphschitz & Lev-Yadum 1986; Rodá et al. 1999). The Southern locations are likely to have a summer stop in addition to the winter stop. It would be interesting to confirm these hypotheses using more precise techniques to detect cambial activity (i.e. dendrometers, cambial marking).

The effect upon plants of increasing temperature in the absence of changes in precipitation will result in an increase in water stress and higher ETP. This, together with last decades increase in CO_2 concentrations (Raupach et al. 2007) is likely to affect tree sensitivity and growth. Different authors report different responses to increasing CO_2 fertilization, although in general it is expected that relative radial growth increases in dry environments due to higher water use efficiency (WUE) (Hattenschwiler *et al*. 1997; Tognetti *et al.* 2000; Knapp *et al*. 2001; Soulé & Knapp 2006). However if ETP increases in Mediterranean ecosystems, water stress could dominate over the CO_2 fertilization effect (if any) and this may result in important changes in species distribution (latitudinal and altitudinal shift). Species growing at low elevations in the Mediterranean, like *Q. ilex* in this study, are more susceptible to climate change than plants growing at higher altitudes. However, stand structure and competition are also influential factors affecting plant response to climate (e.g. Laurent et al. 2003) and these factors are neglected in most studies. Management (e.g. through stand density) might help to preserve some species in certain sites against the effects of climate change (Cescatti & Piutti 1998). *Q. ilex* trees are more sensitive now to precipitation and temperature, and this is one reason why many sites have regeneration problems, particularly in the degraded and overgrazed open stands that characterize the ecosystem today (Pulido & Díaz 2005).

Quercus ilex growth synchronicity with European and Mediterranean forest-growth

Q. ilex seems to be responding to some common climatic signal influencing trees located in latitudes between 39-42º North, except low elevation termophyllous locations and the highest elevations. However, this signal does not explain all of the climatic variation of the chronologies. Differences in aspect may be the reason why some chronologies do not crossdate, and it is well known that (e.g. Richter et al. 1991) the proximity of populations increases synchronicity. We believe that this latitudinal growth correlation is responding to 'annual energy/heat impulses', i.e. a combination of latitude, elevation, and aspect, with the common signal diminishing with distance. The most distant populations that crossdate are 3,000 km apart in the Anatolian Peninsula. This chronology and the chronology crossdating in Greece are from *Quercus* sp. at elevations 600-750 m, hence ecologically very similar to our *Q. ilex* chronology.

The highest elevation series are mostly limited by temperature whereas the lowest elevation series respond mostly to local precipitation phenomena, because at the latter, low temperature barely limits growth of evergreen species in winter. Low elevation *P. pinea* series do not always synchronize between each other, suggesting a stronger dependence on precipitation, which is a more localised variable than temperature (Briffa et al. 2002) or the influence of non-climatic factors. That is the reason why *P. pinea* forests response is independent to the rest of Spanish series analyzed. The *P. halepensis* chronology from France also seems to follow a distinct pattern (Liphschitz & Lev-Yadun 1986). The chronologies in the North-West aspect of the Central Mountain Range crossdate with *Q. ilex* much better than those from an Eastern aspect (more continental, rain shadow) and the highest elevation chronologies, showing the influence of altitude and aspect.

The PCA results show a regionalization of the chronologies: first the big ecological groups (boreal, Mediterranean) were separated, then regional clusters were formed. Spanish chronologies were clearly separated from the others, both boreal and Mediterranean, which could reflect higher oceanicity compared to more Eastern locations. Mediterranean thermophyllous species (*P. halepensis*, *P. pinea*) from the lowest elevations behaved differently than mid-altitude forests, especially in the Iberian Peninsula. This segregation may be predominantly caused by different responses to temperate-winter cambial stop and summer/winter double stress (Liphschitz & Lev-Yadum 1986). The *Q. ilex* chronology (elevation 700 m) is included in the big group of Mediterranean-Mountain forests that still share a temperature limitation with Northern Hemisphere chronologies, but that are also affected by water stress (Briffa *et al*. 2002). This means that they constitute a different group apart from both European taxa (generally in more Northern latitudes) (Richter *et al*. 1991; Briffa *et al*. 2002), responding also to the temperate winter climatic rhythm (Liphschitz & Lev-Yadum 1986), despite the summer water stress. Species adapt to climatic and edaphic patterns, which might be the reason why the PCA and cross-correlation statistics separate regions rather than species. There appear to be three main 'climatic domains' in the Iberian-Mediterranean area, with some species overlapping in different domains and hence, exhibiting a mixture of different and shared climatic signals. These three domains are: i) The highest elevations (mostly occupied by boreal species such as *P. sylvestris*, as Mediterranean mountains can be considered boreal refuges), that are limited mostly (but not only) by temperature, and behave similarly to boreal sites in Northern Europe (Briffa et al. 2002); ii) inland mid elevation sites, that are limited by regional temperature, but also by local precipitation, and still exhibit winter dormancy; iii) low elevation Mediterranean sites that respond mostly to local precipitation as a consequence of mild winter temperatures (Campelo et al. 2006). Northern Hemisphere trees, excluding the tropics, would be placed in between the two extremes of only winter low-temperature limited boreal locations (hence, strong positive correlation with summer temperature) and only summer high-temperature-drought limited locations.

Except in soils with high water accumulation, water is the most strongly limiting factor on growth with decreasing altitude in the Mediterranean region, with temperature following the opposite trend. Among the alpine species of Central Europe, *A. alba* has a distinct response to climate (Frank & Esper 2005) and possesses the highest correlation with *Q. ilex* among those boreal species. Spanish chronologies of *A. alba* seem to have a shared climatic response that separate them from the European chronologies analyzed. Thus, we believe that the PCAs mostly reflect precipitation gradients, whereas Glk and CDI mostly reflect a temperature gradient. Ordination includes *Q. ilex* at mid elevation in Western Spain within the same cluster as mid-elevation mountains (below 2000 m) in Eastern Spain and North-West aspect of the Central Range. Although grouping is similar, less variance is explained by ordination when including *Q. ilex*, compared to studies that have only analyzed conifers at elevations higher than 1000 m a.s.l. (Richter et al. 1991). It is remarkable that there is more synchronicity with series that are located north of *Q. ilex*, than with species located further south, supporting the shared temperature limitation hypothesis discussed. *C. atlantica* series from the Rif Mountains in North Morocco were climatically close to stands from Southern Spain Andalusian mountains (see Figure 7B), forming a climatic unit distinct from the Atlas Mountains. This could suggest North-South temperature bands or bands of increased summer aridity (although, e.g. wet Atlantic winds are influential), similar to those described by Jalut *et al*. (2000) in the last millennia.

Our results agree with the suggested by Cherubini *et al.* (2003), that not all *Q. ilex* locations will share a climatic signal. It is likely that holm oaks from warmer locations have a different climatic response that may be more similar to that of low elevation *P. pinea*. Some species like the holm oak are plastic and able to adapt to a wide spectrum of ecological conditions under specific bioclimates. If warming continues, trees might not be able to continue to adapt as they are currently doing by their increase in sensitivity and growing season adaptations. The warmest and driest sites are likely to experience the biggest changes. Mediterranean forests should be monitored in the future to study any shift in species. *Q. ilex* is likely to adapt in many locations, but if aridity continues increasing it might disappear from the driest sites and most degraded soils, especially in the Southern Mediterranean such as South Iberia and Northern Africa. Jalut et al. (2000) showed how the Mediterranean climate has been expanding northward in latitude since the last glaciation more than 10,000 years ago. If an expansion of summer drought is continuing, it would be important to take this into account. The changes detected in species response could be a sign of this phenomenon, and an increase in summer water stress could have dramatic effects on species distribution.

CONCLUSIONS

The increase in temperature and changes in precipitation observed in the last decades have an influence upon tree growth and are likely to have consequences on species distribution in the short term. Tree response to climate varies with changing climate as seen in this study of the broadleaf *Q. ilex* and in conifers in other studies from mountainous areas of Europe. Holm oak is also showing increasing sensitivity to climate, in common with conifers in high elevations in the Iberian Peninsula. Evergreen oak forests in West Iberia are highly sensitive to early summer precipitation and negatively affected by high temperatures in late summer. The growing season of holm oak is expanding further into fall, and summer has become a greater stressor on growth as a consequence of recent warming. The consequences of climatic change for species distribution will have to be closely monitored from now on, particularly in degraded soils like those found in many locations in the Mediterranean.

In this study we have built the first chronology of a broadleaf Mediterranean species in the Iberian Peninsula. It is also the first *Q. ilex* published chronology, additionally it is highly significant as one of the few mid/low elevation chronologies from Spain and as one of most Westerly chronologies available for the Mediterranean region. Our holm oak tree-ring chronology shared a climatic signal with other chronologies over a Mediterranean latitudinal band up to the Anatolian Peninsula. This signal is likely to be a combination of latitude, altitude and aspect. There is also a more localised response, probably related to precipitation, with the *Q. ilex* series located closer to high elevation *Pinus* sp. than to termophyllous locations such as those inhabited by species like *P. pinea*. Whether it is possible to extrapolate our results to warmer locations occupied by *Q. ilex* remains to be studied. We hypothesise that our chronology will follow a different climatic response pattern than holm oaks at lower elevations and lower latitudes. Monitoring of the future shared responses to environmental changes is crucial to understand ecosystems dynamics.

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ANEXO II

Gea-Izquierdo G, Cañellas I, Montero G. 2008. Site index in agroforestry systems: age-dependent and age-independent dynamic diameter growth models for *Quercus ilex* in Iberian open oak woodlands. Canadian Journal of Forest Research 38, 101-113.

SITE INDEX IN AGROFORESTRY SYSTEMS: AGE-DEPENDENT AND AGE-INDEPENDENT DYNAMIC DIAMETER GROWTH MODELS FOR *Quercus ilex* L. IN IBERIAN OPEN OAK WOODLANDS

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ABSTRACT

Despite *Quercus ilex* being one of the most widespread tree species in the Mediterranean basin, there are no growth models in the literature for this species. In this study, we compare age-dependent and age-independent dynamic diameter growth models, and discuss the concept of dominance in open stands. 'A posteriori' dominance was determined to fit potential growth age-dependent models, and a site index based on diameter growth was defined. Formulations derived from power decline base models (Korf and Hossfeld) best described diameter growth. The best approach for age dependent models was a polymorphic and with variable asymptotes generalized algebraic difference approach formulation. Residual errors in trees between 20-55 cm ranged from circa 7.0% in potential growth models to circa 15% in age-independent models expanded by density. Using a unique age-dependent dynamic equation for all trees, regardless of dominance, did not increase much the error. In age-independent models, the inclusion of the defined site index reduced the prediction error, but requires that the age of trees is estimated to determine the site index. The difficulty of estimating *Q. ilex* age makes age-independent models very attractive for system modelling. Age-independent models could be useful in other ecosystems where age estimation is problematic.

Keywords: holm oak; Mediterranean; dehesa; Spain; site index.

INTRODUCTION

Agroforestry systems share the presence of a woody component, commonly trees, and occupy large expanses across the world (Mosquera et al. 2005). Agrosilvopastoral and silvopastoral systems are different types of agroforestry systems having in common the presence of grazing animals. Management of these systems differs from classical forestry systems. Usually, timber is not the most important output, which is the reason why tree growth has not been paid as much attention as in traditional forest systems. Yet, understanding past tree growth is one of the first steps to sustainable management and prediction of future landscape responses to different management or climate change scenarios. Site index models based on the height growth of dominant trees are the classical way of indirectly estimating site quality (mostly a combination of soil fertility and climate) in forestry management (e.g., Carmean 1975; Goelz and Burk 1992; Cieszewski and Bailey 2000). Applying the site index to modelling the tree component in agroforestry systems is not always straightforward. Compared with forests, agroforestry systems are characterized by low tree densities, as other products (e.g. pasture, crops, fruits, cork) are usually of greater economical interest than the timber (Ares and Brauer 2004; Mosquera et al. 2005). Additionally, in some agroforestry systems trees are pruned (e.g., Balandier and Dupraz 1999), and some of them have originated from fire or thinned 'natural' forests or shrublands. This complicates the selection of true life-span dominant individuals. Therefore, the concept of canopy dominance is not directly applicable as the wide spacing reduces aerial competition, generally resulting in a unique 'dominant-codominant' tree stratum. However diameter is more likely to be affected by density than dominant height, some studies have used diameter from dominant trees instead of dominant height in systems where dominant height was not available (Carmean 1975; Ares and Brauer 2004).

In Western Iberia, an agrosilvopastoral system of high economical and ecological interest called 'dehesa' in Spain and 'montado' in Portugal, occupies more than 3,000,000 ha (San Miguel 1994; Pulido et al. 2001). This is one of the most famous traditional agroforestry systems in the world, having received much attention in the literature. 'Dehesas' are anthropic savannas mostly dominated by *Quercus* sp., with *Quercus ilex* L. (holm oak) being the most common species, followed by *Quercus suber* L. These oak stands are not suitable for traditional, intensive forestry because of the poor sandy soils and Mediterranean variable dry climate in which they thrive. The specific management, applied through time, has modelled this landscape. The history of the dehesas is complex and the origin of the current structure uncertain. It is likely that they result from a combination of thinning, conversion by thinning on coppice, acorn sowing, and holm oak selection in what was probably a mixed landscape several thousand years ago. Most authors today (Manuel and Gil 1999; Pulido et al. 2001; Martín-Vicente and Fernández-Alés 2006) suggest that most current 'dehesas' originate from the XIX century. Therefore, it is very likely that most of them are still in their first rotation cycle, at least with the open tree structure dominated by holm oak encountered today. As in other agroforestry systems, trees are pruned, usually at regular intervals of 10-20 years (Gómez and Pérez 1996). Lack of tree regeneration is a challenging problem, and constitutes a threat for the persistence of these systems (Pulido et al. 2001; Pulido and Díaz 2005).

Quercus ilex is one of the most important and widespread tree species in the Mediterranean Region (Barbero et al. 1992; Rodá et al. 1999). Despite the importance of the species, and the abundant literature on the ecosystems that it dominates, there are no growth models published. There are several possible explanations: (i) it is not a classic timber species; (ii) it has been primarily managed to obtain firewood and many *Quercus ilex* stands are coppice (Rodá et al. 1999); (iii) it is very difficult to obtain permissions to log tree-like holm oaks; (iv) the species wood anatomy makes it difficult to clearly distinguish annual rings (Gené et al. 1993). The formation of annual rings in holm oaks have been described in several dendroecological studies (e.g. Zhang and Romane 1991; Cherubini et al. 2003). However, double rings are sometimes present and because of eccentric growth, absent rings in parts of the circumference are common. It is therefore desirable to analyse whole sections (Gené et al. 1993).

In this study, we discuss the concepts of dominance and site index in low tree density agroforestry systems where trees are pruned using the agrosilvopastoral system called 'dehesa' and *Quercus ilex* as an example. Dynamic age-dependent models are used to define a site index and their fit and applicability is compared to recently proposed age-independent dynamic formulations (Tomé et al. 2006). In addition, the role played by current density in holm oak diameter dynamic growth is analyzed. The main objective is twofold: (i) discuss the concept of dominant growth in low-density agroforestry systems; (ii) compare age-dependent and age-independent formulations for modelling holm oak diameter growth. To do so, we structured our study in three consecutive steps: (1) we fitted age-dependent dominant diameter growth models to study the definition of a site index for these woodlands; (2) we discuss the concept of dominance within this low-density system and the possibility of fitting a single dynamic age-dependent growth model for all trees independent of dominance; (3) we compare the behaviour of age-dependent models with age-independent models as proposed by Tomé et al. (2006), and discuss the role of current density as a proxy to management of stands throughout their history and the suitability of the defined site index.

MATERIAL AND METHODS

Study site and sampling methods

The tree samples were collected in Central-Western Spain, close to the border with Portugal (40º 37' N, 6º 40' W, 700 m a.s.l). The trees were included within a belt of circa 50 m x 9 km clearcut to construct a freeway. The ecosystem is a typical 'dehesa' under a continental-mediterranean climate with mean annual precipitation around 600 mm and summer drougth. The clearcut belt belonged to a large patch of almost pure holm oak woodland of variable density with sparse *Quercus faginea* Lam. and shrubs, such as *Cytisus multiflorus* (L'Hér.) Sweet, *Cistus clusii* Dunal or *Cistus ladanifer* L. intermixed. Soils in the study area were sandy and of granitic origin, with a few plots located on slate.

Data

During the summer of 2005, we set up 25 plots of variable radius that included 10 trees each. The plots were selected to include stands of different densities (from 39.2 to 210.4 trees/ha, with a mean of 129.9±37.9 trees/ha, corresponding to 9.5±3.9 m^2/ha.) and trees from all diameter classes. The five central trees of each plot (i.e., a total of 125 trees) were pushed down with a bulldozer and sections at 1.30 m and at the base were collected. From the 125 trees felled, 115 presented at least one readable radius (absence of rot). Stem discs were air-dried, then sanded and polished (60 to 1200 grit). Annual growth was measured with TSAP software and LINTAB (Rinntech, 2003). To ascertain that we were measuring annual rings, two to three radii were crossdated in a set of subsamples (Fritts, 1976). In addition, all sections at 1.30 had lower age than discs at the base resulting in the following model: $Age_{basal}=11.82+1.01\cdot Age_{DBH}$; $R^2=0.93$, Residual root mean square error-RMSE=7.67. All analyses in this study are referred to growth without bark (bark thickness [mm]=0.02·DBH[cm]-0.39; $R^2=0.55$, RMSE=0.24). Annual diameter increments were averaged at 5-year intervals to reduce autocorrelation and minimize possible measuring errors. Whether the estimated tree ages from basal sections are ‘real-ages’ or ‘stem ages’ from an older stump, is not possible to be ascertained. Nevertheless when the trees were felled, the stumps were not swollen nor presented more than one stem, what could suggest an origin from seedlings.

To fit *Quercus ilex* diameter ‘potential’ growth site index models, tree dominance (assuming in principle that dominance existed) had to be defined ‘a posteriori’. We accepted that, under the current densities, within each plot at least two of the five trees were exhibiting potential growth. The growth measurements by plot were plotted on a graph, and trees showing apparent suppression were removed. From a total of 88 selected ‘dominant-codominant’ trees, two to five trees per plot were averaged to build 25 plot series. We used these 25 series to fit potential growth (dominant) models, whereas general age-dependent models for all trees and age-independent models were fitted using the individual 115 tree-growth series.

Models and analysis

Four three parameter base models among the most commonly used in the literature were selected from a larger set of integral growth models preliminary compared. These models were used to formulate both age-dependent and age-independent equations. Two base models belonged to the power decline group (Hossfeld IV and Korf) whereas the other two belonged to the exponential decline group (Richards in all cases and Weibull when parameter c>1. [Zeide, 1993; Shvets and Zeide 1996; Kiviste et al. 2002]). All the selected integral models are differentiable and share the desirable characteristics for site index models (e.g., Cieszewski and Bailey 2000), namely: (i) polymorphism; (ii) inflection point; (iii) horizontal asymptote as a biological limit to growth; (iv) theoretical basis; (v) logical behaviour; (vi) simplicity. Throughout this study, age-dependent models are referred as E(i) while age-independent models as T(i).

To develop age-dependent models we used GADA (generalized algebraic difference approach) formulations of the base models (Cieszewski and Bailey 2000; Cieszewski 2004), a generalization of the algebraic difference approach (ADA) by Bailey and Clutter (1974). ADA is a particular type of GADA, where only one parameter varies with site. Therefore, E1, E2, E4, E7, E10, and E11 are equivalent to polymorphic ADA, E3 is an anamorphic GADA (equivalent to the models discussed in Cieszewski [2002] and Cieszewski et al. [2006]), the rest (E5, E6, E8, E9) are polymorphic with variable asymptotes GADA. Some of these models have been used in other forestry applications (e.g. Barrio-Anta et al. 2006; Cieszewski et al. 2006; Diéguez-Aranda et al. 2006; Tomé et al. 2006). Base-age invariance was achieved by fitting GADA models using the dummy variables method (Cieszewski et al. 2000; Cieszewski 2003). The unobservable theoretical variable *X* represents the site productivity dimension. *X* is an unknown function of management regimes, soil conditions, and ecological and climatic factors, which cannot be reliably measured or even functionally defined (Cieszewski 2002). This variable might be of particular interest in this study, as we expect the unknown plot management regime to be very influential on diameter growth. GADA were used both for potential growth models and general age-dependent models for all trees. All analyses were programmed using the MODEL procedure in SAS 9.1 (SAS Institute Inc., 2004).

Dynamic growth models are usually age-dependent. However, age estimation can be very challenging or even impossible for some tree species like the holm oak and many tropical tree species. For this reason, the age-independent formulation proposed by Tomé et al. (2006) appears to be an attractive alternative for species or forest stands where age estimation is not possible (like uneven-age stands). Age-independence is achieved by solving the base equations for age in t_1 and then substituting in t_2 expressed as $t_2=t_{1+dif}$, being ‘dif’ the projection length. To generate a family of curves, at least one of the parameters needs to be expressed as a function of site variables and/or stand characteristics (Tomé et al. 2006). In this study we use current density to expand the parameters at first approach and then compare this with age-independent models that were expanded by the previously defined site index and density. Formulations based on site index are not really age-independent as some estimation of age is needed to estimate site index.

In order to remove serial correlation we graphically compared several stationary autocorrelation structures (processes AR(x) and ARMA(x,1)) by plotting autocorrelation functions (ACF) of residuals (data not shown). The most parsimonious autoregressive structure that removed autocorrelation was AR(2) ($\varepsilon_i = \rho_1 \cdot \varepsilon_{i-1} + \rho_2 \cdot \varepsilon_{i-2}$; with ε_i= residual for observation i, and ρ_1, ρ_2=autocorrelation parameters) which was used in all cases. Possible heterokedasticity was examined visually by plotting the residuals against predicted values. When residuals were heterokedastic the models were fitted using generalized non linear least

Table 1. Base models and difference equations considered to develop the age-dependent growth equations.

Base equation	Parameter related to site	Solution for X	Dynamic equation	Id
Hosfeld IV (1822) cited in Peschel (1938): $y=\frac{t^c}{b+at^c}$	b = X	$X_0=t_1^c\cdot\left(\frac{1}{y_1}-a\right)$	$y_2=\frac{t_2^c}{X_0+a\cdot t_2^c}$	(E1)
	c = X	$X_0=\frac{\ln\left(\frac{y_1b}{1-y_1a}\right)}{\ln t_1}$	$y_2=\frac{t_2^{X_0}}{b+at_2^{X_0}}$	(E2)
	a = X b = b₁X	$X_0=\frac{t_1^c/y_1}{b_1+t_1^c}$	$y_2=\frac{t_2^c}{X_0\cdot(b_1+t_2^c)}$	(E3)
Korf (1939) cited in Lundqvist (1957) $y=a\cdot\exp(-b\cdot t^{-c})$	b = X	$X_0=\frac{-\ln(y_1/a)}{t_1^{-c}}$	$y_2=a\cdot\left(\frac{y_1}{a}\right)^{(t_1/t_2)^c}$	(E4)
	a = exp(X) b = b₁+(b₂/X)	$X_0=0.5\cdot(b_1t_1^{-c}+\ln(y_1)+F_0)$ $F_0=\sqrt{((b_1t_1^{-c}+\ln(y_1))^2+4b_2t_1^{-c}})$	$y_2=\exp(X_0)\cdot\exp(-(b_1+(b_2/X_0))\cdot t_2^{-c})$	(E5)
	a = exp(a₂X) b = X	$X_0=\frac{\ln(y_1)}{a_2-t_1^{-c}}$;	$y_2=\exp(a_2X_0)\cdot\exp(-X_0t_2^{-c})$	(E6)
von Bertalanffy (1957)- Richards (1959): $y=a\cdot(1-\exp(-b\cdot t))^c$	b = X	$X_0=-\frac{\ln(1-\sqrt[c]{y_1/a})}{t_1}$	$y_2=a\cdot\left(1-\left(1-\sqrt[c]{\left(\frac{y_1}{a}\right)}\right)^{\frac{t_2}{t_1}}\right)^c$	(E7)
	a = exp(X) c = c₁+(1/X)	$X_0=0.5\cdot(\ln(y_1)-c_1F_0+\sqrt{(c_1F_0-\ln(y_1))^2-4F_0}$ $F_0=\ln(1-\exp(-bt_1))$	$y_2=\exp(X_0)\cdot(1-\exp(-bt_2))^{(c_1+(1/X_0))}$	(E8)
	a = exp(a₂X) c = X	$X_0=\frac{\ln(y_1)}{a_2+F_0}$ $F_0=\ln(1-\exp(-bt_1))$	$y_2=\exp(a_2X_0)\cdot(1-\exp(-bt_2))^{(X_0)}$	(E9)
Weibull (1951)-Yang et al. (1978) $y=a\cdot(1-\exp(-b\cdot t^c))$	b = X	$X_0=-\frac{\ln(1-(y_1/a))}{t_1^c}$	$y_2=a\cdot\left(1-\left(1-\frac{y_1}{a}\right)^{\left(\frac{t_2}{t_1}\right)^c}\right)$	(E10)
	c = X	$X_0=\frac{\ln\left(-\frac{\ln\left(1-\left(\frac{y_1}{a}\right)\right)}{b}\right)}{\ln t_1}$	$y_2=a\cdot(1-\exp(-b\cdot t_2^{X_0}))$	(E11)

squares weighted by 1/Var(ε_i), with Var(ε_i) being the variance function estimated for the residuals.

Diameter growth was analysed in three consecutive approaches using dynamic forms derived from the four integral models selected:

(i) *Potential growth dynamic age-dependent models*: we used the 25 series to define a site index based on holm oak diameter growth and analysed the biological potential growth of the species. Models are shown in Table 1, designated from E1 to E11.

(ii) *Tree diameter dynamic age-dependent growth models*: we considered two hypothesis concerning crown competition and dominance shared by many other agroforestry systems: (i) in the most open stands this competition is almost nil, and hence the stands are mostly a combination of free-grown trees or a dominant-codominant unique canopy layer; (ii) if dominance is expressed in the more dense stands, it is not a continuous feature of trees because after each pruning rotation trees need to rebuild their crowns. To answer these hypothesis and its applications to dynamic growth, we analyzed the effect of current density (expanding parameters ‘a’ or ‘b’ in models E3d and E5d, to compare with $E3_2$, $E5_2$ and $E9_2$ which are non-expanded), as a proxy to stand history. Generally, current density is not a good covariate to use in dynamic models as it is likely to change through time. However in ‘dehesas’, as a consequence of history and management, the tree stratum can be considered as almost ‘static’, with few changes in the stand structure (but a slow decline in oak numbers) at least since the 1950´s (García del Barrio et al. 2004). It might be hypothesised that the trees remaining today were the healthy, dominant trees from the ancient woodland (if we accept healthier, dominant trees produce more acorns and firewood) or at least these would not have been selectively removed, as timber has always been a secondary product in relation to firewood, acorn production and pasture. As it is not possible to determine dominance in the field (pruning, open stands), we fitted age-diameter dynamic models for the whole dataset (115 trees). These models can be applied to any tree of known age. They are formulated as shown in Table 1, but we add the subindexes ‘d’ or ‘2’ to distinguish that they are fitted for the whole dataset either expanded by density (‘d’) or not (‘2’).

(iii) *Tree diameter age-independent dynamic growth models*: in age-independent formulations (Tomé et al. 2006), parameters a and/or b were first expanded by density. We did not expand the models parameters with climate or soil variables because we did not have soil analyses and climate was homogeneous through the study area. Finally, we fitted ‘pseudo-age independent’ models expanding the same model parameters by density and the previously defined site index. Expansion of the model with the defined site index allowed us to test its validity and discuss our results with Tomé et al.´s. Age-independent models were derived from Hossfeld and Korf base models: T1, T2 and T3 are models expanded only by density (age-independent) while T4s is expanded by site index and T5s by site index and density, as follows:

a. Hossfeld IV Models, including T1, T2, T4s and T5s, were expansions from the expression:

$$y_2 = \frac{\left(\sqrt[c]{\frac{y_1 \cdot b}{(1-a\cdot y_1)}} + dif\right)^c}{b + a\cdot\left(\sqrt[c]{\frac{y_1 \cdot b}{(1-a\cdot y_1)}} + dif\right)^c};$$

Particularly, a, b and c are expanded as: in T1, b=(b_1·density); in T2 a=(a_1/density) and b=(b_1·density); in T4s, b=(b_{S1}/SI) and a = (a_{S1}·SI); and in T5s b=((b_{S1}/SI)+b_{d1}·density) and a=((a_{S1}·SI)+(a_{d1}/density)). a_{S1}, a_{d1} b_{S1} and b_{d1} are parameters. The projection length (‘*dif*’) is the number of years between the known diameter and the one to be predicted. The site index SI is defined by the potential growth models expressed in cm (see Results and Discussion).

b. Korf age independent equations:

$$y_2 = a\cdot\exp\left(-b\cdot\frac{1}{\left(\left(\frac{-b}{\log(y_1/a)}\right)^{1/c} + dif\right)^c}\right);$$

used in model T3, with b=(b_1·density).

The following statistics were used to compare models:

Table 2. Age dependent potential growth (25 series) estimation and evaluation goodness of fit statistics for the best candidate models (ADA and GADA). $DBHwb_{350}$=DBH without bark predicted at the age of 350 years in cm for site class I. The asymptote is also calculated for class I. MBias=residual mean bias; RMSE=residual root mean square error; AICd=Akaike´s information criterion differences; EF=efficiency; Adj. R^2=adjusted R^2; MBias=Mean residual error (bias).

Id	Estimation			Model Evaluation (jack-knife)					
	RMSE (cm)	R^2	AICd	MBias (cm)	RMSE (cm)	EF	AICd	$DBHwb_{350}$ (SI=I; cm)	Asymptote (SI=I; cm)
E1	0.7890	0.9967	32.0	0.3593	2.5445	0.9654	47.2	88.5	104.6
E2	0.7646	0.9969	0.0	0.1899	2.4496	0.9679	8.5	81.2	95.6
E3	0.7703	0.9968	7.6	0.0716	2.7467	0.9596	124.8	105.9	133.3
E4	0.7901	0.9967	33.3	0.4147	2.6169	0.9634	75.7	128.0	1679.9
E5	0.7687	0.9968	6.4	0.1189	2.6005	0.9639	68.2	141.5	1564.7
E6	0.7720	0.9968	9.8	0.2326	2.9601	0.9533	197.8	151.1	1944.7
E7	0.7896	0.9967	32.7	0.3804	2.5377	0.9656	41.4	74.8	75.1
E8	0.7745	0.9968	13.1	0.1082	2.7793	0.9586	139.9	96.2	98.8
E9	0.7773	0.9968	16.7	0.1129	3.2070	0.9450	282.2	104.2	107.4
E10	0.7906	0.9967	33.9	0.4047	2.5412	0.9655	45.8	71.2	71.3
E11	0.7666	0.9969	2.6	0.2468	2.4291	0.9685	0.0	67.1	67.1

- Root mean square error: $RMSE = \sqrt{\frac{\sum_{i=1}^{n}(est_i - obs_i)^2}{n-p}}$,

Where: est=estimated values; obs=observed values; n=number of observations; p=number of parameters, when calculating RMSE for a fitted model, and p=1 when calculating RMSE for an age or diameter class. To obtain relative RMSE we divided the previous expression by the mean observed DBH: $RMSE(\%) = 100 \cdot \left(\frac{RMSE}{\overline{Y}}\right)$

- Coefficient of determination (estimation) or efficiency (validation):

$$R^2 \approx EF = 1 - \frac{\sum_{i=1}^{n}(est_i - obs_i)^2}{\sum_{i=1}^{n}(obs_i - \overline{obs})^2}$$

- Mean residual (bias): $Bias = \frac{\sum_{i=1}^{n}(est_i - obs_i)}{n}$
- Akaike´s information criterion differences (AICd) (Burnham and Anderson, 2004): $AICd = n\ln\overline{\sigma}^2 + 2k - \min(n\ln\overline{\sigma}^2 + 2k)$, where $\overline{\sigma}^2 = \frac{\sum_{i=1}^{n}(Y_i - \overline{Y_i})^2}{n}$.

The asymptotic behaviour and DBH at 350 years ($DBHwb_{350}$, used as a ‘naïve’ estimate of maximum potential diameter, rather than the asymptote) were also used as a criterion for model selection, comparing it with the highest diameter values found in the literature. The largest trees reported in the literature for *Q. ilex* do not usually exceed 120 cm in DBH, although it is possible to find exceptions that reach almost 150 cm (DGB 1999). As we lacked an independent data set for validation purposes, and despite some authors consider that crossvalidation usually reports the same information as fitting with the whole data set (Kozak and Kozak, 2003), we carried out a cross-validation (jack-knife) to each model. To do so the models were fitted n times (being n either the number of plots for ‘potential models’ or number of trees for the rest) for n fitting data sets obtained from setting aside one plot/tree each time. Then, the prediction residuals were calculated for the observations split from the fitting dataset obtaining a set of prediction residuals from the n fits to calculate the validation statistics (Myers 1990). Finally, to test for significance in the selected age-diameter general model between expanded and non-expanded, we used the Lakkis-Jones test: $L = \left(\frac{SS_f}{SS_r}\right)^{m/2}$, where SS_f and SS_r are error sum of squares for full and reduced models respectively, m=total number of trees. -2·ln(L) converges to a χ^2 distribution (Khattree and Naik 1995).

RESULTS

The mean DBH with bark from the 115 trees included in our sample was 30.8±13.0 cm, ranging from 10.3 cm to 68.4 cm. The mean age was 89±28.6 years, corresponding to estimated tree ages from 26 to 175 years old. Mean tree height was 6.3±1.8 m (maximum by plot 8.3±2.3 m), mean stem height 2.1±0.3 m and mean crown diameter 6.4±2.3 m. The thickest tree (68.4 cm) was 92 years old and had a mean crown diameter of 14.4 m, also the largest in the sample. It averaged 0.390 cm/year in diameter, while the total mean annual growth for all samples was 0.175 cm.

Table 3. Parameter estimates and goodness of fit statistics for the age dependent models for 115 trees (parameters expanded and non-expanded by density). Estimation statistics were calculated using the weighted residuals. In E3d: $b=(b_1+b_d \cdot \text{Density}) \cdot X$; in E5d: $b=(b_1+b_d \cdot \text{density})+(1/X)$;

Id	Estimation			Model evaluation (jack-knife)			
	RMSE (cm)	R^2	AICd	MBias (cm)	RMSE (cm)	EF	AICd
$E3_2$	0.7234	0.9926	8.5	0.0670	2.6532	0.9508	89.2
$E5_2$	0.7217	0.9927	0.0	-0.0492	2.5887	0.9532	0.0
$E9_2$	0.7327	0.9924	54.4	0.0827	3.0584	0.9347	603.3
E3d	0.7234	0.9926	10.3	0.0767	2.6787	0.9499	122.7
E5d	0.7217	0.9927	1.7	-0.0386	2.6031	0.9527	19.1

Holm oak age-dependent diameter potential growth

In this study (Table 1; Table 2) we have only shown the best models (i.e., the most parsimonious, with a 'logical' graphical behaviour) from many different parameterizations tried. The AR(2) error structure eliminated serial autocorrelation (Figure 1), and the fitting residuals in potential growth models were homocedastic (Figure 2A). All models had similar statistics, differing in the behaviour in the highest DBH classes. In the fitting step, the estimated RMSE and R^2 were similar in all models (the differences in RMSE are ±0.01 cm, smaller than the measuring error), and AIC pointed in the same direction as RMSE (Table 2). The validation statistics showed that ADA formulations were slightly biased compared to GADA formulations, whereas RMSE and EF were similar among models, with small differences around ±0.1 cm in RMSE. E11 was the best model in terms of RMSE and EF both in the estimation and prediction steps. However, its asymptote and diameter at 350 years were too low to be considered as the best model. Formulations derived from Richards and Weibull functions had very low asymptotes and predicted diameters unrealistic in the highest diameter classes, whereas models derived from Hossfeld and especially Korf base models best predicted diameters in the highest classes (DBH at 350 years, Table 2). Among GADA, E3 and E5 were the best: E5 was slightly superior in the goodness of fit statistics (the difference in AIC was greater than 10. Burnham and Anderson 2002) and had the advantage of being polymorphic with multiple asymptotes, in opposition to E3, which is anamorphic (Cieszewski 2002; Cieszewski et al. 2006). The predicted DBH_{350} is in accordance with the National Forest Inventory (DGB 1999).

The final model expression was:

$$DBH_2 = \exp(X_0) \cdot \exp(-(14.77073 + (-37.6516 / X_0)) \cdot t_2^{-0.237368}),$$

where $X_0 = 0.5 \cdot (14.77073 \cdot t_1^{-0.237368} + \ln(DBH_1) + F_0)$, (1)

and $F_0 = \sqrt{((14.77073 \cdot t_1^{-0.237368} + \ln(DBH_1))^2 + 4 \cdot (-37.6516) \cdot t_1^{-0.237368})}$.

(b_1: SE=2.374, $p>|t|$ <0.001; b_2: SE=16.415, $p>|t|$ <0.022; c: SE=0.027, $p>|t|$ <0.001)

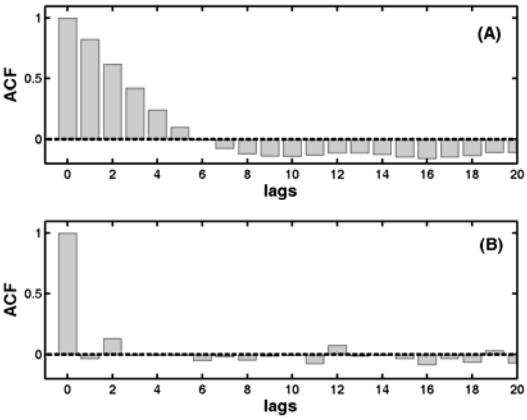

Figure 1: Autocorrelation function (ACF) of: (A) E5 residuals (i.e. predicted-observed) for the 25 plot series without taking into account autocorrelation; (B) E5 residuals for the 25 plot series with AR(2) error structure.

From (1) we defined a site index based on diameter growth. Figure 3A suggested the selection of site index from the ages of 30 to 75-80, as after 80 the number of observations decreased significantly. There are different opinions upon whether reference ages should be greater or lower (Álvarez et al. 2004). We considered 80 years the optimum, as it was the highest age where the error was small and the number of observations was still around 400 observations (Figure 3A), and for comparable purposes with the site index selected for *Quercus suber* in Sánchez-González et al. (2005). The four site indexes corresponded to 50 cm (class **I**), 41 cm (class **II**), 32 cm (class **III**), and 23 cm (class **IV**). The individual plots to compare the behaviour of site index in different age classes (Figure 3B), which remained almost constant over the age of approximately 30 years, they also demonstrate that the indexes selected were appropriate. The original data of the 25 series and the selected potential model are shown in Figure 4A. The error in prediction was around 7% in 'dominant' trees from 10 to 45 cm (Figure 5). Predictive error followed the typical increase in the smallest classes and the proposed model was unbiased in all diameter classes except for trees over 55 cm, because of lack of data from trees over that size (Figure 5). As expected, the longer the prediction interval, the larger the error in prediction (Figure 6). The mean predictive error was lower than 15% for lags shorter than 45 years, and only 3.5% for 5 years.

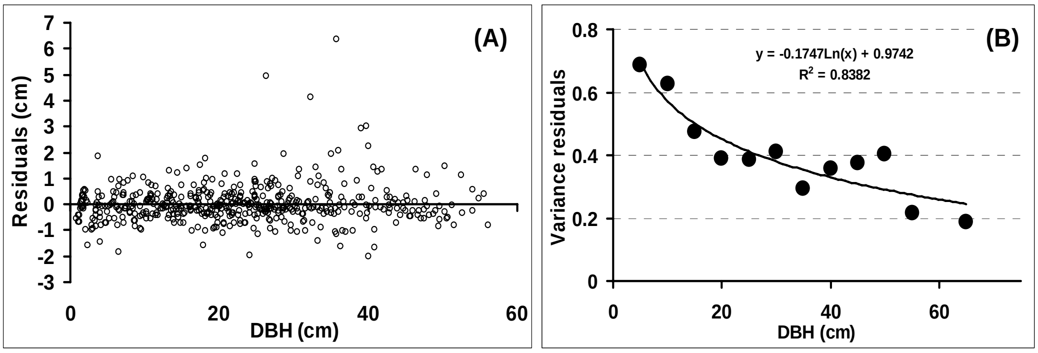

Figure 2: Estimation residuals (predicted-observed) versus predicted DBH as an illustration of potential heterokedasticity for E5 growth model: (A) E5, for 25 series; and (B) $E5_2$ for 115 series, variance for each diameter class and estimated variance function (i.e. weigth , w_i) applied.

Holm oak age-dependent diameter growth in relation to management

As the dataset was different (115 trees instead of 25 series), we compared again some of the best models (GADA) used for potential growth (Table 1) expanding them by density. We did not compare any Weibull models as they were very similar to Richards but with lower, unrealistic predictions in the highest DBH classes. The residuals were heterocedastic, therefore a weighting factor was applied in the regression (see Figure 2B). Again GADA $E5_2$ formulations from the Korf base model were the best ($E5_2$ and E5d, Table 3). When comparing E5d (model with parameter b expanded by density) with $E5_2$ (formulation without expanding parameters), E5d did not increase significantly the information explained by $E5_2$ (Table 3). This was confirmed when we farther tested the significance of the expanded parameter: the Lakkis-Jones test comparing $E5_2$ and E5d was not significant (χ^2 = 0.075; p=1.000). Yet when plotting the non-expanded model $E5_2$ in Figure 4B, the fastest growing trees occurred in plots with density below 100 trees/ha (darkest thin lines).

Table 4: Age independent holm oak diameter growth dynamic models with parameters expanded by stand density (T1, T2, T3) and/or site index (T4s and T5s). Estimation statistics were calculated using the weighted residuals.

Id	Estimation			Model evaluation (Jack-knife)			
	RMSE (cm)	R^2	AICd	MBias (cm)	RMSE (cm)	EF	AICd
T1	0.6762	0.9927	900.0	-0.4007	4.7340	0.8333	6240.8
T2	0.6781	0.9927	981.2	-0.5587	4.6274	0.8407	5549.2
T3	0.6856	0.9925	1317.7	-0.4495	4.7475	0.8323	6327.3
T4s	0.6632	0.9930	307.7	-0.0742	4.0366	0.8788	1400.5
T5s	0.6565	0.9931	0.0	-0.1413	3.8545	0.8895	0.0

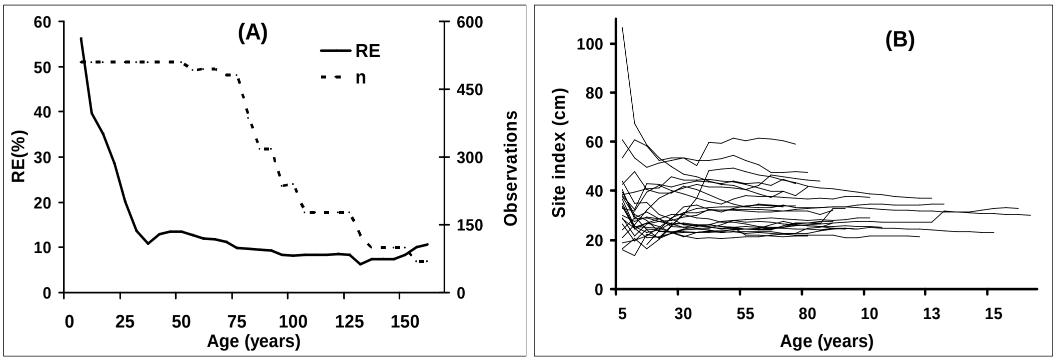

Figure 3. (A) Mean relative error (RE) in DBH prediction and sample size (n=number of observations) according to different choice of reference age for E5 by 5 years classes; (B) Consistency of site index over age estimated using E5 for the 25 series.

The model finally selected (GADA E5, unique for all trees regardless of density) has the expression:

$$DBH_2 = \exp(X_0) \cdot \exp(-(8.310178 + (1/X_0)) \cdot t_2^{-0.264597}),$$

where $X_0 = 0.5 \cdot (\mathbf{8.310178} \cdot t_1^{-0.264597} + \ln(DBH_1) + F_0)$

and $F_0 = \sqrt{((\mathbf{8.31017} \cdot t_1^{-0.264597} + \ln(DBH_1))^2 + 4 \cdot t_1^{-0.264597}})$ (2)

(b_1: SE=0.118, p>|t| <0.001; c: SE=0.016, p>|t| <0.001)

The residual error increased compared to models built for the 25 series (Table 3; Figure 5; Figure 6), as might be expected from the inclusion of suppressed trees. Still the error is acceptable (circa 10% for trees 10<DBH<50 cm), increasing in the smallest and the largest diameter classes in the same way as in potential models. Again, the longer the prediction interval the larger the error, the mean predictive error was smaller than 15% for lags shorter than 25 years, and 5.2 % for 5 years (Figure 6).

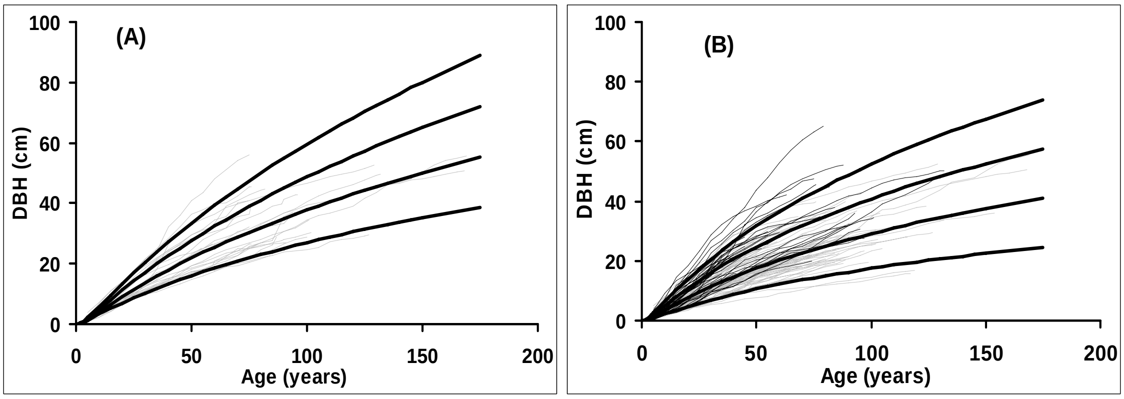

Figure 4: Age-dependent dynamic models: (A) GADA E5 (Korf base model) potential growth curves (25 series) for site indexes 50, 41, 32 and 23 cm at a reference age of 80 years. (B) GADA $E5_2$ (Korf base model) diameter growth curves, 115 trees; the curves where graphed for DBH 45, 35, 25 and 15 cm at 80 years; black thin lines correspond to trees growing in density≤100 trees/ha, whereas grey thin lines to trees growing in density>100trees/ha.

Holm oak diameter growth in relation to management: age-independent dynamic models

Age-independent models shown were only derived from Hossfeld IV and Korf base models, as formulations from these base models behaved better than Richards'. As in general models for all trees, residuals were again not homocedastic (Figure 7), therefore a weighting factor was applied when fitting the models. Age-independent models based on the Hossfeld growth function were the best (Table 4).

T1, T2 and T3 were only expanded by density, thus they were really independent of age. Among these three models T2, an age-independent Hossfeld IV model with a inversely related and b directly related to quantitative density (greater asymptotes in low densities, Figure 8)), was best in the validation statistics (Table 4). Its expression is:

$$DBH_2 = \frac{(F+dif)^{1.007868}}{(0.023114\cdot density)+\left(\frac{0.465367}{density}\right)\cdot(F+dif)^{1.007868}}$$, with (3)

$$F = t_1 = \sqrt[1.007868]{\frac{DBH_1\cdot(0.023114\cdot density)}{(1-\left(\frac{0.465367}{density}\right)\cdot DBH_1)}}$$, and dif=projection length (i.e. T_2-T_1)

(a_1: SE=0.010, p>|t| <0.001; b_1: SE=0.001, p>|t| <0.001; c: SE=0.088, p>|t| <0.001)

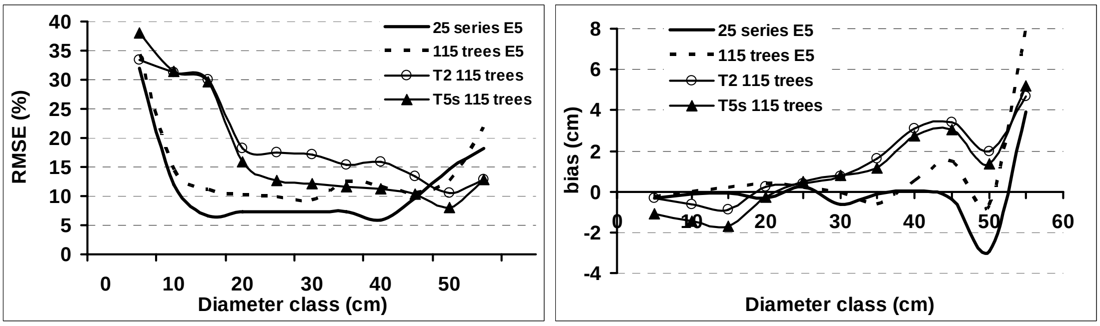

Figure 5. Relative mean root square error and bias in diameter prediction by diameter class for E3 (solid line) and $E3_2$ (dashed line), T2 (white circles) and T5s (dark triangles).

Contrary to GADA age-dependent models, age-independent models only expanded by density were slightly biased in the validation phase, and their RMSE increased 80% as compared to the age-dependent models (Table 4). In figures 5 and 6 the relationship between the predicted errors and diameter class or lag of interval prediction are shown: the lag interval below 15% error was 20 years, the error increasing as usual with lag length.

When expanding the age-independent formulations also by site index, the error greatly decreased compared to real age-independent models T1, T2 and T3. In addition, models T4s and T5s were almost unbiased (Table 4; Figure 5; Figure 6). The inclusion of the site index reduced in T5s the mean residual by 17% and the mean bias to around 75% compared to age-independent T2. The lag of prediction with error below 15% increased to 25 years (Figure 6). The model (T5s) expression is:

$$DBH_2 = \frac{(F + dif)^{0.859611}}{(0.002797 \cdot density + 31.4296 / SI) + \left(\left(\frac{-0.06588}{density}\right) + 0.000123 \cdot SI\right) \cdot (F + dif)^{0.859611}} \text{, with}$$

$$F = \sqrt[0.859611]{\frac{DBH_1 \cdot (0.002797 \cdot density + 31.4296 / SI)}{(1 - \left(\left(\frac{-0.06588}{density}\right) + 0.000123 \cdot SI\right) \cdot DBH_1)}} \qquad (4)$$

dif=projection length, SI= site index in cm.

(a_1: SE=0.000, p>|t| <0.001; a_{d1}: SE=0.0275, p>|t| <0.017; b_1: SE=1.426, p>|t| <0.001; b_{d1}: SE=0.000, p>|t| <0.001; c: SE=0.0084, p>|t| <0.001)

Both models (3) and (4) are polymorphic and with variable asymptotes for different densities and site indexes (Figure 8).

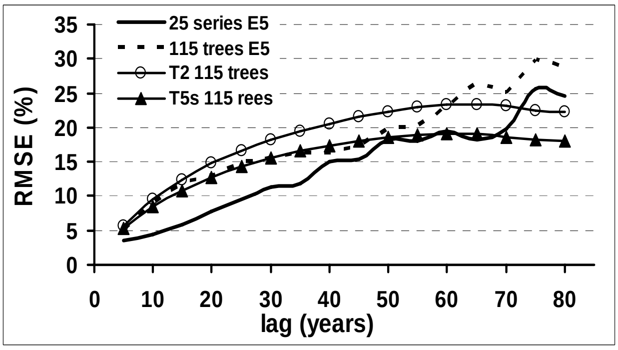

Figure 6. Relative root mean square error (RMSE, %) by lag of prediction for E3 (solid line) and $E3_2$ (dashed line), T2 (white circles) and T5s (dark triangles).

DISCUSSION

This study is the first attempt to model diameter growth in *Quercus ilex* tree-like woodlands. Fitting growth models to this species in this ecosystem is challenging for its particular management and uncertain history. Despite the versatility of the species to thrive in a variety of climates and soils, the historical isolation of tree formations to marginal soils has probably reduced the presence of the species to the worst soil conditions. Nevertheless, it is very likely that trees analysed exhibit near maximal growth for *Q. ilex* in this area as humans, who probably selected the best trees, enforced the current structure, with low tree densities. Holm oak has been traditionally considered a slow-growth species (Ibáñez et al. 1999). In our results mean growth is slightly slower than that of other Mediterranean oaks such as *Q. suber* (Sánchez-González et al. 2005; Tomé et al. 2006) and *Q. pyrenaica* (Adame et al., in press). Diameter growth is expected to be greater in low-density agroforestry systems than in forests (Balandier and Dupraz 1999). The young age range found in this study, and in other analyzed samples not included here (partly described in Plieninger et al. 2003), where the maximum age was also below 200 years, agree with the hypothesis that most dehesas originated since the early XIXth century, mostly after the 1850´s and the first half of the XXth century (Manuel and Gil 1999; Pulido et al. 2001; Martín Vicente and Fernández Alés, 2006).

Formulations derived from power decline base models (Korf and Hossfeld) rather than exponential decline (Richards, Weibull when c>1 [Kiviste et al. 2002]) best described diameter growth in all cases, as stated in the literature (Zeide 1989; Zeide 1993; Shvets and Zeide 1996). The analysis of 'potential' growth describes how species grow and provides tools that can be applied in system models (Porté and Bartelink 2002). What we consider here as 'potential growth' could be more accurately denominated 'maximum diameter growth under traditional 'dehesa' management'. As in other previous studies, GADA formulations had as slight better fit than simpler ADA (e.g. Cieszewski 2002; Barrio-Anta et al. 2006). The model selected (E5), polymorphic and with variable asymptotes GADA formulation derived from the Korf growth function fit the data with a reduced RMSE of 2.6 cm and 7% in DBH classes from 10 to 45, coinciding with the diameter range within which most trees of the 'dehesas' are found (Pulido et al. 2001). The errors yielded (Tables 2, 3 and 4; Figures 5 and 6) are in accordance with site dynamic growth studies for other tree species (e.g. Barrio-Anta et al. 2006; Diéguez-Aranda et al. 2006).

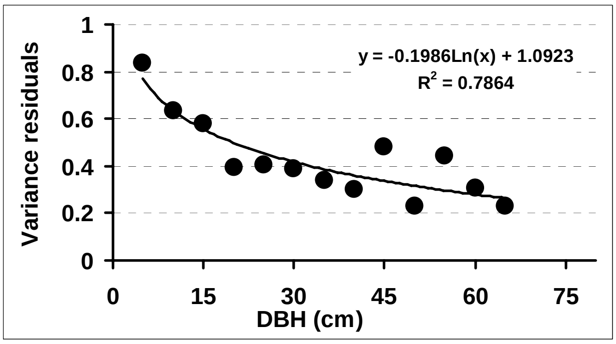

Figure 7: Estimation residuals (predicted-observed) versus predicted DBH as an illustration of potential heterokedasticity for age independent formulations. Residual variance by diameter class and estimated variance function (i.e. weigth , w_i) applied in T2 and T5s.

The wide range of densities included in our plots makes possible the comparison between 'potential models' and the effect of density in general models for all trees regardless of their social position within the stand. However density was not included in the models, the most open stands coincided with the most productive (Figure 4B); the reason could be that humans thinned the most productive sites more intensively and in turn, this has produced better pastures. Thus the positive effect of low density and fertile sites is likely to be combined in these anthropic woodlands. The small increase in the error with respect to 'potential growth' models and the similarity between the model for 25 series and the model for 115 trees would support the hypothesis of codominance of most trees. This could have been expected as only 23.5% of trees had been considered 'suppressed' in the graphical analysis, meaning that the five trees analyzed per plot generally exhibited very similar growth. Our results support the use of a single model for all densities and for any tree in the system as the error does not increase significantly. An average tree would reach circa 15 cm DBH after 30 years, which is in accordance with the approximate age suggested for cattle exclusion on regenerated sites (San Miguel 1994). This mean tree would reach around 27 cm at 60 years and 35 cm at 90 years (see Figure 4B).

Model (2) can be applied to any tree in the system without defining dominance. However, accurately estimating tree age in holm oak is extremely difficult. This is the reason why we compared age-independent formulations (Tomé et al. 2006) to the previous age-dependent dynamic models. When expanding only by density, the models where slightly biased and increased the error except in prediction lags greater than 50-60 years, where age-independent models were better. Yet this increase was acceptable, especially bearing in mind the advantage of neglecting age. Additionally, the highest errors in models (3) and (4) coincided with the smallest and greatest diameter classes. This is a normal feature in growth models that results from a lack of data in the largest classes and worse predictive ability in the youngest ages. When expanding also by site index (model [4]) the error significantly decreased, with a similar behaviour to the general age-dependent model (2), especially when analyzing the mean error by lag of prediction. In both models, the smallest error was again centred in diameter classes from 20 to 50 cm (Figure 5), which are the most abundant in the system today (Pulido et al. 2001). In T5s, density explained less variance than site index, which is in accordance with the non-inclusion of density in $E5_2$. Although T5s is not totally 'age-independent', as site index must be estimated, it enabled us to test the validity of the defined site index and compare our results to Tomé et al. (2006) original paper. The aforementioned increase in error with respect to age-dependent dynamic models found in our analysis is not totally compatible with results of Tomé et al (2006) for *Quercus suber* age-independent formulations in a similar system. In that study, age-independent models had a slight better fit than age-dependent ones. Nevertheless, we consider our results reasonable: when significant covariates are added to an equation ('age' in this case) the error is likely to decrease and the goodness-of fit increase. In addition, T5s is likely to improve if soil and climatic data were available. Although we believe it is unlikely to explain such a great difference in the increase in error with respect to that study, the increase in error found in our models might result from the use of a site index derived from diameter rather than from height. Acknowledging the previous shortcomings and, from the tremendous advantage of neglecting age, we believe the error yielded is acceptable in the middle diameter classes, which are the most common in these woodlands, as discussed. Age-independent models are an alternative to model growth in tree species that do not form annual rings, including many species in the tropics (Verheyden et al. 2005) and can be applied to other agroforestry systems, particularly in Mediterranean climates (e.g. Jackson et al. 1990; Ovalle et al. 1990), and to uneven-aged stands (Tomé et al. 2006).

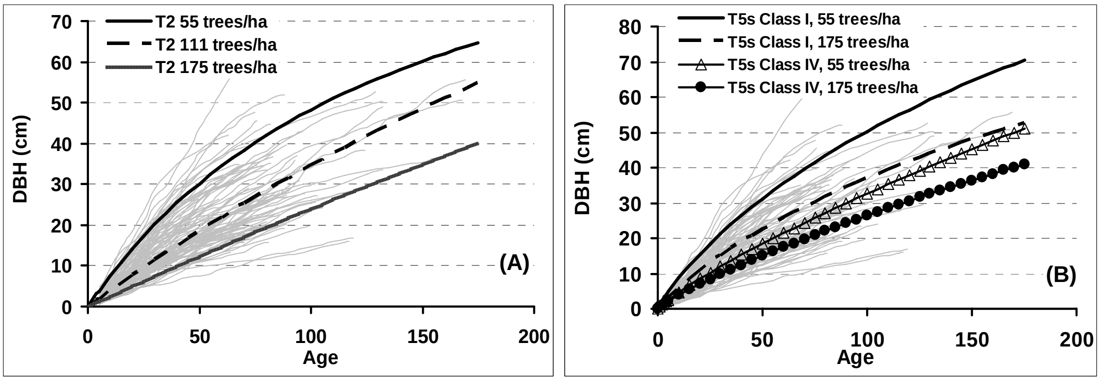

Figure 8. Age independent models: (A) T2 for densities 55, 111 and 175 trees/ha; (B) T5s for site index 50 (Class I) and 23 (Class IV), densities 55 and 175 trees/ha.

The site index based on diameter growth proposed was significant in T5s. This would support the definition of site indexes based in diameter growth in open stands. It is supported by an ecological basis, if we accept that when canopies are competing for light, trees tend to focus growth in height, whereas isolated trees focus growth in increasing their canopies and stem diameter (Hasenauer 1997). Therefore, in open stands we could consider diameter growth as potential at least in terms of competition for light. Finally, the fact that current density was included in age-independent life-span models might reflect the human influence upon these systems: the current woodland structure and density was modified decades ago, the stands are static except for tree death, which is gradually reducing the tree stock. In this study we offer several different possibilities to model diameter growth in *Q. ilex* woodlands that adapt to the particular features of low density stands and tree species where age estimation is problematic.

In this study we offer different possibilities to model diameter growth in *Q. ilex* open woodlands. It would be interesting to study the difference comparing the implementation of a site index based on a general equation for all trees with a site index based on potential growth series, particularly when soil and climate variables were available. Whether these models, based on past growth, are appropriate to predict diameter under different future climatic scenarios is something that should be studied.

CONCLUSIONS

The ‘potential growth’ equations were unbiased and with an error of around 7% in the most abundant diameter classes encountered in the system, modelling the data and the asymptotic growth tendency of the species very well. The general age-dependent model selected, applicable to any tree within any stand density knowing its age, did not increase the error (which was around 10% in DBH from 10-50 cm) much compared to the ‘potential’ models. Density did not provide much information in the age-dependent models, whereas in age-independent models, in spite of being significant, the residual errors decreased when the site index proposed was used to expand the parameters. The inclusion of the defined site index in the models increased the accuracy of age-independent formulations, although it added the same limitation that age must be estimated, in order to define the site index. Age-independent models including site index were similar to general age-dependent models in the most abundant diameter classes in the system (20-55 cm). The discussion of age-independent dynamic models offers managers and researchers of other agroforestry systems and tropical forests new alternatives for modelling dynamic growth in highly altered tree systems and in species or stands where the determination of age is cumbersome.

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ANEXO III

Gea-Izquierdo G, Cañellas I.

Analysis of holm oak intraspecific competition using Gamma regression. En revision.

ANALYSIS OF HOLM OAK INTRASPECIFIC COMPETITION USING GAMMA REGRESSION

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ABSTRACT

Analysis of plant competition is a major issue in ecology and forestry, as it influences plant growth and plant-environment interactions. Different distance dependent and distance independent competition indices have been used in forestry applications. Competition is expected to be lower in the sparse tree stratum of open woodlands and agroforestry systems than in closed forests. We have analyzed competition in open woodlands of *Quercus ilex* in the Iberian Peninsula by studying a 10 year diameter growth increment from collected samples and from consecutive National Forest Inventories. Density was the competition index selected in all models, outperforming more complex distance dependent indices. The models, showed that competition is playing a role in growth, but that the covariate most correlated with growth is age or, DBH as a surrogate of age. Therefore, below-ground competition is likely to be limiting tree growth, but below-ground competition is lower in open woodlands compared with denser forests, and thus potential growth (which is strongly linked to age) is almost expressed. To fit parsimonious models we used Gamma regression instead of Gaussian regression. Our results showed that modelling growth with the Gamma probability distribution resulted in better models compared to classic log-transformed Gaussian linear models. Gamma models offer a great potential for many forestry applications.

Keywords: dehesa, *Quercus ilex*, distance dependent, diameter increment growth, generalized linear model.

INTRODUCTION

There are many studies analyzing competition among trees in closed forests (e.g. Biging and Dobbertin 1995; Canham et al. 2006), where density is usually greater than in agroforestry systems and open woodlands. All agroforestry systems have a low-density woody stratum, where trees are likely to compete for below-ground resources with each other and with the herbaceous and/or shrub layers. Below-ground interactions are complex and poorly understood. In spite of this potential source of competition, low density trees are generally thought to exhibit free growth, which in traditional forestry would be considered as potential growth (Hasenauer 1997). Diameter increment is mostly related to three factors: age, site index (as a surrogate of fertility) and competition (Lessard et al. 2001). Competition can be defined in various ways, emphasising different variables. Bearing in mind that competition is never totally symmetric or asymmetric, competition can be broadly classified as either asymmetric or symmetric. These classifications are usually applied to competition for light, and soil resources - namely nutrients and water (Schwinning and Weiner 1998). The most commonly-used competition indices assume that there is a relationship between the size and proximity of competitor trees and the distribution of resources (Larocque 2002). Tree competition indices used in forestry can be generally classified as distance dependent or distance independent. Distance dependent indices can be further sub-classified as: area overlap indices, point-density indices, distance-weighted size ratio indices, and area-potentially-available indices (Tomé and Burkhart 1989; Biging and Dobbertin 1995; Larocque 2002). The search radius to decide whether a neighbour is competing or not, can be a crucial issue (Biging and Dobbertin 1992). In crowded systems, asymmetric competition for light is in general the primary cause of size inequality. In agroforestry systems the tree stratum is not crowded, therefore symmetric competition (soil-moisture) is likely to be the most important competitive factor affecting tree growth. The herbage component in agroforestry systems is very much affected by tree density and hence asymmetric competition for light; this is particularly evident where management regimes include pruning.

Many authors' results suggest that more complex distance dependent indices are not better than distance independent indices (e.g. Martin and Ek 1984; Biging and Dobbertin 1995) although there are exceptions (e.g. Mailly et al. 2003; Stadt et al. 2007). Often indices calculated from crown features are very much correlated with growth (Biging and Dobbertin 1995; Miina and Pukkala 2000), but those cannot be reliably calculated in pruned stands, common in some agroforestry systems. The conclusion from the numerous studies analyzing competition is that there is no superior competition index (Tomé and Burkhart 1989; Biging and Dobbertin 1995) but, depending on the stand structure and particular environment, certain indices will be better than others. Therefore: (i) each species could require a different index; (ii) each stand structure could require a different index; (iii) variation between datasets has a large influence on whether an index is more or less correlated with growth. Competition among species is not symmetrical, with different species competing distinctly (Canham et al. 2006). Competition can also influence the way trees respond to climate (e.g. Cescatti and Piutti 1998; Andreu et al. 2007), thus analysis of competition is interesting not only from a commercial point of view, but also for conservation.

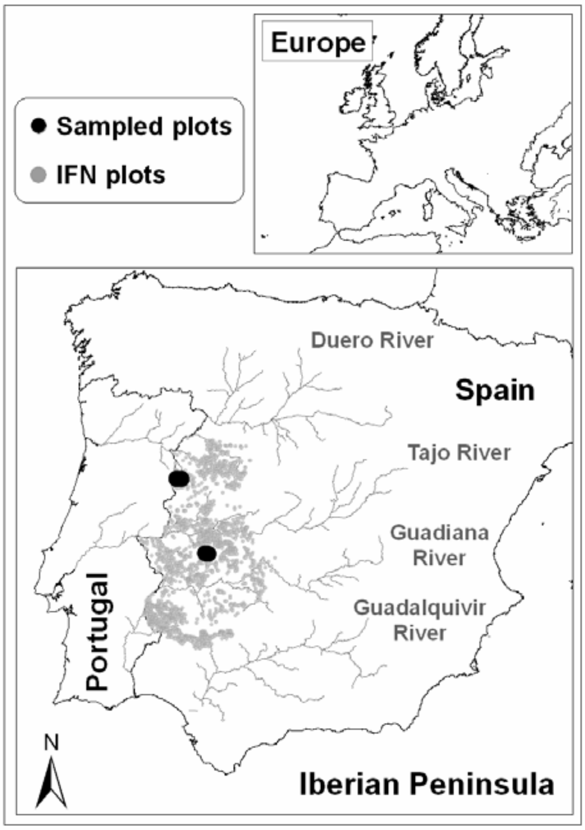

Figure 1. Location of the study plots.

There are a wide variety of different models in the literature to describe diameter growth, which is a key variable in forestry modelling (Porté and Bartelink 2002). Most individual tree diameter models used can be ascribed to two categories, namely empirical or semi-empirical (Vanclay 1994). Examples of empirical models can be found in Miina (1993), Andreassen and Tomter (2003) and Mailly et al. (2003); while semi-empirical examples are found in Biging and Dobbertin (1995), Canham et al. (2006) and Stadt et al. (2007). Empirical models are usually linear in their parameters, although usually linearity is achieved after some transformation (most often logarithmic) to mimic the non-linear, sigmoid shape of plant growth (Wykoff 1990; Schwinning and Weiner 1998). Semi-empiric models have the advantage that they have their foundations in biological theory, but they require the estimation of potential growth, which is difficult and adds an extra source of error (Wykoff 1990; Vanclay 1994). Semi-empiric models are more complex than empirical models because they are non-linear. In addition, Martin and Ek (1984) and Sánchez-González et al (2006) did not detect an improvement in accuracy using semi-empirical models. Other statistical methods (Generalized Additive Models [GAM], Classification and Regression Tree Analysis [CART], and Artificial Neural Networks [ANN]) used in ecological modelling (Guisan et al. 2000) have been used for modelling stand characteristics in Inventory data (Moisen and Frescino 2002). Generally, they were not an improvement on classic linear models, but we do not know of any study using them to model diameter increment. Generalized linear models (GLM) are a class of linear models that relax the Gaussian assumption. Therefore, GLMs are able to fit different shapes of data, including data with heterogeneous variances and probability distributions such as the Gaussian (normal), Poisson, Gamma and Negative Binomial (McCullagh and Nelder 1989). Poisson, and more specifically, Gaussian models are frequently used in forestry and ecology, but Gamma and Negative binomial models, while been used in other biological sciences, are not yet very common in studies of ecology and forestry (e.g. Guisan and Zimmermann 2000; Gea-Izquierdo et al. 2007; Salway and Wakefield 2007).

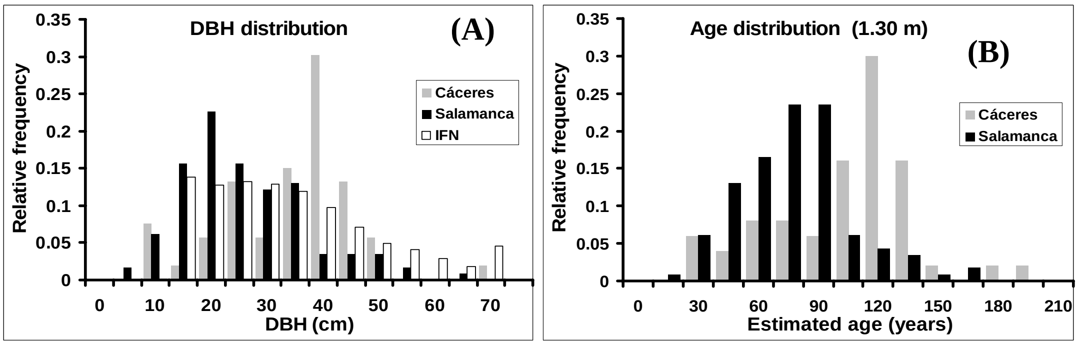

Figure 2. (A) Diameter distribution of plots: (i) Cáceres plots in grey bars; (ii) Salamanca plots in black bars; (iii) IFN plots in white bars. (B) Age distribution at 1.30 m.

Agrosilvopastoral systems are one special type of agroforestry system, these include the *Quercus* sp. dominated open woodlands of West Iberia (called ‘dehesas’ in Spain) that cover more than 3,000,000 ha. *Quercus ilex* L. (holm oak) is the most common tree species in the ecosystem and probably the most important and widespread tree species in the Mediterranean Region (Barbero et al. 1992). These oak stands are not suitable for traditional, intensive forestry because of the poor sandy soils and Mediterranean variable dry climate in which they thrive. The origin and history of the ‘dehesas’ is complex, the specific management applied through time has modelled the landscape, resulting in the low density, open tree stratum encountered today. As in other agroforestry systems, trees are regularly pruned (San Miguel 1994).

The objectives of this study are to: (i) analyze whether it is true or not that holm oaks in this system exhibit free growth, and to what extent competition affects diameter growth; (ii) discuss whether distance dependent indices are better than distance independent indices in this system; and what maximum radius should be used in distance dependent competition indices, as an estimate of the distance within which competition may occur; (iii) compare different empirical models and discuss whether modelling growth with Gamma distributions results in better models than classical transformed Gaussian distributions; (iv) check the possibility of using the National Forest Inventory (IFN) for holm oak growth modelling, as these data are a cheap (for the user) and interesting source of information (Moisen and Frescino 2002).

MATERIAL AND METHODS

Study area and data

Sampled data

The two directly sampled study areas were typical ‘dehesa’ with acidic bedrock (granites, slates, cuarcites) under a continental-mediterranean climate with mean annual precipitation ca. 600 mm and summer drought. Mean annual temperatures at the study areas were 16.0ºC at Cáceres (southern most sampled area), and 13.5ºC in Salamanca. Sampled data were collected from 37 variable radius plots generally including 10 trees: 25 plots in Salamanca (40º 37’ N, 6º 40’ W, 700 m a.s.l.) and 12 plots in Cáceres (39º 28’ N, 6º 11’ W, 393 m a.s.l. [Figure 1]). These plots were all included in different holm oak woodland belts clearcut to construct two freeways. For each of the 10 trees, we measured distance and azimuth to the centre of the plot, two perpendicular crown radii, total height and height to crown base, and two perpendicular diameters at 1.30 m (DBH). We sampled all holm oaks, including shrubs which, when calculating indices, were considered as competing trees having a DBH equal to that of a tree-like holm oak of equivalent crown. This assumption was made because there were no signs of pruning in recent years at Cáceres.

Table 1. Sample characteristics: DBH=diameter at breast height (1.30 m) in cm. BA=plot basal area (m^2/ha); Nn=Density in trees/ha; Age=estimated age in the base. *data from IFN3: plot radius=10 m, DBHtrees>12.5 cm, density<500 trees/ha.

	Ciudad Rodrigo				Cáceres				IFN*		
	DBH	Age	Density	BA	DBH	Age	Density	BA	DBH	Density	BA
Mean	28.9	88	129.9	9.5	39.6	116	45.6	6.5	36.8	70.0	5.7
CV (%)	38.8	32.3	29.2	41.5	33.1	31.4	44.3	36.9	44.6	110.5	64.1
Minimum	10.2	26	39.5	4.6	13.9	42	15.3	3.1	13.4	5.1	0.4
Maximum	68.4	175	210.4	18.0	96.8	212	87.3	10.6	108.2	489.6	31.4
n	115	110	25	250	53	46	12	12	2819	2062	2062

To estimate growth, the five central trees of each plot were pushed down with a bulldozer and sections at 1.30 m and at the base were collected. Data is likely to be slightly biased away from individuals with the widest diameters (and, hence, probably greatest ages) as the oldest and thickest trees tended to be rotten and only trees with at least one readable radius were included in the analysis. In total 168 trees, 115 from Salamanca and 53 from Cáceres, were included in the analyses (Figure 2). Annual ring width was estimated as explained in Gea-Izquierdo *et al*. (2008) and the sum of the period 1995-2004 (hereafter ‘$IncDBH_{10}$’) was used as the dependent variable. We considered bark growth to be negligible compared to DBH growth, and hence was not taken into account in the analyses. Covariates were calculated from plot attributes, site index (IS) from Gea-Izquierdo et al. (2008) and competition indices calculated as explained below (Table 1). Covariates analyzed included DBH^2, as growth is likely to be a paraboloid with an inflection point (Wykoff 1990).

Many competition indices are calculated from crown features, and it has been shown that some of them explain much of the variance in diameter growth (Biging and Dobbertin 1992, 1995). However, at our study areas, the tree pruning cycles could not be determined (each estate prunes following their own criterion) and therefore covariates including crown features are not reliable. Thus we only tested competition indices that do not depend on crown features, i.e. those based on distances, crowding and/or tree diameters. Crown competition is thought to be a minor issue in an open woodland ecosystem because crowns do not compete for light actively as in closed forests. Below-ground competition for water is more likely to be a principal growth limiting factor than crown competition for light or competition for nutrients, similarly to other Mediterranean ecosystems (e.g. Mayor and Rodá 1994; Ogaya and Peñuelas 2007). A total of 18 distance dependent and distance independent indices were studied (Table 2). The distance of influence (the distance within which neighbours are considered to be competing) was also studied; comparing fixed distances with relative distances (from 40 to 140 times the DBH). Density has not changed much during the last decades in the ‘dehesas’ (García del Barrio et al. 2004) and there were no signs of recent logging in the study area, so we assume that density was constant during the last 10 years.

Table 2. List of competition indices used in the study. The index I refers to the subject tree; j refers to a competitor; $dist_{ij}$=distance between i and j; BA= plot basal area; $Dmc = 2 \cdot \left(\sqrt{BA/\pi \cdot Nn}\right)$; n=number of trees in plot k; DBH_i=diameter at breast height of tree i; BA_i=basal area of tree i; r=search radius.

Index	Name	Expression	Reference
Distance Independent Indices			
CII1	Plot density (Nn)	n/plot area (in trees/ha)	
CII2	Plot basal area	$\sum_{i=1}^{n} \pi \cdot (DBH_i / 2)^2$	
CII3	ddg	DBH_i/Dmc	
CII4	Glover	$DBH_i^2 / \overline{DBH}^2$	Glover and Hool (1979)
CII5	BAL	$\sum_{j=1}^{n-1} \pi \cdot (DBH_j / 2)^2$ when $DBH_j>DBH_i$	
CII6r	Number of competitors within r meters (N_r)		Moravie et al. (1999) cited in Paulo et al. (2002)
CII7r	Number of competitors within r meters such that $DBH_j>DBH_i$		Moravie et al.(1999) cited in Paulo et al. (2002)
CII8r	Sum of size of trees within r metres	$\sum DBH_j$	Steneker and Jarvis (1963) cited in Paulo et al. (2002)
CII9r	Size ratio	$\frac{DBH_i}{\sum_{i=1}^{n} DBH_i}$	Daniels et al. (1986) cited in Paulo et al. (2002)
Distance Dependent Indices			
CID10	Clark-Evans	$\left(\sum_{i=1}^{n} \min(dist_{ij}) / n\right) / \left(2 \cdot \sqrt{Nn}\right)$ (Nn in trees/m^2)	Clark and Evans (1954)
CID11	Distance to nearest tree (NN)		Moravie et al.(1999) cited in Paulo et al. (2002)
CID12	Distance to NN such that $DBH_j>DBH_i$		Moravie et al.(1999) cited in Paulo et al. (2002)
CID13r	Size ratio proportional to distance	$\sum_{j=1}^{n} \frac{DBH_j}{DBH_i} \cdot \frac{1}{(dist_{ij}+1)}$	Hegyi (1974) cited in Biging and Dobbertin (1995)
CID14r	Size difference proportional to distance	$\sum_{j=1}^{n} \frac{DBH_j - DBH_i}{(dist_{ij}+1)}$	Moravie et al. (1999) cited in Paulo et al. (2002)
CID15r	Negative exponential size ratio	$\sum_{j=1}^{n} \frac{DBH_j}{DBH_i} \cdot \frac{1}{\exp(dist_{ij}+1)}$	
CID16r	Negative exponential weighted size ratio	$\sum_{j=1}^{n} \frac{DBH_j}{DBH_i} \cdot \exp[-(dist_{ij}+1)/(DBH_i + DBH_j)]$	Martin and Ek (1984)
CID17r	Lorimer	$\sum_{j=1}^{n} \frac{DBH_j / DBH_i}{\sqrt{Dist_{ij}/r}}$	Lorimer (1983) cited in Mailly et al. (2003)
CID18r	Crowding	$\sum_{j=1}^{n-1} (DBH_j / dist_{ij})^{\gamma}$; with γ=1	Miina and Pukkala (2002); Stadt et al. (2007)

IFN data

In the Spanish National Forest Inventory (IFN) plots are located systematically in a 1 km grid and are measured with a periodicity of ten years. Plots are circular with four different radii (from 5 to 25 m) where different tree sizes are sampled. For this study we only used data from the 10 m radius, analyzing trees with DBH>12.5 cm. Other studies with similar inventory design have also selected specific subplots (Canham et al. 2006). By using only this subset of the data we avoided biases from sampling different sizes in the contiguous radii and we reduced data correlation. Due to the differences in plot design, data collection and processing we decided to compare the results derived from fitting models to our data and those derived from fitting models to the IFN data independently without mixing the two data sets.

Plots from the provinces of Salamanca, Cáceres and Badajoz (Figure 1), were selected. Plots were only selected if they were holm oak monospecific and of a density lower than 500 trees/ha. Decreasing density limits (500, 250, 150 trees/ha) were compared, to avoid as much as possible shrub formations from coppice. Following the previous criteria and deleting negative increments (5% of the total) we analyzed 2819 observations from 1566 plots (Figure 1). The difference between DBH in the second and third inventories was used as dependent variable, taking as covariates: the plot density, basal area, tree height, UTM coordinates, slope, meteorological data (Sánchez-Palomares et al. 1999), and river basin (the three last covariates were estimated using a GIS). No other competition indices were calculated from the plot design and the inventory data limitations already described. The holm oak data in IFN is not as complete as for other species, as past diameter increments from increment borers are not available, reducing modelling possibilities (Trasobares et al. 2004).

Models and statistical analyses

Models were fitted to 10 year increments for two reasons: (i) to compare with IFN data; (ii) to reduce climatic variability and measuring error, as the species is slow-growing. Diameter increment was approached in two ways: (i) age-dependent models; (ii) age-independent models. This double approach was done to study the role played by age in the models (potential diameter growth would imply age explaining the most variance with null competition) as age estimation in holm oak is generally impossible to managers. As discussed in the introduction, we decided to use empiric models. Exponential or power models are biologically sound if fitted for the data range over the growth inflection point (or even before in some cases. [Wykoff 1990]), which is usually located at early ages, at least in holm oak (Gea-Izquierdo et al. In press). Similarly, log-transformation has been widely used (e.g. Wykoff 1991; Andreassen and Tomter 2003; Trasobares et al. 2004) as it results in a negative exponential shape close to biological growth. However, transformation alters the error structure, resulting in biases that must be corrected (Myers 1990). In the study, we used the correction proposed by Snowdon (1991) to correct residuals from log-transformed models.

After log-transformation, researchers generally obtain a general linear model with normal errors (i.e. the data is lognormal) and this has been the classic approach to diameter empiric growth models. Classic general linear models with a normal distribution are extended into generalized linear models (GLM) that, using maximum likelihood theory, are able to fit linear models to any probability distribution included in the exponential family (McCullagh and Nelder 1989). Therefore, data fitted by GLMs belong to: $f_Y(y;\theta,\phi) = \exp\{(y\theta - b(\theta))/a(\phi) + c(y,\phi)\}$ where θ and ϕ are the canonical and dispersion parameters respectively. GLMs include probability distributions such as the Normal (where variance=$\phi=\sigma^2$) or the Gamma functions (where variance=$\mu^2 \cdot \phi$ [McCullagh and Nelder 1989]). GLMs directly fit the expected mean of the dependent variable, hence avoiding biases included in transformed general models (McCullagh and Nelder 1989). They have the generic expression $E(Y_i) = \mu_i = g^{-1}(\eta_i)$, with Y_i being the random component or dependent variable (belonging to the exponential family), $g(\cdot)$ the link function, and η_i the linear predictor (McCullagh and Nelder 1989). General models are a particular type of GLM with identity link and Gaussian distribution, whereas a log-transformed model is the same as a lognormal GLM with an identity link. The Gamma function can be used to fit variables with constant coefficient of variation, and is usually used either with identity, log or reciprocal links (Halekoh and Højsgaard, unpublished).

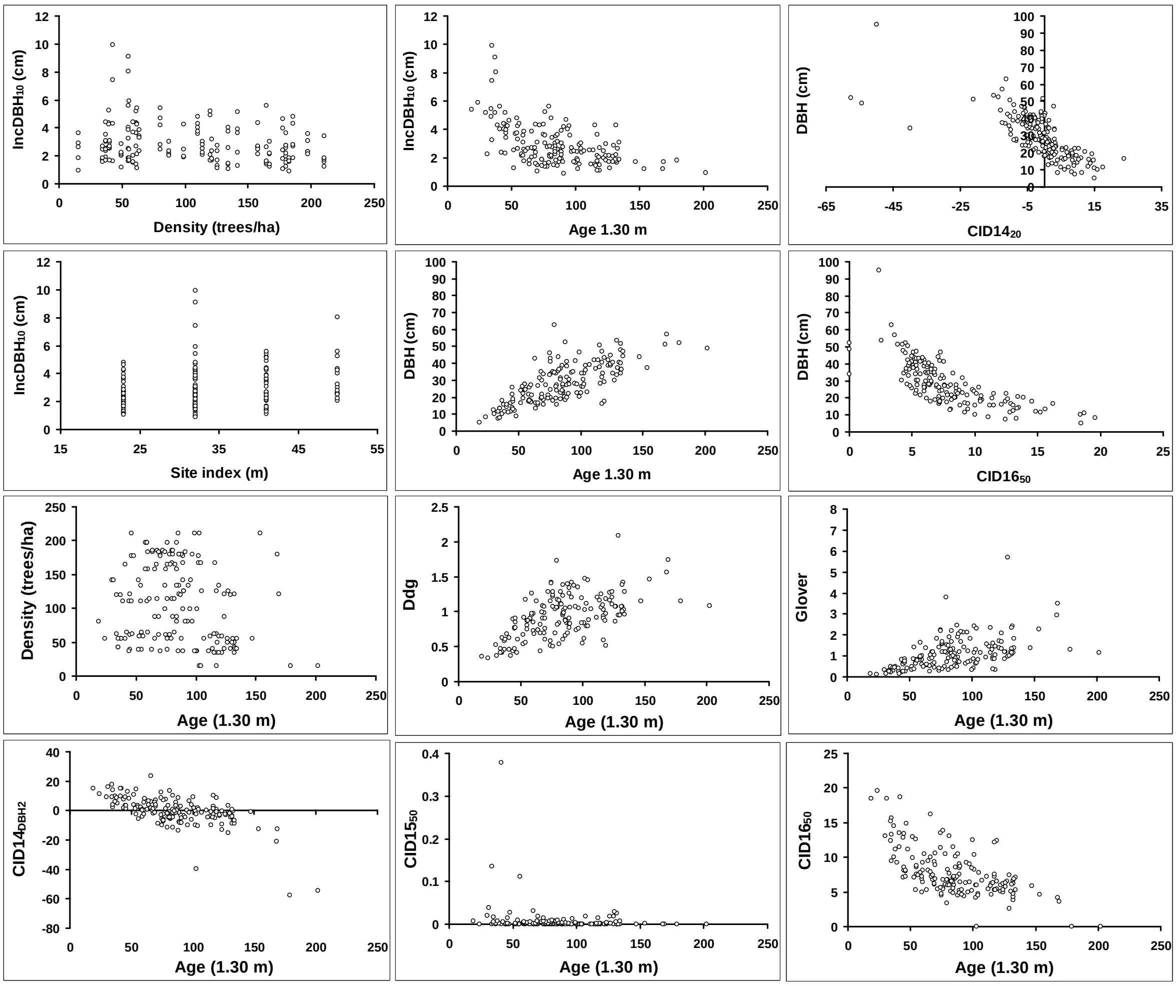

Figure 3. Bivariate plots.

GLMs and general linear models share the same assumptions of independence among observations. In general linear models, correlations within the data can be modelled to obtain more robust and accurate estimates by using linear mixed models. These models include both fixed and random effects and can model correlation in the residual variance-covariance structure (Verbeke and Mohlenbergs 2000). An extension of linear Gaussian mixed models are Generalized linear mixed models (GLMM), similar to normal mixed models in structure, where G and R can be modeled, and with expression (Diggle et al. 2002; Mohlenberghs and Verbeke 2005):

$$f_i(y_{ij} \mid b_i, \beta, \phi) = \exp\{\phi^{-1}[y_{ij}\theta_{ij} - \psi(\theta_{ij})] + c(y_{ij}, \phi)\}\ ;$$

$$\text{and}\ \mu_{ij} = E(Y_{ij} \mid b_i) = g^{-1}(x'_{ij}\,\beta + z'_{ij}\,b_i)\ ;$$

$g(\cdot)$ is the link function; x_{ij} and z_{ij} are matrixes of known covariates; β a *p*-dimensional vector of fixed effects, and b_i a *q*-dimensional vector of random effects, b_i~N(0,G). Y_{ij} are observations from any distribution of the exponential family, with covariance matrix V, and where ϕ is the scale parameter and θ the natural parameter (Diggle et al. 2002, Molenberghs and Verbeke 2005).

In this study we compared linear log-transformed general models with GLMs with Normal and Gamma probability density functions (PDF) and their ability to select significant covariates in parsimonious models. Covariates were selected by comparing nested models fitted using Maximum Likelihood methods by log-likelihood ratio tests compared to a χ^2 distribution (Verbeke and Mohlenberghs 2000) while significance of covariates in GLMs were tested using analyses of residual deviance (McCullagh and Nelder 1989). The final linear log-transformed mixed models were fitted using REML (Verbeke and Mohlenberghs 2000). GLMM´s Maximum likelihood estimates were obtained using linearization methods (pseudo-likelihood estimation) therefore no likelihood ratio tests could be performed (Molenberghs and Verbeke 2005). Random effects were accepted when the standard error was at least two times smaller than the estimated mean. To check for multicollinearity in linear normal models we calculated the variance inflation factor (VIF [Myers 1990]) using PROC

REG. The other analyses were performed using PROC MIXED for linear mixed models, PROC GENMOD for GLM´s and PROC GLIMMIX for GLMM´s, all in SAS 9.1. (SAS Ins. 2004). We did not have an independent dataset and the sample size was too small to be split so we carried out an autovalidation (jack-knife) leaving out one plot each time and calculating the goodness of fit statistics to the residuals obtained (Myers et al. 1990).

To compare behaviour between models we calculated the following goodness of fit statistics:

- Mean residual (bias): $\text{Bias} = \dfrac{\sum_{i=1}^{n}(\text{est}_i - \text{obs}_i)}{n}$
- Root mean square error: $\text{RMSE} = \sqrt{\dfrac{\sum_{i=1}^{n}(\text{est}_i - \text{obs}_i)^2}{n-p}}$,
- Adjusted coefficient of determination (Mittlböck and Heinzl 2002):
  - (i) For general normal linear models:

$$R^2_{SS} = 1 - \frac{(n-k-1)^{-1} \cdot \sum_{i=1}^{n}(y_i - \hat{\mu}_i)^2}{(n-1)^{-1} \cdot \sum_{i=1}^{n}(y_i - \overline{\mu})^2}$$

  - (ii) For GLM (both Gaussian and Gamma):

$$R^2_{D} = 1 - \frac{(n-k-1)^{-1} \cdot D(y;\hat{\mu})}{(n-1)^{-1} \cdot D(y;\overline{\mu})}$$

With n=sample size, k=number of fitted parameters. The R^2 calculated in the autovalidation is called efficiency (EF), and it is the same as R^2_{SS} without the correction for the degrees of freedom (in all models $EF = 1 - (\sum_{i=1}^{n}(y_i - \hat{\mu}_i)^2 / \sum_{i=1}^{n}(y_i - \overline{\mu})^2)$). All R^2 and EF values are calculated for residuals obtained using only the mean response (i.e. the fixed effects, if any random existing in the model). To check for systematic departures in GLMs, McCullagh and Nelder (1989) recommend plotting standardized deviance residuals against predicted values and covariates. We decided to plot raw residuals (observed-predicted) to ease the interpretation and comparison with general models.

RESULTS

At the landscape scale ‘dehesas’ are a mosaic of different plant assemblages, in contrast at the plot scale, trees tended to be displaced following an uniform pattern (Clark-Evans: 1.400±0.214). Plot summary statistics are shown in Table 1 and the distributions of age and DBH can be seen in Figure 2. These distributions are skewed and non-normal, with samples from Salamanca being younger with a smaller mean DBH. Before fitting the final diameter increment models, we explored the relationship between growth and the competition indices. The correlation between the indices (Table 2) was studied both with the Pearson correlation index and fitting a mixed model with random intercept as follows: ‘$\log(IncDBH_{10}+1) = \mu + \beta \cdot CI + b_i$’, with CI being the competition index, μ a fixed intercept, β the fixed slope of the regression, and b_i a random intercept effect. It can be seen in Table 3 that both statistics point in the same direction, with the mixed model coefficients being more conservative. Competition indices that included the size of competitors (i.e. DBH_j) in the numerator or those including larger competitors, were all positively correlated with subject tree growth, whereas indices including the subject tree (DBH_i) were negatively correlated with growth. With the exception of CID15, density (CII1) and basal area (CII2), all indices were particularly correlated with growth in low density stands (< 80 trees/ha), and strong correlations (in low densities) were found in distance dependent indices that included competitor size in their formulation (Tables 2, 3). The relationship between variables can be seen in Figure 3, where only search distances maximizing correlation are included (Figure 4).

Competition in age dependent diameter increment models

As expected, the log-transformed age-dependent model was biased before applying the correction (Snowdon 1991) to the residuals (MBias=0.102 cm; RMSE=0.996 cm; EF=55.2 %). In Table 4 we show the selected covariates using Log-likelihood ratio tests for the log-transformed mixed model (Verbeke and Mohlenbergs 2000). Although in general the threshold level for the VIF is 10 (Wimberly and Bare 1996), the great similarities among some covariates prompted us to consider a more limiting threshold (Table 4). Five covariates were selected (excluding those that were collinear with the previously selected covariates), age was the covariate explaining the most variance, followed by density (CII1) and ddg (CII3). A random intercept was not significant (Table 6) and the previous three covariates were negatively correlated with growth, reflecting the existence of competition. The log-transformed mixed model explained 50% of the variance of the back-transformed dependent variable (Table 5), but it included too many covariates, as demonstrated in comparison with the Gamma model (Table 6). In Table 5 we compared the log-transformed models and the GLM´s with log links including extra covariates as selected from Table 4 to ease the comparison between models. Among GLM´s, the Log-likelihood maximized in Gamma models both with the reciprocal link (-203.8: the maximum, hence, the link used in the final model shown in Table 6) and the log link (-204.0) compared to the Gaussian with a log link (-236.5). Gamma models were better than log-transformed models (equivalent to a lognormal GLM) and Gaussian GLMs with log link (identical to a non-linear exponential model), particularly in terms of the validation statistics and, as mentioned, they maximized the likelihood.

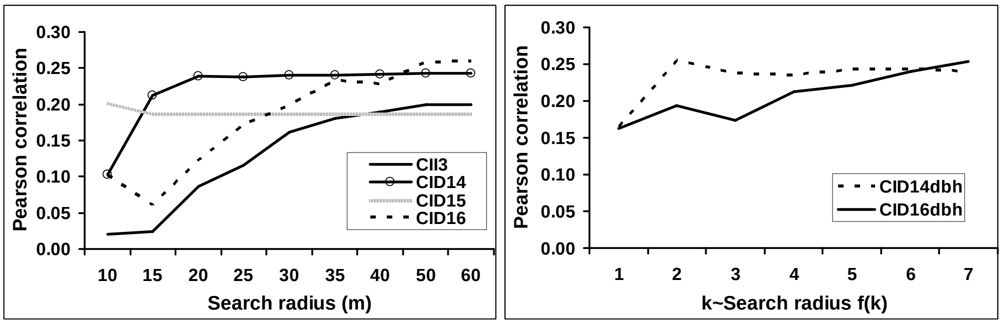

Figure 4. Pearson correlation coefficient between competition indices and the search radius.
k meaning: search radius= 20·k·DBH in m.

In table 6 we show the estimates of the Gamma model with inverse (=reciprocal) link and the log-transformed. The Gamma model reduced the significant covariates to density and age, which were the covariates with the strongest correlation from the beginning, both in the statistics and graphical analysis (Figure 3). It can be seen how using the Gaussian PDF over-inflates the coefficient of variation from the excessive number of covariates selected. The final age-dependent model is a Gamma GLM including an intercept, age at 1.30 m and density, with no random coefficients (the random coefficient in the GLMM was non-significant; Table 6), and it had the expression:

$$\mathrm{Inc10}_i = \hat{\mu}_i = \frac{1}{0.05336 + 0.003095 \cdot \mathrm{Age}_{\mathrm{DBH}} + 0.000889 \cdot \mathrm{Density}} + \varepsilon_i ,$$

with $\varepsilon_i \sim G(\mu, \mu^2/8.6817)$. As age was closely related to DBH, and as estimating age in holm oak is extremely difficult, it would be very useful to estimate ages from DBH (Plieninger et al. 2003). The relationship obtained would be:

$$\mathrm{Age}_{ij} = 21.0457[3.2578] + (2.3742[0.1518] + b_i) \cdot \mathrm{DBH}_{ij} + \varepsilon_{ij} ,$$

with $\varepsilon_i \sim G(\mu, \mu^2 \cdot 0.02820\ [0.003663])$; $b_i \sim N(0,\ 0.3347\ [0.09466])$; MBias=-0.120, RMSE=23.41, and R^2_{SS}=47.24 (standard errors of parameters are between square brackets).

From Table 2, it would seem that there could be two different behaviours in holm oak stands, depending on whether plot densities are over or under 80 trees/ha. However, we discarded fitting different models for the two groups or including a dummy variable (χ^2=0.01; p=0.931) as none of the options seemed to increase significantly the proportion of explained variance in age dependent models (stands>80 trees/ha: n=97, RMSE=0.944, R^2=32.90; stands<80 trees/ha: n=68, RMSE=1.201, R^2=56.70). Distribution of residuals against predicted values and covariates are shown in Figure 5 and Figure 6.

Competition in age independent diameter increment models

Six covariates were first selected in the log-transformed model (Table 4), among which density, the inverse of DBH and a dummy variable for the Cáceres data were most strongly related to diameter increment. However we used only five covariates to compare models in Table 5, excluding (1/DBH), as although this covariate was significantly selected in the estimation phase, the autovalidation statistics were better in all models without its inclusion(not shown), and models depicted more realistic fits.

Table 3. Goodness of fit statistics for model Log(IncDBH$_{10}$+1)= μ+β·CI + b_i and Pearson correlation coefficient for: (i) whole dataset; (ii) plots of density <80 trees/ha; (iii) plots of density >80 trees/ha. Subindex (20/50 or DBH2/DBH7) means search radius either fixed (20 or 50 m) or relative to DBH [2·(0.2·DBH) or 7·(0.2·DBH) m]. **=significant at α=0.05; *=significant at α=0.10. ρ=Pearson correlation coefficient; p=probability associated to test.

Index	Whole Dataset				Density < 80 trees/ha				Density > 80 trees/ha			
	β (SE)	p (t-Value)	EF (%)	ρ (p)	β (SE)	p (t-Value)	EF (%)	ρ (p)	β (SE)	p (t-Value)	EF (%)	ρ (p)
CII1	-0.00121 (0.0006)	**0.0312**** **(-2.18)**	4.339	**-0.208**** **(0.0067)**	0.004399 (0.0038)	0.2573 (1.14)	5.576	0.160 (0.1818)	-0.00188 (0.0011)	0.0811* (-1.77)	7.782	**0.231**** **(0.0230)**
CII2	-0.01717 (0.0101)	0.0934* (-1.69)	2.898	**-0.171**** **(0.0269)**	0.01518 (0.0317)	0.6335 (0.48)	3.679	0.064 (0.5932)	-0.01562 (0.0120)	0.1987 (-1.30)	5.933	-0.186* (0.0677)
CII3	-0.2403 (0.0732)	**0.0013**** **(-3.28)**	4.981	**-0.223**** **(0.0036)**	-0.4138 (0.1155)	**0.0007**** **(-3.58)**	16.541	**0.371**** **(0.0015)**	-0.09069 (0.0913)	0.3237 (-0.99)	3.236	-0.082 (0.4258)
CII4	-0.08050 (0.0265)	0.0029** (-3.03)	2.706	**-0.170**** **(0.0274)**	-0.1188 (0.0395)	**0.0040**** **(-3.01)**	9.744	**-0.266**** **(0.0252)**	-0.03766 (0.0356)	0.2934 (-1.06)	3.103	-0.076 (0.4610)
CII5	0.007663 (0.0075)	0.3062 (1.03)	1.865	0.032 (0.6767)	0.04681 (0.0167)	**0.0069**** **(2.81)**	12.808	**0.315**** **(0.0074)**	0.003642 (0.0080)	0.6478 (0.46)	2.137	-0.022 (0.8310)
CII6$_{20}$	-0.0990 (0.0130)	0.4468 (-0.76)	0.718	-0.087 (0.2645)	0.03307 (0.0218)	**0.1347** **(1.52)**	6.803	**0.191**** **(0.1107)**	-0.06431 (0.0329)	0.0542* (-1.96)	5.811	-0.183* (0.0732)
CII7$_{50}$	0.02275 (0.0086)	**0.0090**** **(2.65)**	3.991	**0.200**** **(0.0094)**	0.04254 (0.01449)	**0.0049**** **(2.94)**	11.653	**0.342**** **(0.0036)**	0.01137 (0.01013)	0.2651 (1.12)	1.100	0.105 (0.3066)
CII8$_{50}$	0.000581 (0.0004)	0.1417 (1.48)	1.676	0.130* (0.0930)	0.000577 (0.000553)	0.3008 (1.04)	1.560	0.127 (0.2920)	-0.00028 (0.000783)	0.7256 (-0.35)	0.310	-0.057 (0.5823)
CII9	-0.7544 (0.3038)	**0.0143**** **(-2.48)**	0.261	-0.106 (0.1720)	-1.3059 (0.3876)	**0.0014**** **(-3.37)**	15.181	**-0.352**** **(0.0026)**	-0.3156 (0.7499)	0.6751 (-0.42)	2.610	-0.022 (0.8344)
CID10	-0.1540 (0.1589)	0.3342 (-0.97)	3.178	-0.091 (0.2476)	0.1826 (0.2510)	0.4702 (0.73)	10.322	0.111 (0.3691)	-0.1434 (0.3679)	0.6978 (-0.39)	2.869	-0.053 (0.6068)
CID11	-0.01546 (0.0087)	0.0772* (-1.72)	0.201	-0.064 (0.4110)	-0.02032 (0.0113)	0.0781* (-1.80)	6.588	-0.187 (0.1175)	-0.02097 (0.0166)	0.2093 (-1.27)	2.049	-0.040 (0.6970)
CID12	-0.0142 (0.0008)	0.0934* (-1.69)	1.389	-0.118 (0.1267)	-0.00198 (0.0013)	0.1477 (-1.47)	6.567	-0.185 (0.1231)	-0.00143 (0.0014)	0.1774 (-1.36)	3.819	-0.113 (0.2710)
CID13$_{50}$	0.1669 (0.0573)	**0.0042**** **(2.91)**	1.0416	**0.202**** **(0.0088)**	0.3107 (0.09126)	**0.0013**** **(3.40)**	15.022	**0.388**** **(0.0008)**	0.1051 (0.07309)	0.1547 (1.44)	2.014	0.142 (0.1652)
CID14$_{20}$	0.007986 (0.0024)	**0.0014**** **(3.27)**	5.678	**0.239**** **(0.0018)**	0.01044 (0.0031)	**0.0016**** **(3.33)**	16.529	**0.371**** **(0.0015)**	0.004296 (0.0039)	0.2791 (1.09)	3.712	0.107 (0.2968)
CID14$_{DBH2}$	0.009696 (0.0029)	**0.0011**** **(3.31)**	6.499	**0.255**** **(0.0008)**	0.01065 (0.0035)	**0.0038**** **(3.02)**	15.059	**0.350**** **(0.0028)**	0.008589 (0.0053)	0.1074 (1.63)	5.578	0.176* (0.0850)
CID15$_{50}$	2.3605 (0.7749)	**0.0019**** **(3.17)**	3.347	**0.187**** **(0.0151)**	3.6320 (1.9614)	0.0695* (1.85)	6.453	0.183 (0.1264)	2.0939 (0.7281)	**0.0052**** **(2.58)**	6.994	**0.218**** **(0.0322)**
CID16$_{50}$	0.02433 (0.0072)	**0.0010**** **(3.31)**	6.668	**0.258**** **(0.0007)**	0.03822 (0.0100)	**0.0004**** **(3.81)**	20.599	**0.423**** **(0.0002)**	0.008250 (0.0102)	0.4130 (4.82)	3.313	0.086 (0.4028)
CID16$_{DBH7}$	0.02390 (0.0072)	**0.011**** **(3.34)**	6.401	**0.253**** **(0.0009)**	0.03762 (0.01004)	**0.0004**** **(3.75)**	17.312	**0.416**** **(0.0003)**	0.008374 (0.009949)	0.4026 (0.84)	0.794	0.090 (0.3834)
CID17$_{50}$	0.008001 (0.0024)	**0.0013**** **(3.24)**	5.758	**0.240**** **(0.0017)**	0.01384 (0.003674)	**0.0004**** **(3.74)**	9.122	**0.422**** **(0.0002)**	0.004195 (0.003197)	0.1934 (1.31)	3.804	0.134 (0.1919)
CID18$_{50}$	0.007571 (0.0027)	**0.0053**** **(2.83)**	1.889	**0.153**** **(0.0480)**	0.01028 (0.0051)	**0.0499**** **(2.01)**	4.663	0.218* (0.0681)	0.007284 (0.0029)	**0.0151**** **(2.59)**	1.8379	0.161 (0.1162)

Table 4. Selection of covariates in linear mixed model: (i) age-dependent models; (ii) age-independent models for our data; (iii) age-independent models for IFN. p (χ^2)=log-likelihood ratio test, probability associated to the χ^2 distribution. EF=efficiency calculated for the residuals without back-transforming. Max VIF=is the maximum variance inflation factor corresponding to covariate x. Models fitted using Maximum Likelihood (ML) estimation. 'DumCac'=dummy variable for Cáceres data. BA=basal area. Tmin=mean of minimum temperatures of coldest month. '$^+$' meaning multicollinearity. In bold characters the last step including significant covariates in the final model. Basic model: $\text{IncDBH}_{10ij}=f(x)+b_i+\varepsilon_{ij}$; plot i, tree j, f(x) linear relationship of fixed effects, b_i is a random intercept plot effect.

Step	Variables added	-2LL	p (χ^2)	EF (%)	Max. VIF (x)
(i) Age-dependent models [$\log(\text{IncDBH}_{10})=f(x_c)$]					
1	**age**	160.2	< *0.0001* (55.5)**	33.19	1.000
2	**Density (CII1)**	151.1	*0.0026* (9.10)**	44.69	1.037
3	**Ddg (CII3)**	134.6	< *0.0001* (16.5)**	50.01	1.608 (age)
4	**(1/DBH)**	126.6	*0.0050* (8.0)**	51.81	2.607 (1/DBH)
5	**CID15$_{50}$**	119.1	*0.0062* (7.5)**	**53.09**	2.608 (1/DBH)
6	CID13$_{50}$	116.2	0.0886 (2.90)*	52.82	5.739 (CID13)$^+$
7	IS	120.4	1.0 (0.0)	55.45	2.658 (1/DBH)
8	BA(CII2)	121.2	1.0 (0.0)	54.76	3.106 (Ddg)
9	CID16$_{50}$	121.8	1.0 (0.0)	52.84	4.837 (CID16)$^+$
(ii) Age-independent models (own data) [$\log(\text{IncDBH}_{10}+1)=f(x_c)$]					
1	**(1/DBH)**	79.1	< *0.0001* (24.0)**	13.47	1.000
2	**Density (CII1)**	68.1	*0.0009* (11.0)**	21.57	1.04
3	**DumCac**	57.9	*0.0014* (10.2)**	26.98	1.83 (DumCac)
4	**CID15$_{50}$**	50.9	*0.0081* (7.0)**	29.88	1.85 (DumCac)
5	**CII7$_{50}$**	45.9	*0.0253* (5.0)**	30.98	2.00 (CII7)
6	**DBH**	41.7	*0.0404* (4.20)**	**33.42**	3.69 (DBH)
7	Ddg (CII3)	33.7	0.0047 (8.0)**	36.17	8.17 (DBH)$^+$
8	CID16$_{50}$	33.6	0.7518 (10.6)	36.01	9.62 (ddg) $^+$
9	BA (CII2)	23.7	0.0016 (10.0)**	39.95	15.42 (ddg)$^+$
(iii) Age-independent models (IFN) [$\log(\text{IncDBH}_{10}+1)=f(x_c)$]					
1	**Y UTM (km)**	2643.2	< *0.0001* (29.7)**	1.407	1.00
2	**Slope**	2611.9	< *0.0001* (31.3)**	3.170	1.04
3	**Density**	2606.7	*0.0226* (5.2)**	3.649	1.07 (slope)
4	**DBH**	2600.6	*0.0135* (6.1)**	3.763	1.23 (density)
5	**Height**	2589.0	*0.0066* (11.7)**	4.306	1.72 (DBH)
6	**Tmin**	2583.8	*0.0226* (5.2)**	4.685	3.89 (Tmin)
7	**DumGuadi**	2577.6	*0.0128* (6.20)**	**4.906**	4.04 (Tmin)

First, all age independent GLMs in Table 5 were also fitted using the log-link for comparative purposes. Both untransformed GLMs were better than the log-transformed classic model. Although the Gaussian GLM had the best goodness of fit statistics, (Table 5) it can be seen in Table 6 that the Gamma model was the best as it reduced significantly the number of selected covariates (Table 6. McCullagh and Nelder 1989). Thus it resulted in more parsimonious models depicting the real relationship between covariates and the dependent variable. The Log-likelihood was maximized in Gamma models both with reciprocal link (-238.9) and with a log link (-241.8), compared to Gaussian with a log link (-264.1) and a reciprocal link (-256.7). As the reciprocal maximized the likelihood with both PDFs, we used the reciprocal link to fit final normal and Gamma age-independent GLMs (Table 6). The variables finally selected in the Gamma model with inverse link were again density and DBH (in lieu of age) and a dummy for the Cáceres province. The three of them were negatively correlated with diameter increment (i.e. positive estimates using a reciprocal link). The final expression was:

$$\text{Inc10}_i = \hat{\mu}_i = \frac{1}{0.1068 \cdot \text{DumCac} + 0.0056 \cdot \text{DBH} + 0.0017 \cdot \text{Density}} + \varepsilon_i \,,$$

where $\varepsilon_i \sim G(\mu, \mu^2/6.3218)$. A random intercept effect was not significant (Table 6). Again, including a dummy variable for plots below 80 trees/ha was not significant ($\chi^2=0.04$; $p=0.833$). Fitting two models would not improve the results, with a similar behaviour to that of age-dependent models (stands>80 trees/ha: n=97, RMSE=1.050, $R^2=16.87$; stands<80 trees/ha: n=71, RMSE=1.443, $R^2=34.66$). Distribution of residuals against predicted values and covariates are shown in Figure 5 and Figure 6.

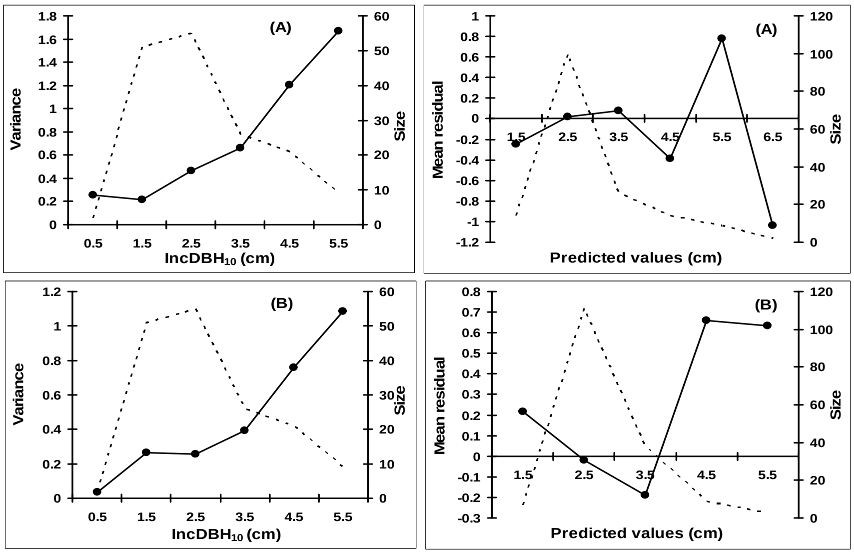

Figure 5. Variance function of residuals and residuals against predicted values: (A) age-dependent models; (B) Age-independent models. Thick lines with dark circles correspond to variance function or mean residual, whereas dashed line to sample size.

Table 5. (i) Comparison of log transformed (i.e. lognormal) linear Gaussian general model; (ii) Gaussian linear generalized model (GLM) with a log link; (iii) Gamma GLM with reciprocal (1/μ) link function. The fitting statistics for the log-transformed linear model are calculated using the corrected predictions: $\text{pred}_{\text{corr}} = \hat{y} \cdot \text{CF}$ (Snowdon 1991); -2LL=-2 times residual log-likelihood.

Model		Estimation				Validation (Jack-knife)		
		-2LL	Mean Bias (cm)	RMSE (cm)	R^2_{SS} (R^2_D)	Mean Bias (cm)	RMSE (cm)	EF (%)
Age-dependent models	Log-transformed Gaussian linear model (≈ lognormal GLM)	-	0.0244	1.0303	50.599	0.0145	1.0964	45.737
	Gaussian GLM with a log link	-236.5	0.0083	1.0176	51.787 (51.787)	-0.0105	1.1422	41.112
	Gamma GLM with log link	-203.95	0.0042	1.0261	50.977 (53.929)	-0.0035	1.0899	46.378
Age-independent models	Log-transformed Gaussian linear model (≈ lognormal GLM)	-	0.0000	1.2084	30.807	-0.0153	1.3021	22.059
	Gaussian GLM with a log link	-264.11	0.0216	1.1690	35.249 (35.249)	0.0252	1.2344	29.952
	Gamma GLM with a log link	-241.81	0.0093	1.1965	32.163 (28.718)	-0.0049	1.2808	24.598

Note: all models include only fixed effects (see text for non-significant tests for random effects). All age-dependent models include the 5 covariates selected in table 4 for the log-transformed linear model, whereas age-independent models include the 6 covariates selected in table 4 except 1/DBH (see text for details).

Applicability of the National Forest Inventory to model *Quercus ilex* L. diameter growth

For IFN data we fitted a log-transformed model (Table 4) as data and residuals were less skewed than in the sampled set and to ease comparison with other published studies. Density was also selected in this model; however the covariates that explained most variance were slope and the Y UTM (Table 4). The final model included six covariates, and its expression was:

$$\mathrm{Inc10} = \mathrm{CF} \cdot (\exp(-4.0376 + 0.001175 \cdot \mathrm{YUTM} - 0.00448 \cdot \mathrm{Slope} - 0.00038 \cdot \mathrm{Density} -$$
$$- 0.00234 \cdot \mathrm{DBH} + 0.02329 \cdot \mathrm{Height} + 0.02842 \cdot \mathrm{Tmin} + 0.08161 \cdot \mathrm{DumGuad} + b_i + \varepsilon_i) - 1)$$

with $\varepsilon_i \sim N(0, 0.1032[0.004049])$ and $b_i \sim N(0, 0.05348[0.004844])$. CF is the correction factor (1.11614 with our data [Snowdon 1991]), YUTM expressed in km, slope in %, density in trees/ha, DBH in cm, height in m, 'Tmin'=mean of minimum temperatures in the coldest month, and 'DumGuad' is a dummy variable for the 'Guadiana and Guadalquivir river basins', which are the southernmost basins in the study area (Figure 1); with MBias=0.000, RMSE=1.548, and R^2=3.931. Results were similar if only plots with a density of <250 trees/ha were analyzed: 2667 obs., MBias=0.000, RMSE=1.551, R^2=4.130. Finally, if only plots with density of <150 trees/ha were used, the model fit was worse (2429 obs., MBias=0.000, RMSE=1.559, R^2=3.369).

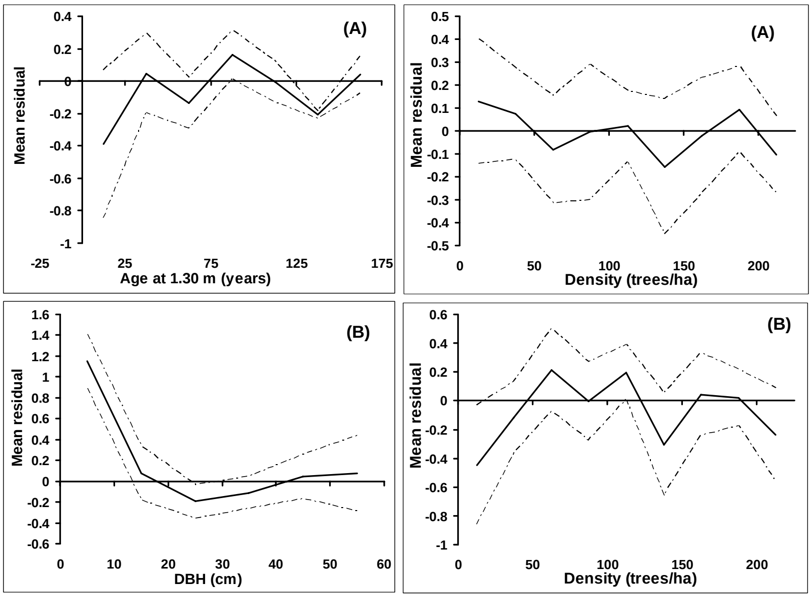

Figure 6. Plots of residuals against selected covariates in the final models: (A) age-dependent model; (B) age-independent model. Dark lines correspond to mean residuals while dashed lines to standard errors of the mean.

DISCUSSION

Holm oak intraespecific competition

Correlation coefficients between the calculated indices and diameter growth were similar to those obtained by Mailly et al. (2003) in denser stands, and similar to results from the widest spaced plots but smaller to those from highest densities of Tomé and Burkhart (1989). Competition indices in Table 2 were formulated to penalize size and distance, meaning that a negative relationship was to be expected between competition indices and growth: the greater the competition index (meaning either more or bigger competitors), the higher the limitation to growth. Nevertheless, not all correlations were negative (Table 3). Only indices where the subject tree was included in the index formulation were negatively correlated with diameter growth (hence depicting a competition gradient). Whereas, indices including size of competing neighbours in their formulation were positively correlated with growth.

The previous result would seem to be contrary to ecological theory. This apparent contradiction (distance dependent competition indices were positively correlated with growth) is explained by the fact that indices are calculated from DBH_j, and DBHs are closely related to age (Figure 3) in this open ecosystem, as extracted from our results and those in Plieninger et al. (2003). Therefore, in this preliminary correlation analysis competition indices would be behaving as surrogates of age. The high correlations found in Table 2 e.g. CID15 or CID16 do not reflect competition, or at least not to a large extent. This is because the youngest trees tend to have smallest DBH, which are very likely to be surrounded by bigger and older competitors, under the current structure of the ecosystem. They are also not included in the final models, because subject tree age and DBH explain the same information. This pattern is likely to be expressed most strongly at the lowest tree densities, when growth is most closely related to age (Table 4, Table 6). However, this could also reflect some competition: another explanation for the positive correlation of distance dependent indices could be a positive sheltering effect upon the subject tree under the water stressed conditions where these holm oaks thrive (Mayor and Rodá 1994; Ogaya and Peñuelas 2007) or that more dense stands are more likely to include saplings from better regeneration conditions. We believe that the hypothesis that the indices are related to age is far more probable, a reflection of the fact that the distance competition indices calculated are not real estimators of competition in this system. The negative relationships between indices and growth (i.e. indices reflecting competition) are below 0.25, depicting low competition compared to that found in previous studies.

Therefore, competition does exist, but age is clearly the most influential covariate, probably because the trees are not competing for light (at least in the lowest densities), as they are in closed forests. As found in many other studies (e.g. Martin and Ek 1984; Biging and Dobbertin 1995; Wimberly and Bare 1996) distance dependent indices do not outperform distance independent indices. Plot density is the best competition index, which might be expected from the uniformity of the stands (Biging and Dobbertin 1992). Distance dependent indices were not selected in the final models; it is remarkable that depending on the index, distances to up of 50 m or 140 times the estimated DBH (i.e. a DBH of 30 cm would have a search radius of 42 m) were the most correlated with growth. This could seem like an excessive distance and, as discussed above, it does not mean that it indeed reflects an effective competition distance from the tree. Rooting studies with holm oaks and the 'dehesa' ecosystem (Canadell and Rodá 1991; Moreno et al. 2005) and from other ecosystems (Canadell et al. 1996; Jackson et al. 1996), show that the distance is not disproportionate. Competition for below-ground resources can occur over greater distances than competition for light (Schwinning and Weiner 1998), hence holm oak trees could be prospecting large areas (both in depth and top soil) outside of their own crown projection.

Table 6. Model parameter estimates and confidence intervals. 'p' values are for the analysis of deviance test compared to the χ^2distribution (McCullagh and Nelder 1989). For test of hypothesis (Log-likelihood ratio tests) of log-transformed model see table 4. ϕ = dispersion parameter in GLM; SE=Standard error. $\sigma i2^{+}$ = variance estimate of random intercept effect GLMM with same fixed parameters as the corresponding GLM; between parenthesis the standard error of prediction. Goodness of fit statistics in transformed model were calculated with the back-transformed corrected residuals (see text for details). ** significant at α=0.05; * significant at α=0.10.

Parameter/Statistic	Age-dependent models			Age-independent models			
	Log-transformed Gaussian linear model	Gamma GLM with reciprocal link		Gaussian GLM with reciprocal link		Gamma GLM with reciprocal link	
	Estimate (SE)	Estimate (SE)	p (χ^2 value)	Estimate (SE)	p (χ^2 value)	Estimate (SE)	p (χ^2 value)
Intercept	1.2884 (0.1833)	0.05336 (0.0238)	0.0051** (7.84)	-0.2400 (0.0512)	< 0.0001** (21.51)	-	0.6737 (0.18)
Age 1.30 m	-0.00989 (0.0011)	0.003095 (0.0003)	0.0001** (14.69)	-	-	-	-
Density	-0.00357 (0.0005)	0.000889 (0.0002)	0.0662* (3.38)	0.0020 (0.0002)	< 0.0001** (102.40)	0.0017 (0.0002)	< 0.0005** (29.05)
Ddg	0.6336 (0.1230)	-	0.1475 (2.10)	-	-	-	-
CID15$_{50}$	1.7446 (0.7970)	-	0.7667 (0.09)	-0.6319 (0.1184)	0.0006** (11.75)	-	0.3326 (0.94)
(1/DBH)	4.0504 (1.6200)	-	0.6512 (0.20)	-	0.8634 (0.03)	-	0.3945 (0.73)
CII7$_{50}$	-	-	-	0.0233 (0.0045)	< 0.0001** (27.92)	-	0.3792 (0.77)
DBH	-	-	-	0.0098 (0.0012)	< 0.0001** (73.07)	0.0056 (0.0007)	< 0.0001** (20.07)
Dummy Cáceres	-	-	-	0.1142 (0.0223)	< 0.0001** (36.59)	0.1068 (0.0260)	0.0863* (2.94)
ϕ	-	8.6817 (0.9380)		1.1154 (0.0609)		6.3218 (0.6723)	
Mean Bias (cm)	0.0244	0.0000		0.0210		-0.0303	
RMSE (cm)	1.0303	1.0595		1.1188		1.2286	
R^2_{SS} (R^2_D)	50.599	48.697 (46.625)		40.692 (40.692)		29.340 (24.889)	
σ_i^{2+}	0.01433 (0.01008)*	0.000 (-)		0.000 (-)		0.000 (-)	

According to Larocque (2002) and Schwininng and Weiner (1998), asymmetric competition is related to crown and symmetric to roots. In semiarid woodlands, competition for water is likely to be more important than competition for light. Changing the plot size could affect the performance of competition indices (Biging and Dobbertin 1995). Correlations are not generally very high, however, as Larocque (2002) states, it is doubtful that the simple indices used in competition studies can fully represent the complex processes involved in competition, and factors affecting competition and their consequences need to be tested with other approaches. Our results confirm this statement: the distance competition indices calculated and used in many studies, are not suitable for estimating competition in our plots.

Holm oak diameter increment models

Mixed models and GLMs rely on maximum likelihood estimation, and it can be seen how models with inverse link function and PDF that maximize the likelihood result in the most parsimonious models. Models fitted with the Gaussian PDF selected too many covariates. In Figure 3 it can be seen how among covariates showing correlation with growth, only density and age-DBH are uncorrelated. Therefore, they are the only covariates expected to be included in the final models. The three individuals growing in the lowest density stands (isolated trees) were among the oldest (ages>175 years), and that is why they seem to break the general decreasing trend between density and diameter increment (Figure 3).

Age and density were negatively correlated with growth in age dependent models (positive coefficients in Gamma model, as we are using the inverse link (Table 6). Gamma models were the best, and they are of interest for two main reasons: (i) we are directly modelling the raw dependent variable, this avoids biases from transformation and makes the models easier to use for managers and researchers; (ii) we are using a flexible PDF that is able to model departures from normality, particularly increasing variance with increasing scores of the dependent variable, and thus weighted regression is not required. In normal models $R^2_D = R^2_{SS}$ are calculated identically (McCullagh and Nelder 1989, pp. 34), whereas in Gamma models the deviance is calculated as $2\cdot\sum[-\log(y/\hat{\mu})+(y-\hat{\mu})/\hat{\mu}]$. The decrease in R^2_D compared to R^2_{SS} in Gamma models was unexpected (Mittlböck and Heinzl 2002).

Age-independent models also show how selecting the appropriate PDF results in more parsimonious models with a lower number of significant covariates, enabling a clearer discussion of the relationship between covariates and the dependent variable. As the Analysis of Deviance is more restrictive in Gamma models than in Gaussian models, because of the way the Deviance is calculated and from the best fit of the dependent data, we decided to accept covariates at $\alpha=0.10$ (Table 6). Again, density was negatively correlated with growth, and DBH was also significant. The dummy for Cáceres is added to DBH as an estimate of older age in that location (Table 1, Figure 2), as it is deduced from its only inclusion in the age-independent model. The same could be thought of DBH: as it is only included in age independent models, it seems that it is in fact being selected as an indirect estimate of age in the system. The IFN data and our observations when measuring the whole life growth of both samples (personal observations) points towards less growth in the southern-most holm oaks from Cáceres compared to those in Salamanca, but age may be a confounding variable.

In some studies the square DBH enters in the final models (e.g. Wykoff 1990; Larocque 2002) to fit the biological point of inflection expected in growth. In our model it was not selected, probably because the inflection point is reached at a very young age (smaller than 10 cm DBH [Anexo II]), or because it was not included sufficiently in the sampled plots (Table 1) or in the ecosystem in general (Pulido et al. 2001). Age-independent models explained less of the variation in the dependent variable (>28%), but efficiencies were similar to those of other studies (Lessard et al. 2001; Sánchez-González et al. 2005; Stadt et al. 2007). The inclusion of age reduced the model error and almost doubled efficiency ($R^2=47.6$, Table 6). This reflects the high correlation between growth and age that was especially noticeable in the lowest density stands, as a consequence of reduced competition. We did not find such a close relationship between DBH and age as that in Plieninger et al. (2003), but it is still good enough to give an estimate, bearing in mind the general difficulty of estimating ages from DBH (Cooks and Kairiukstis 1990). The DBH-age relationship has possibly occurred because aerial competition is reduced to the minimum, particularly in low density stands. This relationship is likely to vary in other holm oak formations, especially if they are not as homogeneous as our stands.

In the sampled plots we only characterized holm oak shrubs, although some plots included high densities of *Cytisus multiflorus* (L'Hér.) and *Cistus* sp. This could be, along with the different parent materials, another reason for differences that were not included in the models. Additionally, we did not sample the holm oak shrubland, which results from logging or coppicing, as seen in Cáceres (personal observation). No random parameters were significant in the final models (neither in log-transformed nor in GLMs), therefore, with the model proposed it is not possible to perform random effects calibrations to improve prediction accuracy. Other diameter increment models usually include random components (Miina 1993; Miina and Pukkala 2000; Calama and Montero 2005) the reasons why random plot parameters were not included in our models could be related to the open stands and management of study areas. Larger data sets might provide more insights in improving model accuracy, especially to test models for different densities.

Finally, when fitting growth models, the question arises as to whether estimations based on past growth, are applicable to future growth, especially under the current conditions of climate change. It has been shown that tree growth responds to climate change, and this is expected to be more patent in tree species growing at the limit of their distribution areas (Andreu et al. 2007) or under climates where limiting factors mean that the vegetation type is on the border between tree-like formations and, for instance, steppe or shrubland. This is the case for the Continental Mediterranean climate ecosystems of our study area. Additionally, when analyzing the effect of density, our results show that the classical forestry assumption is correct: the lower the density, the faster diameter increment growth. Problems could arise if changes in aridity, for instance, changed this tendency, especially in stands like those in Mediterranean ecosystems where timber is not the principal product, and where close stands are likely to be crucial for regeneration and forest preservation (Pulido et al. 2001). These issues should be addressed in future studies, particularly with this species and ecosystem, where preservation of the ecosystem integrity (e.g. top-soil, humidity levels) with tree-like formations should be the principal goal.

Use of the National Forest Inventory to model holm oak diameter growth

The National Forest Inventory data does not seem to be appropriate for modeling growth in *Quercus ilex*. We found poor correlations between covariates and growth (R^2<4%), even when compared with other Forest Inventory studies whose R^2 does not tend to be very high, but in all cases greater than our results (usually over 20%; e.g. Lessard et al. 2001; Andreassen and Tomter 2003; Trasobares et al. 2004; Canham et al. 2006). This can be explained by: (i) the heterogeneity of holm oak stands, including coppice and seedlings, shrubs and tree-like oaks; (ii) the stem profile, which makes it difficult to clearly define the DBH at 1.30 and hence, re-measure it at the same point in different samples; (iii) management of the stands, including pruning and clearing; (iv) assuming a constant error in IFN sampling, independent of the target species. This cannot be assumed, as the slower the growth of the species, the greater the expected relative error.

The IFN models presented are log-transformed linear mixed models. Moisen and Frescino (2002) observed that generally speaking linear models fit Inventory data as well as other more complex techniques. Many covariates were selected, but as seen in Table 4, latitude (calculated as the Y UTM) and slope were the regressors that explained most of the variation and are the only correlations we would consider as hypothesis for further investigations. It is impossible to conclude whether this trend is real or not because the model explains too little variance. However, the relationship with latitude and slope (soil) seems logical from a climatic and edaphic point of view. In general, the southern most plots would be expected to suffer more water stress, especially considering the changes in patterns of precipitation and increases in temperature that have occurred during the last decades (e.g. Esteban-Parra et al. 1998; Easterling et al. 2000; Zhang et al. 2007). The stem diameter increment in holm oak coppices has been shown to be strongly correlated with water availability (e.g. Mayor and Rodá 1994; Ogaya and Peñuelas 2007). Additionally higher slopes have shallower, poorer soils that retain less water (Puerto and Rico 1992).

Checking these trends in the model fitted to the sampled datasets is not as straightforward as mentioned. They were not balanced in the diameter and age probability distributions, which makes the comparisons between them difficult. Finally, we used data only from the 10m ring, to avoid the need of weighting or problems arising from plot definition (different rings containing only greater DBH individuals). In addition the 10 m radius model maximized the goodness of fit statistics compared to models using all radii (not shown). Density was also selected in IFN models, confirming that density affects growth in these open woodlands. Although tree height is not a reliable covariate in this ecosystem, it was included in the models. We allowed the inclusion of tree height to show the best possible fit, but assumed that this equation will not be used for predictive purposes, but only to support what we have discussed about covariates most strongly selected. The IFN model includes a random intercept effect, so in the future, climatic, spatial or plot wise calibrations could be performed to improve the models (Lappi 1991; Miina 1993; Miina 2000; Nanos et al. 2004). By including random effects we obtain more realistic estimates for the fixed effects (Verbeke and Mohlenberghs 2000; Diggle et al. 2002), hence, even for mean fixed effects prediction, estimates are more realistic if we model the random effects. Finally, climate-growth interactions in climate change scenarios and their inclusion in diameter increment models are a must for the future. In this way, climatic calibrations could be tested (Yeh and Wensel 2000) from the basic models proposed in this study as a starting point for describing biological growth. The effect of competition on growth could be also modified if climate changes (Cescatti and Piutti 1998; Yeh and Wensel 2000).

CONCLUSIONS

Although often considered as free grown, we have shown that competition limits holm oak growth to some extent in Iberian open woodlands. Age-dependent models explained circa 50% of diameter increment variation whereas age-independent models explained around 29%. Age was the covariate most correlated with growth, which reflects the reduced competition for light with increased age. This was also supported by the substitution of age by DBH (if we accept that it is closely related to age in the absence of competition) in age-independent models. The analyses of different competition indices showed that density (a simple distance-independent index) outperformed more complex distance-dependent indices. This may be because below-ground competition is limiting holm oak growth in this uniform stands. Our results showed that the distance dependent indices used to estimate competition were in fact not appropriate as they were correlated with subject tree age. Density was selected in all models as the most important competition index, although competition appears to be reduced compared to close forests. Aerial competition is generally minimal as crowns are either isolated or form a unique dominant-codominant layer, however below-ground competition reduced tree growth, especially in densities over 80 trees/ha. Finally, modelling diameter growth with Gamma regression to fit the natural growth trend of increasing variance with increasing growth resulted in more parsimonious models that explained holm oak diameter increment more clearly. These results suggest that data transformations in future empirical models should be avoided and that data should be modelled directly with the most appropriate PDF. This is likely to have great potential for forestry applications.

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ANEXO IV

Gea-Izquierdo G, Cañellas I, Montero G. 2006. Acorn production in Spanish holm oak woodlands. Investigación Agraria, Sistemas y Recursos Forestales 15(3), 339-354.

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Acorn production in Spanish holm oak woodlands

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Abstract

We present a review on the state-of-the-art of fruit prodution in Western Iberia woodlands («dehesas»), and particularly in *Q. ilex* (holm oak) «dehesas». This threatened ecosystem is of very high ecological and economical importance. *Quercus* sp. fruits (acorns) are essential for wildlife, and for pig fattening in «dehesas». In the first part of this review we briefly describe the phenology of the holm oak and the factors affecting acorn morphology and chemical composition. In the second half we analyze the main known factors reported in the literature that determine acorn production: pruning, stand characteristics, and site (weather and soil). We make several suggestions to improve future research and detect the existing gaps in the undertanding of acorn production.

Fruit production is highly variable, both between and within years and individuals. The mean production in «dehesas» (mean density circa 50 trees/ha) is around 250-600 kg/ha (≈100 g/canopy-m^2, CV > 100%). Acorn morphology is also very variable, with mean sound acorn size around 3.5 × 1.6 cm, CV ≈ 10% (3.5 g/acorn, CV > 50%). Silviculture plays an essential role in acorn production. Acorn production per tree seems to be negatively related to density. The effect of pruning is less clear: production seems to be reduced in the first and second years after pruning. After the third year it is not possible to discern from the literature whether there is any response to pruning or not. Weather and soil (site) also impact production and their effects should be explored in future management. The influence of genetics is unknown and should also be addressed. Longer data series are necessary. The dasometric features of the stands need to be characterized, in order to better understand production and compare results from different locations. Much research is still required to understand the functioning of fruiting in these woodlands.

Key words: *Quercus ilex*, holm oak, acorn, fruit production, dehesa, agrosilvopastoral systems.

Resumen

Producción de bellota en las dehesas españolas de encina

El alto interés ecológico y económico de la producción de fruto en las dehesas ibéricas, concretamente las de encina (*Quercus ilex*), nos ha movido a realizar una revisión del estado actual de conocimientos. Los frutos (bellotas) de *Quercus* sp. resultan esenciales para la fauna salvaje y el engorde de ganado porcino en las dehesas. En la primera parte de este trabajo se describen brevemente las características fenológicas de la especie, así como los factores que influyen en la variabilidad morfológica y la composición bromatológica del fruto. En la segunda parte se analizan los factores fundamentales estudiados en la bibliografía que determinan la producción: la poda, las características dasométricas (densidad y distribución diamétrica) y la influencia del sitio (suelo y clima). Se realizan sugerencias para mejorar futuras líneas de trabajo, así como se subrayan áreas de conocimiento deficitarias.

La producción es muy variable tanto intra- como interanualmente. La producción media en las dehesas ibéricas (densidades medias alrededor de 50 pies/ha) es de unos 250-600 kg/ha (100 g/m^2 de copa, CV > 100%), presentando las bellotas una morfología muy variable, con valores medios en bellotas sanas alrededor de 3,5 × 1,6 cm (CV ≈ 10%), correspondientes a 3,5 g/bellota (CV > 50%). Los tratamientos selvícolas juegan un papel fundamental, estando posiblemente la producción de bellota por árbol negativamente relacionada con la densidad de la masa arbórea. El efecto de la poda sobre la producción presenta cierta controversia. Parece que se reduce los primeros uno o dos años, no siendo concluyentes los resultados a partir del tercer año. El clima y el suelo (sitio) también influyen en la producción, aunque sus efectos deben ser estudiados con mayor detalle en futuros trabajos. De igual modo, la influencia del factor genético se desconoce y debería ser estudiada. El nivel de conocimiento alcanzado hasta ahora es del todo insuficiente, siendo necesarias series temporales más largas para caracterizar la producción de fruto. Es estrictamente necesario multiplicar el esfuerzo realizado si queremos llegar a comprender las razones que determinan la producción

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de fruto en este ecosistema y así ser capaces de optimizar de un modo sostenible un recurso tan valioso. La sistematización del modo en que se ofrecen los resultados y el uso de métodos de estimación validados y fiables, resulta fundamental para poder comparar posteriormente diferentes estudios y responder a cuestiones específicas.

Palabras clave: *Quercus ilex*, encina; bellota, producción de fruto, sistema agrosilvopastoral.

Introduction

Acorn production in *Quercus sp.*

Supra-annual variability is the rule among many polycarpic woody plants. Traditionally, this pattern of reproduction, in which there is an intermittent synchronous production of large seed crops by plant populations, has been termed «mast» or «mast-seeding». Mast seeding of woody species is a complex phenomenon that has not yet been perfectly understood (e.g. Herrera *et al.*, 1988; Kelly and Sork, 2002; Rees *et al.*, 2002; Koenig *et al.*, 2003). Two main explanations have been proposed: i) mast seeding is a direct response to environmental variability («resource matching»); ii) it is an evolved reproductive strategy, related to some economy of scale such as wind pollination or predator satiation. These two hypotheses are compatible; masting might be a result of their interaction (Herrera *et al.*, 1998; Kelly and Sork, 2002; Abrahamson and Layne, 2003). Masting seems to be more patent in dominant wind pollinated species and higher in mid-latitudes, paired to the variability of rainfall (Kelly and Sork, 2002; Koenig and Knops, 2000). According to recently published theoretical models, the availability of outcross pollen (pollen coupling) might also be another determining factor in masting (Iwasa and Satake, 2004).

The *Quercus* genus, hereafter oak, is one of the most widespread in the Northern Hemisphere, and is dominant in many forests and woodlands. There is a vast literature in acorn production, the majority from North America. In Europe fewer studies exist despite the great importance of this genus. Particularly in the Mediterranean Region acorns play a basic role in domestic and wildlife feeding and most forests and woodlands are threatened by lack of regeneration. It has been demonstrated for some oak species that climatic conditions during the reproductive stages, from bud initiation to acorn maturation, account for some of the variability in acorn production (Sork *et al.*, 1993; Masaka and Sato, 2002; Abrahamson and Layne, 2003). Some oak species' fruiting patterns can be approached to species specific cycles, meaning either positive or negative annual autocorrelations (synchrony) in annual acorn production. The cycles are partly explained by the acorn maturation pattern, either 1-year or 2-year (Koenig and Knops, 2000; Kelly and Sork, 2002; Liebhold *et al.*, 2004), and are influenced by resource limitations, either light, nutrients or rainfall. So, like mast seeding patterns in other genera, oak acorn production is likely to result from resources interacting with plant endogenous reproductive patterns (Sork *et al.*, 1993; Koenig and Knops, 2000; Kelly and Sork, 2002; Abrahamson and Layne 2003).

Brief review of acorn production estimation methods

Estimating acorn production is a laborious activity as large samples are required and collecting acorns demands a great effort. Different estimation techniques driving to different estimates and indexes of distinct accuracy have been developed, and could be summarized as follows:

Visual surveys

a) Partial or total counts: acorn counts are performed directly from standing acorns on the crown, with the aid of binoculars if necessary. The counts are made during a fixed time period, in sectors of the crown, or in quadrats (Koenig *et al.*, 1994; Garrison *et al.*, 1998; Perry and Thill, 1999). A variation of this method has been extensively applied in [dehesas] (Vázquez *et al.*, 1999), and the traditional way of estimating acorn crops are subjective estimations called «aforos».

b) Score methods: subjective visual estimations are made from standing crops according to ranked categories based on the amount and distribution of acorns in the crown. Several kinds and numbers of scores (generally between 4 and 10 categories) have been used in the literature (Perry and Thill, 1999, 2003; Peter and Harrington, 2002). However, only surveys using fewer than six categories have yielded statistical differences among categories (Perry and Thill, 1999).

Acorn collection

a) Partial acorn collection: acorns are collected in seed traps or quadrats (ground plots) evenly distributed beneath the crown. The number of traps or quadrats is preferably proportional to the crown area (Gysel, 1956; De Zulueta and Cañellas, 1989; Perry and Thill, 1999).

b) Total acorn collection: all acorns reaching the ground, either naturally or man induced by using sticks, are collected in canvases placed beneath the crown (Gysel, 1956).

The election of the estimation method should be based on economy, time, availability of workers, and scientific accuracy required. The visual methods are biased if the procedures are not standardised and the observers well trained before the survey. In traps, only acorns reaching the ground are collected. Therefore the estimation is of acorns available for regeneration and terrestrial animals, rather than total production, since acorn collections are biased from arboreal acorn consumption. If we aim at estimating the total production, every method except the total counts requires a previous estimate to relate either the total acorn production or the production per surface area to the estimative method (scores, counts, traps or quadrats) selected, what adds an extra source of error. As a rule, quantitative methods rather than qualitative should be preferably selected, as more statistical inferences can be applied (Perry and Thill, 1999). Counting methods are more appropriate for wildlife, whereas traps are more appropriate for regeneration (Perry and Thill, 1999) and domestic animals, such as the Iberian pig.

The total collection method is, hence, the most accurate one. Nevertheless, it requires the highest effort and, like all collection methods, does not permit estimating acorn yields in advance. Estimating yields in advance, i.e. counting green acorns in the middle of summer, would be useful e.g. for calculating pig stocking rates in Iberian woodlands, but the actual yield is susceptible to large errors related to irregular weather conditions prior to ripening (e.g., storms, drought, and temperature) and insect infestation. Visual surveys permit estimations in advance of acorn crops. They are more efficient, although they do not detect small differences among individuals and areas. Larger sample sizes can be attained with visual surveys, and can be appropriate to detect from moderate to big differences between individuals and areas (Perry and Thill, 1999). With collection methods, other variables such as incidence of disease, acorn size and weight, and acorn quality can also be analyzed. Although acorn size and weight are frequently neglected in studies of acorn production, we believe that they should be measured in tree subsamples when estimating yields, particularly when using scores. As acorn size and morphology are likely to vary between years and among trees within the same year, the same score can be applied to trees with different acorn features. When using scores, the inclusion of crown size as covariate increases accuracy, as in the way scores are defined, a high ranked tree with a small crown might produce less than the same score in other tree with a bigger crown. Other factors likely to influence acorn estimation are sampling date, whether we consider acorns after or previous ripening, and whether we consider all acorns or just the sound ones.

The holm oak and Iberian dehesas: a Mediterranean anthropic ecosystem

The Mediterranean climate is characterized by large fluctuations in rainfall both within and between years, and by a long summer drought. One of the most abundant *Quercus* tree species in the Mediterranean region is the holm oak (*Quercus ilex* L.). Two main morphotypes have been described, and are variably considered as either two species (*Q. ilex* and *Q. rotundifolia* Lam.), or two subspecies [*Q. ilex* ssp. *ilex* and *Q. ilex* ssp. *ballota* (Desf.) Samp. in Bol.] (Do Amaral, 1990; Barbero *et al.*, 1992; Lumaret *et al.*, 2002). *Q. ilex* ssp. *ballota* (= *Q. rotundifolia*) occurs in Southern France, throughout Iberia, on many islands in the Mediterranean, and in Northern Africa. This evergreen species has broad ecological amplitude, growing in a wide variety of soils within the Mediterranean bioclimate (Afzal-Rafii *et al.*, 1992; Barbero *et al.*, 1992; Lumaret *et al.*, 2002). Throughout the Mediterranean holm oak forests have suffered severe degradation as a consequence of human impacts in history (Lossaint and Rapp, 1978).

In Western Iberia, holm oak occupies large extensions growing either in pure stands or mixed stands, commonly with *Quercus suber* L. (cork oak), *Quercus faginea* Lam., *Quercus pyrenaica* Willd. and *Fraxinus angustifolia* Vahl., as the most conspicuous species. This vegetation community transformed along history by human interaction forms the traditional agrosilvopastoral system called «dehesa» in Spain (Joffre *et al.*, 1988; San Miguel, 1994) and «montado» in Portugal

Figure 1. Broad distribution of «dehesas» (dashed line) and «montados» in the Iberian Peninsula.

(Pinto-Correia, 1993) (Fig. 1). This ecosystem consists of an open-woodland with an understory composed of a mosaic of croplands, grasslands and shrublands, where cattle, sheep, pigs and goats are extensively raised. The dehesas occupy specific geographic and topographic locations that are marginal for agriculture (see Fig. 1 for a broad area of distribution). They are characterized by poor shallow soils (acidic and sandy) with granites and slates as parent materials.

The tree mean density is generally between 30-50 trees/ha, but can vary from isolated trees to complete density (over 100 trees/ha). Pruning to obtain firewood is a traditional activity. In spite of having lost almost all its value, pruning is still quite common because it is traditionally performed and there is a general belief that it increases acorn production (San Miguel, 1994; Gómez and Pérez, 1996). Coppice originated from firewood exploitation is common in the steepest slopes and shallowest soils, and now plays and essential role for wildlife and game species. The ecosystem is in great danger as a result of the changing social and economic structure (Pinto-Correia, 1993; San Miguel, 1994; Gómez-Limón and de Lucío, 1999) and the almost absolute lack of tree regeneration in most stands (Pulido *et al.*, 2001; Leiva and Fernández-Alés, 2003; Pulido *et al.*, 2005). Lack of regeneration is one of the greatest problems of the ecosystem and is likely to become more problematic in the climate change scenarios expected for Mediterranean regions.

Acorns are one of the most profitable products in the dehesa system today, because during the oak fruiting period Iberian pigs are raised extensively feeding on acorns. One animal, fed only on acorns and grass, can consume 7-13 kg of acorns per day while they are in the dehesa, coinciding with the end of their fattening period, when they grow from 100 to 160 kg (López-Bote, 1998; Nieto *et al.*, 2002; Rueda, 2004). Holm oak acorns are preferably consumed than other oak species present. Traditionally, people have selected sweet-acorned trees, as in poor areas even until several decades ago, acorns were still an important food resource for humans in times of scarcity (García-Gómez *et al.*, 2002).

Understanding fruit production in these oak woodlands is crucial in order to achieve a sustainable management assuring regeneration and enhance pig and wildlife feeding. This review is motivated from the extremely high economical and ecological importance of this ecosystem and, particularly, fruit production within the ecosystem. Additionally, we have been encouraged from the many lacks in knowledge we encountered when starting to work in the topic. Although several studies have been conducted in Mediterranean woodlands that explore acorn production, this complex process is still not well understood. In Spain, most studies are at a small scale, sparse and unlinked. In this study, we review the existing literature to determine the current knowledge on oak fruit production, and make recommendations for future research directions. We focus on the holm oak, making comparisons with other ecosystems and, when available, with other species within the same ecosystem. We had to simply discuss qualitatively the bibliography without making any statistical inferences or other quantitative analyses as the data series currently available are too limited. We will first briefly introduce holm oak flowering and fruiting patterns, then analyze the biotic and abiotic factors affecting oak acorn size and acorn chemical composition. Finally we discuss relationships between holm oak acorn production and management and environmental factors.

Flowering and fruiting

Oaks are monoecious species, with separate male and female flowers. Commonly, in some oak species including the holm oak, there are trees that produce almost exclusively female flowers whereas other trees produce male flowers (Sork *et al.*, 1993; Greenberg, 2000). Within the genus *Quercus* two general patterns of acorn development have been described: annual and biennial. *Q. ilex* is traditionally included in the Subgenus *Quercus*, Section *Quercus* (= *Lepidobalanus*). The species included in this group, the white oaks, exhibit an annual pattern of maturation, with acorns maturing around 6 months after pollination (Do Amaral, 1990; Cecich, 1997; Castro-Díez and Montserrat-Martí, 1998). Therefore, the full fruit cycle spans two years: from the spring prior to flowering, when the staminate and pistillate floral buds are initiated, to the autumn of the year when flowers bloom (Abrahamson and Layne, 2003). The time required for the acorn to develop is important because whether flowers mature in 1 or more years influences the acorn production pattern and its relationship to climate (Sork *et al.*, 1993; Koenig *et al.*, 2003). Detailed information on the reproductive morphology of the genus can be found in Kaul (1985).

Weather, especially in spring, affects both flowering and fruiting (Sork *et al.*, 1993; Cecich and Sullivan, 1999). High irradiance is associated with increased flowering in many plants (Peter and Harrington, 2002), which in fruit trees results in differences in flowering and flower morphology depending on the canopy position (Nuzzo *et al.*, 1999). In several oak species there is a positive correlation between acorn crop and total flower crop, which is inversely correlated with colder temperatures in the flowering period (Sork *et al.*, 1993; Masaka and Sato, 2002). Conditions favorable for pollination and fertilization (warm weather, absence of hail and freeze, higher rainfall) are likely to enhance mean annual acorn production (Cecich and Sullivan, 1999). However, the high number of flowers produced many years does not guarantee high acorn crops. Overproduction of flowers and subsequent abortion is a widespread phenomenon (Obeso, 2004). Production of female flowers does not seem to be affected by a certain level of herbivory (Díaz *et al.*, 2004), and according to the same authors herbivory might enhance production of female flowers at the branch level. Stressed trees selectively abort low viable acorns (Díaz *et al.*, 2003), and leaf asymmetry as a reflection of biotic or abiotic stress is related to flower and fruit production (Díaz *et al.*, 2003, 2004). Extreme climatic factors in the acorn growing period, such as drought, or insects can diminish acorn yields.

The holm oak is a wind pollinated dyszoochorous species (Kaul, 1985). The species adapts its phenology to the different environments where it thrives, partly as a response to temperature and water availability. Low air temperature and water stress are limiting factors for bud opening and vegetative activity (Gratani and Crescente, 1993; Gratani, 1996; La Mantia *et al.*, 2003). Holm oaks produce flowers beginning at 8 years old, and start producing acorns when 15-20 years old (Corti, 1959; La Mantia *et al.*, 2003). The flowering flush happens in spring (April-May), and in some years a small secondary flowering occurs in autumn (La Mantia *et al.*, 2003). Acorn growth occurs in summer. Ripening and dispersion occurs from October to February of the same year, varying slightly among locations and years (Castro-Díez and Montserrat-Martí, 1998; Siscart *et al.*, 1999; Nieto *et al.*, 2002; Olea *et al.*, 2004). The establishment of young seedlings occurs during the first spring after acorn dispersion (Siscart *et al.*, 1999; Gómez, 2004; Pulido and Díaz, 2005). In these Mediterranean ecosystems, provisional shade (from shrubs or mature trees) is crucial for the survival of young seedlings (Pulido and Díaz, 2005).

Acorn size and morphology

Most oak studies are based on acorn number estimations (Sork *et al.*, 1993; Abrahamson and Layne, 2003), focused on estimating seed number production rather than fruit crops, per se. Consequently, these studies leave out acorn size and weight, which are important in calculating acorn yields. There is high variation in seed size both within and across oak species (Sork, 1993; Greenberg, 2000). Some authors have suggested the hypothesis that woody species with longer intermast interval are likely to produce larger seeds, likely as an adaptation to increase seedling survival (Aizen and Woodcock, 1992; García *et al.*, 2000; Sork, 1993). It has been shown in some oak species how acorn size correlates positively with the length of its development period and with rainfall (Sork, 1993; Díaz-Fernández *et al.*, 2004).

It is not clear whether seedling establishment is positively related to seed size (Sork, 1993; Díaz *et al.*, 2003; Gómez, 2004). The role of acorn size is controversial: bigger acorns are preferably consumed by predators (Gómez, 2004) including pigs (García *et al.*, 2003), which might hamper regeneration (Leiva and Fernández-Alés, 2003). Seedlings from bigger acorns average higher number of leaves and higher leaf area (Díaz *et al.*, 2003), which might be an advantage for young seedlings. Variability among holm oak individuals in acorn size and weight is high. Holm oak acorn size can vary strongly between years in the same location and between locations (Carbonero *et al.,* 2003; Porras, 1998). The variability of holm oak acorn weight found in the bibliography ranges from 1.2 to more than 6.5 g, and is likely to be explained by tree individual characteristics (genetics), climate, soil properties, and stand structure (Afzal-Rafii, 1992; Porras, 1998). Acorn size seems to be negatively correlated with continentality. Afzal-Rafii *et al.* (1992) report significantly higher mean holm oak acorn weights (around 3.5 g vs. 1.6 g) in non-continental calcareous sites as compared to a continental siliceous Mediterranean climate in Central Spain, although data come from a single year. In Porras (1998), mean acorn diameter (1.60 cm) ranges from 0.69 to 2.07 cm in different locations, which might be related to climate and soil. Gómez (2004) fits acorn weight to a log-normal distribution, with mean varying in two years from 2.25 ± 0.02 g to 2.64 ± 0.03 g, also under a continental Mediterranean climate, however 200 mm more humid in average than Afzal-Raffii *et al.*'s continental site. The reduction of acorn size as a response of the shorter, cooler growing season has been reported elsewhere for other oak species (Aizen and Woodcock, 1992; Díaz-Fernández *et al.,* 2004).

Acorn size and morphology are also likely to be affected by soil properties and stand characteristics. In Álvarez *et al.* (2002) the richest site (foothills) produced heavier acorns during most of the season. Acorn mass in their study ranged from 2.78 to 4.71 g (mean 3.81 g) in the foothills, and from 1.94 to 4.94 g (mean 3.12 g) in the slopes (lower fertility), with acorn weight from holm oaks located in the plains occupying an intermediate position. Additionally, they found heavier acorns in the higher diameter class (DC) trees, with acorn diameter ranging from 2.98 to 4.90 g in DC > 55 cm, and from 1.85 to 3.71 g in DC < 35 cm. However on slopes both the higher tree densities and lower diameter distribution coincided, masking the real influence of each isolated factor. Additionally this study lacks replication. In results from North Eastern Spain, acorn weight in coppice stands (mean around 0.8 g/acorn) is significantly lower compared to isolated holm oaks (mean around 2.9 g/acorn) in a single year (Milla *et al.,* 2002). The studies discussed are only preliminary; the effect of site should be addressed more thoroughly.

Pruning is an additional source of variability in these woodlands. The influence of pruning on acorn size and morphology seems to be minimal (Porras, 1998; Carbonero *et al.,* 2002, 2003; Álvarez *et al.,* 2004), but results are currently inconclusive. The difference between acorn size in pruned and un-pruned trees oscillates between years and stands. Most studies reflect a slight increase in acorn size the first year after pruning, with no effect the following years. In Porras (1998), in some locations the pruned stands produced significant but slightly larger acorns (around 3% in acorn diameter) than the un-pruned stands, whereas other locations show the opposite behaviour. Other authors found similar results. The first year after pruning, Carbonero *et al.* (2003) found an increase in acorn size (trees one year after pruning vs. more than one year after pruning: acorn length 3.8 cm vs. 3.2-3.4 cm; acorn diameter 1.6 vs. 1.4 cm) coinciding with a significant decrease in acorn production in the pruned stands. The second year after pruning acorn production was not different between pruned and un-pruned stands; the difference in acorn length decreases (3.4 vs. 3.2 cm) and acorn width is similar in both stands (around 1.6 cm). A similar effect has been observed in some scrub oaks in North America, where the species with the smallest acorns has the highest number of acorns per bearing ramet (Abrahamson and Layne, 2003). No authors analyzed acorn size and morphology before pruning, so it is not possible to determine whether the differences reported might be partly explained by site and stand characteristics.

Other factors also influence acorn size and morphology. In fruit trees, it is accepted that high light level availability is required for good production. Light availability affects bud quality, by increasing carbohydrate reserves, which positively affects fruit developmental potential (Nuzzo *et al.,* 1999). Following this hypothesis, a difference in acorn size would be expected between crown positions and maybe aspects. Carbonero *et al.* (2002, 2003) did not detect size differences in crown position, although their results were not conclusive and acorns from the south part of the crown were bigger. Throughout the fruiting period, acorn size and acorn dry pulp weight remain constant according to most authors (Carbonero *et al.,* 2003; García *et al.,* 2003; López-Carrasco *et al.,* 2004). Conversely, Álvarez *et al.* (2002) suggest an increase in acorn weight during the fruiting season (total average = 3.32 g), which could be related to insect-infested acorns falling in the first weeks (Soria *et al.,* 2005), or to late ripening. Insects, and to a lesser extent freezing temperatures, have a considerable effect on fallen acorn size. Insect infestation, particularly by *Curculio* *elephas* Gyll., and *Cydia* sp., frequently provokes the early falling of acorns from growth stops as a result of the infestation (Villagrán *et al.*, 2002; Bonal, 2005). It is not clear whether infestation affects size, however it reduces acorn weight. While Soria *et al.* (1996) report a reduction of 4% in mean acorn width (mean 1.54 ± 0.03 cm) and acorn length remains constant (mean 3.42 ± 0.36 cm) in infested acorns, Soria *et al.* (2005) reported bigger infested acorns (2 years: 35.1 ± 0.2 cm × 13.1 ± 0.1 cm; 32.6 ± 0.2 cm × 13.2 ± 0.1 cm), both in length and width, than sound acorns (2 years: 34.6 ± 0.1 cm × 12.4 ± 0.1 cm; 30.4 ± 0.4 cm × 12.3 ± 0.2 cm). Sound acorns are always heavier than acorns injured by insects, sound acorns averaging 3.73 ± 2.10 g and insect infested acorns averaging 2.99 ± 1.79 g (Soria *et al.*, 1996). López-Carrasco *et al.* (2004) report a mean pulp dry weight of 2.55 g for sound acorns with a significant reduction in insect-infested acorns (1.59 g) and frozen acorns (2.25 g). No significant differences have been observed in the effect of the different insect species studied (Soria *et al.*, 1996; López-Carrasco *et al.*, 2004). The average germination rate is reduced in infested acorns, from an average of 2.6% non germinated sound acorns to a mean of 25% non germinated infested acorns (Soria *et al.*, 1996). Pigs selectively consume the biggest acorn sizes according to García *et al.* (2003). These authors report a decrease in acorn size collected on the ground during the fruiting period in plots with pigs (from average 2.75 g to average 1.78 g), whereas they did not detect any differences in plots where pigs were excluded. This reduction in acorn size from pigs feeding coincides with the hypothesis that predator select bigger acorns (Gómez, 2004), and bigger acorns are more likely to be sound. However, we can not exclude from García *et al.*'s study that pigs could be selecting non-infested acorns.

The percentage of kernel/shell ranges from 65 to 79% in the bibliography (Olea *et al.*, 2004; Espárrago *et al.*, 1993). However they only provide preliminary results, Olea *et al.* (2004) observed that, in two years, the kernel/shell ratio was smaller (67.8 against 75.3%) when mean temperatures were warmer (18.0ºC against 16.8ºC) and both annual (888.2 mm against 704.4 mm) and fall (484.8 against 165.2) rainfall were higher. The relation kernel/shell has much interest for pigs and wildlife feeding, as pigs just consume the kernel, rejecting shells. Finally, it should be noticed that not all authors specify whether they report dry matter results when studying either acorn size or production. We will not discuss this point, but it should be kept in mind that it is a potential source of error as the acorn water content varies.

Acorn chemical composition

The nutrient content of holm oak acorns has been widely studied, mostly as a result of the high economic importance of Iberian pigs. Acorn nutrient content values are quite variable in the literature (Table 1), especially when samples are small (Nieto *et al.*, 2002). Acorns have high fat (4-12%) and starch content (more than 50%), but low protein content (4-6%) (López-Bote, 1998. Table 1). However a high fat content seems to be a characteristic of holm oak, the two morphotypes exhibit differences in some nutritional elements: *Q. ilex* ssp. *ballota* has a higher fat content (7.3-11.3%) than *Q. ilex* ssp. *ilex* (3.4-4.2%) (Afzal-Rafii *et al.*,

Table 1. Holm oak dry pulp acorn chemical composition in dehesas according to several authors. Between brackets standard deviations are shown when the authors provided them. Data from Afzal-Rafii *et al.* (1992) are means from location «El Pardo», the only one included in the dehesa range (Northern limit)

Source	**Afzal-Rafii *et al.* (1992)**	**Nieto *et al.* (2002)**	**Cañellas *et al.* (2003)**	**López-Carrasco *et al.* (2004)**	**Olea *et al.* (2004)**
Pulp (%)	—	80.8 (0.4)	—	—	71.5 (4.5)
Dry matter (%)	—	59.3 (0.05)	—	63.5	—
Crude Protein (%)	4.9 (0.1)	4.8 (0.1)	5.0	5.6 (0.7)	4.7
Lipid (%)	6.3 (1.4)	12.1 (0.2)	7.0	11.3 (2.8)	—
Crude fiber (%)	—	—	3.2	0.9 (0.7)	—
Ash (%)	2.2 (0.2)	1.6 (0.1)	2.0	1.8 (0.2)	—
P (%)	0.15 (0.01)	—	0.08	—	0.22
Ca (%)	0.02 (0.01)	—	0.24	—	0.09
Mg (%)	0.04 (0.02)	—	0.07	—	—

1992). Acorns have a high content of oleic acid (> 63% of total fatty acids), and palmitic and linoleic acids concentrations (12-20%). Acorns have a considerable amount of antioxidants such as α-(19-31 mg/kg dry matter) and γ-tocopherol (113-66 mg/kg DM). The latter is in higher concentration in acorns than in grass (63-66 mg/kg DM). These compounds are very important in the pig diet because they affect the Iberian dry ham aging process (Cantos *et al.*, 2003).

The acorn chemical composition can vary depending on several factors. Acorn protein, fiber, fat, C, and P content collected in the ground does not change along the fruiting period (López-Carrasco *et al.,* 2004; Olea *et al.,* 2004). The effect of freezing does not seem to affect the acorn chemical composition. There is a decrease in the acorn fat content in insect infested acorns, while the protein content is not affected by insect infestation. Insects can consume a high proportion of the annual yield (farther discussed below), which would have a negative impact on Iberian pigs as fat is essential in their diet (López-Carrasco *et al.,* 2004). However the effect of acorn position within the canopy which might significantly affect its chemical composition has not been studied. It has been observed in fruit trees that the carbohydrate content of fruits varies according to the position within the crown, responding to light availability (Nuzzo *et al.*, 1999).

The relationship of site and acorn chemical composition has not been studied in much detail. Afzal-Rafii *et al.* (1992) did not find any apparent relationship between soil and acorn chemistry. However, they studied an overall relationship for each location, lacking more specific relationships within site or plot. They detected significant differences in acorn chemical composition between populations within the same morphotype (*ballota* and *ilex*) and among trees within a population, what could be related either or both to individual genetic variability or site. These effects should be addressed in future studies.

Acorn production

Oak acorn production has not been yet well described in any of the species thriving on dehesas. The time series studied are far too short to provide any solid explanation to acorn production. The great variability reported by all authors (Martín *et al.*, 1998; Álvarez *et al.*, 2002; Carbonero *et al.*, 2002; Torres *et al.*, 2004), both between individuals and within individuals between years, is common to most other woody species (Herrera *et al.*, 1998; Koenig and Knops, 2000). From the previously discussed, we might expect the holm oak (as a wind pollinated species) to exhibit a high individual variability, with high population seed production synchrony, that would result in masting (Kelly and Sork, 2002; Koenig *et al.,* 2003). We might also expect an effect of weather and soil nutrient availability, with more pronounced masting in less productive habitats (Kelly and Sork, 2002). However, these trends are still to be demonstrated in *Quercus ilex*.

Synchrony within a species and section (1-year vs. 2-year) and asynchrony among species is common in American mixed oak formations (Sork *et al.,* 1993; Abrahamson and Layne, 2003; Liebhold *et al.,* 2004). This same pattern has been observed in Southern Spain in mixed oak forests and dehesas in seven year data sets. Stands of the same *Quercus* species at close locations exhibited synchrony, whereas asynchrony was found when distinct species (*Q. ilex*, *Q. suber*, *Q. canariensis*) were compared (Martín *et al.*, 1998). This phenomenon would smooth the variability of acorn production within mixed stands as each year there is more probability that at least one species is producing (Sork *et al.*, 1993; Martín *et al.*, 1998; Abrahamson and Layne, 2003).

Production per crown unit area is the most objective way to measure productivity and to compare between different stands and locations. Holm oak acorn annual mean values in the literature in dehesas are between 80 and 300 g/m^2 (Table 2). These figures are higher than productions in forests of NW Spain and SW France reported by Siscart *et al.* (1999). These results (which varied between 15 and 60 g/m^2) were estimated from litter traps. The authors do not specify, but it is likely that the litter traps were not displaced to estimate production per crown unit area, which would explain at least part of the great difference encountered with Table 2. Coefficients of variation over 100% are fairly common in the bibliography. Within the same location it is possible to find individuals with null annual production and trees producing up to 155 kg/tree (Carbonero *et al.*, 2003) or even 300 kg/tree (López-Carrasco, unpublished data). In the northwest foothills of the Sistema Central Range (northernmost range of dehesas, Salamanca province) Álvarez *et al.* (2002) report ranges from 0.1 to 87.9 kg/tree, corresponding to an average of 19.0 kg/tree. These results are similar to some studies, with a tree annual production in 6 years of 20.7 kg/tree (Medina-Blanco, 1963), from the Central West Range of dehesas (Extremadura), but higher than

Table 2. Acorn production of Western Iberian holm oak woodlands according to different authors. Data are averages of several years and different stands. Pruning is not taken into account. Means of annual standard deviations (SD) as naïve estimates of dispersion are between brackets; they were weighted by number of years estimating production when possible. *This work is just an example of a list of studies carried out by the same authors along the last years. See text for farther discussion about these studies

References	Procedence	Estimation method	Sample size (trees)	Sampling design	N.º of years	Stand density (trees/ha)	Mean production		
							(g/crown m^2)	(kg/tree)	(kg/ha)
Porras (1998)	Huelva	Total acorn collection	140	3 sites × 2 pruning treatments/site	From 8 to 2	—	—	22.9 (10.8)	—
Álvarez *et al.* (2002)	Salamanca	Total acorn collection	—	3 × 2,500 m^2 plots	1	25	—	19.0	475
Gómez *et al.* (1980)	Salamanca	Traps	3	—	2	—	86.6	—	—
Escudero *et al.* (1985)	Salamanca	Traps	—	—	3	—	120.1	—	—
Martín *et al.* (1998)	Sevilla	Traps	—	2 × 1 ha plots	7	23	285.8 (194.5)	25.3 (6.5)	
						60	115.8 (83.2)	7.1 (1.9)	
Carbonero *et al.* (2003)	Córdoba	Traps	50	10 trees × 5 pruning years	2	60-78	—	26.7 (5.1)	—
Torrent (1963)	Spain	—	2,000	—	10	—	—	—	587
Medina (1963)	Extremadura	—	—	—	6	—	—	20.8	—
Olea *et al.* (2004)	Badajoz	Traps	20	4 trees × 5 sites	2	20-45	—	—	674.3 (120.4)
García *et al.* (2005)	Extremadura	Visual surveys	2,851	—	1	40	—	12.86 (6.54)	—

other results in that same area (15 kg/tree; Espárrago *et al.*, 1963). In [dehesas] within 8 provinces of Spain, in 10 years, Torrent (1963) visually estimated a mean annual average of 586.4 ± 131.6 kg/ha (this study will be farther discussed later) and similar average values around 550 kg/ha have been reported by other authors (San Miguel, 1994; Martín *et al.*, 1998. Table 2).

The influence of pruning

Assessing the effect of pruning on acorn production is complex; long data series would be required both prior to, and after pruning. Additionally, several types of pruning with different pruning frequencies are applied. Thus, any comparison between two studies will include possible uncontrolled biases coming from the pruning history of the stands. As we previously stated, it is not clear whether pruning enhances acorn production as has traditionally been believed (San Miguel, 1994). It is difficult to obtain any conclusions from the existing studies, as most of them lack many necessary details, e.g. production previous to pruning and stand characterization (especially tree diameter distribution and crown sizes). They also do not study a whole pruning period (between 10 and 20 years) (Gómez and Pérez, 1996; Álvarez *et al.*, 2004). The great variability of acorn production and short datasets mask the influence of pruning. Most authors find a decrease of production the first year after pruning (Porras, 1998; Carbonero *et al.*, 2003; Álvarez *et al.*, 2004; Cañellas *et al.*, in press) that might be related to tree reallocation of resources to rebuild the aboveground biomass. Acorn production results two years after pruning are not conclusive, although it seems that the reduction in acorn production also affects the second year (Porras, 1998). Porras (1998) studied 180 trees divided in three sites in a period of 2 and 6-7 years after pruning. The difference between pruned and un-pruned plots fluctuates between years and stands, although it looks that after the third year the production in the pruned stands increases. In his results the differences were not significant in all years. The differences were clear only when the year production was above the average. In the two sites studied up to seven years, the pruned plots averaged 24.1 ± 15.0 kg/tree-year vs. 18.9 ± 10.8 the un-pruned plots. The authors did not characterize the stands, and since they report acorn production per tree, it is not possible to discern whether these differences are related to other factors such as crown size. Additionally, in one of these sites the production was estimated one year before pruning, and acorn production was higher in the plot to be pruned. In the third stand, studied only up to two years after pruning, the pruned trees averaged significantly lower production than the un-pruned stands (27.8 ± 1.0 kg/tree-year in the pruned; 36.8 ± 8.1 in the un-pruned). Also in dehesas, but in *Q. suber*, Cañellas *et al.* (in press) report a decrease in production per crown unit area up to 5 years after moderate pruning. Acorn production ranged from 0.74 dry matter g/crown-m^2 to 332.85 g/crown-m^2 (average 155.6 g/ crown-m^2 in the un-pruned trees vs. 81.2 g/crown-m^2 in the pruned) and was significantly higher in unpruned trees just the years production was above the average. *Q. suber* flowering and fruiting phenology is more complex than in holm oak (Díaz-Fernández *et al.*, 2004), and this could influence any comparisons between the species.

It is not straightforward to make comparisons between pruning methods, because pruning descriptions are always qualitative. There seems to be an increase when pruning is light (i.e. removing dead and «unproductive» branches) although not significant in Torres *et al.* (2004), which might be a result of the small sample size used. These authors studied acorn production up to three years after different pruning methods. They found the lowest annual mean values in the untreated plot (177.2 ± 293.4 g/crown m^2), and the heavy pruning plot (average 180.6 ± 168.2 g/crown m^2), whereas the most productive were two light pruning plots (269.9 ± 245.5 g/crown m^2). However, these light pruning are seldom applied in practice. Álvarez *et al.* (2004) did not find any difference between two heavy pruning types in holm oaks pruned up to 18 years ago. They do not compare with any plot where pruning was not applied. The effect of pruning on acorn production should be studied in more detail in the future with multi-year data series in stands where acorn production could be estimated several years before pruning (depending on the sample, differences between trees and stands could already exist previous to pruning). We acknowledge the difficulty of performing these experiments, because most stands as they are found today were pruned some time. Pruning provides jobs in rural depressed areas and pruned branches are used as fodder for livestock. However, as the existence of a positive effect of pruning on acorn production has not been observed, and charcoal and firewood are depreciated nowadays, pruning might be unprofitable from an economic point of view.

Tree and stand production

The effect of tree density and stand characteristics

However it has not been studied in depth in «dehesas», acorn production is likely to vary with stand density. Martín *et al.* (1998) estimated a holm oak annual production per crown unit area ranging from 0.5 to 577.2 g dry matter /m^2 (Table 2). Holm oaks in stands of low density (23 trees/ha) averaged higher productions per tree (285.8 g/m^2; 25.3 kg/tree). However, these trees produced less per ha (291.5 kg/ha) than stands with higher densities (59.5 trees/ha), which exhibited the opposite trend (115.8 g/m^2; 7.1 kg/tree; 296.0 kg/ha). The same negative relationship was observed for cork oak stands in the same area: stands with lower density (20 trees/ha) averaged higher production per tree but lower per ha (171.7 g/m^2; 16.9 kg/tree; 250.9 kg/ha) than stands with higher densities from 94 to 253 trees/ha (Martín *et al.*, 1998). The highest mean production per ha (58.5 g/m^2; 399.2 kg/ha) was obtained in the stand with 160 trees/ha, which was located in the more humid and warmer area (Martín *et al.*, 1998). Hence, lower densities seem to account for higher tree production, as a result of increased light availability (Abrahamson and Layne, 2003), and decreased intraspecific competition. Vázquez *et al.* (1996) studied three stands with densities 19, 56 and 133 trees/ha. The stand of middle density averaged the highest acorn production per ha (21.3 ± 32.8 kg/tree), and the stand with lower density the highest acorn production per tree (31.5 ± 3.4 kg/tree). The third plot produced 2.3 ± 0.6 kg/tree. In North America (Healy *et al.*,1999; Perry and Thill, 2003) and Central America (Guariguata and Sáenz, 2002) several oak species average higher productions after thinning, and also it has been shown in two North American *Quercus* species how acorn production decreases with increasing stand basal area (Perry and Thill, 2004). In calcareous holm oak ecosystems in North East Spain, Bellot *et al.* (1992) found mean annual productions of 14.3 ± 11.0 g/m^2 for dense coppice stands. In holm oak closed forests with 1,400 trees/ha, mean dbh (diameter at 1.3 m) 18.0 cm and average height 10-12 m in France, the average reported is 512.3 ± 365.5 kg/ha-year (Lossaint and Rapp, 1978). It is noticeable that the high density forest yields are comparable to the achieved in dehesas with lower density. This indicates the success achieved by this traditional system, in which acorn production seems to be kept at its highest compatible with additional uses such as livestock and cropping.

The stand diameter distribution is also likely to affect acorn production (Abrahamson and Layne, 2003). Tree diameter is directly related to crown volume and age. In other oak species it has been shown that the larger the dbh, the higher the total tree production (Greenberg, 2000), although this is partly related to the greater crown volume. The effect of dbh, crown size, and tree age into production per crown m^2 is not clear. Some authors have stated that trees with dbh under 25 cm are significantly less productive per crown unit area (Greenberg, 2000; Carbonero *et al.*, 2002). This fact could be related to the first age of flowering of trees and maturing of individuals, and should be studied in more detail.

The effect of site

The relationship of acorn production to site characteristics (climate and soil) has been widely reported in other species, meaning that different sites within a taxon can show great differences in acorn production (Kelly and Sork, 2002; Abrahamson and Layne, 2003). In «dehesas» there is also a lack of studies analyzing the effect of site. Álvarez *et al.* (2002) observed differences in acorn production between stands thriving on slopes, plains and foothills. Foothill soils have higher clay and loam content (Puerto and Rico, 1992), and slopes tend to be poorer and more acidic. These plots are very different in density and diameter distribution, which would account for part of the variability. Similarly, Carbonero *et al.* (2004) reported higher production in heavy soils (loamy-clay soils or clay), than in sandy or sandy-loam soils. Siscart *et al.* (1999), in holm oak forests of NW Spain, report an increase in acorn number and biomass in nitrogen fertilized plots. In the same study, irrigation was found to be closely related to fertilization and affected positively annual acorn production just in years with high summer drought. In America, Abrahamson and Layne (2003) also explained part of the variability they found by the occurrence of sandy soils. According to the previously discussed, masting would be likely to be more pronounced in the highest elevations, as lower productivity increases the time required to accumulate resources between high seed crops (Kelly and Sork, 2002; Abrahamson and Layne, 2003). In «dehesas», two authors have studied the relationship between fertility and acorn production (Martín *et al.*, 1998; Carbonero *et al.*, 2004) but neither of them found any significant effect. This can probably be explained by their sampling methodology, e.g., Martín *et al.*, 1998 collected samples just from shallow horizons (10 cm).

The effect of weather on acorn production should also be considered, since its influence has been widely reported for other oak species (e.g., Sork *et al.*, 1993; Koenig and Knops, 2000; Abrahamson and Layne, 2003). We have detected a lack of studies analyzing the relationship between weather and production in Mediterranean oaks. In Southern Spain, Martín *et al.* (1998) did not find any correlation between annual rainfall and acorn production. The lowest annual production in the oak stands he studied coincided with the end of a five-four years dry period, with the minimum annual yield in a site coinciding with the driest and the highest mean temperature year. Maybe the trees are able to reallocate nutrients and resources in bad years, after which they are depleted and need good years to recover and start storing again (Sork *et al.*, 1993; Isagi *et al.*, 1997). This behavior would be particularly important in regions with Mediterranean climates. Intense drought can lead to losing of female flowers (Díaz-Fernández *et al.*, 2004), which would negatively influence both acorn production, and most probably also acorn size for the surviving flowers.

Other factors affecting acorn production

The position within the canopy affects holm oak phenology and flowering (Innes, 1994; Nuzzo *et al.*, 1997; La Mantia *et al.*, 2003). Peter and Harrington (2002) found higher acorn production in the top half of the canopy in *Quercus alba* stands. Carbonero *et al.* (2002) report a non-significant increase in both the outer part and the south facing part of the crown (29.6 g/m^2 in the South-outer; 26.4 g/m^2 in the North-outer; 21.2 g/m^2 in the South-interior; 20.4 g/m^2 in the North-interior) in holm oak trees in dehesas. These differences could be a result of higher light availability (Guariguata and Sáenz, 2002) as acorns in the more shaded branches receive less light for maturation, in a similar way to subcanopy tree species (Kato and Hiura, 1999). Additionally, branches located in different orientations receive different quantities of sap (Infante *et al.*, 2001). Therefore, it might be thought that South and South West aspects would be more productive. This effect has been observed in some North American oaks sites, whereas other stands did not show differences among orientations (Liebhold *et al.*, 2004).

Pre-dispersal and post-dispersal acorn losses owing to biotic and abiotic factors can deplenish year acorn production (Pulido *et al.*, 2005). Insect attack provokes an early fall of acorns (Soria *et al.*, 2005). The negative effect of insects can be very intense some years, with reductions in acorn yield up to 50% (Espárrago *et al.*, 1993; Soria *et al.*, 1996, Cañellas *et al.*, submitted), however these figures are likely to increase some years attending to results in other European oak species (Crawley and Long, 1992). Some authors report an adjustment of some insect life-cycles to two or more year patterns, suggesting that insects would synchronize their diapause to fruit masting (Maeto and Ozaki, 2003). The exudation of sap in acorns, a phenomenon called «drippy nut disease» («melazo») possibly caused transmission of pathogens by insects, is another common source of acorn losses. In García *et al.* (2005) 27.5 ± 10.7 % of trees produced acorns with «melazo», which generally fall earlier from the tree. Finally, Díaz *et al.* (2003) report a negative relationship between the number of acorns/shoot and average leaf asymmetry, a parameter directly related to herbivory. Other activities such as grazing and ploughing could influence acorn production. And tree selection through centuries in dehesas could have led to a genetic differentiation compared to the original forest. However, to our knowledge, no studies have been conducted analyzing the effect of genetic selection and genetic tree variability on acorn production in this ecosystem.

The importance of the estimation method and systematization of acorn results

Finally we would like to make emphasis on the importance of presenting clear complete results, estimated with appropriate, scientifically tested methods. In this study we could not make any inferences and extract clear conclusions from the existing literature, as the results reported in the bibliography are heterogeneous and generally incomplete. The most conspicuous acorn production studies discussed and their sampling main characteristics can be seen in Table 2. We include Medina (1963) and Torrent (1963) studies as the first works found in the literature studying acorn production in this ecosystem. In these studies acorn production was estimated trough traditional visual surveys and in this way some of the results reported are likely to include a big error and, hence, be just mere approximations. We include in Table 2 the study García *et al.* (2005), as an exponent of a list of studies from the same research group, some of them also included in this review (Vázquez *et al.*, 1998, 1999). These authors use visual surveys with a series of ratio corrections. They report production for different tree densities that they calculate proportionally to production estimated for a generic medium density, 40 trees/ha (they multiply by 0.60 and 0.90 to extrapolate to 20 trees/ha and 60-70 trees/ha). Along with Medina (1963) and Torrent (1963), these studies are useful as management plans or informal estimations, but they seem insufficient to be used as a reference to explain acorn production and give an explanation to the factors affecting production, in particular the effect of tree density. Visual surveys have been shown to be useful in some situations, but must be used carefully. It is very important to validate scientifically any method proposed, and in this sense we encourage authors to publish their results in scientific journals that will guarantee the echo of their results.

Other studies showed in Table 2 use more reliable estimation methods, mostly traps. However the method been reliable in most of them, the sampling design is usually insufficient. This makes their results preliminary, and in this way interesting, but it is impossible to compare them to obtain robust conclusions. For all these reasons and as it has been already discussed, most questions posed in this study about the influence of tree density, site, etc., are still to be answered. Acknowledging the difficulty of designing and performing complete and balanced experiments, we believe that more effort should be made to develop longer data series with more balanced, bigger samples.

Conclusions

The most important conclusion from this study should be the need of more detailed, longer studies to explain acorn production patterns in this Iberian ecosystem. The heterogeneity of methodologies and incomplete way in which results are reported in most studies makes impossible the extraction of clear conclusions of any of the factors analyzed. Acorn production is economically and ecologically important enough to deserve more attention that it has received so far. Specific, well designed studies are urgently needed if we want to approach the understanding of this phenomenon and all details involved.

Holm oak acorn production is an extremely variable phenomenon. A variety of factors including weather, soil, genetics, tree density, tree age, and pruning affect production in a way that is not yet well understood. The two first years after pruning, acorn production decreases, but it is not clear whether there is any trend thereafter. It is important to characterize stands in terms of density and diameter distributions; a lack of these stand variables may have masked the results of many studies. Tree production seems to be negatively related with density. However, the optimum density depending on the different objectives pursued in the ecosystem should be studied: the studies analyzing the relationship between density and production are preliminary. With current densities, mean productions around 20-25 kg/tree are common in the literature, corresponding to an average around 250-600 kg/ha. Acorn size and morphology also varies between years, sites, individuals and densities. Mean acorn width values are around 1.5 cm and 3 cm, while acorn weight ranges from 1.2 g to 6.5 g. More research with longer data series is needed, as the comprehension of all factors discussed has shown to be still deficient. Of special interest is to determine the characteristics of great producer individuals. If different sites produced differently, it would be important for management to arrange a fruit index similar to the site-index in traditional forestry.

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ANEXO V

Gea-Izquierdo G, Montero G, Cañellas I. Changes in limiting resources determine spatio-temporal variability in tree-grass interactions. En revisión

CHANGES IN LIMITING RESOURCES DETERMINE SPATIO-TEMPORAL VARIABILITY IN TREE-GRASS INTERACTIONS

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ABSTRACT

Changing biotic and abiotic stress mediate in plant-plant interactions resulting in positive to neutral or negative effects, and these effects can change with gradients of stress or through plant dynamics. In Mediterranean savanna-like open oak woodlands from west Iberia, the presence of trees generally had a positive effect on pasture production in average climatic years although only where soil fertility was low. Facilitation seemed to be driven mainly by nutrient deficiency for pasture growth. However, the interaction changed with increasing abiotic water stress (reduced precipitation). In a dry year, the increase in fertility could not be utilized and the effect of the crown was neutral. The effect of shade turned out to be beneficial for growth, contrary to the situation in an average climatic year when the highest levels of insolation yielded the highest growth in enriched soils below canopies. Soil moisture was lower beneath than outside canopy. Light insolation was positive for legume biomass, which is important for soils and livestock grazing. Legumes were the least abundant functional component but displayed the greatest variability, being dominant in some locations for specific years. Grasses dominate below the canopy, with forbs and legumes being more abundant beyond the influence of the canopy. However, this varies over the course of the growing period as well as from one year to another, thus if sampling is only undertaken at the end of the vegetative period, it may only provide a partial picture of the overall grass composition. Under low levels of other biotic stresses such as livestock grazing or root competition, the limiting factor among light, soil moisture or soil nutrients may determine whether facilitation or competition occurs. The effect of the canopy on the understory is heterogeneous, both in terms of distance to the tree base and orientation. The results of this study would disagree with the stress-gradient hypothesis, as increasing water stress resulted in a neutral interaction and the balance between moisture-light-nutrients changed. This temporal variability in the tree-grass interaction within the ecosystem may be more evident in a climate change scenario.

Keywords: facilitation; competition; legumes; Mediterranean; dehesas; abiotic stress.

INTRODUCTION

Plants compete within ecosystems for resources such as light, water and nutrients. Relationships between plants, whether positive (facilitation), neutral or negative (competition), have been the subject of much attention during recent decades. Formerly, it was believed that increasing abiotic stress favoured facilitation (the so-called stress-gradient hypothesis [Bertness and Callaway 1994]), but recently this relationship has been questioned (Maestre et al. 2005), with current literature providing examples of variable interactions, for example in time or different levels of abiotic or biotic stress. Depending on different ecological factors, the balance of the interaction between the tree and the understory vegetation can sway from facilitation to competition. Within the same system, facilitation and competition can coexist both in time and space making prediction and modelling of plant-plant interactions somewhat complex (Ludwig et al. 2001; Brooker et al. 2008).

The ecological role of trees in low density tree systems has been studied extensively in all kinds of ecosystems, from the tropics to temperate ecosystems (Mosquera et al. 2005). Agroforestry systems share the presence of a woody component, generally not in the form of complete canopy cover, which interacts with understory plants. The overall effect of trees on their herbaceous understory is determined by the balance of both facilitation and competition (Callaway and Walker 1997), and the effect of trees is different depending on the species and stand density, among other factors. Trees increase the nutrient content below their canopies, directly through biomass and atmospheric deposition and leaching (throughfall/stemflow) and indirectly by attracting animals. The soil below canopies has lower bulk density, higher water holding capacity and nutrient content (e.g. Joffre and Rambal 1993; Rhoades 1997), and roots compete for water and nutrients with understory vegetation (Belsky 1994; Ludwig et al. 2004). Precipitation is redistributed by canopies (Bellot and Escarré 1998), trees reduce light availability and soften temperatures (Veetas 1992).

The tree-grass interaction has been studied chiefly from two different angles: (i) from the perspective of grass production in livestock producing systems; (ii) from an ecological point of view either analyzing the role played by the tree in the ecosystem nutrient cycle or tree interactions with other plants. In silvopastoral management, one question currently being asked is: what effect does density have? Most studies have focused on isolated individuals, but in practice, even open woodlands are a combination of clusters of different densities adapted to the microtopography (Puerto and Rico 1992) and shaped by human management. In this regard, Vetaas (1992) emphasized the fact that great care should be taken when extrapolating the results for interactions studied in isolated trees to higher tree densities since tree-grass interactions are unlikely to be lineal.

The ‘dehesas’ in the western part of the Iberian peninsula are an example of an agroforestry system. These are open woodlands dominated by perennial *Quercus* sp. (*Q. ilex* L., *Q. suber* L.) with crops, pastures and shrubland intermixed (Olea and San Miguel 2006). This system was created by humans with a pastoral objective; hence the presence of grazing animals, which play a major role in shaping the landscape. The silvopastoral, rather than agricultural nature of the system, is a consequence of the oligotrophy of its soils under the influence of a Mediterranean climate, with its characteristic summer drought. Water and nutrients are redistributed as a result of the hilly topography leading to a diversification of soils, which in turn creates a mosaic of ecologically different grassland communities (Puerto and Rico 1992; Pérez et al. 1995). These grasslands are composed of different forms of plant-life with different phenologies, particularly annual and perennial species. Thus, the understory vegetation can be summarized as (e.g. Luis 1980; Olea and San Miguel 2006): (i) crops in the best soils; (ii) annual-perennial herbaceous species dominated by grasses in valley bottoms, more fertile and wet non-cultivated soil; (iii) annual-perennial communities dominated by *Poa bulbosa* L. and *Trifolium subterraneaum* L. established through redistribution of nutrients by livestock, mostly sheep; (iv) annual herbaceous species in other non-cultivated soils (where there is no water compensation, as annuals are adapted to summer drought). This, of course, occurs in places where grazing is active and shrub encroaching is controlled, otherwise shrubs tend to colonize (Olea and San Miguel 2006), accompanied by an increase in grassland β-diversity and changes in the previously described communities below trees (e.g. González-Bernáldez 1969; Marañón 1986).

The previously described differences in soil nutrients and moisture availability in the different grasslands, make it unlikely that the interaction with trees will be the same in these understory groups. It might be supposed that they would respond differently as a consequence of the differences in their ecology and particularly, the different soils in which they grow. Facilitation of the herbaceous stratum might prevail particularly in low nutrient soils, which in the Mediterranean usually means annual communities in dry soils. In this study, we draw on existing literature to respond to the following questions: in the temporal scale, (i) do changes in ecologically stressful factors such as very dry years affect the influence of trees on the understory biomass and composition within the same ecosystem?; (ii) does the effect of the tree vary over the course of the year?; and in the spatial scale: (iii) is the interaction of the tree symmetrical within and around its canopy?

Table 1. Summary results of soil attributes (top 20 cm). SD=Standard Deviation. OM=organic matter; CEC=Cation Exchange Capacity; Ca, Mg and CEC are in meq/100 g.

	pH	OM (%)	N (%)	C:N	P (ppm)	K (ppm)	Ca	Mg	CEC	Sand (%)	Clay (%)	Density (g/cm^3)
Mean	5.3	1.2	0.06	16.5	26.9	89.6	1.9	0.3	7.7	84.4	1.3	1.5
SD	0.5	0.4	0.03	7.6	15.1	42.3	1.1	0.1	2.6	4.2	0.3	0.2
Max	6.63	2.3	0.13	47.3	64.8	237.8	5.6	0.7	13.9	91.8	2.4	1.9
Min	4.49	0.4	0.01	8.3	0.0	41.5	0.5	0.1	2.3	70.1	0.8	1.1

MATERIAL AND METHODS

Study area and sampling design

Ten trees were used as replicates at a site in West Central Spain (40ºN 5ºW). Mean tree density was around 10 trees/ha, and always below 30 trees/ha. Trees had a mean diameter (standard deviation in brackets) of 63.5 (26.0) cm, height 8.8 (1.6) m and crown radius 4.9 (1.8) m. The climate is continental Mediterranean, with mean precipitation of 573 mm (September-August period). During the period of the study (2004-2006) annual precipitation (precipitation for March-May in brackets) was 782.3 (214.1), 343.9 (96.5) and 583.0 (205.3) mm respectively, with minimum precipitation registered during the summer period (June-September). This means that 2005 was an extremely dry year whereas 2004 can be considered wet and 2006 average. The mean annual temperature is 15.1 ºC. The soils are generally sandy, and of granitic origin. The top soil is acidic, sandy and has low nutrient and organic matter content (Table 1).

Understory vegetation was composed of annual grassland both below and outside the canopy, dominated by species such as *Ornithopus compressus* L., *Ornithopus sativus* Brot. (these two species are dominant among legumes), *Trifolium campestre* Schreb. (among several other annual *Trifolium* species), *Lolium rigidum* Gaud., *Vulpia myuros K* (L.) C.C.Gmel., *Stipa barbata* Desf., *Bromus diandrus* Roth, *Bromus hordeaceous* L., *Holcus setiglumis* (L.) Gaertn., *Xolantha guttata* (L.) Raf.., *Tolpis barbata* Boiss. & Reu, *Rumex bucephalophorus* L., *Echium plantagineum* L., *Raphanus raphanistrum* L. or *Plantago lagopus* L. Today, grazing is mainly associated with wild animals, especially deer, but traditionally the area was grazed by livestock (sheep and cattle).

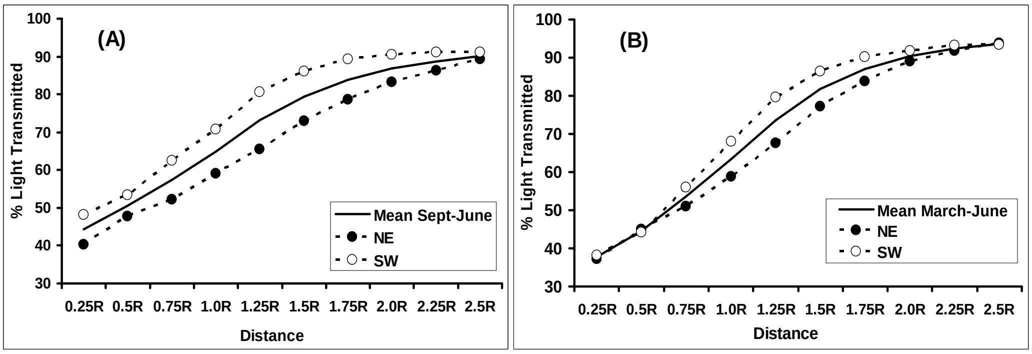

Figure 1. Mean light transmitted in isolated holm oaks in relation to proportional distance to the tree base: (A) complete annual grassland phenological period (21 September-21 June); (B) spring, main growth period (1 March-21 June).

The interaction between the tree and the understory vegetation was studied by analyzing the effect of two factors (independent variables) on the dependent variables herbage yield (‘production’) and grassland abundance (%) of functional groups (grasses, legumes and forbs). The two factors were: (i) distance from the tree (DT), to study the extent of the influence (indirectly reflecting a combination of shade, nutrients, root competition) of the tree; (ii) orientation (OR), to study the differential effect of insolation and the asymmetry of the crown effect. Grazing was excluded by either fencing off the trees or using cages. In 2004 and 2005, 16 sampling points were displaced proportionally to the crown radius (R) within the influence of each tree (hence, from 0.25 times R to 2.0 times R; hereafter 0.25R, 0.5R… and 2.0R) in the most and least shaded aspects: 8 sampling points North-East (NE) and 8 South-West (SW). In the third year of the study (2006) the sampling points were extended to 2.25R and 2.5R for both orientations. Therefore, a total of 200 sampling points per collection date (April and May, resulting in 400 samples in that year) were clipped in 2006 whereas 160 samples per collection date were collected in 2004 and 2005.

Data collection

The herbaceous material was collected in 20x50 cm rectangles in 2004, and 50x50 cm squares the other two years (2005-2006). They were separated into plant functional groups (grasses, legumes and forbs) and then dried for 48 h at 60ºC to estimate the biomass of each group. Sampling points were displaced slightly each year to avoid the influence of previous clippings. Since we were interested in studying within year variability, biomass was collected in mid April and at the end of May to estimate annual yield. Functional groups (hereafter ‘composition’) were separated in May 2004/2006, and April 2005/2006.

Hemispherical photographs were taken from the same 200 sampling points used in 2006. Photographs were obtained in February 2006 and light transmitted was estimated using GLA 2.0 (Frazer et al. 1999). Two periods of radiation were studied: (i) from 21st September to 21st June (‘vegetative period’); (ii) from 1st March to 21st June (‘spring’). To estimate soil moisture, 18x0.5 m tubes were placed on the NE side of three trees at 6 different distances proportional to the crown radius, and moisture was estimated once a month using time domain reflectometry (TDR). Finally, we included temperatures measured around a tree close to our experimental plots. Temperature data were registered at eight probes, 4 placed below canopy and 4 beyond the canopy on the SW side. Data were recorded daily for the period 1996-1999. Probes were situated 30 cm above ground, at ground level, at a depth of 15 cm and at a depth of 30 cm both below and beyond the canopy.

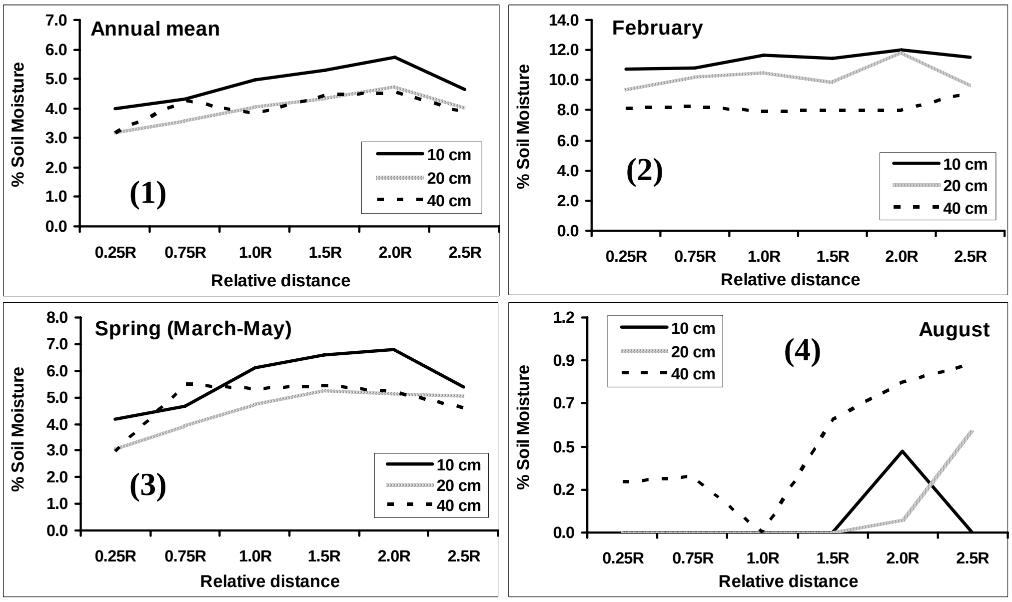

Figure 2. Soil water content in relation to distance to the tree base (measurements from february 2006 to June 2007): (1) Annual mean; (2) maximum moisture content (winter, February); (3) spring (March-May); (4) August (minimum moisture content

Analysis

The dependent variables approached normal distribution. Data gathered included both spatial and temporal correlation; therefore, in order to test for differences between sample points and perform accurate tests, we used linear mixed models with random effects (Verbeke and Moelenberghs 2000). The expression of the model for the dependent variable Y, u tree, v observation would be $Y_{uv}=X_{uv}\cdot\beta+Z_{uv}\cdot b+\varepsilon_{uv}$, where X_{uv} is the fixed effects matrix; β is the vector containing the fixed effects; Z_{uv} is the matrix of random effects associated with that observation; b is the vector containing the random effects associated with the sampling point and is distributed following a normal distribution with mean 0 and variance G; ε_{uv} is the random error term, normal of mean 0 and variance matrix R. The variance function is given by V=ZGZ'+R. All covariates, namely distance, orientation, year, month and their interactions, were treated as independent fixed effects, whereas we included a random intercept (grouping by sampling point) and the R matrix was modelled using a first order autoregressive structure (AR(1)), with submatrixes corresponding to observations within a tree. Wald tests were used to test for significance of variance-covariance parameters. Nested models were compared using likelihood ratio tests with likelihood estimated using maximum likelihood. The final model was fitted using restricted maximum likelihood (Verbeke & Mohlenbergs 2000). To test for differences within fixed effects we used contrasts compared to an F distribution, with degrees of freedom calculated following Kenward and Roger (1997). All tests were at α = 0.05. An estimate of the percentage of variance explained by each covariate was calculated as the difference between the efficiency ($\mathrm{EF}=1-\frac{\sum_{i=1}^{n}(\mathrm{est}_i-\mathrm{obs}_i)^2}{\sum_{i=1}^{n}(\mathrm{obs}_i-\overline{\mathrm{obs}})^2}$) estimated for the full model containing all significant covariates and the reduced model removing one factor each time. Finally, the non-linear relationship (Figure 1) of light interception and distance to the tree was modelled using the coefficients of the relative distance (i.e. 0.25, 0.5,…, 2.5) as dependent variables. All analyses were carried out in SAS 9.1. (SAS Institute Inc., 2004).

	DM	Grasses (%)	Legumes (%)	Forbs (%)
Mean	1901.8	43.1	15.3	41.6
SD	1122.6	27.6	18.9	24.7
Max	5777.0	100.0	95.1	100.0
Min	111.6	0.0	0.0	0.0

Table 2. Summary results of biomass production and grass composition. SD=Standard Deviation; DM=dry matter (kg/ha-year) at the end of the vegetative period (May).

RESULTS

The SW locations received more transmitted light on average over the whole vegetative period, and none of the sampling points were totally exposed to sunlight either throughout the day or the year (Figure 1A). Light intercepted over the whole growth period (September-June) on the NE side was significantly greater than on the SW side (t-value = 8.53; p<0.0001), and the expression was: $\%\text{light} = \exp((4.25182 - 0.108609 \cdot \text{NEdum}) \cdot \text{Dist}^{0.08301})$; R^2=0.851; RMSE=6.828; with 'NEdum', a dummy variable for the NE orientation and 'Dist', relative distance to the tree. In spring, when most grassland growth occurs, the two sampling points closest to and farthest from the tree (0.25R-0.5R and 2.25R-2.5R) received the same light on both sides (Figure 1B).

Soil water was only measured on the NE side, and although accurate estimation of soil water dynamics requires a more intense sampling, our results showed that moisture was greatest in the first 10 cm during winter, spring and fall. In summer the first 40 cm were almost dry, with moisture remaining only in the deepest profile measured (40 cm), particularly at the points farthest from the tree (Figure 2). In general, the closer to the tree the lower the soil moisture was. Average soil surface temperatures were lower below the canopy, with less pronounced maximum and minimum peak values in summer and winter. The annual mean was 14.5±5.8 ºC below canopy (mean maximum temperature 17.0ºC; mean minimum monthly temperature 12.8ºC) and 16.9±9.3ºC outside the canopy (mean monthly maximum, 24.8ºC; mean monthly minimum 11.9ºC).

Table 3. Linear mixed model results. DT=distance to tree base; OR=orientation. σ^2_i (b)=variance component estimate for the random effect. φ (ρ)=estimate for the autocorrelation parameter in variance-covariance residual matrix. **=test significant at α=0.05

	Above-ground biomass (kg/ha)		Grasses (%)		Legumes (%)		Forbs (%)	
	F (df)	p-value	F (df)	p-value	F (df)	p-value	F (df)	p-value
DT	10.11 (9, 145)	< 0.0001**	5.65 (9, 127)	< 0.0001**	2.94 (9, 122)	0.0034**	1.53 (9, 98)	0.1493
OR	27.37 (1, 211)	< 0.0001**	1.39 (1, 139)	0.2409	5.06 (1, 159)	0.0258**	0.10 (1, 172)	0.7465
Year	120.35 (2, 106)	< 0.0001**	34.33 (2, 71)	< 0.0001**	30.47 (2, 71)	< 0.0001**	11.02 (2, 68)	< 0.0001**
Month	98.85 (1, 104)	< 0.0001**	0.05 (1, 67)	0.8311	25.09 (1, 66)	< 0.0001**	12.12 (1, 64)	0.0009**
DT*OR	1.59 (9, 150)	0.1217	1.32 (9, 132)	0.2344	0.50 (9, 128)	0.8698	0.52 (9, 94)	0.8559
DT*Year	3.50 (14, 538)	< 0.0001**	0.45 (14, 357)	0.9554	2.28 (14, 355)	0.0055**	0.88 (14, 341)	0.5756
DT*Month	0.78 (9, 540)	0.6388	1.47 (9, 336)	0.1591	1.54 (9, 335)	0.1310	0.78 (9, 319)	0.6352
OR*Year	11.04 (2, 148)	< 0.0001**	0.78 (2, 105)	0.4628	1.65 (2, 99)	0.1966	0.16 (2, 117)	0.8564
OR*Month	0.02 (1, 149)	0.9019	0.86 (1, 96)	0.3568	1.77 (1, 92)	0.1863	0.02 (1, 96)	0.8989
Year*Month	7.90 (1, 107)	0.0059**	-	-	-	-	-	-
DT*Year *Month	0.45 (7, 526)	0.8695	-	-	-	-	-	-
OR*Year *Month	0.56 (1, 146)	0.4553	-	-	-	-	-	-
DT*OR *Year	1.15 (14, 541)	0.3143	0.77 (14, 361)	0.7035	1.50 (14, 356)	0.1068	0.98 (14, 329)	0.4733
DT*OR *Month	0.24 (9, 534)	0.9890	0.47 (9, 336)	0.8960	1.81 (9, 333)	0.0652*	0.30 (9, 317)	0.9740
DT*OR *Year*Month	0.39 (7, 522)	0.9098	-	-	-	-	-	-
	Z value	p-value	Z value	p-value	Z value	p-value	Z value	p-value
σ^2_i (b)	2.82	0.0024**	2.06	0.0199**	3.07	0.0011**	2.30	0.0106**
φ (ρ)	15.92	< 0.0001**	16.31	< 0.0001**	14.73	< 0.0001**	16.15	< 0.0001**

Average grassland production was higher throughout the vegetative period (in April and May) both below the canopy ($F_{1,415}$=71.42; p<0.0001) and in the sunniest locations (SW) ($F_{1,259}$=22.91; p<0.0001; Figure 3), except for the location closest to the tree base, where production was equal on both sides ($F_{1,228}$=0.03; p=0.8703). The average production was also similar for each aspect at the second closest location to the base of the tree ($F_{1,304}$=0.72; p=0.3968), although in Figure 3 it can be appreciated that the difference fluctuates depending on the year and month. As a rule in Mediterranean ecosystems, production varies greatly in climatically different years. The interaction between DT and year, and OR and year were significant (Table 3; Figure 3), thus differences for each factor varied depending on the other factor categories in different years (hence different precipitation). This variability was produced by the difference results found in 2005, a very dry year (dry spring). That year, mean production was greater below the canopy only in NE locations ($F_{1,223}$=6.80; p=0.0097). The NE orientation was more productive over the whole season (except in April) whereas in the SW locations there was not a significant increase in pasture yield below the canopy ($F_{1,170}$=0.18; p=0.6709). Precipitation was the most important factor, as the effect of 'year' accounted for 49% of the variance explained by the four fixed effects (EF=62.3%), followed by month (28.8%), which reflects the logical growth increase over the life of annuals which occurs in spring. Since only one intercept random effect was introduced, the variance function is additive between the estimated residual and random effect variances; therefore, the calculation of the percentage of the residual variance explained by the random effect was straightforward, giving a result of 22.5 %.

On average, grasses and forbs were dominant in the grassland (Table 2), and tended to play complementary roles, with grasses generally more abundant (on average 0.25R to 1.0R) below canopy ($F_{1,396}$=39.9; p<0.0001) and forbs outside the canopy ($F_{1,322}$=11.93; p=0.0006). Legumes were the least abundant component of the grassland; although they exhibited the highest variability both in space and time (all fixed effects were significant; Table 3). Forbs seemed to be the main component at the beginning of the season, decreasing in importance (in terms of percentage of herbaceous biomass) towards the end of the vegetative season, with grasses and legumes increasing their abundance as the season advances. As with the forbs, legumes were on average more abundant outside rather than below canopies ($F_{1,347}$=10.59; p=0.0012) and were also more abundant in SW locations compared to more shaded NE locations ($F_{1,83}$=51.7; p<0.0001). These results clearly show the preference of legumes for spots with high levels of irradiance.

Grassland composition also varied significantly from one year to another (Table 3). In 2005 there was an increase in grasses in all locations ($F_{1,74.7}$=40.9; p<0.0001) and the difference below canopy and beyond canopy was less evident, especially in the case of the NE locations. Although interactions were not significant for grasses (Table 3), Figure 4 suggests that the results for 2006 differed in the proportion of grasses below canopy for the two orientations. Furthermore, although on average (2004-2006) there was no difference between the two orientations (Table 3), in 2006 there were more grasses to the NE than to the SW below the canopy ($F_{1,79}$=16.11; p<0.0001), whereas this difference was not significant beyond the canopy in that year ($F_{1,78}$=0.06; p=0.8127). For grasses and forbs, the respective decrease or increase in production with increasing distance to the tree appears to be continuous up to 2.5R in an average year (Figure 4), particularly to the NE: thus, the influence of the crown goes beyond the crown border, probably due to the influence of shade (or some other factor indirectly influenced by shade) on the composition. The large increase in legumes recorded in 2006 ($F_{1,83}$=51.7; p<0.0001), directly following the dry year, is a noteworthy occurrence. In 2006, legumes increased from an average of 3.8% in 2005 to 26.7% (33.4% in May 2006, 40.1% to the SW in May 2006; 54.4% at 2.25R to the SW in May 2006. [Figure 4]).

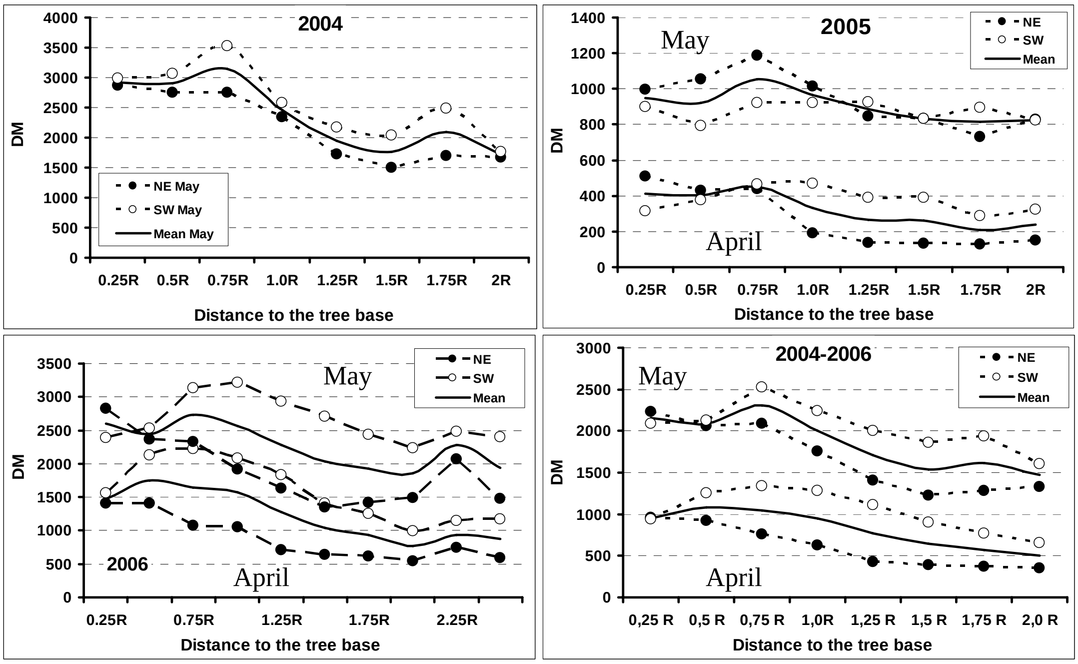

Figure 3. Pasture production by distance and orientation in the three years of study. DM=dry matter (kg/ha).

The percentage of variance explained by the random effect was 20.1% in grasses, 25.2% in legumes and 20.9% in forbs. In the case of grasses, the efficiency of the four fixed effects was 44.2%, of which 48.7% is explained by year. In legumes, the year comprised 75.4% (of a total of 46.6% explained by the four fixed effects) and 46.0% (of 22.7%) in forbs.

DISCUSSION

Facilitation and competition coexist within the same system and can alternate depending on the ecological factor which most limits growth (Belsky 1994; Ludwig et al. 2001; Brooker et al. 2008). Von Liebig´s Law of the Minimum (Von Liebig 1840, cited in Koerselman and Meuleman 1996) states that site fertility for individual plants is governed by the availability of the limiting nutrient. The variability found (Brooker et al. 2008) could mean that growth response to the addition of a limiting nutrient might be extrapolated to any other limiting factor, not only nutritional, such as moisture or light availability (Ludwig et al. 2001). Organic matter, nitrogen, potassium, calcium or magnesium are increased below canopy (González-Bernáldez et al. 1969; Rhoades 1997; Gallardo 2003). In our study the soil is sandy, acidic and has a low nutrient content (Table 1). These characteristics, together with the summer drought typical of the Mediterranean climate, are generally associated with annual grasslands, which in our results were also located below canopies (although some scattered perennials also exist such as *Dactylis glomerata* L., among others).

In Mediterranean ecosystems, the water content generally recovers in fall, bringing the soil close to field capacity until the end of spring, when it decreases until July as the soil dries out (Joffre and Rambal 1993; Cubera and Moreno 2007). The effect of the tree on soil moisture seems to be variable depending on the ecosystem (Vetaas 1992), so it should not be generalized that trees increase or decrease moisture availability below canopies. We found a moisture decrease below canopy for all months, and this decrease was smallest in winter, when the soil was likely to be at its field capacity. The decrease detected in moisture below canopy coincides with some studies conducted in the same ecosystem (Cubera and Moreno 2007) but not others (Joffre and Rambal 1993). Some of the differences might be a consequence of our soils being sandier (generally the first 20 cm are loamy sand) or of differences in precipitation (Cubera and Moreno 2007). Two main factors reduce water below canopies: (i) rainfall interception and redistribution by the canopy (Bellot and Escarré. 1998), although this is likely to be of less importance than in closed forests and temperate climates (Joffre and Rambal 1993); (ii) competition for water from tree roots. There are many examples of reduced moisture below canopy in other ecosystems (e.g. Jackson et al. 1990; Belsky 1994; Ludwig et al. 2004). However evaporation of soil moisture is likely to be lower below canopy, the balance of ETP is likely to be negative for the tree-grass component compared to only grass and soils below canopy have been reported to have higher field capacity, as the tree-grass component is subject to a great evaporative demand (Joffre and Rambal 1993). Whether this could vary in different conditions is a matter which needs to be addressed.

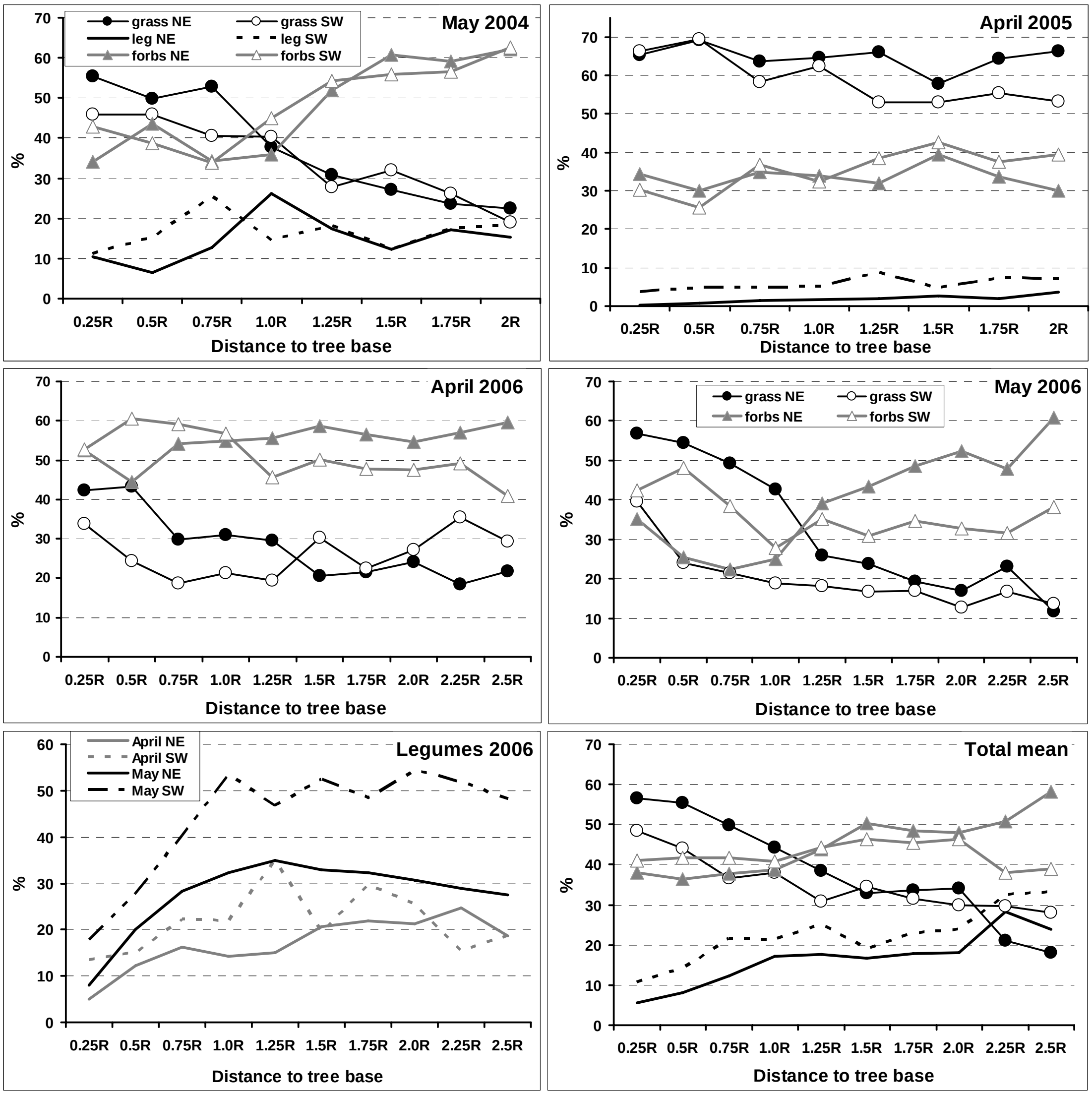

Figure 4. Mean percentage pasture composition by distance and orientation in the three years of study. Grasses are represented by black solid line with circles (dark, NE; white, SW); Legumes by solid line (NE) dashed line (SW); forbs are represented by grey solid line with triangles (dark, NE; white, SW). Legumes are shown in an independent graph in 2006 to ease the interpretation.

The reduction of light by the canopy in spring was similar in both orientations for the two locations closest to and farthest from the tree, with all other southern locations receiving more radiation. The maximum reduction of solar radiation was around 40%, which is similar to results from isolated savanna trees (Veetas 1992). The reduction of light irradiance by the canopy reduces mean temperature values and temperature oscillation by increasing minimum temperatures in winter and decreasing maximum temperatures in summer with respect to locations beyond the canopy. Thus, it follows that the higher the amount of radiation intercepted, the greater the modification of the microclimate (Eviner and Chapin III 2003). Modification of temperatures by trees may be playing an important role in grass ecology, for example as the limiting factor in winter (Vetaas 1992).

Variability in time and space can be considered the rule, both in terms of production and composition in these Mediterranean grasslands. The presence of the tree increases plant diversity in the ecosystem (e.g. González-Bernáldez et al. 1969; Marañón 1986; Puerto and Rico 1994). Pasture yield was within the range found in other studies conducted in the same ecosystem (Olea and San Miguel 2006), and on average, herbage biomass increased below the canopy. Facilitation by nutrient enrichment counterbalanced competition for water and light interference in an average year. Abiotic stress associated with light and nutrients is subordinated to water availability in this ecosystem, as is commonly the case in arid and semiarid ecosystems. Microsite benefits are only apparent when enough water is available to profit from other factors such as nutrients (Maestre et al. 2005), and this might be generalized if any other limiting factor exists. This is similar to other nutrient poor ecosystems, like some African savannas where different nutrients might limit pastures beyond canopy (N) and below canopy (P) when there is enough light below canopy and available water (Belsky 1994; Rhoades 1997). Therefore, depending on the climate and ecosystem (soil, stand density), the balance between facilitation and competition can result in an increase in pasture yield (e.g. Belsky 1994; Rhoades 1997), have no effect (e.g. Ludwig et al. 2004; Thevathasan and Gordon 2004) or lead to yield reduction (e.g. Somarriba 1988).

Locations receiving more light (SW) produced significantly more, reflecting the fact that, in an average year there is no water limitation to annuals in spring, hence they are able to fully utilize nutrient availability and energy. Previous literature on the subject describes the reduction in understory production as a result of excessive shade, even in nutrient rich soils in the absence of drought (e.g. Somarriba 1988). In the ecosystem studied, it seems that the positive effect of trees (facilitation) is most evident in poor soils; hence, these are usually colonized by annuals. In annual-perennial grassland communities in valley bottoms and fertilized crops or grasslands, the balance is negative (competition), reducing understory growth with respect to locations beyond the canopy (Montalvo et al. 1980; Moreno 2008). In the very dry year, the relationship between the tree and the understory production changed, with the most shaded (NE) locations exhibiting the highest growth. In the dry year, the pasture community was unable to utilize the increased fertility below the canopy, and the production was homogeneous both below and beyond the canopy in the sunniest locations (SW). This seems to point towards not only the previously described spatial heterogeneity of pasture production but also a temporal variation depending on the interaction between precipitation and light. The positive effect of light increases in soils with a higher nutrient content. This is particularly evident in studies analyzing the effect of removing trees or absence of competition from dead trees when there is enough precipitation (Bartolome et al. 1994; Jackson and Ash 1998; Ludwig et al. 2004). More production has also been linked to increasing precipitation in other studies within Mediterranean dehesas (Moreno 2008) and African savannas (Belsky 1994). However, Moreno (2008) found a positive effect of shade on herbage growth. In the aforementioned study, the positive effect of shade was recorded at 50% light reduction, equivalent to distance 0.75R, where the maximum growth was registered. Our results would disagree with the ‘stress-gradient hypothesis’ (Maestre et al. 2005, 2006). Facilitation is mainly driven by an increase in soil fertility that will only be beneficial if there is enough water and light for photosynthesis, assuming that root competition from woody vegetation is counterbalanced.

The legume content of plant systems is important because legumes fix atmospheric nitrogen which increases soil fertility, and their high protein content is readily accepted by grazing animals (Hauggaard-Nielsen and Jensen 2005). They are used as an index to estimate pasture quality within the system (Olea and San Miguel 2006). Shade reduced the abundance of legumes whereas in given years or locations it could increase the biomass of grasses. There was an increase in the proportion of legume dry matter over the course of the season, with accumulation of ‘effective growing days’ (Henkin et al. 1998). Forbs do not seem to have a clear response to shade, but rather, appear to be outcompeted by grasses in high nutrient soils. Grasses are dominant in more eutrophic conditions below the canopy and in soils with the highest nutrient content in the system like those found in foothills (Marañón 1986; Pérez et al. 1995), which generally lead to an increase in biomass production. Legumes constitute the fraction which shows the greatest variability (Luis et al. 1980; Pérez et al. 1995) and temporal variability is also evident throughout the life cycle of annuals: forbs were dominant at the beginning of the growing season, with grasses and legumes increasing their presence later, although this varies in other studies (Pérez et al. 1998), probably as a result of different species composition. The preference of legumes for sunny conditions was evident. The effect of the tree was asymmetric, with SW locations displaying a higher presence of legumes. A positive correlation also existed between the abundance of legumes and distance to the tree base. The variables studied also displayed high variability within the canopy (Figure 1). In some years, ‘poor quality’ pastures (from a pastoral point of view) such as those studied, can contain a high proportion of legumes, which is positive for livestock grazing and soil enrichment (Hauggaard-Nielsen and Jensen 2005). Regarding the variability in plant composition, the most important factor was the year, i.e. the climate in the current as well as in previous years, which influences the interannual variations in plant development and seed bank dynamics in this Mediterranean ecosystem.

There are still some unresolved issues regarding tree-grass interaction. Since the biomass of functional groups changes over the course of the vegetative period. Studies where samples are only taken at the end of the vegetative period may miss certain species and therefore the results regarding the abundance of functional groups might be biased. The role played by competition from tree roots is not assessed in this study, but is likely to be influential in the reduction of available soil moisture and hence, reduce growth (Callaway et al. 1991; Ludwig et al. 2004; Moreno 2008). Tree root distribution varies according to the ecosystem; species, climate and soil, and deep extensive root systems are more likely in woody species growing in dry climates, like that of the Mediterranean (Canadell et al. 1996; Jackson et al. 1996). Holm oaks seem to have both deep and shallow roots (Moreno et al. 2005; Moreno 2008). The existence of inhibition associated with allelopathic relationships has been documented in some ecosystems (Callaway et al. 1991). However, this has not been studied in ‘dehesas’. The effect of livestock grazing has not been analyzed in this study either, and overgrazing may shadow the influence of the tree.

In this study, we have centred on functional groups. However, if individual species management were required, it is possible that certain aspects of species specific behaviour would differ from the behaviour of the functional group. Additionally, it is necessary to determine how long it takes for a tree species to have an impact on the characteristics of the upper soil horizons or if trees can establish in sites which are already enriched in soil nutrients (we believe this to be very improbable in the ecosystem studied). The positive effect of nutrient enrichment will be ineffective if tree density is high. It is important for reforestation in this silvopastoral system, to monitor the changes in soil and the impact upon the understory of the different stages of stand development. Shifts from positive or neutral effects to negative effects and viceversa have been found in aridity gradient studies in other plant-plant interactions (Broker et al. 2008). All these aspects should be taken into account in future silvopastoral models including different climatic scenarios.

CONCLUSIONS

The interaction between trees and understory vegetation is a complex phenomenon, as facilitation, interference and competition relationships are involved. The presence of the tree seems to facilitate understory grassland growth by increasing soil nutrients in the nutrient limited ecosystem studied, whereas trees also act as competitors by reducing light availability and by root competition. The balance of facilitation-competition for herbage growth tends to be positive if there is no water limitation during growth (as is the case in Mediterranean annual grassland spring growth on average years) in nutrient-limited ecosystems. The grassland studied seems to be mostly nutrient-limited, and this might be generalized to annual grasslands in the western part of the Iberian Peninsula. Pasture production and the composition of functional groups are variable not only in space but also in time, both within and between years. Legume biomass responded negatively to shade and plant groups were displaced asymmetrically around trees, both within the canopy and around the tree. The contemplation of plant-plant interactions in a simple form in theoretical or management oriented models is not easy due to their complexity and variability. Factors such as light, nutrients, and moisture (ETP) interact within the ecosystem, and the one (or combination) which acts as a limiting factor may determine the understory growth and dynamics. Results from single periods or sites should not be extrapolated to all annual plant stages and sites.

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ANEXO VI

Gea-Izquierdo G, Allen-Díaz B, San Miguel A, Cañellas I.

Tree influence upon mediterranean annual grassland nutrient variability. Manuscrito

TREE INFLUENCE UPON MEDITERRANEAN ANNUAL GRASSLANDS NUTRIENT VARIABILITY

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Abstract

The tree component in agroforestry systems and open woodlands produces spatial and temporal heterogeneity in nutrient cycling, growth and composition of surrounding grasslands. The tree introduces ecological modifications to soil and microclimate, creating heterogeneous gradients of nutrient availability, solar radiation and precipitation redistribution. In this study we analyze the heterogeneity in nutrients and variables of pastoral interest induced by trees in West Iberian Mediterranean open woodlands on a sandy and acidic site. Although mineralization measured by the C:N ratio was not higher in locations receiving more radiation, OM and consequently N, K, Ca and Mg were significantly greater in SW orientations, and there was an increase in OM and all macronutrients (except P) below canopy. The presence of the tree increased soil N, K, Ca, Mg, and CEC, similarly to other studies. Clay content increased in those soils receiving most radiation probably as a result of '*in situ*'clay formation and pH was highest below canopies when compared to the acidic grassland outside. These two results are relevant as they are not reported in other similar studies, probably responding to very low soil pH (≈5.5) and bedrock. Contrary to what it was expected, plant nutrient concentrations did not directly reflect those found in soil, with the exception of K. There might be interactions among nutrients and deciding which is limiting was impossible to detect in this study. The interactions might be responsible for the absence or reduced spatial heterogeneity plant in some nutrients, although there might be other explanation (e.g. botanical composition, soil type). Thus, the studied annual grassland responded to increased nutrient availability by enhancing growth rather than increasing plant nutrient concentrations. Hence there are more total accumulated nutrients in the ecosystem below canopy than outside but mostly as a consequence of plant growth enhancement rather than higher nutrient concentrations. Temporal variability, particularly within the year (plant maturity stage), explained most of the variability in annual plant nutrient concentration, with spatial variability induced by trees of secondary importance. The effect of orientation was not significant, and phenology was likely to be responsible for some reported differences. Plant levels of Ca, Mg, and Na decreased during the drought year, which could have implications if global water stress increases. The spatial and temporal heterogeneity of this oak savanna ecosystem is of interest for both ecological modelling and the management of silvopastoral systems.

Keywords. Dehesa; silvopastoral system; livestock and wildlife feeding; facilitation; competition.

INTRODUCTION

Growth of individual species can be limited by different nutrients (Koerselman and Meuleman 1996; Barker and Pilbeam 2007). The Von Liebig´s Law of the Minimum (Von Liebig 1840, cited in Koerselman and Meuleman 1996) states that the effects of site fertility on individual plants are governed by the availability of the limiting nutrients. Since there is a growth response to an addition of a limiting nutrient, this response could be extrapolated to any other factor that is able to limit growth, such as moisture or light availability. Also, within the same community, different species are likely to respond differently to the same stimuli, and different variables, e.g. biomass growth or nutrient concentration could respond distinctly.

Facilitation and competition processes play a basic role in ecology. They can coexist in time and space within the same system, thus prediction and modelling of plant-plant interactions is not straightforward (Ludwig et al. 2001; Brooker et al. 2008). In ecological systems such as savannas and open woodlands, a tree stratum coexists with either or both an herbaceous and shrub strata, hence understanding plant-plant interactions among strata is a crucial step in modelling the ecosystem.

Trees modify the nutrient content of soils below their canopies through litterfall deposition and leaching (from plants, dry deposition and throughfall/stemflow), and indirectly through the activity of animals (e.g. Escudero et al. 1985; Rodá et al. 1999; Olea and San Miguel 2006). However, not all nutrients are affected identically to the presence of trees. Nutrient response seems to be dependent of tree species, climate or soil type. There is an increase in nutrients in upper soil organic matter (OM) below the canopy, together with an increase in total nitrogen (N), calcium (Ca), potassium (K) and magnesium (Mg). These nutrients are very correlated with OM and in the case of Ca, K and Mg also with leaching (e.g. Chapin III 1980; Rodá et al. 1999; Brady and Weil 2002). Variables such as soil pH or phosphorus (P) vary in different studies (e.g. Rhoades 1997; Rodá et al. 1999; Ludwig et al. 2001; Eviner and Chapin III 2003; Gallardo 2003). Explaining the variation in some elements is not an easy task. Depending on factors such as plant community type (e.g. annuals, perennials), climate or soil bedrock, the nutrient cycle is likely to vary, and utilization of nutrients by plants can obscure differences in nutrient availability if only analyses of soil data are used (Rodá et al. 1999; Ludwig et al. 2001).

Trees reduce solar radiation availability to understory vegetation as trees intercept light. Roots compete for water and nutrients with understory vegetation (Belsky 1994; Ludwig et al. 2004) and precipitation is redistributed by canopies (Rodá et al. 1999). This leads to a series of interactions depending on the variable of interest (i.e. biomass, nutrients, etc). These interactions affect biogeochemical cycles within savanna ecosystems (Eviner and Chapin III 2003) and are important for plant growth and distribution, for livestock and wildlife management, and even for greenhouse gas (GHG) cycles as in the case of N or C.

The most extended landscape in Western Iberia is open woodland of perennial *Quercus* sp. (*Q. ilex* L., *Q. suber* L.) with crops, pastures and shrubland intermixed. This system has been created by humans with a pastoral objective, and its characteristics have been widely described in the literature (e.g. Joffre et al. 1988; Olea and San Miguel 2006), including the variability and dryness of the climate (summer drought characteristic of Mediterranean climate). Soils are generally of low fertility, most often originated from granites, quartzites, schists and slates. Thus it is important to understand the possible sources of increased fertility, such as redistribution of nutrients by topography or trees (e.g. Puerto and Rico 1992; Gallardo 2003). In this system, as a consequence of the multiple strata present, plant-plant interactions are of main interest in system modelling and for understanding savanna dynamics. The understory is composed mostly by two ecological types of herbaceous communities, with different phenology and composition; (i) annual-perennials, either thriving in the most fertile and humid soils (foothills, ‘vallicares’) or in soils where fertility has been increased by livestock (sheep) management (‘majadales’); and (ii) annual species, thriving in the poorest and driest soils. Many studies in tree-understory interactions, either from an ecological or pastoral scope, have been conducted in more productive annual-perennial communities whereas fewer studies in less productive annual grasslands have been published (e.g. Montalvo et al. 1980; Puerto and Rico 1996). Despite the same climate, nutrient cycles in these two different ecological systems are likely to vary, and plant-plant interactions are likely to be different. In this study, we examine the poor, low fertility annual grass/tree ecosystem.

Besides macronutrients such as N, P, K, Mg and Ca, which are important both for plant and animal nutrition, there are other variables important for animal feeding such as micronutrients like Cu and Fe, different types of estimation of fibre content and minerals like Na (De Blas et al. 1987; Barker and Pilbeam 2007). In this study, we will examine Cu, Na, Fe and ash content of plants, neutral detergent fibre (FND, mostly and estimation of cellulose, hemicellulose, lignin and silica), acid detergent fibre (FAD the same as FND but without hemicellulose) and lignin, which are related to cell wall content and hence herbage palatability (De Blas 1987; Vázquez de Aldana et al. 2000).

We are also interested in the influence of trees on the nutrient content concentration of the herbaceous annual understory vegetation, and we discuss the differences with other plant assemblages within the same ecosystem and other ecosystems under different macroclimates. We first study the modification of spatial soil properties influenced by the presence of trees on a location in Western Spain, then discuss the relationship with differences in spatial and temporal variation found in plant nutrient contents of an herbaceous community sampled several years at different distances from the base of isolated trees.

MATERIAL AND METHODS

Study area and sampling design

Ten trees were used as replicates in an open woodland in West Central Spain (40ºN 5ºW). Stand mean tree density was around 10 trees/ha, and tree mean diameter (standard deviation in parenthesis) was 63.5 (26.0) cm, height 8.8 (1.6) m and crown radius 4.9 (1.8) m. The climate was continental Mediterranean, with mean precipitation 573 mm (September-August period) and March-May mean precipitation 150 mm. In the period of study (2004-2006) annual (March-May in parenthesis) precipitation was 782.3 (214.1), 343.9 (96.5) and 583.0 (205.3) mm respectively. Understory vegetation was annual grassland both below and outside the canopy, dominated by species such as *Ornithopus compressus* L., *Vulpia myuros* K (L.) C.C.Gmel., *Helianthemum guttatum* (L.) P. Mill., and *Rumex bucephalophorus* L.

The interaction between the tree and the understory vegetation was studied analyzing the response of soil and plant nutrients as dependent variables to two independent factors, namely: (i) distance from the tree (DT), to study the spatial extent of the influence (indirectly shade, nutrients, competition) of the tree; and (ii) orientation (OR), to study the differential effect of solar radiation and the asymmetry of the crown effect. Grazing (mostly wild animals) was excluded either by fencing trees or using cages. In 2004, 16 sampling points were placed proportionally to the crown radius (R) within each tree (hence, from 0.25 times R to 2.0 times R, hereafter 0.25R, 0.5R,…, and 2.0R) in the most and least shaded aspects: 8 sampling points North-East (NE) and 8 in the South-West (SW). Proportional distances to the tree base were sampled to assure that the sample design is representative of any tree regardless of its size. This resulted on 160 samples that were used to study the spatial variation in plant nutrients. In addition, we studied the temporal variation in plant nutrients in both locations (below canopy, beyond canopy). Sampling was comprised of two samples (0.5R-0.75R, ‘below’; 1.75R-2.0R, ‘beyond’) per orientation (hence, four/tree) were analyzed in 2005 and 2006.

Data collection and chemical analyses

The herbaceous material was collected in 20x50 cm squares in 2004 and 50x50 cm squares the other years, and dried 48 h at 60ºC. Sampling points were slightly moved each of the three years to avoid influence of previous clipping. Plant material was collected in mid April, final May (varying slightly between years depending on year phenology, to estimate annual yield) and July only in 2006 in the NE to analyze the lowest nutrient content of plants and discuss their potential for livestock and wildlife grazing in summer.

Table 1. Soil data in relation to canopy and orientation. Below canopy are means of 0.375R and 0.75R. Beyond canopy vertical influence are calculated as average between 2.0R and 2.5R.

		Below canopy		Beyond canopy		Total mean		
		NE	SW	NE	SW			
pH	Mean	5.674	5.798	4.978	5.014	5.325	Max	6.630
	SD	0.420	0.483	0.312	0.269	0.499	Min	4.490
OM (%)	Mean	1.467	1.631	0.744	0.941	1.165	Max	2.290
	SD	0.333	0.394	0.231	0.205	0.421	Min	0.350
N (%)	Mean	0.072	0.078	0.036	0.048	0.056	Max	0.130
	SD	0.025	0.040	0.012	0.018	0.029	Min	0.010
C:N	Mean	15.173	16.038	16.986	16.932	16.508	Max	47.270
	SD	2.463	10.416	5.748	10.216	7.635	Min	8.310
P (ppm)	Mean	26.792	31.100	28.025	21.275	26.917	Max	64.800
	SD	17.040	15.595	15.293	12.601	15.056	Min	0.000
K (ppm)	Mean	102.478	150.588	57.003	60.700	89.600	Max	237.780
	SD	34.784	40.323	10.205	10.707	42.300	Min	41.450
Ca (meq/100 g)	Mean	2.572	3.251	0.804	1.348	1.859	Max	5.590
	SD	1.018	1.391	0.247	0.402	1.141	Min	0.460
Mg (meq/100 g)	Mean	0.348	0.478	0.135	0.203	0.274	Max	0.720
	SD	0.116	0.142	0.042	0.073	0.146	Min	0.080
CEC (meq/100 g)	Mean	8.685	9.663	6.703	6.849	7.678	Max	13.910
	SD	2.323	2.937	1.893	2.630	2.616	Min	2.340
Sand (%)	Mean	85.020	84.412	86.192	82.496	84.386	Max	91.833
	SD	3.841	2.878	3.329	5.491	4.181	Min	70.085
Silt (%)	Mean	12.564	14.619	12.667	16.063	14.340	Max	27.493
	SD	3.641	2.910	3.182	5.054	3.928	Min	7.214
Clay (%)	Mean	1.224	1.362	1.141	1.440	1.274	Max	2.422
	SD	0.267	0.256	0.195	0.449	0.323	Min	0.785
Density (g/cm^3)	Mean	1.396	1.378	1.664	1.559	1.501	Max	1.883
	SD	0.138	0.154	0.157	0.137	0.173	Min	1.082

Table 2. Results from linear mixed model with plant macronutrient concentration and Cu as dependent variables. DT=distance to tree base; OR=orientation. σ^2_i (b)= variance estimate for intercept random effect. Toeplitz=value for the log-likelihood ratio test (χ^2) testing the model with Toeplitz residual variance against the same model but with variance components residual variance ($I \cdot \sigma^2$). July is not included in the analyses to balance the data. $^+$Toeplitz covariance structure (Verbeke and Mohlenberghs 2000).

Parameter	N (%)		P (%)		K (%)		Ca (%)		Mg (%)		Cu (ppm)	
	F (df)	p-value	F (df)	p-value	F (df)	p-value	F (df)	p-value	F (df)	p-value	F (df)	p-value
DT	3.95 (1, 40)	0.0538*	1.40 (1.08)	0.3042	122.28 (1, 62)	<0.0001**	26.92 (1, 77)	<0.0001**	3.96 (1, 22)	0.0595*	0.76 (1, 48)	0.3892
OR	1.32 (1, 37)	0.2589	0.91 (1, 40)	0.3470	0.00 (1, 65)	0.9603	0.04 (1, 44)	0.8373	0.50 (1, 35)	0.4829	0.57 (1, 48)	0.4536
Year	2.29 (2, 76)	0.0801*	6.77 (2, 96)	0.0018**	3.21 (2, 28)	0.0553*	19.22 (2, 27)	<0.0001**	28.36 (2, 30)	<0.0001**	24.07 (2, 102)	< 0.0001**
Month	48.28 (1, 15)	< 0.0001**	66.65 (1, 95)	< 0.0001**	132.20 (1, 11)	<0.0001**	60.27 (1, 9)	<0.0001**	108.13 (1, 14)	<0.0001**	37.37 (1, 98)	< 0.0001**
DT*OR	0.90 (1, 32)	0.3509	0.40 (1, 47)	0.4979	0.01 (1, 67)	0.9183	0.10 (1, 68)	0.7504	0.47 (1, 31)	0.4989	0.05 (1, 48)	0.8250
DT*Year	0.08 (2, 54)	0.9270	4.27 (2, 96)	0.0167**	4.17 (2, 69)	0.0196**	5.22 (2, 63)	0.0080**	0.80 (2, 79)	0.4544	4.65 (2, 102)	0.0117**
DT*Month	35.82 (1, 13)	< 0.0001**	16.19 (1, 95)	0.0001**	17.64 (1, 30)	0.0002**	6.68 (1.15)	0.0204**	3.03 (1, 22)	0.0962*	2.40 (1, 98)	0.1245
OR*Year	4.94 (2, 44)	0.0116**	3.89 (2, 96)	0.0238**	5.56 (2, 70)	0.0057**	1.79 (2, 45)	0.1794	2.29 (2, 56)	0.1106	1.44 (2, 102)	0.2418
OR*Month	0.77 (1, 16)	0.3938	10.89 (1, 95)	0.0014**	2.49 (1, 28)	0.1261	3.39 (1, 37)	0.0738*	3.72 (1, 33)	0.0623*	0.43 (1, 98)	0.5129
DT*OR *Year	1.06 (2, 47)	0.3536	0.54 (2, 96)	0.5836	0.60 (2, 61)	0.5519	0.63 (2, 53)	0.5359	0.34 (2, 48)	0.7125	0.26 (2, 102)	0.7722
DT*OR *Month	0.08 (1, 30)	0.7851	0.01 (1, 95)	0.9130	0.41 (1, 40)	0.5281	0.06 (1, 32)	0.8099	0.62 (1, 38)	0.4356	3.31 (1, 98)	0.0720*
	test value	p-value	test value	p-value	test value	p-value	test value	p-value	test value	p-value	test value	p-value
σ^2_i (b)	2.37	0.0090**	2.56	0.0052**	0.69	0.2442	0.51	0.3064	1.32	0.0933*	0.20	0.3980
Toeplitz	13.90	0.05298*	10.40	0.1670	20.20	0.0051**	28.20	0.0002**	24.80	0.0008**	1.80	0.9371

Table 3. Results from linear mixed model with plant micronutrients and variables of pastoral interest as dependent variables. DT=distance to tree base; OR=orientation. σ^2_i (b)= variance estimate for intercept random effect. Toeplitz=value for the log-likelihood ratio test (χ^2) testing the model with Toeplitz residual variance against the same model but with variance components residual variance ($I \cdot \sigma^2$). When $^+$ means that it is a compound symmetry matrix instead. July is not included in the analyses to balance the data.

Parameter	FND (%)		FAD (%)		Lignin (%)		Fe (%)		Ash (%)		Na (%)	
	F (df)	p-value	F (df)	p-value	F (df)	p-value	F (df)	p-value	F (df)	p-value	F (df)	p-value
DT	2.10 (1, 80)	0.1510	0.01 (1, 50)	0.9402	0.07 (1, 55)	0.7964	0.08 (1, 34)	0.7806	0.21 (1, 55)	0.6481	0.05 (1, 62)	0.8298
OR	0.84 (1, 80)	0.3630	3.49 (1, 55)	0.0670*	0.05 (1, 51)	0.8277	0.05 (1, 63)	0.8309	3.54 (1, 70)	0.0640*	0.10 (1, 83)	0.7583
Year	1.01 (1, 18)	0.3282	8.17 (1, 24)	0.0087**	51.25 (1, 30)	< 0.0001**	35.22 (1, 27)	< 0.0001**	30.71 (2, 45)	< 0.0001**	22.75 (1, 34)	< 0.0001**
Month	43.80 (1, 80)	< 0.0001**	22.69 (1, 15)	0.0002**	22.04 (1, 17)	0.0002**	38.41 (1, 13)	< 0.0001**	75.37 (1, 25)	< 0.0001**	19.00 (1, 18)	0.0004**
DT*OR	0.44 (1, 80)	0.5110	0.00 (1, 45)	0.9867	0.10 (1, 49)	0.7543	0.02 (1, 48)	0.8809	0.41 (1, 74)	0.5256	3.21 (1, 53)	0.0790*
DT*Year	0.12 (1, 80)	0.7326	0.12 (1, 50)	0.7313	3.88 (1, 55)	0.0540*	3.03 (1, 34)	0.0910*	3.32 (2, 74)	0.0417**	3.74 (1, 62)	0.0578*
DT*Month	6.98 (1, 80)	0.0099**	4.60 (1, 27)	0.0412**	3.17 (1, 30)	0.0854*	7.11 (1, 25)	0.0133**	5.75 (1, 40)	0.0213**	5.28 (1, 31)	0.0285**
OR*Year	3.68 (1, 80)	0.0587*	5.11 (1, 55)	0.0278**	4.12 (1, 51)	0.0475**	1.42 (1, 63)	0.2386	2.55 (2, 80)	0.0845*	2.91 (1, 83)	0.0920*
OR*Month	1.81 (1, 80)	0.1825	16.49 (1, 18)	0.0007**	19.70 (1, 22)	0.0002**	1.40 (1, 22)	0.2498	20.51 (1, 29)	< 0.0001**	2.07 (1, 24)	0.1635
DT*OR *Year	0.38 (1, 80)	0.5402	0.01 (1, 45)	0.9216	0.03 (1, 49)	0.8547	2.26 (1, 48)	0.1390	0.03 (2, 73)	0.9662	2.76 (1, 53)	0.1027
DT*OR *Month	0.44 (1, 80)	0.9596	0.04 (1, 30)	0.8514	0.07 (1, 39)	0.7966	2.62 (1, 25)	0.1183	0.06 (1, 54)	0.8031	0.02 (1, 34)	0.8801
	test value	p-value	test value	p-value	test value	p-value	test value	p-value	test value	p-value	test value	p-value
σ^2_i (b)	0.33	0.3704	-	-	-	-	0.19	0.4241	-	-	1.27	0.1021
Toeplitz	13.40^{+}	0.0371**	22.90	0.0018**	32.90	< 0.0001**	9.60	0.0019**	25.90	0.0005**	26.00	0.0005**

In May 2006, soil data were collected from the top 20 cm of soil in 72 points from 6 trees, at 6 distances proportional to the crown radius (from 0.375R to 2.5R) in the same two orientations (NE, SW). Soil data to estimate bulk density were collected in October 2007. Soil samples were air-dried, then sieved (<2 mm) and analyzed for organic matter (OM) by the Walkey-Black method, total nitrogen (N) by the Kjeldahl method; phosphorus (P) by the Bray procedure; potassium (K), calcium (Ca), magnesium (Mg), and cation exchange capacity (CEC), extracted from an acetate solution; pH, C:N ratio and particle size (following USDA Standards; Brady and Weil 2002). Plant nutrient content was analyzed for N; P, K, Ca, Mg, copper (Cu) all years and iron (Fe), sodium (Na) only in 2005-06; neutral-detergent fibre (FND), acid-detergent fibre (FAD), lignin by the digestion method; and ash by the loss on ignition method at 550ºC.

Statistical Analysis

Data gathered included both spatial and temporal correlation so, to accurately test for differences between sample points and as dependent data could be approached to the normal distribution we used linear mixed models (Verbeke and Mohlenbergs 2000). Data from 2004 were analyzed testing 'DT', 'OR' and the interaction, only modelling the residual variance-covariance matrix with a first autoregressive structure (AR(1)), with submatrixes corresponding to observations within a tree. When data from the period 2004-06 were analyzed (distance coded just as 'below' or 'beyond'), month and year (and their interactions) were also tested, and the linear model also included a random intercept effect to account for the temporal correlation. In this case the residual variance-covariance matrix (R) was either not specified (hence it was just $I\cdot\sigma^2$) or had a Toeplitz structure when the nested log-likelihood ratio test was significant (Mohlenberghs and Verbeke 2000). More details on this second statistical analysis and the sampling structure can be found in Gea-Izquierdo et al. (Submitted). Finally, whenanalyzing the dependent variables of pastoral interest, the R matrix had a more simple compound symmetry structure or Toeplitz(r) (Mohlenberghs and Verbeke 2000). To test for differences within fixed effects we used contrasts compared to an F distribution. Degrees of freedom were calculated following Kenward and Roger (1997), and all tests were at α = 0.05.

RESULTS

Tree effects on the spatial variation of nutrients in annual grasslands

The studied soils have very low nutrient content (Table 1). Soil nutrients were clearly dependent on the distance from the tree, as expected. Except in areas of high sand content at α=0.10 ($F_{5,501}$=2.14, p=0.0756), no DT*OR interaction was significant (e.g. for OM, $F_{5,46}$=0.52, p=0.7609; for pH, $F_{5,48}$=1.30, p=0.2792) Thus conclusions from categories of fixed effects can be extracted from all categories of other effects. OM decreased with distance from the tree until the crown edge (Figure 1. $F_{1,62}$=18.57, p<0.0001), and was similar in positions beyond the canopy ($F_{1,62}$=1.44, p=0.2351). The other soil nutrients directly related to OM followed a similar pattern, with the exception of soil-P, which did not show any significant difference with distance from the tree ($F_{5,57}$=1.37, p=0.2478). Soil-P exhibited high variability in the studied soil (Table 1).

Soil-N ($F_{1,62}$=13.51, p=0.0005), soil-K ($F_{1,61}$=28.05, p<0.0001), soil-Ca ($F_{1,62}$=60.43, p<0.0001), soil-Mg ($F_{1,60}$=51.09, p<0.0001), and CEC ($F_{1,62}$=7.48, p=0.0081) decreased almost monotonically with distance below the canopy. Sampling points located outside the vertical crown projection, hence, the area least influenced by litterfall, did not show significant differences. pH also clearly decreased with distance from the tree ($F_{1,62}$=42.46, p<0.0001) and similar to the previously discussed nutrients, (except soil-P), was highest in the location closest to the tree base.

Bulk density showed the opposite behaviour, increasing with distance from the tree ($F_{1,46}$=29.20, p<0.0001), presenting maximum values in the farthest locations from the tree base. This increment in density can be explained by differences in soil texture and the variation in OM described. Clay content was very low and did not change significantly with distance ($F_{5,56}$=0.94, p=0.4597).

Differences in solar radiation resulted in significant differences in availability of most soil nutrients, generally more nutrients with more insulation (Gea-Izquierdo et al. Submitted). There was more OM in the SW than in the NE ($F_{1,24}$=6.79, p=0.0155), and this increase in the SW was also found in soil nutrients that have a direct relationship with OM, such as N ($F_{1,28}$=5.82, p=0.0226), K ($F_{1,22}$=10.03, p=0.0073), and Mg ($F_{1,22}$=9.47, p=0.0056); with Ca ($F_{1,22}$=3.13, p=0.0904) and bulk density ($F_{1,28}$=3.05, p=0.0918) being significant at α=0.10. In spite of what is suggested by Figure 1, soil-P was not significantly different between orientations ($F_{1,31}$=0.01, p=0.9070) as a consequence of the high variability reported; pH ($F_{1,26}$=0.09, p=0.7686), and CEC ($F_{1,27}$=1.64, p=0.2108) also did not yield significant differences between orientations. Finally, texture varied with solar radiation; there was more clay in the SW orientation ($F_{1,27}$=5.11, p=0.0320), whereas sand was only different between orientations outside the canopy ($F_{1,25}$=5.20, p=0.0312), with NE locations having more sand, complementary to silt (data not shown). Finally, the previous differences in OR or DT were not accompanied by significant differences in mineralization conditions as estimated by the C:N ratio. This ratio did not show any apparent trend either between orientations ($F_{1,29}$=0.06, p=0.8148) or distance ($F_{5,53}$=1.20, p=0.3237), although it is remarkable that variability was much higher with increasing radiation (Table 1), both in orientation and position with respect to the crown.

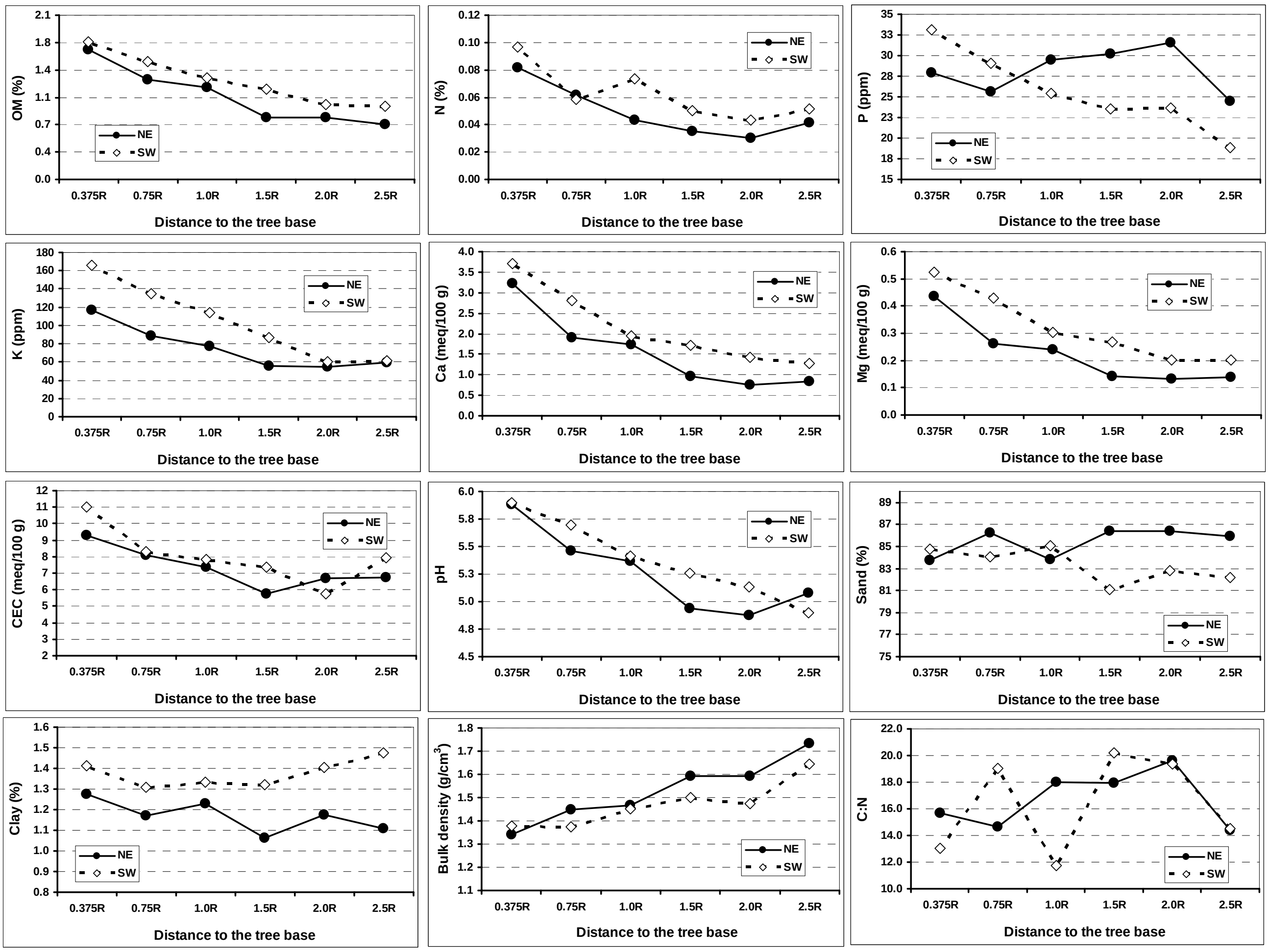

Figure 1. Soil characteristics in relation to distance to tree and orientation.

The higher levels of most soil nutrients found in SW locations and the closer to the tree base did not imply higher levels in plants in May 2004 (when sampling was more intensive to study spatial variation around trees) in those locations. No OR*DT interaction was significant for any plant nutrient in 2004 (e.g. $F_{7,113}$=1.23, p=0.2906 for N). Nitrogen in plants did not follow the same patterns found in soil-N: there was a slight increase of N with distance significant only at 10% ($F_{7,119}$=1.80, p=0.0926), we will discuss later a variation with sampling date. The effect of orientation was non-significant ($F_{1,46}$=0.14, p=0.7081). The only nutrient clearly decreasing with distance from the tree bole in understory plants was K ($F_{1,100}$=34.17, p<0.0001). This decrease was similar in both orientations ($F_{1,42}$=0.07, p=0.7884) and evident both below and beyond the canopy. Conversely, plant-P seemed to increase with distance to the tree only in the NE, in this way the contrast between both orientations excluding 0.25R, 0.5R and 2.0R was significant at α=0.10 ($F_{1,41}$=3.63, p=0.0638). Plant-Ca contents were significantly higher in the two positions closest to the tree ($F_{1,106}$=5.21, p=0.0244), with no difference between orientations. Plant-Mg was not significant with distance ($F_{7,130}$=0.96, p=0.4601) or orientation ($F_{1,44}$=1.25, p=0.2692). However, some of these relationships were modified when analyzing them in different years, as discussed below. Finally, Cu was significantly greater outside canopy than in positions closest to the tree, particularly in the NE ($F_{1,85}$=5.69, p=0.0193), but this seemed to be highly variable, as it will be discussed below.

Tree effects on the temporal variation of nutrients in grasslands

As expected, there was a strong decrease in all plant nutrients as the season progressed (hereafter referred as plant maturity, plant age, phenology or stages of physiological development). This effect was true regardless of location with respect to the canopy (Figure 3; Table 2). For this reason, the small differences between orientation or years were difficult to analyze, as they could just reflecting differences in phenology in locations receiving different insulation (indirect effect of canopy light interception) rather than a response to increased soil nutrients. The significant interactions found in N (Table 2) suggested that the effect of orientation changed with different years and the effect of distance changed with plant age. It seemed that in the early vegetative months (April) the pasture below the canopy contained more N ($F_{1,40}$=21.75, p<0.0001) whereas in May and July the pasture outside the canopy seemed to have higher N levels (Table 2), although this was not significant ($F_{1,76}$=1.08, p=0.3019). Orientation was only significant in 2006 ($F_{1,30}$=1.08, p=0.3019), with the SW having more N than the NE.

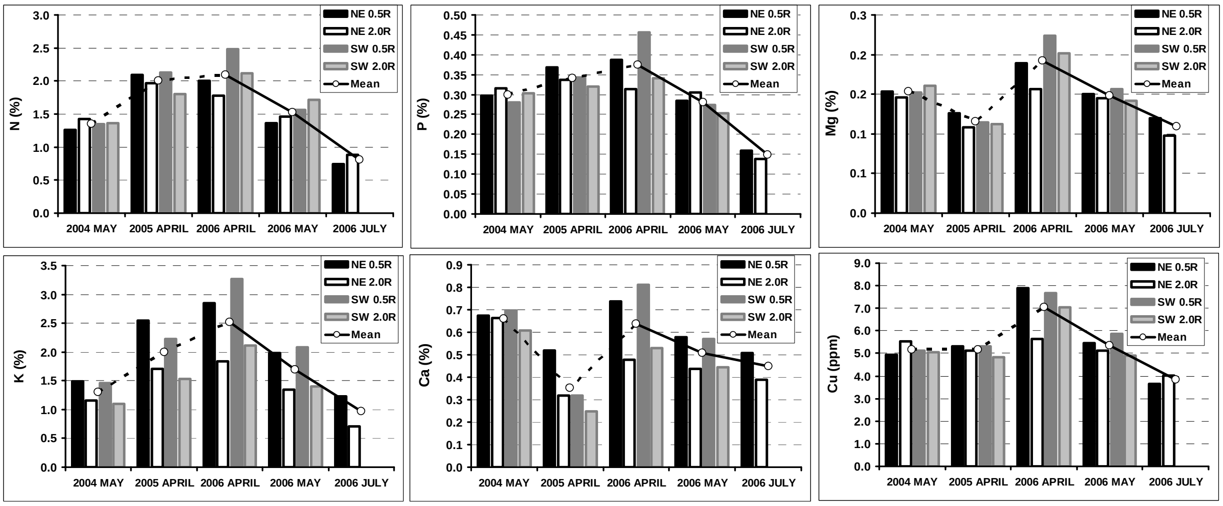

Figure 3. Temporal variation in plant nutrient content (I): macronutrients and copper. Solid lines depicting the mean annual decline along the growing season in 2006. Dashed line serve as a reference for mean values in 2004 and 2005, where only one sampling was carried out.

Plant-P did not show any clear trend with distance or orientation. There were significant interactions (Table 2) most probably related to differences in phenology between orientation or years. Those interactions including ‘month’ had the most significant tests, and month was by far the factor yielding greatest differences. Although there were interactions in plant-K, it can be seen that tests for DT and ‘month’ were clearly significant. Besides the decrease with phenology in plant-K levels, it was clear that plants below the canopy had significantly more K than plants outside (Table 2; Figure 3). The interactions in plant-K were responding to greater differences in earlier sampling (April), but the difference was event significant in July ($F_{1,68}$=11.16, p=0.0014) when grass is dry.

When analyzing plant-Ca, again there were significant interactions involving month and year, but only with distance: Ca was more abundant in plants below canopy (Table 2. Figure 3) but this was not significant all sampling dates, for instance July ($F_{1,39}$=0.64, p=0.4303). Plant-Ca levels decreased with phenological stage (Figure 3. Table 2) and in 2005, the dry year, plant-Ca levels were significantly lower ($F_{1,34}$=32.78, p<0.0001). Finally, in plant-Mg the most important factors were again differences in phenology (decreasing Mg with time) and, the same as Ca, in the dry year the Mg levels were the smallest ($F_{1,34}$=32.78, p<0.0001). There were no interactions at α=0.05 in Mg, and month and year were significant (Table 2). Distance was significant only at α=0.10, the same as the interaction with month (Table 2) reflecting that the Mg contents are likely to be greater in plants growing below canopy, as it was seen in April 2006 (Figure 3) and July ($F_{1,59}$=4.34, p=0.0417), but this increase is not consistent in all dates.

Finally, there was no difference between orientation in Cu (Table 3), with most variability being related to sampling month (Table 3), hence plant age. There was an increase in plant Cu with distance to the tree only some years (Table 3). In this way, there was more Cu in plants below the canopy in April-May in 2006 ($F_{1,141}$=13.44, p=0.0003) but not in July ($F_{1,158}$=0.38, p=0.5390), whereas it was not significant in 2005 ($F_{1,141}$=0.34, p=0.5587) and only at α=0.10 in 2004 ($F_{1,141}$=2.97, p=0.0872) if analyzed pooled.

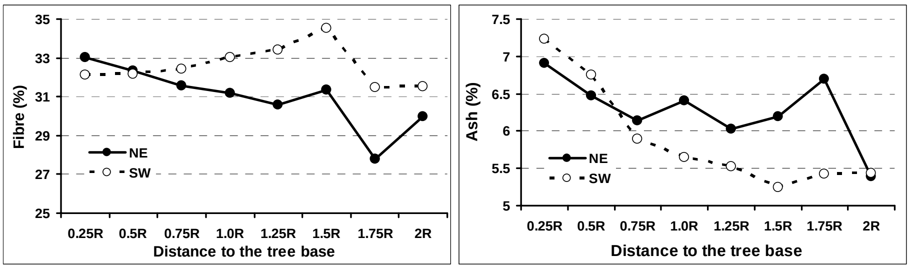

Figure 4. Spatial variation in plant nutrient content in year 2004 (II): crude fiber and ash.

Implications for livestock and wildlife grazing

Fibre and ash were analyzed in 2004 to study the spatial variation between canopy and open (Figure 4). Crude fibre significantly decreased that year with distance from the tree ($F_{7,89}$=4.82, p<0.0001) in the NE orientation ($F_{1,29}$=4.45, p=0.0452). Ash decreased with distance ($F_{7,120}$=4.93, p<0.0001), being greater in the NE outside. These two differences with orientation were probably responding to differences in plants' stage of physiological development. The decline in pasture quality along as the growing season progressed (as it was also seen above for N, P, K, Ca, Mg and Cu) resulted in lower Fe, Ash and Na, and higher FND and FAD into the summer (Figures 3, 5). Both FND and FAD greatly increased with plant age; month was the factor explaining the most variance, especially in FND. Lignin fluctuated from April to July (Table 3; Figure 5) with the most variance explained by year. In 2005, the dry year, lignin was significantly lower ($F_{1,28}$=54.01, p<0.0001; Table 3; Figure 5). There were no differences between orientation in FND (Table 3) and although FND used to be greater the canopy, this was only significant in May ($F_{1,86}$=7.45, p=0.0077). FAD levels were most related to month (Figure 5; Table 3), and plants growing below the canopy had lower levels of FAD which was only significant in April ($F_{1,54}$=4.09, p=0.0482). There was no difference in lignin with distance from the tree bole (Table 3).

Fe, ash and Na responded differently, but all responded to temporal variation and not spatial variation. In 2005 (the dry year) plant mineral levels were significantly lower than in 2006 (Figure5; Table 3). In Fe, ash and Na there were no differences between orientation or distance, and although there were significant interactions involving DT (Table 3), we did not detect any clear trend (Figure 5) as a consequence of the differential response of the position 2.0R in NE in 2006. Finally, both ash (F_{179}=4.83, p=0.0309) and Na were greater below the canopy in July, although this difference was not significant in Na ($F_{1,65}$=0.99, p=0.3223). Fe levels were similar both below and beyond the canopy when the pasture was dry.

DISCUSSION

Tree influence on spatial soil nutrient variability in Mediterranean open woodlands

The impact of a tree species on soil fertility is likely to vary depending on the type of bedrock, climate and forest management (Augusto et al. 2002). The negative correlation with distance from the tree of top-soil OM, N, K, Ca and Mg found is a constant in the literature (e.g. Puerto and Rico 1988; Rhoades 1997; Gallardo et al. 2000; Gallardo 2003; Moreno et al. 2007). Here we only analyze the top 20 cm of the soil, thus when we speak about soil modifications we can not assess whether these modifications are also found at depth or not, although the influence of trees upon soil tend to be maximum in the upper soil (Augusto et al. 2002). Trees modify the soil beneath them, but the time necessary for a tree to modify soil properties at depth is something to be addressed, as tree influences on soil increases with age (Ludwig et al. 2001). The influence of the gradient in light, temperature and nutrient input from the tree base goes beyond the crown limit. In some nutrients, particularly in the SW, the decrease with distance goes beyond the canopy projection and is spatially heterogeneous and asymmetric. Summer water stress is the key in Mediterranean ecosystems, but precipitation induced stress is likely to be secondary in annual grasslands in comparison to nutrient availability and soil texture, as annuals have adapted to drought through ephemeral life cycles centred in the rainy periods.

The increased fertility with the presence of the tree is positive in the studied nutrient limited ecosystem both for plant development and animals. The increase in OM with proximity to the tree is related to litterfall deposition (Escudero et al. 1985), and this is likely to increase levels of other nutrients, especially N, which depends mostly on organic inputs (Rodá et al. 1999; Brady and Weil 2002; Barker and Pilbeam 2007). Ca, Mg, K and P depend not only on organic inputs but also inorganic (bedrock, precipitation, dry deposition), with K being particularly increased by throughfall/stemflow (canopy leaching) as a result of its high solubility and mobility, followed by Ca and Mg (Escudero et al. 1985; Rodá et al. 1999; De Schrijver et al. 2007). It seems that, independently of the substrate, holm oak litterfall chemical composition is in average (leaves, bark, wood, twigs, inflorescences, fruits) particularly rich in Ca, followed by N, K and Mg, with P content being lowest compared to the other macronutrients (Escudero et al. 1985; Rapp et al. 1999; Rodá et al. 1999).

Deficiency in P is common in many soils around the world (Brady and Weil 2002). The lack of clear trends found in soil-P is not in accordance with most other studies within the system, that report higher P supply below canopy (Joffre et al. 1988; Puerto and Rico 1988; Moreno et al. 2007), although there are exceptions (Montoya 1982). P availability is controlled through chemical interactions with the soil and other nutrients (Brady and Weil 2002; Eviner and Chapin III 2003). Soil-P levels were > 20 ppm, which is not an exception in the ecosystem (Puerto and Rico 1988), and did not present much variation (Table 1). Traditionally these soils have been considered to be deficient in P and Ca, particularly if compared with agronomic soils in the same area. Low soil fertility is one of the explanations of the silvopastoral use of this system (Olea and San Miguel 2006).

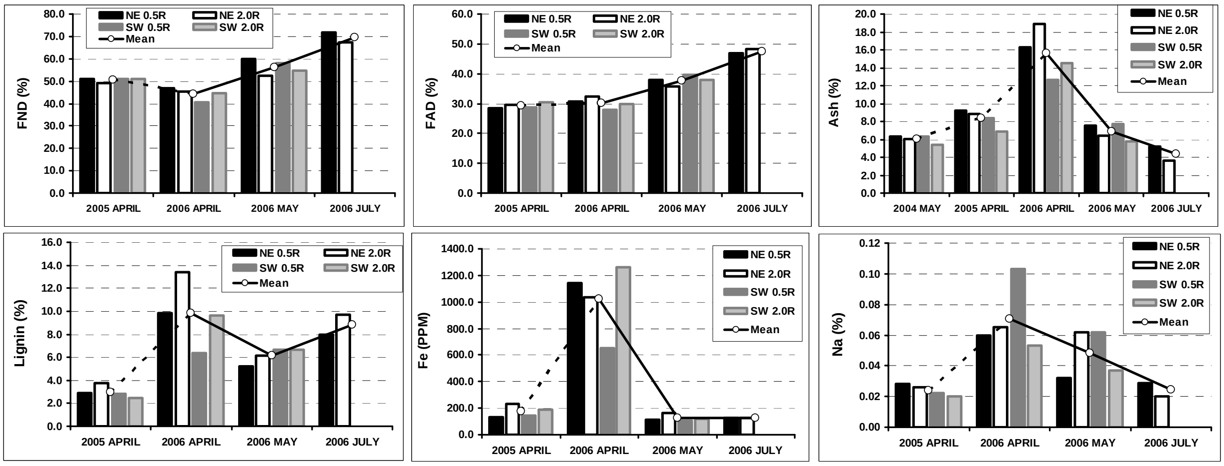

Figure 5. Temporal variation in plant nutrient content (II): micronutrients and variables of pastoral interest. Solid lines depicting the mean annual decline along the growing season in 2006. Dashed line serve as a reference for mean values in 2004 and 2005, where only one sampling was carried out.

The increase in pH with proximity to the tree could be expected from the behaviour of other variables studied (mostly Ca, but also CEC and OM). In the literature some studies (with pH around 5.5) report an increase in pH (González-Bernáldez et al 1969; Puerto and Rico 1988; Rhoades 1997) whereas other studies do not (Montoya 1982; Gallardo et al. 2000; Moreno et al. 2007). Plants can both increase or decrease the pH depending on the composition of the organic matter they produce and the soil pH and texture (Augusto et al. 2002; Brady and Weil 2002). Holm oaks might increase the soil-pH only in very acid soils, with the consequent benefits to plants. This was true in most studies discussed, but not all (Moreno et al. 2007). CEC was inversely related to distance from the tree, whereas soil bulk density was directly related. Density is directly dependent on the abundance of OM (decreasing with distance from the tree bole implying increasing density) and fine particles (more clay in the SW implies lower bulk density) (Brady and Weil 2002), and that is why it was maximum in locations farthest from the tree. Sand did not change significantly with distance but was lower beyond the canopy in the SW, complementary to silt and the increase in clay under highest radiations, as discussed below.

In addition to the spatial variation with distance from the tree, nutrients respond to differences in solar radiation induced by different orientations of the canopy. OM and K, Mg, Ca and N were more abundant in SW soils. Clay increased in those locations receiving most radiation (SW), what could be reflecting "*in situ*" formation of clay in those locations where biogeochemical cycles are faster (temperature, moisture) or greater migrations to depth in most shaded locations. A similar effect on soil texture has been reported in some studies (Puerto and Rico 1988) but not others (Moreno et al. 2007). Some of these studies do not differentiate between orientation. Although we found no significant spatial differences in C:N, there was much more variability in the SW in C:N than in NE. High C:N is generally related to low mineralization rates (Brady and Weil 2002; Eviner and Chapin III 2003). We assumed that nutrients are similar in different years and sampling dates, but this does not have to be totally true for all variables analyzed.

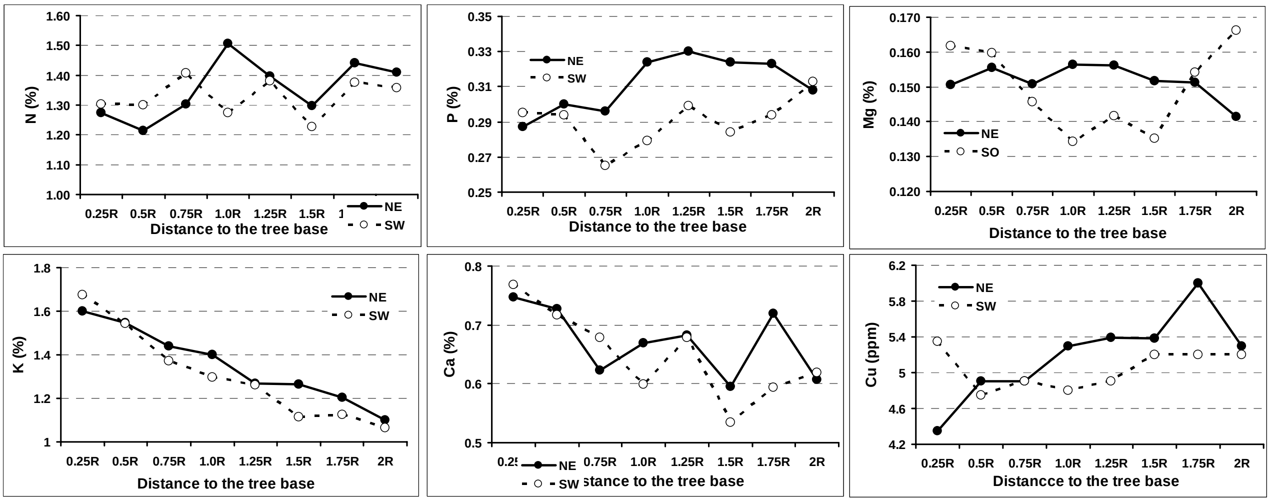

Figure 2. Spatial variation in plant nutrient content in year 2004 (I): macronutrients and copper.

Tree effects upon spatio-temporal variability in plant nutrients in Mediterranean open woodlands

Annual species in the Mediterranean environment studied experience a growth flush focused in spring, and it might be that most nutrients utilized in the rapid growth were stored in seeds produced the previous year spring, with probably low impact upon soil pools in nutrients easiest to allocate (Chapin III 1980). The spatial heterogeneity just discussed (Figure 2) complicates the plant-nutrient temporal analyses, where we only compared one pooled sample below to one outside the canopy, as some nutrients are not totally homogeneous in the two environments compared (below-beyond canopy). Plant nutrient concentrations were expected to respond directly to soil nutrient availability (Belsky 1992; Ludwig et al. 2001; Barker and Pilbeam 2007). In other studies in the 'dehesas', increases in plant nutrient concentration below the canopy were most clearly in those soils with original lowest nutrient contents (Puerto and Rico 1996). Therefore we expected plants growing in the studied soil to respond to enhanced fertility below trees by a significant increase in nutrient concentration, but this was not the case except in K and Ca (Figures 2, 3). It is difficult to ascertain which nutrient is limiting, if any, as there are many interactions among nutrients that could be determining growth (e.g. antagonistic relationships between plant uptake of Mg^{2+} with K^+ and Ca^+), or deficiency of specific nutrients could be triggered by an increase in other nutrients (e.g. Cu or P when N fertilizer is applied [Barker and Pilbeam 2007]). Factors such as plant maturity, nutrient supply, and botanical composition are directly related to plant nutrient concentration (Barker and Pilbeam 2007), and these factors can be highly correlated (e.g. botanical composition and soil nutrient availability). Our results suggest that, in the studied annual grassland, plant maturity and plant botanical composition might be the most important factors determining plant nutrient concentrations. More radiation accumulated outside the canopy is likely to change the nutrient status of plants both by different photosynthetic rates and stage of maturity (difference in 'growing days' [Henkin et al. 1998]), as plants allocate different nutrient concentrations to stems, roots, leafs or fruits (Barker and Pilbeam 2007).

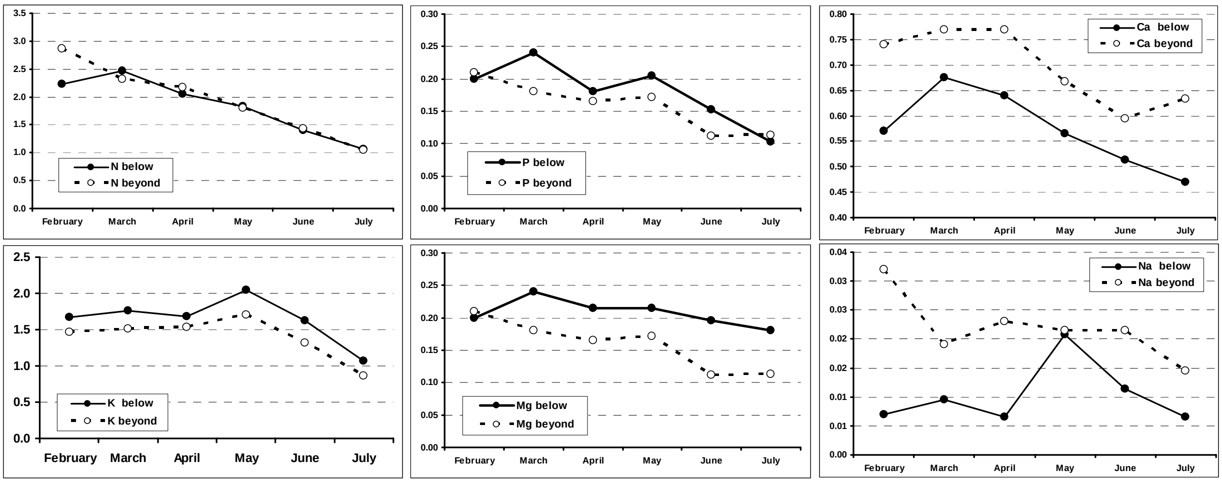

Figure 6. Calculated based on data from Montalvo et al. (1980). Four annual-perennial grasslands ('vallicares') dominated by grasses; 1 sq-m sampled under canopy and outside; data from three years, sampling each 15 days.

Grass macronutrient concentrations decreased with plant maturity (Figure 6, Montalvo et al. 1980; Barker and Pilbeam 2007). All nutrients analyzed exhibited greater temporal variability than spatial, and the most important factor deciding plant nutrient concentration was the phenological stage of annual species (e.g. Montalvo et al. 1982; Olea et al. 1990-91; Pérez Corona et al. 1998). Among functional groups, grasses are more abundant below canopy (e.g. Montalvo et al. 1980; Puerto and Rico 1996), and are negatively related to nutrient concentration (N, P, K, Ca, Mg, N, and Fe). Legumes have the greatest levels of nutrients including N, P and Ca, (García Ciudad et al. 1997; Pérez Corona et al. 1998; Barker and Pilbeam 2007).

Yield increased below canopy (Gea-Izquierdo et al. Submitted) but this was not reflected on a higher concentration of N in plant tissues. Several authors report an increase in plant N with increased N supply (Belsky 1992; Puerto and Rico 1996; Barker and Pilbeam 2007), whereas other authors' results are similar to ours (Montalvo et al. 1980). Plant-N concentration could be responding to higher legume content in less shaded conditions beyond the canopy, rather than to N supply and/or to interactions with other nutrients. The high variability of legumes and their greater abundance in the late season in the studied grassland (Gea-Izquierdo et al. Submitted) could explain the oscillating differences found in plant-N between years and sampling date, also reported by Puerto et al. (1984). The N:P ratio has been suggested as a tool to test whether plants are limited by N or P in wetlands (Koerselman and Meuleman 1996) and have also been used in other grasslands (e.g. Ludwig et al. 2001). This ratio (mean=5.6, SD=1.7; min=1.6; max=13.0, no difference between below/beyond) would indicate N limitation, instead of P limitation, but the great differences between wetlands and annual grasslands could invalidate this hypothesis. Within the studied annual grasslands in 'dehesas', it is a common belief that growth is mostly limited by P and Ca, and P fertilization is common (Olea et al. 1990-91; Olea and San Miguel 2006). Moreover, the studied soils are very sandy and have very low nutrient content compared to other grasslands in the same ecosystem (e.g. Joffre et al. 1988; Puerto and Rico 1988). It would support the N limitation hypothesis since N is likely to present luxury consumption, if it is not limiting (Chapin III 1980; Koerselman and Meuleman 1996). According to Barker and Pilbeam (2007), the plant-P levels reported here are considered sufficient for most crops, whereas plant-N levels would be considered low according to the same authors who were studying different plant species. Maybe more N availability in soils, might imply a change in grassland species composition rather than a change in plant nutrients and this can be extrapolated to other nutrients.

Plant-P did not show any clear trend with distance or orientation similarly to Pérez Corona et al. (1998) but contrary to most other studies in the system (Figure 6, Montalvo et al. 1980; Puerto and Rico 1984, 1996). K was the only nutrient that clearly increased below canopy in all studies found regardless of the grassland type (Figure 6, Montalvo et al. 1980; Puerto and Rico 1984, 1996). K monotonically decreased with distance from the tree base, with no differences between orientation. Hence, it could be responding to soil-K availability, probably through luxury consumption, as K is generally less limiting than P or N (Koerselman and Meuleman 1996; Brady and Weil 2002; Barker and Pilbeam 2007). Ca levels were greater only in positions closest to the tree, but this was not shared by all other studies (Figure 6, Montalvo et al. 1980), probably responding to pH or plant composition (grasses), as differences in pH between samples below and beyond canopy seem to be more evident in poorest soils (Puerto and Rico 1996). Ca concentration could be responding to higher Ca availability through higher soil pH below canopy. Ca is likely to be deficient as a consequence of low soil pH (Table 1) and from plant concentrations accepting as a reference *Lolium perenne* L. (Barker and Pilbeam 2007). There was no increase in Mg below canopy. This nutrient seemed to respond to canopy fertilization only in some situations and sampling dates similarly to N (Figure 6; Montalvo et al. 1980; Puerto and Rico 1984, 1996). Differences in botanical composition were proposed again as the explanation, but it is difficult to know how soil nutrients affect botanical composition and how this is responsible for community nutrient concentration. Radiation did not significantly change most plant nutrient content, but scarce precipitation (maybe through lower solubility) like that found in 2005, could explain the greater reduction in Ca levels and Mg (Brady and Weil 2002).

Implications for livestock and wildlife grazing

The quality of the studied pasture is poor, even if compared to other studies within the same ecosystem, which are also of poor quality for livestock (Olea et al. 1990-91; Olea and San Miguel 2006). Some of the previous nutrients, such as N, P, K, Ca and Mg, are essential to animal feeding, and hence what we have discussed is also of interest to livestock and wildlife management. Other variables such as different estimations of cell wall components (here we analyze FND, FAD and lignin) and micronutrients such as Cu, Fe or Na, which are important for animal feeding and plant nutrition (Cu, Fe [Barker and Pilbeam 2007]), were also analyzed here. Similar to the macronutrients just discussed, there was a decrease in plant tissue nutrients throughout the growing season, and this was the factor which explained the most variability. The presence of the tree increased ash whereas fibre was lower in the NE probably as a consequence of differed phenology (Figure 2). Cu, Fe, ash and Na were lowest in summer whereas FND and FAD were highest, responding to the stage of plant maturity (Pérez Corona et al. 1998; Vázquez de Aldana et al. 2001) or allocation of nutrients to seeds at the end of the annual cycle. Lignin fluctuated and no trend was detected, which was unexpected, as other studies had reported an increase likewise FND and FAD (Pérez Corona et al. 1998). Temporal variation was again more important than spatial variation. The decrease found in Na concentration with grass senescence has not been observed in other studies in the system. Other studies report more Na beyond the canopy (Montalvo et al. 1980, 1982; Puerto et al. 1984; Pérez Corona et al. 1998) whereas we did not find any difference. Cu is generally the most readily available in acidic soils like that in this study, although plant-Cu levels found are not very high (Barker and Pilbeam 2007).

Spatial variation was not remarkable for in any of the pastoral variables, and differences reported could be explained by phenological differences between orientation. In other ecosystems such as African savannas, grasslands below canopy had lower content of FND and FAD and higher lignin than beyond canopy (Belsky 1992). The delay in plant maturity (differences in phenological stage) in the presence of the tree is positive for animal feeding (Montoya 1982). We did not observed more wall content (FND, FAD, and lignin) in the driest year beneath the tree canopy. Cell wall estimations are lowest in legumes compared to grasses, hence they are more palatable to animals (Pérez Corona et al. 1995).

Pasture growth in these annuals communities happens mostly in April-May (Olea et al. 1990-91), thus, except spring, the rest of the year shows a shortage of grass for livestock, that either find very little biomass or dry biomass of very low quality. Pastures in ‘dehesas’ are generally of very low quality, presenting occasional levels of some nutrients (such as N) below the minimum required by livestock (García Ciudad et al. 1997). In this way, an increase in nutrient content in summer (for instance, driven by legume increase [Olea and San Miguel 2006]) could increase the number of animals supported by natural vegetation.

CONCLUSIONS

Temporal variability, particularly related to plant phenological development, is the most influential factor determining plant nutrients in the annual grassland studied. The increase in soil OM, N, K, Mg, Ca and CEC supply, and enhancement of absorption conditions through increases in pH was promoted by trees, but was not followed by an increase in grassland plant nutrient concentrations, with the exception of K and Ca. Plant-K is shown in all studies to increase below canopies, with all other nutrients varying depending on the interaction between soil properties (pH, soil fertility) and grass composition, which also closely depended on soil properties and precipitation. Soil nutrients around trees are displaced heterogeneously, with greater levels of most macronutrients and clay in locations receiving more radiation. However, and different from many other studies, this was not reflected in plant concentrations but in increased biomass growth resulting in more accumulated nutrients. These results are important for nutrient availability to livestock and wildlife management, as well as should be considered in ecosystem ecological modelling.

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ANEXO VII

Inventario florístico parcelas Capítulos 7 y 8

ANEXO VII

Inventario florístico parcelas Dehesón del Encinar Capítulos 7 y 8.

1. *Agrostis castellana* Boiss. & Reuter
2. *Agrostis pourretii* Willd.
3. *Aira caryophyllea* L. subsp. *multiculmis* (Dumort.) Bonnier & Cayons
4. *Anagallis arvensis* L.
5. *Andryala integrifolia* L.
6. *Anthemys arvensis* L.
7. *Anthemys mixta* L.
8. *Anthriscus caucalis* Bieb
9. *Anthyllis lotoides* L.
10. *Anthyllis vulneraria* L.
11. *Anthoxanthum aristatum* Boiss.
12. *Aphanes microcarpa* (Boiss. & Reut.) Rothm
13. *Astragalus hamosus* L.
14. *Avena barbata* Pott ex. Link.
15. *Bellardia trixago* (L.) All.
16. *Bellis annua* L.
17. *Biserrula pelecinus* L.
18. *Brassica fruticulosa* Cirillo
19. *Briza maxima* L.
20. *Bromus diandrus* Roth.
21. *Bromus hordeaceus* L.
22. *Bromus madritensis* L.
23. *Bromus tectorum* L.
24. *Calendula arvensis* L.
25. *Campanula lusitanica* L.
26. *Capsella bursa-pastoris* (L.) Medicus
27. *Cardamine hirsuta* L.
28. *Carduus tenuiflorus* Curtis
29. *Carduus pycnochepalus* L.
30. *Cerastium gracile* L. Dufoura
31. *Chaetonychia cymosa* (L.) Sweet
32. *Coincya monensis* (L.) Greuter & Burdet
33. *Coronilla juncea* L.
34. *Corrigiola litoralis* L. subsp. *litoralis* L.
35. *Corynephorus fasciculatus* Boiss. Et Reuter
36. *Crepis capillaris* Wallr.
37. *Cynodon dactylon* (L.) Pers.
38. *Cynosurus echinatus* L.
39. *Dactylis glomerata* L.
40. *Diplotaxis harra* (Forsk.) Boiss.
41. *Diplotaxis muralis* (L.) DC.
42. *Echium plantagineum* L.
43. *Evax carpetana* Lange
44. *Elymus hispanicus* (Píos.) Talavera
45. *Eragrostis curvula* (Schrader) Nees
46. *Erodium aethiopicum* (Lam.) Brumh. et Thell. (66)
47. *Erodium moschatum* (L.) L'Hér.
48. *Eryngium campestre* L.
49. *Euphorbia* sp.
50. *Festuca costei* (St. Yves) Markgr.-Danneb.
51. *Galium aparine* L.
52. *Gaudinia fragilis* (L.) Beauv.
53. *Geranium molle* L.
54. *Hedypnois cretica* (L.) Dum.-Courset
55. *Hipsidella hispanica* Barnades ex Lam

56 *Holcus setiglumis* Boiss. & Reuter
57 *Hordeum murinum* L.
58 *Jasione montana* L.
59 *Lamium amplexicaule* L.
60 *Lamium purpureum* L.
61 *Lathyrus* sp.
62 *Leontodon salzmannii* (Schultz Bip.) Ball.
63 *Leontodon* sp.
64 *Linaria spartea* (L.) Chaz.
65 *Lolium rigidum* Gaudin
66 *Lupinus angustifolius* L.
67 *Lupinus hispanicus* Boiss. & Reuter
68 *Malcomia* sp.
69 *Medicago orbicularis* (L.) Bartal
70 *Medicago truncatula* Gaertn.
71 *Mibora minima* L. Desv
72 *Myosotis* sp.
73 *Moenchia erecta* (L.) P. Gaertn.
74 *Molineriella minuta* (L.) Rouy
75 *Myosotis ramosissima* Rochel
76 *Muscari comosum* (L.) Millar.
77 *Muscari neglectum* Guss. ex Ten.
78 *Ornithogalum* sp.
79 *Ornithopus compressus* L.
80 *Ornithopus pinnatus* (Miller) Druce
81 *Ornithopus sativus* Brot.
82 *Orobanche* sp.
83 *Parentucellia latifolia* (L.) Caruel
84 *Plantago coronopus* L.
85 *Plantago lagopus* L.
86 *Quercus ilex* ssp. *ballota* (Desf.) Samp.
87 *Raphanus raphanistrum* L.
88 *Rumex bucephalophorus* L.
89 *Rhynchosinapis hispida* (Cav.) Heywood
90 *Sanguisorba minor* Scop.
91 *Sedum* sp.
92 *Senecio sylvaticus* L.
93 *Senecio vulgaris* L.
94 *Silene vulgaris* (Moench) Garcke
95 *Sisymbrium irio* L.
96 *Spergula arvensis* L.
97 *Spergularia purpurea* (Pers.) D. Don.
98 *Stachys arvensis* (L.) L.
99 *Taeniatherum caput-medusae* (L.) Nevski
100 *Taraxacum erythrospermum* Adrz. Ex Besser.
101 *Taraxacum obovatum* (Willd.) DC.
102 *Teesdalia nudicaulis* (L.) R. Br.
103 *Teucrium* sp.
104 *Tolpis barbata* (L.) Gaertner
105 *Trifolium angustifolium* L.
106 *Trifolium arvense* L.
107 *Trifolium campestre* Schreb.
108 *Trifolium cherleri* L.
109 *Trifolium glomeratum* L.
110 *Trifolium ligusticum* Balb. ex Loisel
111 *Trifolium retusum* L.
112 *Trifolium striatum* L.
113 *Trifolium tomentosum* L.
114 *Trifolium subterraneum* L.
115 *Tuberaria guttata* (L.) Fourr.

116 *Valerianella* sp.
117 *Vicia lutea* L.
118 *Vicia sativa* L.
119 *Viola kitaibeliana* Schultz in Roem. & Schult
120 *Vulpia bromoides* (L.) S. F. Gray
121 *Vulpia membranacea* (L.) Dumort.
122 *Vulpia myuros* (L.) Gmel.

“[…] Finalmente, Sancho se quedó dormido al pie de un alcornoque, y don Quijote dormitando al de una robusta *encina*; pero poco espacio de tiempo había pasado cuando le despertó un ruido que sintió a sus espaldas, y […]”.