Variabilidade anatómica e da densidade da madeira de *Quercus faginea* em diferentes idades e condições ambientais

Tese apresentada para obtenção do grau de Doutor
em Engenharia Florestal e dos Recursos Naturais

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Resumo

A importância e a valorização das espécies autóctones em Portugal motivou a realização do presente estudo para avaliar o potencial tecnológico e aprofundar o conhecimento das propriedades e variabilidade da madeira de *Quercus faginea* Lam., de nome comum carvalho português ou cerquinho.

Estudaram-se os anéis de crescimento, a formação do cerne, as características anatómicas do lenho e da casca e a densidade da madeira em diferentes idades e locais. A madeira apresenta porosidade em anel, elevada proporção de fibras e raios, e densidade elevada. A proporção de cerne foi relativamente alta com decréscimo da base para o topo de acordo com o perfil do tronco. A espessura de borne manteve-se aproximadamente constante. As fibras e os raios multisseriados apresentaram uma tendência de aumento de dimensões da medula para a casca, assim como a área média dos vasos do lenho inicial. A largura dos anéis de crescimento e a densidade da madeira decresceram no sentido radial. As fontes de maior variação foram determinadas atendendo à importância da idade, árvore e das condições ambientais, mostrando os efeitos consideráveis do local, seguido das árvores e da idade do câmbio. As correlações existentes entre as variáveis estudadas evidenciaram a possibilidade de obter estimativas de crescimento e qualidade da madeira com base, nomeadamente, na largura do anel.

A caracterização obtida e a relativa homogeneidade encontrada na árvore possibilitam a sua exploração e reforçam o carácter desta espécie para a diversificação da floresta.

Palavras – chave

Quercus faginea, variabilidade da madeira, cerne, anatomia, densidade

Wood anatomy and density variability of *Quercus faginea* at different ages and environmental conditions

Abstract

The importance and valorization of the species that occur naturally in Portugal motivated the present study to evaluate the properties, variability and the technological potential of the wood of *Quercus faginea* Lam., commonly referred as Portuguese or Lusitanian oak.

Growth rings, heartwood development, anatomical characteristics of wood and bark and wood density were studied at different ages and sites. The wood showed growth ring porosity, high fibre and rays proportion and high wood density. The heartwood proportion was relatively high and increased from the base to the top following the trunk profile. Sapwood thickness was approximately constant. The fibre and multiseriate rays showed an increasing tendency towards the bark as well as the mean earlywood vessels area. The ring width and wood density decreased from pith to bark. The variation sources included age, trees and environmental conditions. Site was responsible for the main variations followed by tree and cambial age. The correlations between the studied variables showed that growth and wood quality might be estimated namely with ring width.

The wood characterization and relative stem homogeneity allow exploitation of this species and reinforce its role in forest diversity.

Keywords

Quercus faginea, wood variability, heartwood, anatomy, density

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Capítulo 1

Introdução e objectivos

1.1. Introdução e justificação de interesse

A importância do estudo e valorização das espécies que constituíram a floresta natural portuguesa não se reflecte no conhecimento actual que se tem sobre as mesmas, nomeadamente as propriedades da madeira e da sua variabilidade. Nestas espécies inclui-se a *Quercus faginea* Lam., conhecida como carvalho português ou cerquinho, cuja madeira já foi largamente valorizada no passado mas que caiu em desuso, de que resultaram efeitos ecológicos, sociais e económicos negativos (Paiva 2007; Carvalho 1997).

O interesse actual na valorização das espécies autóctones e da biodiversidade reforça a importância do carácter multifuncional da floresta mediterrânica. Os produtos lenhosos representam 20-40% do valor económico total das florestas, estando o restante associado aos produtos não lenhosos e serviços ambientais como a protecção do solo e dos recursos hídricos, conservação da biodiversidade e fixação de carbono (Croitoru 2007; Alves et al. 2012). Em Portugal, salienta-se a contribuição do sector florestal para o Produto Interno Bruto, mas considera-se que a diversidade de espécies florestais é reduzida pelo que a reintrodução de folhosas ganha maior importância para garantir a continuidade da paisagem florestal e sustentabilidade da floresta (Fabião et al. 2007; Maltez-Mouro et al. 2005; Capelo e Catry 2007; Louro et al. 2003).

Do ponto de vista da conservação, os carvalhais de *Q. faginea* (cercais) constituem um dos habitats naturais reconhecidos e documentados na Directiva do Conselho 92/43/CEE (de 21 de Maio de 1992) da União Europeia. Nas áreas ocupadas por carvalho português, a composição do sub-bosque é bastante diversa, incluindo espécies como urze, murta, giesta, tojo, carrasco (*Q. coccifera*), pilriteiro, rosa brava, silva, hera, fetos, gramíneas e leguminosas herbáceas (Natividade 1929; Bingre e Damasceno 2007). A fauna característica também é bastante diversificada desde artrópodes a mamíferos, incluindo mamíferos de grande porte como o javali e o veado, embora estes últimos sejam de observação difícil (Bingre e Damasceno 2007).

Na perspectiva da floresta multifuncional, as espécies sem valor actual de mercado como o carvalho português poderão proporcionar, de uma forma sustentada, para além dos diversos bens e serviços ambientais atrás referidos, também a produção de bens lenhosos de valor acrescentado. Na Europa, apenas 20 em 100 espécies com distribuição natural têm interesse comercial e são essas as mais estudadas no que diz respeito às propriedades anatómicas e estruturais da madeira e à análise das relações de crescimento e influência de factores internos e externos (Marja-Sisko e Ilvessalo-Pfäffli 1995; Spiecker et al. 2000).

A madeira de *Q. faginea* destina-se, hoje em dia, principalmente a lenha e produção de carvão, mas nos sécs. XV e XVI destinava-se também para a construção de caravelas (Natividade 1929; Ayanz 1986, Fabião et al. 2007). A casca era também utilizada para extracção de taninos para a produção de curtumes (Natividade 1929). Por um lado, estas utilizações eram já fruto de algum conhecimento das propriedades da madeira, nomeadamente do seu poder calorífico, resistência e durabilidade nomeadamente quanto a impactos e atritos e capacidade de resistência à imersão e ao contacto com humidade (Natividade 1929; Ayanz 1986). Por outro, estas utilizações eram também consequência da sua abundância no território, que viria a diminuir consideravelmente devido aos sucessivos abates para consumo de lenha, saldo de dívidas do Estado e substituição por espécies de crescimento rápido, com características mais atractivas para produção como o eucalipto e o pinheiro bravo ou preferência por outros carvalhos como, por exemplo, o carvalho americano (*Q. rubra*) (Natividade 1929).

A madeira de *Q. faginea* é potencialmente interessante para uma gama de produtos estruturais e de maior qualidade, nomeadamente para aplicações de pequenas dimensões para fins estruturais ou de interiores, tendo em conta o seu carácter estético, as propriedades mecânicas, a densidade elevada e a durabilidade moderada que apresenta (Carvalho 1997; Ramos et al. 2009; Silva 2011; Knapič et al. 2011).

Neste sentido, a caracterização e o estudo da variabilidade da estrutura da madeira, ao nível dos anéis de crescimento e dos elementos estruturais tais como as fibras e vasos (biometria e distribuição), é importante para a análise do crescimento e avaliação das suas propriedades, nomeadamente da densidade que serve de critério base para avaliação de outras propriedades e características tecnológicas da madeira (Tsoumis 1991). Os elementos anatómicos e a densidade estão intimamente relacionados, permitindo estudar a adequação da madeira de *Q. faginea* e o seu valor tecnológico para fins mais nobres.

1.2. Objectivos

O trabalho tem como objectivo geral reforçar o conhecimento sobre a madeira de *Quercus faginea* (carvalho português), espécie importante da floresta autóctone portuguesa, através da avaliação do seu potencial tecnológico, contribuindo para a diversificação da floresta e da indústria de produtos florestais de qualidade. Em particular, pretendeu-se estudar a variabilidade dos elementos anatómicos e da densidade da madeira de *Q. faginea* na árvore (variação radial e axial), entre árvores e entre diferentes condições ambientais, avaliando os efeitos das diferentes fontes de variação e seleccionando elementos estruturais que permitissem indicar linhas de orientação para a gestão de povoamentos de *Q. faginea*. Assim, os principais objectivos específicos do trabalho foram:

- Estudar a formação e proporção de borne e cerne e o crescimento anual da *Q. faginea* e a sua variação na árvore (variação radial e axial), entre árvores e locais (4.1);

- Caracterizar a anatomia da madeira de *Q. faginea* e a variabilidade dos principais elementos anatómicos (fibras, raios multisseriados e vasos) na árvore, entre árvores e em diferentes condições ambientais (4.2.);

- Caracterizar a casca da *Q. faginea,* a sua variabilidade e potencial (4.3);

- Analisar o padrão de variabilidade da densidade da madeira nas árvores de *Q. faginea* com idade média de 125 anos em povoamento de regeneração natural (4.4);

- Compreender a magnitude e os efeitos de locais com diferentes condições ambientais na variação da densidade da madeira de *Q. faginea* num período de 30 anos de idade do câmbio (4.5);

- Identificar os efeitos dos vasos do lenho inicial, da madeira de *Q. faginea*, na variação e correlação com a largura e densidade dos anéis de crescimento e potencial como indicador de crescimento e densidade da madeira (4.6).

1.3. Estrutura da tese

O estado de arte é apresentado no Capítulo 2 incidindo em especial na literatura relativa ao género *Quercus*. O delineamento da amostragem é descrito no Capítulo 3 e as conclusões e perspectivas incluídas no Capítulo 5. Estes capítulos são expostos em português.

O trabalho experimental está apresentado sob a forma de artigos científicos[1], escritos em inglês, de acordo com o estilo e formatação da revista onde foram publicados ou submetidos:

- 4.1: "Ring width variation and heartwood development in *Quercus faginea*" - Wood and Fiber Science, 45: 405-414;

- 4.2: "Age trends in the wood anatomy of *Quercus faginea* Lam" – IAWA Journal, em revisão;

- 4.3: "Bark anatomy and cell size variation in *Quercus faginea* Lam" – Turkish Journal of Botany, 37: 561-570;

- 4.4: "Age trends of ring width and wood density in *Quercus faginea* mature trees" – Wood Science and Technology, submetido (WST-13-0240);

- 4.5: "Influence of site in wood density components in *Quercus faginea* in the juvenile and early mature periods" – European Journal of Forest Research, submetido (EJFOR-13-00354);

- 4.6: "Earlywood vessels features in *Quercus faginea*: relation to ring width and wood density at two sites" –Journal of Wood Science , submetido (JOWS-13-00219).

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[1] As publicações aqui apresentadas como submetidas ou aceites poderão vir a sofrer alterações de conteúdo de acordo com as notas dos revisores ou editores.

Capítulo 2

Revisão de conhecimentos

2.1. Características do carvalho português

2.1.1. Classificação taxonómica e descrição botânica

A *Quercus faginea* Lam. pertence à secção *Quercus*, subgénero *Quercus*, género *Quercus*, família *Fagaceae*. Esta designação foi proposta pelo francês Jean-Baptiste Lamarck, em 1785. O restritivo específico *faginea* provém do latim *fagineus*, que significa de faia, de madeira de faia (Paiva 2007). É reconhecida como carvalho português ou cerquinho, *quejigo* (espanhol), *quercia lusitanica* (italiano), *chêne de Portugal* (francês) e *Portuguese oak* ou *Lusitanian oak* (inglês). A designação cerquinho evoluiu a partir do étimo em latim *Quercinu,* caso genitivo do substantivo *Quercus* (carvalho) (Bringe e Damasceno 2007).

Existe alguma controvérsia em relação à sua designação científica no seio da comunidade botânica, sendo que o carvalho português pode ser designado como *Q. faginea* subsp. *broteroi*, *Q. broteroi* e *Q. hibrida* (Bringe e Damasceno 2007).

Existem várias subespécies e variedades, sendo a sua distinção por vezes difícil e alvo de discussão, à semelhança do que acontece com outras *Quercus* spp. (e.g. Cañellas e San Miguel 2003). As três subespécies que se destacam são as subespécies *broteroi*, *faginea* e *alpestris.*

É uma árvore de porte médio, não ultrapassando em geral os 20 m, com tronco normalmente tortuoso mas também com fuste direito (Oliveira et al. 2001). É uma espécie de meia-luz, relativamente intolerante ao ensombramento e à competição (Ayanz 1986). Apresenta um sistema radicular grande e extenso adaptado ao clima mediterrânico (Oliveira et al. 2001), subsistindo em diferentes tipos de solos (Capelo e Catry 2007), mas tendo preferência por solos profundos com maior disponibilidade de água (Villar-Salvador et al. 1997). É considerada uma espécie de crescimento lento e de grande longevidade (e.g. Natividade 1929; Oliveira et al. 2001).

É uma espécie decídua que apresenta uma folhagem pouco densa (Oliveira et al. 2001). As folhas mantêm-se marcescentes durante muito tempo e algumas conservam-se verdes durante o Inverno até à Primavera seguinte, destacando-se de outras quercíneas (Oliveira et al. 2001; Goes 1991).

As folhas são simples e alternas, apresentam um pecíolo bem desenvolvido normalmente superior a 4 mm, limbo simples e relativamente coriáceo, com 8 a 14 pares de nervuras (Oliveira et al. 2001; Bringe e Damasceno 2007; González 2004). As folhas de Inverno e Verão apresentam ligeiras diferenças. A página superior começa por estar coberta de pêlos que acabam por cair ressaltando um tom mais verde e lustroso contrastando com o anterior tom acinzentado originado pela camada de pêlos e que se mantêm na página inferior mesmo no estado adulto (González 2004).

As flores masculinas estão dispostas em amentilhos e medem cerca de 20 a 75 mm e as flores femininas isoladas ou em pequenos grupos (Oliveira et al. 2001; Bringe e Damasceno 2007). O período de floração ocorre entre Abril e Maio. Os frutos são bolotas, com cerca de 25 por 17 mm, que apresentam pedúnculo curto e escamas ovado-triangular (Oliveira et al. 2001; Bringe e Damasceno 2007). A frutificação ocorre por volta dos 15 anos tornando-se abundante aos 30 anos (Oliveira et al. 2001).

A Figura 1 apresenta alguns aspectos botânicos da *Q. faginea* desde o hábito, folhas, flores, fruto e casca.

Figura 1. Porte, folhas, flores (adaptado de González 2004), fruto (adaptado de AJ Pereira, www.flora-on.pt) e casca característicos da *Q. faginea*.

2.1.2. Distribuição e condições edafo-climáticas

A *Q. faginea* ocorre naturalmente em Portugal, Espanha, norte de Marrocos, Argélia, Tunísia, sul de França e residualmente na ilha de Maiorca (Oliveira et al. 2001; Capelo e Catry 2007; Bringe e Damasceno 2007).

Em Portugal terá sido abundante no passado nas zonas de Trás-os-Montes, Beira Litoral e Estremadura, mas a sua distribuição actual é pontual e limitar-se-á a alguns milhares de hectares (Capelo e Catry 2007). Os carvalhos, excluindo a azinheira e o sobreiro, ocupam cerca de 2% do território florestal nacional (ICNF 2013). Oliveira et al. (2001) referiam para o ano de 1995 cerca de 1221 ha de povoamentos com mais de 2 hectares com regeneração natural ou vegetativa.

A ocorrência e a distribuição das subespécies estão relacionadas com diversos factores, nomeadamente geográficos e edafo-climáticos (Bringe e Damasceno 2007). A *Q. faginea* subsp. *broteroi* distribui-se, em Portugal, na região da Estremadura (norte de Lisboa, região de Tomar, Leiria e Pombal) e nas regiões de Estremadura e Andaluzia, em Espanha (Capelo e Catry 2007). A *Q. faginea* subsp. *faginea* está associada à região de Trás-os-Montes em Portugal, à Espanha continental e sul de França (Capelo e Catry 2007). A *Q. faginea* subsp. *alpestris* ocorre pontualmente no Algarve, sendo mais abundante nos países do Magreb (Capelo e Catry 2007). O mapa com as áreas de ocorrência potencial e dos povoamentos actuais é apresentado na Figura 2.

A *Q. faginea* encontra-se frequentemente associada a outros carvalhos, como o carvalho-negral (*Q. pyrenaica* Willd.), a azinheira (*Q. rotundifolia* Lam.) e o sobreiro (*Q. suber* L.) (Fabião et al. 2007). A ocorrência de híbridos e outras espécies como o castanheiro (*Castanea sativa* Mill.) ou pinheiro bravo (*Pinus pinaster* Aiton) é frequente nas manchas existentes.

No contexto geológico, ocorre na orla ocidental meso-cenozóica (Estremadura e Beira Litoral) onde predominam os calcários, encontrando-se no Maciço Calcário Estremenho, por exemplo, na serra da Arrábida, Aire e Candeeiros, alguns bosques de referência da *Q. faginea* (Bringe e Damasceno 2007; Capelo e Catry 2007). A *Q. faginea* é considerada como uma espécie bem adaptada a vários tipos de solos, embora ocorra principalmente em solos de natureza siliciosa (Oliveira et al. 2001). Em altitude estende-se do nível basal (300 m) até cerca de 700 a 1000 m (nível montano), preferindo os vales e encostas frescas (Oliveira et al. 2001).

Trata-se de uma espécie que se desenvolve em clima temperado a temperado-frio (Figueras 1979). Em Portugal, o clima onde prevalece é de transição entre as duas regiões climáticas: a Atlântica e a Mediterrânica (Bringe e Damasceno 2007). Necessita, em média, de uma temperatura anual de 15 ºC a 26 ºC no Verão e de -4 ºC e 8 ºC no Inverno, com precipitações anuais que podem variar desde 350 mm até 2000 mm (Ayanz 1986). Convém referir que estes dados climáticos são relativos à ocorrência e vegetação da espécie com base em estudos realizados em Espanha, não havendo até ao momento dados concretos para Portugal.

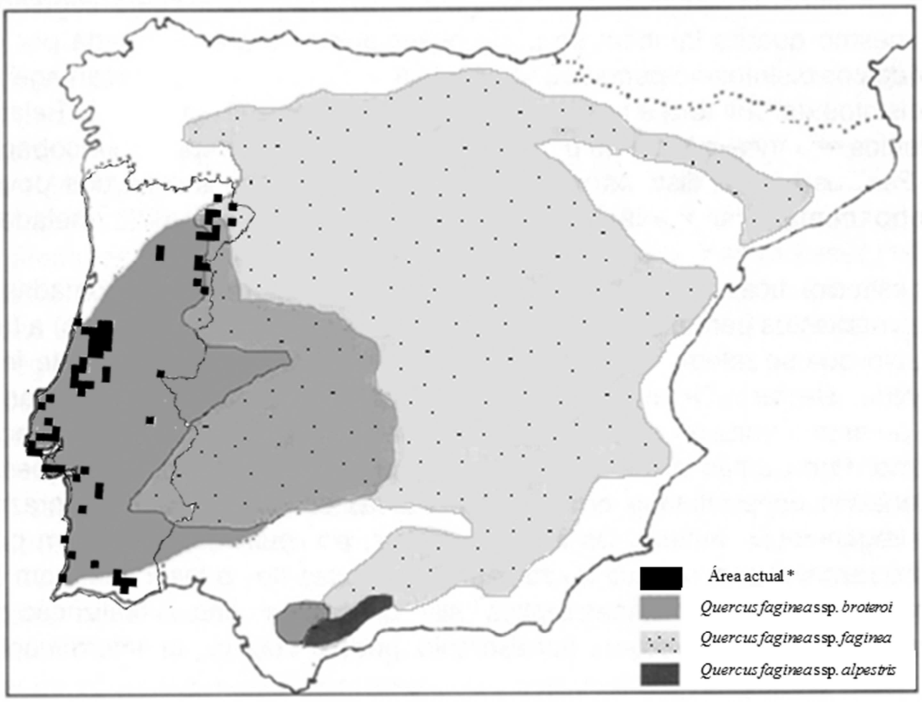

Figura 2. Área de distribuição natural e actual da *Quercus faginea* na Península Ibérica (Adaptado de Oliveira et al. 2001 e www.flora-on.pt). * Estes dados podem estar desactualizados.

2.1.3. Tipos de povoamento

As produções tradicionais da *Q. faginea* são a madeira, lenha, carvão, casca, bolota e silvopastorícia, sendo o regime de talhadia aquele que está associado à produção de lenha e casca e o regime de alto fuste aos restantes produtos (Oliveira et al. 2001). Os povoamentos explorados em alto fuste têm rotações de cerca de 100 a 150 anos, ou seja, semelhante a outros carvalhos, como por exemplo, a *Q. petraea* em França (Ayanz 1986; Zhang et al. 1993). As talhadias teriam rotações de 10 a 20 anos (Natividade 1929; Ayanz 1986).

A diminuição da área de carvalho português ocorreu por variados motivos, alguns já citados, entre os quais a baixa produtividade e rentabilidade associada aos povoamentos de *Q. faginea*, que, segundo Natividade (1929), deveriam ser convertidos em povoamentos de *P. pinaster* e *Eucalytus globulus* Labill.. Oliveira et al. (2001) sugerem, com base em estudos de diferentes parcelas, um conceito de gestão multifuncional. Aqui, poderiam incluir-se os regimes de talhadia composta (coexistência de talhadia e alto fuste), talhadia com reservas para fornecer peças de maior dimensão e os montados ou povoamentos abertos que incluiriam outras espécies de carvalhos e em que existiria uma componente arbórea associada a uma pastoril/agrícola (Fabião et al. 2007).

Em geral, os povoamentos resultam de regeneração vegetativa e a gestão é semelhante à de outros carvalhos (Alves et al. 2012). A regeneração natural por via seminal é uma alternativa viável, atendendo a que uma plantação requer algumas exigências iniciais e cuidados de manutenção e que a utilização de abrigos não foi conclusiva (Oliveira et al. 2001; Fabião e Silva 1996).

No caso de plantação, a densidade pode variar de 400 a 600 árvores por hectare no caso de montados e de 1100 a 2500 no caso de produção de madeira (Fabião et al. 2007).

2.2. Características da madeira e sua variabilidade

A madeira é designada em termos fisiológicos de lenho ou xilema e é o resultado da actividade do meristema lateral ou câmbio vascular (Fahn 1990). Embora a sua estrutura geral pareça homogénea, os seus elementos exibem uma grande variabilidade (Larson 1963). Trata-se de uma característica inerente à própria madeira e está relacionada com o facto de se tratar de um material biológico sujeito à influência de factores internos e externos (Zobel e van Buijtenen 1989). Os processos fisiológicos e de diferenciação celular da madeira, assim como os factores genéticos, determinam parte da variabilidade na árvore (e.g. Esau 1974; Fahn 1990; Larson 1994). Os factores externos que incluem as condições geográficas e ambientais, assim como as intervenções culturais, podem influenciar o processo de crescimento da árvore, alterando a sua estrutura. No estudo da variabilidade dentro da espécie interessa analisar a variabilidade na árvore (radial e axial), entre árvores e entre locais. De um modo geral, esta heterogeneidade permite que haja diferentes aptidões e aplicações, de acordo com as diferentes características da madeira. O estudo da variabilidade da madeira permite definir períodos de rotação, selecção de árvores e locais assim como a realização de operações culturais em função dos objectivos de gestão e produção florestal.

2.2.1. Anatomia

A descrição anatómica de uma madeira e da casca é feita a nível macroscópico e microscópico, qualitativa e quantitativamente. A caracterização, proporção e biometria dos diferentes tipos de células são importantes para determinar diversas propriedades da madeira e casca, nomeadamente a permeabilidade, densidade e resistência, assim como a sua utilização final.

A madeira de carvalho é uma das mais complexas do grupo das Angiospérmicas, podendo apresentar elementos de vaso, traqueídos (vasicêntricos e vasculares), fibro-traqueídos, fibras libriformes, parênquima axial e parênquina radial de diferentes dimensões (Evert 2006). É importante referir a distribuição, o calibre dos vasos na camada de crescimento (porosidade) e o seu agrupamento; o arranjo do parênquima axial e a sua abundância; presença ou não de fibras septadas; presença de estrutura estratificada; dimensão e tipo dos raios; tipo de perfuração dos vasos; forma, dimensão e abundância de cristais (Evert 2006). A identificação de uma espécie de carvalho com recurso apenas à caracterização anatómica da madeira é bastante difícil, por exemplo, a diferenciação da *Q. robur* L., *Q. petraea* (Matt.) Liebl. e *Q. pubescens* Willd. não pode ser feita apenas com recurso à anatomia (Schoch et al. 2004), embora tenham sido feitas tentativas baseadas na forma, tamanho e proporção de tecidos com relativo sucesso (Feuillat et al. 1997; Bakour 2003). A textura, a proporção de tecidos e as características dos vasos do lenho inicial e dos raios lenhosos mostraram diferenças significativas entre a *Q. petraea* e *Q. robur* (Bakour 2003) (Figura 3).

Sobre a estrutura da madeira do carvalho português salientam-se as descrições de Carvalho (1997) e García Esteban et al. (2003). As descrições são em geral concordantes com algumas excepções em relação ao tipo de porosidade, ao número de linhas de vasos largos e/ou vasos agrupados, existência de fibras septadas, composição celular dos raios e presença de fibro-traqueídos.

Alguns autores descrevem a madeira de *Q. faginea* como tendo porosidade em anel (Baas e Schweingruber 1987; Villar-Salvador et al. 1997; Carvalho, 1997), outros variando entre porosidade difusa e porosidade em anel (García Esteban et al. 2003; García Esteban e Guindeo Casasús 1990).

As fibras são em geral libriformes com poucas e pequenas pontuações (Carvalho 1997; Schweingruber e Landolt 2005). A existência de traqueídos vasicêntricos (com pontuações maiores e mais abundantes) é destacada na descrição feita por Carvalho (1997) para a *Q. faginea* e por Ferreirinha (1958) no género *Quercus* e na *Castanea sativa* Mill.. Os raios são descritos como homocelulares por Carvalho (1997) e Schweingruber e Landolt (2005) e como heterocelulares por García Esteban et al. (2003). A presença de cristais no parênquima radial e axial é referida por Carvalho (1997) e García Esteban et al. (2003). A ocorrência de tilos também é frequente na madeira de carvalho português (Carvalho 1997; Schweingruber e Landolt 2005).

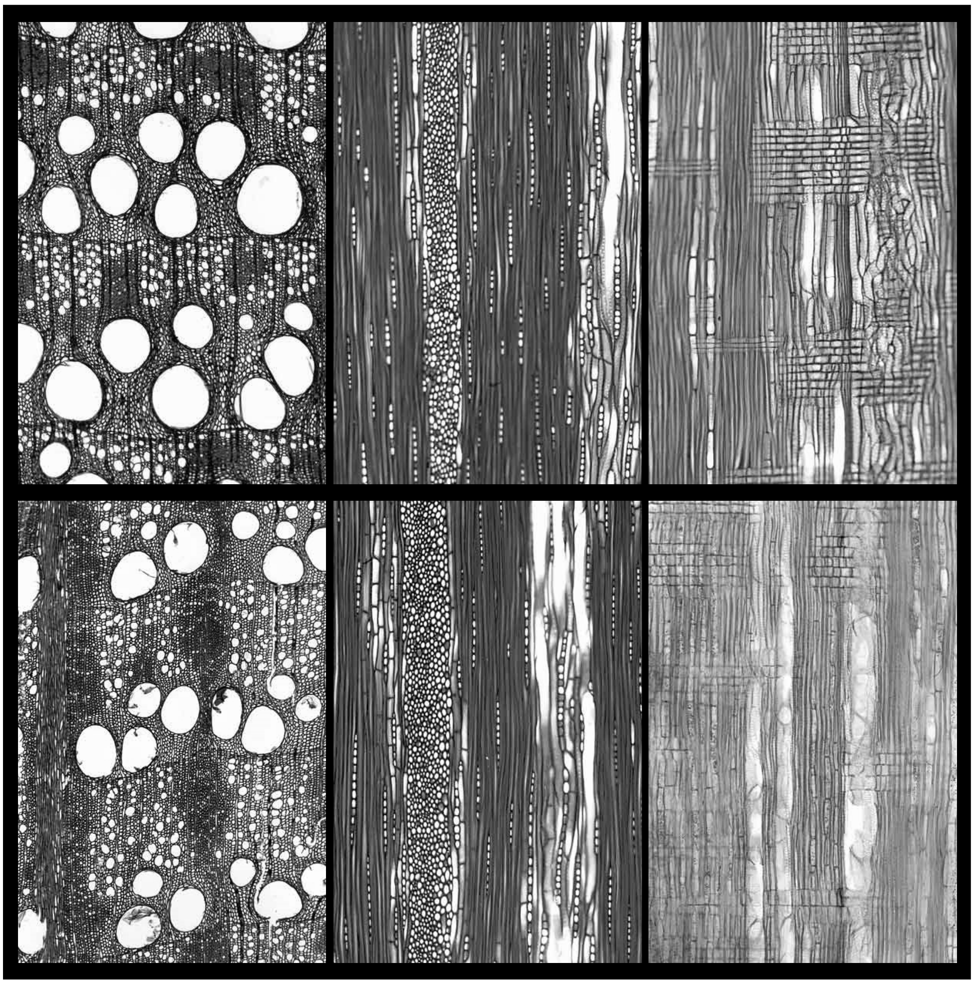

Figura 3. Secção transversal, tangencial e radial da madeira de *Q. petraea* (em cima) e *Q. robur* (em baixo) (Adaptado de Schoch et al. 2004).

2.2.1.1. Fibras

As fibras têm como principal função a sustentação mecânica da árvore. As suas características morfológicas têm influência na flexibilidade, plasticidade e resistência da madeira na fase de processamento industrial e nas propriedades ópticas e físico-mecânicas do produto final. No entanto existem relativamente poucos estudos sobre as dimensões, proporção e variabilidade das fibras nas folhosas e mais em concreto carvalhos quando comparados com os estudos efectuados em resinosas ou em folhosas com vista à produção de pasta para papel.

Na madeira de *Quercus* spp, as fibras são o seu constituinte principal e representam cerca de 50% da área transversal (Zobel e van Buijtenen 1989). Nos estudos, já realizados em carvalhos foi possível verificar que, por exemplo, o comprimento das fibras na *Q. suber* variou entre 1100 µm e 1230 µm (Sousa et al. 2009), na *Q. garryana* Dougl. aproximadamente entre 1000 µm e 1200 µm (Lei et al. 1996) e de 1100 a 1350 µm em *Q. conferta* Kit., *Q. ilex* L. e *Q. coccifera* L. (Voulgaridis 1990). Relativamente à *Q. faginea*, os autores García Esteban e Guindeo Casasús

(1990) referem uma maior amplitude de variação do comprimento das fibras, isto é, de 800 a 1600 µm.

O estudo da variabilidade radial do comprimento das fibras (libriformes) nos carvalhos mostra que a tendência geral de crescimento em função da idade aumenta no período inicial de forma mais significativa, sendo menos acentuada com o avançar dos anos (Lei et al. 1996; Leal et al. 2006). Para além disso, e mais frequentemente nas resinosas, o comprimento das fibras/traqueídos tem permitido identificar a região de demarcação do lenho juvenil para o lenho adulto (Chauhan et al. 2006). É de referir que também no caso de alguns carvalhos os resultados obtidos foram bastante satisfatórios comparativamente às resinosas, sendo que a idade (do câmbio) em que começa a ocorrer uma maior estabilidade dimensional varia entre as espécies (Voulgaridis 1990; Helinska-Raczkowska e Fabisiak 1991; Lei et al. 1996; Tsuchiya e Furukawa 2009).

Em relação à largura das fibras, no caso do sobreiro verificou-se que variou entre 20 e 21 µm (Sousa et al. 2009). A largura média das fibras de *Q. faginea* referida por García Esteban e Guindeo Casasús (1990) é de 17 µm.

A espessura da parede das fibras de *Q. suber* foi em média de 8 µm (Sousa et al. 2009) e na *Q. faginea* variou de 3 a 8 µm (García Esteban e Guindeo Casasús 1990). Estas fibras são consideradas espessas (IAWA 1989) e caracterizam, em geral, a madeira dos carvalhos (García Esteban e Guindeo Casasús 1990).

Os estudos efectuados em *Quercus* spp. em termos de variabilidade da largura e espessura da parede das fibras evidenciaram uma tendência de aumento da medula para a casca (Leal et al. 2006). Este padrão também se encontra noutras espécies de folhosas, como a *Eucalyptus globulus* (Jorge et al. 2000).

A estabilização biométrica está relacionada com os mecanismos fisiológicos (actividade meristemática e enzimática) inerentes ao envelhecimento da árvore, sendo que os factores genéticos e ambientais podem influenciar os referidos mecanismos (Zobel e van Buijtenen 1989).

A existência de correlações fortes entre os diferentes parâmetros biométricos poderia permitir efectuar boas estimativas das mesmas características. Por exemplo, no sobreiro foi obtida uma relação linear significativa entre a largura e a espessura da parede das fibras (Leal et al. 2006) ou de outras propriedades da madeira, como a densidade (ver 2.2.3. Densidade).

2.2.1.2. Raios

Os raios são células parênquimatosas não lenhificadas com função de armazenamento de diversas substâncias como, por exemplo, gomas e amido. Butterfield (2006) refere também como função importante o transporte radial de carboidratos nas fases de divisão e expansão celular. A dimensão e distribuição dos raios influenciam a qualidade e utilização da madeira (Zobel e van Buijtnen 1989). A existência de raios largos visíveis a olho nu é uma característica importante na madeira e, em particular, nos carvalhos. A presença destes raios, que representa de acordo com Butterfield (2006) cerca de 50 % do volume da madeira, reflecte-se na imagem a nível macroscópico através de uma estética bastante apreciada na madeira de carvalho (Figura 4).

A identificação do tipo de raios numa determinada madeira é essencial para a sua caracterização e identificação. Os raios no género *Quercus* são essencialmente de dois tipos: unisseriados e multisseriados, mas a sua morfologia e distribuição não são suficientes para fazer identificação ao nível da espécie (e.g. Feuillat et al. 1997). No estudo biométrico dos raios é preciso ter em atenção os efeitos ontogénicos e ambientais (Carlquist 2001). Em geral, a altura e a largura dos raios são medidas muitas vezes apenas para estudos comparativos e os trabalhos sobre a biometria dos raios e sua variabilidade são escassos. Ferreinha (1965) refere a existência de uma forte correlação entre a altura e a largura dos raios ao nível da espécie.

A madeira de carvalho português apresenta raios unisseriados e multisseriados (Carvalho 1997; García Esteban e Guindeo Casasús 1990; García Esteban et al.2003; Schweingruber e Landolt 2005).

A altura média dos raios multisseriados na *Q. faginea* é de 20 mm e pode variar de 6 a 50 mm de altura segundo Carvalho (1997). Comparativamente, na *Q. suber* a altura média foi de 5,16 mm e a largura de 0,48 mm (Leal et al. 2006). Na *Q. petraea* e *Q. robur* a largura média dos raios foi de 0,2 e 0,18 mm (Bakour 2003). Porém, diferentes metodologias de medição terão sido aplicadas pelo que é necessário alguma moderação na apreciação e comparação de resultados.

Verificou-se um aumento relativo no sentido radial na altura e largura dos raios multisseriados na *Q. suber* (Leal et al. 2006). Noutras espécies, a proporção de raios manteve-se relativamente constante da medula para a periferia (Lei et al. 1996; Gartner et al. 1997; Bakour 2003), sendo esta a tendência esperada nas folhosas (Zobel e van Buijtenen 1989; Carlquist 2001). Observou-se uma elevada variabilidade entre árvores na dimensão dos raios da *Q. suber* (Sousa et al. 2009; Leal et al. 2006). A variabilidade entre locais foi significativa para a altura dos raios (Sousa et al. 2009). Segundo os mesmos autores a largura dos raios multisseriados em *Q. suber* não sofreu influência do local contrariamente ao observado em *Q. robur* e *Q. petraea* por Bakour (2003).

Vale a pena referir que os raios correspondem a zonas de densidade elevada, sendo parcialmente apontados como responsáveis pela variabilidade da densidade na madeira (Polge e Keller 1973; Guilley e Nepveu 2003). O estudo da sua variabilidade é importante para determinar ou adequar processos de secagem da madeira, pois influenciam diversas propriedades, nomeadamente a retracção da madeira (Tsoumis 1991).

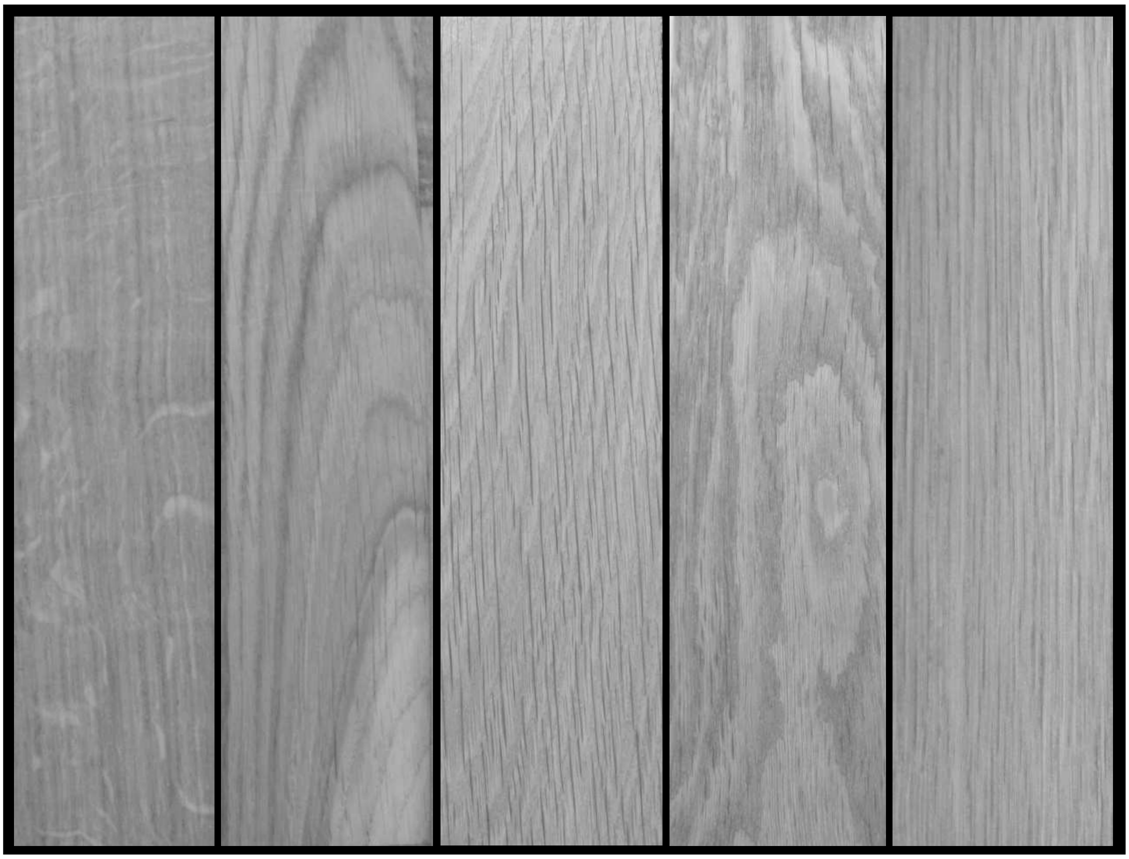

Figura 4. Exemplos do padrão da madeira de soalho de carvalho de acordo com o tipo de corte efectuado.

2.2.1.3. Vasos

O estudo da distribuição dos vasos e das suas características contribui para um maior conhecimento do ponto de vista fisiológico sobre as relações de condução na árvore, e do ponto de vista tecnológico sobre a laboração e utilização final.

A classificação da porosidade de uma madeira é função principalmente da distribuição e morfologia dos vasos ao longo da camada de crescimento. Os três principais tipos são: porosidade em anel, porosidade difusa e porosidade semi-difusa. Em geral, as espécies de folha caduca apresentam porosidade em anel, enquanto as perenifólias apresentam porosidade semi-

-difusa (Butterfield 2006). Salienta-se que factores externos podem influenciar a porosidade como o clima, nomeadamente os períodos de seca (Esau 1974).

A denominada porosidade em anel é característica do género *Quercus* e das espécies de folha caduca (ver secção seguinte), isto é, os vasos do lenho inicial são muito largos comparativamente com os vasos do lenho final, originando uma mudança abrupta da dimensão dos vasos entre as camadas de crescimento. Os vasos largos característicos, do lenho inicial, da madeira de carvalho são largamente responsáveis pela sua estética muito apreciada. No caso da madeira de carvalho português, os vasos que se formam no início da época de crescimento são menores quando comparados com outras madeiras de carvalho com porosidade em anel como o carvalho roble e o negral, segundo Carvalho (1997). Os vasos de *Q. faginea* são muito maiores em comparação com a *Q. ilex* e *Q. coccifera*, espécies de porosidade difusa (Corcuera et al. 2004; Villar-Salvador et al. 1997).

Importa referir que a descrição da forma e arranjo dos vasos na camada de crescimento é muito importante para a identificação, caracterização e estética da madeira (Figura 4). No caso da *Q. faginea*, os vasos do lenho inicial são relativamente circulares e estão distribuídos segundo linhas relativamente tangenciais e os vasos do lenho final tem formas mais poligonais e dispõem-se em bandas radiais que dilatam para o final da camada de crescimento (Carvalho 1997; García Esteban e Guíndeo Casasús 1990).

A existência de tilos é característica do cerne e dos vasos do lenho inicial dos carvalhos, mas não se trata de uma característica sistemática e a sua formação está, por exemplo, relacionada com os fenómenos fisiológicos de cavitação. Nas espécies pertencentes à secção *Quercus*, como a *Q. petraea*, *Q robur* e *Q. faginea* é esperada a ocorrência destas proliferações celulares (Carvalho 1997). Em termos de utilização da madeira, os tilos conferem maior impermeabilidade e dificuldade de secagem à madeira, tornando-a adequada, por exemplo, para a produção de barris.

Usualmente os parâmetros biométricos mais estudados são: o diâmetro tangencial dos vasos, a área, a densidade (nº de vasos/mm^2), a proporção dos vasos (área de vasos/área total) e os demais índices de condutividade. A área média dos vasos do lenho inicial da *Q. faginea* variou entre 0,020 mm^2 e 0,034 mm^2 segundo Alla e Camarero (2012) para árvores com idades aproximadas de 30 anos e entre locais com características contrastantes. Os vasos de *Q. robur* variaram entre 0,035 mm^2 e 0,081 mm^2, com máximos de 0,125 mm^2 (Savill 1986; García-González e Eckstein 2003).

A variação das medidas biométricas dos vasos tem sido estudada em função da idade em algumas espécies de carvalhos e tem evidenciado que a área média de vasos tende a aumentar da medula para a periferia e o número de vasos a diminuir (Leal et al. 2007; Preston et al. 2006;

Bakour 2003). A densidade dos vasos mantém-se relativamente constante ou diminui ao passo que a proporção dos vasos sofre um ligeiro aumento radial (Leal et al. 2007; Phelps e Workman 1994; Bakour 2003). A relação destes parâmetros anatómicos com a idade e o crescimento radial da árvore revelou, por exemplo, em *Q. alba* L. uma relação significativa entre a proporção da área de vasos do lenho inicial e a posição radial, mas não com a largura do anel (Phelps e Workman 1994).

A potencial utilização dos parâmetros anatómicos dos vasos para o estudo e explicação da variação da densidade da madeira tem ganho importância, nomeadamente no género *Quercus* (Leal et al. 2011; Rao et al. 1997; Zhang e Zhong 1992). Em geral, o calibre dos vasos (área) e o número de vasos tendem a ser inversamente proporcionais à densidade da madeira (Savidge 2003). A proporção dos vasos é um dos parâmetros que mais contribui para a variação da densidade (Rao et al. 1997; Zhang e Zhong 1992). Na *Q. suber* concluiu-se que o calibre e o número de vasos também contribuem significativamente para a variação da densidade desta madeira (Leal et al. 2011).

A utilização dos vasos como indicadores fisiológicos ou climáticos também se tem revelado bastante interessante no género *Quercus* (Woodcock 1989; Leal et al. 2007; Tardif e Conciatori 2006; Matissons e Brumelis 2012). Embora no caso dos vasos de *Q. faginea*, os estudos efectuados não sejam conclusivos, por exemplo, Villar-Salvador et al. (1997) refere que os vasos não apresentaram nenhum padrão de variação em relação aos factores climáticos, mas Alla e Camarero (2011) notaram uma correlação negativa da área de vasos do lenho inicial com a temperatura de inverno.

2.2.1.4. Anéis de crescimento

A actividade do câmbio é condicionada por diversos factores entre os quais os factores ambientais. Nas regiões de clima temperado, o câmbio inicia a sua actividade em condições favoráveis, normalmente na Primavera, entrando num estado de dormência a partir do Outono até à Primavera seguinte (Esau 1974). Esta periodicidade da actividade do câmbio dá origem ao anel de crescimento no xilema secundário (Esau 1974). O anel de crescimento caracteriza-se por apresentar duas zonas distintas: o lenho inicial e o lenho final. O lenho inicial caracteriza-se por apresentar células mais largas com paredes mais finas, em relação ao lenho final que apresenta células com paredes mais espessas e de menor diâmetro.

A largura do anel de crescimento e a sua variação na árvore são consideradas características primárias de avaliação da qualidade da madeira, pois estão relacionadas com a variação da densidade e de outras propriedades físico-mecânicas da madeira (Chauhan et al. 2006; Zhang et al. 1993; Nepveu 1984).

Existem diferentes tipos de anel de crescimento classificados de acordo com a presença e arranjo estrutural dos elementos anatómicos (Carlquist 2001). Nos carvalhos, espécies de crescimento lento, os anéis tendem a ser mais estreitos comparativamente com as espécies de crescimento rápido. Por exemplo, a largura do anel de crescimento em *Q. petraea* para um período de 30 anos foi de 2 mm (largo), 1,65 mm e 0,97 mm em árvores com idade média de 165 anos e próxima dos 300 anos, respectivamente (Helińska-Raczhowska e Fabisiak 1991; Bakour 2003; Lebourgeois 2004). A *Q. robur* apresentou maiores valores comparativamente à *Q. petraea*, média de 2,0 mm de largura do anel para 150 anos de idade (Bakour 2003). O sobreiro (*Q. suber*) apresenta em média valores entre 2,5 e 3,9 mm (Leal et al. 2008; Knapič et al. 2007). Na *Q. pyrenaica* (carvalho-negral) verificou-se um decréscimo da largura do anel de 1,6 mm para 0,5 mm da medula para a periferia, em árvores com 35-41 anos de idade (Corcuera et al. 2006). A *Q. cerris* L. apresenta em média 2,6 mm nos primeiros 15 anéis e 1,6 mm nos dez anéis seguintes (Manetti 2002).

Na *Q. faginea*, espécie de porosidade em anel, os anéis de crescimento são nitidamente distintos com poros grandes (Carvalho 1997). Oliveira et al. (2001) referem um crescimento anual de 1,5 mm/ano para um período de 30 anos. Recentemente, Knapič et al. (2011) indicam uma largura média de 2,4 mm para as árvores de *Q. faginea* oriundas de Macedo de Cavaleiros, com idades compreendidas entre 34 e 65 anos.

O factor idade é muito importante para o estudo da variação da largura e estrutura dos anéis de crescimento. O padrão de tendência dos carvalhos corresponde a um decréscimo da largura do anel com a idade seguido de um período de alguma estabilização (Paul 1963; Lei et al. 1996; Zhang et al. 1993; Lebourgeois et al. 2004). Dentro do anel de crescimento diferencia-se o lenho inicial e o lenho final. A variação da proporção do lenho final na espécie, na *Q.petraea* é função da idade e apresenta uma forte correlação com a largura total do anel (Polge e Keller 1973; Zhang et al. 1993; Lebourgeois et al. 2004).

A largura do anel no género *Quercus* também é influenciada pelas condições ambientais e do povoamento, nomeadamente a sua densidade e outros aspectos silviculturais (Guilley et al 1999; Zhang et al. 1993; Bakour 2003; Lebourgeois et al. 2004; Bergès et al. 2008). Por sua vez estas condições irão influenciar a utilização final da madeira, por exemplo, a anéis mais largos corresponde geralmente madeira mais densa que será menos adequada à produção de folheado.

2.2.2. Borne e cerne

À medida que a árvore cresce e que o lenho se vai formando, ocorrem diversas alterações fisiológicas que permitem diferenciar duas regiões: o cerne e o borne. O cerne caracteriza-se por ser a região interna e fisiologicamente inactiva do tronco e o borne a região externa em actividade que assegura funções de armazenamento e condução (Bierman 1996; Hillis 1987). As células de parênquima radial são responsáveis pelo depósito de extractivos (compostos orgânicos como fenóis e óleos) nas células vizinhas resultando na formação do cerne (Kramer e Kozlowski 1960; Hillis 1962; Desch e Dinwoodie 1996; Buchanan et al. 2000).

As principais funções associadas ao cerne são de carácter fisiológico ou de suporte. Existem algumas teorias sobre a formação de cerne mas esta é bastante complexa e ainda não está totalmente explicada.

O cerne e o borne são bastante diferentes devido ao conteúdo de extractivos, densidade e algumas propriedades físicas, como estabilidade dimensional e durabilidade (Pereira et al. 2003; Tsoumis 1991). Em geral, o cerne é preferido para a maior parte das utilizações de madeira maciça devido à sua cor mais escura e elevada durabilidade natural. Estas duas características estão relacionadas com uma acumulação elevada de extractivos relativamente ao borne, que possui menor teor de extractivos e é rico em amido e gorduras, sendo mais facilmente deteriorado e mais claro. Assim, o cerne como material apresenta vantagens para aplicações em ambientes exteriores e/ou bastante húmidos, mas pode ter implicações negativas aquando da laboração (e.g. presença de sílica), colagem e preservação da madeira. Isto é, a proporção de cerne é uma característica importante para a avaliação da qualidade da madeira.

Embora seja economicamente importante, o desenvolvimento de cerne não está devidamente caracterizado em diversas espécies, sendo o caso de várias *Quercus* spp. incluíndo a *Q. faginea*. A maior parte dos estudos tem incidido nas propriedades químicas, de cor, durabilidade dos carvalhos (e.g. Mosedale et al. 1996; Humar et al. 2008) ou nas relações com a área foliar e condução (e.g. Meadows e Hodges 2002; Granier et al. 1994).

A madeira de carvalho português apresenta cerne acastanhado e borne amarelado (Carvalho 1997). Em relação à área e desenvolvimento de cerne, apenas Natividade (1929) refere para um conjunto de seis árvores de *Q. faginea*, da região do Vimeiro, uma média de 30 cm de diâmetro de cerne e 3 cm de espessura de borne a 1,30 m de altura, com formação a iniciar aos 18/20 anos. Noutros carvalhos, como a *Q. petraea* e *Q. robur* a espessura de borne foi de 3,07 cm e 2,78 cm para idades médias de 161 e 150 anos, respectivamente (Bakour 2003).

Em termos de formação têm sido encontrados diferentes padrões de desenvolvimento de acordo com as diversas espécies. Axialmente, a tendência mais comum é a diminuição da área de cerne com a altura (Hillis 1987) mas têm sido observadas algumas flutuações nesta variação (Pinto et al. 2004; Knapič e Pereira 2005; Knapič et al. 2006). Em relação ao borne, em geral a sua espessura é relativamente constante ao longo do tronco (Hillis 1987; Bamber 1976). Entre espécies é de notar algumas diferenças na tendência de variação, por exemplo, a espessura de borne decresce em altura em *P. pinaster* (Pinto et al. 2004) e aumenta na *E. grandis* x *E. urophylla* (Gominho et al. 2001).

Vários estudos evidenciaram uma relação entre o crescimento em diâmetro e a área de cerne, mas não com a espessura de borne (Pinto et al. 2004, 2005; Knapič e Pereira 2005; Gominho e Pereira 2000, 2005; Knapič et al. 2006). As correlações entre estas e outras variáveis biométricas têm sido realizadas para algumas espécies economicamente viáveis, permitindo obter modelos de crescimento do cerne, ou seja, estimando de forma aproximada os volumes de produção.

A área de borne e cerne varia bastante entre espécies e entre árvores de diferentes idades, sendo a proporção de borne maior nas árvores mais novas quando comparada com a proporção de cerne, e condicionada pelos factores ambientais inclusive nos carvalhos europeus (Hillis 1987; Beck 2005; Bakour 2003). Também os factores genéticos influenciam a formação de cerne como por exemplo foi demonstrado na *Q. petraea* e *Q. robur* (Mosedale et al. 1996).

2.2.3. Densidade

A densidade ou massa volúmica[2] (g/cm^3) pode ser definida como a razão entre massa e o volume da amostra de madeira, sob condições ambientais específicas, normalmente 0% ou 12% de humidade. É uma das características consideradas mais importantes para a avaliação da qualidade da madeira (Zobel e van Buijtnen 1989). A sua determinação pode ser realizada por diferentes métodos, relativamente simples, tornando-a numa característica de medição acessível e de baixo custo que permite estimar com boa precisão outras propriedades da madeira.

A densidade da madeira traduz a relação entre a quantidade de matéria lenhosa (parede celular) e os espaços vazios existentes na madeira por unidade de volume. Assim, as diferenças de densidade estão relacionadas com as diferenças anatómicas como o tipo de células, a sua distribuição quantitativa, espessura de parede e lúmenes celulares (Tsoumis 1991). Em geral, os elementos anatómicos com paredes mais espessas e lúmenes reduzidos (por exemplo as fibras do lenho final) contribuem para um aumento da densidade, ao contrário dos elementos com paredes mais finas e lúmenes largos (por exemplo os vasos e fibras do lenho inicial).

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[2] A utilização da designação *massa volúmica* está de acordo com as convenções e resoluções internacionais e com as normas portuguesas contudo é usalmente utilizada a designação *densidade* neste contexto o que parece devirar do termo <<*density*>> na língua inglesa que designa a massa volúmica.

Os carvalhos de maior valor comercial, *Q. petraea* e *Q. robur*, apresentam densidades médias de 0,52 a 0,83 g/cm^3 e para a mesma largura de anel a *Q. robur* apresenta densidades mais baixas (Bergès et al. 2008; Nepveu 1984; Bakour 2003; Genet et al. 2012). Outros, como o sobreiro (*Q. suber*) e o carvalho turco (*Q. cerris*), apresentam em média densidades mais elevadas desde 0,75 a 1,07 g/cm^3 (Knapič et al. 2007, 2008; Dilem 1995).

Em relação à madeira de *Q. faginea*, foi realizado recentemente um estudo detalhado com as amostras provenientes de Macedo de Cavaleiros (correspondente ao local 1 do presente trabalho) por Knapič et al. (2011). Os referidos autores concluíram que a madeira apresenta em média densidade elevada de 0,848 g/cm^3. Estes resultados vieram corroborar as descrições encontradas na literatura que referiam a densidade elevada como característica da madeira de *Q. faginea* (Carvalho 1997; Natividade 1929).

Face à importância da homogeneidade da densidade da madeira enquanto material, alguns estudos têm sido desenvolvidos sobre a sua variabilidade ao nível da espécie, nomeadamente na árvore, entre árvores e diferentes condições da estação ou local. A variabilidade entre árvores tem sido apontada como uma das que mais contribui para a variação total, como por exemplo, em *Q. petraea* e *Q. robur* (Bergès et al. 2008; Guilley et al. 2004; Ackermann 1995; Zhang et al. 1993).

O decréscimo da densidade com a idade do câmbio é considerado a tendência padrão em *Quercus* spp, desde a *Q. garryana*, *Q. suber*, *Q. petraea*, *Q. robur* e *Q. nigra* L. entre outras (Knapič et al. 2008; Lei et al. 1996; Bergès et al. 2000; Bakour 2003; Paul 1963). Na *Q. faginea* em árvores com idade média de 40 anos, para um período de 30 anos de idade do câmbio, foi observada esta mesma tendência (Knapič et al. 2011). A largura do anel segue a mesma tendência de variação radial (Paul 1963; Lei et al. 1996; Zhang et al. 1993). Os estudos de correlação entre a largura do anel e a densidade média têm originado resultados contraditórios, desde boas correlações como na *Q. faginea* nas árvores estudadas por Knapič et al. (2011), em *Q. alba* (Paul 1963) e em *Q. petraea* e *Q. robur* (Bakour 2003) ou fracas como refere Zhang (1994) para espécies de porosidade em anel e Polge e Keller (1973) para a *Q. petraea*. Os perfis de densidade com a largura do anel e idades fixadas podem ser fundamentais para a distinção entre espécies (e.g. Bakour 2003). Nas espécies com porosidade em anel, em geral, a anéis mais largos correspondem densidades mais elevadas devido à maior proporção do lenho final (Chauhan 2006). Porém, a complexidade da estrutura nestas espécies tem justificado o interesse em avaliar quais as componentes mais importantes. Estudos recentes referem a importância dos elementos anatómicos nomeadamente as fibras, raios e vasos para explicar as variações de densidade ao nível da espécie (Guilley e Nepveu 2003; Bakour 2003).

Nos carvalhos, incluindo o carvalho português, em termos axiais, tem sido verificada uma tendência de diminuição da densidade com a altura na árvore (Knapič et al. 2008, 2011; Guilley et al. 1999; Lei et al. 1996). Esta variação estará relacionada com a influência da formação de lenho final como efeito da proximidade da copa.

A densidade, estando associada à estrutura anatómica do anel e à formação de lenho final, poderá estar dependente de factores fisiológicos e ambientais. A densidade dentro do anel diminuiu com a idade do câmbio na *Q. petraea* e *Q. robur* (Bakour 2003). Por exemplo, a largura de lenho final e a densidade da madeira também foram afectadas pelas condições ambientais (Nepveau 1984; Ackermann 1995; Bergès et al. 2008). No entanto existem resultados contraditórios (Guilley et al. 2004) e o mais consensual até agora parece ser que os factores ecológicos afectem mais o crescimento do que a densidade (Bergès et al. 2008; Guilley et al. 1999).

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Capítulo 3

Material e métodos

3.1. Amostragem

O planeamento da amostragem foi desenvolvido no âmbito do projecto OAKWOODS – "Propriedades da madeira de carvalhos portugueses para produção de produtos sólidos e compostos de madeira de valor elevado / *Properties of wood from Portuguese oaks for high value solid and assembled wood products*" (PTDC/AGR-AAM/69077/2006). Esta selecção foi condicionada por alguns factores administrativos e logísticos externos ao estudo.

A selecção dos locais foi realizada na área de distribuição natural da *Q. faginea* (Capelo e Catry 2009). O primeiro local (local 1) seleccionado foi, na região nordeste, em Macedo de Cavaleiros (distrito de Bragança) e o segundo (local 2), na região centro-oeste, em Vimeiro (distrito de Alcobaça) (Figura 5). Ambos os povoamentos são de regeneração natural e não existem dados das operações silviculturais realizadas, sendo admitido no trabalho apenas terem existido limpezas de mato. O clima é do tipo mediterrânico com influência atlântica e segundo o sistema de classificação de Köppen-Geiger podem ser designados por Csa e Csb em Macedo de Cavaleiros e no Vimeiro, respectivamente.

A vegetação no local 1 caracteriza-se pela ocorrência casual de *Q. suber*, *Q. rotundifolia* e *P. pinaster* e arbustos como *Cistus ladanifer* L., *Lavandula* spp., *Daphne gnidium* L., *Cytisus multiflorus* (L'Hér.) Sweet. No local 2 registam-se exemplares de *Q. suber*, *C. sativa* e *P. pinaster* sendo o estrato arbustivo composto por, entre outras espécies, *Arbutus unedo* L., *Ulex europeaus* L. ssp., *Erica arborea* L. e fetos (*Pteridium aquilinum* (L.) Kuhn). O Quadro 1 apresenta um resumo das principais características edafo-climáticas e biométricas dos dois locais. Estes são referidos como local 1 e local 2 à excepção do quarto trabalho onde se referem como MC e VI, respectivamente.

Foram seleccionadas 10 árvores dominantes ou co-dominantes em cada um dos locais, tendo em consideração o bom estado fitosanitário das mesmas. A idade média estimada, através da contagem do número de anéis na base, das árvores foi de 40 anos em Macedo de Cavaleiros e de 125 anos no Vimeiro. Mediu-se o diâmetro à altura do peito (DAP), altura total, altura do tronco (ou altura do fuste limpo), altura da copa (diferença entre altura total e do tronco) e 8 raios da copa (na projecção horizontal a partir do tronco e segundo os pontos cardeais) por cada árvore. Os Quadros 2 e 3 apresentam os dados biométricos para as árvores seleccionadas no local 1 e 2, respectivamente. Em cada árvore abatida foram cortadas rodelas de 2 em 2 metros, isto é, foram retiradas rodelas ao nível da base, 1,3 m, 3,4 m, 5,5 m, 7,6 m e 9,7 m. No local 2 apenas em 8 árvores foram retiradas rodelas a 7,6 m e em 6 árvores a 9,7 m de altura, dada a respectiva dimensão. Em cada nível de altura foram seleccionadas as amostras de acordo com o estudo a realizar.

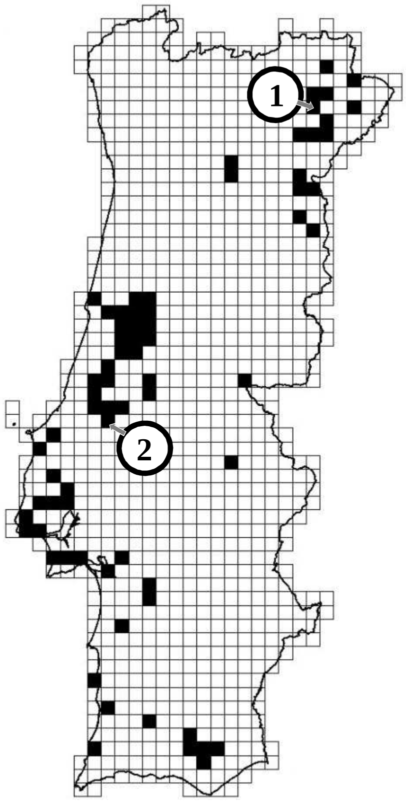

Figura 5. Identificação dos locais de amostragem em relação à distribuição natural da *Q. faginea*: Macedo de Cavaleiros (1) e Vimeiro (2) (Adaptado de www.flora-on.pt).

Quadro 1. Caracterização edafo-climática dos locais selecionados para o estudo e respectivos povoamentos de *Q. faginea*.

	Macedo de Cavaleiros (local 1/MC)	**Vimeiro (local 2/VI)**
Latitude	41° 31′ N	39º 29' N
Longitude	06° 51’ W	09º 01' W
Altitude (m)	540	100
Precipitação total (mm)	700	890
Temperatura média anual (ºC)	12	15
Solos	Leptossolos dístricos órticos e êutricos órticos	Cambissolos crómicos
Área basal (m^2)	18	102
Densidade (árv/ha)	327	300

Quadro 2. Caracterização das árvores de *Q. faginea* no local de Macedo de Cavaleiros. Desvio padrão entre parêntesis.

Árvore	Idade estimada*	DAP (cm)	Altura total (m)	Altura do tronco (m)	Área da copa ** (m^2)
1	60	29.0	9,5	2,3	50,9
2	34	24.1	10,1	1,2	7,4
3	34	24.5	11,7	0,5	10,6
4	43	20.5	10,4	1,9	24,1
5	36	15.5	10,0	3,9	9,1
6	42	22.3	11,0	2,2	26,6
7	39	19.9	10,8	3,3	22,6
8	38	19.5	10,5	2,9	16,1
9	39	15.9	11,0	2,6	11,5
10	39	17.6	9,7	1,4	21,9
Média	40 (8)	20,9 (4,2)	10,5 (0,7)	2,2 (1,0)	20,1 (12,8)

* com base no número de anéis na base

**Média de 8 raios.

Quadro 3. Caracterização das árvores de *Q. faginea* no local do Vimeiro. Desvio padrão entre parêntesis.

Árvore	Idade estimada *	DAP (cm)	Altura total (m)	Altura do tronco (m)	Área da copa ** (m^2)
1	122	42,2	17,1	11,2	77,4
2	120	29,0	14,2	6,5	61,8
3	122	31,1	13,7	5,0	70,3
4	128	42,0	16,2	8,9	41,1
5	121	33,5	15,6	6,0	68,8
6	132	46,3	18,0	6,5	99,4
7	132	40,8	15,5	2,7	65,4
8	112	37,1	14,2	6,3	103,9
9	112	30,4	13,0	4,7	31,4
10	150	34,8	10,0	4,4	61,0
Média	125 (11)	36,7 (5,9)	14,8 (2,3)	6,2 (2,4)	63,4 (28,0)

* com base no número de anéis na base

** Média de 8 raios.

3.2. Determinação da proporção de cerne e borne

A identificação do borne e cerne é feita geralmente com base nas diferenças de cor natural, sendo mais acentuada ainda com o material em verde devido às grandes diferenças de humidade das duas zonas. Os testes químicos facilitam essa diferenciação e os mais utilizados baseiam-se na diferença de pH e presença de amido entre o cerne e o borne.

No caso da madeira de *Q. faginea*, o cerne distinguiu-se bastante bem do borne devido à diferença de cor natural. Para obter uma maior precisão na distinção e sucessiva medição, recorreu-se à utilização do corante alaranjado de metilo que aumentou o contraste de cor devido às variações de pH.

Mediram-se a área total (sem casca) e a área de cerne, em cada rodela retirada a cada nível de altura em cada árvore e em cada local, com recurso a técnicas de análise de imagem (Analysis software, version 3.2, AnalySIS Soft Imaging System GmbH). Para cada rodela, calculou-se a área de borne por diferença entre a área total e área de cerne, a largura média de borne e o diâmetro médio de cerne.

Para efeitos do estudo dos anéis de crescimento, as amostras foram previamente polidas e observadas a uma ampliação de 7 x (1 pixel = 0,0217 mm) e a medição efectuada, com precisão de 0,1 mm, num programa de análise de imagem (Leica Q Win Standard). O número e a largura média dos anéis do borne e cerne foram calculados com base na medição efectuada em 3 raios relativamente equidistantes em cada uma das rodelas.

As delimitações da área de cerne e borne não são inteiramente correspondentes aos anéis de crescimento, tornando por vezes necessário efectuar uma aproximação no que diz respeito à contagem dos anéis correspondentes.

O trabalho experimental foi desenvolvido no Laboratório de Dendrocronologia e Análise de Imagem, no Centro de Estudos Florestais do ISA.

3.3. Caracterização anatómica

Foi seleccionada uma rodela ao nível do DAP de cada árvore em cada local e cortaram-se amostras radiais, da medula para a periferia.

Para as observações microscópicas cortaram-se amostras de 1 x 1 x 2 cm^3 (direcção radial x tangencial x axial) em três pontos de amostragem: próximo da medula (20% do raio), intermédio (50% do raio) e periférico (90% do raio). De seguida procedeu-se ao seu amolecimento e corte com um micrótomo de deslize. Foram realizados cortes radiais, tangenciais e transversais com cerca de 15-20 µm de espessura em cada ponto de amostragem radial. As preparações finais foram obtidas depois da gradação alcoólica dos cortes, coloração simples com safranina ou dupla coloração com verde malaquita (no caso da quantificação dos tecidos) e montagem em Euparal.

Na secção transversal foram medidos os diâmetros dos poros do lenho inicial nos três pontos de amostragem radiais e feita a quantificação dos tecidos com recurso a uma malha de 28 pontos ao longo do anel de crescimento também em cada um dos três pontos de amostragem radiais. Na secção tangencial mediram-se os raios unisseriados por cada posição radial.

Foi realizado o estudo da variação radial do comprimento, largura e espessura da parede das fibras; e do comprimento dos elementos vasculares. As medições foram efectuadas em elementos dissociados, após maceração com solução 1:1 de ácido acético e peróxido de hidrogénio durante 48 h em estufa a 60 ºC.

A medição da largura e altura dos raios multisseriados foi feita na secção tangencial depois de polida e de se aplicar óleo para salientar os raios.

A distribuição e a variação da área de vasos do lenho inicial foram estudadas da medula para a periferia. A secção transversal das amostras foi polida aplicando-se a seguir cera branca para preencher os poros e obter um contraste maior com os tecidos adjacentes. A sequência radial dos vasos foi captada em imagens sucessivas em formato digital e posteriormente efectuada a medição dos diversos parâmetros, de acordo coma metodologia proposta por Leal et al. (2007). O número de vasos e a respectiva área foram medidos em cada anel. Determinou-se ainda a densidade dos vasos (nº de vasos por mm^2) e a proporção de vasos total (área de vasos por mm^2).

Para o estudo qualitativo da casca, as amostras foram previamente incluídas em polietileno-glicol de acordo com o processo descrito por Quilhó et al. (1999) e os cortes efectuados num micrótomo de deslize. Foi feita uma coloração dupla com azul astral-crisoidina (solução aquosa), seguida de desidratação gradual dos cortes e montagem permanente com Eukitt. O estudo da variação axial do comprimento, largura e espessura da parede das fibras e dos elementos de tubo crivoso foi realizado, em três níveis de altura (base, DAP e a 75% de altura), em elementos dissociados obtidos por maceração.

Todas as medições foram feitas em programas de análise de imagem (Leica Qwin standard e Leica Application Suite) com as ampliações apropriadas aos respectivos parâmetros anatómicos.

A caracterização anatómica da casca de *Q. faginea* foi feita com base nas amostras provenientes de Macedo de Cavaleiros (local 1) e a caracterização da madeira e o estudo da variação radial das fibras, raios e vasos do lenho inicial foi realizado nos dois locais. No caso das fibras e raios multisseriados as amostras foram obtidas em cada 5 anéis no local 1 e no local 2 de 10 em 10 anéis. Os vasos foram estudados da medula para a periferia, em cada anel.

No Quadro 4 apresenta-se o esquema de amostragem para a biometria realizada na madeira de *Q. faginea*.

A preparação dos cortes e medições através de programas de análise de imagem foi desenvolvida no Laboratório de Anatomia do Centro de Estudos Florestais do ISA e do IICT.

Quadro 4. Medições biométricas realizadas nas amostras de madeira de *Q. faginea* para o estudo anatómico.

	Local	**Nº medições**	**Ampliação**	**Pontos de amostragem**	**Observações**
Lenho					
Elementos de vaso					
Comprimento (µm)	1,2	25	125 x	20, 50 e 90% do raio	Elementos dissociados
Diâmetro tangencial (µm)	1,2	25	50 x	20, 50 e 90% do raio	Secção transversal
Área (mm^2)	1,2	Variável	20 x	Da medula para a periferia	Secção transversal
Número	1,2	Variável	20 x	Da medula para a periferia	Secção transversal
Raios unisseriados (Nº de células em altura)	1,2	50	250 x	20, 50 e 90% do raio	Secção tangencial
Percentagem de tecidos (%)	1,2	Variável	62,5 x	20, 50 e 90% do raio	Secção transversal
Fibras					
Comprimento (mm)	1,2	40 (20 por lâmina)	125 x	5 em 5 anos (local 1)	Elementos dissociados
Largura (µm)			500 x	10 em 10 anos (local 2)	
Espessura da parede * (µm)			500 x		
Raios multisseriados	1,2	Variável	1 x	5 em 5 anos (local 1)	Secção tangencial
Altura (mm)				10 em 10 anos (local 2)	
Largura (mm)					
Casca					
Fibras	1			Um ponto	
Comprimento (mm)		40 (20 por lâmina)	125 x		Elementos dissociados
Largura (µm)			500 x		
Espessura da parede * (µm)			500 x		
Elementos de tubo crivoso	1			Um ponto	
Diâmetro (µm)		40 (20 por lâmina)			Elementos dissociados
Comprimento (µm)			500 x		
			125 x		

*(largura total da fibra - largura do lúmen)/2

3.4. Microdensitometria

A densidade pode ser determinada por vários métodos entre os quais se destaca o método de determinação por raios X, desenvolvido por Polge (1966). As amostras de madeira (bem orientadas na direcção radial e com espessura uniforme) são submetidas à radiação de raios X, obtendo-se uma imagem negativa das amostras impressa em película adequada seguindo-se a leitura da densidade óptica, por um microdensitómetro, que depois será correlacionada e convertida em densidade real da madeira. Este método tem a vantagem de ser bastante expedito, consistente e de possibilitar estudar a variação entre anéis e dentro dos anéis de forma contínua (e.g. Echols 1973; Koubaa et al. 2002; Louzada 2000). O registo contínuo permite obter e estudar várias componentes da densidade.

Para o presente trabalho, por cada árvore e em cada nível de altura, foi retirada uma amostra da medula para a casca, prependicular ao eixo da árvore, tendo o cuidado de evitar o lenho de tensão. De seguida cortaram-se tiras de 5 mm de largura (direcção tangencial) e 2 mm de espessura (direccão axial) através de uma tupia de disco duplo. Estas amostras foram condicionadas a 12% de humidade.

As amostras foram de seguida radiografadas por raios X no sentido perpendicular à secção transversal, sendo colocadas a 2,5 m de distância do tubo de radiação e submetidas ao feixe de radiação durante 350 s, com uma voltagem de 12kV e intensidade de corrente de 18mA. A imagem das amostras foi impressa numa película Kodak Industrex CX (Figura 6). A leitura das películas de raios-x foi efectuada num microdensitómetro de duplo feixe Joyce Loebl MK3, equipado com um sistema duplo de saída de dados. O registo da densidade da madeira foi realizado a cada 100 µm (direcção radial) por 455 µm (direcção tangencial) na superfície da película. Este registo foi feito primeiramente numa fita perfurada e traçador de gráficos e depois calculados os valores da densidade real da madeira com base numa equação de regressão (R^2~100%) entre a densidade óptica e a densidade real dos padrões (de acetato de celulose). Uma descrição mais detalhada do método microdensitométrico utilizado é dada por Louzada (2000).

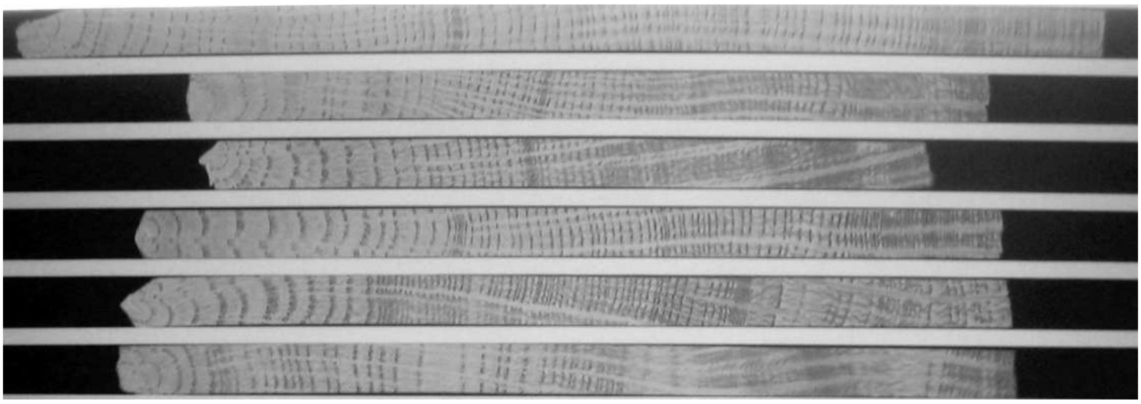

Figura 6. Superfície transversal de amostras de madeira de *Q. faginea* impressas em película de raios X.

A distinção dos anéis nas amostras de *Q. faginea* foi feita tendo em consideração a variação da densidade ao longo do anel de crescimento e com recurso à observação macroscópica das amostras, mais concretamente sobre a variação abrupta do calibre dos poros do lenho inicial (poros largos) e final (poros muito estreitos). Para cada anel foram calculadas as seguintes componentes da densidade: densidade média do anel, densidade média do lenho inicial, densidade média do lenho final, índice de heterogeneidade, largura do anel, largura do lenho inicial, largura do lenho final e percentagem de lenho final. Salienta-se que a transição entre o lenho inicial e final por cada anel foi obtida através da média dos valores mínimos e máximos de cada anel (Rozenberg et al. 2001). O índice de heterogeneidade, que quantifica a variação da densidade dentro do anel, foi calculado através do desvio padrão de todos os valores individuais de densidade em cada anel (Ferrand 1982).

Para o estudo da variação da densidade nas árvores com média de 125 anos, do Vimeiro (Local 2), optou-se por analisar uma série fisiológica (ou vertical) composta pelos 100 primeiros anéis comuns aos primeiros quatro níveis de altura das árvores. Nesta série os anéis têm a mesma idade fisiológica do câmbio e pretende-se estudar o efeito da idade do câmbio, árvore, níveis de altura e respectivas interacções.

Para o estudo de comparação entre os dois locais, ou seja entre as árvores com média de 40 anos e aquelas com média de 125 anos, considerou-se uma série vertical dos primeiros 15 anéis, número que foi condicionado pela rodela do último nível da árvore mais jovem. Esta série pretende ser indicativa do comportamento do lenho juvenil. Considerou-se também para este estudo, uma série oblíqua composta por 10 anéis iniciando ao nível da base no anel 31º ao 40º em ambos os locais que foi analisada para interpretar as diferenças numa idade fisiológica mais avançada, correspondendo a uma fase inicial do lenho adulto, incluindo o efeito da variação de cerne e borne ao longo do tronco.

O trabalho experimental foi efectuado no Laboratório dos Produtos Florestais da UTAD.

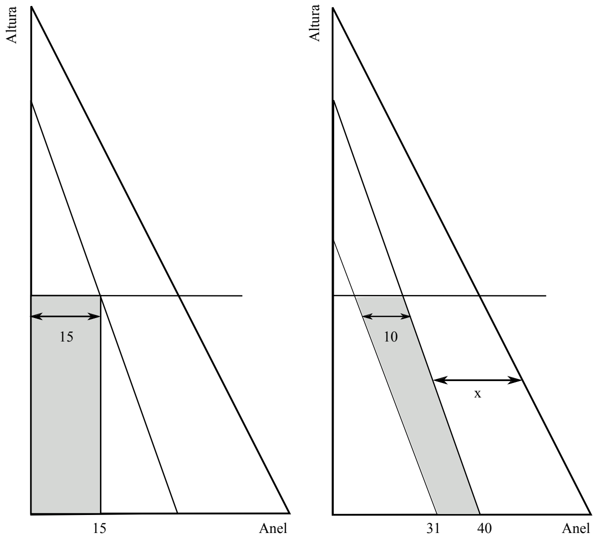

Figura 7. Esquema representativo das séries vertical e oblíqua, analisadas no estudo da variação da densidade da madeira de *Q. faginea*.

3.5. Análise estatística

Foi realizada a análise estatística descritiva dos dados para avaliar as suas características de distribuição, incluindo as médias, mínimos, máximos, desvios padrão e coeficientes de variação. A respectiva transposição gráfica permitiu uma melhor apresentação e interpretação dos resultados.

Para quantificar a relação entre algumas características e obter modelos de ajustamento mais ou menos aproximados da variação, principalmente radial, foram feitas regressões lineares ou polinomiais, estas geralmente de segundo grau, para algumas variáveis.

As correlações entre as diferentes variáveis medidas foram feitas recorrendo aos coeficientes de correlação de Pearson.

A análise de variância foi escolhida para identificar quais as principais fontes de variação nas características anatómicas e da densidade avaliando a sua significância estatística e quantificando a sua participação na variação total. Foram desenvolvidos diversos modelos adaptados aos conjuntos ou subconjuntos de dados a analisar e calculados os respectivos graus de liberdade, soma de quadrados dos desvios e quadrado médio. A escolha dos efeitos fixos e casuais foi feita para cada modelo. Na generalidade dos casos pretendeu-se estudar os efeitos da:

- Árvore (variação entre árvores);
- Idade do câmbio (variação radial na árvore);
- Nível de altura (variação axial na árvore);
- Locais (variação na espécie);
- E respectivas interacções.

Salienta-se que os efeitos podendo ser por vezes significativos contribuem pouco para a variação total. Daqui a importância da variância esperada que é calculada e expressa em função da variação total, obtendo-se assim uma medida da importância relativa de cada origem de variação. Para a comparação posterior das médias foi utilizado o teste múltiplo de Duncan.

Os diferentes tipos de análise foram feitos para alfa de 0,05 obtendo-se quatro níveis de significância: não significativo ($P > 0{,}05$), estatísticamente significativo para um nível de probabilidade de $P < 0{,}05$; estatísticamente significativo para um nível de probabilidade de $P < 0{,}01$ e estatísticamente significativo para um nível de probabilidade de $P < 0{,}001$ (altamente significativo).

Recorreu-se à utilização de programas informáticos comerciais, nomeadamente SPSS (LEAD Technologies Inc.) e JMP (SAS Institute Inc.), assim como a folhas de cálculo Microsoft Excel.

3.6. Referências

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Capítulo 4

Trabalho experimental

4.1. Ring width variation and heartwood development in *Quercus faginea*

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Keywords: *Quercus faginea,* Portuguese oak, heartwood, sapwood, ring width, wood quality.

Abstract:

High value exploitation of endogenous forest species may help fighting the threat to their sustainability, as it is the case for *Quercus faginea* Lam. (Portuguese oak) for which research is underway to determine the wood potential for high quality products. Ring widths were measured in 20 trees in two sites in Portugal and within-tree heartwood and sapwood development were determined. The wood shows distinct ring porosity. The mean annual radial growth at dbh was 2.3 mm and 1.0 mm for the two sites respectively. Ring width decreased with cambial age i.e. 3.1±1.2 mm in the first 10 rings to 1.3 ± 0.8 mm at around 40 years (site 1). Ring width decreased axially from the tree base upwards but the variation was small. The trees showed a relatively high proportion of heartwood, i.e. 60-70% heartwood for 20-25 cm wood diameters that decreased with height, and followed the stem profile. Heartwood diameter was modeled as a function of stem diameter, to be used for heartwood estimation in standing trees. Sapwood width was relatively constant. Overall the stem quality was found to be good for production of solid wood products as regards to ring and heartwood features.

Introduction

Quercus faginea Lam. (Portuguese or Lusitanian oak) is a deciduous oak, belonging to the white oaks sub-group, that is a native species in the western Mediterranean part of the Iberian Peninsula and Maghreb Africa. *Q. faginea* forests have been subject to extensive destruction over the centuries and the long-term future of the species is under threat. The oak forests that once covered Portugal were intensively exploited for timber for various applications, for example for naval construction during the XV and XVI centuries or as railway sleepers in the last two centuries, and many stands were converted to agriculture, or to industrial pine and eucalypt plantations (Capelo and Catry 2007). Now *Q. faginea* is restricted to only a few scattered stands. However, the wood potential and the environmental and cultural importance of the species are acknowledged (Fabião et al. 2007, Paiva 2007). More knowledge on tree growth, stem development, and wood properties is an essential tool to strengthen the efforts of producing high-value wood products with this species ie as in the EU Woodtech research project.

Most studies on this species have dealt with seedling sensitivity and response to environmental conditions (e.g., Sanz-Pérez et al. 2007), as well as with edaphic and environmental and climatic questions (e.g., Maltez-Mouro et al. 2009). Villar-Salvador et al. (1997) studied the response of xylem features to climate and Corcuera et al. (2004) the effects of severe drought.

Knowledge of *Q. faginea* wood properties is scarce. It has distinct ring porosity and overall oak-type anatomical features, high mechanical strength and high density (Carvalho 1997; Knapič et al. 2011). The utilization of *Q. faginea* wood, which currently is not commercially significant, and the acceptance of the species as providing high value timber should help in guaranteeing the sustainability of *Q. faginea* forests. The detailed wood characterization requires evaluation of a number of anatomical, physical and mechanical properties. Among them, two characteristics that are important for determining wood quality and performance are ring width and heartwood proportion. The width of annual growth rings and their within-tree variation is one of the primary wood quality factors since it is related to wood density variation and consequently to other physical and mechanical wood properties, especially in ring-porous woods (Nepveu 1984, Zhang et al. 1993,Chauhan et al. 2006).

Heartwood is also an important stem quality characteristic regarding its use value. Heartwood develops as a physiologically inactive region in the inner part of the stem while the outer region of sapwood remains active in storage and conduction (Hillis 1987). Heartwood and sapwood are very different in their extractives content, density, and some other physical properties (Pereira et al. 2003). Heartwood is generally preferred for most timber applications because of its darker color and higher natural durability. Despite its economic importance, the heartwood development of *Q. faginea*, as for many other species, has not been fully characterized.

The present article reports data for *Q. faginea* on radial stem growth measured by ring analysis, and its between-tree and within-tree variation, together with information on heartwood and sapwood within-tree distribution, based on 20 trees that were harvested in two stands in Portugal. Previous work on variation of wood density components within and between *Q. faginea* trees (at site 1) showed that density decreased with height and from pith to bark, i.e. the larger rings had higher wood density values (Knapič et al. 2011). The present study adds knowledge on *Q. faginea* heartwood and sapwood within-tree distribution and on between-site and tree radial stem growth based on ring analysis. This information is a first step in the development of an understanding of the growth and wood mechanical quality of this tree. It is our objective to contribute to the efforts of preserving *Q. faginea* by determining its potential for high-quality end uses and simultaneously gathering information on the characteristics of its growth and development under the general rationale that a high value exploitation of endogenous forest species is a method for fighting threats to their sustainability.

Material and methods

For this study, two stands of *Q. faginea* were selected for sampling: Site 1 was located in the northeast of Portugal, near Macedo de Cavaleiros, Bragança (latitude 41°30’N, longitude 7°01’ W, 554 m mean altitude) and Site 2 in the center of Portugal, near Vimeiro, Alcobaça (latitude 39º 29' N, longitude 9º 01' W, 100 m mean altitude). The trees were aged 34-60 yr and 112-150 years at Site 1 and Site 2, respectively. From each stand, 10 dominant or co-dominant trees free of visible signs of decay were randomly selected. Total tree height, crown height, crown diameter and tree diameter at breast height (1.3 m) were measured on the standing trees. Site and tree characteristics are shown in Table 1. The stands were unmanaged and no records of eventual silvicultural operations exist.

The trees were felled and sampled along the stem: at stem base height, at 1.3 m, 3.4 m, 5.6 m, 7.7 m and 9.7 m (Site 2 only) above ground level. A disc of about 10 cm thickness was collected at each of the sampling heights of each tree. Each disc surface was prepared by sanding. Tree ring widths were measured with 0.1 mm precision along three approximately equidistant radial directions (≈120º) on each disc in successive images with 7x optical magnification (1 pixel = 0.0217 mm) using a microscope coupled to a digital camera and image analysis software (Leica Q Win Standard).

Heartwood was visually distinct from sapwood (Fig. 1) but for measurement distinction was enhanced by applying a methylorange solution to the disc surface. The images of the discs were acquired using image analysis software (Analysis software, version 3.2, AnalySIS Soft Imaging System GmbH) and measurements of total disc area and heartwood area were taken. Calculations were made of sapwood area, sapwood mean radial width and heartwood mean diameter. The number of rings included in the heartwood and in the sapwood was also determined. The height limit of the heartwood was calculated as the intercept of the linear regression of heartwood areas with tree height levels.

Statistical and correlation analysis were performed at 0.05 confidence level using SPSS for windows version 19.0 (LEAD Technologies, Inc .). Analysis of variance was made considering tree, ring and height level as fixed effects, as well as their interactions. Relationship among the studied variables was assessed through correlation analysis.

Figure 1. Stem cross-section of *Quercus faginea* showing the natural colour differences between heartwood and sapwood (bar = 2 cm).

Table 1. Site and *Quercus faginea* trees characteristics.

	Site 1	**Site 2**
Location	Bragança (Macedo de Cavaleiros) Latitude 41°31′ N, longitude 6°51’ W	Alcobaça (Vimeiro) Latitude 39º 29' N, longitude 9º 01' W
Altitude (m)	540	100
Soil	Orthic Dystric and Eutric Leptosols	Chromic Cambisols
Annual precipitation (mm)	700 ± 141(289-1299)	890 ± 249 (469-1477)
Annual Mean temperature (ºC)	12 ± 1 (11-13)	15 ± 3 (10-19)
Köppen-Geiger Climate Classification	Csa	Csb
Tree height (m)	10.5 ± 0.7 (9.5 – 11.7)	14.8 ± 2.3 (10.0-18.0)
Diameter at 1.3m (cm)*	20.9 ± 4.2 (15.5 – 29.0)	36.7 ± 5.9 (29.0 - 46.3)
Crown height (m)**	8.3 ±1.3 (6.1 – 11.2)	8.5 ± 2.3 (5.6-12.8)
Radius crown (m)	2.4 ± 0.7	4.4±1.1
Tree age ***	40 ± 8 (34-60)	125 ± 11 (112-150)

[a] Mean values and standard deviation with min – max values in parentheses.

[b] Over bark diameter.

[c] Crown height = Tree height - trunk height.

[d] Measured at stem base.

Results

The sampled *Q. faginea* trees showed similar characteristics to those reported for the species (Table 1). The trees were medium-sized with a maximum tree height of 18 m and an average diameter at breast height of 37 cm for 125-yr-old trees (site 2). The trees had a short stem and on average 8 m of crown height.

Q. faginea showed distinct tree rings that were visible to the naked eye. It is a ring-porous wood (Fig. 2) with very wide pores in the earlywood in comparison with the pores in the latewood. The pores were arranged in lines, usually up to three lines, producing distinct ring boundaries. Rings were eccentric to undulating, and sometimes very narrow, but discontinuous rings were not frequent. Overall ring distinction was very good and allowed easy ring counting and measurement.

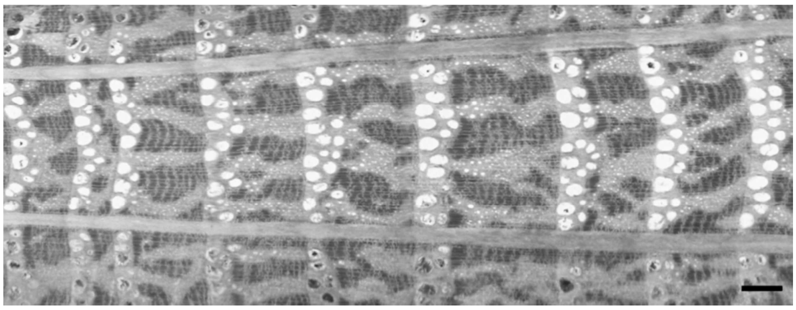


Figure 2. *Quercus faginea* wood observed in cross-section showing the wood vessels and ring porosity (scale bar = 1 cm).

Ring width and radial growth

The radial variation of the average tree ring width at 1.3 m height is shown in Fig. 3 for sites 1 and 2. The pattern of radial variation was similar at both sites with a higher growth rate in the first 10 years of cambial age (2.8 and 1.2 mm for site 1 and site 2, respectively) that decreased gradually at about 30-40 yr of cambial age (1.5 and 1.0 mm respectively for site 1 and site 2) and from this age on remained relatively constant. Overall growth rate was higher at Site 1 compared to Site 2 for similar cambial ages. The between-tree variability of ring width was high within Site 1, as shown by the deviation of the mean with differences that were statistically significant ($p < 0.0001$) during the first 30 yr of growth. At site 2 the between-tree variability of ring width for growth during the first 30 yr was not significant.

Figure 4 plots the mean accumulated radial growth for the 10 *Q. faginea* trees at each site. The pattern of radial growth variation was similar in both sites although with differences in the absolute values with a tree mean radial growth that was higher at site 1. For instance, at an age of 50 yr, the underbark diameter of *Q. faginea* trees was 21.2 cm (site 1) and 13.4 cm (site 2).

The within-tree variation is shown in Table 2 by summarizing the mean ring width for different cambial age classes (radial variation) at the different tree height levels (axial variation). Ring width varied with height in the tree for the same cambial age with an overall decreasing trend i.e. the mean annual ring width was highest at the stem base and lowest at the top of the stem. The radial variation showed a decrease with cambial age at all height levels, which was more accentuated in the regions near the pith.

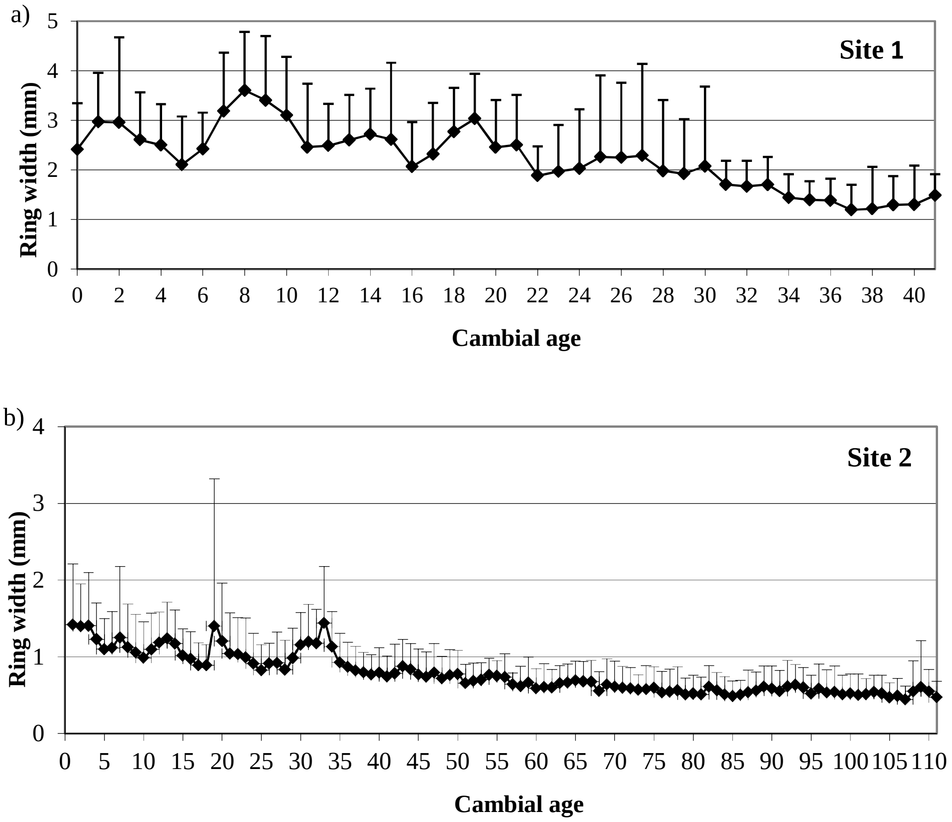


Figure 3. Ring width variation with cambial age at 1.3 m height in *Quercus faginea* trees at Sites 1 and 2. Average of 10 trees with error bars representing standard deviation. Note that the XX scale differs between sites.

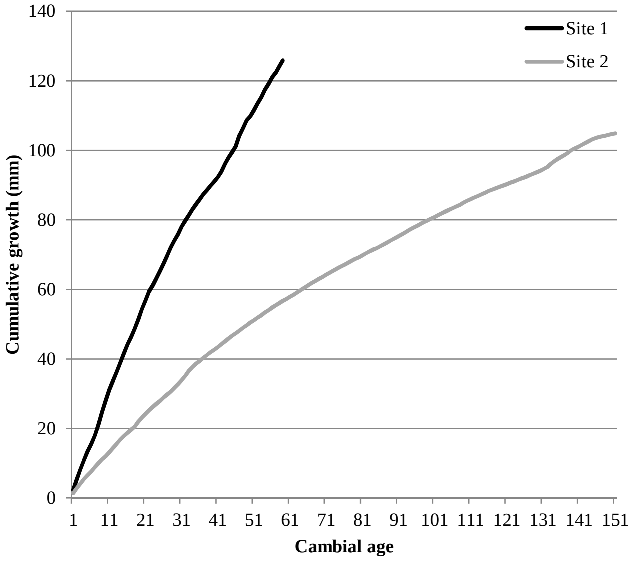


Figure 4. Accumulated radial growth with cambial age at 1.3 m height in *Quercus faginea* trees at Site 1 and 2. Mean of 10 trees.

Table 2. Within-tree variation of ring width according to cambial age classes and stem for *Quercus faginea* trees at Site 1 and Site 2.

Site	Age Class	Ring width (mm)					
		0 m	1.3 m	3.4 m	5.6m	6.7 m	9.7 m
1	[0-10]	2.8 ± 0.7	2.8 ± 0.7	2.4 ± 0.6	2.0 ± 0.6	1.5 ± 0.3	
	]10 - 20]	3.1 ± 0.5	2.6 ± 0.4	2.4 ± 0.6	2.0 ± 0.6	1.5 ± 0.3	
	]20 - 30]	2.8 ± 0.8	2.1 ± 1.1	2.4 ± 0.9	1.5 ± 0.9	1.0 ± 0.0	
	]30 - 40]	2.0 ± 0.6	1.5 ± 0.4	1.6 ± 0.3	1.5 ± 0.3	- ±	
	]40 - 50]	1.9 ± 0.7	1.6 ± 0.5	2.0 ± 0.6	1.5 ± 0.3	- ±	
	Mean	2.6 ± 0.8	2.3 ± 0.8	2.3 ± 0.7	1.9 ± 0.7	1.4 ± 0.3	
2	[0-10]	1.9 ± 0.5	1.9 ± 0.6	1.8 ± 0.3	2.1 ± 0.4	1.9 ± 0.3	1.2 ± 0.6
	]10 - 20]	1.8 ± 0.3	1.2 ± 0.2	1.5 ± 0.4	0.8 ± 0.3	0.9 ± 0.3	1.1 ± 0.2
	]20 - 30]	1.5 ± 0.3	1.2 ± 0.4	1.0 ± 0.2	1.4 ± 0.3	1.0 ± 0.2	1.1 ± 0.3
	]30 - 40]	1.7 ± 0.4	1.1 ± 0.1	1.3 ± 0.2	1.3 ± 0.3	0.8 ± 0.2	0.8 ± 0.1
	]40 - 50]	1.5 ± 0.2	1.3 ± 0.2	1.1 ± 0.3	1.0 ± 0.1	0.8 ± 0.2	0.8 ± 0.2
	]50 - 60]	1.4 ± 0.2	1.0 ± 0.2	1.0 ± 0.1	1.1 ± 0.1	0.8 ± 0.2	0.7 ± 0.1
	]60 - 70]	1.5 ± 0.3	0.7 ± 0.2	1.0 ± 0.2	0.7 ± 0.1	0.8 ± 0.2	0.6 ± 0.1
	]70 - 80]	1.2 ± 0.2	0.6 ± 0.1	0.7 ± 0.1	0.6 ± 0.1	0.7 ± 0.3	1.1 ± 0.6
	]80 - 90]	0.9 ± 0.1	0.8 ± 0.1	0.6 ± 0.1	0.5 ± 0.1	0.8 ± 0.3	0.7 ± 0.1
	]90 - 100]	1.1 ± 0.1	0.9 ± 0.2	0.7 ± 0.2	0.6 ± 0.1	0.6 ± 0.2	0.9 ± 0.2
	]100 - 110]	0.9 ± 0.1	0.9 ± 0.1	0.6 ± 0.1	0.6 ± 0.2	0.5 ± 0.2	0.5 ± 0.2
	]110 - 120]	0.7 ± 0.2	0.8 ± 0.2	0.7 ± 0.2	0.7 ± 0.2	0.6 ± 0.4	- ±
	]120 - 130]	0.9 ± 0.3	0.7 ± 0.1	0.7 ± 0.2	0.5 ± 0.1	0.3 ± 0.1	- ±
	Mean	1.3 ± 0.4	1.0 ± 0.3	1.0 ± 0.4	0.9 ± 0.5	0.8 ± 0.4	0.9 ± 0.2

[a] Average of 10 trees at each site plus standard deviation.

Heartwood and sapwood development

The heartwood of *Q. faginea* was clearly visible on the wood discs because of its brown color and generally well-defined borders (Fig. 1). Heartwood area decreased within the tree from the base upward and the heartwood vertical profile within the tree followed approximately the stem profile, resulting in an uniform thickness of sapwood along the tree. This also happened when there were clear taper variations along the stem (for example see Figure 5 representing one tree at each site).

The heartwood content differed considerably between sites (Fig. 6). At Site 1 the heartwood proportion was relatively constant in the lower part of the stem, representing 35.0% and 37.1% of the cross-sectional area at tree base and 1.3 m height respectively, and decreased regularly up the stem to 11.3% at 5.6 m, whereas at 7.7 m none of the trees contained heartwood. At Site 2, the proportion of heartwood was considerably higher: 67.9% at the base, 73.1% at 1.3 m, 69.9% at 3.4 m, and then decreasing to 54.5% at 7.6 m height and 45.6% at 9.7 m. The within-tree heartwood variation was statistically significant ($p < 0.001$ at site 1 and $p < 0.05$ at site 2) as well as the differences between sites ($p < 0.001$).

The sapwood width was relatively constant along the height axis of the tree (Fig. 6), and varied between 47.6 mm and 37.2 mm (site 1) and 31.2 mm and 23.1 mm (site 2). The within-tree sapwood variation was not statistically significant in either case. The sapwood contained, on average, 21 rings at the tree base and 17 rings at 5.6 m height at site 1, and 31 rings at the base and 31 at 7.7 m height at site 2. The difference in sapwood width between sites was statistically significant ($p < 0.001$).

Heartwood diameter was related to tree size with the smallest trees having less heartwood (Fig. 7a). In fact, the diameter of heartwood in *Q. faginea* was strongly correlated with stem diameter (R^2=78.3 and 92.9% at site 1 and site 2 respectively, $p < 0.0001$). The sapwood width was independent of stem diameter while ($p < 0.001$) the sapwood area showed a tendency to increase with tree diameter (R^2= 83.6 and 57.2% at Site 1 and 2 respectively, $p < 0.001$) (Fig. 7c).

The results show that in *Q. faginea* heartwood starts to form when the stem diameter reaches about 10-20 cm and subsequently increases with tree diameter, maintaining a constant sapwood width at about 2-4 cm (Fig. 6a).

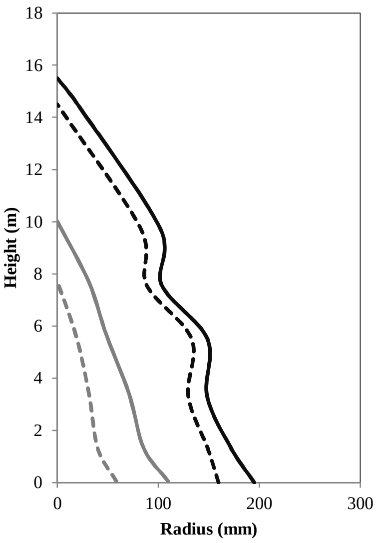


Figure 5. Tree radius (full line) and heartwood (dashed line) profiles for one tree at site 1 and site 2 (outside).

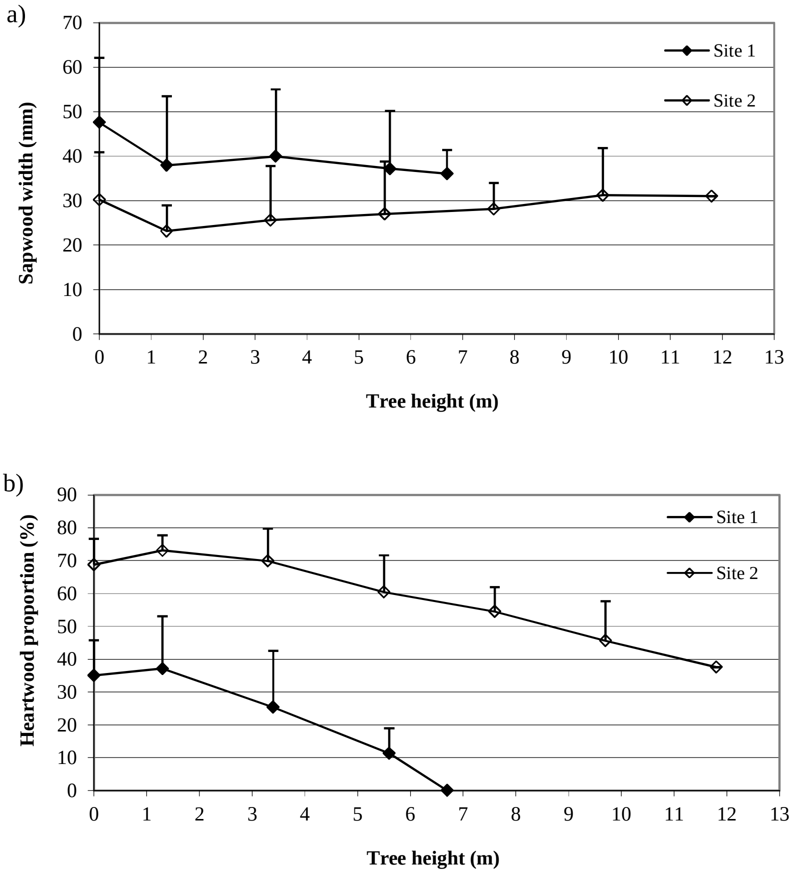
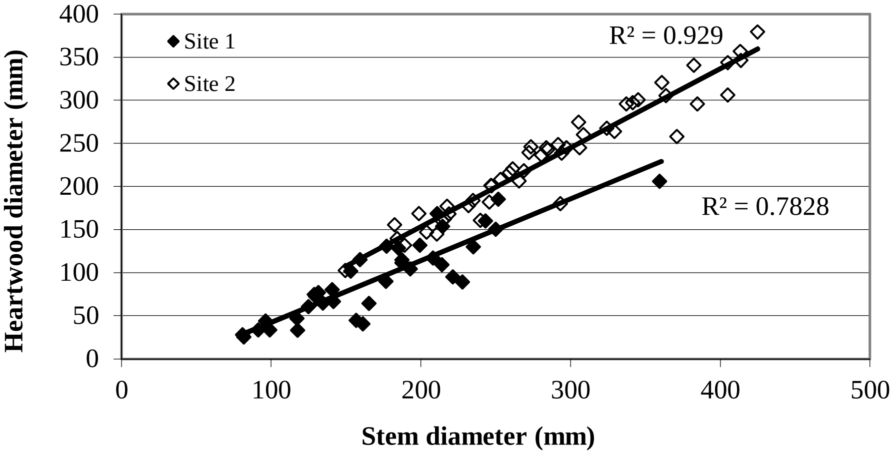
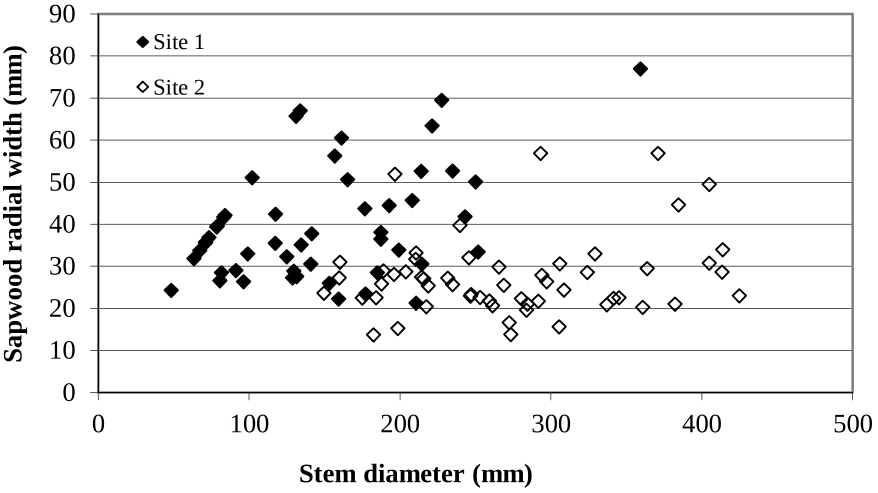


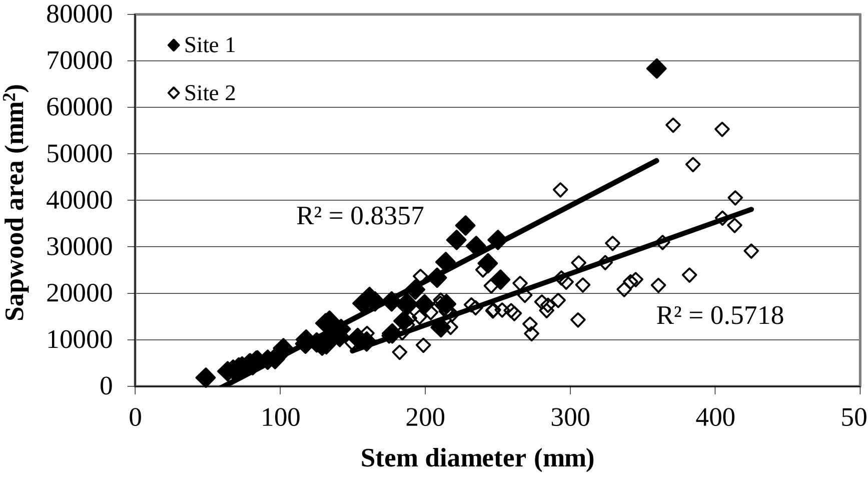
Figure 6. Sapwood width, heartwood proportion and heartwood area variation along the stem at site 1 and site 2. Mean of 10 trees with bars as standard deviation.



(a)



(b)



(c)

Figure 7. Scatter-plots representing the relationship between stem diameter and: a) heartwood diameter, b) sapwood radial width, and c) sapwood area at site 1 and site 2.

Discussion

Only one reference was found in the literature regarding *Q. faginea* growth rate, with a report of 1.5 mm year $^{-1}$ over 31 years (Oliveira 2001). In the present study, the growth rate for a similar period of 30 yr (Table 2) was 2.5 mm year $^{-1}$ and 1.4 mm year $^{-1}$ for samples taken from site 1 and site 2, respectively. The annual growth rate (Table 2) found in this study of *Q. faginea* is similar to other oak species, namely *Q. suber* another native oak species from Portugal, both in terms of mean ring width and radial variation (Leal et al. 2008; Costa et al. 2003; Gourlay and Pereira 1998). In *Q. pyrenaica*, Corcuera et al. (2006) found that the radial ring width decreased from approximately 1.6 mm to 0.5 mm from the inner to the outer part of the stem at a cambial age of 35-41 yr. *Q. petraea* produces annual rings of 2 mm or more in the first 30 rings (Helińska-Raczhowska and Fabisiak 1991), which is similar to *Q. cerris* with a growth rate of 2.2-2.9 mm in the first 15 yr and 1.5-1.7 mm afterwards until 25 yr of age (Manetti 2002).

Overall the radial growth rate of *Q. faginea* was in the range of values reported for other oak species and larger for site 1. This leads to the inference that under favorable conditions, growth of *Q. faginea* is comparatively high. In this case, commercial stems for the solid wood industry would require a rotation of 70-80 yr for a stem diameter of 30-35 cm. The within-tree radial and axial variation of ring width that was found in the *Q. faginea* trees was of moderate magnitude as shown by coefficients of variation of the radial and axial means of respectively 30-40% and 30-50% Table 2). These differences are not sufficient to produce excessive heterogeneity within the stem and a variation in properties that would be detrimental to product performance and value.

There are no results published for *Q. faginea* regarding heartwood content. In fact, scant information is available in the bibliography regarding the amount of heartwood and sapwood in other oak species. Most works on oak heartwood deals with durability, and chemical and color properties (e.g. Mosedale et al. 1996; Humar et al. 2008), while sapwood area is related to leaf area (e.g. Meadows and Hodges, 2002) or sap flow (e.g. Granier et al. 1994).

The patterns of within-tree axial variation of heartwood and sapwood (Fig. 6) are in agreement with previous results on heartwood development for most species (Hillis 1987). The slight increase in percentage of cross-sectional area corresponding to heartwood at 1.3 m of tree height is found in some species where an enlargement of heartwood from the base to a point in the lower part of the stem has been reported (Pinto et al. 2004; Knapič and Pereira 2005), although not all species show this tendency (Knapič et al. 2006).

A number of studies report a positive relationship between tree growth measured by diameter and heartwood dimension while the sapwood maintains a relatively constant width range independent of tree diameter (Gominho and Pereira 2000, 2005; Pinto et al. 2004, 2005; Knapič and Pereira 2005; Knapič et al. 2006). These results support the theory that heartwood formation is a cumulative process that increases during tree growth at the pace required to maintain an approximately constant sapwood width as required by the physiological conditions of the species (Bamber 1976). In the case of the *Q. faginea* trees in this study, the results support this theory. The sapwood width followed the stem profile (Fig. 5) without a significant within-tree axial variation (Fig. 6) and showed no correlation with tree diameter (Fig. 7b) while the sapwood area (at 1.3 m) that ranged between 87 cm^2 and 345 cm^2 at site 1 and between 133 cm^2 and 405 cm^2 at site 2 was correlated with tree diameter (Fig. 7c).

The heartwood of *Q. faginea* was well correlated with tree diameter (Fig. 7) and represented a substantial proportion of the stem cross-section, ie 20-25 cm wood diameters correspond to a 60-70% heartwood proportion. The previous conclusions on wood density from trees at site 1 as reported by Knapič et al. (2011) and more recent data (not shown) from trees at site 2 corroborates the decrease tendency of wood density ie heartwood is denser compared to sapwood and is related to ring width. An important practical consequence for the high value utilization of *Q. faginea* timber is the possibility of modeling and estimating heartwood content in standing trees from the measurement of tree diameter.

Conclusions

Q. faginea trees show a mean annual radial growth at 1.3 m height of between 2.3 mm and 1.1 mm, depending on site. The ring width decreased radially within the tree with cambial age and axially from the base upward but the magnitude of the ring width variation was small and allows a stem homogeneity that is valued for technological processing.

Q. faginea showed substantial heartwood development that follows the stem profile and allows prediction of heartwood area based on the stem diameter in standing trees. The sapwood width was small and rather constant along the stem.

Overall the stem wood quality of *Q. faginea* trees appears to be good for production of solid wood products with regard to its ring and heartwood distribution features. Other characteristics, ie color and chemical composition, should be studied in the future since them largely contribute to appearance and durability properties of wood products.

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4.2 Age trends in the wood anatomy of *Quercus faginea* Lam

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Abstract

The wood anatomy of *Quercus faginea*, an oak native to the Iberian Peninsula and the Maghreb in Africa, is described and age trends of fibres and ray dimensions are recorded. The analysis was made on a total of 20 trees from two different sites in Portugal. The wood structure within both sites was similar. *Q. faginea* shares its microscopic characteristics with other species of the white oak group; i.e., it was not easily distinguishable from other European oaks. The wood is ring porous with wide multiseriate rays and a high proportion of fibres and vasicentric tracheids. There was an increase of fibre and ray dimensions from the pith outwards. Fibre length started to stabilize around 30 years of age up to 50-60 years and decreased afterwards under a traditional rotation period (100-150 years). Linear and polynomial adjustments fitted better the fibre variation at younger and older ages. Rays were quite homogenous within the trees. Cambial age accounted less to total variation compared to tree at both sites i.e. tree-to-tree variation is greater than variation related to maturation or cambial age. The average dimensions of fibres and rays were similar between sites.

Introduction

Quercus faginea Lam., Portuguese or Lusitanian oak, is native to Portugal and Spain, and also occurs in the Maghreb in Northern Africa.

Q. faginea is a deciduous species that is found in mixed stands with other oaks such as *Q. coccifera* L., *Q. pyrenaica* L., *Q. rotundifolia* L. and *Q. suber* L., as well as with other species e.g. *Castanea sativa* Mill. and *Pinus pinaster* Ait.. *Q. faginea* is adapted to differing soils and was abundant in former times, but its distribution is now sparse and limited to a few thousand hectares (Capelo & Catry 2007).

The tree is of medium height up to 20 m, usually with a straight trunk but sometimes reduced to shrub habit under unfavourable growth conditions. The bark is dark and narrow, about 0.4-1.6 cm thick (Quilhó *et al*. 2013).

There are very few detailed studies on *Q. faginea* wood. General descriptions refer to white yellowish sapwood and brown yellowish heartwood, and distinct growth rings with conspicuous vessels and large rays (Carvalho 1997). The wood is dense (0.848-0.920 g/cm^3) with a considerable mechanical strength (Knapič *et al*. 2011; Silva 2011) and moderate durability (Ramos *et al*. 2009). Schweingruber (1990) gives some wood anatomical details of *Q. faginea*. Other wood anatomical studies on *Q. faginea* focus on the response of xylem features to climate (Villar-Salvador 1997; Corcuera *et al*. 2004b; Alla and Camarero 2012).

Oaks were important for shipbuilding in Europe and America until the mid-19th century (Johnson *et al*. 2002). This was also the case with *Q. faginea*, although its commercial value has been forgotten and the wood is nowadays used as firewood (Fabião *et al*. 2007). The present demand for oak wood products is however high, mainly focusing on high value applications. Also the perception of the ecological role of oaks has increased, often in the context of a multifunctional forestry approach and in association with a renewed interest in valuing native species.

The aesthetic character and properties of *Q. faginea* wood make it an interesting timber species with a potential for high value products (Ramos *et al*. 2009; Knapič *et al*. 2011). This economic valuing of *Q. faginea* would support its conservation and spread through extension of habitat by plantation or regeneration in secondary forests, in line with the framework of increasing forest sustainability. For this purpose more knowledge is needed on *Q. faginea* wood regarding its technological quality evaluation, including the study of many characteristics that range from anatomical to physical features.

The aim of this paper is to characterize in detail, for the first time, the wood anatomy of *Q. faginea* and age trends of the main wood anatomical features in trees grown in two sites. The study includes an analysis of the between and within-tree variation of fibre and multiseriate ray biometry. The information will allow establishing relationships to technological properties and help in dealing with various aspects of oak wood processing and proper commercial utilization. It will also give insight into the impact of forest management options, including optimal rotation times.

Material and methods

The wood samples were taken from 20 healthy and dominant or co-dominant trees of *Q. faginea* that were randomly selected and harvested from two sites: one with 34-60 year aged trees in the northeast of Portugal (site 1), near Macedo de Cavaleiros (554 m of altitude); the other with 112-150 year aged trees in the center of Portugal (site 2), near Vimeiro (100 m mean altitude). Both regions are in the natural geographic distribution area of *Q. faginea* (Capelo & Catry 2007). The climate is of the Mediterranean type with Atlantic influence. The mean annual temperature is 12 ºC and 15 ºC, and annual precipitation 700 mm and 890 mm at site 1 and 2, respectively. Soils are classified as leptosols at site 1 and cambisols at site 2.

Both stands are naturally regenerated and unmanaged. Basal area is 18 m^2/ha and 102 m^2/ha and tree density is 327/ha and 300/ha at site 1 and 2, respectively. The vegetation at site 1 is mainly characterized by minor occurrence of *Q. suber, Q. rotundifolia* and *P. pinaster* trees, and mainly *Cistus ladanifer* L., *Lavandula* spp., *Daphne gnidium* L., *Cytisus multiflorus* (L'Hér.) Sweet shrubs; at site 2 there were sparse *Q. suber*, *C. sativa* and *P. pinaster* trees, shrubs such as *Arbutus unedo* L., *Ulex europeaus* L. ssp., and *Erica arborea* L. and the fern *Pteridium aquilinum* (L.) Kuhn. The tree characteristics are shown in Table 1.

The trees were harvested and one stem cross-sectional disk (2 cm thickness) was cut at 1.30 m above ground level from each tree. Radial strips (2 cm wide) were cut from pith to bark and samples (1 x 1 x 2 cm^3, radial x tangential x axial) were prepared for anatomical observations and measurements.

For microscopy, the samples were taken at three radial positions, one adjacent to the pith (inner region, about 20% of the radius), one located centrally in the radius (mid region, 50% of radius), and one adjacent to the bark (outer region, about 80% of the radius). The wood samples were first softened in boiling water and then sectioned with a sliding microtome. Transverse, radial and tangential sections (15-20 µm thickness) were prepared from each radial position. The sections were washed in alcohol, stained with safranin and mounted in euparal. The tangential diameter (including the wall) of the earlywood vessels was measured of at least 25 vessels at each radial position in the transverse sections. The height of uniseriate rays was measured in tangential sections of 50 rays at each radial position. The proportion of axial parenchyma, fibres, rays and vessels was measured in the transverse sections that were double-stained with safranin and malachite green, using a 28 point-grid on successive areas along the growth ring.

Cell dimensional variation with cambial age (radial variation) was studied by taking one radial strip for each tree and sampling it at different positions from pith to bark: at every fifth annual ring in site 1 and at every tenth annual ring in site 2. The height and width of multiseriate rays were measured in tangential surfaces with incident light. For that, surfaces were polished, and oil was applied to highlight the rays, and the surfaces were scanned at 1200 dpi for measurement using image analysis. For fibre measurement of length, width and wall thickness, small wood slivers were macerated with Jeffery's solution during 48 h at 60 ºC, washed in water and stored in 70% alcohol. Temporary slides were prepared and measurement of fibre length, width and wall thickness (40 fibres) was performed using an image analysis system (Leica Application Suite) using light microscopy. Vessel element length was measured (at least 25 measurements including tails if present).

Terminology follows the IAWA list of microscopic features for hardwood identification (IAWA Committee 1989).

Analysis of variance was used to determine effects of sites, individual trees, and cambial age (ring number from the pith) on fibre and multiseriate ray biometry, and was performed with commercial software.

Table 1. Characteristics of the sampled *Quercus faginea* trees from Macedo de Cavaleiros (site 1) and Vimeiro (site 2).

	Site	**1**			**Site**	**2**	
Tree no.	**Height (m)**	**Diameter* (cm)**	**Age***	**Tree no.**	**Height (m)**	**Diameter* (cm)**	**Age***
1.1	9.5	29.0	60	2.1	17.1	42.2	122
1.2	10.1	24.1	34	2.2	14.2	29.0	120
1.3	11.7	24.5	34	2.3	13.7	31.1	122
1.4	10.4	20.5	43	2.4	16.2	42.0	128
1.5	10.0	15.5	36	2.5	15.6	33.5	121
1.6	11.0	22.3	42	2.6	18.0	46.3	132
1.7	10.8	19.9	39	2.7	15.5	40.8	132
1.8	10.5	19.5	38	2.8	14.2	37.1	112
1.9	11.0	15.9	39	2.9	13.0	30.4	112
1.10	9.7	17.6	39	2.10	10.0	34.8	150

* Diameter (over bark) measured at 1.3 m of tree height and and age based in ring counts at stem base.

Results

Macroscopic structure

The wood of *Q. faginea* is characterized by generally distinct heartwood with a dark brown colour and yellowish sapwood. The pith is small and star-shaped in cross-section.

The wood is ring-porous. A gradual transition in vessel size along the annual growth ring was observed only occasionally.

The general anatomical structure of *Q. faginea* wood was identical at both sites.

Microscopic structure

The microscopic anatomical features of *Q. faginea* wood are shown in Figure 1. Earlywood vessels round to oval in shape were mostly solitary or in groups of two and sometimes three vessels, distributed in up to three rows. A well-defined diagonal to radial arrangement in strips of more or less polygonal latewood vessels that widen towards the end of the annual growth is observed. Earlywood vessel elements 469 (214-696) µm long; vessel diameter 205 (71-358) µm wide, at site 1 while at site 2 earlywood vessel elements were longer and narrower (Table 2). The earlywood vessel dimensions increased radially from pith to bark. The vessel elements showed simple perforation plates. The vessel walls were conspicuously pitted with bi-bordered intervessel pits and tracheid-to-vessel pits and irregularly shaped, large and simple ray-to-vessel-pits.

The apotracheal parenchyma was arranged in concentric lines of 1-3 cells. The paratracheal parenchyma was difficult to distinguish in cross section.

The average fibre dimensions were: length 1149 µm, width 20 µm and cell wall thickness 8.1 µm at site 1; and length 1339 µm, width 19 µm and cell wall thickness 7.5 µm at site 2. Fibres were very thick-walled with simple to minutely bordered pits. Fibre-tracheids and abundant vasicentric tracheids were present.

Numerous uniseriate with 9 (2-30) cells in height and broad multiseriate rays were found, with occasional biseriate rays (Table 2). Rays were generally homocellular.

Prismatic crystals were observed in parenchyma cells and tyloses were frequent.

Overall tissue proportion was15-17% vessels, 32-36% fibres, 13-21% rays and 33-34% axial parenchyma and tracheids (Table 2).

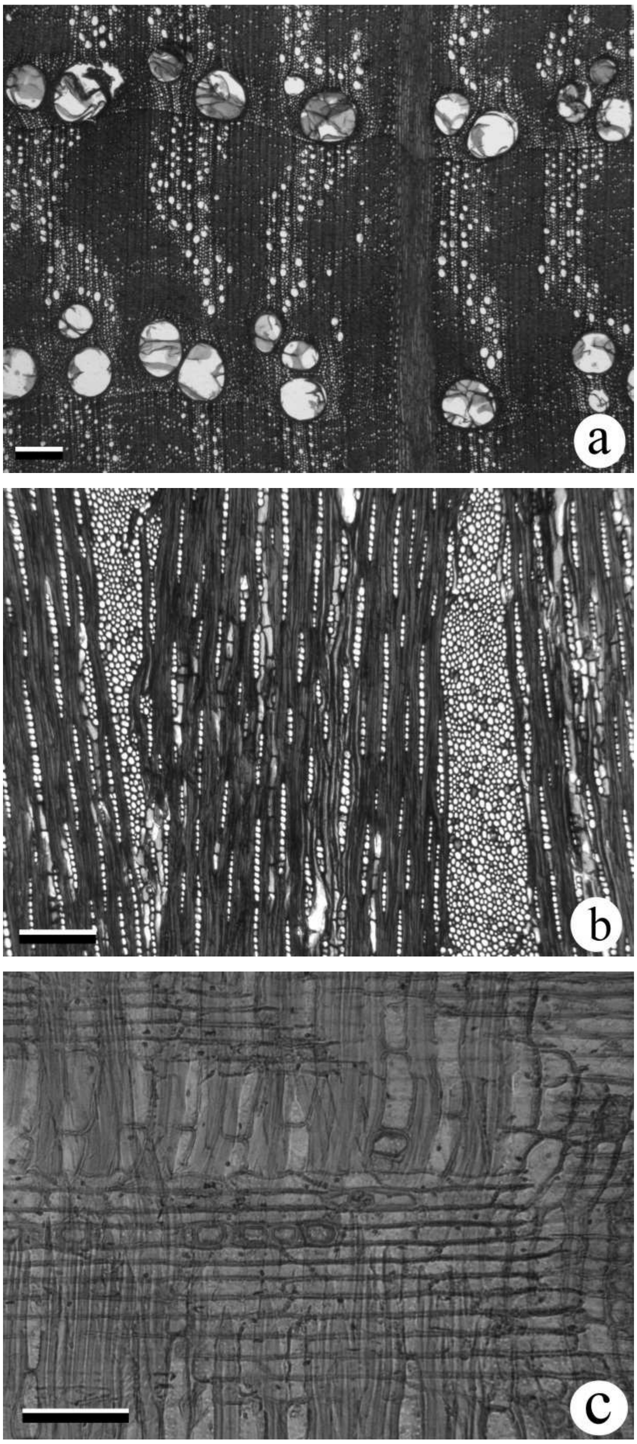


Figure 1. *Quercus faginea* microscopic wood sections. a) Transverse section showing a typical growth ring. b) Tangential section with uniseriate and multiseriate rays. c) Radial section with visible crystals. Scale bars: a, b) 200 µm and c) 100 µm.

Table 2. Radial variation of anatomical features *Quercus faginea* wood measured in inner, middle and outer radial positions. Mean of 10 trees from both sites and standard deviation; range in parenthesis.

	Site 1			**Site 2**		
	Inner	**Middle**	**Outer**	**Inner**	**Middle**	**Outer**
Tissue						
Vessels (%)	14 ± 6	16 ± 6	16 ± 5	13 ± 9	16 ± 6	22 ± 10
Rays (%)	22 ± 5	18 ± 10	22 ± 13	18 ± 12	9 ± 7	12 ± 9
Fibres (%)	31 ± 11	34 ± 8	31 ± 10	44 ± 7	42 ± 14	23 ± 12
Others (%)	31 ± 7	35 ± 7	34 ± 13	25 ± 10	33 ± 12	43 ± 13
Uniseriate rays						
Height (# cells)	10 ± 4	9 ± 4	9 ± 4	10 ± 4	9 ± 4	9 ± 4
	(2 - 24)	(3 - 28)	(2 - 26)	(2 - 29)	(2 - 27)	(3 -30)
Earlywood Vessels						
Diameter (µm)	184.8 ± 54.8	207.8 ± 50.0	223.4 ± 56.8	161.8 ± 93.7	168.0 ± 57.3	186.1 ± 62.5
	(71.0 - 309.9)	(103.3 - 328.5)	(95.8 - 358.0)	(35 - 491.4)	(35 - 317)	(35 - 345)
Element length (µm)	453.2 ± 91.9	474.4 ± 80.5	477.8 ± 72.7	589.1 ± 125	596.8 ± 101.2	598.5 ± 81.5
	(282.3 - 696.0)	(252.3 - 650.8)	(214.3 - 611.5)	(343.9 ± 777.7)	(315.2 ± 806.9)	(445.2 ± 749.4)

Radial variation of fibre dimensions

The radial variation of fibre dimensions shown by individual trees is presented on Figure 2. Fibre dimensions increased from pith to bark at both sites. Fibre length increased from 969 to 1195 µm, width from 17 to 21 µm and wall thickness from 7 to 8 µm for the younger trees at site 1, while for trees at site 2 fibre length increased from 1269 to 1349 µm, width from 19 to 21 µm and wall thickness from 7 to 8 µm. The pattern of increasing dimensions with cambial age was very similar for all the trees at each site. The trees at site 2 showed an increase in fibre length until 50-60 years, subsequently levelling off.

Tree, ring and tree x ring interaction were significant in fibre biometry ($p<0.001$) at both sites (Table 3 and 4). The statistically significant effects to explain the variation of fibre biometry at site 1 were mainly the trees (accounting for 7-17% of the total variation), the rings (10-14% of the total variation) and their interaction (4-8% of the total variance). At site 2 the trees also accounted for the main variation (10-18% of the total variation), followed by the rings (3-6% of the total variation) and their interaction (5-18% of the total variance).

Between-tree variation was higher (7-23% of the total variation at site 1; 10-30% of the total variation at site 2) when compared to cambial age (1-14% of the total variation at site 1; 0-6% of the total variation at site 2) at both sites. Tree-to-tree variability was higher at site 2. In general the ring effects were more evident above 40 years of cambial age and in fibre length and wall thickness. The ring and tree effects at site 1 on fibre wall thickness increased with cambial age (2 to 4% and 19 to 23%, respectively). The residual effect was high and 63-74% of the total variation of the fibre biometry of *Q. faginea* trees at both sites is due to other factors than the between and the within-tree (radial) variation.

Fibre width was linearly related to fibre wall thickness at site 1 (R^2=0.56) and site 2 (R^2=0.80). No relationship was found between fibre length and width (Fig. 3).

In the first common physiological stages at both sites the fibre length was significantly different ($p<0.001$) while fibre width and wall thickness showed no significant differences between sites.

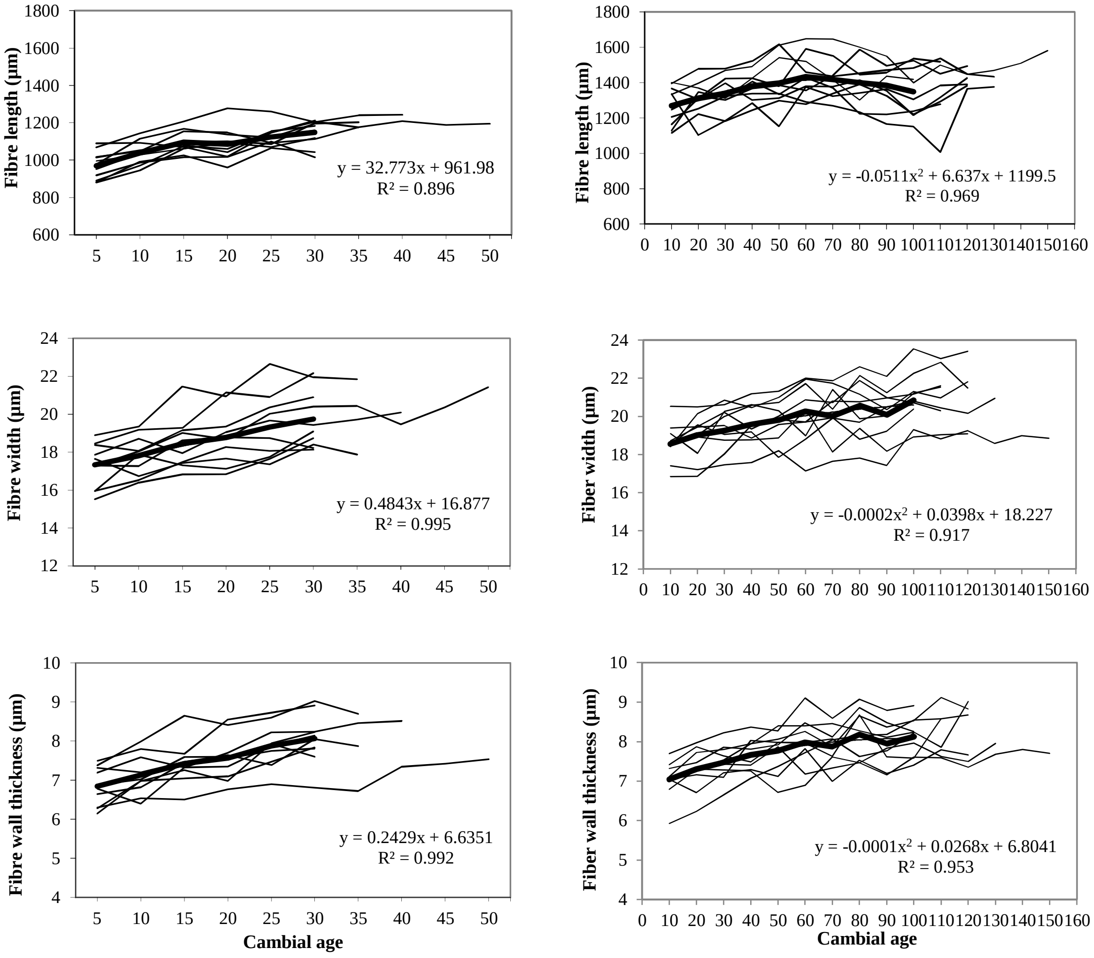
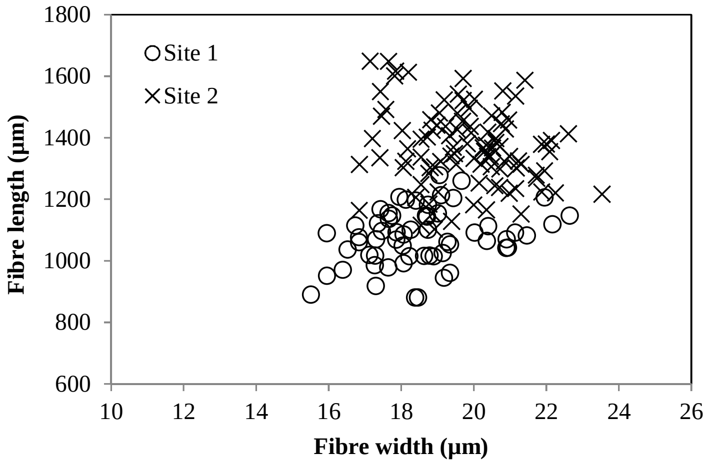


Figure 2. Radial variation of fibre biometry (length, width and wall thickness) of *Quercus faginea* trees at Macedo de Cavaleiros (site 1, mean as bold line for the common period - 30 years) at left and at Vimeiro (site 2, mean as bold line for the common period -100 years) at right.



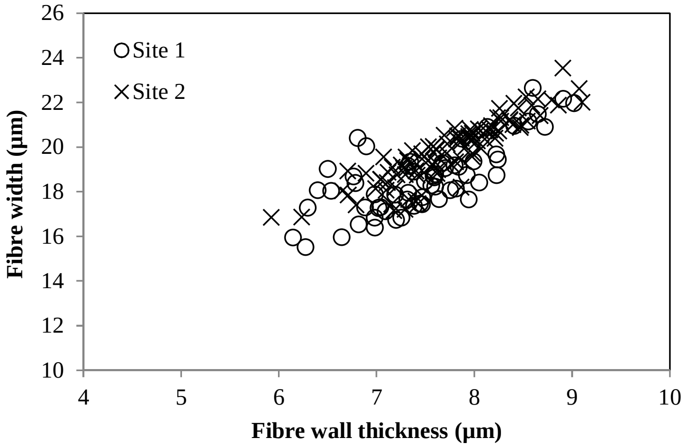


Figure 3. Scatter plots representing the relation between fibre dimensions (µm) of *Quercus faginea* wood from trees at both sites.

Table 3. Site 1. Expected variance (%) from the analysis of variance for fibre length, width and wall thickness for all inner rings (5-30) and intervals of rings (5-10; 10-20; 20-30) with $p < 0.001$. Tree (T), Ring (R), Tree x Ring (TxR), Error (E), Fibre length (FL), Fibre width (FW) and fibre wall thickness (FWT).

Source	**Dependent variable**	**Rings**			
		5 - 30	**5-10**	**10-20**	**20-30**
T	FL	7	14	10	8
	FW	17	15	19	22
	FWT	16	19	18	23
R	FL	12	3	5	2
	FW	10	1	4	2
	FWT	14	2	4	4
T x R	FL	8	13	4	8
	FW	4	6	4	3
	FWT	7	7	9	4
E	FL	72	70	81	83
	FW	69	78	74	72
	FWT	63	73	70	68

Table 4. Site 2. Expected variance (%) from the analysis of variance for fibre length, width and wall thickness for all rings (1-100) and intervals of rings (10-20; 20-40; 40-60; 60-80; 80-100) with p <0.001, p<0.01 (**), p<0.05 (*) and non-significant (ns). Tree (T), Ring (R), Tree x Ring (TxR), Error (E), Fibre length (FL), Fibre width (FW) and fibre wall thickness (FWT).

Source	**Dependent variable**	**1-100**	**10-20**	**20-40**	**40-60**	**60-80**	**80-100**
T	FL	18	16	21	26	22	27
	FW	15	18	14	18	21	22
	FWT	10	30	17	16	17	16
R	FL	5**	2	3	1*	0**	1
	FW	6**	2**	1	1**	1	2
	FWT	3	3*	0	2	1**	1
T * R	FL	11	16**	2	8	9	6
	FW	5ns	1	4*	1	4**	2
	FWT	18	31	11	3	4**	3
E	FL	66	66	74	65	69	66
	FW	74	79	81	79	74	75
	FWT	69	36	71	80	78	80

Radial variation of multiseriate rays

Average values of multiseriate rays width were similar at both sites but height was higher at site 2. Ray size increased radially (Fig. 4): at site 1 ray height varied between 2.5 mm and 4.5 mm, and width from 0.2 mm to 0.4 mm from the innermost to the outermost ring; at site 2 the multiseriate rays varied between 5.6-7.1 mm in height and 0.2-0.3 mm in width. Ray height increased with age until the 70th ring slowing down afterwards.

In general, the between-tree variability was more evident in ray height compared to ray width (Fig. 4). This variability was significant when analyzing the effects by cambial age intervals.

Ring, tree and tree x ring interaction had significant effects in ray width and height (p<0.001). The between-tree variation in ray biometry accounted for 8% to 13% of its total variation during the first 30 years of cambial age (site 1), the ring effects for 2-3% of the total variation and their interaction for 9% of the total variation. During the first 100 years of cambial age at site 2, the trees accounted for 8% of the total variation, ring effects for 5-9% and their interaction for 13-18% of the total variation (Table 5 and 6).

Most of the variation found in ray biometry was not explained by the analyzed factors and the residual effect was the main source of variation (69-80%). The effect of directions within the stem and site conditions were not studied and probably account for part of the residual effects.

No strong correlation was found between ray width and height either at site 1 or 2 (Fig. 5).

Between sites and within the same cambial age the ray biometry of *Q. faginea* was significantly different (p<0.001).

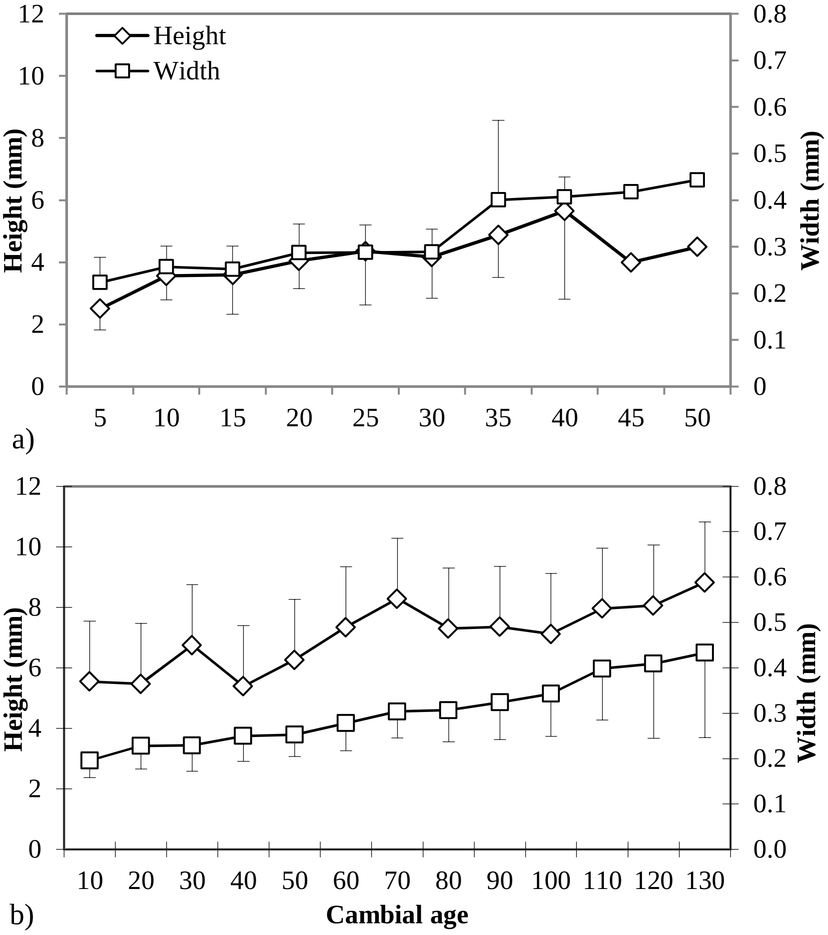


Figure 4. Radial variation of multiseriate rays dimensions of *Quercus faginea* wood from trees at a) Macedo de Cavaleiros (site 1) and b) at Vimeiro (site 2).

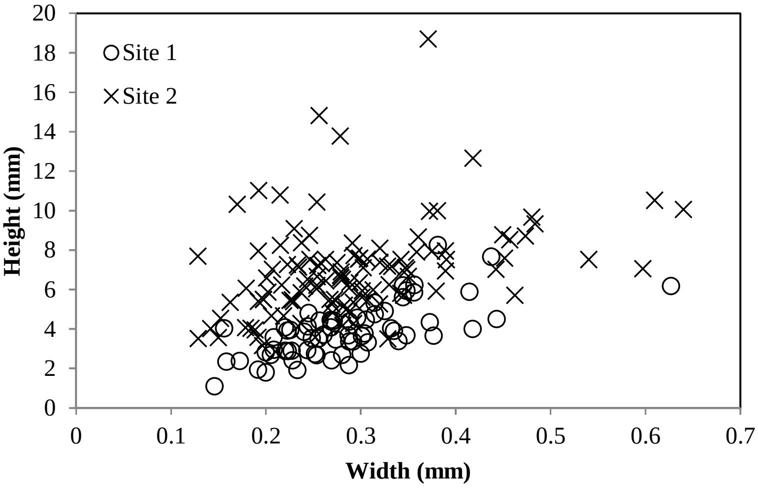


Figure 5. Scatter plot representing the relation between ray dimensions of *Quercus faginea* wood from trees at both sites.

Table 5. Site 1. Analysis of variance of ray height and width for all rings (1-30) and intervals of rings (5-10; 10-20; 20-30) with p <0.001, p<0.01 (**), p<0.05 (*) and non-significant (ns) and expected variance (%). Tree (T), Ring (R), Tree x Ring (TxR), Error (E), Ray height (RH) and Ray width (RW).

Source	**Dependent variable**	**5 - 30**	**5-10**	**10-20**	**20-30**
		% var	% var	% var	% var
T	RH	8	8	7	8
	RW	13	20	12	18
R	RH	3	1*	1ns	2**
	RW	2	ns	3	ns
T x R	RH	9	ns	3**	11
	RW	9	3*	12	7
E	RH	80	88	89	79
	RW	76	76	73	75

Table 6. Site 2. Analysis of variance of ray height and width for all rings (1-100) and intervals of rings (10-20; 20-40; 40-60; 60-80; 80-100) with p <0.001, p<0.01 (**), p<0.05 (*) and non-significant (ns) and expected variance (%). Tree (T), Ring (R), Tree x Ring (TxR), Error (E), Ray height (RH) and Ray width (RW).

Source	**Dependent variable**	**1-100**	**10-20**	**20-40**	**40-60**	**60-80**	**80-100**
		% var	% var	% var	% var	% var	% var
T	RH	8	18	19	9	8	22
	RW	8	13	19	11	17	7
R	RH	9	ns	1	ns	ns	2**
	RW	5	ns	2	5	1*	ns
T x R	RH	13	ns	9	11	6**	12
	RW	18	9**	16	18	15	4*
Error	RH	71	81	72	79	85	65
	RW	69	78	63	66	67	89

Discussion

General attributes and variablity

Q. faginea wood is reported as ring-porous (Baas & Schweingruber 1987; Schweingruber 1990; Carvalho 1997; Villar-Salvador 1997) or between semi-ring and ring-porous (García-Esteban *et al*. 2003; García-Esteban & Guindeo-Casasús 1990).

In the two studied sites, the ring porosity was evident and only very few rings showed a more gradual size transition between earlywood and latewood vessels. This indicates that there was no considerable effect of seasonal drought on wood porosity, as reported for the Mediterranean climate (Cherubini *et al*. 2003). In fact, according to Villar-Salvador (1997), *Q. faginea* dominates in submediterranean areas where soils are deeper and water availability is higher, therefore achieving a relative independence from the regional rainfall regime by developing a deep root system and habitat selection. More recently Corcuera *et al*. (2004b) found that latewood vessels of *Q. faginea* were more sensitive to climatic variability than the earlywood ones.

The diameter of *Q. faginea* early- and latewood vessels were within the range reported by García-Esteban and Guíndeo-Casasús 1990 (80 to 350 µm and 15 to 120 µm, respectively). Comparing earlywood vessel diameters among ring porous *Quercus* spp., the earlywood vessels of *Q. faginea* are smaller than *Q. robur* and *Q. pyrenaica* according to Carvalho (1997), and for example larger than *Q. boissori* (30-200 µm) (Baas *et al*. 1983). Other co-existing evergreen oaks as *Q. ilex*, characterized by diffuse porous wood, show much smaller diameters (54 µm) (Corcuera *et al*. 2004a).

The increasing tendency of earlywood vessel diameter is reported for *Quercus* spp. (Corcuera *et al*. 2004b; Lei *et al*. 1996; Helinska-Raczkowska 1994) which according Anfodillo *et al*. (2013) is size dependent i.e. conduit are gradually wider as trees grow taller. As in ring-porous species the earlywood formation is generated before leaves development, the fact that *Q. faginea* is a deciduous species may affect vessel characteristics along ring growth. The latewood vessels and tracheids are the safety conductive component of the xylem especially under unfavourable conditions as embolism of earlywood vessels (Granier *et al*. 1994). In the case of *Q. faginea* the sets of vasicentric tracheids participate on this role contributing to its adaptive capacity for adverse environment conditions.

Fibre-tracheids presence is described for *Q. faginea* by most authors although the distinction and classification between fibre (libriform), fibre tracheid and tracheid is sometimes difficult.The parenchyma, vasicentric tracheids and rays cell composition and arrangement were similar to other *Quercus* spp, as well as the common occurrence of tyloses (Carvalho 1997, Sousa *et al*. 2009, Gasson 1985, 1987).

Variation with cambial age

Overall fibre length was slightly higher in the older trees (site 2) compared to the younger trees (site 1) while fibre width and wall thickness did not vary between the two sites. The average values were similar to García-Esteban and Guindeo-Casasús‘s (1990) data on *Q. faginea* with 800 to 1600 µm in height, 17 µm of width, and 3 to 8 µm of wall thickness. Fibre length of *Q. faginea* was similar to *Q. suber* (1100 µm – 1230 µm) as well as fibre width (19.8 µm - 21.4 µm) and wall thickness (on average 8.1 µm) (Sousa *et al*. 2009). Bark fibres of *Q. faginea* are shorter (878 µm), and have similar width (20 µm) and wall thickness (9 µm) (Quilhó *et al*. 2013).

The increasing trend of fibre length along the radial direction is summarized in Zobel and Buijtenen (1989) and referred by many other authors (e.g. Dickson 2000). The age trend of fibre length in *Q. faginea* is similar to other *Quercus* spp. such as *Q. suber* (Leal *et al*. 2006), *Q. robur* and *Q. falcata* (Zobel & Buijtenen 1989), *Q. ilex*, *Q. conferta* and *Q. coccifera* (Voulgaridis 1990), *Q. petraea* (Helinska-Raczkowska & Fabisiak 1991), *Q. garryana* (Lei *et al*. 1996) and *Q. serrata* (Tsuchiya & Furukawa 2009). This trend is characterized by a high initial increase and a later shortening when the trees get old. In the case of *Q. faginea* this stabilization was clearly around 50-60 years of age at site 2 while in site 1 the highest increase was observed up to 15 years of age. Differences between and within the same species are related to the number of years to reach the typical fibre length. In *Quercus* spp the initial increase phase lasts generally 8-30 years (15, *Q. garryana*), (18, *Q. conferta*), (30, *Q. petraea*) and (8-27, *Q. serrata*) (Voulgaridis 1990; Helinska-Raczkowska & Fabisiak 1991; Lei *et al*. 1996, Tsuchiya & Furukawa 2009).

Between-tree variation of fibre length in *Q. faginea* was highly statistically significant, contrary to what was reported for *Q. garryana* (Lei *et al*. 1996) and more important than in 40-year old *Q. suber* trees (Leal *et al*. 2006). High tree-to -tree variation was also reported for *Q. serrata* (Tsuchiya & Furukawa 2009). The hypothesis that cambial age is not the only factor that determines anatomical properties is reinforced by the present study that showed the potential for individual selection.

The linear relationship between fibre width and wall thickness was stronger at site 2 suggesting that this is maintained with tree age (Figure 6). Leal *et al*. (2006) also found a strong relationship between fibre width and wall thickness.

Rays size and distribution have a major effect on wood quality, utility and figure (Zobel & Buijtenen 1989). Multiseriate rays of *Q. faginea* reported in this study were shorter than those found by Carvalho (1997) (6-50 mm) and Esteban and Guindeo-Casasús (1990) (3 to 23 mm) but with width values comparable to the range (170 to 350 µm) reported by Esteban and

Guindeo-Casasús (1990). Regarding other *Quercus spp*., *Q. suber* rays were higher with 5.2 mm height and 0.5 mm width (Sousa *et al*. 2009, Leal *et al*. 2006). There was no significant relation between multiseriate ray width and height as reported for *Q. suber* (Leal *et al*. 2006).

In hardwoods the changes in ray volume are of small magnitude (Zobel & Buijtenen 1989) with a tendency for wider rays in the outer wood (Carlquist 1988). This was shown in *Q. suber* (Leal *et al*. 2006), *Q. garryana* (Lei *et al*. 1996) and *Alnus rubra* (Gartner *et al*. 1997).

Between-tree variation of ray biometry was statistically significant in *Q. faginea* (Fig.6 and 7), accounting for 7-22% of the total expected variation (Table 5 and 6).

Q. faginea showed a relative homogeneity of ray size and structure within the tree; i.e., cambial age accounted for little of the total ray variation. This should simplify industrial processing and gives uniformity to wood pieces. The multiseriate rays of *Q. faginea* do not seem to be responsible for the decreasing radial pattern of wood density with cambial age (Knapič *et al*. 2011).

Conclusions

Q. faginea is a ring porous wood with large multiseriate rays, a high proportion of thick-walled fibres and a significant presence of vasicentric tracheids.

The dimensions of fibres and multiseriate rays showed an increasing trend from pith outwards. Overall the tree-to-tree and cambial age of the rings accounted for little of the total variation of fibres and multiseriate ray biometry, and there was a considerable homogeneity within the tree populations. This homogeneity is a favourable characteristic for processing and timber performance, giving perspectives for high value wood products.

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4.3. Bark anatomy and cell size variation in *Quercus faginea* Lam

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Key words: *Quercus*, bark, anatomy, fibre, sieve tubes elements

Abstract

The bark structure of *Quercus faginea* in 30-60 year old trees grown in Portugal is described. The rhytidome consists of 3-5 sequential periderms alternating with dilated secondary phloem. Phellem is composed of 2-5 layers of cells with thin suberised walls, and narrow (1-3 seriate) tangential band of lignified thick-walled cells. Phelloderm is thin (2-3 seriate). Secondary phloem is formed by few tangential bands of fibres alternating with bands of sieve elements and axial parenchyma. Formation of conspicuous sclereids and the dilatation growth (proliferation and enlargement of parenchyma cells) affect the bark structure. Fused phloem rays give rise to broad rays. Crystals and druses were mostly seen in dilated axial parenchyma cells.

Bark thickness, sieve tube element length and secondary phloem fibre wall thickness decreased with tree height. The sieve tube width did not follow any regular trend. In general, the fibre length had a small increase toward breast height, followed by a decrease towards the top. Fibre width decreased with height in most of the cases, but in some trees a slight increase was noticed at the top.

Introduction

The Portuguese oak (*Quercus faginea* Lam.) is a species native to the western Iberian Peninsula and the North African countries of Morocco, Tunisia, and Algeria. The species grows well in the temperature range of 15 ºC-25 ºC in summer and from - 4 ºC to 8 ºC in the winter, with annual precipitation between 350 and 2000 mm (Oliveira et al., 2001). It is a medium-sized deciduous or semievergreen tree growing to a height of 20 m and a diameter of 80 cm.

In Portugal, *Q. faginea* coexists with other oak species such as *Quercus ilex* L., *Quercus suber* L., *Quercus pyrenaica* Willd., and *Quercus robur* L. The distribution has became fragmented along the last centuries (Fabião & Silva, 1996) and there are concerns on future area reduction with warming and reduced rainfall trends, since drought is the main limiting factor of sub-Mediterranean oaks (Cotillas et al., 2009), specifically for *Q. faginea* (Corcuera et al., 2004; Montserrat-Marti, 2009).

Studies on bark anatomy are scarce when compared to previous studies on wood. However, knowledge on bark structure and its variation within and between individuals of a species, as well as age-related trends are important to assess bark's diagnostic value and to determine its potential uses (Roth, 1981). In this area, literature is also scarce (i.e. Trockenbrodt, 1994; Quilhó et al., 2000; Jorge et al., 2000; Babu et al., 2010; Arhan & Guvenç, 2011; Tavares et al., 2011).

Only very limited information was published on the bark of *Quercus* L. species. Bark anatomy of white and northern red oak barks was first described by Chang (1954). Whitmore (1962) compared the bark structure and surface pattern of mature trees of *Q. robur,* Howard (1977) observed the bark structure of 11 *Quercus* species, Trockenbrodt (1991, 1994, 1995) studied the qualitative and quantitative anatomy of *Q. robur* bark, and Sen et al. (2011 a, 2011b) described in detail the bark of *Q. cerris* L. var. *cerris*. One exception is the research effort and detailed knowledge gathered on *Q. suber* bark, which is due to the economic importance of its cork component, as reviewed by Pereira (2007).

The present study investigated the bark structure as well as between- and within-tree size variation of the sieve tube elements and secondary phloem fibres in *Q. faginea*. The results are the first to be published on the bark of this species, thereby also adding new information on the structural characteristics of *Quercus* spp. barks. We also think that this knowledge, besides being necessary to assess potential bark uses, has a role in the research on sustainability of *Q. faginea* in its indigenous regions.

Material and methods

The anatomical studies were made from the bark of 10 randomly selected *Quercus faginea* Lam. trees, growing in pure stands in north-eastern Portugal, in the district of Bragança (41° 30’41’’N, 7° 01’06’’ W; altitude 554 m, 600 - 800 mm annual rainfall, and 12–14 ºC mean temperature). Tree characteristics are shown in Table 1. The soils are mainly Orthic Dystric Leptosols on shale or granite rocks and Orthic Eutric Leptosols on basic rocks. The pH varies from acid to neutral and the hard rock is found within 50 cm of the surface.

Table 1 – Characteristics of the *Quercus faginea* trees (mean and standard deviation, min. and max. of 10 trees).

	Mean ± Std. dev.	Min. – Max.
Tree age	40.4 ± 7.50	34 - 60
Total tree height (m)	10.5 ± 0.67	10 - 12
Height of living crown (m)	8.3 ± 1.34	6 - 11
Stem height (m)	2.2 ± 1.02	1 - 4
Diameter at bh (cm)	20.9 ± 4.20	16 - 29
Bark thickness at bh (cm)	1.0 ± 0.29	1 - 1

Cross-sectional 5-cm-thick discs were cut from each tree along the stem at different height levels and 2 crossdiameters were measured for bark thickness determination.

For qualitative anatomical characterisation, bark samples were collected at breast height (bh), i.e. at 1.30 m above ground. The samples were impregnated with DP1500 polyethylene glycol, and transverse and longitudinal microscopic sections of approximately 17 µm thickness were prepared with a Leica SM 2400 microtome using Tesafilm 106/4106 adhesive (Quilhó et al., 1999). The sections were stained with a double staining of chrysodine/astra blue. Sudan 4 was also used for selective staining of suberin. The stained sections were mounted on Kaiser glycerine, and after 24 h drying, the lamellas were submerged into xylol for 30 minutes to remove the Tesafilm, dehydrated on 96% and 100% alcohol and mounted on Eukitt.

For quantitative studies, specimens were taken from bark samples collected at 3 tree height levels (base, bh and 75% of total height), and samples were taken sequentially from the cambium towards the periphery. Specimens were macerated in a 1:1 solution of 30% H_2O_2 and CH_3COOH at 60° C for 48 h and stained with astra blue. Length, width and cell wall thickness of 40 fibres and 40 sieve tube elements were measured on each specimen using a microscope and a semiautomatic image analyzer. The number of measurements was previously calculated to give an accuracy of 95% at the 0.05 probability level. The tangential diameter of parenchyma cells, sclereids and cluster of sclereids were also measured to estimate their range of values.

A light microscope Leica DM LA with camera Nikon Microphot-FXA was used for light microscopic observations.

Mean values for the tree were calculated as the arithmetic mean of the 3 height levels in each tree. Analysis of variance (ANOVA) was applied to determine if the differences on sieve tube elements and bark fibre size within and between trees were statistically significant at a 0.05 confidence level. Statistical calculations were carried out with IMB SPSS Statistics v.19, software.

The descriptive terminology for bark structure follows Trockenbrodt (1990), Junikka (1994) and, Richter et al. (1996).

Results and discussion

The bark of the *Quercus faginea* trees showed a scaly surface of grey-brown colour, with short but deep longitudinal furrows (Figure 1). The visual appearance was similar to other *Quercus* spp. (Whitmore, 1962; Howard, 1977). The bark thickness ranged between 0.5 cm and 1.4 cm at bh (Table 1) corresponding to 10% of the total tree radius. Table 2 presents the data for each tree showing that bark thickness tends to increase with age i.e. higher values occur in the base of the tree, agreeing with observations in other taxa (Trockenbrodt, 1994; Quilhó et al., 2000). There was a significant difference between the bark thickness of each tree at the 3 height levels, indicative of a significant axial variation of bark thickness in the tree.

Table 2 – Mean bark thickness of 10 *Q. faginea* trees at three height levels (base, bh and top).

	Bark thickness (cm)									
	1	2	3	4	5	6	7	8	9	10
Top	0.43	0.35	0.15	0.50	0.23	0.50	0.40	0.43	0.33	0.43
bh	1.18	1.03	0.50	0.75	0.63	1.20	1.23	1.38	0.85	1.00
Base	1.88	1.00	0.68	1.18	0.85	3.83	1.28	2.08	2.13	1.88

Bark structure

The bark structure of *Q. faginea* was identical in the 10 trees. It was possible to distinguish macroscopically in the bark cross-section the phloem, the periderm and the rhytidome.

Abundant clusters of sclereids were observed across the whole section of the bark and constituted a conspicuous feature as shown in Figure 1. In general the *Q. faginea* bark showed many similarities with those described for other *Quercus* species (Whitmore, 1962; Howard, 1977; Sen et al., 2011 a).

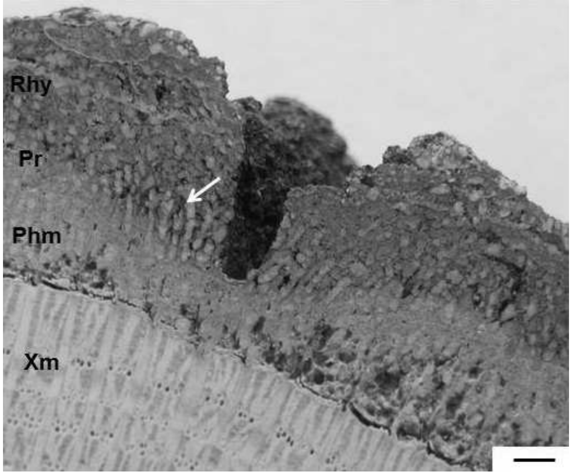

Figure 1. Transverse section of Q. faginea bark: (Phm) secondary phloem; (Pr) periderm and (Rhy) rhytidome; clusters of sclereids (arrow). (Xm) Xylem. Scale bar = 2 mm

The rhytidome was persistent and represented a substantial proportion of the bark (Figure 1). It consists of 3-5 sequential periderms alternating with the layers of dilated secondary phloem (Figure 2). In contrast to other oak species (Witmore, 1962), no shedding of the outermost periderms was observed in *Q. faginea*.

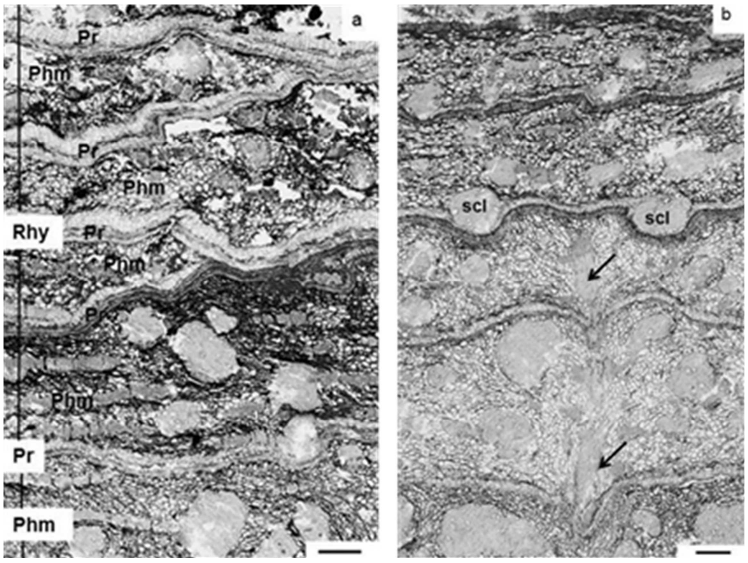

Figure 2. Transverse section of *Q. faginea* bark. a - (Phm) Secondary phloem; (Pr) periderm and (Rhy) rhytidome. b - The irregular course of the periderm is due to the formation of clusters of sclereids (Scl) and fused rays (arrow).Scale bars; a and b =125 µm

The periderm appeared undulated, and its phellem curved slightly forming discontinuous arching layers in cross-section (Figure 2). Sometimes the irregular course of the periderm was a consequence of the presence in its path of sclereid clusters and fused rays (Figure 2). *Q. faginea* did not produce extensive phellem or cork layers, as it is the case in the discontinuous phellem of *Q. cerris* (Sen et al., 2011 a, b) or in the continuous phellem of *Q. suber* (Pereira et al., 1992; Graça & Pereira, 2004).

Each phellem layer comprises 2-5 layers of isodiametric or sometimes radially flattened cells arranged into more or less distinct radial pattern with evenly thin suberised walls, and a narrow (1-3-seriate) band of radially flattened cells with evenly thick and pitted lignified walls (Figure 3). On the inside, these lignified cells are also accompanied by 1-3 layers of thin-walled phellem cells, which are, however, somewhat crushed, and their radial pattern is distorted due to the compressive strain against this more rigid layer. This band of sclerified cells in the phellem was also observed in *Q. cerris* (Sen et al., 2011b) but was not reported in the phellem layer of *Q. suber* (Pereira, 2007).

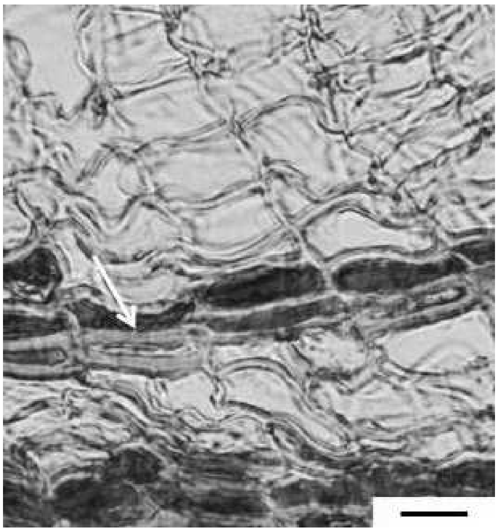

Figure 3. Phellem layer of *Q. faginea* (transverse section) with suberized phellem cells with tangential and radial walls uniform thickened aligned radially and phellem cells with thickened sclerified walls (arrow) filled with dark compounds. Scale bar = 25 µm

The phelloderm was poorly developed, composed of 2-3 thin-walled cells in radial rows and resembling the adjacent parenchyma cells, except for their radial alignment. Dark stained material was observed in the cells of phellem and phelloderm. The phellogen with rectangular and thin-walled cells was difficult to distinguish in cross-section.

The secondary phloem of *Quercus faginea* (Figures 4) is nonlayered, and growth rings were not observed, in the contrast to *Q. robur* (Trockenbrodt, 1991), *Q. cerris* var. *austriaca* (Babos, 1979 a) and *Q. cerris* var. *cerris* (Sen et al., 2011 a).

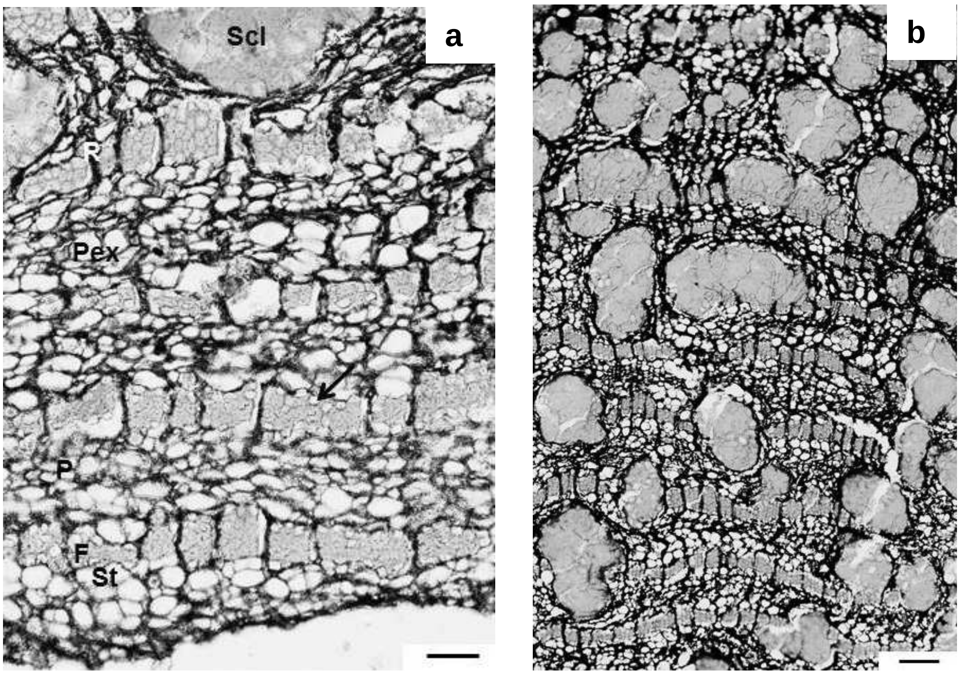

Figure 4. Transverse section of the secondary phloem of *Q. faginea*. a - near the vascular cambium and outward; St (sieve tubes); (f) fibres bordered by crystalliferous axial parenchyma (arrow); (P) axial parenchyma; (R) ray; (Pex) expanded parenchyma cells and clusters of sclereids (Scl). b – collapsed secondary phloem. Clusters of sclereids increased significantly throughout the collapsed secondary phloem towards the periderm. Scale bars; a = 50 µm; b = 125 µm

The noncollapsed phloem in *Q. faginea* is a narrow layer. A thin layer of noncollapsed phloem is also described by Sen et. al. (2011 a) in another *Quercus* species and Roth (1981) and Cufar et al.(2011) in another genus. In the transverse section the initial portion of secondary phloem was characterised by the occurrence of multiseriate tangential bands of axial parenchyma cells and sieve tube elements alternating with tangential rows of fibres (3-5 cells wide). These rows are crossed by secondary phloem rays (Figure 4).

When the secondary phloem ceases its conducting function, the cells collapse and the tangential fibre bands are interrupted by small groups of sclereids, forming clusters (Figure 4). The size of the clusters is variable (132-312-675 µm; values are given as ranges with means), and their quantity increased throughout the collapsed secondary phloem towards the periderm, giving rise to an altered structure of the secondary phloem, accompanied by a slight distortion of the secondary phloem rays (Figure 4) and some dilatation of the axial parenchyma cells. These features represent the adjustment of the secondary phloem to tree growth (Quilhó, 1999).

The sieve tube elements had a round to an irregular shape in transverse section, about 22-38-58 µm in diameter and 206-311-338 µm in length with unlignified thin walls and with companion cells, which are recognized either in transverse or longitudinal sections (Figures 5). The sieve elements were solitary or in groups of 2 or 3 with a tangential arrangement; the sieve plates were inclined, compound, with 3-8 sieve areas in a scalariform pattern with numerous sieve pores (Figure 5) and lateral sieve areas. Similar observations were made by Chang (1954) for white and northern red oaks.

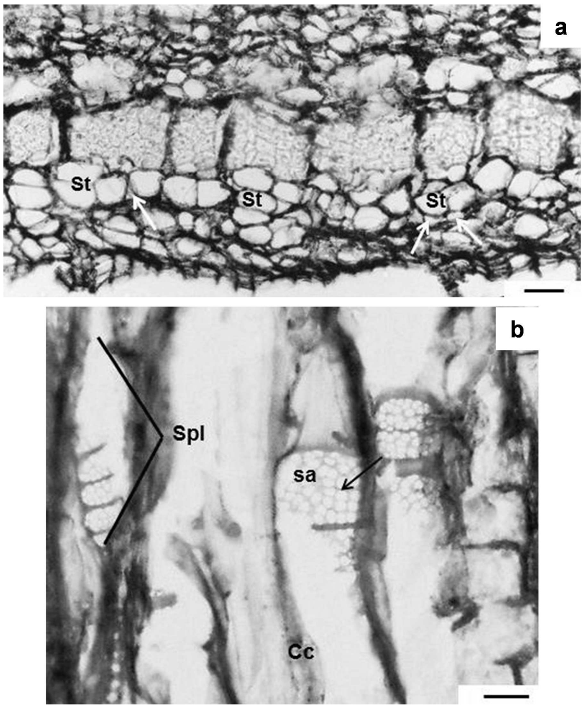

Figure 5. Sieve tubes of *Q. faginea*. a - Sieve tubes (St) and companion cells (arrow) in non-collapse secondary phloem in transverse section and. b - Sieve plate (Spl) with sieve areas (sa) sieve pores (arrow) and companion cells (Cc) in a longitudinal view. Scale bars; a = 12.5 µm; b = 25 µm

The axial parenchyma of the secondary phloem appears in strands of 3-6 cells and has round to rectangular thin-walled cells of irregular size in transverse view (Figure 4). It was located between the tangential bands of fibres and interspersed with sieve elements that were sometimes difficult to distinguish from the axial parenchyma cells. Strands of crystal-bearing axial parenchyma of approximately equal length (6 to > 10 cells) were found along the margins of the fiber band (Figures 6 and 7), as it occurs also in other *Quercus* (Howard, 1977; Trockenbrodt, 1991; Quilhó et al., 2003; Sen et al., 2011 a). Druses and prismatic crystals occurred profusely in the axial chambered parenchyma cells (Figure 7). Although crystals occur in the noncollapsed phloem, Evert and Eichhorn (2006) mentioned their accumulation in cells bordering those undergoing sclerification in the collapsed phloem.

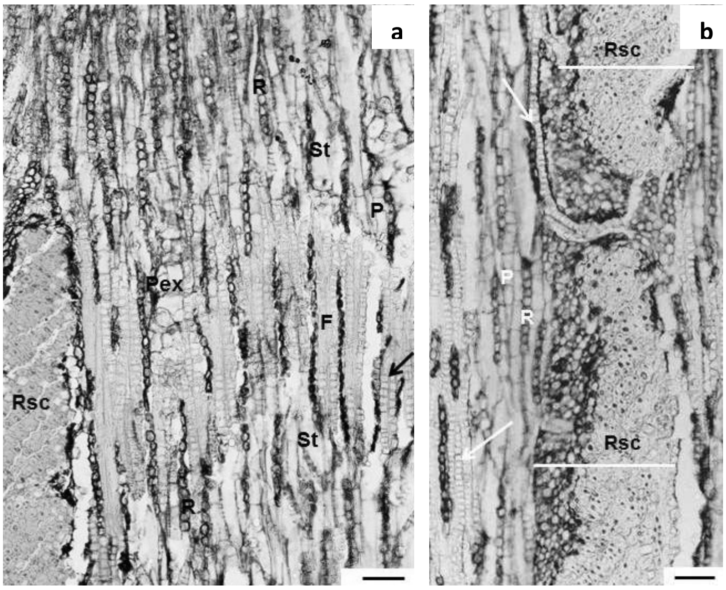

Figure 6. Tangential section of non-collapsed secondary phloem in *Q. faginea*: a - (St) sieve tubes; (f) fibres bordered by crystalliferous axial parenchyma (arrow); (P) axial parenchyma; (R) uniseriate ray; (Rsc) multiseriate ray with all cells sclerified and (Pex) expanded parenchyma cells. b - Fused ray (_) partially sclerified (Rsc), radial parenchyma cells became highly sclerified. Crystalliferous parenchyma cells (white arrow). Scale bars; and b = 50 µm.

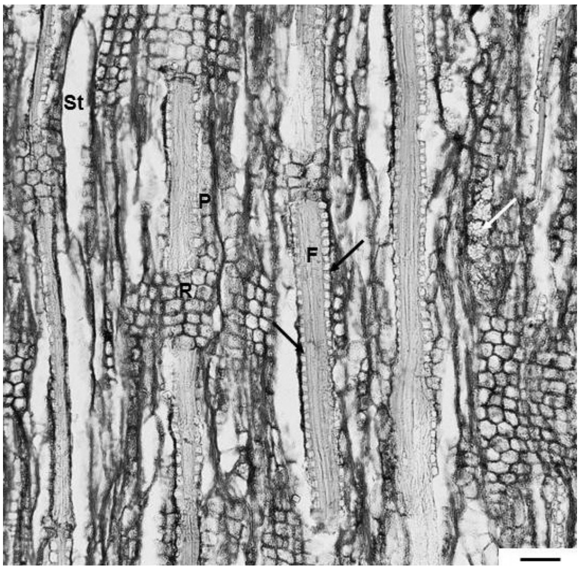

Figure 7. Radial section of non-collapsed secondary phloem in *Q. faginea* (St) sieve tubes; (F) fibres bordered by crystalliferous axial parenchyma (black arrow); (P) axial parenchyma; (R) Rays homocellular with frequently short procumbent cells. Druses (white arrow) Scale bar = 50 µm.

The axial parenchyma cells proliferated and enlarged (22 to 56 µm) in the outer portion of the phloem forming the dilatation tissue (Figure 8). The development of this tissue due to the increase of stem diameter is in agreement with observations of Trockenbrodt (1991) in *Q.*

robur, and Sen et al. (2011 a) in *Q. cerris* var *cerris*, and was also described by Evert and Eichhorn (2006) in another genus.

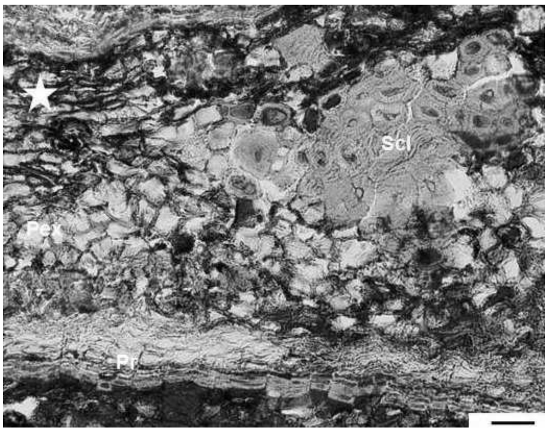

Figure 8. Dilatation tissue in the rhytidome of *Q. faginea*: proliferation of parenchyma cells (*) expanded axial parenchyma cells (Pex) and sclereids (Scl) isolated by the periderm (Pr), in transverse view. Scale bar = 50 µm

Secondary phloem fibres were arranged parallel to the vascular cambium in continuous tangential bands, about 2 to 4 cells wide, sometimes interrupted by groups of sclereids (Figure 4). The fibres were 0.799-0.878-1.016 mm long and 19-20-22 µm wide; the fibres were slender with narrow lumens and with tapered overlapping end, although sometimes bifurcated (Figure 9), caused by the adjustment to adjacent cells during elongation and intrusion, as stated by Iqbal and Ghouse (1983). They were usually thick walled (7.93-8.84-9.66 µm) and lignified.

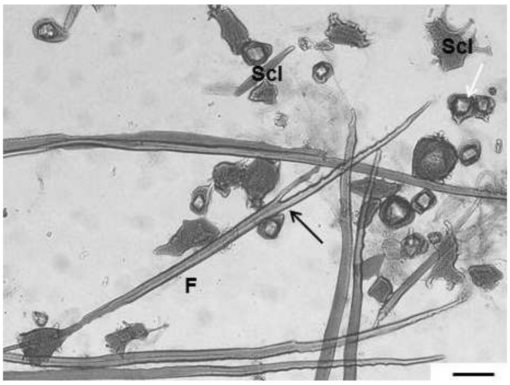

Figure 9. Maceration of *Q. faginea* bark; sclereids with crystals (white arrows) and (F) fibres sometimes are bifurcated (black arrow). Scale bar = 50 µm

Secondary phloem rays are the outward continuation of the wood rays and occurred in 2 sizes: narrow uniseriate rays (uniseriate, 3 to 10 cells high) and broad rays (multiseriate up to 20 cells wide and > 100 cells high) (Figures 6). Both were homocellular frequently with short procumbent cells (Figure 7) as in the bark of other *Quercus* (Howard, 1977, Sen et al., 2011 a). The narrow rays followed a straight to undulated direction in the beginning of the noncollapsed secondary phloem, but towards the periphery showed a moderate dilatation due to the tangential stretching and anticlinal cell divisions. In the outer phloem close to the periderm, the ray dilatation tissue could be confused with the axial parenchyma.

Sclerification of radial parenchyma cells occurred early in the noncollapsed phloem near the cambium, mostly in fused broad rays. This is in agreement with Evert and Eichhorn (2006), who reported the differentiation of sclereids in oaks first in the rays and later in dilatation tissue, in clusters of variable size; the radial parenchyma cells sclerification was also reported in *Quercus* spp. (Howard, 1977; Babos, 1979 a; Trockenbrodt, 1991; Graça & Pereira, 2004; Sen et al., 2011 a). Figures 2 and 6 show sclerified broad rays in the rhytidome and in a portion of the noncollapsed phloem, respectively.

Sclereids were abundant and formed a high proportion of *Q. faginea* bark, as in other oaks (Howard, 1977). In general they were isodiametric (31-126 µm, in tangential size), although they may attain various shapes and had thick and polylamellate walls transversed by minute pit channels, when seen in transverse section (Figure 8) or in dissociated cells (Figure 9). Sclereids originated from axial parenchyma cells and lacked the typical intrusive growth of the phloem fibres, in accordance with Evert and Eicchorn (2006). The “expanded parenchyma cells” (Quilhó et al., 1999) or cells of intermediate type (Richter et al., 1996) undergo gradually changes in shape, form, and cell wall thickness (Figures 4 and 6). Finally those cells develop into sclereids by the progressive sclerification of their walls. Sclereids frequently included large prismatic crystals (Figure 9) and dark compounds.

Sclereids occurred mostly in groups that might fuse, giving rise to prominent clusters that sometimes attained large tangential or radial diameters. In the transverse section, the clustered sclereids (Figure 4) showed a tangential or radial arrangement: they were adjacent to the fibre groups, or formed radial bands near or within the broad rays, as in other *Quercus* (Trockenbrodt, 1991; Sen et al., 2011 a). The highest proportion of sclereids was observed in the outer and dilated portion of the phloem near the periderm, although sclerified cells also differentiated near the vascular cambium. The increase of sclereids with growth is according to observations of Trockenbrodt (1991, 1994) in *Q. robur*. The occurrence of sclereids is of practical relevance since they can limit the use of bark (Hoffmann & Ouellet, 2005).

Size variation of sieve tube elements and secondary phloem fibres

Table 3 summarises the sieve tube element and secondary phloem fibre dimensions and their range of variation in each tree height level.

Table 3 – Sieve tube elements and fibre dimensions in secondary phloem of *Q.faginea* (mean, standard deviation, min. and max. of 10 trees in each tree height level).

	Sieve tube element		Fibre		
	Length (μm)	Width (μm)	Length (mm)	Width (μm)	Wall thickness (μm)
Top	290.2±7.87	39.3±1.30	0.82±0.046	20.2±0.80	8.6±0.41
	(207-385)	(22-61)	(0.43-1.29)	(14-30)	(5-13)
bh	305.8±5.26	37.8±1.87	0.92±0.116	20.0±3.12	8.9±1.49
	(200-450)	(22-61)	(0.60-1.75)	(10-31)	(4-14)
Base	336.6±29.86	37.4±0.67	0.90±0.054	20.6±0.93	9.1±0.39
	(188-431)	(23-52)	(0.46-1.42)	(13-29)	(5-13)

The tree mean and range of values for length and width of sieve tube elements were 299-311-431 μm and 37-38-40 μm, respectively. Sieve tube elements of *Q. faginea* fit into the length categories I (> 400 μm) and II (250 - 400 μm) defined by Richter et al. (1996).The average values of sieve tube elements sizes fit into the range of values reported by Trockenbrodt (1994) in some individual trees of the genus *Quercus*. The analysis of variance for length and width of sieve tube elements showed that the height level was highly significant ($P < 0.001$) to explain their variation. A decrease of sieve tube elements length with tree height was observed in all the trees (Fig. 10). This trend of variation could reflect the increase of the cambial initials with age causing a corresponding increase of the length of sieve tube elements. In contrast, the sieve tube width did not follow any regular trend within the tree (Figure 10), although sieve tube elements tend to be larger in the in upper part of the stem (Table 3). Similar pattern of axial variation of length and width of sieve tube elements was reported by Iqbal and Ghouse (1983), Trockenbrodt (1994) and Quilhó et al. (2000) in some individuals in various species such as *Q. robur, Populus tremula* L., *Acacia spicigera* (L.) Druce, and *Eucalyptus globulus* Labill.

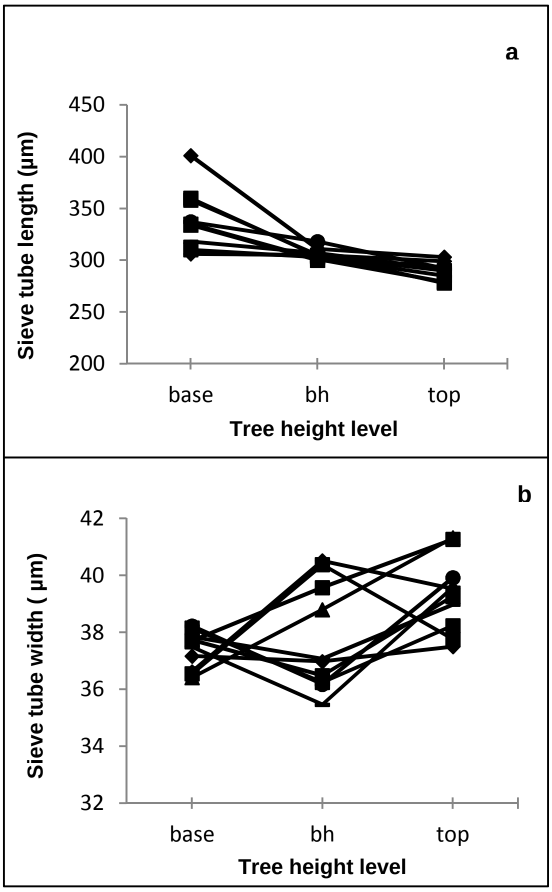

Figure 10. Axial variation of sieve tube elements in 10 *Q. faginea* trees. a - length. b –width.

The between-tree variability of secondary phloem fibre length, width and wall thickness was highly significant (P < 0.001). No correlations were found between fibre size and tree diameter.

The average secondary phloem fibre length of 0.88 mm fits in the range reported by Trockenbrodt (1994) for *Q. robur* (0.72 mm to 0.91 mm in 12 to 33 year old trees) and by Sen et al. (2012) for *Q. cerris* var. *cerris* (0.73 mm to 1.68 mm in 70 to 80 year old trees). The secondary phloem fibre width and wall thickness were on average 20 µm and 9 µm, respectively. Babos (1979 b) reported the average secondary phloem fibre diameter in *Q. cerris* bark as 15.1 µm.

It is frequently referred that secondary phloem fibres are longer than wood fibers (Jorge et al., 2000; Parameswaran & Liese, 1974). In this study the secondary phloem fibers of *Q. faginea* were shorter than the wood fibres (0.88 mm vs. 1.13 mm long) although the maximum value of fibre length was found in the bark (Table 3) since wood fiber length ranged 0.8 to 1.4 mm, as determined by Sousa et al. (2009) in the same trees. There was a significant difference (P < 0.001) between wood and bark fibre length at bh. The secondary phloem fiber width and wall thickness values are close to those referred for the wood of the same trees of 15-23 µm and 5-8 µm, respectively (Sousa et. al., 2009).

There was not a linear relationship between length, width and fibre wall thickness with tree age at bh, although the oldest tree (60 year old) had the widest and thickest fibers (22 µm and 9.7 µm, respectively).

There was a highly significant ($P < 0.001$) axial variation of secondary phloem fibre length with a small increase from the base to bh, followed by a decrease towards the top in the majority of individuals (Figure 11). This is in accordance with the dimensions of the cambial fusiform initials that generally increase from stem base to a certain tree height and then decrease towards the uppermost part of the tree (Larson, 1963; Ridoutt & Sands, 1994). This pattern of variation was found in *Acacia nilotica* and *Prosopis spicigera* (Iqbal & Ghouse, 1983), but the inverse was shown by Trockenbrodt (1994) in *Q. robur* with longer fibres in the top of the tree. Fibre length depends also on the degree of intrusive growth (Ghouse & Siddiqui, 1976; Khan & Siddiqui, 2007; Lev-Yadun, 2010) and on maturation and outlines of surrounding cells (Jura-Morawiec, 2008) which can justify the different patterns of axial variation described for other genus i.e *Eucalyptus* (Quilhó et al., 2000) or *Acacia* (Tavares et al., 2011). As Bailey and Tupper (1918) showed, the vessel element length is approximately equal to the length of fusiform cambial initials. Sousa et al. (2009) determined the length of vessel elements in wood at bh in the same trees as 214-459-696 µm. The comparison of the mean length of secondary phloem fibres at bh (Table 3) with the mean length of vessel elements at the same height level allows us to estimate that the secondary phloem fibres grow about 1.9 times the size of the fusiform cambial initials.

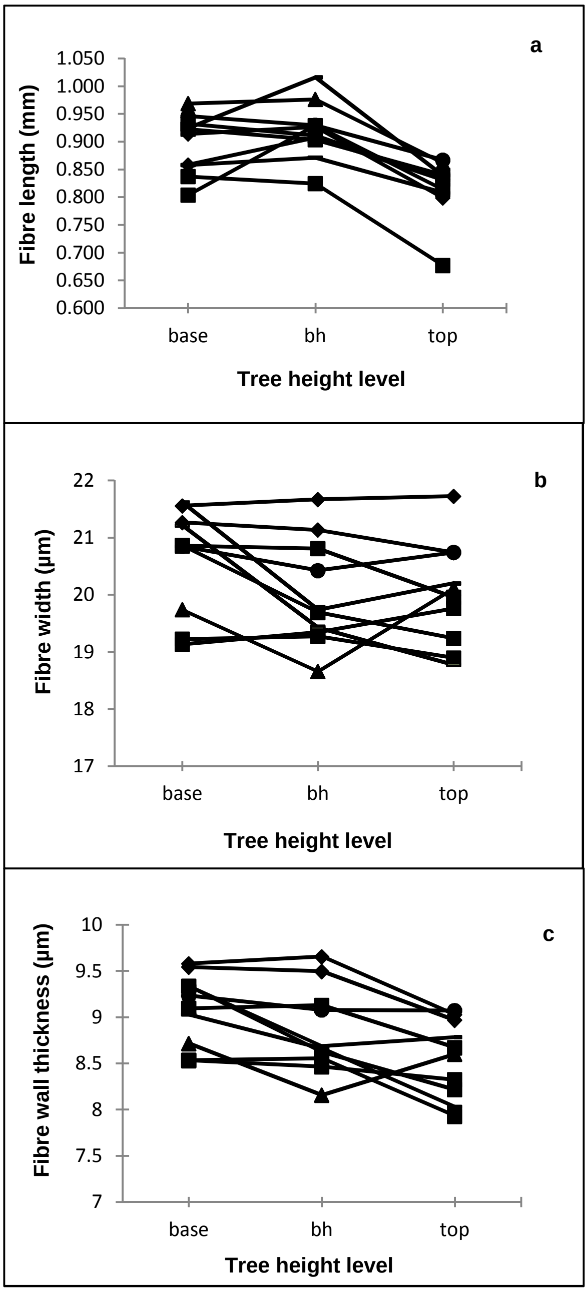

Figure 11. Axial variation of secondary phloem fibres in 10 *Q. faginea* trees. a - length. b - width. c - wall thickness

In general, secondary phloem fibre width and wall cell thickness decreased only slightly from the base to the top (Figures 11). However, regarding the width of fibres, this trend of axial variation was not recognized in all the trees, and a slight increase was also noticed at the top. In the tree the variations of fibre width ($P < 0.05$) and cell wall thickness ($P < 0.01$). were of small magnitude. There are no comparable studies concerning the axial variation of the secondary phloem fibre width and wall thickness for *Quercus*, but the same pattern of variation was also described for *E. globulus* (Quilhó et al., 2000) and is sustained by studies of Ridoutt and Sands (1994).

Width and fibre wall thickness could be affected by alterations of hormonal content i.e a longitudinal decreasing auxin concentration is responsible for fibre enlargement (Lev-Yadun & Aloni, 1991). However, information is still scarce on hormone interaction during cambial development, and genetic regulation of secondary vascular growth and cell differentiation (Elo et al., 2009; Lev-Yadun, 2010; Spicer & Groover, 2010).

Conclusions

The bark anatomy of *Quercus faginea* was characterised for the first time. The rhytidome of *Q. faginea* includes successive periderms with a substantial amount of secondary phloemic tissue, with abundant compact nodules of sclereids and sclerified broad rays. *Q. faginea* does not produce an extensive phellem or cork layers and phelloderm is poorly developed.

The sequence of tissues in the secondary phloem, the type of sieve tube elements, sieve plates, fibres, axial and radial parenchyma, formation of sclereids, and type of crystals were similar to other *Quercus* spp.

Q. faginea bark thickness, sieve tube element length and phloem secondary fibre cell wall thickness decreased with tree height; in contrast the sieve tube element width did not follow any regular trend within the tree. The secondary phloem fibre length had a small increase from the base to bh, followed by a decrease towards the top in the majority of individuals. Fibre width decreased within the tree for most trees, but in some a slight increase was observed at the top.

Acknowledgments

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4.4. Age trends of ring width and wood density in *Quercus faginea* mature trees

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(Submetido)

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Abstract

Quercus faginea Lam. (Portuguese or Lusitanian oak) is a native oak species of the Iberian Peninsula and Maghreb Africa with good potential to high quality end uses which could be of importance in a context of multifunctional forestry management and species preservation.

The study aim is to describe age trends, quantify and compare between and within-tree variations in ring width and wood density components in 125 year old *Q. faginea* trees, of 40 cm dbh class. X-ray microdensitometry was used in all rings per each stem height level in 10 trees.

The overall wood density was high ranging between height levels from 0.864 g/cm^3 to 0.957 g/cm^3. Wood density decreased from pith to bark and with stem height. Heartwood and sapwood were distinguishable by wood density differences. Cambial age was strongly correlated with wood density showing a good linear adjustment and was the most important effect to explain variation in wood density. The intra-ring and axial homogeneity was good within tree. Ring width was positively correlated with all wood density components and latewood percentage.

Mature trees of *Q. faginea* showed high wood density and wood potential is comparable with that of other commercial oaks. Cambial age and ring width are important factors to explain wood density and improve wood quality, namely throughout growth rate by adequate stand management.

Introduction

Oak wood is highly prized to produce a wide variety of value products, such as indoor flooring, furniture, and cabinets, due to its strong textural features, density and mechanical properties. In central Europe, native oaks such as *Quercus robur* and *Q. petraea* are the most studied in relation to wood anatomical characteristics and properties due to their present market value (e.g. Bergès et al. 2008; Zhang et al. 1993; Guilley et al. 1999, 2004), but other oaks have also attracted attention namely species growing in more southern regions (e.g. Leal et al. 2006, Knapič et al. 2008).

Quercus faginea Lam. (Portuguese or Lusitanian oak) is native to the Iberian Peninsula and Maghreb Africa and its wood was used in the past for demanding products e.g. shipbuilding. However intensive exploitation and replacement by plantation species such as *Pinus pinaster* and *Eucalyptus globulus* have led to declining areas, abandonment of silvicultural management and low value wood utilization i.e. nowadays it is mainly used as fuel. There are therefore serious concerns regarding the sustainability of such endogenous oak forests and the overall impoverishment of forest diversity. Valorization of the wood from *Q. faginea* may be important in this context and more effectively contribute to fight the species' decline by giving an economic value for such potential multifunctional forests that will go beyond conservation (Habitat Directive).

Density is one of the main wood properties, largely used to evaluate wood technological characteristics and quality. Wood density is very variable between and within species, and also shows within tree variation that includes axial, radial and within growth ring variation (Saranpaa 2003; Panshin and Zeeuw 1980; Zobel and van Buijtenen 1989). Growth ring variation is related essentially to the cellular structure, and earlywood and latewood characteristics and proportion. In wood ring porous species, the growth rate affects wood properties due to its effect on earlywood and latewood proportion, and high growth rates result generally in higher density in spite of some controversy (Walker 2006; Zobel and van Buijtenen 1989).

The study of wood density variation is therefore one supporting line for the effort of valorizing *Q. faginea*. A previous study with young adult trees (on average 40 year old trees, with a dbh of 21 cm) showed favourable features in what regards the high density (ca. 0.848 g/cm^3) and a within-tree density variation of small magnitude, leading to a quite homogenous wood (Knapič et al. 2011). However information is lacking on mature *Q. faginea* trees at rotation age for timber products i.e. with a 40 cm dbh class. This is the object of the present paper which addresses the question of the within-tree variation of wood density components and ring width, which is an important issue for an industrial timber use. Although a decreasing pattern from pith to bark and from base to top may be expected as it occurs in other *Quercus* spp. (e.g. Lei et al. 1996; Bergès et al. 2000), the wood density range is quite diverse within this genus and there is little information on variation patterns in high density woods (Woodcock 2002; Nepveu 1984; Dilem 1995). The knowledge obtained will be important for forest management of the actual *Q. faginea* stands targeted towards solid wood products and for increasing the interest in the economic exploitation of this autochthonous species in the future.

Material and methods

For this study *Quercus faginea* trees were selected for sampling in the center of Portugal, at Vimeiro (39º 29' N, 9º 01' W, 100 m mean altitude). The climate is of the Mediterranean type with Atlantic influence, with a mean annual temperature of 15 ºC and annual precipitation of 890 mm. The highest temperatures occur during July-August (19 ºC) and the precipitation is concentrated from October to February (77 mm to 99 mm monthly rainfall). It is an unmanaged stand of public nature and kept for conservational targets, essentially constituted by *Q. faginea* with some *Q. suber*, *Castanea sativa* and *Pinus pinaster* sparse trees. Vegetation is diverse with ferns, gorses, heathers and grasses among others. The soils are classified as chromic cambisols.

Ten dominant or co-dominant trees aged on average 125 years and free of visible signs of decay were harvested. Total tree height, crown height, crown diameter and tree diameter (over bark) at 1.30 m were measured on the standing trees (Table 1). The trees were felled and sampled at stem base, and at 1.3 m, 3.4 m, 5.6 m, 7.7 m and 9.7 m above ground level. Only 8 trees attained the 7.7 m height level and 6 trees the 9.7 m height level. A disk of about 10 cm thickness was collected at each of the sampling heights of each tree. A wood sample from pith to bark was selected from each tree avoiding tension wood.

The samples were sawn along the radial direction into strips with 5 mm on the tangential direction and 2 mm of thickness (axial direction) using especially designed dual-saw equipment and conditioned at 12% moisture content. These radial samples were X-rayed perpendicularly to the transverse section and their images scanned by microdensitometric analysis as described by Louzada (2000). The time of exposure to radiation was 350 s, at an intensity of 18 mA and an accelerating tension of 12 kV, with a 2.5 m distance between X-ray source and film. Density was recorded at every 100 μm of the radial strip length with a slit height (tangential direction) of 455 μm.

The growth ring boundaries were identified on the radial profiles by locating the sharp density variations and with a cross-examination using a visual observation of the macroscopic anatomical features, namely the vessel distribution that is characterized by an abrupt transition in pores size from earlywood to latewood (Sousa et al 2009). The earlywood-latewood boundary for each growth ring was set by the average of the minimum and maximum density values within each ring (Rozenberg et al. 2001). For each ring, average ring density, earlywood density, latewood density, heterogeneity index, ring width, earlywood width, latewood width and latewood percentage were determined. The heterogeneity index quantifies the intra ring density variation and is given by the standard deviation of all density values across each annual ring (Ferrand 1982).

The heartwood and sapwood were identified by visual natural color differences and whenever necessary methylorange solution was applied to highlight the contrast. Then the rings were counted and cross-exanimated with the densitometry profiles of ring width to analyze 10 rings in four different radial regions: inner heartwood (IH), mid heartwood (HW), heartwood-sapwood transition wood (TW) and sapwood (SW).

To measure and analyse the relationship between ring density and radial growth parameters the cambial age was used as reference for arranging the data obtained from the microdensitometric profiles.

Analysis of variance for all ring and wood density components was performed according to the model presented in Table 2 to find significant differences between trees, height levels, rings and their interactions. In order to perform the analysis 100 rings from pith to bark were analysed within the first four stem heights of all trees adding up a total of 4000 rings. Expected variance was calculated to identify the contribution of the sources of variation. Correlation analysis was performed between wood density and ring number, and distance from pith as well as between the wood density and ring width components. Duncan Multiple test was performed to find the statistically significant differences between the variable means. Statistical analysis was performed using commercial software.

Table 1. Estimated age (number of rings at stem base) and biometric characteristics of the 10 sampled *Quercus faginea* trees. Standard deviation in brackets.

Tree	Estimated Age*	Diameter at 1.3 m (cm)	Total height (m)	Stem height (m)	Heartwood radius (cm)	Sapwood width (mm)
1	122	42.2	17.1	11.2	12.8	27.0
2	120	29.0	14.2	6.5	8.4	28.6
3	122	31.1	13.7	5.0	12.1	16.0
4	128	42.0	16.2	8.9	13.1	23.2
5	121	33.5	15.6	6.0	9.9	25.4
6	132	46.3	18.0	6.5	11.6	42.5
7	132	40.8	15.5	2.7	11.5	28.8
8	112	37.1	14.2	6.3	11.6	29.7
9	112	30.4	13.0	4.7	9.9	22.9
10	150	34.8	10.0	4.4	10.5	23.8
Mean	125 (11)	36.7 (5.9)	14.8(2.3)	6.2 (2.4)	11.0 (3.6)	27.4 (9.5)

*Ring numbers at the base

Table 2. Model for analysis of variance for the ring and density components.

Source of variation	Degrees of freedom	Expected variance	Error Term
(1)Trees (T)	t-1	$\sigma^2\varepsilon + lr\,\sigma^2 T$	(7)
(2)Levels (L)	l-1	$\sigma^2\varepsilon + r\,\sigma^2 TL + rt\,\sigma^2 L$	(3)
(3)T x L	(t-1)(l-1)	$\sigma^2\varepsilon + r\,\sigma^2 TL$	(7)
(4)Rings (R)	r-1	$\sigma^2\varepsilon + l\,\sigma^2 RT + lt\,\sigma^2 R$	(5)
(5)R x T	(r-1)(t-1)	$\sigma^2\varepsilon + l\,\sigma^2 RT$	(7)
(6)R x L	(r-1)(l-1)	$\sigma^2\varepsilon + t\,\sigma^2 RL$	(7)
(7)Residual (R x L x T)	(r-1)(l-1)(t-1)	$\sigma^2\varepsilon$	

t = trees (10); l = height levels/tree (4); r = rings/level/tree (100)

σ^2 T, σ^2 L, σ^2TL, σ^2R, σ^2RT, σ^2RL and $\sigma^2\varepsilon$ are variance components due to trees, levels, trees x levels, rings, rings x trees, rings x levels and residual.

Results

Age related patterns

Tree ring boundaries were clearly signalled by differences in wood density as well as by visual observations due to the abrupt transition of pore size between latewood to earlywood (Fig. 1). The less distinct rings were very narrow, presenting almost only earlywood tissues, and were more frequent at the lower stem height levels and near the bark.

Overall ring width decreased with cambial age at each height level and ring width differences between levels decreased also from pith to bark. The higher ring width variation found in the first 80 years of cambial age was present at all height levels (Fig. 2). At breast height, the ring width presented the highest values within the first four rings close to the pith with an average of 2.4 mm. Ring width decreased abruptly to 1.5 mm for the 5th ring and remained rather constant at an average of 1.6 mm till the 36th ring, decreasing further to 1.0 mm from the 40th to the 80th ring, and subsequently to 0.54 mm. Higher ring-to-ring width variation was found in the first 80 years of cambium age (Fig. 3a).

There was a gradual decrease of ring width from stem base to 5.5 m of tree height with respectively 1.42 mm and 0.98 mm mean ring width (Table 3). At the highest tree level of 9.7 m, the mean value was 1.00 mm. The between-tree variation, as observed by the standard deviations values of the means, showed higher ring-to-ring fluctuations compared to height levels differences (Fig. 4a, Table 3).

The latewood proportion varied between the extreme values of 44% and 72% but without any clear tendency of variation (Fig. 3b). Between-trees variation was slightly higher at the initial cambial ages and similar between height levels (Fig. 4b).

The mean ring wood density decreased gradually from pith to bark with some ring-to-ring fluctuations at all height levels (Fig. 2). Heartwood density that ranged between 1.00 g/cm^3 and 0.88 g/cm^3 from the inner to heartwood-sapwood transition was clearly different from sapwood density that was on average 0.69 g/cm^3 (Table 4).

The wood density was very high with an average of 0.859 g/cm^3 at breast height (Table 3). Level profiles and absolute wood density values were similar in the first 20 rings of cambial age and afterwards the differences became more evident (Fig. 2). Most differences were observed after about 60 years of cambial age at the higher levels which showed lower density values (Fig. 2). Overall wood density values decreased from the initial years of cambium activity to the last years that were studied, and stem lower levels showed higher values compared to upper levels (Table 3). The between-trees variation was high i.e. ranging between 0.76 g/cm^3 and 1.10 g/cm^3 at 1.3 m (Table 3). Differences in wood density become more evident after 40-60 years of cambial age at all height levels (Fig. 4 c). The existing statistically significant differences refer to the lower stem height levels (base and 1.3 m) and the higher levels (3.4 m and 5.5 m) (Table 3).

The general trends of earlywood and latewood density were parallel to the mean density and showed annual similar fluctuations (Fig. 3b) and the same height level variation (Table 3). The earlywood density varied less (0.825–0.807 g/cm^3) in the heartwood region than the latewood density that showed significant differences from mid heartwood to transition wood (0.971–0.922 g/cm^3) (Table 4).

The ring heterogeneity index was very low with a minimum of 0.01 g/cm^3 and an average of 0.06 g/cm^3 with smaller values in the early cambial ages, increasing afterwards till the 20th ring and decreasing again after around 60 years notwithstanding the observed ring-to-ring fluctuations (Fig. 2b). Tree-to-tree variability was relatively constant along the stem height level and with cambial age (Fig. 4d).

Regardless of tree level, the strongest correlation between wood density and tree growth was found between wood density and ring number ($-0.544 < r < -0.715$), followed by wood density and distance from pith ($-0.427 < r < -0.602$) and wood density and ring width ($0.398 < r < 0.532$) (Table 5). Both linear and nonlinear models fitted quite well the radial variation of wood density according to cambial age (Table 6). The relationship between wood density and ring width were better described with a polynomial model (Fig. 5).

When considering cambium age according the heartwood formation it was found that wood density was significantly different between the inner heartwood and the mid heartwood and between the transition wood and the sapwood at all height levels (Table 7).

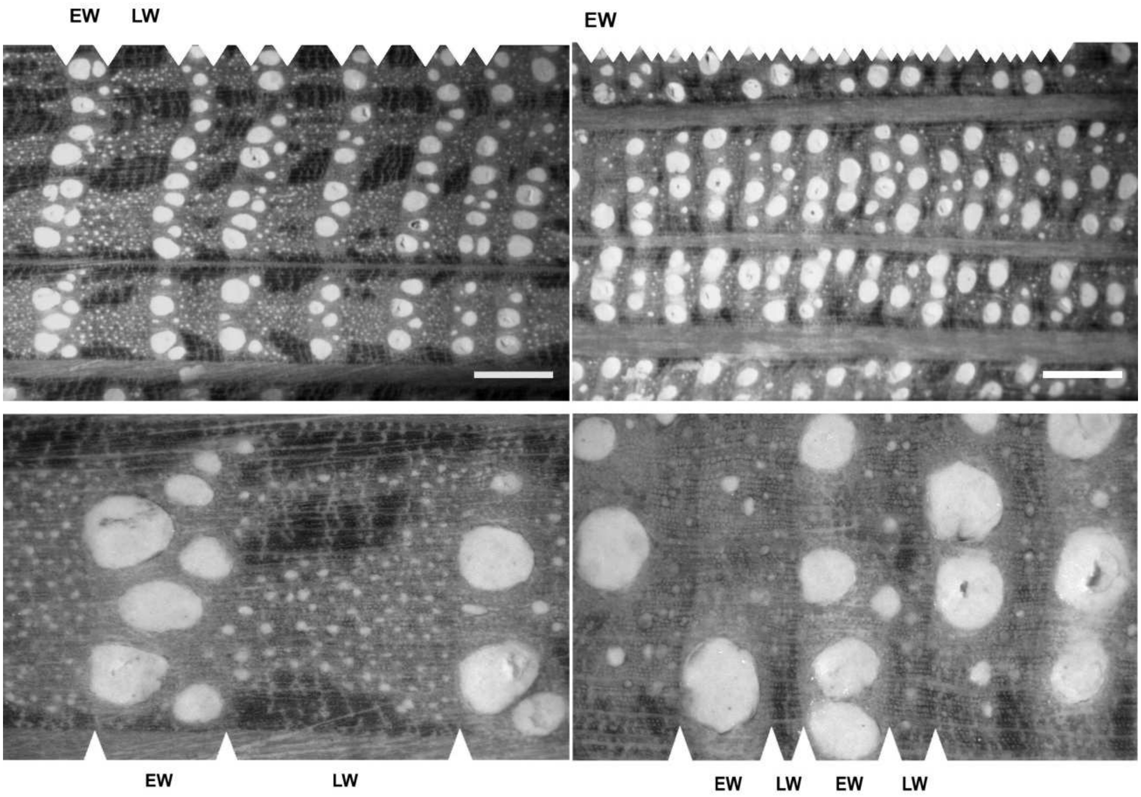

Figure 1. Growth rings distinctiveness in *Quercus faginea* trees due to pore size differences from earlywood (EW) and latewood (LW) within: a) large and b) narrower rings. Scale bar = 1mm.

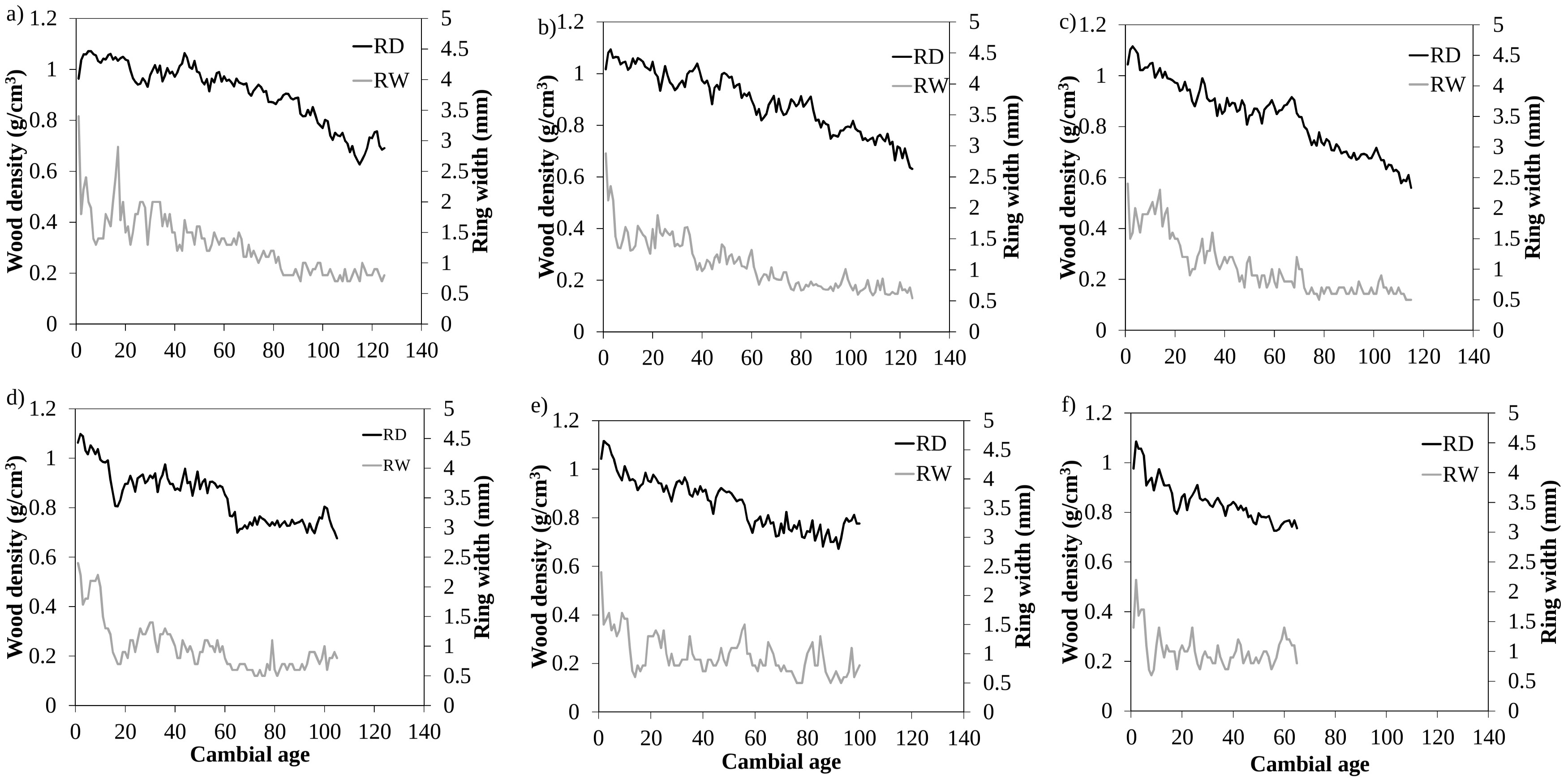

Figure 2. Ring width and wood density profiles for Quercus faginea mature trees at different height level: a) at the base, b) 1.3 m, c) 3.4 m, d) 5.6 m, e) 7.7 m and f) 9.7 m.

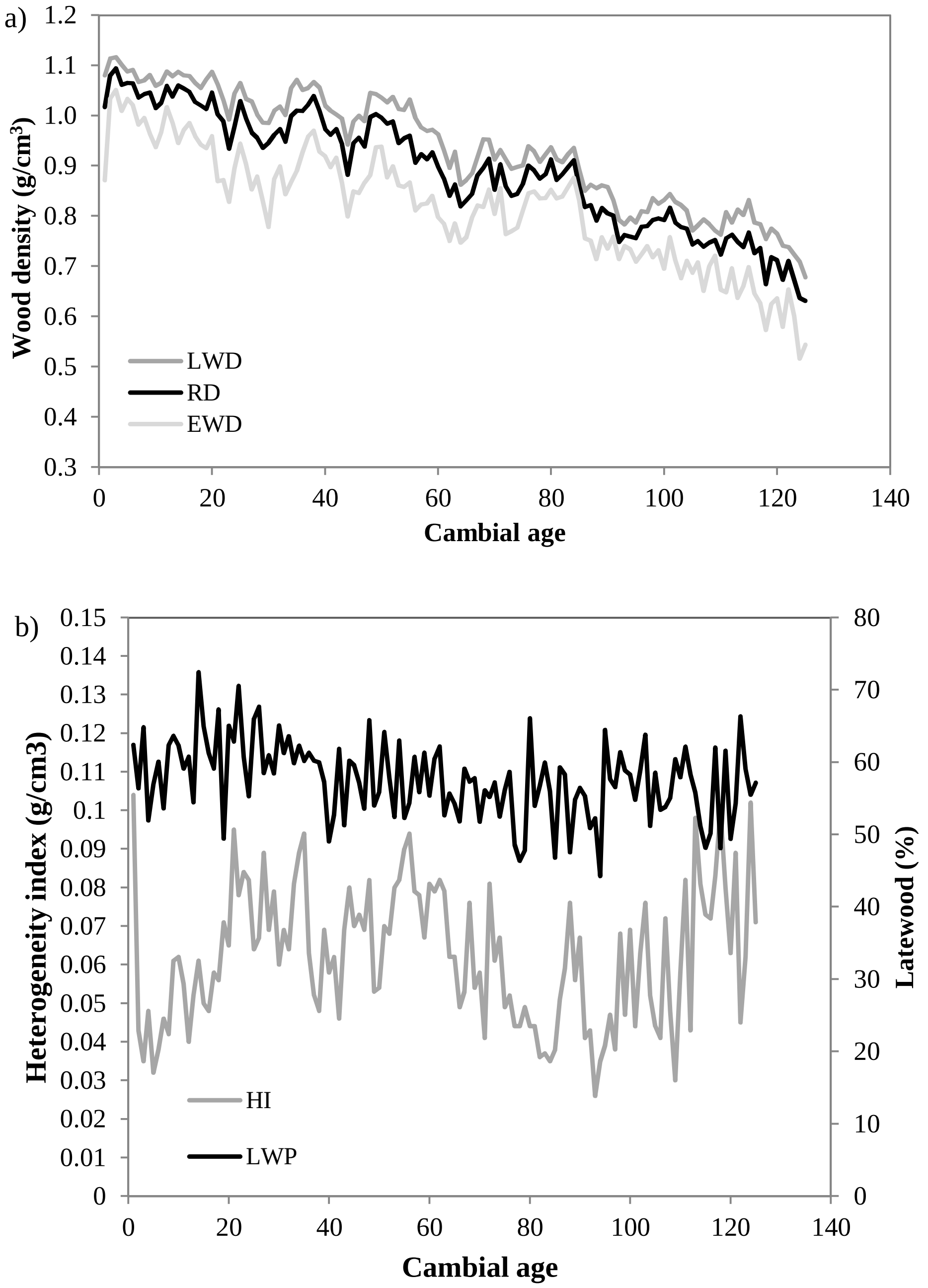

Figure 3. Radial variation of a) ring density, earlywood and latewood density, and b) latewood percentage and heterogeneity index for the first 125 rings at 1.30 tree height level.

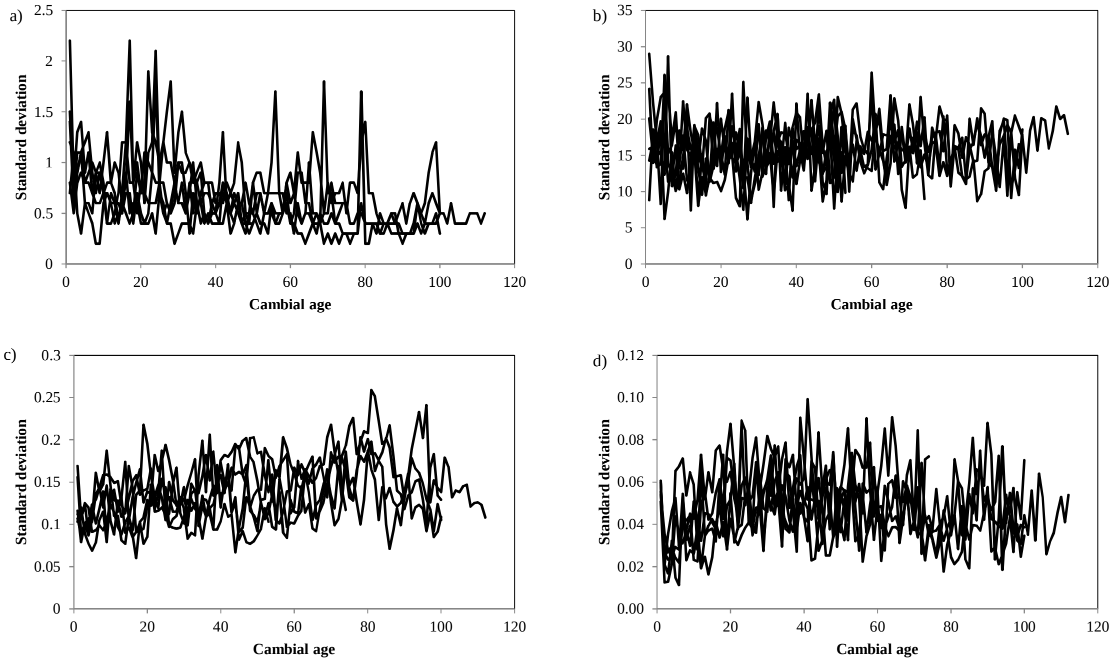

Figure 4. Standard deviations plotted for a) ring width, b) latewood percentage, c) wood density and d) heterogeneity index by cambial age at each height level (1= base, 2= 1.3 m, 3= 3.4 m, 4= 5.6 m; 5= 7.7 m and 6= 9.7 m) from the 10 *Q. faginea* sampled trees.

Tree, height and cambial age effects

The variance analysis was performed for the first 100 rings that were common to all trees and the first four stem height levels (till 5.6 m of tree height) (Table 8).

The effects that explained significantly the variation of the density components were mainly the rings (cambial age) accounting for 17-26% of the total variation. Tree, level and interaction effects accounted for 5-9%; tree and ring interaction 6-8%; and level and ring interaction 1-2% of the total variation. Other factors than those associated to between- and within- tree variations accounted for 42% to 53% of the total variation of the density components of *Q. faginea* wood.

In relation to ring width, ring and tree x ring interaction were the most significant factors of variation accounting for 19% and 10% of the total variation, respectively. Tree x level interaction accounted for 5%, level for 4%, tree for 3%, and level x ring interaction for 2% of the total variation. The residual effects were also high with 57% of the total variation unexplained by the analysed factors. Latewood percentage was only slightly explained by cambial age, tree and level (2 to 3 %) and mainly due to residual effect (87%).

Overall the between-tree variation was smaller for ring width components (3 %) than for density components (6 to 9 %).

The intra-ring variation (heterogeneity index) was less influenced by the analysed factors and the residual effect accounted for 74% of the total variation. Between tree variation explained more than cambial age (8% and 4%, respectively) and height levels were not a significant factor of variation.

Correlation with ring width was significant and positive for mean ring density (r=0.432), earlywood density (r=0.257) and latewood density (r=0.464) (Table 9). The density components were not strongly correlated to latewood percentage. Latewood density showed the strongest correlation of all variables with mean ring density (r=0.969).

Table 3. Mean values for wood density and ring width components for the studied *Q. faginea* trees. Mean values by stem height level (1= base, 2= 1.3 m, 3= 3.4 m, 4= 5.6 m, 5= 7.7 m and 6= 9.7 m) plus standard deviation for the maximum rings common at each level (n=1000).

Level	RD (g/cm^3)	EWD (g/cm^3)	LWD (g/cm^3)	HI (g/cm^3)	EWW (mm)	LWW (mm)	RW (mm)	LWP (%)
1	0.957 ± 0.147 b	0.88 ± 0.17 b	0.998 ± 0.148 b	0.061 ± 0.054 a	0.51 ± 0.63 b	0.91 ± 0.8 c	1.42 ± 1 b	60.3 ± 16.4 c
2	0.932 ± 0.169 b	0.859 ± 0.189 b	0.975 ± 0.163 b	0.061 ± 0.049 a	0.45 ± 0.3 ab	0.73 ± 0.61 b	1.18 ± 0.78 a	58.0 ± 16.6 bc
3	0.868 ± 0.18 a	0.799 ± 0.189 a	0.913 ± 0.178 a	0.062 ± 0.05 a	0.43 ± 0.31 a	0.65 ± 0.58 ab	1.08 ± 0.79 a	57.2 ± 15.6 ab
4	0.851 ± 0.166	0.783 ± 0.181 a	0.901 ± 0.164 a	0.064 ± 0.052 a	0.41 ± 0.29 a	0.57 ± 0.51 a	0.98 ± 0.7 a	54.9 ± 16.0 a
Mean	0.899 ± 0.169	0.826 ± 0.186	0.944 ± 0.166	0.063 ± 0.052	0.44 ± 0.32	0.7 ± 0.62	1.14 ± 0.81	57.6 ± 16.3

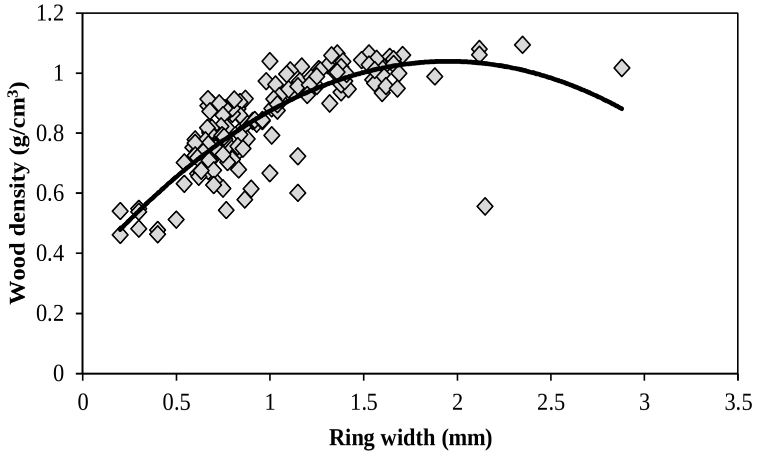

Figure 5. Wood density and ring width relationship for the first 100 rings at 1.30 tree height level and fitted model ($y = -0.1828x^2 + 0.7132x + 0.3436$).

Table 4. Average values for the wood density and ring width components at different regions from pith to bark (IW= Inner heartwood, HW= Mid heartwood, TW= heartwood-sapwood transition wood, SW= Sapwood). Average values on the same column with the same letter are not statistically different by Duncan Multiple test with alpha 0.05.

	RD (g/cm^3)	EWD (g/cm^3)	LWD (g/cm^3)	HI (g/cm^3)	RW (mm)	LWP (%)
IW	1.006 ± 0.126 a	0.936 ± 0.162 a	1.047 ± 0.113 a	0.058 ± 0.044 a	1.53 ± 0.82 a	59.19 ± 15.39
HW	0.917 ± 0.153 b	0.825 ± 0.184 b	0.971 ± 0.143 b	0.076 ± 0.059 b	1.09 ± 0.63 b	59.01 ± 15.82
TW	0.879 ± 0.171 c	0.807 ± 0.196 b	0.922 ± 0.162 c	0.06 ± 0.052 a	0.96 ± 0.06 c	57.4 ± 16.97
SW	0.692 ± 0.128 d	0.629 ± 0.147 c	0.736 ± 0.13 d	0.058 ± 0.051 a	0.84 ± 0.53 d	55.37 ± 16.16
Mean	0.873 ± 0.185	0.799 ± 0.205	0.919 ± 0.18	0.063 ± 0.052	1.1 ± 0.7	57.74 ± 16.16

Table 5. Correlation of wood density, ring width (RW), ring number (RN) and distance from pith (DP) at each height level sampled (1= base, 2= 1.3 m, 3= 3.4 m, 4= 5.6 m; 5= 7.7 m and 6= 9.7 m). Correlation is significant at the 0.01 level (2-tailed).

	Level					
	1	2	3	4	5	6
RW	0.398	0.436	0.532	0.488	0.399	0.407
RN	-0.654	-0.621	-0.715	-0.609	-0.59	-0.544
DP	-0.572	-0.556	-0.602	-0.511	-0.484	-0.427
N	1276	1255	1201	1107	825	528

Table 6. Fitted models for wood density of *Q. faginea* as function of cambial age at each height level sampled (1= base, 2= 1.3 m, 3= 3.4 m, 4= 5.6 m; 5= 7.7 m and 6= 9.7 m). N values were the mean of 10 trees.

Level	n	Model		R^2
1	112	Linear	$y = -0.0019x + 1.1024$	0.729
		Nonlinear	$y = -2E-05x^2 + 0.0015x + 1.0045$	0.858
2	100	Linear	$y = -0.0028x + 1.0755$	0.847
		Nonlinear	$y = -1E-05x^2 - 0.0019x + 1.0591$	0.853
3	100	Linear	$y = -0.0038x + 1.062$	0.911
		Nonlinear	$y = -6E-07x^2 - 0.0038x + 1.0609$	0.911
4	100	Linear	$y = -0.0032x + 1.0107$	0.756
		Nonlinear	$y = 9E-06x^2 - 0.0041x + 1.0264$	0.760
5	74	Linear	$y = -0.0039x + 1.0442$	0.828
		Nonlinear	$y = -6E-06x^2 - 0.0035x + 1.0388$	0.829
6	58	Linear	$y = -0.0042x + 0.9769$	0.750
		Nonlinear	$y = 6E-05x^2 - 0.0076x + 1.0112$	0.783

Table 7. Average values for the wood density at different regions from pith to bark (IW= Inner heartwood, HW= Mid heartwood, TW= heartwood-sapwood transition wood, SW= Sapwood) at each height level (1= base, 2= 1.3 m, 3= 3.4 m, 4= 5.6 m; 5= 7.7 m and 6= 9.7 m). Average values on the same column with the same letter are not statistically different by Duncan Multiple test with alpha 0.05. Note: C. age is the mean of cambial age of the analysed data at each height level.

	Level					
	1	2	3	4	5	6
IW	1.048 a	1.044 a	1.023 a	0.987 a	0.974 a	0.923 a
C. age	11	11	11	11	11	11
HW	0.988 b	0.953 b	0.876 b	0.910 b	0.915 b	0.823 b
C. age	47	47	45	39	37	31
TW	0.955 c	0.910 b	0.810 c	0.838 c	0.908 b	0.843 b
C. age	80	79	74	67	63	50
SW	0.678 d	0.700 c	0.639 d	0.704 d	0.712 c	0.743 c
C. age	121	119	114	104	97	82

Table 8. Results of the analysis of variance for each wood density and ring components, with the significance and percentage of total expected variation by source of variation (EV%). Average of the first 100 rings at 4 height levels for the 10 studied *Q. faginea* trees. Note: RD= ring density, EWD= earlywood density, LWD - latewood density, HI - heterogeneity index, EWW - eralywood width, LWW - latewood width, RW - ring width and LW - latewood percentage.

Source of variation	RD		EWD		LWD		HI		EWW		LWW		RW		LWP	
	P	EV	P	EV	P	EV	P	EV	P	EV	P	EV	P	EV	P	EV
Tree (T)	0.0001	7.7	0.0001	9.4	0.0001	6.4	0.0001	7.7	0.0001	1.7	0.0001	3.1	0.0001	3.0	0.0001	2.8
Level (L)	0.0001	7.6	0.0011	5.1	0.0002	6.8	0.8902	0.0	0.0245	1.3	0.0003	4.2	0.0005	4.2	0.0039	1.6
T x L	0.0001	7.6	0.0001	7.8	0.0001	7.9	0.0001	8.3	0.0001	4.1	0.0001	4.8	0.0001	5.3	0.0001	2.6
Ring (R)	0.0001	24.4	0.0001	17.1	0.0001	26.4	0.0001	3.8	0.0001	13.5	0.0001	15.1	0.0001	18.6	0.0001	1.8
T x R	0.0001	7.1	0.0001	6.0	0.0001	7.7	0.0001	6.2	0.0001	4.7	0.0001	9.3	0.0001	9.6	0.0001	4.1
L x R	0.0001	2.0	0.0026	1.4	0.0001	2.3	0.1841	0.6	0.1264	0.7	0.0001	2.5	0.0001	2.2	0.3778	0.2
Residual		43.6		53.3		42.4		73.		74.0		60.9		57.0		86.9

Table 9. Correlation matrix for density components and ring width (average values of the first 100 rings at 4 height levels from 10 *Q. faginea* trees, n=4000). Values marked in bold are significant at P<0.05. Note: RD - ring density, EWD - earlywood density, LWD - latewood density, HI - heterogeneity index, EWW - eralywood width, LWW - latewood width, RW - ring width and LW - latewood percentage.

	RD	EWD	LWD	LWP	RW	EWW	LWW
RD	1.000						
EWD	**0.920**	1.000					
LWD	**0.969**	**0.839**	1.000				
LWP	**0.234**	0.019	**0.188**	1.000			
RW	**0.432**	**0.257**	**0.464**	**0.331**	1.000		
EWW	**0.319**	**0.292**	**0.385**	**-0.262**	**0.725**	1.000	
LWW	**0.403**	**0.190**	**0.412**	**0.560**	**0.940**	**0.447**	1.000

Discussion

The average diameter at breast height of the studied trees (36.7 cm, Table 1) is in line with Loewenstein et al. (2000) age models predicted for white oaks under a managed uneven-aged oak forest. The mean annual growth of *Q. faginea* trees for a 100-year period was 1.2 mm (at 1.3 m of height, Table 3). There is a previous study using the same microdensitometric methodology focusing on younger *Q. faginea* trees with 34-60 years of age for which 2.4 mm wide rings were reported (Knapič et al. 2011). For the same cambial age period i.e. the first 30 years, the mean ring width was smaller in this study. In theory this difference should be the consequence, at least partially, of the fact that the forest from where the trees were taken had no silvicultural management and was kept as a conservational area, from which a slow tree radial growth is expected; differences in soil and climate conditions probably are also involved.

Regarding growth rate of other oaks with similar ages, Guilley et al. (1999) referred 1.7 mm ring width for *Q. petraea* with a slow growth under a classic silviculture, which could be increased to 2.5 mm with a dynamic silviculture and accelerated tree growth. Predictive models for *Q. petraea* and *Q. robur* by Zhang et al. (1993) showed similar results under these two types of silvicultural regimes. Other ring width values were reported for *Q. petraea* ranging from 1.3 to 3.9 mm for 61-224 years (Guilley et al. 2004) and 0.8 to 3.1 mm for 110 years (Bergès et al. 2008). Zhang et al. (1993) reported an average 1.5 mm ring width for *Q. petraea* and *Q. robur* with 151 years of age from natural forests.

There was a significant effect of cambial age on ring width, with a decreasing trend, although stabilization occurred after about 80 years. Cambial age and its interaction with tree were the most important sources for the total variation found in ring width (Table 4). This decreasing tendency of ring width with ageing is a common pattern in ring-porous species (e.g. Paul 1963; Lei et al. 1996; Zhang et al. 1993).

The axial variation of ring width, representing the effect of tree age (maturation), although highly significant, only contributed in a small degree to explain the ring width variation (Table 7) and the mean values at most of the different stem height levels were not statistically different (Table 3). Stem analysis on other *Quercus* spp corroborates our results (Knapič et al. 2008, Guilley et al. 1999, Lei et al. 1996). This is important from the point of view of wood processing and suitability since an axial homogeneity is favourable.

Latewood percentage was rather constant along the years under a 100-year lifetime period. Latewood accounted for 57% of the ring. In ring-porous species, a retardation of radial growth brings the rows of large pores closer together in the successive annual rings, as seen in cross sections (Fig. 1), and reduces the ring region of latewood containing the thicker latewood cells (Chauchan 2006). Therefore ring porous species show a positive correlation between latewood proportion and ring width (Polge and Keller 1973; Zhang et al. 1993). In the present case, this relationship was significant (Table 8) with a positive trend, reflecting that latewood width in wider or narrow rings was proportional to total ring width (Fig. 1). However residual effects were high and should be related for instance with site characteristics and circumference heterogeneity.

Q. faginea mature trees showed high wood density values (mean density of 0.86 g/cm^3, Table 3). This density is in the range of *Q. suber* density values from 0.75 to 1.07 g/cm^3 (Knapič et al. 2007, 2008) and *Q. cerris* 0.96 g/cm^3 (Dilem 1995). The density is higher than the values found for the presently highly valued oaks as *Q. petraea* (0.66 - 0.83 g/cm^3) (Bergès et al. 2008), *Q. rubra* (0.54-0.76 g/cm^3), and *Q. robur* (0.52-0.63 g/cm^3) (Nepveu 1984, Genet et al. 2012).

These results followed the general trend of ring-porous hardwood species from temperate climate that are characterized by differences between earlywood and latewood density and present a radial decrease of density from pith to bark (Woodcook 2002). Earlywood and latewood density differences are related to anatomical characteristics such as vessel size and arrangement along the growth ring with large pores (about 200 µm) in earlywood and small pores in latewood (about 50 µm) and the latewood proportion. Bergès et al. (2008) noted that cambial age influenced earlywood and latewood density and reduced latewood proportion, leading to a significant effect of age on mean density in *Q. petraea*. In contrast, Rao et al.

(1997) found that density in *Q. robur* was independent from latewood width due to a relative uniformity of latewood width with cambial age.

As regards to the radial pattern of wood density, a decreasing tendency was observed. This corroborates the results of previous studies in other oaks i.e. in 70-110-year-old *Q. suber* trees (Knapič et al. 2008), in 80-year-old *Q. garryana* (Lei et al. 1996) and in mature trees of *Q. petraea* (Bergès et al. 2000), in 80 and 250 year-old as well as in other American oaks (*Q. nigra, Q. rubra, Q. falcata, Q. velutina*) (Paul 1963).

Heartwood formation and accumulation of extractives during ageing may also increase density, as it was found in *Q. suber* trees (Knapič et al. 2008). Heartwood formation is characterized by an accumulation of extractives that increase the wood density (Hillis 1987). In the present case, the lower density region of the stem that corresponds to the outermost rings, namely after 80 years, approximately coincides with the measurements of sapwood width that ranged 23-43 mm. The sapwood width tendency is to follow the stem profile irrespectively of taper variations (Sousa et al. 2013). The abrupt wood density variation between the heartwood-sapwood transition region and the sapwood (0.879 and 0.692 g/cm^3 respectively, Table 4 and 7) reinforces this hypothesis at all stem heights.

Similar observations on the axial profile of wood density were made in younger *Q. faginea* trees (Knapič et al. 2011) and in other *Quercus* spp: *Q. suber* (Knapič et al. 2008), *Q. petraea* (Guilley et al. 1999; Degron and Nepveu (1996) and *Q. garryana* (Lei et al. 1996). Explanations for the wood density decrease with increasing tree age have been suggested to be related with the crown effects on latewood formation inhibition leading to lower values of density in the upper levels of the stem based mostly in softwoods (Saranppa 2003). However this subject is lacking on conclusions and no crown effects on wood density have also been reported (Gartner et al. 2002).

The residual effect in the variance analysis was high. One of the unaccounted factors was the heartwood and sapwood distinction, for which that our results showed the importance, and extractive depositions (Zobel and van Buijtenen 1989; Woodcook 2002). Other factors could be, for instance, the effect of the directions in the cross-sections within levels and crown effects. The genetic factors also contribute to explain the high residual effect found in the *Q. faginea* mature trees, as suggested for *Q.petraea* by Guilley et al. (2004). Site effects i.e. edaphic and climatic factors, can have or not an influence on ring density (Bergès et al. 2008; Guilley et al. 2004).

Correlation between ring width and density was significant and higher than in younger trees as previously found by Knapič et al. (2011). These findings corroborate Paul (1963) studies in unmanaged stands of *Q. alba* and *Q. velutina*, where the variation in density was significantly related to changes in ring width with increasing tree ages as well as in managed stands (Zhang et al. 1993, Degron and Nepveu 1996, Guilley et al. 1999). Zhang (1994) concluded that in ring porous species ring width had little influence in density while other studies refer inconsistent relationships between ring width and wood density for other oaks (Polge and Keller 1973).

The relationship between density and ring width was close to the classic positive hyperbolic curve. The variation pattern from pith outwards of density and ring width was similar which in case of the ring-porous species, as *Q. faginea*, is related with ring structure development during the year. Since earlywood varies less in amount than latewood under unfavourable growth conditions, the narrow rings contain a higher earlywood proportion, leading to lower mean ring density (Paul 1963). In fact, the latewood proportion tended to be more constant with tree ageing in these mature trees of *Q. faginea*.

Between-tree variability was higher for the ring wood density components than for the ring width components and was very important to explain the wood density variation as also previously found for *Q. petraea* and *Q. robur* (Bergès et al. 2008; Guilley et al. 2004; Zhang et al. 1993; Ackermann 1995). Tree variability is related to external factors as silviculture practices and internal factors such as genotype (Zobel and Buijtenen 1989). Under this perspective more homogenous wood might be obtained using tree selection and forestry breeding programs.

In conclusion, this study with mature trees of *Q. faginea* showed the high density of this wood and an overall small magnitude of within tree density variation. Such wood density characteristics confirm the value of *Q. faginea* as a timber species for use in solid products comparable with other commercial oaks.

It was also clear that ring width is important for defining wood density and that there is scope for improving growth rate by adequate stand management avoiding excessive tree competition. Our results suggest that the already available *Q. faginea* trees growing in unmanaged stands are valuable as high wood density timber and can be economically exploited.

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4.5. Influence of site in ring width and wood density components in *Quercus faginea* trees in the juvenile and early mature periods

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(Submetido)

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Abstract

Ring width and wood density components were studied in two naturally regenerated stands of *Quercus faginea* in Portugal. The site influence was compared in the juvenile and early mature periods, within the axial and radial directions.

A juvenile-mature wood density variation was observed for *Q. faginea* trees regardless of site. The results also confirmed the importance of heartwood presence to increase wood density. Site effects were found to be the main source of variation for the wood growth and density components and were higher for density and for mature wood. The radial growth in *Q. faginea* was influenced by stand characteristics, e.g. tree competition, that may overrule the site specific environment conditions, thereby stressing the importance of forest management for increased tree growth.

Relative uniformity of wood density was observed within the tree, since radial and axial variations were of small magnitude, thereby contributing to an overall favorable wood processing quality.

Wood density and ring width components showed only weak correlations, thus allowing tree selection for both traits.

Introduction

Wood density is largely used for raw-material evaluation because it relates to various wood properties and product performance, and it can be precisely measured with relatively simple equipment (Zobel and van Buijtenen 1989). Wood density has a large range of variation i.e. between species and within the same species, between locations, trees and within the tree. Wood density variation is also a good indicator of the transition between juvenile and mature adult in some species. Knowledge on wood density variation within a specific species is important for better designing a product-oriented silvicultural management e.g. stand density, rotation age and tree selection towards production of high valued wood products.

One important factor of density variation is site, resulting from a combination of many factors e.g. edaphic and climatic. In the case of ring-porous hardwoods such as oaks, different growing conditions may affect tissues composition i.e. latewood percentage, and therefore wood density (Zobel and van Buijtenen 1989). In *Quercus robur* and *Q. petraea* latewood width and wood density were affected by environment effects (Nepveau 1984; Ackermann 1995; Bergès et al. 2008), although Guilley et al. (2004) found that the wood density in *Q. petraea* with fixed age and growth rate did not vary between sites. In general, it seems that in oaks ecological factors affect more the radial growth than the wood density (Bergès et al. 2008, Guilley et al. 1999). For several oak species it has been reported that mature wood is already present around 30 years of cambial age (e.g. Voulgaridis 1990; Helinska-Raczkowska 1994; Lei et al. 1996).

Q. faginea is an oak mainly distributed in the Iberian Peninsula and Maghreb Africa, that is being considered as a potential timber species for high quality wood products namely structural and flooring components (Ramos et al. 2009; Knapič et al. 2011; Silva 2011). *Q. faginea* wood density is high and its between and within tree variation was already studied separately in two sites in trees of different ages about 40 (Knapič et al. 2011) and 125 years (data not shown) respectively, and with different growth rates. Alla and Camarero (2012) and Corcuera et al. (2004) refered that *Q. faginea* ring width and anatomy are affected by climatic conditions, while Villar-Salvador et al. (1997) reported no wood response to precipitation.

These findings motivated us to examine the site effects on ring width and wood density components in *Q. faginea*. The analysis is based on a 20-tree sampling on two differing sites in the centre and northeast of Portugal, with radial density measurements by X-ray microdensitometry made at six stem height levels, and takes into account the combined effects of cambial age of the rings (radial variation) and the tree age (stem height levels).

Since *Q. faginea* is well adapted to different soils and locations (Capelo and Catry 2007), the results of this study will show the site related differences in ring width and if site can explain the production of more or less dense wood and how it impacts on ring and density components variation.

Material and Methods

Sites and sampling

The study was carried out in two locations, near Macedo de Cavaleiros (MC, northeast of Portugal), and near Vimeiro (VI, center of Portugal), both within the *Quercus faginea* geographical natural distribution (Capelo and Catry 2007). Stands result from natural regeneration, were unmanaged, mixed and uneven-aged and VI is kept for state conservational purposes. The vegetation at MC is mainly characterized by minor occurrence of *Q. suber*, *Q. rotundifolia* and *Pinus pinaster* trees, and mainly *Cistus ladanifer*, *Lavandula* spp., *Daphne gnidium*, *Cytisus multiflorus* shrubs; at VI there were *Q. suber*, *Castanea sativa* and *P. pinaster* sparse trees, shrubs such as *Arbutus unedo*, *Pteridium aquilinum*, *Ulex europeaus*, and *Erica arborea*.

The climate is of Mediterranean type classified as Csa and Csb according the Köppen-Geiger Climate system at site MC and VI, respectively. Figure 1 shows the mean monthly variation of precipitation and temperature.

Basal area was 18 m^2/ha and 102 m^2/ha, and density 327 trees /ha and 300 trees /ha at MC and VI, respectively. Trees were in average 40 and 125 years old at site MC and VI, respectively. Ten dominant or co-dominant healthy trees were randomly selected per each site. Tree and site characteristics are shown in Table 1. The trees were harvested and from each of the 20 trees, a disk was taken at stem base, at 1.3 m, 3.4 m, and every 2.1 m along the stem to the top level.

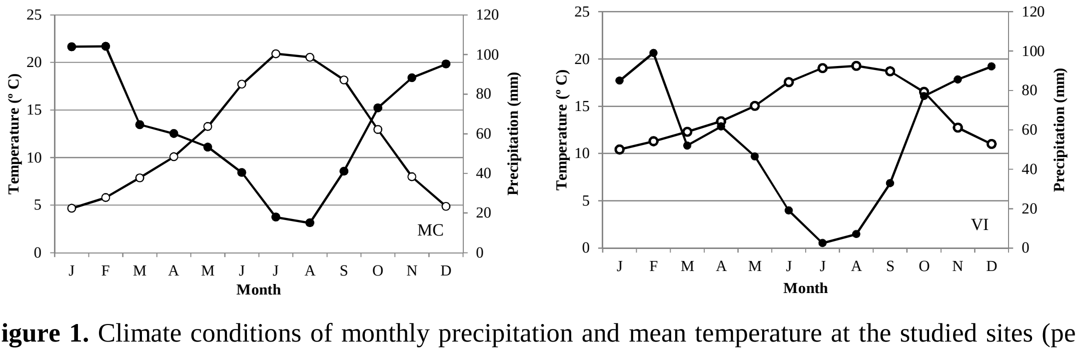

Figure 1. Climate conditions of monthly precipitation and mean temperature at the studied sites (period 1959-1988).

Table 1. Description of the two studied sites and sampled *Quercus faginea* trees. Mean values and standard deviation.

	Macedo de Cavaleiros (MC)	**Vimeiro (VI)**
Latitude	41° 31′ N	39º 29' N
Longitude	06° 51’ W	09º 01' W
Altitude (m)	540	100
Soil	Orthic Dystric and Eutric Leptosols	Chromic Cambisols
Tree height (m)	10.5 ± 0.7	14.8 ± 2.3
Diameter at 1.3m (cm)*	20.9 ± 4.2	36.7 ± 5.9
Crown height (m)**	8.3 ±1.3	8.5 ± 2.3
Radius crown (m)	2.4 ± 0.7	4.4±1.1
Tree age	40 ± 8 (34-60)	125 ± 11 (112-150)

* Over bark diameter; ** Crown height = Tree height - trunk height

X-ray microdensitometry

A radial sample from pith to bark was cut from each disk avoiding tension wood and knots. The radial samples were trimmed down to strips with 2 mm thickness (longitudinal) and 5 mm width with a specially designed dual-saw equipment and conditioned at 12% moisture content. These radial strips were X-rayed perpendicularly to the transverse section with an accelerating tension of 12 kV, an intensity of 18 mA and a time of exposure to radiation of 350 s, at 2.5 m distance between X-ray source and film. The images were scanned by microdensitometric analysis and film density was recorded at every 100 μm (radial) by 455 μm (tangential). Detailed descriptions of the method are given in the literature (Louzada 2000). Simultaneously with the wood pieces, standards of cellulose acetate with various thicknesses and previously gauged densities were also X-rayed. Since these standards have an X-ray affinity very similar to that of the wood, the regression calculated between the film optical density and the material density of the standards was used for conversion of film optical density to wood density of the studied samples.

The ring boundary was identified on the radial profiles by locating the sharp density variations set by the earlywood and latewood and by visual cross-examination focusing on the pores distribution that is characterized by an abrupt size transition.

For each ring, ring density and its components (earlywood and latewood density) as well as ring width, and latewood percentage were determined. Within-ring distinction of earlywood and latewood was made using the average of the minimum and maximum density values in each ring (Rozenberg et al. 2001; Knapič et al. 2011). The heterogeneity index for quantification of the intra ring density variation was calculated as the standard deviation of all density values across the ring (Ferrand 1982).

Data analysis

Since the number of rings at each tree height level is not the same (decreasing with height) and given the fact the average tree age is different in the two sites,.it is necessary to orthogonalize the data in order to maximize the information regarding the within and between tree variation of the different wood characteristics. The analysis was limited to the number of rings allowed by the dimension of the limiting sample (the uppermost height level of the youngest tree).

Data analysis was performed making use of two approaches:

i) the first analysis concerns the central part of the trees (juvenile wood) made up by the innermost 15 rings present in all the levels (core analysis), thereby comparing rings with the same physiological age at different levels of the tree; and

ii) the second analysis concerns a sheath analysis of a sequence of 10 rings with the same chronological age in the different height levels of the tree. As the age of the sampled trees was different in the two sites, to ensure that the analysis referred to an identical stem phase in the two sites, this sheath analysis was conditioned by the number of rings of the youngest tree, for which the outermost 10 rings at bottom level corresponded to the sequence of the 31st to the 40th ring, thus representing the early mature wood. Therefore all the trees were virtually reduced to 40 rings at the bottom level and then the outermost sequence of 10 rings was taken at all height levels.

Analysis of variance for wood density and ring components was performed according to the model presented in Table 2, to assess significant differences and the effect of sites, trees, rings, height levels and their interactions. Sites, rings, and height levels were considered to be fixed sources of variation and trees at sites were random sources of variation. Variance components were calculated to identify the main sources of variation for density components and ring width. Differences between means were assessed by Duncan Multiple test. Correlation analysis was performed between ring width and density components.

Table 2. Model for analysis of variance for the ring and density components.

Source of variation	**Degrees of freedom**	**Expected Variance**	**Error Term**
(1) Sites (S)	s-1	$\sigma^2\varepsilon$ + rl σ^2 T/S + rlt σ^2 S	(2)
(2) Trees/Sites (T/S)	(t-1)s	$\sigma^2\varepsilon$ + rl σ^2 T/S	(11)
(3) Levels (L)	l-1	$\sigma^2\varepsilon$ + rts σ^2 L	(11)
(4) L x S	(l-1)(s-1)	$\sigma^2\varepsilon$ + r σ^2 LT/S + rt σ^2 LS	(5)
(5) L x T/S	(l-1)(t-1)s	$\sigma^2\varepsilon$ + r σ^2 LT/S	(11)
(6) Rings (R)	r-1	$\sigma^2\varepsilon$ + lts σ^2R	(11)
(7) R x S	(r-1)(s-1)	$\sigma^2\varepsilon$ + l σ^2RT/S + lt σ^2RS	(8)
(8) R x T/S	(r-1)(t-1)s	$\sigma^2\varepsilon$ + l σ^2RT/S	(11)
(9) R x L	(r-1)(l-1)	$\sigma^2\varepsilon$ + ts σ^2RL	(11)
(10) R x L x S	(r-1)(l-1)(s-1)	$\sigma^2\varepsilon$ + t σ^2RLS	(11)
(11) Residual (R x L x T/S)	(r-1)(l-1)(t-1)s	$\sigma^2\varepsilon$	

t = trees (10/Site); l = height levels/tree (4); r = rings/level (15 or 10); σ^2 S, σ^2 T/S, σ^2L, σ^2LS, σ^2LT/S, σ^2R, σ^2RS, σ^2RT/S, σ^2RL, σ^2RLS and $\sigma^2\varepsilon$ are variance components due to Sites, Trees/Sites, Levels, Levels x Sites, Levels x Trees/Sites, Rings, Rings x Sites, Rings x Trees/Sites, Rings x Levels, Rings x Levels x Sites and Residual.

Results

Variation of ring width and density components within juvenile wood

The mean values for ring width and wood density components for the juvenile wood (1-15 years) are summarized in Table 3 for each site. Table 4 summarizes the results for the corresponding analysis of variance.

Ring width was in average 1.83 mm at Site VI and 2.52 mm at Site MC for the first 15 rings (Table 3). Site was the most important factor of variation of ring width, accounting for about 14% of the total variation. The between-tree variation was also highly significant and accounted for 7% of the total variation, as well as the axial variation given by the stem height levels and their interactions with site and trees that altogether accounted for 19% of the total variation (Table 4). The effect of cambial age given by the ring effect was very small (0.5%) in this young juvenile phase, as also the interaction of the rings with site, tree or height level. The general radial variation showed a decrease from the pith to the 5th ring followed by a rather constant region (Fig. 2). Ring width trend decreased from base to top (Table 5), although this levels effect only explained 3.1% of the total variation of ring width.

The mean latewood percentage was higher at site MC (69%) than at site VI (60%) (Table 3). Site was the most important factor of latewood percentage variation, accounting for 11% of the total variation (Table 4). Within the tree, the latewood percentage was quite constant radially and axially. The levels and the ring effects only explained 0.6% and 4.2%, respectively, of the total variation. From pith outwards the latewood percentage decreased only from the 1st to the 2nd ring, remaining rather constant in the following rings (Fig. 2). Regarding the levels effect, *Q. faginea* showed an axial decrease only for the upper level of the trees. The residual effect accounted for 71% of the total variation (Table 4).

Average wood density was 0.914 g/cm^3 and 1.037 g/cm^3 at sites MC and VI, respectively for the first 15 years of cambial functioning (Table 3). There were also site differences in earlywood and latewood density which were greater for earlywood density.

The wood density components showed statistically significant differences between the two sites (Table 3). The site explained the main variation accounting for 30-35%, followed by the tree effect (16-21%) and the interaction between trees and height level (12-14%) (Table 4). Despite the wood density trend to decrease from base to top of the trees (Table 5), the height level effect represented only 3-5% of the total variation. The cambial age (rings), although highly significant, only accounted for a small proportion of the total variation (2-4%) expressed by a slight radial reduction of the wood density (Fig. 3). The residual effect (the contribution of variance due to other factors that were not studied) was relatively small (21%).

As regards the index of heterogeneity within the ring, the wood produced in site MC was more heterogeneous than in site VI (Table 3), and irrespective of site the heterogeneity increased with cambial age and decreased from base to top (Table 5). The differences of the heterogeneity index were mainly due to site, trees, height levels and rings that accounted for 14%, 10%, 5% and 7% of the total variation respectively (Table 4).

Ring density correlations with ring width and latewood percentage were not statistically significant. Ring width was positively correlated with latewood percentage and negatively with earlywood density (Table 6).

Table 3. Mean values (± standard deviation) of the ring width and wood density compoments measured within the juvenile core sequence (rings 1 to 15) and the sheath sequence corresponding to an early mature period (31-40 rings) at bottom level. Mean of 10 trees per site and four stem height levels (RD - ring density, EWD - earlywood density, LWD - latewood density, HI - heterogeneity index, RW - ring width and LWP - latewood percentage).

Sequence	**Site**	**RD (g/cm^3)**	**EWD (g/cm^3)**	**LWD (g/cm^3)**	**HI (g/cm^3)**	**RW (mm)**	**LWP (%)**
Core (1-15 yrs)	MC	0.914 ± 0.114a	0.790 ± 0.148a	0.963 ± 0.103a	0.057 ± 0.039a	2.52 ± 1.27a	68.54 ± 14.11a
	VI	1.037 ± 0.117b	0.965 ± 0.144b	1.076 ± 0.108b	0.085 ± 0.042b	1.83 ± 0.92b	60.25 ± 15.80b
Sheath (31-40 yrs*)	MC	0.751 ± 0.136a	0.611 ± 0.161a	0.827 ± 0.126a	0.073 ± 0.053a	2.11 ± 1.09a	63.01 ± 13.59a
	VI	0.944 ± 0.132b	0.858 ± 0.160b	0.996 ± 0.129b	0.114 ± 0.055b	1.33 ± 0.82b	58.63 ± 15.62a

Different letters correspond to significant ($P<0.05$) differences between sites.

*At bottom level

Table 4. Variance analysis for each wood density components and ring width for the juvenile period (the first15 rings from the pith), showing their significance and the expected variation (EV) for each source of variation (RD - ring density, EWD - earlywood density, LWD - latewood density, HI - heterogeneity index, RW - ring width and LWP - latewood percentage).

Source of variation	**RD**		**EWD**		**LWD**		**HI**		**RW**		**LWP**	
	P	**EV**	**P**	**EV**	**P**	**EV**	**P**	**EV**	**P**	**EV**	**P**	**EV**
Sites (S)	0.0009	29.7	0.0002	34.5	0.001	30.8	0.0017	13.8	0.0005	13.6	0.0008	11.4
Trees/Sites (T/S)	0.0001	19.6	0.0001	16.1	0.0001	20.8	0.0001	10.2	0.0001	7.1	0.0001	6.4
Levels (L)	0.0001	4.7	0.0001	4.4	0.0001	2.9	0.0001	4.8	0.0001	3.1	0.0121	0.6
L x S	0.0156	4.2	0.0288	3.0	0.0093	4.8	0.1506	1.1	0.0015	6.2	0.2877	0.3
L x T/S	0.0001	13.5	0.0001	11.8	0.0001	13.4	0.0001	10.6	0.0001	9.2	0.0001	5.9
Rings (R)	0.0001	2.3	0.0001	4.2	0.0001	1.9	0.0001	7.4	0.0424	0.5	0.0001	4.2
R x S	0.0003	1.1	0.0001	1.6	0.0584	0.4	0.0001	3.4	0.0163	1.7	0.3907	0.1
R x T/S	0.1774	0.5	0.1518	0.6	0.1437	0.6	0.1683	1.1	0.0151	3.2	0.5134	0
R x L	0.0001	3.0	0.0001	2.2	0.0001	3.2	0.1648	0.5	0.0046	1.8	0.783	0
R x L x S	0.4006	0.1	0.3661	0.1	0.3865	0.1	0.0987	1.4	0.2017	1.0	0.735	0
Residual		21.2		21.4		21.0		45.7		52.7		71.1

Table 5. Mean values (± standard deviation) for the wood density components and ring width within the juvenile period (the first 15 rings) by each height level at both sites . (RD - ring density, EWD - earlywood density, LWD - latewood density, HI - heterogeneity index, RW - ring width and LWP - latewood percentage)

Heigth level	**RD (g/cm^3)**	**EWD (g/cm^3)**	**LWD (g/cm^3)**	**HI (g/cm^3)**	**RW (mm)**	**LWP (%)**
5.5 m	0.943 ± 0.102a	0.842 ± 0.134a	0.998 ± 0.097a	0.056 ± 0.034a	1.9 ± 1.4a	62.1 ± 16.8a
3.4 m	0.958 ± 0.124b	0.849 ± 0.165a	1.006 ± 0.116a	0.070 ± 0.040b	2.1 ± 1.1b	65.0 ± 14.7b
1.3 m	0.980 ± 0.144c	0.881 ± 0.187b	1.022 ± 0.130b	0.078 ± 0.046c	2.3 ± 1.0b	65.2 ± 14.6b
bottom	1.021 ± 0.137d	0.938 ± 0.177c	1.053 ± 0.125c	0.080 ± 0.047c	2.4 ± 1.0c	65.3 ± 15.6b

Different letters correspond to significant ($P<0.05$) differences between height levels.

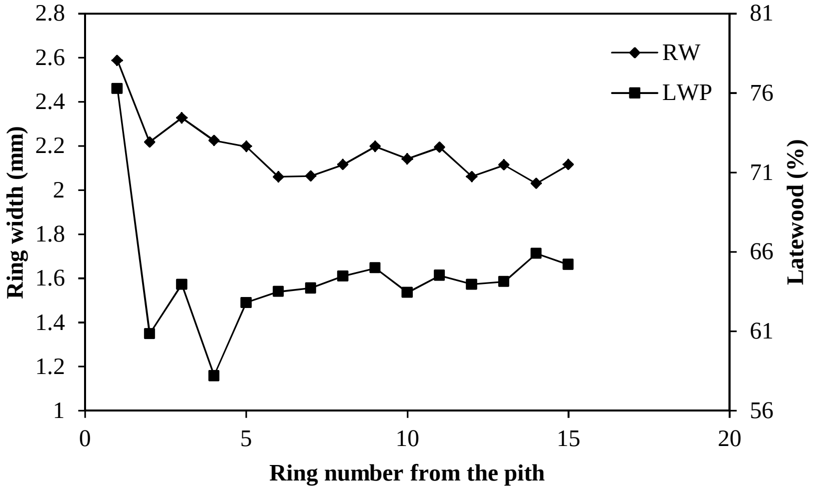

Figure 2. Ring width and latewood percentage variation within the first 15 rings from the pith at both sites. Mean of 20 trees.

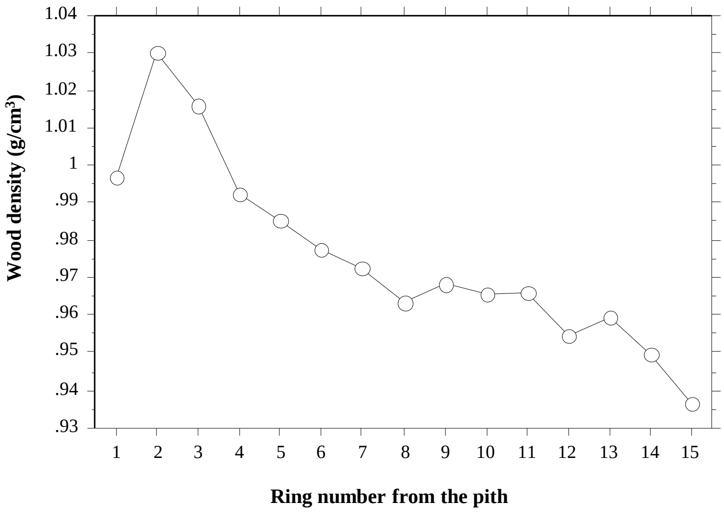

Figure 3. Wood density profile variation within the first 15 rings from the pith at both sites. Mean of 20 trees.

Table 6. Correlation matrix (Pearson bivariate) for ring width and density components within the juvenile wood period (the first 15 rings) (RD - ring density. EWD - earlywood density, LWD - latewood density, RW - ring width and LWP - latewood percentage) (n=1200).

	RD	EWD	LWD	RW	LWP
RD	1				
EWD	**0.904**	1			
LWD	**0.969**	**0.842**	1		
RW	-0.037	**-0.186**	-0.044	1	
LWP	-0.013	**-0.287**	**-0.072**	**0.371**	1

Values statistically significant (P<0.05) are in bold.

Variation of ring width and density components within early mature wood

The mean values for ring width and wood density components for the sheath sequence of rings of 31 to 40 years at the bottom level (corresponding to an early mature wood) at each site are summarized in Table 3. Table 7 summarizes the results for the analysis of variance.

The ring width was significantly different between sites i.e. 2.12 mm at MC and 1.33 mm at VI (Table 3). Within the stem there was a decrease of ring width from the bottom to the top at both sites (Table 8).

Wood density was significantly different between sites, as well as earlywood and latewood density (Table 3). The variability of the density components and growth was primarily due to the effects of site (18-50%), and trees (10-22%) being the wood produced at site VI denser (both in the earlywood and latewood), more heterogeneous and with the narrowest ring widths (Table 7). The only exception was observed for the latewood percentage, whose difference between sites was statistically not significant, and their effect only explained 2.8% of the total variation.

The effects associated with the variation within the tree (rings and levels) were often not significant and showed a very small contribution to the total variation, thus confirming a reduced axial and radial variation in this early mature phase of the trees (Table 7 and 8).

Ring density was positively correlated with all components. Ring width and latewood percentage were only negatively correlated with earlywood density (Table 9).

Table 7. Variance analysis for each wood density components and ring width within the 10-ring sheath sequence corresponding to an early mature wood period at tree bottom level (31th to the 40th rings), showing their significance and the expected variation (EV) for each source of variation (RD - ring density, EWD - earlywood density, LWD - latewood density, HI - heterogeneity index, RW - ring width and LWP - latewood percentage).

Source of variation	**RD**		**EWD**		**LWD**		**HI**		**RW**		**LWP**	
	P	**EV**	**P**	**EV**	**P**	**EV**	**P**	**EV**	**P**	**EV**	**P**	**EV**
Sites (S)	0.0001	47.3	0.0001	50.2	0.0002	43	0.0007	19.2	0.0071	18.3	0.0771	2.8
Trees/Sites (T/S)	0.0001	18.1	0.0001	12.6	0.0001	19.1	0.0001	10.8	0.0001	21.8	0.0001	9.5
Levels (L)	0.0001	0.8	0.0811	0.2	0.0003	0.7	0.5455	0	0.0001	2.1	0.0218	0.8
L x S	0.2802	0.3	0.9928	0.0	0.2457	0.5	0.6397	0	0.1601	1.3	0.0044	5.6
L x T/S	0.0001	8.6	0.0001	10.5	0.0001	8.8	0.0001	18.1	0.0001	14.5	0.0001	7.6
Rings (R)	0.6203	0	0.3888	0	0.5472	0	0.1672	0.3	0.0001	1.4	0.1324	0.5
R x S	0.0135	0.8	0.0154	0.8	0.0896	0.5	0.0996	0.9	0.0001	5.8	0.698	0
R x T/S	0.4395	0.1	0.7402	0	0.5044	0	0.1803	1.4	0.0001	14.1	0.258	4.6
R x L	0.1938	0.3	0.1897	0.3	0.2475	0.2	0.0812	1	0.1857	0.3	0.1763	0.9
R x L x S	0.8987	0	0.8497	0	0.6919	0	0.3643	0.4	0.7437	0.0	0.3626	0.5
Residual		23.6		25.4		27.1		48.0		20.4		67.3

Table 8. Mean values (± standard deviation) for the wood density components and ring width for the 10 rings included in the sheath sequence corresponding to an early mature period at tree bottom level (31th to the 40th rings) by each height level at both sites (RD - ring density, EWD - earlywood density, LWD - latewood density, HI - heterogeneity index, RW - ring width and LWP - latewood percentage).

Height level	**RD (g/cm^3)**	**EWD (g/cm^3)**	**LWD (g/cm^3)**	**HI (g/cm^3)**	**RW (mm)**	**LWP (%)**
5.5 m	0.823 ± 0.183a	0.716 ± 0.218a	0.890 ± 0.169a	0.090 ± 0.055a	1.5 ± 1.1a	59.6 ± 15.4a
3.4 m	0.846 ± 0.173b	0.736 ± 0.202ab	0.908 ± 0.166ab	0.093 ± 0.057a	1.7 ± 1.1b	60.0 ± 15.1a
1.3 m	0.851 ± 0.147bc	0.738 ± 0.188ab	0.917 ± 0.137bc	0.093 ± 0.059a	1.7 ± 1.0b	60.5 ± 14.1a
bottom	0.869 ± 0.159c	0.748 ± 0.207b	0.930 ± 0.141c	0.096 ± 0.061a	2.0 ± 0.9c	63.2 ± 13.9b

Different letters correspond to significant ($P<0.05$) differences between height levels.

Table 9. Correlation matrix (Pearson bivariate) for ring width and density components of sheath sequence (31th to the 40th rings at bottom level) (RD - ring density. EWD - earlywood density, LWD - latewood density, RW - ring width and LWP - latewood percentage) (n=800).

	RD	**EWD**	**LWD**	**RW**	**LWP**
RD	1				
EWD	**0.915**	1			
LWD	**0.962**	**0.824**	1		
RW	0.008	**-0.148**	0.022	1	
LWP	**0.09**	**-0.149**	0.033	**0.404**	1

Values statistically significant ($P<0.05$) are in bold.

Discussion

Ring width of *Quercus faginea* differed between sites either at a younger (beginning of wood formation) and older physiological phases: it was higher at site MC (Table 3), and site accounted for the main (or one of the main) effects of ring width variation (Tables 4 and 7).

Two types of considerations may be made to explain such growth differences: one type relates to climatic and edaphic conditions; the other relates to stand characteristics.

As regards climate and soil, both sites are within the natural area of occurrence of the species and *Q. faginea* is known as being well adapted to different soil conditions (Capelo and Catry 2007). The conditions would however favour a higher growth in VI since *Q. faginea* prefers deeper soils with higher water availability (Villar-Salvador et al. 1997) which would be more probable in the cambisols of site VI than in leptosoils (Table 1). Also the higher rainfall and the over-the-year higher temperatures in VI (Fig. 1) would also a priori call for a higher growth at this site.

However the opposite was found, with growth significantly higher in MC over VI (Table 3). Therefore the explanation should rely on the specific stand and silvicultural conditions. In both cases, the stands were unmanaged but the between-tree competition as well as the competition with other trees and shrubs was lower in MC (Table 1). This calls attention to the importance of forest management to increase wood radial growth as shown for *Q. petraea* and *Q. robur* (Guilley et al. 1999; Zhang et al. 1993).

The average ring density values of *Q. faginea* were higher in site VI compared to site MC by 12% and 20% within the core and sheath sequences, respectively. The site effects were considerable for the density components (30-50% of total variation), indicating that differences in wood density of *Q. faginea* may be found between different edaphic-climatic and stand conditions despite the between-tree variability that was also observed. The influence of site on wood density was also reported for *Q. petraea* (Bergès et al. 2008).

The present study confirms that part of the high residual effect for the variation of *Q. faginea* density that was found when studying separately each site (Knapič et al. 2011; data not shown) is in fact explained by the site effect. However contrasting results were referred by Guilley et al. (2004) who suggested that different geographical locations and site qualities do not explain radial density variations in *Q. petraea*. Between-site differences were not found also in *Acacia melanoxylon* (Tavares et al. 2013). This certainly calls attention to the importance of stand characteristics and forest management to wood development features.

Higher density values may be related with accumulation of heartwood extractives and tension wood (Zobel and van Buijtenen 1989). As tension and knot wood were avoided, the extractives content should be more important to explain density variations in *Q. faginea* wood between sites and between the juvenile and mature wood at each site. The accumulation of extractives depends mainly of heartwood formation (Pereira et al. 2003). In the studied trees, the extractives in heartwood represented 19.3% vs. 14.2% in the whole wood disk (Sousa et al. 2009), and the sapwood radial width was on average 47 mm at site MC and 26 mm at site VI within the four stem height levels (Sousa et al. 2013).

Therefore in site VI both the analyzed juvenile and early mature periods contained only heartwood due to the fact that the trees were on average 125 years old. On the contrary, in MC, the early mature wood was for the most part sapwood, while the juvenile core was formed mostly by heartwood. This explains the larger density differences between juvenile and mature wood at MC (Table 3). Lower density in sapwood in contrast to heartwood was also found for *Q. petraea* (Guilley and Nepveu 2003).

The wood density decreased only slightly with tree age (given by the height levels, Tables 5 and 8) and although highly significant tree age effects accounted for a minor portion of the expected total variance (0.2-5%). When considering sites separately it was seen that at site MC the levels explained about 14-17% of the total variance of the density components (Knapič et al. 2011) and at VI site its influence decreased to 5-8% when considering the first 100 rings (data not shown). The importance of heartwood vs. sapwood in the analyzed samples, as discussed above, is certainly an explanation for this difference. This calls attention to the care that should be given to comparisons between trees and stem cross-sections of different ages and to the influence that heartwood presence may have on wood characteristics. However even though there were differences in the upper levels due to the presence of juvenile wood (especially in MC) they did not account as much as it would be expected to wood density variability.

Latewood proportion was more affected by site in the earlier years (Table 3) as confirmed by statistical analysis: significant site differences in the juvenile wood and no significant differences in the mature wood. The environmental conditions should have more influence on latewood formation in the young *Q. faginea* plant development, and the cambisols and softer summers from site VI should contribute to a longer earlywood growth period, as it was the case.

Growth components i.e. ring width and latewood proportion were closely correlated (Tables 6 and 9), as also found in *Q. petraea* and *Q. robur* (Bergès et al. 2008; Polge and Keller 1973; Zhang et al. 1993). There were also close to very close correlations between density components in *Q. faginea*, as found in other *Quercus* spp. (Bergès et al. 2008; Ackermann 1995). Ring density was not correlated with ring width, as also found by Bergès et al. (2008) in 110 year aged *Q. petraea* trees at plot scale although a correlation was present at tree scale thereby suggesting scale dependence as a possible explanation.

The explanation for the variation of wood density, in addition to the accumulation of extractives in heartwood as discussed previously, should also be given by the anatomical structure of the wood, namely of the wood vessels (Zobel and van Buijtnen 1989) since vessel proportion in oaks is a key factor to determine wood density (Rao et al. 1997; Zhang and Zhong 1992; Leal et al. 2011).

Conclusions

In the juvenile and early mature stages of *Quercus faginea* trees site was the main source of variation of ring width. Stand characteristics, e.g. tree competition, may overrule the site specific edapho-climatic conditions in relation to radial growth, thereby stressing the importance of forest management for increased tree growth.

Site was also the main factor of variation of wood density and their components, with the effects being higher within mature wood than in juvenile wood. The results also confirmed the importance of heartwood presence to increase wood density. Relative wood uniformity was observed within the tree, and radial and axial variations were of small magnitude, thereby contributing to an overall favorable wood processing quality of *Q. faginea* trees.

Ring width and wood density showed only weak correlations, therefore allowing simultaneous selection for both traits.

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4.6. Earlywood vessel features in *Quercus faginea*: relation to ring width and wood density at two sites

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(Submetido)

Key words: *Quercus faginea*, earlywood vessels, wood density, ring width, variation

Abstract

The earlywood vessel distribution and its relation with radial growth and wood density were studied in *Quercus faginea* Lam. The anatomical earlywood vessel features (area, number, density and proportion) were investigated along the radius in 20 trees at two different locations in Portugal within the species natural distribution. Mean earlywood vessel area increased with cambial age for the first 60-70 years and then leveled off. An inverse pattern was found for vessel number beyond that age. Similar radial patterns of all vessel features were found at both sites and no significant differences were found in earlywood vessel area.

The within-tree development of earlywood vessels was age and but not growth related. Overall it was found that wood density of *Q. faginea* was strongly negatively correlated with mean vessel area and proportion. Earlywood vessel features showed a clear physiological pattern within this ring-porous species that explained its wood density variation.

Introduction

Vessels are considered to have great influence on wood characteristics such as texture and density, and their distribution within the annual ring (growth ring pattern) greatly affects the quality and utility of the final product (Zobel and van Buijtnen [1]). Measurement of vessel features such as area and diameter was very time consuming, but today's use of digital microscopy and image analysis software makes data acquisition and processing more expedite (Gasson [2]; Sass and Eckstein [3]; Fonti et al. [4]; Leal et al. [5]). Therefore the number of studies on vessel features variation e.g. with age, growth and site, as well as their relation to other wood characteristics e.g. density, has increased, although data is still scarce and results may be contradictory or species' specific.

Vessels should be key contributors to wood density since they have large lumina in comparison with the other wood cell types, and vessel size and number tend to be inversely proportional to density (Savidge [6]). In oaks, vessel proportion is the major anatomical factor to determine wood density (Rao et al. [7]; Zhang and Zhong [8]). For instance, in *Q. suber*, a semi-ring porous wood, vessel size and number were found to contribute significantly to wood density (Leal et al. [9]).

As regards the variation of vessels with age and tree growth, different results have been reported. In *Q. alba*, the percentage of earlywood vessel area was influenced by radial position, but not by ring width (Phelps and Workman [10]). Earlywood vessel area was larger in faster grown compared to slower grown Juglans nigra trees, but no correlation was found between earlywood vessel area and ring width (Phelps and Workman[10]). Denne et al. [11] verified that total vessel proportion decreased significantly with increase in ring width in Nothofagus nervosa, a diffuse porous hardwood species. In *Q. suber*, the vessel size which increased from pith outwards explained 32% of wood ring density variation (Leal et al.[5,9]). In *Q. rubra*, vessels percentage was also found to be significantly important and independent of soil types (Hamilton and Knauss [12]).

It is generally accepted that earlywood width is relatively constant in ring porous species and therefore it is the latewood width that is the responsible for wood ring density variation (Chauchan [13]). The vessel lumen area contributes to diminish the wood density, thereby leading to a lower earlywood density. However if earlywood width is related with vessel area, smaller vessels would result in higher ring density.

In *Quercus faginea* Lam., a ring porous oak, earlywood vessels are in average four times the size of latewood vessels, and vessels represent about 23% of the xylem tissue with an increasing radial trend towards the bark (Sousa et al. subm.). Recent studies showed that *Q. faginea* wood density components (ring density, earlywood density and latewood density) vary radially and are influenced by site conditions and tree growth (Knapič et al.[14]; Sousa et al.subm.). The first question that may be put forward is if the distribution of earlywood vessels within the ring is a function of cambial age and which is the variation magnitude of earlywood vessel features between trees and sites. A second question regards their relationship with growth and density components. To address these questions, earlywood vessel features (area, number and proportion) were analyzed in *Q. faginea* trees grown in two sites within the species natural area of distribution in Portugal, and analyzed in relation to ring width and wood density. The sampling included 10 trees with an average 40 years of age and 10 trees with on average 125 years of age.

Material and methods

The *Q. faginea* trees were selected in naturally regenerated unmanaged forests in Portugal, near Macedo de Cavaleiros (site 1) and Vimeiro (site 2). The climate is of Mediterranean type tempered by oceanic influence. The mean annual temperature is 12 and 15ºC, and the mean annual rainfall 700 and 890 mm at site 1 and 2 respectively. The soils are classified as orthic dystric and eutric leptosols at site 1 and chromic cambisols at site 2.

Ten dominant or co-dominant trees and free of visible signs of decay were harvested at each site. The trees were on average 40 and 125 years in age at the time of sampling in site 1 and 2, respectively. A disc was taken at 1.3 m above ground level and the wood analyzed individually for each tree within a radial strip from pith to bark.

The wood density was determined by X-ray microdensitometry following the methods described by Louzada [15] on a 5 mm wide wood strip cut from pith to bark. For each ring, mean ring density, earlywood density, latewood density, heterogeneity index, latewood percentage and ring width were determined at every 100 μm of the radial length by 455 μm wide. The results on wood density variation have already been reported (Knapič et al.[14]; Sousa et al. subm.).

The transverse surface of the wood strips used for X-ray measurements were smoothed by fine sanding until pores (vessels) were clearly visible under a light power microscope. White wax was applied on the surface to fill the vessels and allow a better distinction from the surrounding tissues. Sequential images were acquired along the radial direction from the pith to the periphery, and converted to grey pixels following the methodology proposed by Leal et al.[5]. A light microscope with 8x optical magnification (1 pixel = 0.00704 mm) was coupled to a digital camera and image analysis software (Leica Q Win Plus) to capture images and perform measurements of earlywood vessel area and number of earlywood vessels. The minimum size of earlywood vessel measured was 0.001 mm^2.

The vessel proportion (total vessel area per ring width unit area, in %), the average vessel area, and the vessel density (number of vessels per mm^2) were determined for each annual ring. The measurements were made within a frame window of ca. 2.3 mm of tangential width and radial dimension varied with each earlywood width, from the inner to the outermost ring. A total of 13379 vessels were measured. For vessel density and vessel proportion determinations the total window measurement frame area excluding rays was used.

Statistical and correlation analysis were performed at 0.05 confidence level using SPSS (v. 19.0) procedures to analyze the cambial age (i.e. ring), tree and site effects on earlywood vessel features (mean area, number, density and proportion). Correlations with ring width and ring density components were determined and regression curves estimated.

Table 1. Mean values of earlywood vessel area (MVA), number of vessels (NV), vessels density (VD) and vessels proportion (VP) by tree at site 1 (mean of 30 rings) and site 2 (mean of 100 rings). Coefficient of variation in brackets.

Site	**Tree**	**MVA (mm^2)**		**NV**		**VD (nr/mm^2)**		**VP %**	
1	1	0.013	(89)	19.0	(84)	4.6	(47)	1.1	(273)
	2	0.017	(67)	16.0	(75)	3.2	(44)	5.4	(42)
	3	0.021	(68)	8.0	(63)	2.0	(64)	3.8	(58)
	4	0.020	(80)	12.0	(75)	2.9	(52)	5.9	(52)
	5	0.019	(83)	16.0	(69)	3.5	(41)	6.7	(53)
	6	0.031	(66)	7.0	(57)	2.4	(40)	8.0	(59)
	7	0.034	(57)	7.0	(57)	2.3	(36)	7.6	(58)
	8	0.027	(65)	7.0	(57)	3.2	(56)	8.0	(47)
	9	0.026	(61)	8.0	(63)	2.9	(49)	7.7	(52)
	10	0.014	(67)	12.0	(75)	3.6	(34)	5.5	(52)
	Mean	0.020	(78)	18.0	(59)	3.1	(52)	6.0	(67)
2	1	0.029	(57)	8.1	(36)	8.0	(42)	11.4	(64)
	2	0.018	(60)	7.1	(65)	3.4	(46)	6.6	(53)
	3	0.029	(65)	8.9	(31)	3.3	(57)	9.4	(60)
	4	0.028	(73)	8.7	(52)	4.0	(63)	12.1	(67)
	5	0.018	(73)	8.1	(41)	4.6	(124)	6.3	(67)
	6	0.030	(61)	10.1	(46)	4.3	(60)	14.2	(69)
	7	0.027	(56)	6.9	(28)	3.6	(47)	10.1	(57)
	8	0.028	(54)	6.2	(39)	2.1	(79)	5.3	(63)
	9	0.024	(52)	6.8	(43)	3.0	(59)	7.5	(56)
	10	0.028	(55)	9.9	(33)	5.5	(52)	15.9	(60)
	Mean	0.026	(78)	8.1	(45)	4.2	(77)	9.9	(74)

Results

General earlywood vessel anatomy

Quercus faginea is a ring porous wood. Vessels are solitary, round to oval, and arranged in radial strips that widen towards the end of the annual growth ring (Fig. 1). The earlywood vessels were relatively aligned in tangential lines. This was more evident when only one line of earlywood vessels was present. However the number of earlywood vessels tangential lines varied usually from 1 up to 3.

The wood showed conspicuously large vessels together with smaller sized vessels. The narrow earlywood vessels were mixed with wider earlywood vessels with apparently no specific order. The structure of the inner growth rings was quite different from the mature and outermost rings: at younger cambial ages the vessels size decreased gradually thorough the growth ring resembling to a semi-ring-porous pattern, while at later years (above ca. 30 years) the ring porosity became evident. In very narrow growth rings e.g. at the outermost rings of the older trees (125 years) the ring porous pattern was less evident.

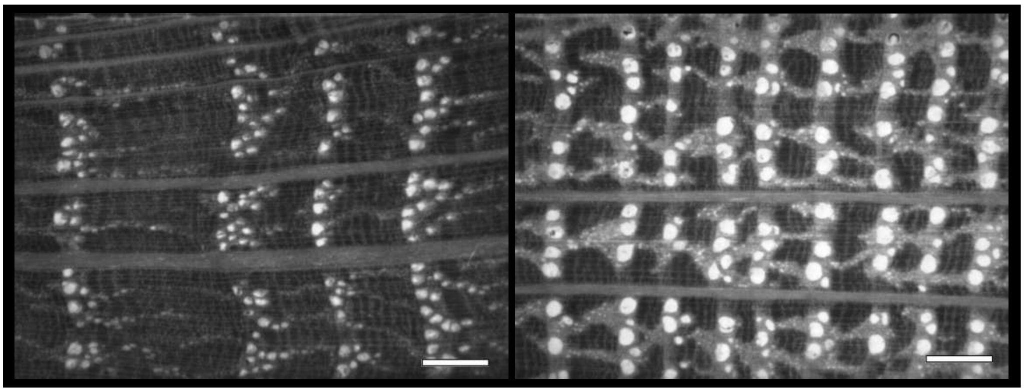


Figure 1. Macroscopic view of transverse sections of the *Quercus faginea* wood. The a) inner and b) outer growth ring structure showing vessels highlighted with white wax. Bar = 1mm.

Variation of earlywood vessels

The distribution of earlywood vessel area is skewed to the left at both sites, even though more pronounced at site 1 (Fig. 2). When analyzing earlywood vessel frequency by age intervals, it is observed that vessels with ca. 0.020 mm^2 or less are much more frequent in the initial years while above 60 years the distribution is no longer skewed.

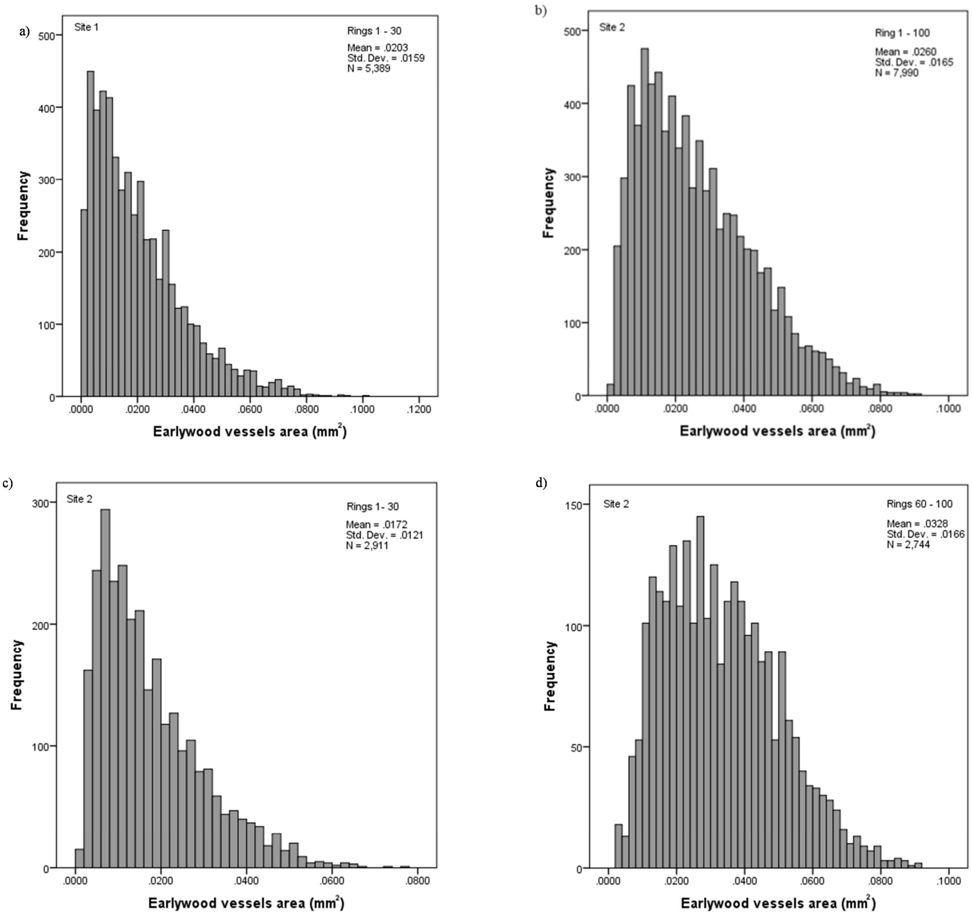


Figure 2. Frequency distribution of all measured earlywood vessel areas at a) site 1 and b) site 2 and from ring c) 1 to 30 and from d) 60 to 100 at site 2.

The radial variation of earlywood vessel area is characterized by a high increase in the initial years up to the 60/70th rings with a slowdown and slight decrease onwards (Fig. 3) e.g. at site 2 the maximum earlywood vessel area was 0.0384 mm^2 and decreased to 0.0318 mm^2 (ca. of 200 µm of tangential diameter) near the bark. The increment of earlywood vessel area was higher at site 1 compared to site 2 for the same cambial age period.

Table 1 shows the data for vessel features by tree at each site. The overall mean of earlywood vessel area was 0.020 ± 0.016 mm^2 at site 1 and 0.026 ± 0.017 mm^2 at site 2. The maximum individual earlywood vessel area was 0.1000 mm^2 and 0.091 mm^2 at site 1 and 2, respectively (data not shown).

Regression analysis indicated that a second degree polynomial model best predicted the mean earlywood vessel area (MVA) as a function of cambial age (CA) (Fig. 3):

$\mathrm{MVA} = -2\mathrm{E}\text{-}05\ \mathrm{CA}^2 + 0.0014\ \mathrm{CA} + 0.0057$ ($R^2 = 0.97$, $p<0.001$ – site 1);

$\mathrm{MVA} = -5\mathrm{E}\text{-}0.6\ \mathrm{CA}^2 + 0.0007\ \mathrm{CA} + 0.0062$ ($R^2=0.93$, $p<0.001$ – site 2).

Considering the common period between the two sites i.e. the first 30 rings, a combined regression analysis was made showing that:

$$MVA = -1E\text{-}05\ CA^2 + 0.0011\ CA + 0.0064\ (R^2 = 0.98, p<0.001)$$

The average earlywood vessel number decreased at both sites from pith to bark, although more pronounced at site 1 (Fig. 3). Average vessel number varied from 7 to 19 and 6 to 10 between trees at site 1 and 2, respectively (Table 1). For predicting vessels number based on cambial age, both second degree polynomial and linear regression proved to fit well (R^2= 0.72, p < 0.001 at site 1 and R^2= 0.60, p < 0.001 at site 2).

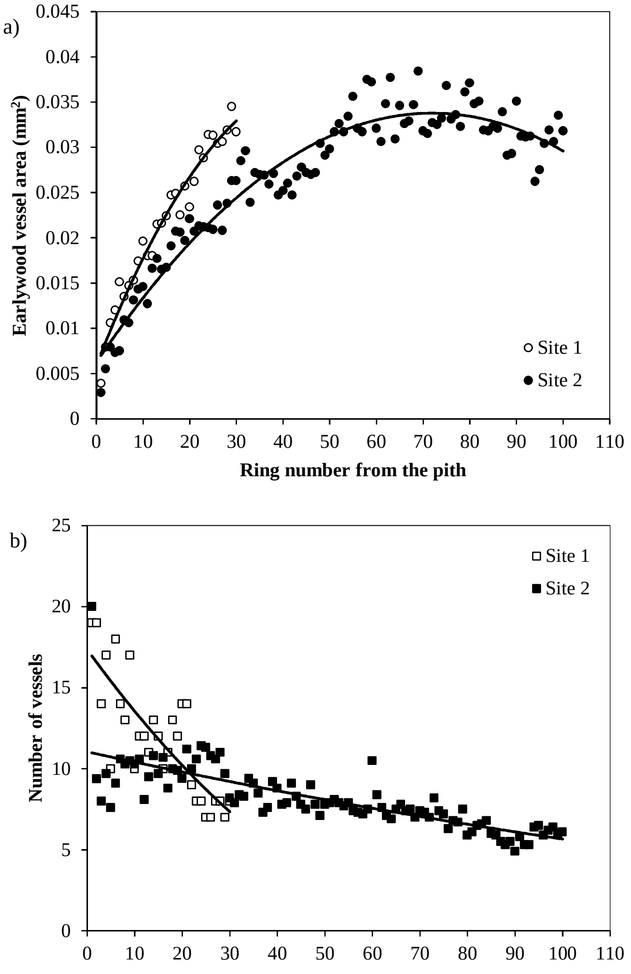
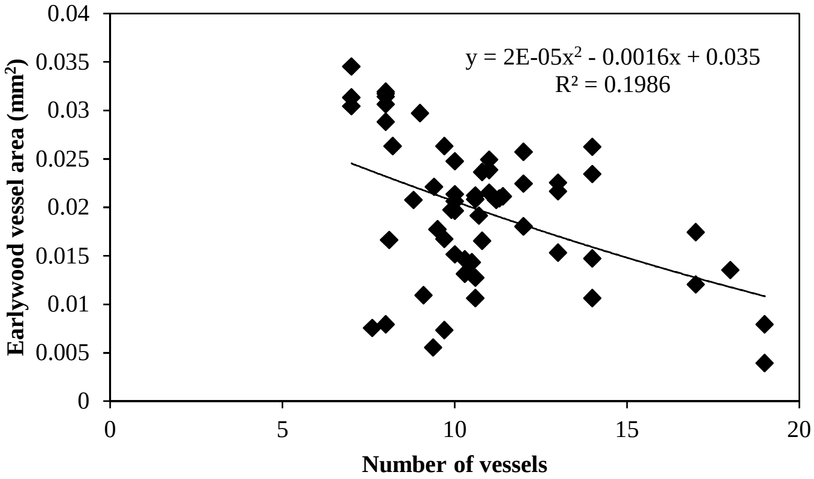
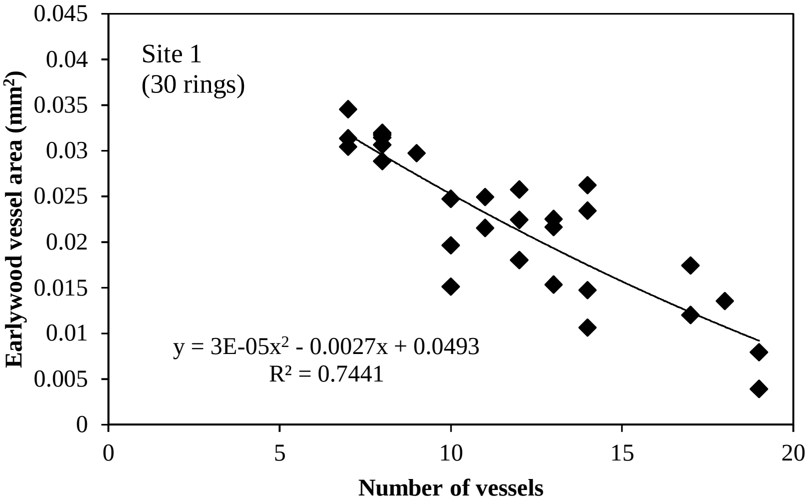


Figure 3. Radial variation of a) mean earlywood vessel area and b) number of vessels per growth ring in *Quercus faginea* wood in two sites. Mean of 10 trees at each site.

The relation between the number of vessels and the mean earlywood vessel area per ring fitted well both linear and second degree polynomial curves (R^2 = 0.74, p < 0.001) at site 1 but when analyzing both sites and site 2 separately a lower correlation coefficient was found (Fig. 4), although statistically highly significant ($p < 0.001$). In fact, medium to strong negative correlations were found between the number of vessels and mean earlywood vessel area (r=-0.162 at both sites; r=-0.461 at site 1; r=-0.216 at site 2) (Table 2, 3 and 4).





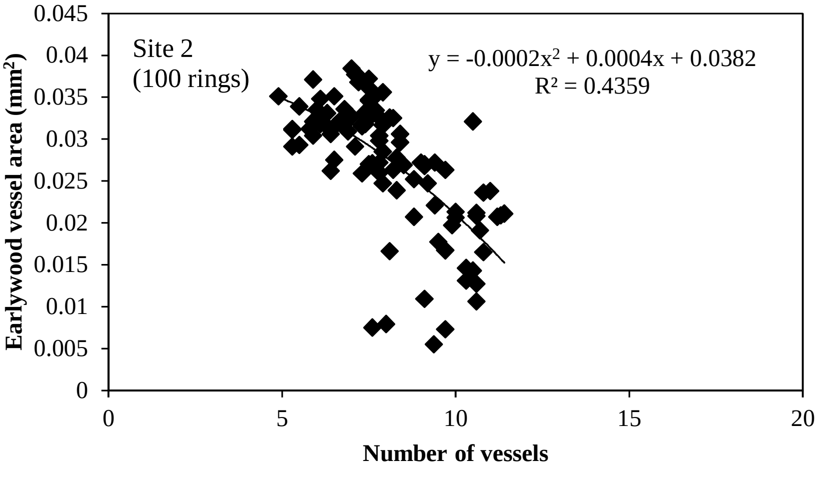


Figure 4. Relationship between the number of earlywood vessels and the mean earlywood vessel area at both sites. Mean of 10 trees.

Table 2. Correlation coefficients between vessel variables, wood density and ring width within the first 30 rings at site 1. NV = number of vessels, MVA = Mean vessels area, VD = vessels density per ring, VP = vessels proportion per ring, MD = mean wood density, EWD = earlywood density, LWD = latewood density, LWP = latewood percentage, RW = ring width. Significant correlations at the 0.01 level (2-tailed) are in bold. Mean values by tree and ring (n=300).

	NV	**MVA**	**VD**	**VP**	**MD**	**EWD**	**LWD**	**LWP**	**RW**
NV	1	**-0.461**	**0.357**	**-0.233**	**0.157**	0.071	**0.16**	0.119	**0.486**
MVA		1	**-0.21**	**0.627**	**-0.419**	**-0.395**	**-0.36**	**-0.229**	**-0.225**
VD			1	**0.315**	-0.064	0.053	-0.03	**-0.322**	**-0.411**
VP				1	**-0.455**	**-0.399**	**-0.39**	**-0.304**	**-0.477**
MD					1	**0.858**	**0.975**	**0.251**	**0.194**
EWD						1	**0.791**	-0.1	0.04
LWD							1	**0.178**	**0.166**
LWP								1	**0.377**
RW									1

Table 3. Correlation coefficients between vessel variables, wood density and ring width within the first 100 rings common to all trees at site 2. NV = number of vessels, MVA = Mean vessels area, VD = vessels density per ring, VP = vessels proportion per ring, MD = mean wood density, EWD = earlywood density, LWD = latewood density, LWP = latewood proportion, RW = ring width. Significant correlations at the 0.01 level (2-tailed) are in bold. Mean values by tree and ring (n=898), rings without vessels were excluded).

	NV	MVA	VD	VP	MD	EWD	LWD	LWP	RW
NV	1	**-0.216**	**0.154**	-0.023	**0.204**	**0.123**	**0.244**	0.071	**0.462**
MVA		1	**-0.086**	**0.489**	**-0.322**	**-0.337**	**-0.287**	0.004	**-0.174**
VD			1	**0.579**	**-0.211**	**-0.135**	**-0.229**	**-0.172**	**-0.391**
VP				1	**-0.374**	**-0.254**	**-0.383**	**-0.265**	**-0.557**
MD					1	**0.909**	**0.975**	**0.217**	**0.385**
EWD						1	**0.841**	-0.022	**0.19**
LWD							1	**0.179**	**0.424**
LWP								1	**0.352**
RW									1

Table 4. Correlation coefficients between vessel variables, wood density and ring width within the common years period (the first 30 rings) at both sites. NV = number of vessels, MVA = mean vessel area, VD = vessel density per ring width, VP = vessel proportion per ring width, MD = mean wood density, EWD = earlywood density, LWD= latewood density, LWP = latewood proportion, RW = ring width. Significant correlations at the 0.01 level (2-tailed) are in bold. Mean values by tree and ring (n=589), rings without vessels were excluded).

	NV	**MVA**	**VD**	**VP**	**MD**	**EWD**	**LWD**	**LWP**	**RW**
NV	1	**-0.162**	0.075	-0.07	**-0.166**	**-0.228**	**-0.147**	**0.164**	**0.541**
MVA		1	**-0.16**	**0.519**	**-0.449**	**-0.449**	**-0.401**	-0.013	-0.003
VD			1	**0.462**	-0.063	0.008	-0.084	**-0.15**	**-0.331**
VP				1	**-0.367**	**-0.277**	**-0.352**	**-0.228**	**-0.425**
MD					1	**0.895**	**0.978**	0.044	-0.074
EWD						1	**0.842**	**-0.242**	**-0.221**
LWD							1	0.003	-0.061
LWP								1	**0.377**
RW									1

The tendency of vessel density (number of vessels per mm^2 per growth ring) variation from pith to bark was relatively constant at both sites, with on average 3.1 ± 0.7 vessels/mm^2 and 4.1 ± 1.2 vessels/mm^2 at site 1 and 2, respectively (Table 1). A specific age pattern was not observed although some year to year fluctuations occurred (Fig. 5).

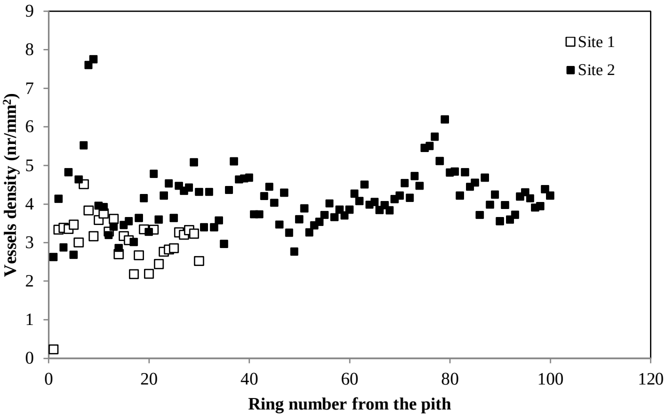


Figure 5. Radial profile of earlywood vessel density per growth ring in *Quercus faginea* wood. Mean of 10 trees at each site.

Between-tree variability ranged between 2.0 ± 1.3 and 4.6 ± 2.2 vessels/mm^2 at site 1 and 2.1 ± 1.6 and 8.0 ± 3.4 vessels/mm^2 at site 2 (Table 1). Earlywood vessel proportion (percentage of cross sectional area occupied by the earlywood vessels per growth ring) showed an increase with age from the pith up to the 70th ring with a maximum of 18.4 ± 14.0 % and then a slight decrease to the bark (Fig. 6). This radial pattern was similar to that of MVA (Fig. 3). On average the proportion of vessels varied from 1.1 to 8.0 % between trees at site 1 and 5.3 and 15.9 % at site 2 (Table 1).

An ANOVA analysis showed that differences in earlywood vessel area between sites were not statistically significant while Trees and Rings were highly significant ($p < 0.001$) factors of variation accounting for 15 and 18% of the total variation, respectively.

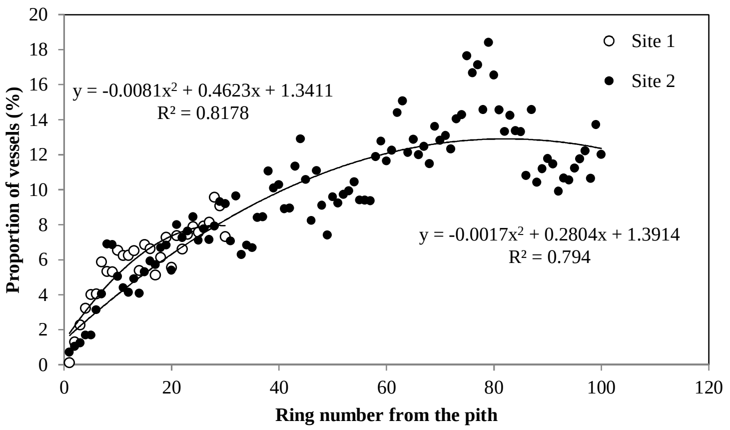


Figure 6. Radial profile of proportion of earlywood vessels per growth ring in *Quercus faginea* wood. Mean of 10 trees at each site.

Variation of earlywood vessel features with ring width

The proportion of vessels was related with the ring width i.e. highest proportion was found in the narrowest rings and vice versa. Strong correlations were found between ring width and the number of vessels per ring ($0.462 < r < 0.541$), vessel density ($-0.331 < r < -0.411$) and vessel proportion ($-0.425 < r < -0.557$) (Table 2, 3 and 4).

The best-fitted models between the earlywood vessel features and ring width are presented in Figure 7. Regardless of site, the wider rings showed higher latewood percentage and number of vessels and less mean vessel area, vessel density and proportion.

Influence of earlywood vessel features on wood density

Considering the common period of 30 rings in the trees of the two sites, the mean wood density and the earlywood density were inversely correlated with the mean earlywood vessel area ($r=-0.449$), as well as the mean wood density with the vessel proportion per ring ($r=-0.367$). The number of vessels was negatively correlated with wood density ($r=-0.166$) and earlywood density ($r=-0.228$) but the correlation of vessel density was not significant (Table 4).

Overall, the wood density components (mean density, earlywood and latewood density) were inversely correlated with mean vessel area ($-0.287 < r < -0.449$) and vessel proportion ($-0.254 < r < -0.455$) (Table 2, 3 and 4). The correlations between the wood density components and either the number of vessels and vessel density were positive and weak within each site separately.

Figure 8 shows the trend adjustment curves between the wood density and earlywood vessel features.

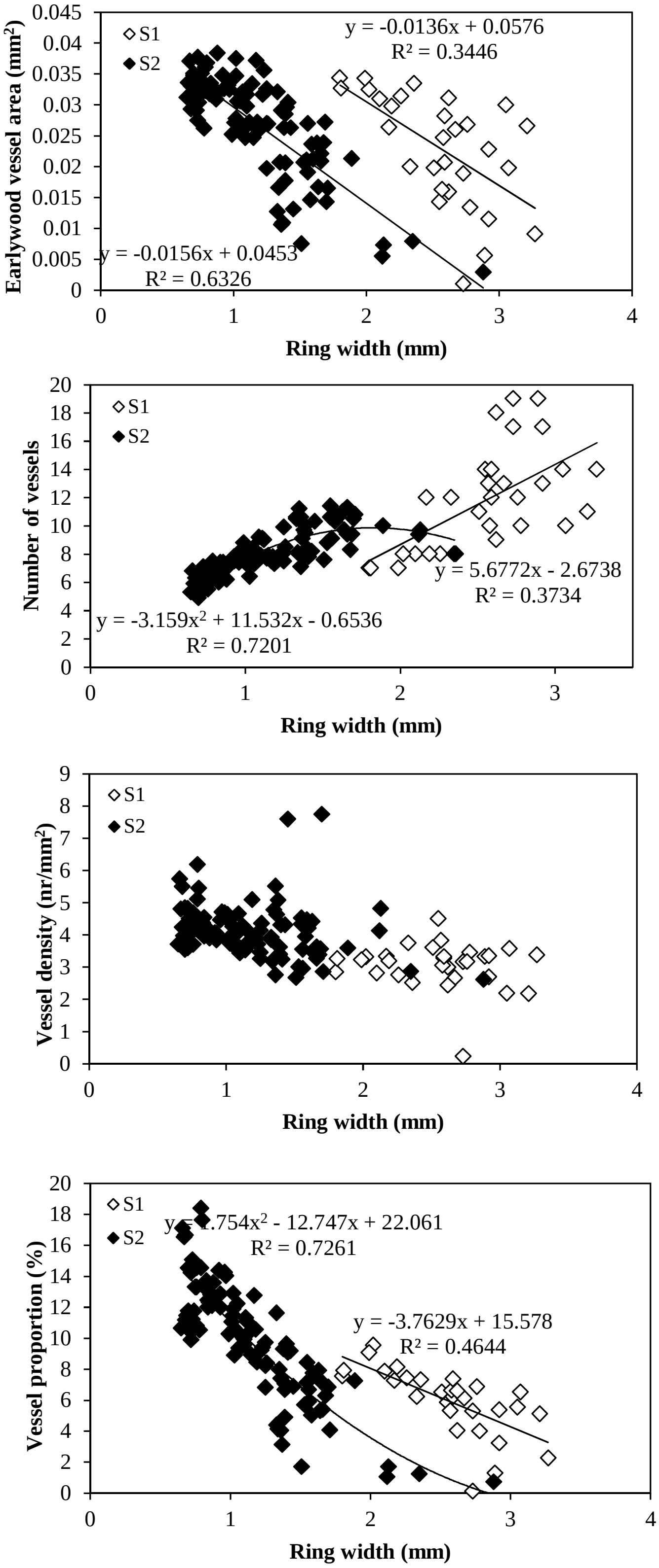


Figure 7. Relationships between ring width and earlywood vessel features at site 1 (S1) and 2 (S2). Mean of 10 trees by each site.

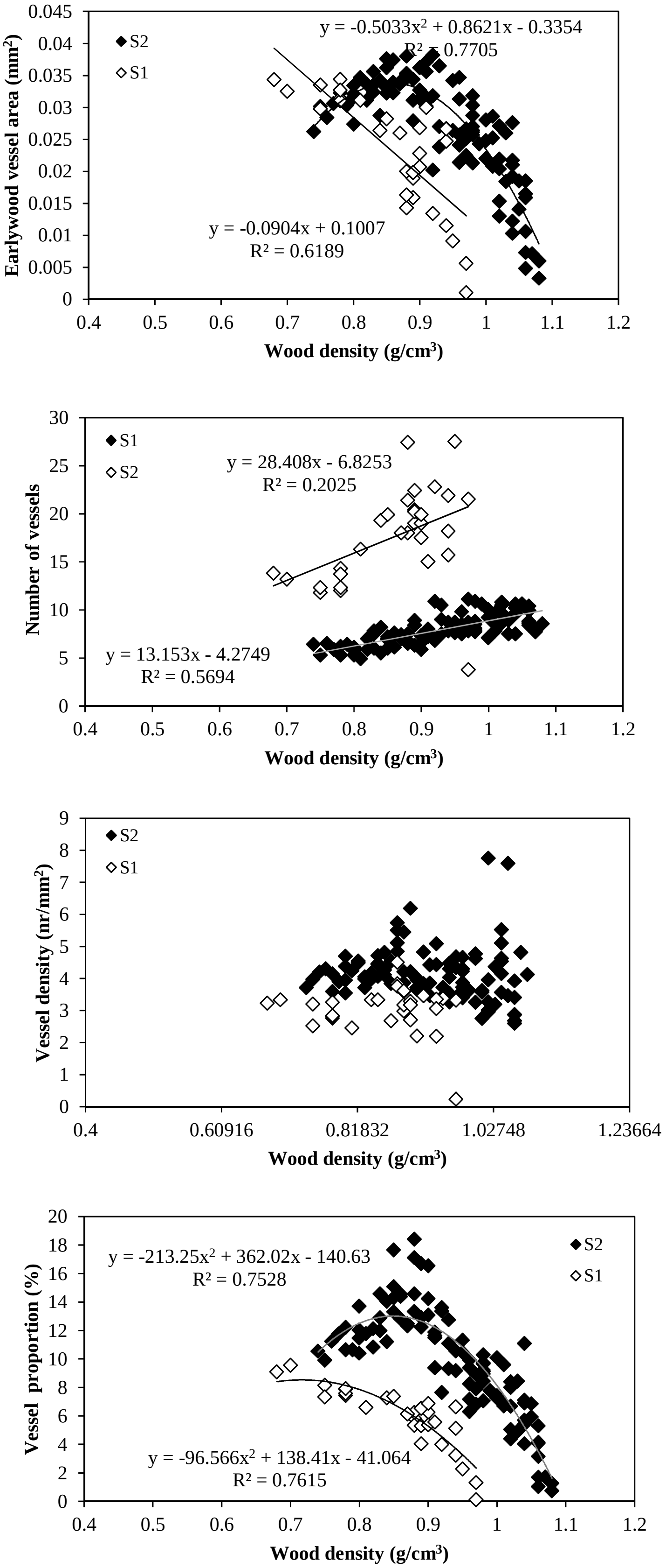


Figure 8. Relationships between wood density and earlywood vessel features at site 1 (S1) and 2 (S2). Mean of 10 trees by each site.

Discussion

The growth ring pattern of *Q. faginea* in mature wood was ring porous. The different porosity patterns found in inner and outer rings (Fig. 1) are consequence of the tree ageing process and environmental conditions (e.g. stand density). Overall vessel distribution was similar to Corcuera et al. [16]and Alla and Camarero [17] findings. This pattern was also found in other *Quercus* spp as *Q. robur* and *Q. ilex* (García-González and Eckstein [18]; Campelo et al. [19], Corcuera et al. [20]). It seems that vessel distribution is age related and that the small vessel size in the initial years is largely responsible for this type of frequency distribution.

The mean area of earlywood vessels was comparable to the range referred by Alla and Camarero [17] from 0.020 to 0.034 mm^2, although for the same tree's life period, smaller sizes (0.019 mm^2 and 0.015 mm^2 at site 1 and 2, respectively) were found in the studied trees. Such differences can be explained by climatic conditions e.g. the less precipitation in the summer period since mean annual precipitation did not show any significant relationship with wood anatomy (Villar-Salvador et al. [21]) and was within the range of the species adaptability (Ayanz [22]).This agrees with the hypothesis that the size of vessels of deciduous trees reflects the availability of water during their formation (e.g. Woodcock [23]; Sass and Eckstein [24]).

The size of *Q. faginea* vessels was larger compared to other evergreen species such as *Q. coccifera* and *Q. ilex,* and similar to *Q.suber* (Villar-Salvador et al.[21]; Campelo et al. [19]; Leal et al.[5]). In contrast *Q. robur* and *Q. petraea* showed higher vessel area (García-González and Eckstein[18]; Savill[25]).

The increase of earlywood vessel area with cambial age in *Q. faginea* (Fig. 3) was also found in other oaks such as *Q. suber* (Leal et al.[5]), *Q. garrayana* (Lei et al.[26]), *Q. macrocarpa* (George et al.[27]) and *Q. serrata* (Tsuchiya and Furukawa[28]) or in other species, for example, *Nothofagus nervosa* (Denne et al.[11]). The larger initial increase of earlywood vessel area is associated with the juvenile wood and, for example, the stabilization period was similar to that found in *Q. macrocarpa* (George et al.[27]). This corroborates that the age trend of vessel area is related with the porosity pattern.

The vessel number and vessel density are inversely related to average vessel area across species (Preston et al.[29]; Pourtahmasi et al. [30]). This was also the case in this study in *Q. faginea* (Fig. 5) which is in agreement with previous findings (Alla and Camarero[17]).

The radial profile of the proportion of earlywood vessels of *Q. faginea* (Fig. 6) was similar to *Q. alba* although the values were smaller in *Q. faginea* (Phelps and Workman[10]). This is related to differences in earlywood vessel diameter (Richter and Dallwitz[31]; Sousa et al. [32]) and the growth ring width decrease radial tendency (Paul[33]; Knapič et al.[14]; Sousa et al.[34]). These results are also comparable with those found for *Q. suber* (Leal et al.[5]).

There were weak negative correlations between ring width and mean earlywood vessel area (Fig. 7) that may be related with the occurrence of small vessels throughout the growth ring in *Q. faginea*. The ring width narrowing with age corresponded to a more constant earlywood vessel area and vessel number, and increasing vessel density and proportion in comparison to what occurred in the early years. In *Fagus orientalis* (semi-ring porous) and *N. nervosa* (diffuse porous) the ring width was found to be positively correlated with mean vessel area, in contrast to what was found in *Q. faginea*, but similarly negatively correlated with proportion of vessel and vessel density (Denne et al. [11], Pourtahmasi et al.[30]).

The relation between the mean wood density of *Q. faginea* with mean earlywood vessel area (Fig. 8) was expected to be considerable as well as with the proportion of vessels since they affect the void volume of the wood. The results found in this study were consistent with this reasoning. It was previously observed in several angiosperms that the average vessel area largely contributed to wood density variation but the proportion of vessels could explain it even better (Preston et al.[29]; Rao et al. [7] ; Zhang and Zhong[8]). In *Q. faginea* strong negative correlations were found between wood density and the mean earlywood vessel area and vessel proportion. On the contrary, the earlywood vessel density of *Q. faginea* showed only weak correlations with wood density. Similar results were obtained for *Q. suber* (Leal et al.[9]).

The results obtained show that vessel features in part explain the positive correlations between ring width and wood density that were reported (Knapič et al.[14]). Overall the pattern of vessels in the wood of *Q. faginea* make it suitable for applications where vessels are required, as for veneer products and barrels, notwithstanding the need for industrial process specific adjustments due to the high wood density pattern.

Conclusions

In *Quercus faginea*, mean earlywood vessel area and vessel number showed respectively an increasing and decreasing age trend. The radial patterns of the earlywood vessel features were relatively similar between sites and no significant differences were found for earlywood vessel area.

The evidence found here for the *Q. faginea* showed that earlywood vessel development within the tree is age related and also to a smaller extent by growth i.e. ring width. The mean vessel area and proportion explain variations in wood density of *Q. faginea* by strong negative correlations.

Acknowledgments

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Capítulo 5

Conclusões e perspectivas

O presente trabalho permitiu estudar em detalhe o crescimento da madeira de *Q. faginea* através da análise dos anéis de crescimento, do desenvolvimento do cerne e borne, das características anatómicas e da sua densidade. Com o estudo da variabilidade foram estabelecidos padrões de tendência em função da idade da árvore e do câmbio, assim como identificadas as fontes de maior variação, dentro da árvore, entre árvores e entre locais, nas diferentes variáveis estruturais e de qualidade que foram analisadas.

O estudo da variação da largura do anel de crescimento na madeira de *Q. faginea* mostrou que existe uma tendência de decréscimo da medula para a casca e axialmente da base para o topo, correspondendo ao padrão comum nas quercíneas, embora a informação bibliográfica seja muito escassa em termos da variação axial. Em média, a largura do anel, a 1,3 m de altura na árvore, foi de 2,4 mm e 1,3 mm, no local 1 (Macedo de Cavaleiros) e no local 2 (Vimeiro), respectivamente. As diferenças entre locais estarão relacionadas com os factores genéticos mas também com as condições do povoamento e ambientais, pois ambos os povoamentos são de regeneração natural, sem histórico de operações florestais. Estes valores são comparáveis a outras *Quercus* spp nomeadamente aos carvalhos vulgarmente denominados de europeus (*Q. petraea* e *Q. robur*).

O carvalho português apresentou um desenvolvimento substancial do cerne, que a 1,3 m de altura com uma proporção média de 37% e 73% no local 1 (árvores com média de 40 anos) e no local 2 (árvores com média de 125 anos), respectivamente. Verificou-se um decréscimo relativo da base para o topo de acordo com o perfil do tronco, viabilizando a obtenção de estimativas da proporção de cerne em função do diâmetro da árvore. A espessura de borne manteve-se relativamente constante ao longo do tronco, mas significativamente diferente entre locais.

A madeira de *Q. faginea* apresenta porosidade em anel, raios largos, uma elevada proporção de fibras e uma presença significativa de traqueídos vasicêntricos. Em geral, os anéis de crescimento são bem distintos entre si, embora nas árvores, com idade média de 125 anos, se tenha verificado, sobretudo na zona próxima da casca, um estreitamento tal que dificultou, por vezes, a sua identificação. Este facto está relacionado com os processos fisiológicos de envelhecimento da árvore e características do povoamento e sua condução, como a densidade e área basal.

As dimensões das fibras (comprimento, largura e espessura da parede) e dos raios multisseriados (largura e altura) aumentaram da medula para a casca. Em geral, a árvore e a idade do câmbio contribuíram pouco para a variação total das dimensões das fibras e dos raios multisseriados, garantindo uma relativa homogeneidade estrutural no tronco. Embora se tenham verificado diferenças significativas na árvore e entre árvores, a sua contribuição para a variação total foi de 2-4% e 8-27%, respectivamente.

A casca da *Q. faginea* é semelhante à de outras espécies do género *Quercus*. O ritidoma inclui várias peridermes e nódulos de esclereídos e raios esclerificados do floema secundário. A periderme não produz a quantidade de células de felema como se verifica na *Q. suber*. A disposição dos tecidos no floema e o tipo de cristais são semelhantes a outras quercíneas. Em geral, a espessura da casca diminuiu da base para o topo assim como o comprimento das fibras e elementos de tubo crivosos.

O estudo da densidade da madeira, nas árvores com idade média de 125 anos, mostrou que a madeira apresenta densidade elevada (0,862 g/cm^3) e que a idade do câmbio é importante para determinar as componentes da largura do anel e densidade da madeira. Os valores de densidade estabilizaram por volta do 60º ao 70º anel relacionada com a falta de condução do povoamento e o número de árvores por hectare. Os valores obtidos para estas árvores foram comparáveis com os valores observados nas árvores com idade média de 40 anos. Esta avaliação do comportamento da densidade, em relação ao factor idade, foi essencial para o estudo da sua variação. No estudo simultâneo dos dois locais este factor revelou-se o mais significativo para a explicação da variação total da largura do anel e das componentes da densidade da madeira. A formação de cerne explica parte da variabilidade e contribuiu para os efeitos residuais. Embora se trate de uma espécie com porosidade em anel, o índice de heterogeneidade obtido foi relativamente baixo.

Os dados biométricos dos vasos do lenho inicial revelaram-se importantes para definir os padrões de crescimento na *Q. faginea* e variabilidade da densidade da madeira. A área média e a proporção de vasos apresentaram fortes correlações positivas com as componentes da densidade. A largura do anel e a proporção do lenho final apresentaram também correlações positivas. A área média dos vasos não foi estatisticamente significativa entre os dois locais. Os efeitos da formação de cerne, das direcções e da constituição genética, entre outros factores, terão contribuído para o efeito residual total encontrado nas diferentes análises efectuadas.

Os resultados obtidos constituem informação importante, quer a nível nacional quer internacional, para a caracterização tecnológica desta madeira com vista à sua produção e utilização, no sentido de dinamizar a floresta portuguesa de espécies autóctones, contribuindo para a sua preservação e valorização.

Embora o número de locais tenha sido limitado, concluiu-se que o local contribuiu mais para a variação das propriedades da madeira do que a idade árvore e do câmbio de *Q. faginea*, verificando-se uma relativa homogeneidade dentro do anel de crescimento e no tronco. A exploração dos povoamentos actuais de carvalho português com diferentes idades é, portanto, possível permitindo obter madeira com boas características tecnológicas. A condução dos povoamentos, no futuro, poderá englobar rotações mais curtas ou mais longas, com retirada parcial de árvores para obtenção de madeira, essencialmente, para pequenas peças. Em geral, o desenvolvimento do cerne, as características anatómicas e da densidade da madeira de *Q. faginea* confirmaram o seu potencial em termos de adequação e qualidade de produtos sólidos de maior valor comparáveis a outros carvalhos comerciais.

No futuro pretende-se incluir a informação climática de uma forma mais detalhada atendendo às características do clima mediterrânico, verificando qual a influência da precipitação e da temperatura no crescimento, nas características anatómicas e da densidade da madeira de *Q. faginea*. Prevê-se a realização de um estudo sobre modelos de densidade e sua validação, com base nos dados recolhidos, de modo a perceber a influência climática na variação nas componentes da largura do anel e da densidade, estrutura anatómica e possíveis relações entre as diferentes variáveis. A avaliação das características anatómicas e biométricas dos vasos do lenho inicial da madeira de *Q. faginea* permitirá equacionar a sua utilização como indicadores de ocorrência de variações climáticas ou ecológicas em Portugal. A inclusão de informação relativa a outros povoamentos de *Q. faginea*, mediante a possibilidade de recolha de material adicional, aumentará o nível de robustez dos resultados do conhecimento da dinâmica de crescimento entre locais e condições ambientais.

Neste seguimento, a intenção é aprofundar o conhecimento sobre os carvalhos representativos em Portugal, reunindo e interligando os conhecimentos agora obtidos da *Q. faginea* e aqueles existentes da *Q. suber*, assim como, e após desenvolver trabalho experimental, na *Q. pyrenaica* e a *Q. rotundifolia.* Esta interligação de conhecimentos é fundamental para estudar o crescimento e as características estruturais e tecnológicas da madeira relacionando-as com o local, clima e gestão florestal. Deste modo, será possível fazer uma avaliação crítica sobre o crescimento, qualidade da madeira e sustentabilidade destas espécies.