Variation in carbon concentration and basic density along stems of sessile oak (Quercus petraea (Matt.) Liebl.) and Pyrenean oak (Quercus pyrenaica Willd.) in the Cantabrian Range (NW Spain)

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ORIGINAL PAPER

Variation in carbon concentration and basic density along stems of sessile oak (*Quercus petraea* (Matt.) Liebl.) and Pyrenean oak (*Quercus pyrenaica* Willd.) in the Cantabrian Range (NW Spain)

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Abstract
• ***Context*** Information about variations in basic density (BD) and carbon content (%C) along tree stems is key to assessing forest carbon sinks.
• ***Aims*** The aim of the study was to determine any differences in %C and BD between different woody tissues (bark, sapwood and heartwood) in two widespread European oak species (*Quercus pyrenaica* and *Quercus petraea*).
• ***Methods*** Twenty trees were felled in northern Spain, and 317 discs cut from the trees were dried and analysed to determine %C and BD.
• ***Results*** There were significant differences in %C between bark, heartwood and sapwood, and between species. There were also significant differences in BD between the tissues (heartwood>sapwood>bark), and the BD was higher in *Q. petraea* than in *Q. pyrenaica*. Both %C and BD varied along the stem.
• ***Conclusion*** More accurate estimates of carbon contents were obtained by using specific values for different heights and anatomical parts, than by using single values.

Keywords Carbon · Basic density · Sapwood · Heartwood · Bark · Oak

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Contribution of the co-authors Javier Castaño-Santamaría: carried out the laboratory analyses, ran the data analysis, wrote the manuscript and corrected the referees' comments and editor's comments in the following versions of the manuscript.
Felipe Bravo: designed the experiment, supervised the work and corrected the first version of the manuscript.

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1 Introduction

Forest biomass is one of the sinks recognised by the Intergovernmental Panel on Climate Change (IPCC) as having the potential to reduce concentrations of atmospheric carbon dioxide (CO_2) (Nabuurs et al. 2007). This has led to increased interest in forests and forest management as potential mitigators of climate change (Canadell and Raupach 2008).

Accurate estimation of forest carbon (C) stocks and fluxes is a prerequisite for assessing the contribution of forest ecosystems to net global C budgets (Zhang et al. 2009). The carbon content of trees is usually calculated from wood volume equations (cubic meters) that include basic wood density (megagram of dry biomass per cubic metre) and a conversion factor for the C concentration in dry biomass (%C) (Houghton et al. 1990).

Basic wood density (BD) is defined as the oven dry weight of the wood divided by the green volume of wood (Simpson 1993). It is commonly considered as an indicator of wood quality (Bergès et al. 2008) and varies widely among species (FIMCI 2003). On the other hand, a C concentration ratio of 50% is used to convert dry tree biomass to carbon stock at an operational level (Lamlom and Savidge 2003). This simplification has been proposed as a default value by the IPCC (Houghton et al. 1990), even though the carbon content varies between tree species (Zhang et al. 2009). Accurate estimates of carbon concentrations would therefore be useful for more precise assessment of carbon stocks in tree biomass (Bert and Danjon 2006). In fact, the use of generic simplifications may produce misleading estimates, with errors as large as 70% (e.g. Ravindranath and Ostwald 2008).

Species- and tissue-specific basic wood density and carbon concentration measurements are required to reduce uncertainties as regards biomass C estimation. This specific problem has rarely been addressed because such studies are very laborious (Huet et al. 2004; Zabek and Prescott 2006). Tree stems are known to display longitudinal differences in carbon concentration (Bert and Danjon 2006; Herrero et al. 2011) and basic density (Nogueira et al. 2008). However, as far we know, no previous studies have tested both radial and longitudinal variation in carbon concentration and basic density in oaks.

The Sessile oak (*Quercus petraea* (Matt.) Liebl.) and Pyrenean oak (*Quercus pyrenaica* Willd.) are indigenous to Europe and widely distributed throughout the continent (Adame et al. 2006; Timbal and Aussenac 1996). The water and soil requirements of both of these oak species are intermediate between those of pure Atlantic (e.g. *Quercus robur* L.) and pure Mediterranean oaks (e.g. *Quercus ilex* L.) (Costa et al. 2005). Management of oak forests is one of the biggest problems that forestry research is facing in Spain (Adame et al. 2006). The increase in rural–urban migration is leading to abandonment of traditional uses of oak (for firewood and charcoal), so that the environmental functions of these forests, particularly as carbon sinks, have become more important. However, according to Sabaté et al. (2002), both of the aforementioned oak species and their hybrid (*Quercus x trabutii* Hy) may be included in the list of species that will be transformed from C sinks to C sources as a result of global warming. If we know the size of the C sink formed by these forests, we will then be able to estimate the potential C source.

The main objective of the present study was to estimate %C and BD in sessile and Pyrenean oak stems in northern Spain, in order to clarify certain aspects of biomass C estimation (Zhang et al. 2009). The specific objectives of the study were: (1) to test for any differences in %C and BD between the two species and amongst different woody tissues along the tree stems, (2) to test for variations in the percentage (in weight) of specific tissues along the tree stem, and (3) to calculate the probability of the presence of heartwood in a specific woody location, defined by its relative height in the stem and by the tree diameter.

2 Materials and methods

2.1 Data

This study was carried out in northern Spain, in an inland area called La Castillería valley, located on siliceous terrain at an altitude of around 1,340 m, with average precipitation of 942 mm and average annual temperature of 10.7°C (Alcalde Crespo 2001). The geographic coordinates of its centre of the area are 4° 26′ 32.23″W, 42° 55′ 14.99″N. The climate is Mediterranean with Atlantic influence and the main forest types are extensive stands of Pyrenean oak, as well as sessile and pedunculate oak and beech. The study forests are natural mixed stands of sessile and Pyrenean oak of around 60 years old, and are managed as shelterwood. The stand density is 1,020 trees/ha with an average height of 10.83 m and an average diameter of 22.54 cm.

Twenty dominant oaks (ten of each species) were destructively sampled in the study stands in 2007. A basic description of these trees by species is shown in Table 1. Each tree was felled as close to the ground as possible. Cross-sectional discs of ~20 mm width were taken from each section, starting at stump height, at a height of 0.50 and 0.80 m above ground, at breast height (1.30 m) and thereafter at 1 m intervals along the stem until the apex. These cross-sectional discs were physically separated into different woody tissues (heartwood, sapwood and bark). The different parts were delimited by visual observation.

To calculate the BD, samples from eight randomly selected trees (two trees per diameter class and species, i.e. four trees of each species) were dried in a forced air oven at 95°C for 2-3 weeks until constant dry weight. They were then immersed in water for 6-8 weeks until they reached a constant wet weight. The volume of the wet samples was determined, in a calibrated container, by applying Archimedes' principle.

To measure the %C, the dried samples from the 20 trees were first ground in a centrifugal mill (10 mm) and then in a mixed mill (5 μm). This fine powder was placed in open containers inside a forced air oven at 95°C for 10 days. Each sample of dry wood powder (~1 mg) was then analysed in a C/N analyzer (CHN-2000 LECO® Corp., St. Joseph, MI, USA; analytical error, C: ±0.07%). The samples were burned completely at 1,200°C in a vial containing pure oxygen, and the concentration of CO_2 emitted was measured by the non-dispersion infrared ray method. The C content

Table 1 Summary statistics for the two species analysed

Variable	Mean	Maximum	Minimum	SD	*n*
Q. petraea					
DBH (cm)	23.77	27.40	18.40	4.35	10
Height (m)	12.38	15.10	9.80	2.69	10
Q. pyrenaica					
DBH (cm)	16.44	19.10	13.30	2.62	10
Height (m)	9.72	13.60	8.30	3.77	10

was calculated and expressed as a percentage (milligram C mass per 100 mg dry mass).

The original database consisted of 805 observations for %C and 172 for BD. Values more than 2 SD from the mean ($\mu \pm 2\sigma$, where μ=mean, σ=SD) were considered as outliers. After removal of outliers, the database was reduced to 797 and 167 observations, for %C and BD, respectively. The elementary statistics for these variables are shown in Table 2.

Given the variation in the number of samples measured for each real height—because the heights of the dominant trees analysed were similar but not identical—the relative height (h_{rel}) of the samples was calculated, and ranked by deciles. This new independent variable (h_{rel}) replaced the sample height, thus ensuring that the results for all the trees were comparable. Thus, the largest h_{rel} (1.0) refers to the apex of the tree while the smallest refers to the stump (0.0). Likewise, the intermediate values (0.1-0.9) refer to the rest of the stem. Similarly, BD was ranked using seven groups with a common range of 0.1 g/ml.

2.2 Statistical analysis

The variation in BD and %C was tested by three-way analysis of variance (α=0.05) considering tree species, woody tissue, and h_{rel} as fixed factors and incorporating the specific tree as a random factor. Both analyses were fitted by the SAS/STAT® GLM procedure (SAS Institute Inc. 2004). The general model can be expressed as:

$$Y = \mu + \alpha_i + \beta_j + \gamma_k + (\alpha\beta)_{ij} + (\beta\gamma)_{jk} + (\alpha\gamma)_{ik} + (\alpha\beta\gamma)_{ijk} + \left(\delta * (\alpha\beta\gamma)_{ijk}\right) + \varepsilon$$

Table 2 Summary statistics for the 20 oak trees used to analyse the variations in carbon concentration and basic density

Variable	Mean	Maximum	Minimum	SD	*n*
Q. petraea					
%C_Bark (%)	46.86	51.69	42.48	2.44	109
%C_Sapwood (%)	45.49	47.82	38.60	3.61	111
%C_Heartwood (%)	46.01	47.75	41.08	3.45	72
DB_Bark (Mg/m^3)	0.26	0.31	0.21	0.03	50
DB_Sapwood (Mg/m^3)	0.62	0.89	0.42	0.15	41
DB_Heartwood (Mg/m^3)	0.64	0.87	0.46	0.13	26
Q. pyrenaica					
%C_Bark (%)	45.82	50.72	40.04	2.94	208
%C_Sapwood (%)	45.58	54.85	38.54	5.02	184
%C_Heartwood (%)	45.78	48.43	42.81	1.61	113
DB_Bark (Mg/m^3)	0.26	0.38	0.19	0.06	24
DB_Sapwood (Mg/m^3)	0.53	0.76	0.42	0.13	18
DB_Heartwood (Mg/m^3)	0.57	0.73	0.43	0.09	8

where, Y is the %C or BD of the sample, μ is the mean value, α_i is the effect of the tissue on Y, β_j is the effect of species on Y, γ_k is the effect of h_{rel} on Y, $(\alpha\beta)_{ij}$ is the effect of the interaction between tissue and species, $(\beta\gamma)_{jk}$ is the effect of the interaction between species and h_{rel}, $(\alpha\gamma)_{ik}$ is the effect of the interaction between tissue and h_{rel}, $(\alpha\beta\gamma)_{ijk}$ is the effect of the interaction between the three variables, $(\delta^*(\alpha\beta\gamma)_{ijk})$ is the random effect of each tree on the fixed factors, and ε is the error. In addition, a Pearson correlation analysis between BD and %C was determined for each species and tissue, by the SAS/STAT® CORR procedure (SAS Institute Inc. 2004).

An additional analysis was carried out to determine if the percentage (by weight) of different tissues varies along the tree stem. A new GLM procedure was applied separately for each species and tissue, with a significance level of 5%. The model expression was %tissue = $\mu + \beta_i + \varepsilon$, where μ refers to the mean value, β_i shows the effect of height on the percentage of each woody tissue in a specific sample, and ε corresponds to the error. The Lakkis-Jones test (Khattree and Naik 1995) was used to compare the differences amongst all these models. This method requires fitting the data to two models (reduced and full). While the reduced model has the same set of parameters for all models, the full model corresponds to different sets of parameters for each group and is obtained by expanding each parameter through an associated parameter and a dummy variable to differentiate the models. Its expression is:

$$L = \left(\frac{\mathrm{SSE}_F}{\mathrm{SSE}_R}\right)^{\frac{n}{2}}$$

where, SSE_F refers to the error sum of squares of the full model, SSE_R is the error sum of squares of the reduced model and n is the number of data in the reduced model.

A logistic model for determining the probability of presence of heartwood was fitted by the SAS/STAT® LOGISTIC procedure (SAS Institute Inc. 2004). The logistic model has the following structure:

$$p = \frac{1}{1 + e^{-z}}$$

in which P is the probability that there will be heartwood at a specific height and z is a linear function, expressed as follows: $(z = a_0 + a_1 \times h + a_2 \times Dn + a_3 \times d)$, where h is the h_{rel} of the sample, DBH is the tree diameter at breast height of the sample, and d is the specific diameter of the sample disc. Prior analysis was conducted to determine the Pearson correlation between DBH and d.

The Akaike information criterion (Venables and Ripley 1999) and the Hosmer and Lemeshow (2000) test were used to assess the goodness of fit. In terms of prediction, the

Table 3 Main results of the GLM procedure for %C (n=797, R^2=96.55%) and BD (n=167, R^2=86.41%)

Source	DF	Type III SS	Mean square	F value	Pr>F
Carbon concentration					
Tissue	2	106.6130	53.3065	99.66	<0.0001
Species	1	27.7374	27.7374	51.86	<0.0001
Height	10	81.3364	8.1366	15.21	<0.0001
Tissue×species	2	59.4492	29.7246	55.57	<0.0001
Tissue×height	19	109.0499	5.7395	10.73	<0.0001
Species×height	10	16.7816	1.6781	3.14	0.001
Tissue×sp×height	18	47.0766	2.6153	4.89	<0.0001
Tree	455	2314.6155	4.2007	7.85	<0.0001
Error	765	2844.3760	3.3376	–	–
Basic density					
Tissue	2	3.3438	1.6719	263.77	<0.0001
Species	1	0.0589	0.0589	9.30	0.0028
Height	10	0.1901	0.0190	3.00	0.0017
Tissue×species	2	0.0549	0.0274	4.33	0.0130
Tissue×height	17	0.2010	0.0118	1.87	0.0262
Error	134	0.8493	0.0061	–	–

coefficient of determination is not appropriate in this type of analysis when independent variables (such as diameter and h_{rel} of the sample) are modelled (Neter and Maynes 1970). However, the area under the receiver operating characteristic (ROC) curve may be considered as an estimator of accuracy (Bravo-Oviedo et al. 2006), because it indicates the ability of the logistic model to predict the presence or absence of heartwood in a specific sample.

3 Results

3.1 Variation in %C and BD

The results showed that oak species, woody tissue, h_{rel}, all interactions between the variables and also the tree random effect had significant effects on %C. However, only oak species, woody tissue, h_{rel}, tissue-species and tissue-h_{rel} interactions had significant effects on BD (Table 3).

The %C was significantly higher in *Q. petraea* than *Q. pyrenaica* in bark (46.86% compared with 45.82%) and heartwood (46.01% compared with 45.78%), while %C was higher in *Q. pyrenaica* (45.58%) than *Q. petraea* (45.49%) in sapwood (Fig. 1). In addition, the following

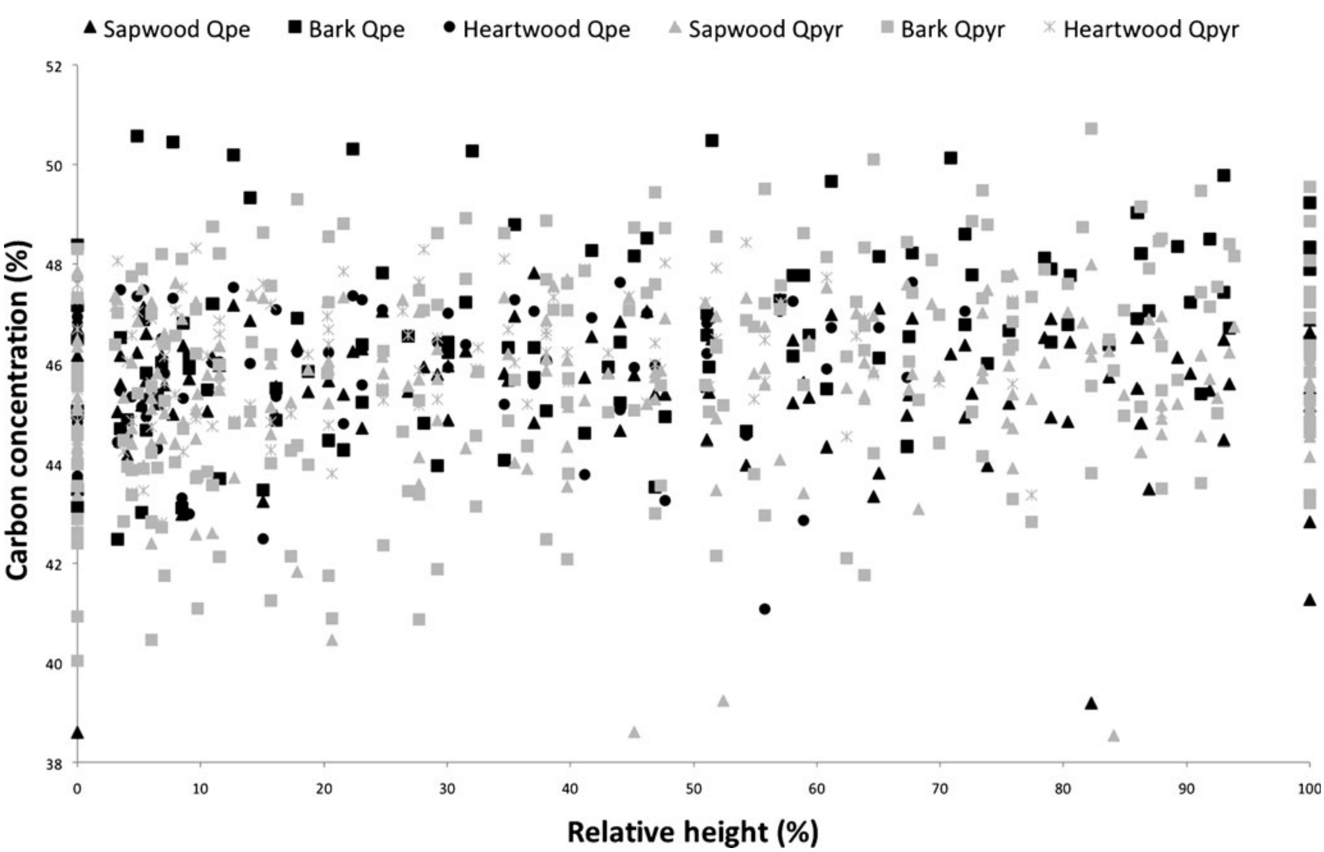

Fig. 1 Variation of carbon percentage in relation to species and h_{rel} by woody tissue

pattern was observed in both species: %C was significantly higher in bark than in heartwood, which also was significantly higher than sapwood. Moreover, the interaction between tissue and h_{rel} for each species showed that %C increased significantly along the stem in both species, in bark (from 45.57% and 45.13% at the stump to 46.12% and 45.44% at the apex for *Q. petraea* and *Q. pyrenaica*, respectively) and sapwood (from 44.92% and 45.01% at the stump to 45.53% and 45.94% at the apex for *Q. petraea* and *Q. pyrenaica*, respectively). However, the %C in the heartwood did not vary significantly along the stem in either species (45.47% and 45.41% at stump to 45.43% and 45.45% for *Q. petraea* and *Q. pyrenaica*, respectively). The %C was higher in *Q. petraea* than in *Q. pyrenaica* at all heights, but the differences were only significant for heights closest to the stump, where there is no heartwood.

The BD was significantly higher in *Q. petraea* than in *Q. pyrenaica*, in heartwood (0.64 and 0.57 Mg/m^3, respectively) and sapwood (0.62 and 0.57 Mg/m^3, respectively) but there were no significant differences as regards bark (0.26 Mg/m^3 in both species). In addition, the interaction between tissue and h_{rel} also had different effects on the tissues studied. The BD decreased significantly along the stem in heartwood and sapwood (from 0.84 Mg/m^3 at stump to 0.61 Mg/m^3 at to the highest height at which there was heartwood, and from 0.66 Mg/m^3 at stump to 0.53 Mg/m^3 at apex for sapwood). However, the BD of the bark did not vary significantly along the stem (0.26-0.28 Mg/m^3). In both species, BD was significantly higher in the stump than in the rest of the tree (Fig. 2).

The Pearson correlation analysis for BD and %C for each species and tissue revealed a lack of correlation between these parameters in all situations. For sessile oak, the values obtained were r=0.045 (p=0.693), r=0.068 (p=0.599) and r=0.014 (p=0.928) for bark, sapwood and heartwood, respectively, while for Pyrenean oak the values were r=0.076 (p=0.595), r=0.097 (p=0.503) and r=0.177 (p=0.384) for bark, sapwood and heartwood, respectively (Fig. 3).

3.2 Variation in percentage of tissues along the tree stem

There were significant differences in the percentage of the different tissues along the stem, but no significant differences between the species (Table 4). In fact, the sample height had a similar significant effect on the percentage of sapwood and heartwood in both species (Table 5). However, height had no effect on the percentage of bark, although the value was always close to 18-22%, with minor variations

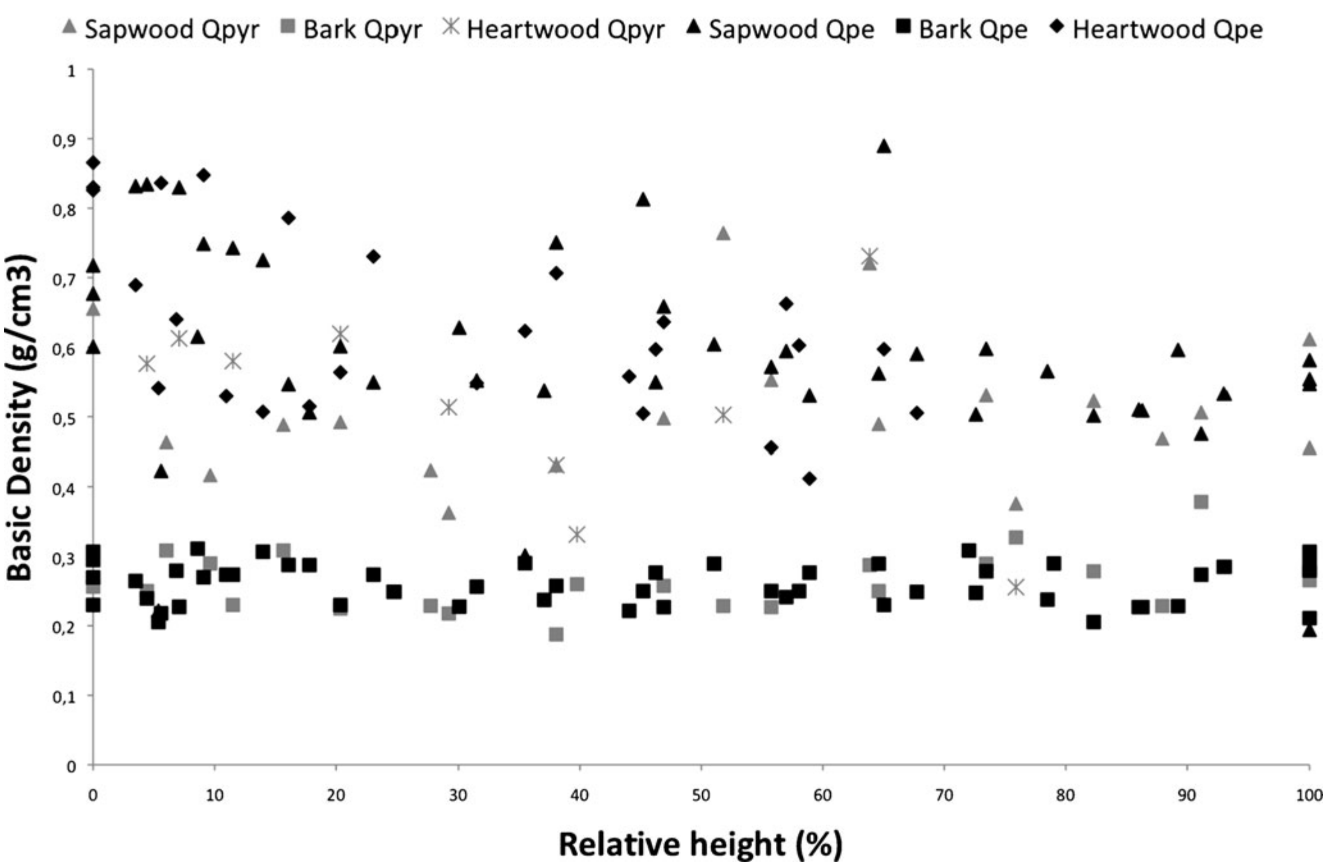

Fig. 2 Variation of basic density in relation to species and h_{rel} by woody tissue

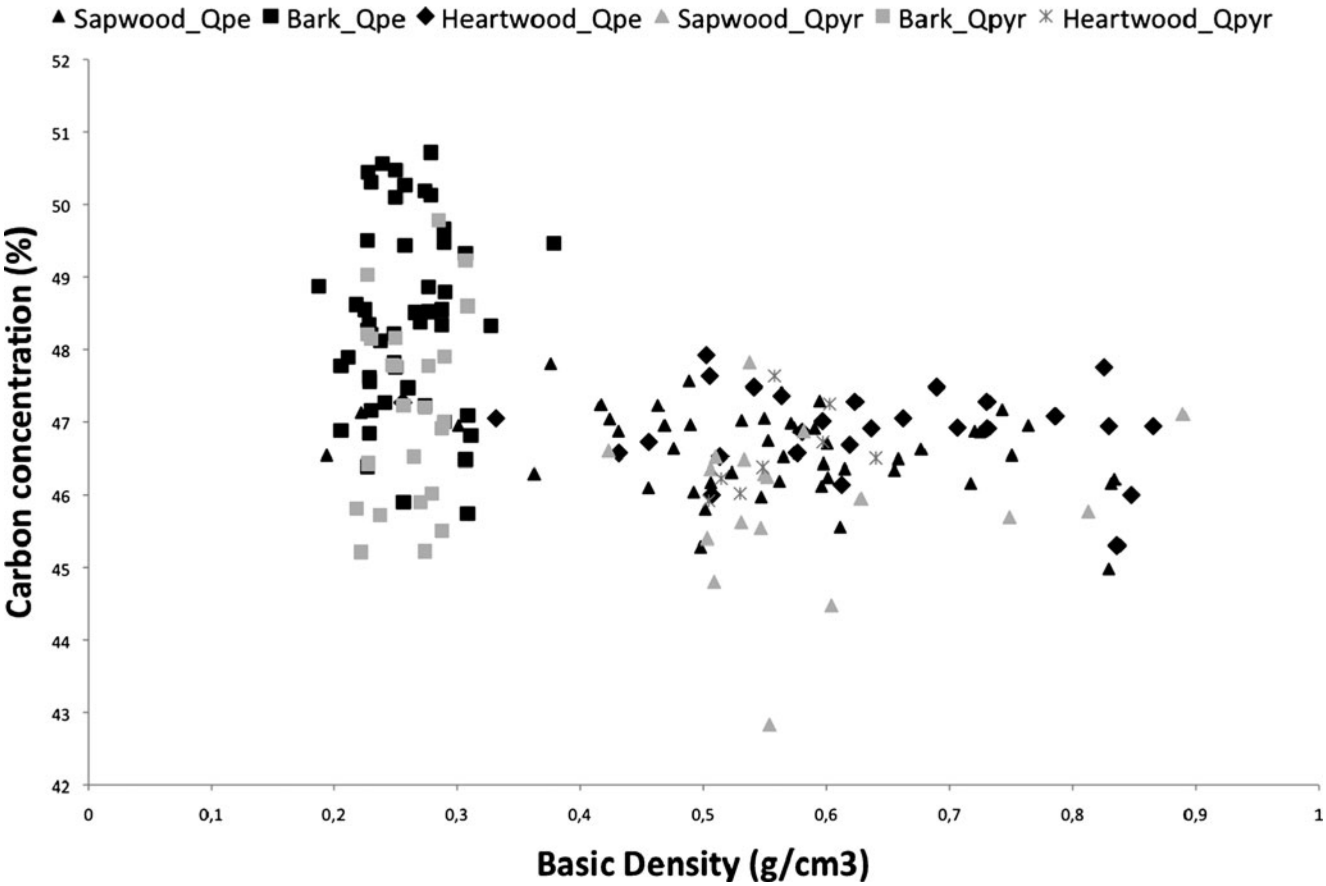

Fig. 3 Lack of correlation between %C and BD for each tissue and species

that were not statistically significant (Table 5). As the height increased, the presence of heartwood decreased to zero, and the percentage of sapwood increased (Fig. 4). For practical purposes, the average tissue percentages obtained from the specific data obtained in the present study were: bark=18.41%, sapwood=54.27% and heartwood=27.32%.

3.3 Model of the probability of presence of heartwood

A single logistic model was fitted jointly for both species, because there were no significant differences between the percentages of the different tissues along the stem (Table 4).

The Pearson correlation analysis for *DBH* and *d* revealed a correlation between *DBH* and *d* for the three woody tissues in the dominant trees (r=0.630 (p<0.0001) for bark, r=0.624 (p<0.0001) for sapwood and r=0.748 (p<0.0001) for heartwood). Therefore, *d* was removed from the model because *DBH* is a more common and measurable variable.

DBH and h_{rel} had significant effects on the probability of the presence of heartwood in a specific woody section (p< 0.0001 and p=0.0088, respectively; Table 6). Diameter at breast height is closely related to the tree age (growth), and the proportion of heartwood increases with age (Bert and Danjon 2006; Zabek and Prescott 2006). The value of the area under the ROC curve was 0.676, indicating a good discriminatory ability. The Akaike Information Criterion value was equal to 690.32 (and 789.68 when the independent variables were not considered), and the Hosmer-Lemeshow test (Pr>0.706) confirmed a good fit. The resulting model is as follows:

$$P = \frac{1}{1 + e^{(1.0408 + 0.218Hrel - 0.0355DBH)}}$$

Table 4 Lakkis–Jones test results

Comparison	*n*	Lakkis	*P*>Lakkis
Q.petraea–Q.pyrenaica	797	8.4425	0.1853
Bark–sapwood	612	29.6765	<0.0001
Bark–heartwood	502	20.8555	0.0020
Sapwood -heartwood	480	21.9517	<0.0001

3.4 Carbon sink estimation

The forest carbon stock existing in medium site quality oak stands in northern Spain was calculated according to Torre

Table 5 Effect of height on %C in different tissues

Source	Type III SS	Mean square	F value	$P>F$	Model	
					R^2 (%)	P value
Both sp.						
h-bark	264.0412	16.5025	0.50	0.9389	11.87	0.9389
h-sapwood	17,490.3613	1,093.1476	8.31	<0.0001	69.27	<0.0001
h-heartwood	20,455.8267	1,278.4892	5.34	<0.0001	59.16	<0.0001

(1994) and Reque (2008), for *Q. pyrenaica* and *Q. petraea*, respectively, in order to compare the estimates with current simplifications (FIMCI 2003; Houghton et al. 1990). The values obtained in the present study were significantly lower (14.68% for sessile oak and 21.91% for Pyrenean oak) than the current approximations (Table 7).

4 Discussion

The present study examined the basic density and carbon concentration of three woody tissues (bark, heartwood and sapwood) and their variations along the stem in *Q. petraea* and *Q. pyrenaica*. Both parameters are highly variable and some gradients were found to be related to woody tissue and position within the tree.

In oak species, low basic wood density is positively correlated with mechanical strength and shrinkage (Zhang et al. 1994), which implies high wood quality (Zobel and Van Buijtenen 1989). Basic density is also important from a biological perspective because it is correlated with growth rates (Roderick 2000). Many studies on oaks have therefore focused on understanding the within- and between-tree variability in BD because it is not influenced by climate, soil or topography (Bergès et al. 2008). Guilley and Nepveu (2003) observed variations in BD between different tissues in *Q. petraea*, and made comparisons at the level of the parenchyma. The present study did not involve comparison of tissues in such detail.

However, on a larger scale, the present results showed that BD differed significantly between heartwood, sapwood and bark, as previously reported (e.g. Herrero et al. 2011; Nogueira et al. 2008). These authors showed that BD decreases towards the apex. The present results also revealed decreases in BD in heartwood and sapwood towards the apex. The BD is higher in the lower part of the stem because there is a greater proportion of late wood in this part of the stem (Zobel and Van Buijtenen 1989). As the tissues age, they become lignified (Magel et al. 1995) and there is an increase in the percentage of heartwood (Fig. 4), which has a higher BD (Correia et al. 2010). However, the BD did not vary significantly along the stem in bark, although in a previous study (Herrero et al. 2011), the BD of bark decreased towards the top of the stem, as in heartwood and sapwood. The present results are not consistent with the latter finding.

Moreover, there are two completely opposing points of view as regards %C. Some authors have used a common %C value, close to 50% (e.g. Clifton et al. 1979 (51.4%); Elliot 1980 (52%)), in accordance with the suggestion of Wenzl (1970), who stated that absolutely dry wood of any species containing about 50% carbon because all species had similar elemental composition. However, these authors gave no source for their values. On the other hand, other authors have used different %C values depending on the species (e.g. Lamlom and Savidge 2003; Löwe et al. 2000; Zhang et al. 2009) or depending on the woody tissue (e.g. Fukatsu et al. 2008; Peri et al. 2010), etc. However, a common value is usually used because of the complexity of estimating specific %C values.

Previous studies of specific %C have mainly considered wood as a whole and its variation among plant species. For

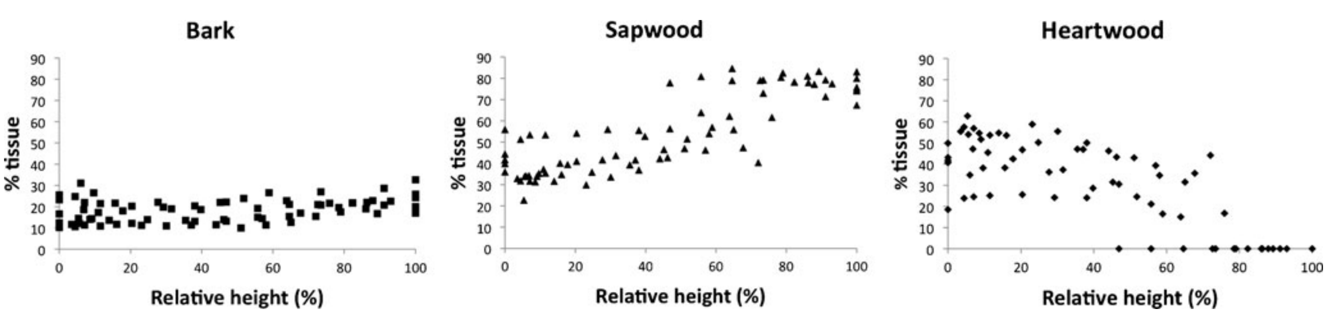

Fig. 4 Variation in the tissue mass percentage in relation to height

Table 6 Main results of the LOGISTIC procedure $f(h_{rel}$, DBH)

Parameter	DF	Estimated value	SD	χ^2	*P* value
β_0	1	−1.0408	0.3034	11.7660	0.0006
H_{rel}	1	−0.2180	0.0339	41.4611	<0.0001
DBH	1	0.0355	0.0136	6.8667	0.0088

Area under ROC curve=0.676

example, Löwe et al. (2000) reviewed the %C of dry matter estimations used by European countries for their national forest carbon reporting. The values ranged from 43% (conifers in Portugal) to 51.9% (pine and spruce in Finland). In other examples of such studies, the %C ranged from 46.3% to 55.2% for 41 North American species (Lamlom and Savidge 2003), and from 43.4% to 55.6% for 10 Chinese species (Zhang et al. 2009).

Other studies that analysed tissue variations in %C reported significantly higher variations in bark than in wood (e.g. Huet et al. 2004). In addition, the %C is usually higher in heartwood than in sapwood, mainly because of differences in the physical and chemical properties in these tissues (e.g. Bert and Danjon 2006; Fukatsu et al. 2008; Herrero et al. 2011). The present results showed significant differences in %C between the three tissues (bark>heartwood>sapwood), as also reported by Fukatsu et al. (2008) and Huet et al. (2004), amongst others.

Longitudinal variations in %C were also observed in previous studies (e.g. Bert and Danjon 2006; Campbell et al. 1990). The present results showed increases in %C along the stem in bark and sapwood towards the top of the stem, where there is a higher proportion of juvenile wood (Zobel and Van Buijtenen 1989). This may be due to the higher degree of cell activity in juvenile wood. Indeed, %C is higher in juvenile wood than in mature wood (Bert and Danjon 2006). However, the present results showed that the %C did not vary significantly along the stem in heartwood. Although heartwood is a biologically dead tissue (Climent et al. 1998), its composition is not the same along the stem (Bert and Danjon 2006; Herrero et al. 2011), so that the %C in heartwood varies, as shown in previous studies (e.g. Campbell et al. 1990).

Moreover, the tree as a random effect only had a significant effect on %C but not on BD. Other authors have showed that there are significant differences in %C and BD between trees in the same stand because each tree is "unique" (e.g. Guilley et al. 2004; Henry et al. 2010; Thomas and Malczewski 2007). The present results are consistent in terms of %C.

In conclusion, the results of the present study showed that as woody tissue grows and ages, the BD increases and the %C decreases. However, the trend in %C is punctually reversed through the transformation of sapwood into heartwood. Over the course of time, the heartwood becomes denser, whereas the %C does not vary significantly.

This study expands our knowledge of C in biomass, taking into consideration different values at different heights and parts of the stem, rather than using a single value as at present. However, the present results should be viewed with caution. Given that the samples were dried at 95°C, direct cross-study comparison is difficult, because different temperature regimes of sample treatment are considered. The %C estimated in this study cannot be used directly to convert biomass usually dried at 65°C into carbon stock (the most common temperature). Thomas and Malczewski (2007) showed that biomass dried at 65°C loses ~2.2% of volatile carbon when samples are dried at 105°C. A small correction factor is therefore required for rigorous calculations. Nonetheless, it is not known exactly how the gradient "temperature-%C loss" varies (Zhang et al. 2009). If the carbon loss occurs linearly, the values determined in the present study would have been ~1.6% higher if the samples had been dried at 65°C. However, there are no data allowing us to describe this relationship. Given that all our samples were dried at the same temperature, the error can probably be considered as systematic and common to all data.

Table 7 Carbon sink estimation in a hectare of sessile and Pyrenean oak (Reque 2008; Torre 1994)

Species	Class	Yield (m^3/ha)[a]	Basic Density (Mg/m^3)			%C			Mg C /ha
			Bark	Sap	Heart	Bark	Sap	Heart	
Q. petraea	Default values	720.1	0.6	0.6	0.6	50	50	50	216.03
	Own estimation	720.1	0.26	0.62	0.64	46.86	45.49	46.01	184.30
Q. pyrenaica	Default values	402.06	0.6	0.6	0.6	50	50	50	120.62
	Own estimation	402.06	0.26	0.57	0.57	45.78	45.58	45.82	94.18

Comparison between default values and our results

[a] Average percentage of tissues: bark=18.41%, sapwood=54.27%, heartwood=27.32%

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