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Original article

Carbon and nutrient stocks in mature *Quercus robur* L. stands in NW Spain

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Abstract – In the present study, the distribution of C and nutrients in biomass (above- and below-ground) and soil were estimated in native *Quercus robur* stands in NW Spain. This information can be used to design future strategies to preserve and improve these forests, which are subjected to severe degradation as a consequence of poor management and fire damage. Biomass equations for tree components were fitted simultaneously using the data corresponding to 31 trees felled in 4 representative mature stands. The C accumulated in aerial biomass, roots, litter layer and mineral soil made up 40, 10, 8 and 42% respectively, of the C in the whole forest system. Tree biomass contained higher amounts of macronutrients than the available reserves in the soil. Stem wood was the major tree compartment for most nutrients, with the exception of Ca, which was mainly accumulated in stem bark. In comparison with commercial forest plantations in the region, particularly high amounts of nutrients were accumulated in the litter layer because of the high amounts of litterfall and higher foliar concentrations of nutrients.

***Quercus robur* L. / biomass / forest nutrition / carbon / seemingly unrelated regression**

Résumé – Estimation des stocks de carbone et d'éléments minéraux dans des peuplements matures de *Quercus robur* L. du NO de l'Espagne. Dans la présente étude, une estimation de la distribution du Carbone et des éléments minéraux dans de la biomasse (aérienne et souterraine) et le sol des forêts primaires de *Quercus robur* du NO de l'Espagne est faite. Cette information pourra être utilisée pour établir une stratégie de conservation et d'amélioration de ces forêts très dégradées par manque de gestion et à cause des incendies. Pour l'estimation des biomasses, une procédure d'équations simultanées a été développée en utilisant les données issues de 31 arbres abattus dans 4 peuplements matures représentatifs. Le carbone accumulé dans les biomasses aériennes et racinaires, la litière et le sol représentait respectivement 40, 10, 8 et 42 % du carbone recensé dans tout l'écosystème. La biomasse des arbres contenait plus de macronutriments qu'il n'en était disponible dans le sol. Les troncs représentent le principal compartiment d'accumulation des nutriments, à l'exception de Ca, qui est principalement accumulé dans l'écorce du tronc. En comparaison avec les autres forêts issues de plantations à vocation commerciale, les quantités de nutriments accumulés dans la litière sont importantes. Ceci peut s'expliquer par une importante production de feuilles et des concentrations foliaires plus importantes.

***Quercus robur* L. / biomasse / nutrition forestière / carbone / régression apparemment sans rapport**

1. INTRODUCTION

In comparison with commercial plantations, which are subject to net losses of C as a consequence of site perturbations and low inputs from litterfall [42, 47], natural forests play an important role as long-term C sinks in soil and tree components [6, 23, 24, 50]. However, disturbances can disrupt the C cycle through direct effects on tree biomass (the age-class distribution of the forest shifts to younger stands containing less C, [28]) and soil organic matter decomposition [17] and, therefore, leading to reduction in C stocks. In other words, conservation measures undertaken in natural forests in Europe are leading to substantial increases in the forest C stock [49].

Although C storage in tree biomass reaches high values, assessment of C budgets in these ecosystems should also take into account the litter layer and soil, as these are major storage compartments [7, 10]. The potential of soils as long-term C sinks is, however, much less well understood than that of tree C [29, 38], even though mineral soil is the compartment of the system that stores most stable C.

Furthermore, in natural forests, nutritional status is very dependent on the amounts of nutrients replenished by internal processes, such organic matter mineralization, biological fixation and weathering. Nutrient concentrations in soil, litter and biomass are important indicators of forest vitality and growth. Forest nutrient budgets, which include data on nutrient stores in soil and vegetation, provide useful information for characterizing nutrient supplies. In natural forests, litter is a major pathway for the return of organic C and nutrients from the vegetation to the soil [18]. For this reason, forest management, which implies changes in tree structure and species composition, can lead to substantial changes in this compartment, altering the nutrient turnover [17].

Near natural forest dominated by *Quercus robur* (pedunculate oak) is the most important natural forest community

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in northern Spain, occupying 15% of forest land [53]. During the last few centuries, these native oak forests have been severely depleted, in terms of fragmentation, habitat loss and genetic composition, and relegated to sites outwith their optimal ecological conditions [6]. However, in recent decades, abandonment of rural areas has reduced the intensity of the harvesting. Furthermore, in recognition of the importance of the environmental issues associated with oak forests (biodiversity, C accumulation, [6, 16, 27, 43, 45]), they are currently protected by different regional and national regulations. Less intensive management, along with the implementation of conservation measures can contribute to restoring forest structure and therefore, C stocks and nutrient cycling. Above- and below-ground biomass and nutrient pools in oak forests have been partially documented in Europe [3, 22, 39, 41, 52]. However, there is a need for further, more complete, studies on ecosystem C and nutrient amounts to assess the effects of management practices and to reach the implementation of conservation measures.

The aim of the present study was to characterize the distribution of biomass, C and nutrients in mature oak forests in NW Spain. Assessment of the C and nutrient distribution in the plant-soil system is required for evaluation of future strategies aimed at preserving and improving the stands and therefore also the associated important environmental functions of these forests.

2. MATERIALS AND METHODS

2.1. Site characteristics

Four mature even-aged stands of pedunculate oak located in northwest Spain were selected for study (Tab. I). These even-aged or two-aged stands represent the oak forests in most of the area, and show a low degree of silvicultural intervention (mainly a variety of undefined partial cuttings of large-diameter trees for at least the past 100 years). In most cases it is difficult to know if the stands have been managed as coppices, coppices with standards or even high forest, and all are characterized by natural regeneration and high growing stock. No land preparation or land treatment is considered in these forests. The silviculture management has involved non-natural development of the stands. The size of the stands ranged from 3 to 11 ha (see Tab. I). The age of most of trees in the stands ranged from 80 to 140 years. Most of the trees belonged to at least four diameter classes, and a minority of dominated trees to lower diameter classes.

The climate of the study area is characterized by mild temperatures (annual average temperature 11 °C). The soils are developed on granitic rocks (2 stands) and acid schist (2 stands) (Tab. I). The soils are of moderate depth, with an intermediate proportion of gravel and a low water-holding capacity. They are rich in organic matter and show low pH (predominantly in the range of pH 4.0–4.5).

The stands selected for the study were in many cases coppice stands with apparently well developed trees showing no phytosanitary problems, and belonging to a *Myrtillo-Quercetum roboris* association, where *Vaccinium myrtillus* and *Erica arborea* are also present [45]. The oak stands had not been previously subjected to any management regime, the only interventions consisting of a single tree selection system of the best specimens, a practice that has historically been used with this species in Galicia [12]. Finally, in many cases, leaf litter from the forests has been removed for use as a soil supplement for growing subsistence crops.

2.2. Tree biomass models

In the summer of 2003 destructive biomass harvesting was carried out on 31 oak trees for subsequent construction of equations for predicting tree biomass. The methodology used was similar to that described in other studies [36]. A complete inventory (sampling plot area of 900–1400 m^2) was carried out in each stand to characterize the stem diameter distribution. Six to nine trees in each sampled stand were subjectively selected to represent the diameter classes defined from the inventory, and were felled. Tree aerial biomass was separated in the field and then in the laboratory into leaves, twigs, branches of diameter larger than 7 cm, thick branches (diameter 2–7 cm), thin branches (diameter 0.5–2 cm), twigs (diameter lesser than 0.5 cm), stem bark and wood (debarked logs with a thin-end diameter of 7 cm). For below-ground biomass, destructive harvesting was carried out with 11 of the 31 sampled oaks. A tractor with a hydraulic ram was used to pull the root system from the soil. For the purpose of the study, a 5 m diameter circle around the sampled tree was considered for analysis of the root system, thus the biomass of thin roots (< 5 mm) may have been underestimated. Representative composite samples of tree components were used to determine the moisture content at 65 °C and the dry weight (Tab. II).

A multilinear regression technique was used to establish equations predicting biomass contents of each tree component, in two stages. In the first stage, regression equations were fitted separately for each fraction using single or combined tree characteristics (diameter at breast height: d and total height: h) and stand measurements (basal area: BA, dominant height: H and mean height: $\overline{H}$) as independent variables. Two methods of achieving minimum variance in parameter estimates and reducing heteroscedasticity were analyzed: logarithmic models and weighted regression, using a weighting factor, x^{-w}, which depended on the independent variables (x) included in the model. The optimum value of w was selected on the basis of Furnival index [20]. Six log-transformed and six weighted models further reported in the biomass literature (i.e. [46]) were tested for each tree fraction. The best prediction models were chosen on the basis of the following statistical criteria: goodness of fit (characterised by four statistics: R^2, bias, residual mean square and most importantly, the Furnival index) and the absence of multicollinearity, as indicated by the condition number. In the second stage, selected equations for each biomass component were fitted simultaneously in order to ensure compatibility between the estimates of total biomass and each of their fractions [25,37], that is, the estimates of the different components should have the property of additivity. The regression methodology proposed by Zellner [54] known as weighted SUR (Seemingly Unrelated Regression), was then applied using the SAS statistical package [44]. When necessary, Meyer's correction was applied to correct for the bias resulting from log transformation [35].

Assessment of biomass at the stand level was performed using established models and the diameter and height distributions of the sampling plots. The error of the estimates was calculated following the approach proposed by Cunia [14].

Table I. General characteristics of the four *Quercus robur* stands selected for the study.

Location	Parent material	Slope (%)	Size (ha)	Altitude (m)	dg (cm)	Stocking (stems/ha)	G (m^2/ha)	Hm (m)	Ho (m)
1. Lanzós	Granite	25	3.0	490	34.1	610	55.92	15.8	17.6
2. Santaballa I	Schist	3	4.5	450	29.2	427	28.56	18.4	20.4
3. Santaballa II	Schist	16	11.0	470	25.5	620	31.84	16.9	19.6
4. Ramil	Granite	15	7.0	510	23.1	665	27.81	12.7	14.1

dg: quadratic mean diameter; G: stand basal area; Hm: mean height; Ho: dominant height.

Table II. Tree biomass descriptive statistics for the data analysed (average, maximum, minimum, S.D., coefficient of variation).

Statistic	dbh (cm)	h (m)	Stem wood (kg)	Stem bark (kg)	Branches > 7 cm (kg)	Thick branches (kg)	Thin branches (kg)	Twigs (kg)	Leaves (kg)	Total aerial biomass (kg)	Coarse Roots (kg)
Average	34.07	18.83	586.86	80.17	167.07	104.14	22.10	7.74	34.24	1002.31	267.30
Maximum	67.48	27.55	2297.55	412.56	909.41	330.97	69.42	22.91	95.44	3611.27	752.52
Minimum	14.60	11.34	13.16	2.57	0.00	7.56	1.99	1.19	3.42	31.07	19.54
S.D.*	16.09	3.93	596.73	91.99	249.05	99.22	18.76	5.38	27.28	1049.11	257.38
VC**	47.21	20.89	101.68	114.74	149.07	95.27	84.85	69.52	79.68	104.67	96.29

* Standard deviation; ** coefficient of variation (%); dbh: diameter at breast height; h: total height.

2.3. Nutrient contents in biomass and soil

Total element storage in the soil was calculated from the depth of each horizon, bulk density, the mean nutrient concentration and that adjusted for gravel content.

Three soil pits were dug at random points in the sampling plots in each stand when tree biomass sampling was carried out. To determine bulk density, samples were taken from the horizons of the tree pits using a brass core (40 mm long, 55 mm inside diameter), and dried to constant weight at 105 °C. Soil samples for chemical analysis were oven-dried and sieved with a 2 mm screen. The pH was measured in H_2O and 0.1 M KCl (soil:solution ratio 1:2.5) with a glass electrode. Soil macro and microelements were extracted using the Mehlich 3 procedure [32]. At the same time, samples from the litter layer (O horizon) were collected at random at six points within each stand and combined to form three bulked samples. Samples were taken using a metal ring (diameter 30 cm) and all plant material was removed from the ring. The oven-dried (65 °C) samples of the plant material (tree components and soil litter layer) were ground (0.25 mm) and digested with HNO_3 in a microwave oven. Carbon, N and S in ground plant and soil samples were analyzed by combustion, using a Leco analyzer. The concentrations of P, K, Ca, Mg, Fe, Mn, Ni, Zn, Cu and B in the digested plant samples and in soil extracts were determined by ICP-EOS. The C and nutrient contents in each tree fraction was calculated by multiplying the concentration by the dry weight calculated for the respective fraction. These values were expressed as concentrations per hectare. Since the coarse fraction (> 2 mm) was not analysed, these contents may have been underestimated. However, the loss of accuracy will be minimal because most of the rock fragments were quartz with a low percentage of weathered rocks in which C and other nutrients are more abundant [48].

3. RESULTS AND DISCUSSION

3.1. Biomass prediction equations and stand biomass amounts

The biomass equations for each oak component finally selected were as follows:

Stem wood	$W_{sw} = -5.714 + 0.018 \cdot d^2h$	$R^2 = 0.939$	(1)
Stem bark	$W_{sb} = -1.500 + 0.032 \cdot d^2 + 0.001 \cdot d^2h$	$R^2 = 0.801$	(2)
Branches > 7 cm	$W_{b7} = 3.427 \cdot 10^{-9} \cdot (d^2h)^{2.310}$	$R^2 = 0.575$	(3)
Thick branches (7–2 cm)	$W_{thickb} = 4.268 + 0.003 \cdot d^2h$	$R^2 = 0.858$	(4)
Thin branches (2–0.5 cm)	$W_{thinb} = 0.039 \cdot d^{1.784}$	$R^2 = 0.799$	(5)
Twigs (< 0.5 cm)	$W_{tw} = 1.379 + 0.00024 \cdot d^2h$	$R^2 = 0.617$	(6)
Leaves	$W_l = 0.020 \cdot (d^2h)^{0.737}$	$R^2 = 0.832$	(7)
Roots	$W_r = 0.0851 \cdot d^{2.151}$	$R^2 = 0.783$	(8)

where W represents the dry weight of the different tree components (kg), d, the diameter at breast height (cm) and h, the total height (m). All parameters of these equations were statistically significant at the 5% level.

The best results were obtained by including the term d^2h as an independent variable in linear or allometric models, except for thin braches and roots where the diameter at breast

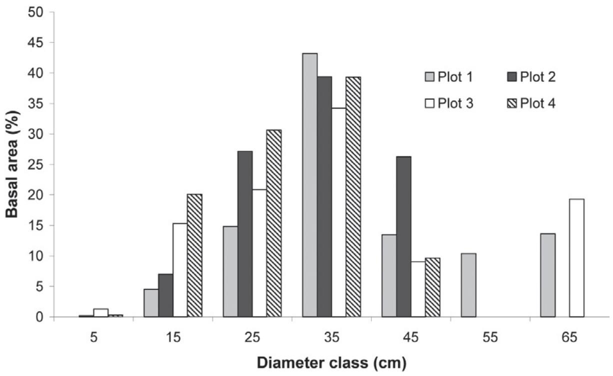

Figure 1. Relative basal area distribution by diameter classes for the four *Quercus robur* stands studied.

height (*d*) was the only independent variable included in the allometric model. Addition of stand variables to take into account the differences in stand structure and density did not lead to substantial decreases in the standard errors of estimates, indicating a good performance of the general equations for all the sample stands. These equations provide a good balance between accurate predictions and low data requirements because they use the most commonly and easily measured variables in forest inventory (diameter at breast height and total height). The use of these regression equations as well as data from diameter and total height distributions allowed us to estimate amounts of tree biomass at stand level.

The sampled stands differed in terms of tree biomass production but not in terms of component distribution. The same pattern as observed for stocking density was obtained for tree biomass amounts, thus differences in biomass among the four stands reflected the different amount of harvesting carried out in the past. Thus, relative differences were found for stand 1 (Lanzós), in which the highest stand basal area was measured. Moreover, the greater amount of biomass in this stand is attributable to the presence of trees larger than 50 cm dbh (Fig. 1). The mean value of the total aerial biomass accumulated in the stands was 238 Mg ha^{-1} (see Tab. VI), and ranged between 136 and 385 Mg ha^{-1}, which corresponded to the stands with lowest and highest basal area respectively. The average root biomass was 65.9 Mg ha^{-1} (interval of confidence 40.0–91.8 Mg ha^{-1}), representing 20% of the total tree biomass (Fig. 2).

The average proportions of stem wood, stem bark, branches and leaves, expressed as a percentage of total tree aerial biomass, were 61.6, 8.8, 27.6 and 2.1%, respectively. Very similar distributions in stem and crown have been observed for other species of *Quercus* (*Quercus pyrenaica, Quercus ilex* and *Quercus faginea*) in the region [11, 22, 41]. However, the present data differed from that corresponding to other oak species in Central Europe (*Quercus petraea*, [3]) and the USA (*Quercus alba*, *Quercus coccinea*, *Quercus prinus*, *Quercus rubra*; [31]), where stem biomass has been found to range from 73 to 84%. The proportion of crown fractions in the oak forests under study (30%) was considerably higher than those of commercial plantations of *Eucalyptus globulus*, *Pinus radiata* and *Pinus pinaster*, in which it made up between 10 and 19% of the aerial tree biomass [5, 33].

3.2. Soil properties

The characteristics of the soils under study (Tab. III) were similar to those of most pedunculate oak stands in the region [16]. They are humic Umbrisols of total depths ranging from 60 to 110 cm. The bulk density values, slightly higher in the two granitic soils, were relatively low, with average values of 0.66 and 0.95 g cm^{-3} for the surface mineral horizon and the subsurface horizons, respectively. The soils are acidic and contain particularly low reserves of extractable P, Ca, Mg and K. The differences between soils are attributable to the different coarse element contents (which are higher in the two soils on granite) and available nutrient concentrations (which are especially low in stand 4).

3.3. Nutrient concentrations in plant fractions

3.3.1. Tree biomass

The lowest concentrations of nutrients were found in stem wood, whereas the highest concentrations occurred in leaves, twigs and stem bark (Tab. IV). Mean concentrations of P and K in tree fractions decreased in the following order: leaves > stem bark > twigs > thin branches > thick branches = stem wood = roots (Tab. V). For Ca and Mg, the pattern of decreasing concentration was as follows: stem bark > twigs > leaves = thin branches > stem wood = roots > thick branches. Similar trends of nutrient accumulations in tree fractions have been reported for *Quercus robur* [9] and for other species in temperate regions [19, 33, 41].

Nutrient concentrations in leaves decreased in the following order N > K > Ca > P = Mg (Tab. V), which is consistent with the data reported for other mature [4, 15, 43] and young stands [13] of pedunculate oak. According to the concentrations reported by Van der Burg [51] for broadleaf forest species, the stands on granite (1 and 4) showed low concentrations of P, K, Ca and Mg. The poorer nutritional status of these stands, however, was not found to be related to lower nutrient stores in soil (Tab. III). Foliar N concentrations in the four stands were adequate or high attributable to the high contents of this element in these soils, as well as to favourable mineralization rates [27,34,40]. Low soil acidity favours the solubility of most micronutrients, therefore deficiencies of such elements were not expected. The concentrations of micronutrients were consistent with the average values reported by Aboal et al. [1] for non polluted areas of the same region.

Nutrient concentrations in stem-bark, branches and stemwood in the present study were similar to those reported for other pedunculate oak stands in Europe [15, 21] and Northern America [31], although higher than those recorded by Bosman et al. [9] in Belgium for P, K, Ca and Mg. We also found higher concentrations of P, K, Ca and Mg in stemwood than those reported by Penninckx et al. [39]. In addition,

Table III. Characteristics of the upper soil horizon in the four stands selected for study.

Plot	Soil profile	(Soil A horizon properties)									
	Horizon	Gravel (%)	pH_{KCl}	Bulk density ($g\ cm^{-3}$)	C* (%)	S* (%)	N* (%)	P** ($mg\ kg^{-1}$)	Ca** ($mg\ kg^{-1}$)	Mg** ($mg\ kg^{-1}$)	K** ($mg\ kg^{-1}$)
1	Ah (0–13 cm); AB (13–40 cm); B (40–75 cm)	43	3.75	0.76	5.1	0.08	0.39	10.5	94.5	48.6	182.3
2	Ah (0–10 cm); AB (10–40 cm); B (40–110 cm)	24	4.13	0.72	3.2	0.05	0.26	5.0	116.8	41.9	47.3
3	Ah (0–10 cm); AB (10–35 cm); B (35–60 cm)	28	3.74	0.57	9.4	0.11	0.63	6.2	104.8	60.9	168.1
4	Ah (0–10 cm); AB (10–35 cm); B (35–70 cm)	32	4.03	0.58	7.9	0.10	0.69	4.2	55.6	39.3	93.7

* Total concentration; ** extractable with Mehlich-3 solution.

Table IV. Average concentrations ($mg\ g^{-1}$) of nutrients in tree components for the four plantations selected for study. Standard deviations are given in parentheses.

Tree fraction	C	S	N	P	K	Ca	Mg	Fe	Mn	Ni	Zn	Cu	B
	($mg\ g^{-1}$)												
Stem wood	484.4	0.17	2.57	0.21	1.57	0.63	0.28	0.064	0.271	0.001	0.015	0.004	0.011
	(37.0)	(0.09)	(1.78)	(0.14)	(0.86)	(0.24)	(0.24)	(0.038)	(0.291)	(0.000	(0.011)	(0.002)	(0.006)
Stem bark	512.0	3.26	13.28	0.83	3.45	9.75	1.48	0.070	0.279	0.001	0.021	0.004	0.012
	(12.8)	(4.26)	(5.65)	(0.36)	(0.72)	(3.90)	(0.32)	(0.039)	(0.286)	(0.000)	(0.026)	(0.002)	(0.006)
Branches d > 7 cm	490.9	0.17	2.23	0.21	1.37	1.52	0.30	0.066	0.264	0.001	0.020	0.004	0.011
	(8.2)	(0.05)	(0.57)	(0.03)	(0.25)	(0.48)	(0.14)	(0.038)	(0.290)	(0.000)	(0.026)	(0.002)	(0.006)
Thick branches	484.0	0.56	3.85	0.39	2.37	4.27	0.53	0.068	0.267	0.001	0.020	0.004	0.011
	(20.7)	(0.38)	(0.37)	(0.08)	(0.92)	(0.76)	(0.06)	(0.037)	(0.288)	(0.000)	(0.026)	(0.002)	(0.006)
Thin branches	502.7	0.46	7.51	0.68	2.55	5.59	0.88	0.069	0.274	0.001	0.021	0.004	0.011
	(1.1)	(0.04)	(0.73)	(0.02)	(0.32)	(2.13)	(0.02)	(0.037)	(0.286)	(0.000)	(0.026)	(0.002)	(0.006)
Twigs	506.8	0.80	12.39	0.79	2.75	6.78	0.85	0.068	0.271	0.001	0.020	0.004	0.011
	(5.0)	(0.19)	(3.15)	(0.03)	(0.24)	(4.09)	(0.18)	(0.037)	(0.286)	(0.000)	(0.026)	(0.002)	(0.006)
Leaves	503.8	1.48	23.41	1.23	5.54	4.39	1.25	0.070	0.281	0.001	0.019	0.004	0.011
	(25.3)	(0.81)	(12.94)	(0.82)	(2.61)	(0.89)	(0.59)	(0.037)	(0.286)	(0.000)	(0.026)	(0.002)	(0.006)
Roots	486.4	0.16	2.52	0.19	1.52	0.72	0.32	0.065	0.057	0.009	0.002	0.001	0.005
	(39.0)	(0.11)	(1.66)	(0.11)	(0.73)	(0.22)	(0.21)	(0.023)	(0.101)	(0.004)	(0.001)	(0.001)	(0.003)

Table V. Concentrations of elements ($mg\ g^{-1}$) in oak leaves and litter layer in the four stands selected for study.

Plot	Fraction	C	S	N	P	K	Ca	Mg	Fe	Mn	Ni	Zn	Cu	B
		($mg\ g^{-1}$)												
1	Leaves	519.2	1.71	29.10	0.68	3.68	3.15	1.11	0.094	0.28	0.001	0.012	0.003	0.010
	Litter layer	311.0	3.72	16.13	0.75	2.20	3.60	3.74	12.78	0.43	0.012	0.053	0.016	0.008
2	Leaves	517.1	2.01	30.57	2.16	8.12	4.96	1.83	0.112	0.91	0.001	0.025	0.006	0.011
	Litter layer	115.0	0.71	11.22	0.32	0.75	2.44	1.61	11.35	0.44	0.013	0.030	0.005	0.002
3	Leaves	513.4	1.93	29.95	1.68	7.42	4.34	1.58	0.131	1.13	0.001	0.017	0.005	0.015
	Litter layer	432.0	4.81	19.34	0.84	1.57	3.38	1.64	5.360	0.66	0.008	0.038	0.010	0.002
4	Leaves	514.0	1.60	25.33	0.80	3.93	5.12	0.90	0.080	0.40	0.001	0.007	0.003	0.011
	Litter layer	395.0	4.35	19.11	0.67	0.95	5.24	0.88	3.570	0.76	0.005	0.037	0.008	0.007

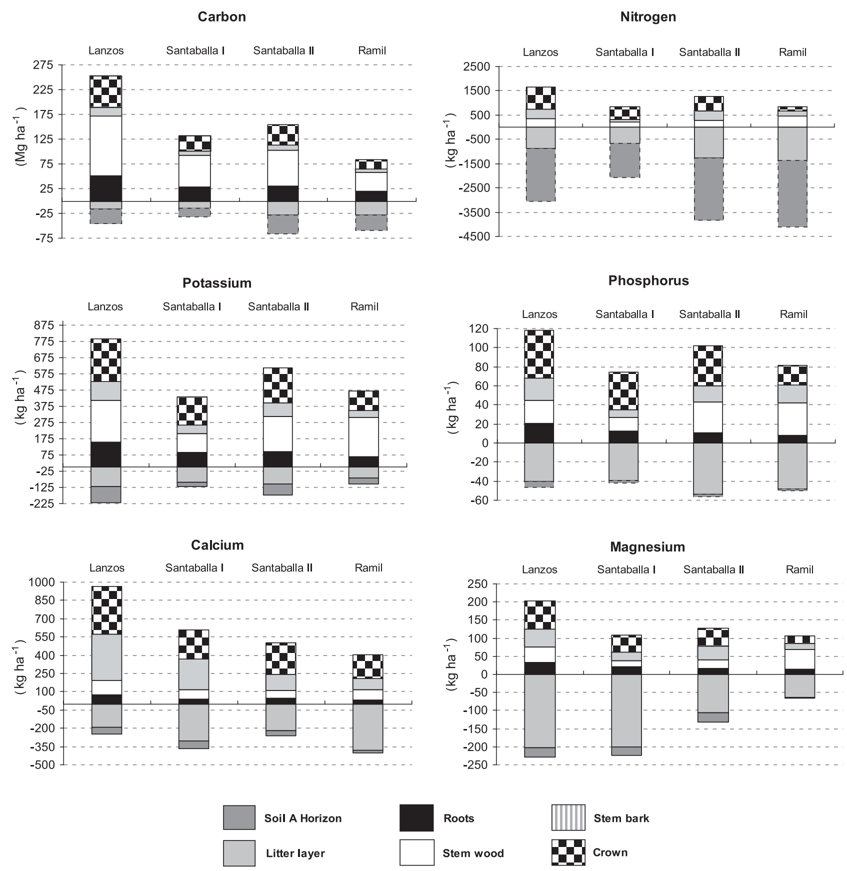

Figure 2. Accumulation of C, N, P, Ca, K and Mg in tree biomass and soil A horizon in the four *Quercus robur* stands studied.

the concentrations of nutrients in roots decreased in the order N > K > Ca > Mg > P > S, which differs from the pattern observed by Bakker [4] for fine-roots of oak trees.

3.3.2. Litter layer

The litter layer mass (Fig. 2 and Tab. VI), which was mainly composed of leaves and fine branches and, to a lesser extent, remains of shrubs and grasses, was much higher than those in commercial plantations in the region [33]. This is attributable to the higher mass of foliage and branches in the oak stands. Thus, the crown mass in living trees accounted for 87% of the differences in litter accumulation among species. With the exception of stand 2, the mass of the litter layer was closely related to the tree density ($r = 0.91$, $P < 0.05$). The higher accumulation of litter in stand 2 may have been due to lower decomposition rates as a consequence of the high humidity of the soil.

Furthermore, concentrations of N, K and B in the litter layer were lower than in the foliage (Tab. V). In contrast, the concentrations of Fe and Zn were lower in green leaves than in the litter. No clear pattern in the concentrations of P, Ca and Mg was evident. The processes involved in the different trends are translocation before leaf abscission, as well as different biotic and abiotic factors regulating the decomposition process (e.g. [2]).

3.4. Nutrient distribution in the system

In the four stands studied, the amounts of P, K, Ca and Mg in the tree biomass were higher than the available reserves in the soil (litter layer plus extractable amounts in the mineral soil, Fig. 2 and Tab. VI). Because of the large amount of biomass, stem wood was the major tree compartment for most nutrients, with the exception of Ca, which was mainly accumulated in the stem bark. Stem wood and stem bark, which accounted for 54% of the whole tree biomass, accumulated between 35 and 50% of the macronutrients contained in the whole tree biomass. For the stand crown biomass, which represents 25% of the whole tree biomass, the corresponding range was 33–42%.

The oak forests under study contained larger quantities of nutrients per kg of biomass than other commercial forest species in the region, such as *Eucalyptus globulus*, *Pinus radiata* and *Pinus pinaster* [33]. Thus, one ton of oak aerial biomass accumulated three times more Ca, and twice as much N, P and K as the other species. The main differences can be attributed to the higher concentrations of Ca (in the crown fraction), N, P and K (in the stem wood) of the oak trees, as well

Table VI. Average biomass, C and nutrient distribution in trees, litter and soil for the four pedunculate oak stands studied. Standard deviation and error of the estimates proposed by Cunia (1986) are given in brackets.

	% with respect to aerial biomass	Biomass (Mg ha^{-1})	C* (kg ha^{-1})	N*	P	K	Ca	Mg	Fe	Mn	Zn	Cu	Ni
Leaves	**4.4 %**	**11.6**	6014	337	14.6	64.8	48.6	15.6	1.2	7.4	0.18	0.05	0.01
	(0.6 %)	(4.1**)	(1998)	(119)	(6.7)	(22.9)	(4.6)	(5.3)	(0.4)	(4.1)	(0.08)	(0.01)	(0.01)
Twigs	**1.0 %**	**2.7**	1359	33	2.1	7.3	18.1	2.3	0.2	0.7	0.07	0.02	0.00
	(0.1 %)	(0.9**)	(403)	(10)	(0.7)	(1.9)	(11.4)	(0.8)	(0.1)	(0.3)	(0.04)	(0.01)	(0.00)
Branches	**22.8 %**	**61.4**	30238	232	21.9	120.7	200.7	31.4	2.2	6.4	0.47	0.19	0.05
	(7.1 %)	(35.5**)	(16130)	(105)	(9.2)	(48.7)	(79.3)	(12.5)	(1.2)	(2.5)	(0.17)	(0.08)	(0.02)
Stem bark	**8.3 %**	**22.2**	11345	289	17.4	77.2	223.4	33.2	2.6	8.4	0.98	0.09	0.03
	(1.2 %)	(9.8**)	(4227)	(119)	(6.9)	(31.7)	(124.7)	(15.4)	(1.0)	(5.6)	(0.77)	(0.03)	(0.01)
Stem wood	**59.1 %**	**140.4**	69161	303	24.7	195.1	81.5	32.3	7.1	7.5	1.09	0.35	0.12
	(1.8 %)	(63.4**)	(32833)	(93)	(8.7)	(57.6)	(22.7)	(13.6)	(3.6)	(6.4)	(0.70)	(0.14)	(0.04)
Aerial biomass		**238.4**	118119	1194	80.8	465.2	572.2	114.9	13.3	30.5	2.79	0.70	0.22
		(113.9**)	(58240)	(384)	(16.4)	(128.3)	(227.4)	(38.1)	(3.6)	(6.3)	(0.22)	(0.27)	(0.08)
Roots		**66.3**	32248	167	12.6	100.7	47.2	21.2	4.0	5.2	0.59	0.17	0.06
		(27.8**)	(12456)	(39)	(4.0)	(21.3)	(17.6)	(9.0)	(1.8)	(4.8)	(0.35)	(0.07)	(0.02)
Total biomass		**304.5**	150291	1361	93.4	565.3	619.8	136.0	17.2	34.3	2.92	0.77	0.81
		(131.7**)	(57876)	(312)	(19.5)	(139.6)	(178.2)	(35.5)	(3.5)	(6.7)	(0.15)	(0.23)	(0.30)
Litter layer		**79.0**	24750	1177	50.5	108.2	289.9	55.6	652.5	45.0	3.08	0.71	0.71
		(31.4)	(11178)	(521)	(18.1)	(52.1)	(92.4)	(97.1)	(354.7)	(12.6)	(0.80)	(0.39)	(0.32)
Soil A hor*			29043	2238	3.2	58.5	45.5	19.7	84.3	4.8	0.86	0.19	0.28
			(8611)	(591)	(1.8)	(34.3)	(17.8)	(10.8)	(27.7)	(2.7)	(0.31)	(0.16)	(0.19)
Soil upper 30 cm*			64246	5415	6.2	119.8	61.3	26.8	199.5	8.5	1.13	0.58	0.52
			(19416)	(1829)	(2.2)	(56.3)	(14.8)	(11.8)	(82.6)	(6.2)	(0.39)	(0.34)	(0.39)
Soil*			131051	11709	14.5	242.9	103.0	40.6	482.9	19.4	1.54	1.75	0.74
			(12438)	(815)	(7.0)	(124.3)	(27.8)	(18.4)	(290.0)	(15.2)	(0.86)	(1.44)	(0.57)

* C and N are total amounts, the others are extractable with Mehlich-3 solution.

** Error of the estimate calculated as Cunia (1986) suggests.

as to the higher proportion of crown fractions, with higher nutrient concentrations than in wood and branches.

Higher concentrations of elements were accumulated in the soil litter layer of these systems than in tree biomass and soil, thereby reflecting the importance of the litter layer as a source of nutrients [19, 30]. On average, this compartment accumulated 32% of the P and 24% of Ca and Mg of the whole forest system (Tab. VI). The litter layer of these oak forests accumulated between 2 and 3 times the amounts of nutrients in commercial plantations in the region [33]. Higher nutrient concentrations in the litter layer under native forests have also been described elsewhere and have been attributed to the higher rates of litterfall nutrient cycling [8]. The leaf litter from these natural oak forests has commonly been removed for use as a soil supplement for subsistence crops in the region, indicating that it is considered as a good source of nutrients [6].

The amounts of some nutrients in tree biomass were related to nutrient availability in the soil. Thus, the tree biomass stocks of P, Ca and particularly, K were correlated with the available storages in the soil upper mineral horizon (r = 0.75, 0.71 and 0.99, respectively, $P < 0.05$). We also found significant correlations between the amounts of Mg and Ca accumulated in leaves and the available amounts stored in the upper mineral horizon (r = 0.99 and 0.76 respectively, $P < 0.05$).

3.5. Carbon pools in the system

In the present study, the average C stock of total tree biomass at stand level amounted to 150 Mg ha^{-1} (range 82–243 Mg ha^{-1}, Fig. 2 and Tab. VI), which accounted for 50% of the C accumulated in the whole system (tree biomass, litter layer and total mineral soil). The high number of larger trees in stand 1 led to a substantial increase in the C stock in the system. The average C accumulation in aboveground tree biomass of these stands, 118 Mg ha^{-1} (range 62–194 Mg ha^{-1}), was comparable to that of *Pinus pinaster*, 99 Mg ha^{-1}, *Pinus radiata*, 135 Mg ha^{-1} (in the latter calculation biomass removed by thinning was considered for a rotation length of 30 years; [5]) and *Eucalyptus globulus*, 117 (for rotation length of 18 years, [33]). For root biomass, the

C stock reached 32.2 Mg ha^{-1}. The amounts of C in biomass were consistent with those reported by Vande Walle et al. [52] for oak-beech stands in Belgium.

The average C storage in the mineral soil amounted to 131 Mg ha^{-1} (range 73–144 Mg ha^{-1}), which makes up 43% of the whole ecosystem. Carbon storage in the mineral soils under study was correlated with the C stocks in the litter layer ($r = 0.99$, $P < 0.01$) and the amounts of C in tree biomass ($r = 0.50$, $P < 0.01$), possibly indicating that the organic matter contents of the soils are in equilibrium with the litter production.

The biomass equations fitted in the present study, as well as a height-diameter relationship for pedunculate oak [6] were applied to data from the Spanish National Forest Inventory [53]. The availability of the biomass data, along with the C concentrations in tree components, allowed us to carry out preliminary estimations of the C storage in pedunculate oak forest in NW Spain (Galicia surface, 3 000 000 ha). Thus, for a total of around 93 000 000 measurable trees, C stocks in tree biomass (including roots) may reach almost 14 500 000 Mg. Nevertheless, further estimates that take into consideration the different management regimes applied to these systems will allow improvement of this preliminary estimate, as well as of the data corresponding to C accumulation in the soils.

4. CONCLUSIONS

The data obtained in the present study confirm the important function of near natural forests as long-term C sinks, in both forest biomass and soil. The long term C storage potential of these systems is very high, especially in less- intensively managed forests that include large trees. Non wood components should be considered in carrying out accurate estimates of C storages in these systems, not only because of the large amounts of C accumulated in these compartments, but also because of their effect on C stocks in soils. To avoid further degradation of these systems, management schedules and harvesting programmes should take into account the importance of the litter layer and the crown fractions as major reservoirs of nutrients. Moreover, protection of these ecosystems may enhance their role as long-term C sinks.

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