

Litterfall and litter decomposition in chestnut high forest stands in northern Portugal

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Abstract

This research aimed to: estimate the inputs of litterfall; model the decomposition process and assess the rates of litter decay and turnover; study the litter decomposition process and dynamics of nutrients in old chestnut high forests. This study aimed to fill a gap in the knowledge of chestnut decomposition process as this type of ecosystems have never been modeled and studied from this point of view in Portugal. The study sites are located in the mountains of Marão, Padrela and Bornes in a west-to-east transect, across northern Portugal, from a more-Atlantic-to-less-maritime influence. This research was developed on old chestnut high forests for quality timber production submitted to a silviculture management close-to-nature. We collected litterfall using littertraps and studied decomposition of leaf and bur litter by the nylon net bag technique. Simple and double exponential models were used to describe the decomposition of chestnut litterfall incubated *in situ* during 559 days. The results of the decomposition are discussed in relation to the initial litter quality (C, N, P, K, Ca, Mg) and the decomposition rates. Annually, the mature chestnut high-forest stands (density 360-1,260 tree ha⁻¹, age 55-73 years old) restore 4.9 Mg DM ha⁻¹ of litter and 2.6 Mg ha⁻¹ yr⁻¹ of carbon to the soil. The two-component litter decay model proved to be more biologically realistic, providing a decay rate for the fast initial stage (46-58 yr⁻¹ for the leaves and 38-42 yr⁻¹ for the burs) and a decay rate related to the recalcitrant pool (0.45-0.60 yr⁻¹ for the leaves and 0.22-0.36 yr⁻¹ for the burs). This study pointed to some decay patterns and release of bioelements by the litterfall which can be useful for calibrating existing models and indicators of sustainability to improve both silvicultural and environmental approaches for the management of chestnut forests.

Key words: *Castanea sativa* Mill.; decomposition rate; turnover; nutrient use efficiency; double exponential model.

Resumen

La hojarasca y su descomposición en bosques de castaño de monte alto en el Norte de Portugal

Esta investigación tuvo como objetivo calcular los aportes de hojarasca; modelar el proceso de descomposición y evaluar las tasas de descomposición de la hojarasca y el *turnover*; estudiar el proceso de descomposición de la hojarasca y la dinámica de nutrientes en bosques de castaños de monte alto. Asimismo, se quiso llenar un vacío en el conocimiento del proceso de descomposición del castaño ya que este tipo de ecosistemas no han sido modelados y estudiados desde este punto de vista en Portugal. El estudio se realizó en las montañas de Marão, Padrela y Bornes situados en un transecto que va de oeste a este, en el norte de Portugal, de mayor a menor influencia Atlántica. La investigación se desarrolló en bosques de castaños antiguos dedicados a la producción de madera de calidad sometida a una gestión silvícola cercana a la naturaleza. Se emplearon colectores de hojarasca y se estudió la descomposición de hojarasca y erizos mediante el empleo de bolsas de red de nylon. Para describir la descomposición de hojarasca del castaño mediante la incubación *in situ* durante 559 días se utilizaron modelos exponenciales simple y doble. Los resultados de la descomposición se discuten en relación a la calidad de la hojarasca inicial (C, N, P, K, Ca, Mg) y las tasas de descomposición. Anualmente, las masas de castaño (densidad 360-1.260 árboles ha⁻¹, edad 55-73 años) producen 4,9 Mg DM ha⁻¹ de hojarasca al suelo y 2,6 Mg ha⁻¹ año⁻¹ de carbono. El modelo exponencial doble de descomposición de hojarasca demostró ser biológicamente más realista, con una tasa de descomposición para la fracción lábil (46-58 años⁻¹ para las hojas y 38-42 años⁻¹ para los erizos) y una tasa de descomposición para la fracción recalcitrante (0,45-0,60 años⁻¹ para

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las hojas y $0,22-0,36 \text{ años}^{-1}$ para los erizos). Los resultados obtenidos mostraron la existencia de patrones de descomposición y liberación de los bioelementos de la hojarasca que pueden ser útiles para la calibración de los modelos existentes y indicadores de sostenibilidad que permitan mejorar los enfoques silvícolas y medioambientales de cara a una gestión sostenible de los bosques de castaño.

Palabras clave: *Castanea sativa* Mill.; tasa de descomposición; *turnover*; eficiencia en el uso de nutrientes; modelo exponencial doble.

Introduction

The sweet chestnut constitutes an important species in Europe occupying 2.53 million hectares. Nowadays, there is a growing interest in the species as a form of economic and environmental enhancement of mountain areas. In Portugal, the species is located essentially in the North from 400-1,100 m above sea level and there are three major management systems: groves, coppices and high forest for quality timber production. In the mountain areas, the coppices and high forest are particularly relevant, especially in deep forest soils. These chestnut areas are natural ecosystems and constitute discontinuities between conifer forests and are important for forest fire prevention, biodiversity and environmental protection. The sustainable management of these areas is crucial and depends on the knowledge of the inputs and outputs of the system.

The litter on the forest floor works as an input-output system of nutrients and the rates at which forest litter falls and decays are the main regulators of primary productivity, energy flow and nutrient cycling in forest ecosystems (Olson, 1963; Bray and Gorham, 1964). Litterfall is a major component of net primary productivity and may provide important information as a phenological indicator of climate change effects on forests (Hansen *et al.*, 2009). One of the ways of evaluating the efficiency of litter decomposition and release of bioelements in low nutrient forest ecosystems is to analyze ratios of dry mass to nutrient flux in litterfall (Vitousek, 1984). Decomposition studies in chestnut high forest for quality timber production are rare in literature. The most related studies are those developed on chestnut coppices (e.g. Gallardo *et al.*, 1995; Martins *et al.*, 2009; Santa-Regina and Gallardo, 1985; Santa-Regina, 2000; Santa-Regina *et al.*, 2005) but of different ages and silviculture managements in particular, density, time period of wood production and dimensions of the wood produced. The modeling of chestnut litter decomposition has been usually done

using the simple exponential model. To our knowledge, no study has applied the double exponential model for the chestnut, addressing the questions of how this model fits to the decay process for this species and how the mass loss takes place in different situations.

Our research was developed on old chestnut high forests for quality timber production submitted to a silviculture management close-to-nature. The study considered three sites, representative of these areas, located in a west-to-east transect, across northern Portugal, from a more-Atlantic-to-less-maritime influence. The study sites are located in the mountains of Marão (the most Atlantic), Padrela (intermediate location) and Bornes (the most inland).

The aim of this research is to (a) estimate the inputs of litterfall, (b) model the decomposition process and assess the rates of litter decay and turnover, (c) study the litter decomposition process and dynamics of nutrients along the considered transect. Furthermore, the nutrient use efficiencies in the three sites are compared. The outcome of this study will be useful to define the indicators of sustainability, in order to improve the management of forest chestnut ecosystems and assess their services, since such studies are scarce. The results of decomposition and nutrient pools can serve as an indicator in characterizing the ecosystems and this information can be used to calibrate existing models filling a gap in the knowledge of chestnut decomposition process as this type of ecosystems have never been modeled and studied from this point of view in Portugal.

Material and Methods

Study site and sampling design

The present study was carried out in three high forest mature chestnut stands located in three mountains: Marão, Padrela and Bornes, following a west-to-east

transect across northern Portugal, from a more-Atlantic-to-less-maritime influence, respectively. The soils in the stands have developed over metamorphic rocks (schist).

In each chestnut stand, a permanent plot of 1,000 m² was established to evaluate the growth and yield of the trees. General characteristics of the stands are in Table 1.

Litterfall was estimated by randomly placing seven circular 1m² litter traps in Padrela and Marão and eight in Bornes. Litter traps were laid out in September 2008 and litter was collected at monthly intervals for 2 years (September 2008 until September 2010). The leaf litter and bur decomposition at the 3 sites were studied by the nylon net bag technique (Bocock *et al.*, 1960), during 559 days, through weight loss and nutrient concentration evolution. Mature fallen leaves and burs were collected separately in each site and air-dried in the laboratory. The initial chemical composition, ash and C/N ratio for the leaf and bur litter are presented in Table 2. A total of 75 nylon-net bags (15 × 15 cm, 1 mm mesh) containing 20 g of air-dried leaf litter and 30 bur-bags (15 × 15 cm, 1 mm mesh) containing 30 g

of air-dried bur litter for each site were prepared and placed randomly at five different group locations on the floor of every stand next to the litter traps, inside and near the permanent dendrometrical plots. The bags were fixed to the soil surface by a u-shaped wire. The bags were kept side by side, at the same location, during the observation period. At least five bags containing decomposing leaf litter and 2 bags containing bur litter were randomly recovered at 1.5 month intervals from each site. After being recovered, the bags were placed in individual polyethylene bags and transported to the laboratory.

Chemical analyses

The collected litter samples were separated into leaves, branches, fruits and burs, oven dried to constant weight at 70 °C and finely ground. Subsamples of each fraction were subjected to wet digestion with sulphuric acid (Houba *et al.*, 1986) subsequently followed by colorimetric method measurements of N and P concen-

Table 1. General characteristics of the studied chestnut stands (northern Portugal)

Chestnut stands	Marão	Padrela	Bornes
Latitude	41° 14' 46" N	41° 30' 41" N	41° 29' 42" N
Longitude	7° 55' 04" W	7° 37' 15" W	6° 55' 12" W
Altitude (m a.s.l.)	900	850	800
Slope (°)	5-10	25-30	15-20
Main soil type ¹	<i>Umbric Regosols</i>	<i>Dystric Regosols</i>	<i>Dystric Cambisols</i>
Soil type profile ²			
pH	4.8	4.9	5.4
FH layer (Mg ha ⁻¹) ³	15.3	15.0	8.4
Organic matter (Mg ha ⁻¹)	371.8	259.7	154.7
N (g kg ⁻¹)	5.8	3.2	1.6
P (mg kg ⁻¹)	4.5	4.3	0.7
Ca (cmol _c kg ⁻¹)	0.05	0.40	0.86
Mean annual temperature (°C) ⁴	11.5-12.0 ^a	12.5 ^b	11.9 ^c
Mean annual precipitation (mm yr ⁻¹) ⁴	2505 ^d	1132 ^e	1009 ^f
Density (tree ha ⁻¹)	360	470	1260
Age (yr) ⁵	73	66	55
Mean DBH (cm) ⁶	40.5 ± 9.0	34.0 ± 6.3	26.8 ± 6.1
Mean height (m) ⁶	29.9 ± 2.7	21.3 ± 2.4	23.8 ± 2.7
Basal area (m ² ha ⁻¹) ⁶	157.9	135.2	223.8
LAI	4.9	4.9	4.4

¹ According to World Reference Base for Soil (FAO, 1988); ² Weighted mean values of 0-65cm in Marão and Padrela and 0-60 cm in Bornes (Patrício *et al.*, 2010); ³ FH fermentative (F) and humus (H) horizons together; ⁴ Mean values for the period 1951-1981 (INMG, 1991); ⁵ Age in 2010; ⁶ Values obtained in 2008.

^a National Environment Commission (CNA, 1975); ^b Meteorological Station (41° 33' N; 7° 36' W; 613 m a. s. l.); ^c Meteorological Station (41° 48' N; 6° 44' W; 690 m a. s. l.); ^d Udometric Station (41° 34' N; 7° 30' W; 950 m a. s. l.); ^e Udometric Station (41° 17' N; 7° 54' W; 800 m a. s. l.); ^f Udometric Station (41° 28' N; 6° 44' W; 700 m a. s. l.).

Table 2. Initial chemical composition (g kg⁻¹), ash, C/N and C/P ratios for the leaf and bur litter of chestnut stands

	Marão		Padrela		Bornes	
	Leaves	Burs	Leaves	Burs	Leaves	Burs
C	597.70	538.75	525.93	473.10	541.29	459.27
Ash	54.00	22.30	43.00	22.60	49.00	30.60
N	12.73	11.17	7.83	9.13	5.65	6.10
P	0.79	0.86	0.35	0.70	1.29	0.74
K	2.90	4.03	4.60	6.30	3.11	4.90
Ca	4.95	2.89	4.51	2.89	6.56	3.43
Mg	2.45	1.19	2.43	1.53	3.42	1.64
C/N	46.97	48.24	67.19	51.79	95.81	75.25
C/P	747.45	625.72	1,488.68	673.93	418.43	623.44

trations using a segmented flow autoanalyzer (SanPlus, Skalar, Breda, The Netherlands). For the K, Ca, Mg and S determinations, samples were digested with nitric-perchloric acid (Mills and Jones, 1996). Ca and Mg being determined by atomic absorption spectrophotometry (AAS 3100, Perkin-Elmer, USA), K by flame photometry (flame photometer PFP7, Jenway, UK) and S by the turbidimetric method (Coutinho, 1996). Total organic C was determined with a PRIMA-SC carbon analyzer (Skalar, Breda, The Netherlands). Residual ash was determined by incineration at 450 °C for 6 h in a muffle furnace.

Statistical analysis

A One-way ANOVA was performed to compare the total amounts of litterfall among the three study sites using the SPSS 17.0 for Windows. A Tukey HSD test ($\alpha = 0.05$) was done for mean multiple comparisons to detect significant differences. The same statistical analysis was used to compare the mineral concentrations in the biomass of the litterbags.

Two different models were fitted to the decomposition data (mass loss) of leaves and burs over time: the single exponential decay model (Olson, 1963) and the double exponential decay model (Wieder and Lang, 1982).

The decomposition constant (k) of leaves and burs for the simple negative exponential decay model was calculated from the following equation: $X_t/X_o = e^{-kt}$, where X_o is the original mass of litter, X_t is the amount of litter remaining after time t and t is the time (years).

The double exponential decay model separates litter material into two components, one that is soluble or easy to decompose (e.g., soluble matter and non-lignified organic carbon) and another that is recalcitrant or

insoluble. The model was fitted as: $X_t/X_o = A e^{-k_1 t} + (1-A) e^{-k_2 t}$, where A is a constant that indicates the easily decomposable fraction of the litter material, and $(1-A)$ is the recalcitrant fraction. This model is considered to be more realistic as it separates decomposition into two stages (O'Connell, 1987). The k_1 represents the decay rate for the faster initial stage and involves soluble components leaching out, and easily degraded compounds (sugars, starches, proteins). The k_2 is the decay rate related to the recalcitrant pool. Non-linear regression analysis of decomposition results were performed using the SPSS non-linear procedure and the Marquardt iterative method (SPSS 17.0 for Windows). The fit index (FI) was calculated as $[1 - (\text{Residual Sum of Squares}) / (\text{Corrected Sum of Squares})]$. The comparison of the goodness of fit of the models was made based on FI and on the biological meaning of the regression coefficients checked graphically.

For every site, the time required for 50% mass loss (half-life) of leaves and burs was calculated as $t_{50} = 0.693/k$ and the turnover as $1/k$.

Nutrient use efficiency (NUE) was calculated according to Vitousek (1984) and Pandey *et al.* (2007): $NUE = \text{Litterfall mass (kg ha}^{-1} \text{ year}^{-1}) / \text{Nutrient content in litterfall (kg ha}^{-1} \text{ year}^{-1})$.

Pearson's correlation coefficients (2-tailed) were calculated between several variables related to the decomposition process using the SPSS 17.0 for Windows.

Results

Litterfall

The overall mean annual litterfall was 4.9 Mg DM ha⁻¹ yr⁻¹. The total litterfall quantities by site

were not significantly different (Tukey test $p > 0.05$). The annual quantities of C returned to the soil were also similar among sites ($2.6 \text{ Mg ha}^{-1} \text{ yr}^{-1}$). Significant differences in partial components of litterfall were observed, i.e., for the leaves, burs and fruits (Table 3). The leaf litter component contributed 66-70% of the total litterfall (Table 3) and was the main pathway of potential return of carbon and nutrients to the soil, being responsible for 61-74% of the total N, 51-70% of P, 61-67% of K, 65-77% of Ca, 83-85% of Mg, 76-87% of S and 69-73% of C (Table 4). There were significant differences between the potential nutrients returned in the soil in the three sites. The overall N return of all the fractions in Bornes ($26.4 \text{ kg ha}^{-1} \text{ yr}^{-1}$) was lower ($p = 0.03$) than in Marão ($59.4 \text{ kg ha}^{-1} \text{ yr}^{-1}$), and similar to Padrela ($p > 0.05$) (Table 4). The overall P return of all the fractions in Bornes presented the highest value ($5.1 \text{ kg ha}^{-1} \text{ yr}^{-1}$) and was different ($p = 0.01$) from Padrela ($2.4 \text{ kg ha}^{-1} \text{ yr}^{-1}$), and similar to Marão ($p > 0.05$). Padrela presented the highest value of potential return of K ($26.0 \text{ kg ha}^{-1} \text{ yr}^{-1}$) which was different ($p = 0.02$) from the other sites. The return of Ca and Mg was similar ($p > 0.05$) in the three places. The potential return of S was different ($p < 0.03$) among locations and the highest value was observed in Marão ($1.7 \text{ kg ha}^{-1} \text{ yr}^{-1}$).

Mass loss

The tendency of average mass loss from litter contained in the bags was similar in the three locations, both for leaves and burs, as shown in Figure 1. The

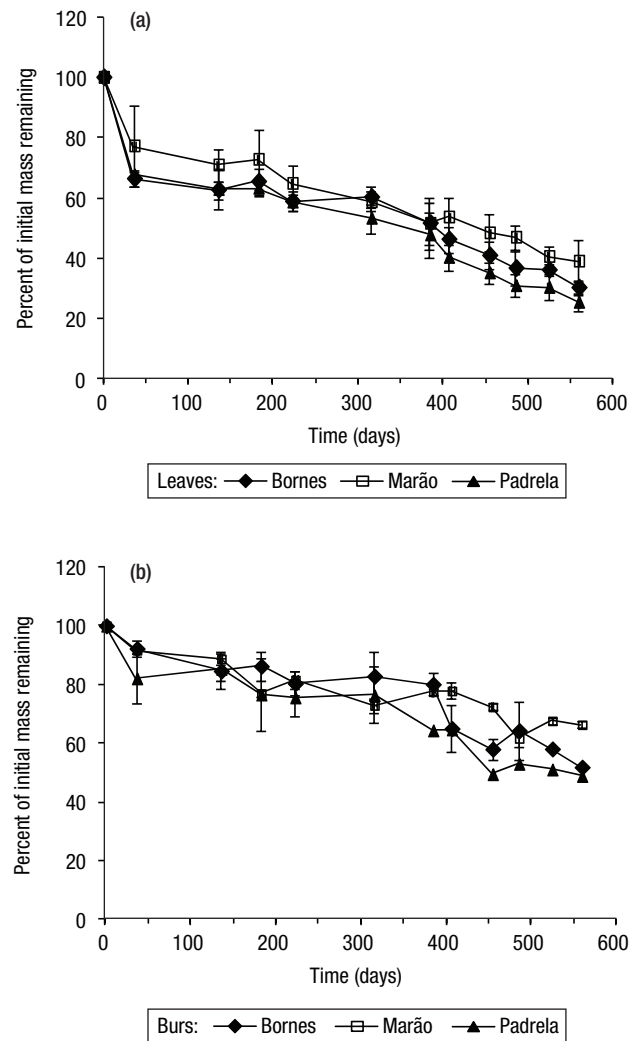


Figure 1. Percent of initial dry-mass remaining as a function of incubation period in (a) decomposing leaf and (b) bur litter. Bars indicate means \pm standard deviation.

Table 3. Average annual litter production of litterfall components in the three high forest mature chestnut stands

Litter fraction	$F_{(2,41)}$	P -values	Marão		Padrela			Bornes			
			Litter production	SE	Litter production	SE	Litter production	SE	Litter production	SE	
			(Mg DM $\text{ha}^{-1} \text{ yr}^{-1}$)		(Mg DM $\text{ha}^{-1} \text{ yr}^{-1}$)		(Mg DM $\text{ha}^{-1} \text{ yr}^{-1}$)		(Mg DM $\text{ha}^{-1} \text{ yr}^{-1}$)		
Leaves	5.18	0.01	3.46 b	0.10	68.56	3.43 b	0.10	66.43	3.09 a	0.07	69.51
Branches	0.81	0.45	1.00 a	0.47	19.82	0.49 a	0.13	9.62	0.63 a	0.15	14.24
Burs	9.75	0.00	0.30 a	0.04	6.02	0.70 b	0.10	13.66	0.41 a	0.05	9.26
Fruits	4.41	0.01	0.28 a	0.04	5.60	0.53 b	0.08	10.29	0.31 a	0.06	6.99
Total	1.63	0.21	5.05 a	0.44	100	5.16 a	0.24	100	4.45 a	0.20	100

The same letter in lines indicates, for the respective litter fraction, no significant differences at $p > 0.05$ among means (Tukey HSD test); SE standard error.

Table 4. Average amounts of N, P, K, Ca, Mg, S (kg ha⁻¹ yr⁻¹) and C (Mg ha⁻¹ yr⁻¹) of litterfall components in the three high forest mature chestnut stands

	Marão							Padrela							Bornes						
	Leaves	Branches	Burs	Fruits	Total	SE	NUE	Leaves	Branches	Burs	Fruits	Total	SE	NUE	Leaves	Branches	Burs	Fruits	Total	SE	NUE
N	44.10	6.66	3.40	5.26	59.42b	6.61	84.99	26.85	3.52	6.44	7.47	44.28ab	4.05	116.53	17.49	3.86	2.52	2.52	26.38a	2.93	168.69
P	2.75	0.29	0.26	0.60	3.90ab	0.33	1294.87	1.21	0.16	0.50	0.51	2.38a	0.19	2168.07	4.00	0.38	0.30	0.39	5.08b	0.28	875.98
K	10.05	1.52	1.22	2.43	15.22a	1.54	331.80	15.78	0.81	4.44	4.96	26.00b	1.61	198.46	9.61	1.00	2.02	1.74	14.38a	0.90	309.45
Ca	17.17	7.12	0.88	1.11	26.28a	5.88	192.16	15.45	2.11	2.04	0.56	20.16a	2.49	255.95	20.29	5.77	1.41	0.60	28.07a	4.31	158.53
Mg	8.50	0.88	0.36	0.43	10.17a	0.97	496.56	8.33	0.35	1.08	0.32	10.08a	0.84	511.90	10.59	1.00	0.68	0.22	12.48a	0.83	356.57
S	1.45	0.09	0.04	0.09	1.67c	0.12	3023.95	0.8	0.06	0.05	0.14	1.05b	0.08	4914.28	0.13	0.01	0.004	0.02	0.16a	0.00	27812.5
C	2.07	0.54	0.16	0.15	2.93a	0.47	1.72	1.80	0.23	0.33	0.24	2.61a	0.28	1.98	1.67	0.30	0.19	0.13	2.30a	0.24	1.93

Results of One-Way ANOVA by site: N - $F_{(2,3)} = 11.93$ $p = 0.03$; P - $F_{(2,3)} = 24.69$ $p = 0.01$; K - $F_{(2,3)} = 21.84$ $p = 0.01$; Ca - $F_{(2,3)} = 0.87$ $p = 0.50$; Mg - $F_{(2,3)} = 2.37$ $p = 0.24$; S - $F_{(2,3)} = 77.26$ $p = 0.00$; C - $F_{(2,3)} = 0.82$ $p = 0.52$; The same letter in lines indicates, for the respective element, no significant differences at $p > 0.05$ among means (Tukey HSD test); NUE - nutrient use efficiency; SE Standard error.

ash-free percentages of original mass remaining of leaves and burs at the end of the experiment (559 days) were 30% and 52%, respectively in Bornes, 39% and 66%, respectively in Marão and 25% and 49%, respectively in Padrela (Fig. 1). After 559 days, Padrela had lost 75% of its original leaf litter dry weight whereas Bornes had lost 70% and Marão 61% of its initial leaf litter dry weight. At the end of the study period, the mass loss was higher in Padrela followed by Bornes and Marão, respectively, both for leaves and burs.

Decomposition rates

The double exponential decay model for the leaves and burs litter fitted better than the single exponential model based on the biological meaning of the regression coefficients and the goodness of fit of the model, given by the fit index (FI) equivalent to the coefficient of determination in linear regression (R^2) (Table 5 and 6). Values of kinetic parameters estimated according to this model showed a labile pool (constant A) that ranged from 0.21-0.30 for the leaves (Table 5) and from

Table 5. Kinetic parameters for the single and double exponential decay models for the leaves in the three study sites

	Marão	Padrela	Bornes
	Simple exponential model for the leaves ($X_t/X_0 = e^{-kt}$)		
K _{1s} (yr ⁻¹)	0.66	0.80	0.72
FI	0.81	0.56	0.26
K _{1.5s} (yr ⁻¹)	0.61	0.84	0.73
FI	0.92	0.91	0.84
Double exponential model for the leaves ($X_t/X_0 = A e^{-k_1t} + (1-A) e^{-k_2t}$)			
A	0.30	0.21	0.29
K ₁ (yr ⁻¹)	58.00	46.11	55.00
K ₂ (yr ⁻¹)	0.60	0.45	0.47
FI	0.98	0.98	0.96
Half-life1 (days)	4.36	5.49	4.60
Turnover1 (days)	6.29	7.92	6.64
Half-life2 (yr)	1.15	1.54	1.47
Turnover2 (yr)	1.67	2.22	2.12

Simple exponential model: K_{1s}, decomposition rate for the 1st year of incubation. K_{1.5s}, decomposition rate for the 1.5 years of incubation. FI, goodness of fit of the model (fit index).

Double exponential model: A, labile fraction; K₁ and K₂, decomposition rates.

Table 6. Kinetic parameters for the single and double exponential decay models for the burs in the three study sites

	Marão	Padrela	Bornes
Simple exponential model for the burs ($X_t/X_0 = e^{-kt}$)			
K _{1s} (yr ⁻¹)	0.32	0.41	0.26
FI	0.71	0.66	0.59
K _{1.5s} (yr ⁻¹)	0.29	0.46	0.36
FI	0.80	0.89	0.86
Double exponential model for the burs ($X_t/X_0 = A e^{-k_1t} + (1-A) e^{-k_2t}$)			
A	0.08	0.12	0.04
K ₁ (yr ⁻¹)	40.00	42.00	38.00
K ₂ (yr ⁻¹)	0.22	0.36	0.35
FI	0.93	0.95	0.90
Half-life1 (days)	6.32	6.02	6.66
Turnover1 (days)	9.13	8.69	9.61
Half-life2 (yr)	3.19	1.94	1.99
Turnover2 (yr)	4.61	2.79	2.86

Simple exponential model: K_{1s}, decomposition rate for the 1st year of incubation. K_{1.5s}, decomposition rate for the 1.5 years of incubation. FI, goodness of fit of the model (fit index).

Double exponential model: A, labile fraction; K₁ and K₂, decomposition rates.

0.04-0.12 for the burs (Table 6). The leaves showed that the decomposition rates for the recalcitrant pools were faster in Marão (0.60 year), followed by Bornes (0.47 year) and Padrela (0.45 year). In relation to the burs (Table 6), the decomposition rates followed a different pattern (Padrela > Bornes > Marão).

Based on the selected model, the time required for 50% mass loss of labile pool for the leaves ranged from 4.4-5.5 days and the turnover from 6.3-8.0 days (Table 5). For the burs (Table 6), the half-life of the labile pool ranged from 6.0-6.7 days and the turnover from 8.7-9.6 days. In regard to the recalcitrant pool of the leaves, the half-life ranged from 1.1-1.5 years and the turnover from 1.7-2.2 years (Table 5). As for

the burs, the half-life ranged from 1.9-3.2 years and the turnover from 2.8-4.6 years (Table 6).

Nutrient balances and NUE

The percentage of nutrients remaining in leaves and burs after 559 days of incubation, is presented in Table 7. The remaining quantity of the nutrients during the decomposition process of leaf and bur litter showed a general decreasing trend (Fig. 2), although two distinct groups can be considered: Ca and Mg with a more pronounced decrease and N and P with a gradual decrease. In general, leaves presented a nutrient mass

Table 7. Nutrient mass remaining (%) and C/N and C/P ratios, at the end of the incubation period (559 days), for the leaves and burs of chestnut stands

	Marão		Padrela		Bornes	
	Leaves	Burs	Leaves	Burs	Leaves	Burs
C	22.19	56.02	25.26	53.10	25.84	55.20
N	41.11	74.31	52.28	95.27	55.05	88.34
P	46.43	58.59	63.91	61.45	24.58	61.62
K	47.13	70.76	18.28	29.85	51.08	59.29
Ca	17.79	62.00	29.91	66.38	36.85	66.37
Mg	37.89	116.48	22.03	78.16	33.38	96.59
C/N	25.31	36.37	32.46	28.87	44.98	47.02
C/P	363.18	598.29	589.87	582.33	411.92	558.51

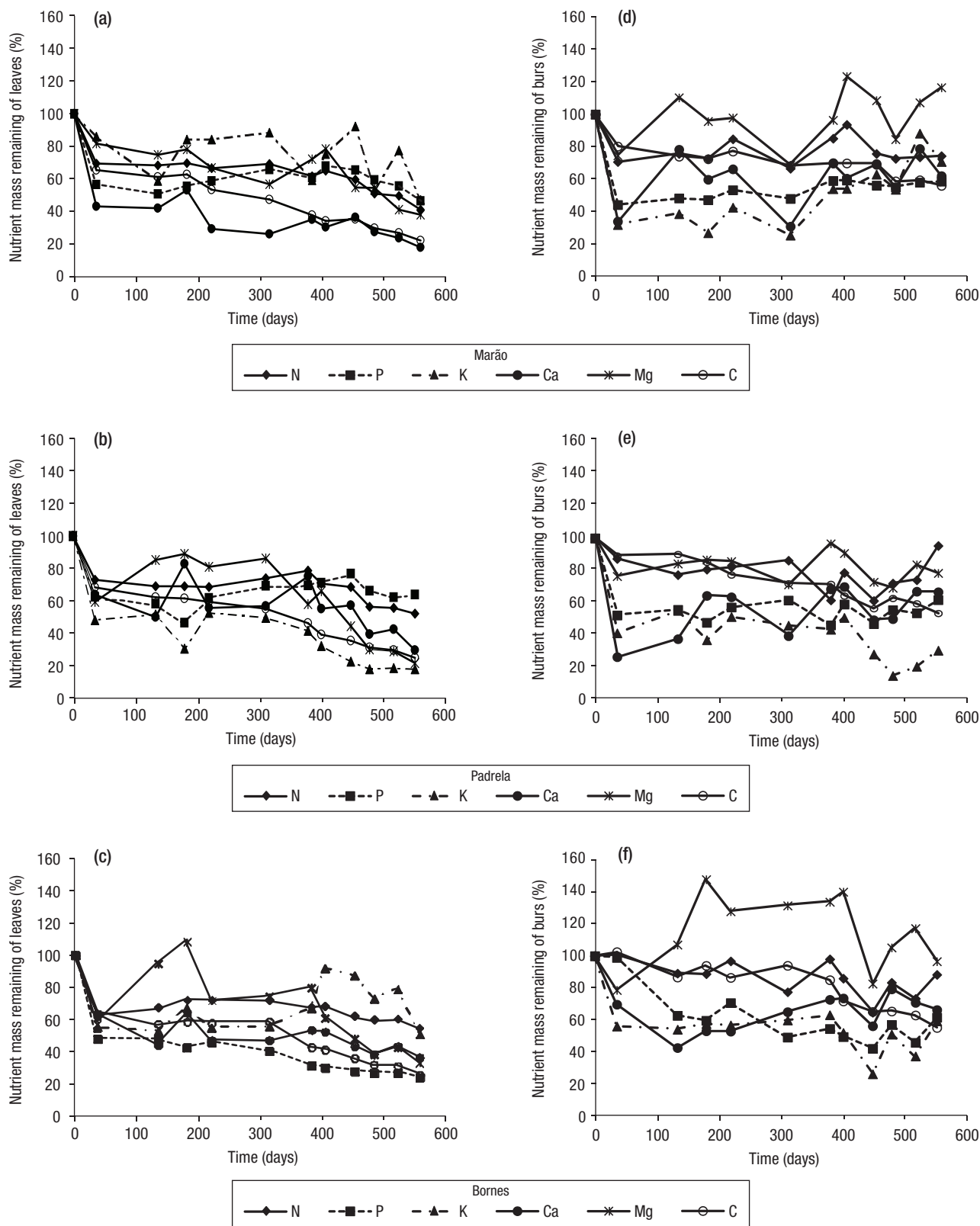


Figure 2. Percent dry-mass remaining of nutrients (N, P, K, Ca and Mg) as a function of incubation period in (a, b, c) decomposing leaf and (d, e, f) bur litter.

remaining lower than burs and the C/N and C/P ratios as well (Table 7). Slight negative correlations with k_1 ($r = 0.37$, $p < 0.03$, $n = 36$) and k_2 ($r = -0.41$, $p < 0.01$, $n = 36$) for the remaining Ca were observed.

The N and S use efficiency (Table 4) was lower in Marão followed by Padrela and Bornes, respectively. The lowest use efficiency for P, Ca and Mg was observed in Bornes > Marão > Padrela. The use efficiency of K was lower in Padrela > Bornes > Marão (Table 4). High positive values of Pearson's correlation were observed between the use efficiency of P and the use efficiency of Ca ($r = 1.00$, $p = 0.01$, $n = 3$), as well as between the use efficiency of Mg and the total biomass ($r = 0.99$, $p = 0.03$, $n = 3$). High negative values of Pearson's correlation were observed between the use efficiency of Mg and its total mineralomass ($r = -0.99$, $p = 0.03$, $n = 3$) as well as between the use efficiency of N and the total mineralomass of S ($r = -0.99$, $p = 0.02$, $n = 3$).

Discussion

Litterfall, mass loss and decomposition rates

The results obtained in this study for total litterfall of high forest chestnut ($4.9 \text{ Mg DM ha}^{-1} \text{ yr}^{-1}$) are similar to the values reported by Santa-Regina (2000) for chestnut coppice. Other studies, also for chestnut coppice, indicated values of $5.9 \text{ Mg DM ha}^{-1} \text{ yr}^{-1}$ (Santa-Regina and Gallardo, 1985) and $5.1\text{-}5.8 \text{ Mg DM ha}^{-1} \text{ yr}^{-1}$ (Santa-Regina *et al.*, 2005). For chestnut groves values of $3.9 \text{ Mg DM ha}^{-1} \text{ yr}^{-1}$ were reported by Pires *et al.* (1994).

The leaves represented 66-70% of total litterfall and constituted the main pathway of the potential return of all bio-elements to the soil, especially for the N, K and Ca. The mineral concentration in the litterfall and fluxes are associated with soil nutrient status at the sites (Hansen *et al.*, 2009). In fact, the lowest amount of N input through litterfall observed in Bornes resulted from the scarcity of this element in its soil (Patricio *et al.*, 2010).

The decomposition process of litterfall has a fundamental role in the nutrient flux to the soil. In the considered west-to-east transect, the remaining mass of leaves and burs was lower than that referred by Raimundo *et al.* (2007) for a similar period in a chestnut grove in the region of Bragança, indicating a faster decomposition rate in high forest stands. This

situation could be related to the differences in climatic conditions, namely higher precipitation in our sites which could have increased the leaching of the soluble components of the litter, as well as the different systems of chestnut management. Although there is no available data to make a comparison, the labile pool in our study reached up to 30% of mass loss for the leaves and 12% for the burs. A number of studies found that litter decomposition was lower in larger gaps than in smaller gaps or under a closed canopy (Zhang and Zak, 1995; Ritter, 2005). Soil properties such as moisture and temperature regimes and pH, affect litter decomposition rates by influencing the activity of decomposers microorganisms (Swift *et al.*, 1979).

In Portugal, the process of litterfall decomposition of the chestnut has been modeled using the single exponential decay model of Olson (1963).

According to the Olson's model the annual decomposition rates in our study were greater than that referred by Raimundo *et al.* (2007) (0.39 and 0.17 for the leaves and burs, respectively) for chestnut groves. For chestnut coppices, using also the simple exponential model, Gallardo *et al.* (1995) showed a decay rate (k_{1s}) of 0.21 in Western-Central Spain. Martins *et al.* (1998) found a k_{1s} of 0.55 in the Padrela and Martins *et al.* (2009) found a k_{1s} of 0.60 in a 15 year old coppice located in the same region.

However, in the present study the double exponential decay model fitted better to the decomposition data for both leaves and burs than the single exponential decay model (Tables 5 and 6). The analysis of the kinetic parameters of the model was in accordance to the observed decay pattern for the leaves. This was also verified for the burs, although the initial fast decomposition stage was not very pronounced (Fig. 1). The k_1 decay rates were considerably higher than k_2 for both leaves and burs. In general, the burs showed slower decomposition rates (k_1 and k_2) than the leaves due to their higher recalcitrant pools. The lowest decomposition rate observed in burs in relation to leaves could be due to the higher lignin/N ratio in burs and their contact with the soil surface not being as good as that of the leaves.

In similar conditions of moisture and temperature, the differences between decomposition rates of organic residues are attributed to the variations of N quantity, C/N and lignin/N ratios (Berg and Staaf, 1980; Taylor *et al.*, 1991; Schomberg *et al.*, 1994). Although the lignin concentration was not considered in our research, the values reported in literature indicate

211 g kg⁻¹ (Sariyildiz, 2008), 246 g kg⁻¹ (Martins *et al.*, 2009) and 272 g kg⁻¹ (Raimundo *et al.*, 2008) for the chestnut leaves. In fact, lignin can dominate litter decomposition rates irrespective of other constituents when the values of initial lignin concentration are higher than 200 g kg⁻¹ (Sariyildiz, 2008).

Nutrient released from decomposing litter

During the decomposition process, the leaf remaining quantities of N, P, K, Ca, Mg and C decreased in all sites, though with more evident variations for K in Bornes and Marão. A decreasing trend was also observed for the burs, except for Mg in Marão and Bornes and K in Marão. These observed exceptions were probably due to contaminations or temporary immobilization. At the end of the study period (559 days), in general, the leaves presented the lowest quantity of nutrients remaining. The fast decay of K observed in the beginning of the decomposition process of leaves and burs (Fig. 2) was due to its leaching. This situation was also referred in the literature (Santa-Regina *et al.*, 1986; Raimundo *et al.*, 2007; Martins *et al.*, 2009). The release of K did not depend on the fast decomposition of leaves because it is not a structural element of the organic residues (Waring and Schlesinger, 1985; Blair, 1988). A strong fluctuation of K during the decay period was observed in Bornes and Marão, probably due to its high abundance in plant tissues in its free form and due to leaching from the forest canopy and heterotrophic immobilization (Berg, 1980). A similar situation was referred by Santa-Regina (2000).

The correlation of Ca with k_1 and k_2 suggested that the release of Ca could depend on the intensity of the biological activity in the decomposition process as reported by Ribeiro *et al.* (2002) and Martins *et al.* (2009).

The dynamics of P depends on its concentration in the substrate. Since a higher concentration of this element in the leaves was observed in Bornes, a greater release of P was also verified (75.4%). In this site, a slight decrease in the C/P ratio was observed at the end of the study period in relation to the beginning, indicating a higher release of P (Fig. 2) which was more evident for the leaves. In the other sites, the remaining P was higher due to its lower concentration and consequent immobilization by the biological activity. The higher C/P ratios observed at the end of the study period were considered inadequate for the mineralization

of P in the organic residues (Stevenson and Cole, 1999). This fact indicated a slow release in the long term, especially in Padrela and Marão which presented a greater reduction of C/P ratios relatively to the initial values, which means that the rate of release of P in the residues was lower than that of C. The C/P ratio of Bornes was greater than Marão because of its higher release of P. The remaining quantity of P correlated slightly with that of N ($r = 0.60$, $p < 0.001$, $n = 36$) as well as that of Ca ($r = 0.51$, $p < 0.01$, $n = 36$) and the remaining quantity of Mg ($r = 0.34$, $p < 0.05$, $n = 36$) suggesting that the mineralization of P could depend on that of the others.

Leaves of Padrela and Bornes presented a faster release of Mg than Ca as is reported by several authors (Waring and Schlesinger, 1985; Wesemael, 1993; Stevenson and Cole, 1999; Martins *et al.*, 2009). The final remaining quantity of Mg (37.9%) in Marão was higher than that of Ca (17.8%) without any plausible explanation except for the highest use efficiency of K and lower use efficiency of Ca than K. Santa-Regina (2000) mentions that the highest K concentration in the plant organs was linked to a lower concentration in Ca which was attributed to the known antagonism between these two elements. When the use efficiency of K is higher than Ca, the remaining quantity of Ca is lower than that of K. The Ca contents were among the lowest found in the literature (Santa-Regina, 2000, Raimundo *et al.*, 2007). The scarcity of Ca could lead to a strong biological immobilization (Duchaufour, 1984) that would also explain the higher percent mass remaining of Ca. However, the remaining quantity of Mg had a slight positive correlation with that of Ca ($r = 0.61$, $p < 0.001$, $n = 36$) as well as that of K ($r = 0.42$, $p = 0.01$, $n = 36$). The same was observed for the burs that presented a slower release of Mg than Ca. This situation was also reported by Martins *et al.* (2009) for *Pseudotsuga menziesii* in Padrela. An irregular trend was observed for the Mg because, as Rapp (1971) suggested, Mg is a readily leachable bioelement reflecting a balance between losses and contributions to the system. For the leaves, the Mg content was within the limits reported in the literature (Khanna and Ulrich, 1991; Raimundo *et al.*, 2007; Martins *et al.*, 2009).

In Padrela, K in the leaves was released faster than Ca or Mg in accordance with many studies (*e.g.*, Edmonds, 1980; Hart and Firestone, 1992; Ribeiro *et al.*, 2002; Martins *et al.*, 2009). However, the release of K from leaves in Bornes and Marão was lower than Ca and Mg. A similar situation was referred by Martins

et al. (2009) for *Pinus nigra*. The lower concentration of K in leaves Marão < Bornes < Padrela led to its immobilization by microorganisms in the decomposition process (Fig. 2). Immobilization of K was referred by several authors (Gosz *et al.*, 1973; Lousier and Parkinson, 1978; Raimundo *et al.*, 2007) and could be related with the availability of K in the organic material or in the soil (Cortina and Vallejo, 1994). The lowest nutrient use efficiency for this element was observed in Padrela.

In regard to the burs, the release of K in Bornes and Padrela was lower than Ca and Mg. The immobilization of Mg in the burs was observed especially in Bornes and Marão following the initial fast decay. This immobilization was less pronounced for Ca. A similar situation was referred by Raimundo *et al.* (2007) and could be due to the biological activity or the lower Mg concentration in the organic material (Blair, 1988).

The release of N from leaves and burs did not depend on the decomposition rates. The highest decay observed for N, which occurred in Marão (58.9%), was due to a higher concentration of N in the leaves and a lower C/N ratio. The remaining N quantity was in accordance with many studies of decomposition (*e.g.*, Stevenson and Cole, 1999; Ribeiro *et al.*, 2002; Raimundo *et al.*, 2007; Martins *et al.*, 2009), indicating that the release of N depends on its concentration in the organic material. During the study period, a strong immobilization was not observed for N in all study sites but, a slight release was evident (Fig. 2). The intense decrease of the C/N ratios observed during the decomposition process indicated a slow release of N in the long term.

Conclusions

Annually, the mature chestnut high-forest stands (density 360-1260 tree ha⁻¹, age 55-73 years old) restore 4.9 Mg DM ha⁻¹ of litter to the soil and 2.6 Mg ha⁻¹ yr⁻¹ of carbon. The leaves are the most important fraction of the total litterfall, representing 66-70%. The results showed that the fraction of leaves in the litterfall is the main vector of potential return of all bioelements to the soil. The decomposition process for the chestnut high forest litterfall can be described by the double exponential decay model. The fitted models can be used to predict the decay process for the leaves as well as for the burs in similar conditions. These models allow a more realistic prediction of the decomposition because they separate a faster initial stage, easily decomposable

(labile pool), from a slower and more recalcitrant one. The decay rates for the labile pool were: 46-58 yr⁻¹ for the leaves and 38-42 yr⁻¹ for the burs. For the recalcitrant pool were: 0.45-0.60 yr⁻¹ for the leaves and 0.22-0.36 yr⁻¹ for the burs. At the end of the study period (559 days), the mass loss was 61-75% for leaves and 34-51% for burs. The mass loss decreased in the following order: Padrela > Bornes > Marão. After the 559 days of incubation a considerable percentage of nutrients in the mass still remained. In general, an initial period of strong mineralization was detected for all analyzed minerals. This phase was followed by a period of stabilization or a progressive slight release, safeguarding the exceptions of K and Mg. The intense decrease of the C/N ratios observed during the decomposition process indicated a slow release of N in the long term. Only remaining Ca showed a significant low to moderate correlation with the decay rates.

This study pointed to some decay patterns and release of bioelements by litterfall of chestnut high forest areas that can be useful for improving both silvicultural and environmental approaches for the management of these forest ecosystems.

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