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Leaf decomposition of cork oak under three different land uses within a *montado* of southern Portugal

Maria Luísa Arosa[A,D], *Sofia R. Costa*[B,C], *and Helena Freitas*[A]

[A]Centre for Functional Ecology, Department of Life Sciences, University of Coimbra, PO Box 3046, 3001-401 Coimbra, Portugal.
[B]Mountain Research Center (CIMO), ESA, Polytechnic Institute of Bragança, Campus de Santa Apolónia, 5300-253 Bragança, Portugal.
[C]Centre of Molecular and Environmental Biology (CBMA), Department of Biology, University of Minho, Campus de Gualtar, 4710-057 Braga, Portugal.
[D]Corresponding author. Email: merisinha@hotmail.com

Abstract. This study compared litter decomposition dynamics of cork oak at three sites under different land-uses (grassland, shrubland and woodland), in a *montado* ecosystem in Southern Portugal. The *montado* is a protected habitat within the EU Habitats Directive, but the long-term persistence of cork oak is endangered in these ecosystems, with health of poor cork oak and low natural regeneration rates being the main causes of degradation. Moreover, human management has resulted in the conversion of woodlands to grasslands and may have long-term effects on soil nutrient availability, eventually modifying soil nutrient budgets. Knowledge of the ecological processes is therefore relevant for ecosystem management and species conservation. In the study, the estimated amount of leaf fall from cork oak showed no significant differences between land uses, despite the positive influence of tree crown size on leaf fall. Decomposition was affected by season, vegetation cover, leaf thickness and litter quality. Differences in land use that exposed soil to harsh climate conditions negatively affected soil microbial dynamics, resulting in lower decomposition rates in the more disturbed sites with lower canopy cover.

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Introduction

Cork oak (*Quercus suber*) is an evergreen tree species native to the western part of the Mediterranean Basin (Pausas *et al.* 2009). The largest cork oak woodlands are found in the Iberian Peninsula and have been used for agricultural, pastoral and forestry purposes at least since the Middle Ages (Joffre *et al.* 1999; Olea *et al.* 2005; Bugalho *et al.* 2011). In Portugal, this ecosystem is known as *montado* and it is characterised by open woodlands (20–80 trees ha^{-1}) with only one or a few tree species besides cork oak, mainly holm oak (*Q. rotundifolia*) and pines (*Pinus* spp.). Because *montados* are found in different climatic and edaphic environments, but mainly in marginal soils and under harsh conditions, their structure and understorey composition are variable (Joffre *et al.* 1999; Pinto-Correia and Mascarenhas 1999). Human management has favoured habitat heterogeneity and biodiversity at local and regional levels, creating a multiplicity of ecotones, and the *montado* represents a model of a sustainable ecosystem with coexisting human activities and natural resources (Blondel 2006). This ecosystem is a protected habitat within the EU Habitats Directive (92/43/EEC, http://ec.europa.eu/environment/nature/legislation/habitatsdirective/index_en.htm, verified 12 September 2016) but the long-term persistence of cork oak in *montados* is a subject of serious concern among the public and the scientific community. The main causes of degradation are poor cork oak phytosanitary conditions and low natural regeneration rates (Díaz *et al.* 1997; Pulido and Díaz 2005; Acácio *et al.* 2007; Camilo-Alves *et al.* 2013; Acácio and Holmgren 2014; Arosa *et al.* 2015).

Ecological processes are frequently controlled by the availability of nutrients; thus, knowledge of the limiting nutrients is relevant for ecosystem management and species conservation. Nutrient limitation may affect species composition and richness through its effects on productivity; the maximum productivity levels attainable may differ depending on nitrogen (N), phosphorus (P) or potassium (K) limitation (Olde Venterink *et al.* 2001; Wassen *et al.* 2005). Foliar nutrient content, litter decomposition and litter dynamics are widely recognised as effective measures of the nutritional status of plants, and they are key processes in nutrient cycling and energy transfer in terrestrial ecosystems, influencing their stability (Chapin *et al.* 1980; Maguire 1994; Vitousek *et al.* 1994; Aerts and Chapin 1999). Litter fall, together with nutrient resorption and foliar leaching, is a principal pathway to return carbon (C) and nutrients (particularly N and P) to the soil, and litter decomposition contributes 70% of the total annual carbon flux (Miller 1984; Raich and Schlesinger 1992; Cadisch and Giller 1997; Piatek and Allen 2000; Luyssaert *et al.* 2005). Litter decomposition involves the mineralisation and humification of lignin, cellulose and hemicellulose, and the leaching of soluble compounds, C, N and P, which are mineralised or immobilised in the soil (Aber and Melillo 1982; Gallardo and Merino 1993; Coûteaux *et al*. 1995). Multiple factors control litter decomposition, including climate, litter chemistry and quality, and soil organisms, with litter being the strongest determinant of the decomposition processes within the same climate region (Hart *et al*. 1992; Lavelle *et al*. 1993; Lisanework and Michelsen 1994; Cornwell *et al*. 2008).

The main objective of this study was to evaluate the decomposition process as leaves fall to the ground in three *montados* subjected to different land uses (grassland, shrubland and woodland). Reduced fitness of cork oak trees will unfavourably affect their mineral nutrition (Robert *et al*. 1996); thus, an understanding of nutritional dynamics of cork oak can aid decision-making for the management of this ecosystem. We estimated the amount of foliar litter fall per site and analysed how it was influenced by tree crown size and tree density. The concentrations of N, C, P, lignin, cellulose and hemicellulose in foliar litter were determined before the decomposition process started and after 18 months in the soil. This was done to improve understanding of nutrient cycling in the *montado*, because the sclerophyllous leaves of cork oak could affect decomposition owing to the high content of structural compounds such as lignin and cellulose that confer impermeability and resistance to microbial degradation (Kolattukudy 1980; Gallardo and Merino 1993). Leaf thickness can help to explain decomposition rates; hence, we compared leaf thickness and tested for differences in litter decomposition rates among the three sites.

The hypotheses tested were that: (i) there is a direct relationship between canopy size and the quantity of foliar litter fall among sites, independently of land use, because aerial biomass in the canopy may condition the amount of litter fall (Chertov *et al*. 1999); (ii) lower decomposition rates occur in grassland from the absence of tree and shrub cover and consequent exposure of the soil to harsh climate conditions during the summer (Gaxiola and Armesto 2015); and (iii) leaf thickness influences decomposition rates because of the negative effect of the presence of lignin and cellulose (Kolattukudy 1980; Cornelissen *et al*. 1999).

Methods

Study area

Fieldwork was carried out from March 2011 to May 2014 in Montemor-o-Novo, southern Portugal, in the Herdade do Freixo do Meio (38°42′N, 8°19′W), a farm that manages 1140 ha of cork oak–holm oak *montado*. The area has a Mediterranean climate with hot, dry summers and rainfall mostly in autumn and winter (mean annual rainfall 660 mm, mean annual evaporation 1760 mm; INMG 1991). In order to test the hypotheses, we selected three sites (grassland, shrubland and woodland) within the study area and nine subplots, three under each site. Site size was 1200 m^2 and distance between each subplot was 250 m.

Cork oak is the dominant tree species and each site has been historically subjected to a different type of management. Detailed description of the three sites is provided in Table 1. Air temperature and relative humidity were recorded at the three sites hourly with thermohygrometers (HOBO Pro v2 logger; Onset Computer Corporation, Bourne, MA, USA) placed 1.5 m aboveground under the tree canopy, and the values in Table 1 represent the mean for each of the three sites calculated during a single year.

Table 1. Description of locality, soil, forest structure and land uses of the three sites
DBH, Diameter at breast height

	Grassland	Shrubland	Woodland
Locality:			
Latitude	38°41′	38°42′	38°42′
Longitude	8°19′	8°19′	8°20′
Altitude (m)	150	175	150
Size (ha)	32	35	29
Air temperature (°C)	15.67	14.75	15.54
Relative humidity (%)	73.80	76.88	73.68
Slope exposure	SSW	SW	W
Soil:			
Bedrock type	Granite	Granite	Granite
pH (H_2O)	4.90	5.15	5.05
Organic matter (%)	1.82	1.85	1.70
Carbon (%)	1.06	1.07	0.98
Nitrogen (%)	0.09	0.09	0.08
Soil moisture (%)			
Spring	18.09	19.89	20.49
Winter	16.29	29.17	18.56
Forest structure:			
Density (trees ha^{-1})	25	40	45
Cork oak trees (%)	69	76	93
Crown diameter (m)	11.1	10.8	9.2
DBH (cm)	163	164	138
Shrub density	Low	Medium	High
Land uses:			
Agriculture	Yes	No	No
Livestock	Yes	Yes	No
Forestry	Yes	Yes	Yes

The grassland site had a density of 25 trees ha^{-1}, and the mean crown diameter of cork oak trees was 11.1 m. Soil ploughing was carried out every 1–2 years to enhance pasture growth for livestock rearing or to produce fodder and grain; therefore, shrubs were almost absent from this site.

The shrubland site had a density of 40 trees ha^{-1}, and the mean crown diameter of cork oak trees was 10.8 m. The site was used for extensive livestock rearing only. Encroaching shrubs were periodically cut with chains to allow livestock grazing and browsing. During the study, there was a dense shrubby undergrowth of *Cistus* spp. and *Asparagus acutifolius*.

The woodland site had a density of 45 trees ha^{-1}, and the mean crown diameter of cork oak trees was 9.2 m. This site was used for forestry only and had a dense, heterogeneous, shrubby understorey composed of *Cistus* spp., *A. acutifolius*, *Ulex australis* subsp. *welwitschianus*, *Pistacia lentiscus*, *Arbutus unedo*, *Phillyrea angustifolia*, *Crataegus monogyna*, *Q. coccifera* and *Lavandula pedunculata*.

Leaf fall

Leaf fall was determined by means of litter traps. Traps were constructed of circular nets of area 0.25 m^2 attached to the canopy with a string. Three traps were installed per tree in 20 cork oak trees per site, making 180 traps in total at the three sites. The contents of each trap were inspected every 15 days from January to December 2011 and leaf fall was restricted to the period between May and mid-July. Litter was collected and dried at 60°C, and leaves were weighed for each litter trap. The projection area of the tree crown was calculated for each selected tree by measuring maximum and minimum crown diameters, in order to estimate foliar litter fall per tree (kg tree^{-1}). To estimate the amount of foliar litter fall per site (kg ha^{-1}), we multiplied the foliar litter fall per tree by the tree density in each site.

Litter quality and decomposition

Chemical composition of cork oak leaf litter was determined at the start of the study and after harvesting litterbags in the soil for 18 months. All leaf material was oven-dried at 60°C. Total C and N concentrations were determined with a CHN elemental analyser (FlashEA1112; Thermo Fisher Scientific, Waltham, MA, USA). Total P concentration was determined by using an ICP-MS (ELEMENT XR; Thermo Fisher Scientific). Lignin and cellulose contents were determined following AOAC (1995) methods and hemicellulose contents were determined following the procedures described by Van Soest and Wine (1967). These results were used to calculate three indices, the ratios C : N, N : P and lignin : N. The C : N ratio expresses the N concentration in organic matter, a low C : N suggesting a high decomposition rate in the early stages of decomposition (Berg and Ekbohm 1983). The variation in the relative supply of N and P among ecosystems influences the decomposition process, which is mostly bacterial-driven at low N : P ratio and fungal-driven at high N : P ratio (Güsewell 2004; Güsewell and Gessner 2009). Knowledge of the limiting nutrient is relevant for ecosystem management and species conservation (Wassen *et al*. 2005). The lignin : N ratio assumes that N and lignin have opposite effects on the decomposition rate, and is a good predictor of mass loss during the initial stages of decay (Melillo *et al*. 1982).

Litter decomposition rates were evaluated by using the litterbag technique (Garnier *et al*. 2007). Leaves were collected in June 2012, at the peak of leaf senescence, and dried at room temperature for 3–4 days until weight stabilised. A standard 1-mm mesh fabric was used to make flat polyester bags of ~10 cm by 10 cm, and then 2.0 ± 0.1 g leaf matter was placed in each bag. Thirty litterbags were distributed per site. The experiment began in November 2012 and lasted for 18 months, with three harvests: April 2013 (6 months), November 2013 (12 months) and April 2014 (18 months). After harvesting, bags were cleaned with a paint brush and dried, first at room temperature and then at 60°C for 3 days, and the clean litter was weighed. Mass loss over time was based on the single exponential decay model that assumes a constant fraction of mass loss per time unit (Olson 1963); mean litter decomposition rates (*k*-values) are presented in Table 2 as fractional mass lost per year.

Leaf thickness (mm) was calculated by using measurements of specific leaf area (SLA, cm^2 kg^{-1}) and leaf dry matter content (LDMC, mg g^{-1}), given that leaf thickness = 1/(SLA × LDMC) (Gallardo and Merino 1993; Pérez-Harguindeguy *et al*. 2000; Vile *et al*. 2005). SLA was determined on 15 full-grown cork oak fresh leaves per site, and LDMC was measured after drying the leaves, following standard methodologies (Pérez-Harguindeguy *et al*. 2013).

Statistical analyses

Data exploration was done with Brodgar 2.6.6 (Highland Statistics Ltd, Newburgh, UK), an interface supported by software R version 2.9.1 (R Development Core Team, Vienna). Analysis of variance (ANOVA) was performed with Statistica 8.0 (StatSoft Inc., Tulsa, OK, USA) to test for differences in mean daily air temperature and relative humidity among sites.

Mean leaf litter mass loss values for each site and harvest were calculated, and the analysis was performed with each of the three plots per site as a replicate. Differences between sites in leaf fall, leaf thickness and litter mass remaining were tested by two-way ANOVA (site and time as factors) followed by the Tukey test ($\alpha = 0.05$). Analyses were carried out with Statistica 8.0. Data were first examined with Levene's tests, and the arcsine transformation was applied to remaining litter mass data for homogeneity of variances. Results are presented as mean ± standard error.

Results

Leaf fall

Foliar litter fall recorded in litter traps during 2011 was 289.9 ± 42.7 g m^{-2} in grassland, 221.9 ± 42.4 g m^{-2} in shrubland and 187.2 ± 22.2 g m^{-2} in woodland (232.4 ± 21.4 g m^{-2} for the

Table 2. Decomposition rates (*k*-values) and litter chemical composition in decomposition bags (each bag with 2.0 ± 0.1 g cork oak leaves) placed at the three sites at the beginning of the decomposition experiment (0 months) and after 18 months in the soil

Values are means of three replicates

Site	*k* (year^{-1})	Nitrogen	Carbon	Phosphorus	Cellulose (mg)	Hemicellulose	Lignin	C : N	N : P	Lignin : N
					0 months					
Grassland	0	35.2	989.6	3.0	465.8	191.8	167.2	28.1	10.7	4.8
Shrubland	0	35.0	995.6	3.4	362.8	175.0	122.8	28.5	10.3	3.5
Woodland	0	34.8	1001.4	3.2	457.4	173.8	164.0	28.8	10.9	4.7
					18 months					
Grassland	0.9	15.5	271.3	0.8	81.4	65.5	54.2	17.5	18.3	3.5
Shrubland	1.6	8.2	141.1	0.2	97.2	44.4	66.8	17.5	44.8	8.2
Woodland	1.1	12.5	241.5	0.1	57.5	73.2	40.9	19.4	120.8	3.3

study area). Marginally significant differences were found among sites for estimated foliar litter fall per tree (grassland 34.4 ± 8.0 kg $tree^{-1}$, shrubland 22.6 ± 5.3 kg $tree^{-1}$, woodland 14.9 ± 2.9 kg $tree^{-1}$; $F_{2,57} = 2.97$, $P = 0.060$). Significant differences were not found for foliar litter fall per site (grassland 859.7 ± 201.2 kg ha^{-1}, shrubland 903.0 ± 211.8 kg ha^{-1}, woodland 671.9 ± 131.3 kg ha^{-1}; $F_{2,57} = 0.46$, $P = 0.633$).

Litter quality and decomposition

Initially, values of C, N and P, and the C : N and N : P ratios, were only slightly different among sites (Table 2). On the other hand, leaves from the shrubland site had very low values of cellulose and lignin, and low lignin : N ratio, whereas the highest values for these parameters, as well as hemicellulose, were found for leaves at the grassland site (Table 2).

After 18 months in the soil, litter content of C, N and P was variable among sites. The C : N ratio showed small differences among sites; however, the lignin : N ratio was very high at the shrubland site (Table 2). The highest concentration of cellulose in remaining litter mass at 18 months was also found in this site. The N : P ratio at the woodland site was very high compared with values obtained for the grassland and shrubland sites.

Respective percentages of litter mass remaining at 6, 12 and 18 months were 51%, 49% and 27% in grassland, 28%, 23% and 14% in shrubland and 44%, 35% and 24% in woodland (Fig. 1). Overall, litter decomposition rates were lowest during spring–summer (6–12 months), whereas the highest decomposition rates occurred during the initial autumn–winter (0–6 months) (Fig. 1). Significant differences were found among sites for remaining litter mass at 6 months ($F_{2,27} = 4.82$, $P = 0.019$) and 12 months ($F_{2,27} = 9.67$, $P = 0.010$), but not at 18 months ($F_{2,27} = 1.49$, $P = 0.251$).

The results may have been influenced by air temperature and relative humidity. These were recorded throughout the study, and are in agreement with the typical Mediterranean climate of long, hot, dry summers and mild, humid winters (mean annual air temperature 15.5°C, mean annual relative humidity 73.6%, INMG 1991). Mean daily air temperature was lowest and relative humidity highest in areas with high tree density and a dense shrub layer (air temperature: $F_{2,1095} = 2.96$, $P > 0.05$; relative humidity: $F_{2,1095} = 5.06$, $P < 0.01$).

Leaf thickness was 0.228 ± 0.001 mm in grassland, 0.205 ± 0.001 in shrubland and 0.184 ± 0.001 mm in woodland, being significantly different among all three sites and least in woodland ($F_{2,42} = 6.99$, $P = 0.002$).

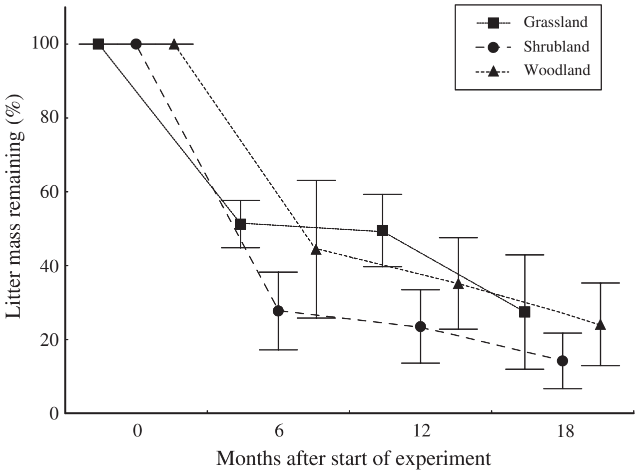

Fig. 1. Litter mass remaining in litterbags placed under the canopy of cork oaks at the three sites (grassland, shrubland and woodland). The experiment started in November 2012 (0 months) and litterbag harvesting was carried out in April 2013 (6 months), November 2013 (12 months) and April 2014 (18 months). Values are mean ± s.e. of 10 replicates per site.

Discussion

Leaf fall can be an adaptation to the water deficit that occurs during the dry summer period in the Mediterranean region (Rodrigues *et al.* 1995), and evergreen cork oaks shed their old leaves mainly during spring in order to reduce transpiration surface (Andivia *et al.* 2010). Mean values of leaf fall of cork oak in our study (0.23 kg m^{-2} $year^{-1}$) are consistent with other previous estimations for cork oak: 0.23 kg m^{-2} $year^{-1}$ (Andivia *et al.* 2010), 0.26 kg m^{-2} $year^{-1}$ (Caritat *et al.* 2006), 0.29 kg m^{-2} $year^{-1}$ (Aponte *et al.* 2013). The amount of litter fall has a direct relationship with aerial biomass in the canopy (Chertov *et al.* 1999), and accordingly, we found marked differences among sites in leaf fall per tree given that wider tree crowns provided a greater amount of foliar litter fall. Nevertheless, these differences did not represent an overall increase in foliar litter fall per site because tree crowns were wider where tree density was lower.

Differences in land use and the resulting plant communities can influence decomposition through changes in the quality of the litter produced and alterations to the temperature and moisture regime at the soil surface. The quality and chemical composition of the litter, environmental conditions, soil fauna and microorganisms can affect the rate of decomposition (Singh and Gupta 1977; Berg and McClaugherty 2008; Castro *et al.* 2010). Litter decomposition rates were significantly different among the three sites. Leaf thickness can also help to explain the decomposition rates of sclerophyllous leaves, negatively affecting loss of litter mass. A negative relationship between leaf thickness and leaf decomposition has been attributed to both dense leaves and the presence of chemically resistant components such as lignin and cellulose (Cornelissen *et al.* 1999; Pérez-Harguindeguy *et al.* 2000; Cornwell *et al.* 2008; Kurokawa and Nakashizuka 2008).

Leaves are structurally organised so that cellulose and hemicellulose are found in the primary cell wall and lignin in the secondary cell wall; thus, the decomposition process occurs in different stages because the larger lignin macromolecules hinder leaf decomposition (Berg and McClaugherty 2008). In addition, N and P have an important role in the regulation of decomposition rates (Enríquez *et al.* 1993). Contents of N and P in leaves at the beginning of our study were similar to those found previously (Passarinho *et al.* 2006; Andivia *et al.* 2010). The low decomposition rates observed at the end of the study can be attributed to the high N : P ratio in shrubland and woodland, where the limiting factor to decomposition seemed to be low P values (Güsewell and Gessner 2009). The higher lignin and cellulose concentrations, together with the low values of N in shrubland relative to grassland and woodland, could have negatively affected the decomposition process. The lower initial concentrations of lignin and cellulose in cork oak leaves in shrubland might have facilitated decomposition compared with the other sites in the early stages; however, the proximity of an artificial pond to this site may have affected the decomposition process. The water level in the pond increased during winter, increasing the soil moisture in its vicinity (Table 1). The resulting lowered soil pH and/or anoxic conditions could have caused the death of some microbial communities, leading to incomplete mineralisation (Enríquez *et al*. 1993; Coûteaux *et al*. 1995). Contents of lignin are presumably altered in wet soils (Berg *et al*. 1993*a*), and this could explain the observations at the late decomposition stage of cellulose and lignin decomposition slowing down, also affecting the lignin : N ratio. On the other hand, early decomposition in grassland was hampered by the higher initial concentrations of cellulose, hemicelluloses and lignin, and by leaf thickness. Moreover, tree density was low at this site (25 trees ha^{-1}), and in the absence of shrubs, soil exposure to harsh climatic conditions during summer could have had a large, negative impact on ecosystem functioning. Thus, soil microbial dynamics, given by nutrient release and immobilisation cycles, and nutrient availability for plants (Berg *et al*. 1993*b*; Aponte *et al*. 2010; Matías *et al*. 2011) can significantly reduce the decomposition rates (Corre *et al*. 2002; Quilchano and Marañón 2002; Gurlevik *et al*. 2003; Blanco *et al*. 2011; Gaxiola and Armesto 2015).

Our study has highlighted important differences in cork oak leaf fall, litter quality and litter decomposition according to the main land uses in the *montado*. Because tree density and tree crown size showed a strong inverse relationship in this ecosystem, the estimated amount of cork oak leaf fall was identical at all sites, even though the wider tree crowns provided more leaf fall. Furthermore, lower values of leaf thickness were associated with a higher tree density, which, together with a lower content of cellulose, hemicellulose and lignin, is likely related to the higher decomposition rates found in shrubland. Litter quality and deficient soil microbial activity due to soil exposure to severe climate conditions in the absence of shrubs were the probable causes of the lowest decomposition rates in grassland. Overall, our results demonstrate that a faster nutrient cycling can occur in *montados* with high tree density and a dense shrub layer.

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References

Aber JD, Melillo JM (1982) Nitrogen immobilization in decaying hardwood leaf litter as a function of initial nitrogen and lignin content. *Canadian Journal of Botany* **60**, 2263–2269. doi:10.1139/b82-277

Acácio V, Holmgren M (2014) Pathways for resilience in Mediterranean cork oak land use systems. *Annals of Forest Science* **71**, 5–13. doi:10.1007/s13595-012-0197-0

Acácio V, Holmgren M, Jansen PA, Schrotter O (2007) Multiple recruitment limitation causes arrested succession in Mediterranean cork oak systems. *Ecosystems* **10**, 1220–1230. doi:10.1007/s10021-007-9089-9

Aerts R, Chapin FS (1999) The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. *Advances in Ecological Research* **30**, 1–67. doi:10.1016/S0065-2504(08)60016-1

Andivia E, Fernández M, Vázquez-Piqué J, González-Pérez A, Tapias R (2010) Nutrients return from leaves and litterfall in a mediterranean cork oak (*Quercus suber* L.) forest in southwestern Spain. *European Journal of Forest Research* **129**, 5–12. doi:10.1007/s10342-009-0274-6

AOAC (1995) 'Official methods of analysis.' (Association of Official Analytical Chemists: Washington, DC)

Aponte C, Marañón T, García LV (2010) Microbial C, N and P in soils of Mediterranean oak forests: influence of season, canopy cover and soil depth. *Biogeochemistry* **101**, 77–92. doi:10.1007/s10533-010-9418-5

Aponte C, García LV, Marañón T (2013) Tree species effects on nutrient cycling and soil biota: a feedback mechanism favouring species coexistence. *Forest Ecology and Management* **309**, 36–46. doi:10.1016/j.foreco.2013.05.035

Arosa ML, Ceia RC, Costa RS, Freitas H (2015) Factors affecting cork oak (*Quercus suber*) regeneration: acorn sowing success and seedling survival under field conditions. *Plant Ecology & Diversity* **8**, 519–528. doi:10.1080/17550874.2015.1051154

Berg B, Ekbohm G (1983) Nitrogen immobilization to decomposing needle litter at variable carbon–nitrogen ratios. *Ecology* **64**, 63–67. doi:10.2307/1937329

Berg B, McClaugherty C (2008) 'Plant litter. Decomposition, humus formation, carbon sequestration.' (Springer Science + Business Media: Berlin)

Berg B, Berg MP, Bottner P, Box E, Breymeyer A, Calvo de Anta R, Coûteaux M, Escudero A, Gallardo A, Kratz W, Madeira M, Mälkönen E, McClaugherty C, Meentemeyer V, Muñoz F, Piussi P, Remacle J, Virzo de Santo A (1993*a*) Litter mass loss rates in pine forests of Europe and Eastern United States: some relationships with climate and litter quality. *Biogeochemistry* **20**, 127–159. doi:10.1007/BF00000785

Berg B, McClaugherty C, Johansson MB (1993*b*) Litter mass-loss rates in late stages of decomposition at some climatically and nutritionally different pine sites. Long-term decomposition in a Scots pine forest. VIII. *Canadian Journal of Botany* **71**, 680–692. doi:10.1139/b93-078

Blanco JA, Imbert JB, Castillo FJ (2011) Thinning affects *Pinus sylvestris* needle decomposition rates and chemistry differently depending on site conditions. *Biogeochemistry* **106**, 397–414. doi:10.1007/s10533-010-9518-2

Blondel J (2006) The 'design' of Mediterranean landscapes: a millennial story of human and ecological systems during the historic period. *Human Ecology* **34**, 713–729. doi:10.1007/s10745-006-9030-4

Bugalho MN, Caldeira MC, Pereira JS, Aronson J, Pausas JG (2011) Mediterranean cork oak savannas require human use to sustain biodiversity and ecosystem services. *Frontiers in Ecology and the Environment* **9**, 278–286. doi:10.1890/100084

Cadisch G, Giller KE (1997) 'Driven by nature: plant litter quality and decomposition.' (CABI: Wallingford, UK)

Camilo-Alves CSP, da Clara MIE, Ribeiro NMCA (2013) Decline of Mediterranean oak trees and its association with *Phytophthora cinnamomi*: a review. *European Journal of Forest Research* **132**, 411–432. doi:10.1007/s10342-013-0688-z

Caritat A, García-Berthou E, Lapeña R, Vilar L (2006) Litter production in a *Quercus suber* forest of Montseny (NE Spain) and its relationship to meteorological conditions. *Annals of Forest Science* **63**, 791–800. doi:10.1051/forest:2006061

Castro H, Fortunel C, Freitas H (2010) Effects of land abandonment on plant litter decomposition in a Montado system: relation to litter chemistry and community functional parameters. *Plant and Soil* **333**, 181–190. doi:10.1007/s11104-010-0333-2

Chapin FS III, Johnson DA, Mc Kendrick JD (1980) Seasonal movement of nutrients implants of differing growth form in Alaskan Tundra ecosystem: implications for herbivory. *Journal of Ecology* **68**, 189–209. doi:10.2307/2259251

Chertov OG, Komarov AS, Tsiplianovsky AM (1999) A combined simulation model of Scots pine, Norway spruce and Silver birch ecosystems in the European boreal zone. *Forest Ecology and Management* **116**, 189–206. doi:10.1016/S0378-1127(98)00456-3

Cornelissen JHC, Pérez-Harguindeguy N, Díaz S, Grime JP, Marzano B, Cabido M, Vendramini F, Cerabolini B (1999) Leaf structure and defence control litter decomposition rate across species and life forms in regional floras on two continents. *New Phytologist* **143**, 191–200. doi:10.1046/j.1469-8137.1999.00430.x

Cornwell WK, Cornelissen JHC, Amatangelo K, Dorrepaal E, Eviner VT, Godoy O, Hobbie SE, Hoorens B, Kurokawa H, Pérez-Harguindeguy N, Quested HM, Santiago LS, Wardle DA, Wright IJ, Aerts R, Allison SD, Van Bodegom P, Brovkin V, Chatain A, Callaghan TV, Díaz S, Garnier E, Gurvich DE, Kazakou E, Klein JA, Read J, Reich PB, Soudzilovskaia NA, Vaieretti MV, Westoby M (2008) Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecology Letters* **11**, 1065–1071. doi:10.1111/j.1461-0248.2008.01219.x

Corre MD, Schnabel RR, Stout WL (2002) Spatial and seasonal variation of gross nitrogen transformations and microbial biomass in a Northeastern US grassland. *Soil Biology & Biochemistry* **34**, 445–457. doi:10.1016/S0038-0717(01)00198-5

Coûteaux MM, Bottner P, Berg B (1995) Litter decomposition, climate and litter quality. *Trends in Ecology & Evolution* **10**, 63–66. doi:10.1016/S0169-5347(00)88978-8

Díaz M, Campos P, Pulido FJ (1997) The Spanish dehesas: a diversity of land use and wildlife. In 'Farming and birds in Europe'. (Eds D Pain, M Pienkowski) pp. 178–209. (Academic Press: London)

Enríquez S, Duarte CM, Sand-Jensen K (1993) Patterns in decomposition rates among photosynthetic organisms: the importance of detritus C : N : P content. *Oecologia* **94**, 457–471. doi:10.1007/BF00566960

Gallardo A, Merino J (1993) Leaf decomposition in two Mediterranean ecosystems of southwest Spain: influence of substrate quality. *Ecology* **74**, 152–161. doi:10.2307/1939510

Garnier E, Lavorel S, Ansquer P, Castro H, Cruz P, Dolezal J, Eriksson O, Fortunel C, Freitas H, Golodets C, Grigulis K, Jouany C, Kazakou E, Kigel J, Kleyer M, Lehsten V, Leps J, Meier T, Pakeman R, Papadimitriou M, Papanastasis V, Quested HM, Quétier F, Robson M, Roumet C, Rusch G, Skarpe C, Sternberg M, Theau JP, Thébault A, Vile D, Zarovali MP (2007) Assessing the effects of land use change on plant traits communities and ecosystem functioning in grasslands: a standardized methodology and lessons from an application to 11 European sites. *Annals of Botany* **99**, 967–985. doi:10.1093/aob/mcl215

Gaxiola A, Armesto JJ (2015) Understanding litter decomposition in semiarid ecosystems: linking leaf traits, UV exposure and rainfall variability. *Frontiers in Plant Science.* doi:10.3389/fpls.2015.00140

Gurlevik N, Kelting DL, Allen HL (2003) The effects of vegetation control and fertilization on net nutrient release from decomposing loblolly pine needles. *Canadian Journal of Forest Research* **33**, 2491–2502. doi:10.1139/x03-182

Güsewell S (2004) N : P ratios in terrestrial plants: variation and functional significance. *New Phytologist* **164**, 243–266. doi:10.1111/j.1469-8137.2004.01192.x

Güsewell S, Gessner MO (2009) N : P ratios influence litter decomposition and colonization by fungi and bacteria in microcosms. *Functional Ecology* **23**, 211–219. doi:10.1111/j.1365-2435.2008.01478.x

Hart SC, Firestone MK, Paul EA (1992) Decomposition and nutrient dynamics of ponderosa pine needles in a Mediterranean-type climate. *Canadian Journal of Forest Research* **22**, 306–314. doi:10.1139/x92-040

INMG (1991) 'Normais climatológicas da região de Alentejo e Algarve, correspondentes a 1951–1980.' O Clima de Portugal, Fascículo XLIX, 4ª Região, Vol. 4. (Instituto Nacional de Meteorologia e Geofísica: Lisboa, Portugal)

Joffre R, Rambal S, Ratte JP (1999) The dehesa system of southern Spain and Portugal as a natural ecosystem mimic. *Agroforestry Systems* **45**, 57–79. doi:10.1023/A:1006259402496

Kolattukudy PE (1980) Biopolyester membranes of plants: cutin and suberin. *Science* **208**, 990–1000. doi:10.1126/science.208.4447.990

Kurokawa H, Nakashizuka T (2008) Leaf herbivory and decomposability in a Malaysian tropical rain forest. *Ecology* **89**, 2645–2656. doi:10.1890/07-1352.1

Lavelle P, Blanchart E, Martin A, Martin S, Spain A (1993) A hierarchical model for decomposition in terrestrial ecosystems: application to soils of the humid tropics. *Biotropica* **25**, 130–150. doi:10.2307/2389178

Lisanework N, Michelsen A (1994) Litter fall and nutrient release by decomposition in three plantations compared with a natural forest in the Ethiopian highland. *Forest Ecology and Management* **65**, 149–164. doi:10.1016/0378-1127(94)90166-X

Luyssaert S, Staelens J, De Schrijver A (2005) Does the commonly used estimator of nutrient resorption in tree foliage actually measure what it claims to? *Oecologia* **144**, 177–186. doi:10.1007/s00442-005-0085-5

Maguire DA (1994) Branch mortality and potential litter fall from Douglas-fir trees in stands of varying density. *Forest Ecology and Management* **70**, 41–53. doi:10.1016/0378-1127(94)90073-6

Matías L, Castro J, Zamora R (2011) Soil-nutrient availability under a global-change scenario in a Mediterranean mountain ecosystem. *Global Change Biology* **17**, 1646–1657. doi:10.1111/j.1365-2486.2010.02338.x

Melillo JM, Aber JD, Muratore JF (1982) Nitrogen and lignin control of hardwood leaf litter dynamics in forest ecosystems. *Ecology* **63**, 621–626. doi:10.2307/1936780

Miller HG (1984) Dynamics of nutrient cycling in plantation ecosystems. In 'Nutrition of plantation forest'. (Eds GD Boven, EKS Nambiar) pp. 53–78. (Academic Press: London)

Olde Venterink H, van der Vliet RE, Wassen MJ (2001) Nutrient limitation along a productivity gradient in wet meadows. *Plant and Soil* **234**, 171–179. doi:10.1023/A:1017922715903

Olea L, López-Bellido RJ, Poblaciones MJ (2005) Europe types of silvopastoral systems in the Mediterranean area: dehesa. In 'Silvopastoralism and sustainable land management. Proceedings International Congress on Silvopastoralism and Sustainable Management'. April 2004, Lugo, Spain. (Eds MR Mosquera, A Rigueiro, J McAdam) pp. 30–35. (CABI: Wallingford, UK)

Olson JS (1963) Energy storage and the balance of producers and decomposers in ecological systems. *Ecology* **44**, 322–331. doi:10.2307/1932179

Passarinho J, Lamosa P, Baeta JP, Santos H, Cândido P (2006) Annual changes in the concentration of minerals and organic compounds of *Quercus suber* leaves. *Physiologia Plantarum* **127**, 100–110. doi:10.1111/j.1399-3054.2006.00655.x

Pausas JG, Pereira J, Aronson J (2009) The tree. In 'Cork oak woodlands on the edge. Ecology, adaptive management, and restoration'. (Eds J Aronson, JS Pereira, JG Pausas) pp. 11–21. (Island Press: Washington, DC)

Pérez-Harguindeguy N, Díaz S, Cornelissen JH, Vendramini F, Cabido M, Castellanos A (2000) Chemistry and toughness predict leaf litter decomposition rates over a wide spectrum of functional types and taxa in central Argentina. *Plant and Soil* **218**, 21–30. doi:10.1023/A:1014981715532

Pérez-Harguindeguy N, Díaz S, Garnier E, Lavorel S, Poorter H, Jaureguiberry P, Bret-Harte MS, Cornwell WK, Craine JM, Gurvich DE, Veneklaas EJ, Reich PB, Poorter L, Wrigth IJ, Ray P, Urcelay C, Enrico L, de Vos AC, Buchmann N, Funes G, Quétier F, Hodgson JG, Morgan HD, ter Steege H, van der Heijden MGA, Sack L, Pausas JG, Thomson K, Blonder B, Poschold P, Vaieretti MV, Conti G, Staver AC, Aquino S, Cornelissen JHC (2013) New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany* **61**, 167–234. doi:10.1071/BT12225

Piatek KB, Allen HL (2000) Site preparation effects on foliar N and P use, retranslocation, and transfer to litter in 15-years old *Pinus taeda. Forest Ecology and Management* **129**, 143–152. doi:10.1016/S0378-1127(99)00150-4

Pinto-Correia T, Mascarenhas J (1999) Contribution to the extensification/intensification debate: new trends in the Portuguese montado. *Landscape and Urban Planning* **46**, 125–131. doi:10.1016/S0169-2046(99)00036-5

Pulido FJ, Díaz M (2005) Regeneration of a Mediterranean oak: a whole cycle approach. *Ecoscience* **12**, 92–102. doi:10.2980/i1195-6860-12-1-92.1

Quilchano C, Marañón T (2002) Dehydrogenase activity in Mediterranean forest soils. *Biology and Fertility of Soils* **35**, 102–107. doi:10.1007/s00374-002-0446-8

Raich JW, Schlesinger WH (1992) The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. *Tellus. Series B, Chemical and Physical Meteorology* **44**, 81–99. doi:10.1034/j.1600-0889.1992.t01-1-00001.x

Robert B, Caritat A, Bertoni G, Vilar L, Molinas M (1996) Nutrient content and seasonal fluctuations in the leaf component of coark-oak (*Quercus suber* L.) litterfall. *Vegetatio* **122**, 29–35. doi:10.1007/BF00052813

Rodrigues ML, Pacheco CA, Chaves MM (1995) Soil-plant relations, root distribution and biomass partitioning in *Lupinus albus* L. under drought conditions. *Journal of Experimental Botany* **46**, 947–956. doi:10.1093/jxb/46.8.947

Singh JS, Gupta SR (1977) Plant decomposition and soil respiration in terrestrial ecosystems. *Botanical Review* **43**, 449–528. doi:10.1007/BF02860844

Van Soest PJ, Wine RH (1967) Use of detergents in the analysis of fibrous feeds. IV. Determination of plant cell-wall constituents. *Journal of Association of Official Analytical Chemists* **50**, 50–55.

Vile D, Garnier E, Shipley B, Laurent G, Navas M-L, Roumet C, Lavorel S, Díaz S, Hodgson JG, Lloret F, Midgley GF, Poorter H, Rutherford MC, Wilson PJ, Wright IJ (2005) Specific leaf area and dry matter content estimate thickness in laminar leaves. *Annals of Botany* **96**, 1129–1136. doi:10.1093/aob/mci264

Vitousek PM, Turner DR, Parton WJ, Sanford RL (1994) Litter decomposition on the Mauna Loa environmental matrix, Hawaii: patterns, mechanisms, and models. *Ecology* **75**, 418–429. doi:10.2307/1939545

Wassen MJ, Venterink HO, Lapshina ED, Tanneberger F (2005) Endangered plants persist under phosphorus limitation. *Nature* **437**, 547–550. doi:10.1038/nature03950