Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria (INIA)
Available online at www.inia.es/forestsystems
doi: http://dx.doi.org/10.5424/fs/20112003-11083

Forest Systems 2011 20(3), 485-495
ISSN: 1131-7965
eISSN: 2171-9845

Aboveground soil C inputs in the ecotone between Scots pine and Pyrenean oak in Sierra de Guadarrama

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Abstract

Aboveground litterfall from Pyrenean oak (*Quercus pyrenaica* Willd. a semi-deciduous species), mixed Pyrenean oak-pine and pine (*Pinus sylvestris* L.) forest stands was surveyed in two sites in a Mediterranean mountain area during a period of 36 and 29 months, respectively. Separation in different litterfall fractions was performed, and C content of each fraction was measured to calculate the C flux to the soil due to litterfall. Our results showed that litterfall input was higher in pine stands than in Pyrenean oak stands (1.8-2.4 Mg C ha^{-1} year^{-1} at pine plots and 0.9-1.4 Mg C ha^{-1} year^{-1} at oak plots) and mixed plots showed intermediate values. Needles or leaves contributed about 50% to total litterfall, underpinning the importance of the rest of materials in the soil C input. The seasonal pattern showed a maximum in Pyrenean oak stands in autumn-early winter, while the pine stands had the maximum in summer, which is in consonance with the physiology of fall of broadleaves and coniferous trees in these latitudes , but clearly differs from needle-shed in Central and Northern Europe. A dry-spring year corresponded to a lower leaf fall during the following autumn, and leaf abscission came some weeks earlier than a year with a rainy spring.

Key words: litterfall; *Pinus sylvestris*; *Quercus pyrenaica*; ecotone; Mediterranean mountain.

Resumen

Caída de hojarasca en un ecotono *Pinus sylvestris* L.-*Quercus pyrenaica* Willd. en la Sierra de Guadarrama

La tasa de caída de hojarasca en parcelas puras de rebollo (*Quercus pyrenaica* Willd.), parcelas mixtas de rebollo y pino silvestre y parcelas puras de pino (*Pinus sylvestris* L.) fue estudiada en dos localizaciones de montaña mediterránea durante 36 y 29 meses, respectivamente. Se llevó a cabo una separación de los componentes de la hojarasca, y se determinó el porcentaje de C en cada una de las fracciones, para calcular un flujo de entrada de C al suelo debido al desfronde. Nuestros resultados muestras que la tasa de caída de hojarasca fue más alta en parcelas de pino que de rebollo, alrededor del doble (1.8-2.4 Mg C ha^{-1} año^{-1} en pino frente a 0.9-1.4 Mg C ha^{-1} año^{-1} en rebollo); las parcelas mixtas mostraron valores intermedios. Las acículas u hojas contribuyeron alrededor del 50% al total de caída de hojarasca. El patrón estacional mostró un máximo de caída de hojarasca de rebollo en otoño y comienzos de invierno, mientras que en las parcelas de pino, dicho máximo se produjo en verano, lo que es congruente con la fisiología de la caída de hojas o acículas en frondosas y coníferas en estas latitudes, pero desmarcándose de los valores obtenidos en Europa Central y del Norte. Un año con primavera seca coincidió con un desfronde de hojas de rebollo menor; asimismo, la caída de la hoja se adelantó algunas semanas con respecto al año con una primavera lluviosa.

Palabras clave: caída de hojarasca; *Pinus sylvestris; Quercus pyrenaica;* ecotono; montaña mediterránea.

Introduction

In the frame of global change, a full understanding of the components and dynamics of the terrestrial C cycle is needed, especially in forest ecosystems, which store a large amount of C, both aboveground (*e.g.* Körner, 2003) and belowground (*e.g.* Jobbágy and Jackson, 2000). Accurate assessments of C stocks in different compartments, as well as of C fluxes between these compartments are desired, in order to predict possible changes in C storage after land

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Received: 30-11-10. Accepted: 03-08-11.

use changes, disturbances or different management practices.

Inputs of C to the soil are due to root decomposition (belowground input) and litterfall (aboveground input), while soil C outputs are due to soil respiration (Trumbore, 2006). Both types of soil C inputs (aboveground litterfall and root descomposition) are known to be related in a global scale (Raich and Nadelhoffer, 1989). C and organic matter inputs to the soil are crucial in terms of nutrient recycling and to sustain soil fertility: this flow of C establishes a clear link between vegetation and soil.

Soil C input rates depend on several factors, which are closely interconnected: higher productivity may lead to higher litterfall rates (Berg *et al.*, 1999), but not necessarily to enhanced root C allocation (Giardina *et al.*, 2003). Reduced forest density through thinning may decrease litterfall rates (Blanco *et al.*, 2006; Roig *et al.*, 2005); however, thinning residues may compensate for declining litterfall rates (Jandl *et al.*, 2007). Tree species have a strong effect on litterfall rates (Binkley and Giardina, 1998; Kavvadias *et al.*, 2001; Vesterdal *et al.*, 2008). Latitude, although with limitations (Berg *et al.*, 1999) has also an effect, likely related to productivity and climate. Finally, precipitation and soil moisture, temperature (Caritat *et al.*, 2006), and soil fertility (Sariyildiz and Anderson, 2005) may play a important role. Some of these factors can be controlled by forest management, such as tree species selection, and thus, forest measures can be conducted in order to choose the best tree species in terms of C sequestration, including soil C.

Scots pine (*Pinus sylvestris* L.) has been intensively monitored in terms of litterfall (Astel *et al.*, 2009; Berg *et al.*, 1999; Blanco *et al.*, 2006; Kouki and Hokkanen, 1992). However, number of studies analysing Scots pine litterfall sharply decreases from Northern to Southern Europe. We consider this to be an important omission, since the Iberian Peninsula is the most southwestern limit of the world distribution of this tree species, and findings from this disjoint population could be different than from the rest of its distribution (Díaz-Pinés *et al.*, in press). In the Iberian Peninsula, the majority of studies were carried out in northern Spain Scots pine stands (Blanco *et al.*, 2006; Pausas, 1997; Santa Regina and Tarazona, 2001), and just one recent paper deals with Scots pine litterfall in Central Spain (Martínez-Alonso *et al.*, 2007). The information related to Pyrenean oak (*Quercus pyrenaica* Willd.) is much more scarce, with data from one single location in the whole Iberian Peninsula (Gallardo *et al.*, 1998), although this tree species covers several hundred thousand hectares in the Iberian Peninsula (Ministerio de Medio Ambiente, 1998).

Thus, more knowledge about litterfall patterns in Mediterranean forest lands is needed, where conditions differ from the rest of Europe. Differential behaviour of Mediterranean Scots pine forests was put on evidence by Berg *et al.* (1999) who found a gradient of increasing litterfall with decreasing latitude from Northern Europe to South France. For the Iberian Peninsula, a variety of litterfall rates was found. Knowing the litterfall pattern of different tree species in Mediterranean ecotonal zones, where the same location may be occupied by different forest types, it is crucial to predict changes after shifts in the tree species distributions. These shifts have been already observed in *Quercus* tree species which are displacing Scots pine stands in northern Spain (Galiano *et al.*, 2010).

In this work, we studied (1) litterfall rates; (2) composition of litterfall and (3) seasonally behaviour of litterfall rates in two ecotones between Scots pine and Pyrenean oak in the Sierra de Guadarrama (Central Spain). The working hypotheses were as follows (1) pines have higher litterfall rates, based on productivity; (2) needles and leaves may be the main contributors of litter-fall and (3) coniferous and broadleaves may have different temporal patterns of litter-fall, since the phenology of the process is different in each tree species.

Material and methods

Site description and experimental design

Experimental sites are located in the Sierra de Guadarrama, in Central Spain: Valsaín (40° 51' N, 4° 3' W) and Rascafría (40° 53' N, 3° 52' W), in the northern and middle area of Sierra de Guadarrama, respectively. Sites are about 1,300 m.a.s.l., over granites and gneisses. Although both experimental sites are in close vicinity (less than 20 km), mean annual precipitation is about 1,000 mm for Rascafría and 500 mm for Valsaín (Table 1). The entire study area is characterized by a Mediterranean climate, with about two-months summer drought, and high temperature fluctuations across the year. Both experimental areas have been and are still managed. A full description of the soil characteristics can be found in Díaz-Pinés *et al.* (in press).

Table 1. Mean (± 1 SD) climatic features for the two experimental areas

	Valsaín (1998-2009)			Rascafría (1984-2009)		
	MMT (°C)	MmT (°C)	MAP (mm)	MMT (°C)	MmT (°C)	MAP (mm)
Spring	14.7 ± 3.3	2.0 ± 2.9	191 ± 50	14.3 ± 3.1	1.2 ± 2.4	220 ± 89
Summer	27.0 ± 1.8	10.2 ± 2.5	60 ± 25	25.4 ± 2.3	7.8 ± 1.5	77 ± 52
Autumn	16.3 ± 5.9	4.2 ± 4.0	195 ± 58	16.2 ± 5.0	2.8 ± 3.2	264 ± 113
Winter	7.4 ± 2.1	–2.9 ± 2.3	159 ± 61	7.9 ± 2.0	–2.9 ± 2.4	337 ± 143
Annual mean	16.3 ± 0.5	3.3 ± 1.5	538 ± 93	16.7 ± 0.7	3.0 ± 1.2	1,060 ± 205

MMT: mean maximum daily temperatures. MmT: mean mimimum daily temperatures. MAP: mean annual precipitation.

At each site, we defined a transect located within the ecotone between Pyrenean oak (hereafter, oak) and Scots pine (hereafter, pine) composed by a pure oak plot, a mixed oak- pine plot and a pure pine plot. Pines are about 80 years old, whereas oaks are about 60 years old. Corresponding basal areas are about 15 m^2 ha^{-1} at the oak plots and 50-60 m^2 ha^{-1} at the pine ones. The mixed plots are composed by 5-10 m^2 ha^{-1} of oaks and 25-30 m^2 ha^{-1} of pines. At each plot (with an area of 2,000 m^2), seven galvanised steel funnel litterfall-collectors (1 meter height, 80 cm diameter), with a cotton cloth bag in the bottom, were randomly placed. Litterfall collection started in October 2005 in Valsaín and in March 2006 in Rascafría and stopped in October 2008 for both sites.

Litterfall was periodically collected and transported to the lab. Once in the lab, material was air-dried and separated according to the following fractions: pine needles, oak leaves, pine branches, oak branches, other pine-origin material (mainly bark and inflorescences), other oak-origin material (mainly inflorescences) and other material of unknown origin. Each fraction was weighted and a sub-sample from each fraction was oven-dried (105°C) to constant weight and dry weight of each fraction was calculated. C content was measured by means of a of a Total Organic Carbon analyser (*TOC-5000*, Shimadzu Corporation, Kyoto, Japan) equipped with a solid sample module (*SSM-5000*, Shimadzu Corporation) (Table 2).

We integrated collected amounts of litterfall in order to get an annual litterfall rate. Litterfall inputs were expressed in Mg C ha^{-1} $year^{-1}$, as the aim of this study is focused on the C cycle. Based on previous experience and visual observations, we assumed that no *in situ* decomposition occurred between litter-fall time and sampling time. For comparison purposes, we defined two «meteorological seasons»: the first one from the beginning of March 2006 to February 2007, and the second one from March 2007 to February 2008. We established the limit between seasons according to the moment of minimum total litterfall rate.

Meteorological data

Meteorological data were obtained from nearby meteorological stations: *Embalse del Pontón Alto* (Valsaín) and *El Paular*, *Rascafría* (Rascafría), from the State Meteorological Agency. We obtained maximal and minimal temperature and accumulated precipitation in a daily resolution, covering the whole measurement period. Long series from previous years were also used to characterize climatically both areas. Due to differences in altitude between meteorological stations and experimental plots, a correction was applied: 0.65°C decrease per 100 m of increasing altitude, and a precipitation increase of 8% for each increase of 100 m in altitude, (but for summer precipitations when convective regime is predominant) (Gandullo, 1994).

Statistical analyses

Differences in litterfall rates between sites and vegetation types were analysed with a two-ways repea-

Table 2. Carbon percentage of each considered litterfall fraction

Material	% C
Pine needle	50.2
Pine branch	49.1
Pine others	48.1
Oak leaf	40.9
Oak branch	45.8
Oak others	45.6
Others	47.7

Table 3. Main meteorological features during the surveying period in both sites

	Valsaín			Rascafría		
	MMT (°C)	**MmT (°C)**	**Prec (mm)**	**MMT (°C)**	**MmT (°C)**	**Prec (mm)**
Summer 2005	27.9	12.2	28	27.1	7.8	32
Autumn 2005	16.8	4.5	168	15.8	1.5	260
Winter 2006	5.8	–2.9	183	7.0	–5.7	350
Spring 2006	16.5	3.7	120	15.5	1.2	165
Summer 2006	27.7	11.9	86	26	7.4	102
Autumn 2006	18.4	7.5	197	17.6	3.5	403
Winter 2007	8.1	–1.4	189	8.7	–4.4	348
March 2006-Feb 2007	*17.7*	*5.4*	*592*	*17.0*	*1.9*	*1,018*
Spring 2007	13.4	2.9	251	13.1	0.0	293
Summer 2007	25.1	9.8	44	24.1	5.8	92
Autumn 2007	16.7	3.8	97	17.5	–0.5	108
Winter 2008	9.9	0.01	82	9.7	–4.3	199
March 2007-Feb 2008	*16.3*	*4.2*	*474*	*16.1*	*0.3*	*692*
Spring 2008	13.6	3.4	290	13.5	0.1	430
Summer 2008	25.4	11	92	24.3	5.3	61
Autumn 2008	14.2	4.5	192	14.4	0.5	260

MMT: mean maximum daily temperatures. MmT: mean mimimum daily temperatures. Prec: precipitation.

ted measures analysis of variance. Univariate repeated measures analysis of variance was used to identify in which collection dates the differences were significant among vegetation types or sites. Subsequently, p*ost hoc* Tukey tests were performed for vegetation type. Correlations were assessed by Pearson correlation test. Significance level was established at $\alpha = 0.05$ for all tests.

Results

The first meteorological season (March 2006-February 2007) was characterized by a relatively dry spring, followed by a common dry summer and rainy autumn and winter, in the range of the historical data (Table 3). During the second meteorological season (March 2007-February 2008), a very rainy spring was observed in comparison to historical data (Table 1), followed by a very long dry period, which resulted in a lower precipitation amount during the whole year 2007 in comparison to 2006 or to historical data (Table 1, Table 3).

Pine plots exhibited higher litterfall rates than oak plots: mean annual litterfall rates were 0.9-1.4 Mg C ha^{-1} year^{-1} for oak plots and 1.8-2.4 Mg C ha^{-1} year^{-1} for pine plots. Mixed stands exhibited intermediate values ranging from 1.5 to 2.1 Mg C ha^{-1} year^{-1} (Fig. 1, Fig. 2). Considering the whole surveying period, Rascafría showed significantly higher litterfall rates than Valsaín. Comparing each vegetation type, the difference between Rascafría and Valsaín litterfall rates was statistically significant in oak plots (1.4 ± 0.2 *vs.* 0.9 ± 0.1 Mg C ha^{-1} year^{-1}, $p = 0.013$) and nearly significant in mixed stands (2.1 ± 0.2 *vs.* 1.8 ± 0.2 Mg C ha^{-1} year^{-1}, $p = 0.08$) and in pine stands (2.4 ± 0.3 *vs.* 1.8 ± 0.1 Mg C ha^{-1} year^{-1} $p = 0.07$). We did not find a significant interaction effect of site and vegetation ($p = 0.57$). We found significant correlations between litterfall rates and basal area, when separately considering the two tree species. R^2 values were high if considering total litterfall rates or only needle- or leaf-fall, respectively (pine litterfall, $R^2 = 0.86$, $p = 0.08$; oak litterfall, $R^2 = 0.84$, $p = 0.02$; needle fall, $R^2 = 0.89$, $p = 0.008$; leaf fall, $R^2 = 0.77$, $p = 0.01$; Fig. 3)

Maximum litterfall occurred in summer for the pine stands, whereas it occurred in autumn-early winter for oak plots. This pattern was similar in the two experimental sites (Fig. 1, Fig. 2). The peak in litterfall was due to high needle- and leaf-fall rates for pine and oak plots, respectively. In the case of mixed plots, contribution of needles during the summer and of leaves during autumn and winter prolonged high litter-fall

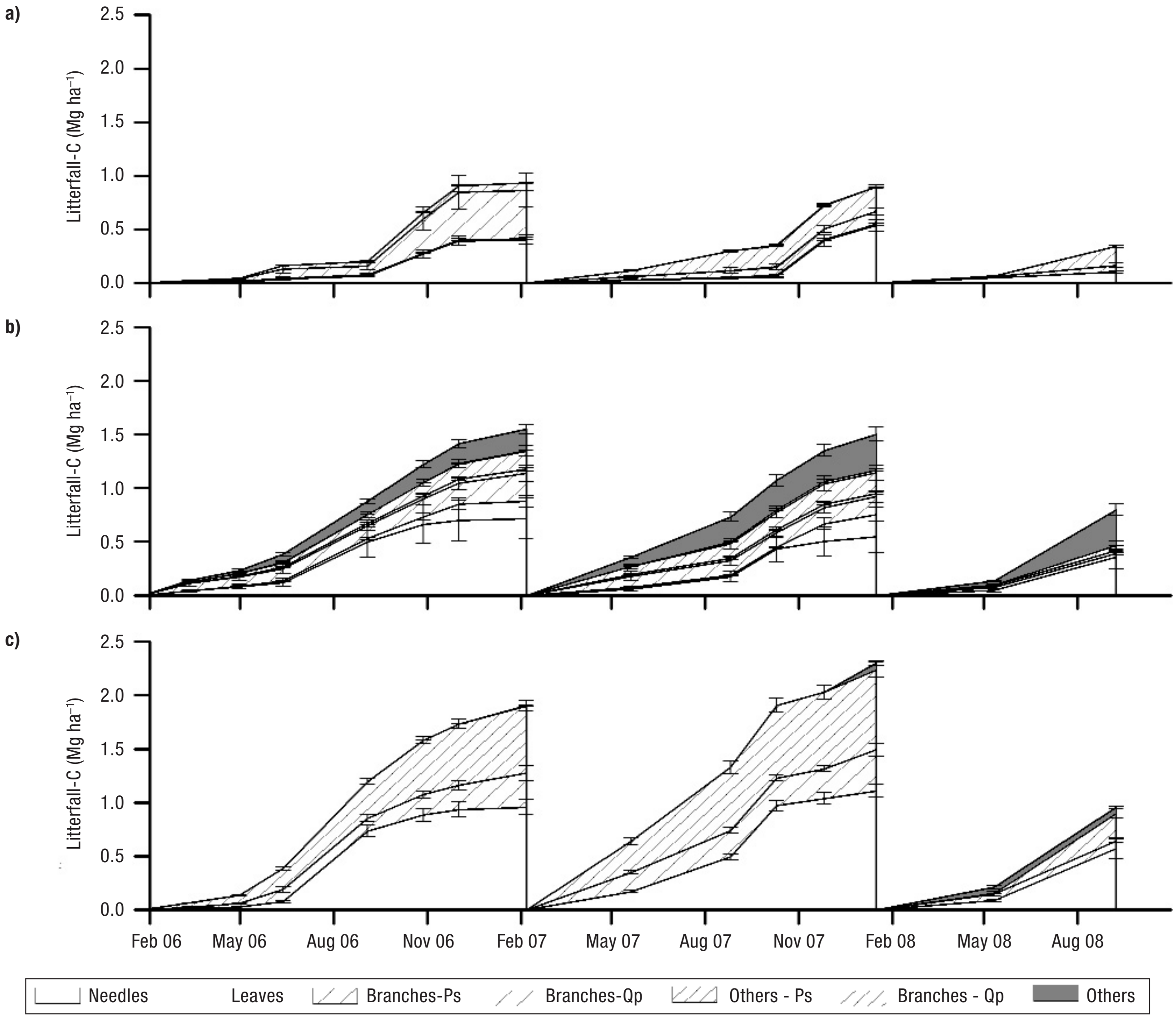

Figure 1. Cumulative litter fall (mean ± 1 SE) along the surveyed years in Valsaín for pure Pyrenean oak (a), mixed (b) and pure Scots pine (c) stands.

rates from June to December (Fig. 1, Fig. 2). From May to September litterfall rates were significantly higher in pine plots in comparison to oak ones whereas from October to December oak plots exhibited the highest litterfall rates.

Maximum leaf-fall rate during meteorological year 2006 lasted from the second half of September to the beginning of November. In 2007 the maximum leaf-fall was observed between end of October and beginning of December. No differential temporal pattern was observed between meteorological years for litterfall in pine plots.

Oak leaves contributed roughly 50% to the total litterfall amounts, and a similar percentage was observed for pine needles (Fig. 4, Fig. 5). Branches contributed up to 40% in oak stands (Valsaín, meteorological season 2006, Fig. 4e), with a mean percentage of about 20%. In the case of pine plots, other material (mainly reproductive material, such as inflorescences) contributed between 30 and 40% to the total litterfall. For oak plots, other materials ranged from 10 to 25% of total litterfall (Fig. 4, Fig. 5).

In the oak plot from Valsaín, oak leaf-litter increased from 0.40 in 2006 to 0.54 Mg C ha^{-1} year^{-1} in 2007 (Table 4, $p = 0.07$). In the mixed plot from Valsaín, there was a significant increase ($p = 0.04$) from 0.16 in 2006 to 0.21 Mg C ha^{-1} year^{-1} in 2007 in oak

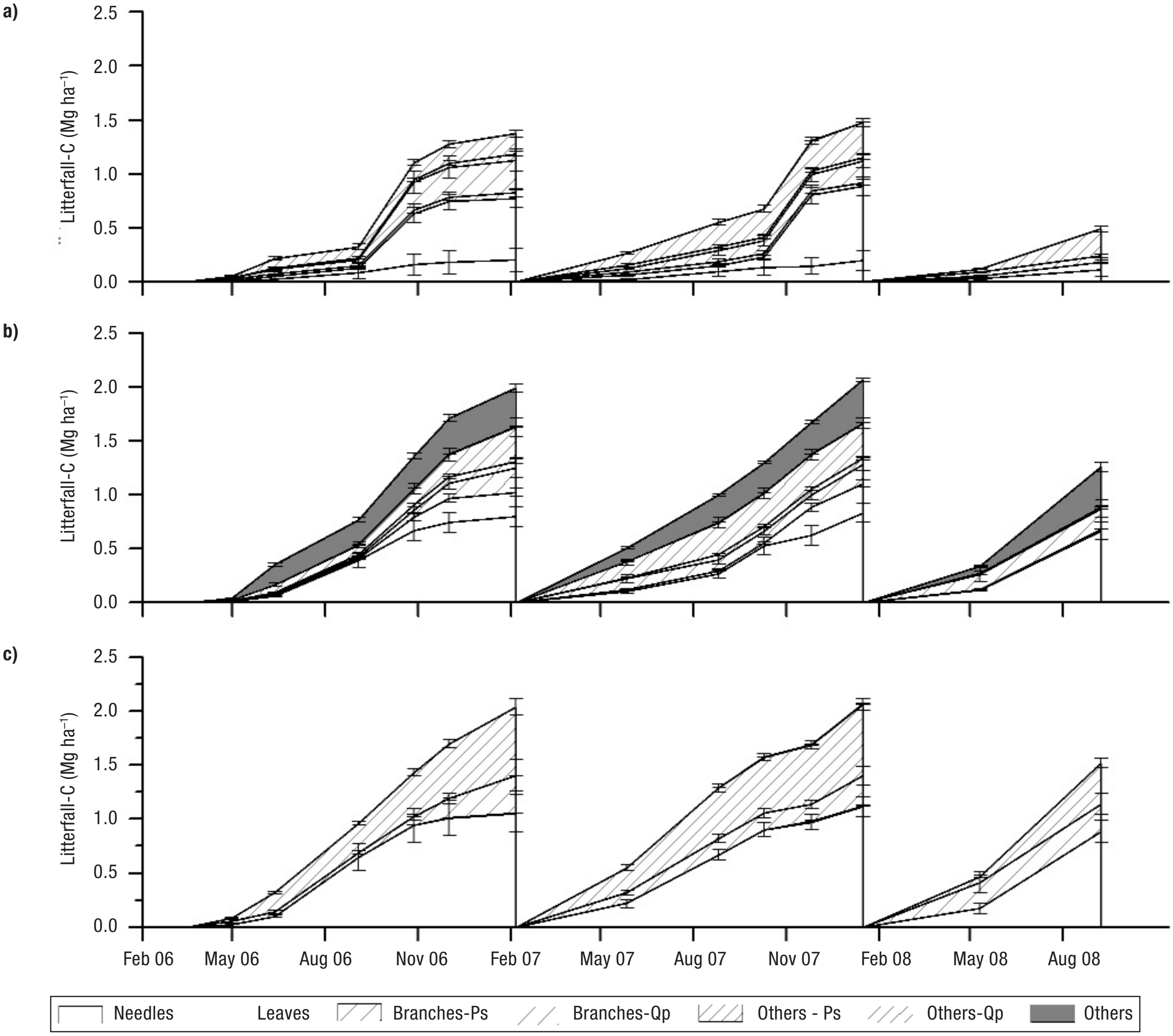

Figure 2. Cumulative litter fall (mean ± 1 SE) along the surveyed years in Rascafría for pure Pyrenean oak (a), mixed (b) and pure Scots pine (c) stands.

leaf-litter. In Rascafría, we observed a similar increase (0.57 in 2006 *vs.* 0.69 Mg C ha^{-1} year^{-1} in 2007, $p = 0.006$). For the mixed plot in Rascafría, the increase in oak leaf-litter (0.22 in 2006; 0.27 Mg C ha^{-1} year^{-1} in 2007) was also significant ($p = 0.025$) (Table 4).

Discussion

In several cases, an accurate comparison between our litterfall rates results and others was not possible in terms of C units, since C percentage for each considered fraction is not included in many papers (Blanco *et al.*, 2006; Martínez-Alonso *et al.*, 2007; Pardo *et al.*, 1997; Pausas, 1997). We found low C percentages in senescence oak leaves (Table 2) and using 50% C —as it is usually made— overestimates C inputs to the soil up to 20%.

Our litterfall-C values are similar to those of other publications of Scots pine forests in Central Spain (Martínez-Alonso *et al.*, 2007), other northern Spanish locations (Blanco *et al.*, 2006; Pausas, 1997) although slightly higher values have been found in these latter areas (Santa Regina and Tarazona, 2001). However, our pine plots exhibited slightly higher litterfall C rates

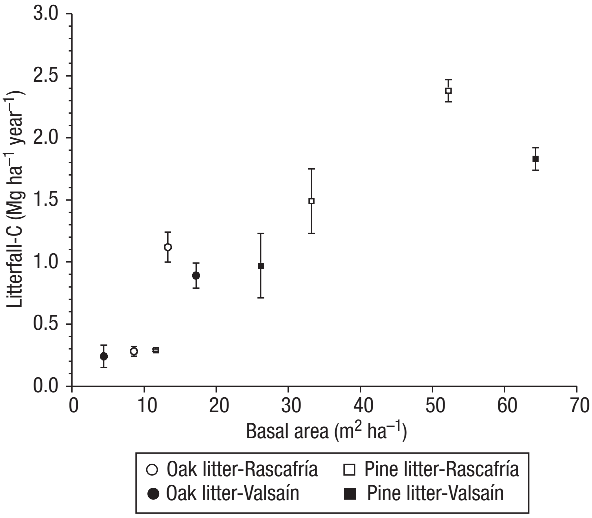

Figure 3. Litterfall rates *vs.* basal area, for oak (circles) and pine (squares) in Rascafría (open symbols) and Valsaín (full symbols). Vertical bars denote standard error of the mean.

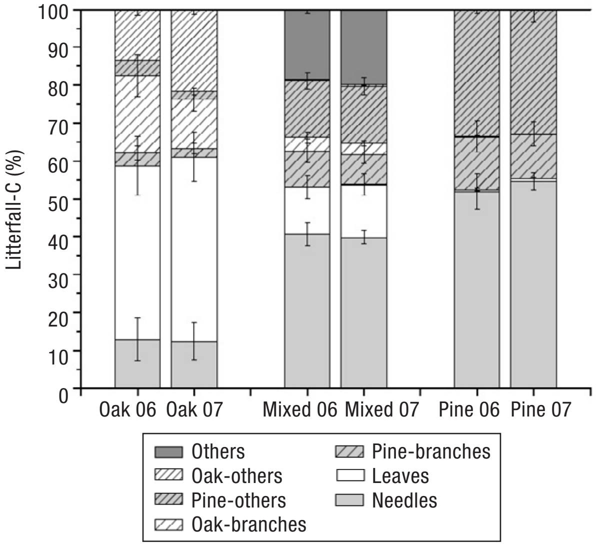

Figure 5. Mean relative contribution (± 1 SE) of each litter fraction to the total litterfall-C in Rascafría for the growing season of 2006 and 2007.

than those recently reported in Poland (Astel *et al.*, 2009) but much higher than those compiled by Starr *et al.* (2005) from Finland (0.5-0.9 Mg C ha^{-1} year^{-1}). It is noteworthy comparing our values with data from other Mediterranean pines, since the behaviour within the genus *Pinus* might by similar in terms of litterfall (Berg *et al.*, 1999). Roig *et al.* (2005) analysed litterfall of *Pinus pinaster* Ait., under different thinning regimes in Central Spain, and found needle-fall mean values of approximately 1.6 Mg C ha^{-1} year^{-1} (ranging from 0.6 to 2.9). Michopoulos *et al.* (2007) found similar values (1.9 Mg C ha^{-1} year^{-1}) in *Pinus halepensis* Mill. urban forests in Athens, Greece. Also in Greece, Kavvadias *et al.* (2001) found lower litterfall rates for *P. pinaster* (0.7 Mg C ha^{-1} year^{-1}) and *Pinus nigra* Arn. v. *pallaciana* (1.3 Mg C ha^{-1} year^{-1}), but the contribution of no-needle litterfall was surprisingly low (less than 5%). Thus, upon the scarce information of genus *Pinus* in Mediterranean areas, litterfall rates seems to be in a range between 1.5-2 Mg C ha^{-1}, (with our data fitting in this threshold) far away from values of 3 Mg C ha^{-1} year^{-1} found in semi-arid areas (Pérez-Suárez *et al.*, 2009) or up to 5 Mg C ha^{-1} year^{-1} in tropical areas (Smith *et al.*, 1998).

Regarding oak litterfall rates, information is even more limited. The values obtained are below the scarce studies carried out in Spain (Gallardo *et al.*, 1998; Pardo *et al.*, 1997) with this almost endemic tree species, and slightly lower than results from a recent study of *Quercus canariensis* Willd., 1.5-1.6 Mg C ha^{-1} year^{-1} (Aponte *et al.*, 2010). Our values are within the range of some studies made on evergreen *Quercus ilex* L in Spain (Bellot *et al.*, 1992; Martin *et al.*, 1996), but far below with results from *Q. ilex* in Central Italy (Bussotti *et al.*, 2003). Our results are also lower than those from deciduous oaks in northern Atlantic Spain (Díaz-Maroto and Vila-Lameiro, 2006).

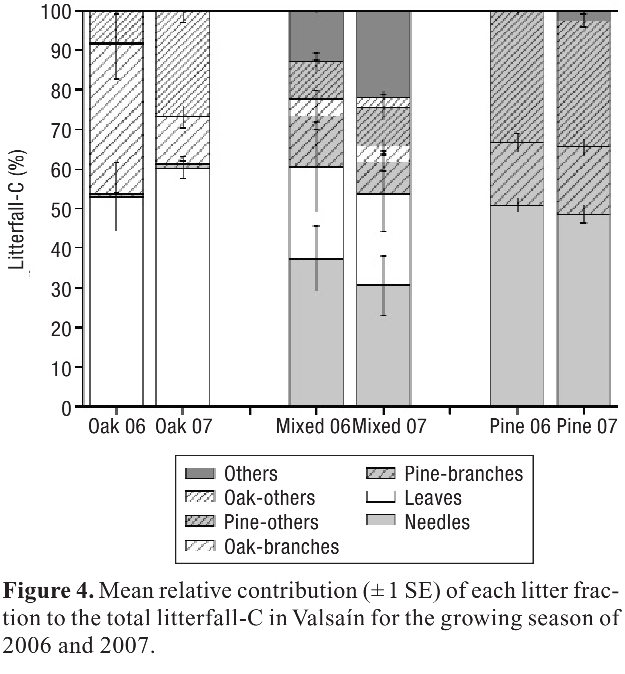

Figure 4. Mean relative contribution (± 1 SE) of each litter fraction to the total litterfall-C in Valsaín for the growing season of 2006 and 2007.

Table 4. Mean (± 1 SE) oak and pine derived litterfall in the monitored meteorological years

Oak Valsaín Qp litter (leaf litter)	Mixed Valsaín Qp litter (leaf litter)	Mixed Valsaín Ps-litter (needle litter)	Pine Valsaín Ps-litter (needle litter)	Oak Rascafría Qp litter (leaf litter)	Mixed Rascafría Qp litter (leaf litter)	Mixed Rascafría Ps-litter (needle litter)	Pine Rascafría Ps-litter (neddle litter)
Season 2006							
0.92 ± 0.18 (0.40 ± 0.05)	0.20 ± 0.07 (0.16 ± 0.05)	1.15 ± 0.30 (0.72 ± 0.19)	1.90 ± 0.18 (0.96 ± 0.07)	1.06 ± 0.15 (0.57 ± 0.09)	0.29 ± 0.06 (0.22 ± 0.04)	1.34 ± 0.25 (0.79 ± 0.10)	2.04 ± 0.32 (1.05 ± 0.17)
Season 2007							
0.88 ± 0.08 (0.54 ± 0.05)	0.26 ± 0.09 (0.21 ± 0.07)	0.90 ± 0.25 (0.54 ± 0.11)	2.24 ± 0.12 (1.11 ± 0.06)	1.21 ± 0.14 (0.69 ± 0.09)	0.34 ± 0.05 (0.27 ± 0.04)	1.33 ± 0.17 (0.83 ± 0.08)	2.06 ± 0.20 (1.11 ± 0.09)

Quercus pyrenaica origin (Qp-litter), *Pinus sylvestris* origin (Ps-litter). Leaf and needle litter (two latter in brackets). All values expressed in Mg C ha^{-1} year^{-1}.

Mixed stands presented intermediate litterfall rates values, as found with the soil C stocks (Díaz-Pinés *et al.*, in press). We were not able to find any reference in the scientific literature reporting litterfall values for coniferous-broadleaves mixed stands on Mediterranean areas. However, our results contrast the study made in a Mexican semi-arid region comparing *Pinus cembroides* Zucc. and *Quercus potosina*, Trel. in which the mixed stands showed the highest litterfall values (Pérez-Suárez *et al.*, 2009). In the same work, the pine plot had the highest basal area and, surprisingly, lower litterfall rates.

Productivity is closely related to litterfall rates (Berg *et al.*, 1999). In our case, we found a strong correlation between basal area and litterfall rates (Fig. 3), which reflects the link between aboveground and belowground C allocation patterns (Raich and Nadelhoffer, 1989). For instance, a significant correlation between litterfall rates and forest floor C stocks, as well as between litterfall rates and soil C stocks in the first cm of the mineral soil has been found (Díaz-Pinés *et al.*, in press), underpinning the importance of litterfall rates as the main soil C input and driver of soil C allocation.

Some authors have related the relative contribution of needle to total litterfall to the state of development of the stand (Martínez-Alonso *et al.*, 2007). However, in a summarising study across Europe, no correlation between needle/total litterfall and age was found; but they found a positive correlation between the contribution of needles and the magnitude of litterfall (Berg and Meentemeyer, 2001). It is somewhat surprising that in some studies it is reported that no-needles litterfall was negligible (Kavvadias *et al.*, 2001; Roig *et al.*, 2005). Oak leaves contributed to about 50% to total oak-derived litterfall, a much lower value than other studies on *Q. pyrenaica* (Gallardo *et al.*, 1998), *Q. ilex* (Rapp *et al.*, 1999) or *Quercus robur* L. (Díaz-Maroto and Vila-Lameiro, 2006; Hansen *et al.*, 2009; Vesterdal *et al.*, 2008). The only studies with similar relative contribution of leaves to total litterfall were those in which a high proportion of acorns was found (Callaway and Nadkarni, 1991; Díaz-Maroto and Vila-Lameiro, 2006), but that was not our case during the sampling period. Besides leaf and/or needle-fall, there is not much information in the scientific literature regarding other components of litterfall. Lehtonen *et al.* (2004) analysed the branch-fall in a chronosequence of Scots pine forests in Sweden, and obtained values from 0.04 to 0.1 Mg C ha^{-1} year^{-1}. This is in contrast to our findings, which show much higher values: 0.3-0.4 Mg C ha^{-1} year^{-1} of branches in pine plots; and 0.2-0.3 Mg C ha^{-1} year^{-1} in mixed plots, with a relatively lower Scots pine presence. Thus, branches contributed significantly to the total litterfall, as well as reproductive organs, and such contribution was consistent across sampling years and experimental sites (roughly, 20% each, Fig. 4, Fig. 5). The ecological importance of reproductive organs or coarse woody debris is high (Montes and Cañellas, 2006) and further research is needed in this direction. Size of the trap may play a role: if the trap is too small (Blanco *et al.*, 2006; Roig *et al.*, 2005), coarse branches may be underestimated, and a key component of the soil C input may be missed. For instance, needle-fall has been proposed as a simple indicator of total litterfall (Berg *et al.*, 1999), but more accurate estimations are needed, since we consider that needle fall can be only a rough estimator of total litterfall, and heterogeneity of coarse debris is high (Pausas, 1997).

Scots pine in Central Spain exhibits the highest needle-fall during summer (Fig. 1, Fig. 2, Martínez-

Alonso *et al.*, 2007), but some weeks before than studies carried out in northern Spain (Blanco *et al.*, 2006; Pausas, 1997; Santa Regina and Tarazona, 2001) or in Central and Northern Europe (Kouki and Hokkanen, 1992). This differential behaviour of Scots pine in Mediterranean regions is likely due to summer water stress. However, water deficit appears not to limit tree growth (Cañellas *et al.*, 2000), high litterfall rates or high soil C stocks (Díaz-Pinés *et al.*, in press). Further studies should be carried out to study whether an early needle fall would promote high soil C stocks. Decomposition taking place in late-summer or autumn might improve nutrient cycling and allow for a higher incorporation of organic C to the soil during the mineralization process.

Pyrenean oak is a semi-deciduous tree: this oak can maintain its dead leaves on the branches during the winter (Do Amaral, 1990), until the buds from the following year sprout to protect the buds from freezing (Blanco *et al.*, 1997). In the Sierra de Guadarrama, the maximum leaf-fall occurred between September and December. We sampled during two contrasting meteorological years: 2006 exhibited a consistent and significant lower leaf-fall than 2007, and precipitation was much lower in 2006 than in 2007 (Table 3). Relatively scarce water during spring (and also during the former winter) likely contributed to a decrease on leaves production of *Q. pyrenaica*. Since oak renews all the leaves every year, this lower leaves production resulted in a lower input of leaves to the soil in 2006 than in 2007. Interestingly, we also observed a delay of some weeks in the maximum leaf fall during 2007. Such trends (different needle-fall amount or different temporal pattern between years) were not evident for pine needles fall. Vogt *et al.* (1986) concluded that broadleaves tree species were more sensitive to climatic factors than coniferous trees in relation to litterfall, at the global scale. In addition, deeper tap roots from Scots pine may somewhat alleviate water stress during summer. More research is needed to know how and to which extent within-years litterfall heterogeneity and variations of litterfall temporal patterns influence the C cycle in this pine-oak ecotone, since both amount of C inputs and decomposition conditions may vary in the frame of global change.

Acknowledgments

We would like to thank Beatriz Ortiz and the people who worked in the lab performing litterfall separation, and to forest managers for facilitation of the working environment. Gratitude is shown to the State Agency of Meteorology for providing the meteorological data. This work was partially funded by the Projects AGL2007-64707/FOR and AGL2010-16862 from the Spanish Ministry of Education

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