Seasonal patterns of litterfall in the floodplain forest of a large Mediterranean river

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ABSTRACT
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Litterfall is a key process controlling trophic and nutrient dynamics in coupled river-floodplain ecosystems. Litterfall quantity, quality and timing may be partly controlled by the local hydrology and forest structure. In the Middle Ebro (a large Mediterranean river in NE Spain), the importance of those factors has recently been assessed for litterfall quantity and quality but never for litterfall timing. In this study, the litterfall seasonal patterns (i.e., the intra-annual phenology of total vertical litterfall, the contribution of different species as well as the litter fractions and their nutrient concentration) in the floodplain forest of the Middle Ebro in 2007 were described to assess the role of their controlling factors. To that end, litterfall was collected monthly in a series of 12 plots representing the variety (in terms of forest structure and hydroperiod) of forest patches existing in the floodplain. The sampled material was sorted by litter fractions and species, and their C, N and P concentrations were analysed. The results showed that, as in most deciduous temperate forests, the bulk of litterfall occurred in autumn (42 % of total) with leaf fall (57 % of all litter fractions) for the 6 dominant tree species. However, the amount of litterfall collected during the rest of the year (especially in spring = 25 % and summer = 20 %) and from other litter components (woody = 22 % and reproductive = 10 %, with significantly higher N and P concentrations) was not negligible. This litterfall leads to seasonal imbalances in the quantity and quality of litter inputs to the riparian system throughout the year, which consequently might control the detritus-based community structure, food webs and nutrient cycling. Two species of Populus (P. nigra and P. alba) exhibited a second leaf fall peak in the summer. However, cross correlation analyses showed that the temporal dynamics of litter and leaf fall were similar between plots and dominant tree species. This result suggests that, unlike litterfall quantity and quality, litterfall phenology was not controlled by the differences in forest structure and hydrology at the patch level but rather by some other factors operating at a broader spatial scale, such as the regional climate.

Key words: Litterfall seasonal phenology, floodplain forest, litter input, organic matter, Populus, Tamarix.
INTRODUCTION

Litterfall is a critical pathway for nutrient transfer in riparian zones. The amount and quality of litter inputs to coupled terrestrial-aquatic ecosystems drive consumer community structure (Wallace et al., 1997; 1999; Bailey et al., 2001; Tibbets & Molles, 2005) and key ecosystem processes, such as decomposition and nutrient cycling (Fisher & Likens, 1973; Vannote et al., 1980; Xiong & Nilsson, 1997; Baker et al., 2001; Follstad Shah & Dahm, 2008). The temporal dynamics of litter inputs (i.e., litterfall phenology) also play an important role in ecosystem functioning because they determine the temporal variation in the supply of organic matter and in light availability to aquatic systems (Gregory et al., 1991; Acuña et al., 2007). For example, some studies have shown that the life cycles and structure of the riparian detritus-dependent animal communities are in synchrony with litterfall timing (e.g., Abelho and Graça, 1996; Wantzen & Wagner, 2006).

Tree species composition and the hydrologic regime of rivers are the main factors that contribute to explain litter quantity, quality and phenology in floodplain forests. First, some species produce more litter than other species (Meier et al., 2006), whereas flood type, duration and frequency determine organic matter production (Megonigal et al., 1997; González et al., 2010c). Second, species and functional groups may use and process nutrients differently in terms of uptake, resorption, storage and loss, ultimately affecting litter quality (e.g., N2-fixing vs. non N2-fixing species, Follstad Shah et al., 2010; ruderal vs. competitive species, González et al., 2010b). Moreover, litter-leaf nutrient concentrations also vary as a function of the flooding regime (Tibbets & Molles, 2005; Follstad Shah & Dahm, 2008; González et al., 2010b). Third, litterfall quantities display seasonal peaks in deciduous forests, typically in autumn in the temperate zone (Benfield, 1997; Abelho, 2001) but also in summer, in some cases (e.g., Eucalyptus spp., Lamb, 1985; Pozo et al., 1997; McIvor, 2001; sclerophyllous vegetation, King et al. 1987; Stewart & Davies, 1990). Hydrology may play a role in litterfall timing by triggering the onset of the process under severe drought conditions (Lake, 1995; Rood et al., 2000). Conversely, evergreen trees display an irregular litterfall pattern throughout the year. Unfortunately, both forest composition and hydrology have been altered in most rivers during recent decades. This alteration is not expected to be reverted in the near future but instead is expected to be aggravated by increasing global pressure on the natural water resources (Tockner & Stanford, 2002). Under these circumstances, a greater knowledge of litterfall patterns in floodplain forests seems necessary for understanding eventual alterations in associated food webs and key ecosystem processes (e.g., litterfall breakdown rates, microbial activity, composition and the structure of detritus consumers and predators).
As part of a larger study aimed at describing the factors controlling total annual litter production (González et al., 2010c) and its quality (González et al., 2010c; 2010b), the objectives of this work were to report the phenology of litterfall in the floodplain forest of a large Mediterranean river and to discuss the potential role of the local hydrology and forest structure as drivers of litterfall timing. It was hypothesised that, as observed for litterfall quantity and quality, litterfall phenology could be partly influenced by the local hydrology, most likely exhibiting earlier litterfall in the more disconnected patches along the floodplain. Similarly, tree species could display different phenological patterns depending on their leaf architecture and overall drought tolerance. The results could also be used to assess future studies that examine key litterfall-dependent riparian ecosystem processes in the context of global change because drier conditions and dominance by drought-tolerant taxa are expected; thus, their characteristic litterfall phenology might eventually predominate in the floodplain.

METHODS

Study area

This study was carried out in the floodplain forest of an 8 km river segment located 12 km downstream from the city of Zaragoza (NE Spain, 41°39’ N, 0°52’ W), which is representative of the Middle Ebro River, the 2nd largest river in the semi-arid Mediterranean region. The Ebro River naturally has a year-to-year irregular pluvionival hydrological regime and a meandering-to-braided geomorphology in the middle section (Ollero, 2007). However, flow regulation and channel embankment since the 1950’s is currently leading to a substantial stabilisation in the hydrologic (i.e., reduced flood duration and frequency) and geomorphic (i.e., reduced channel migration) regime (Cabezas et al., 2009; Magdaleno & Fernández, 2011). Reduced overbank flooding and sediment deposition are partially responsible for decreased litter production (González et al., 2010c) and for a lower concentration of nutrients in leaves (González et al., 2010b) at the more disconnected forest patches. River regulation is also causing progressive changes in the composition of the tree community in the study area (González et al., 2010a; 2012). Currently, forests are dominated by relatively senescent and declining populations of the pioneer trees Populus nigra L., Salix alba L., Tamarix gallica, T.africana and T. canariensis; alternately, forests can be dominated by healthier formations of P. alba L., with the frequent presence of small stems of late-seral species such as Fraxinus angustifolia Vahl. and Ulmus minor Mill. in the sub-canopies of both successional pathways. However, the lack of geomorphic dynamism and dry conditions seem to be especially detrimental to S. alba and, to a lesser extent, to P. nigra and Tamarix spp., while their effects on P. alba are more uncertain (i.e., healthy populations but not colonising new gravel bars). All tree species present in the floodplain forest are deciduous.

Selection of forest patches and plot establishment

Within the floodplain forest under study, a total of 12 forest patches were selected according to the following criteria: (i) patches were distributed according to the local proportion of geomorphic landforms (1 patch on a gravel bar, 5 patches on the natural levee of a permanent or intermittent channel, 6 patches on floodplain terrace); (ii) the gradient of tree species composition, forest structure and flooding regime existing in the floodplain had to be represented; and (iii) all patches were ≥ 9 years old as confirmed by the examination of a 1998 aerial photograph and hence had a well-developed overstory layer. The last condition was set to deliberately avoid sampling young successional forests as litter traps are not designed to capture materials growing close to the ground, which are common in early-seral stages (Naiman et al. 2005).

Once the 12 forest patches were chosen, 12 corresponding study plots were set up with the following characteristics: (i) only 1 plot in each forest patch to avoid pseudoreplication bias; (ii) variable plot dimensions to geometrically
adapt to each distinctive riparian forest patch (but always with an area of 500 m$^2$ and a rectangular size to fit within the usually elongated forest patches); and (iii) a buffer distance of at least 5 m from the plot to the forest edge.

A summary of the plot characteristics (forest structure and hydrology) is provided in Table 1. Plots were numbered by flood duration in decreasing order. Therefore, one may expect that, due to global change, patches with characteristics such as those in the plots with higher numbers will be more common in the future.

**Litterfall collection and processing**

In 2007, litterfall was collected monthly in a series of 120 litterfall traps (10 traps / plot). A litterfall trap was made of a 0.25 m$^2$ square metallic frame elevated 1 m above the soil, hanging from nearby trees by ropes. A synthetic 75 cm deep bag with a 1 mm mesh was attached to the frame, allowing rapid drainage of rainwater to reduce weight loss by leaching. Two small stones were placed in each bag to weigh down the trapped material and keep the bag extended.

Each month, the material was taken to the laboratory to be sorted into 5 fractions: woody (bark and twigs $\leq$ 1 cm diameter), buds and scales, reproductive (flowers, fruits and seeds), leaves (by species) and unidentifiable debris. Large woody material (bark and twigs $> 1$ cm diameter) and animal remains were removed from the samples. Samples were dried in the oven at 60°C for at least 72 h until a constant mass was attained and then weighed. Subsamples of each fraction were ground to a homogeneous powder using an IKA A10 mill and then stored in a dark desiccator until they were analysed for quality (% C, N and P concentration). Litter C and N concentrations were measured by combusting subsamples of each litter fraction collected in litter traps with a varioMAX N/CN elemental analyser. Litter P

| Table 1. Forest structure and hydrogeomorphic characteristics of the 12 study plots. The mortality rate was calculated as the frequency of dead plus dying (i.e., mortality already affecting the main axis) stems of the phreatophytic species ($P$. nigra, $P$. alba, $S$. alba and *Tamarix* spp.). The hydrologic parameters were calculated from weekly measurements using a piezometer that was installed in each plot. The depth to groundwater was the annual water level mean. G-Gravel bar, L-Natural levee, T-Floodplain terrace. *Estructura forestal y características hidrológicas de las 12 parcelas de estudio. La tasa de mortalidad se calculó como la frecuencia de pies muertos más pies terminales (i.e., mortalidad ya afectando al eje principal) de especies freatófitas (*P*. nigra, *P*. alba, *S*. alba y *Tamarix* spp.). Los parámetros hidrológicos fueron calculados a partir de medidas semanales en un piezómetro instalado en cada parcela. La profundidad al acuífero era el nivel freático medio anual. G-Playa de gravas, L-Ribera, T-Terraza de la llanura de inundación. |
|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|
| Forest structure | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 |
| Live basal area (m$^2$/ha) | 27.8 | 51.7 | 77.7 | 59.0 | 30.1 | 40.1 | 38.2 | 31.7 | 36.2 | 14.0 | 67.2 | 62.2 |
| Populus nigra | 27.8 | 17.9 | 77.7 | 53.4 | 21.6 | 15.2 | 12.8 | 28.1 | 10.9 | 11.8 | 0 | 0 |
| Populus alba | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Tamarix spp. | 0 | 11.6 | 0 | 2.9 | 4.5 | 15.2 | 12.8 | 28.1 | 10.9 | 11.8 | 0 | 0 |
| Salix alba | 0 | 22.2 | 0 | 1.7 | 1.9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Ulmus minor | 0 | 0 | 0 | 0.3 | 1.8 | 0 | 0.4 | 0.5 | 4.1 | 0 | 0 | 4 |
| Fraxinus angustifolia | 0 | 0 | 0 | 0 | 0.1 | 0.1 | 0 | 0.3 | 0 | 0 | 0 | 0 |
| Other | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Dead basal area (m$^2$/ha) | 0.9 | 4.9 | 2.9 | 3.3 | 2.1 | 0.8 | 11.0 | 5.8 | 11.2 | 3.0 | 14.9 | 5.3 |
| Mortality rate (%) | 14 | 22 | 8 | 22 | 25 | 17 | 70 | 47 | 48 | 55 | 21 | 20 |
| Hydrogeomorphic characteristics | | | | | | | | | | | | |
| Geomorphic landform | G | L | L | L | L | L | T | T | T | T | T | T |
| Depth to groundwater (cm) | 16 | 58 | 70 | 78 | 86 | 129 | 97 | 135 | 137 | 64 | 222 | 227 |
| Flood duration (weeks$ \cdot$y$^{-1}$) | 14 | 12 | 10 | 9 | 9 | 8 | 7 | 4 | 4 | 3 | 3 | 2 |
| River distance (m) | 36 | 45 | 125 | 68 | 46 | 169 | 722 | 889 | 260 | 918 | 213 | 115 |
concentration was determined by ashing the sub-
samples at 450 °C for 3 h followed by digestion in a 3.5 mol · L⁻¹ HNO₃-HCl (1:3) solution and
spectrophotometric analysis using the standard
vanadate-molybdate method (Allen et al., 1976).

Vandalism, tree falls and flooding caused the
loss of 11% of the samples. The damaged bags
were replaced during weekly patrols to maintain
10 traps per plot each month. Missing data were
estimated using averaged daily litterfall rates per
month and plot and were calculated with the
available data.

The correlations in the total litterfall monthly
time series between the 12 plots and in leaf fall
monthly time series between the abovementioned
6 dominant tree species (leaves from the three
Tamarix spp. were treated as a group due to the
impossibility of identifying the species in the ab-
sence of in
florescence) were compared using a
cross correlation statistical procedure (Jenkins &
Watts, 1968; Box & Jenkins, 1976) available in
SPSS 13.0 software. The analysis compares pairs
of time series, including a particular number of
observations (n) collected on a temporal regular
basis (i.e., k = lags), and produces a series of cor-
relation coefficients at a chosen maximum num-
ber of time-lag delays between the two time se-
ries under analysis (m). In our case, n = 12, k = 1
month and m = 0 months (as we were only inter-
ested in the degree of simultaneity between the
monthly time series).

RESULTS

Annual litterfall

Total litterfall ranged from 199 to 916 g m⁻² y⁻¹
between the studied plots (Table 2). In gen-
eral, litter production increased in the plots with
higher basal area and deeper groundwaters and
decreased with higher river distance (squared
Spearman’s coefficients = 0.26, 0.05, 0.24, re-
spectively, p < 0.05, n = 120). Leaves were the
most abundant fraction, followed by woody and
reproductive tissues. Populus nigra clearly dom-
ninated leaf fall, although P. alba and Tamarix
spp. contributions were also considerable. The
high structural variability of the forest in terms
of species composition and dominance (Table 1)
was reflected by the high standard errors within
each leaf litter fraction of the different species.

| Table 2. Total litterfall (g of dry matter m⁻² y⁻¹) and contribution of the different litter fractions and species in the Middle Ebro floodplain forest during 2007. SE±1 standard error of the mean. Letters indicate homogeneous groups after t-tests (p < 0.05) between litter fractions and between species leaf fall, with plots (n = 12) as replicates. Hojarasca caída total (g peso seco m⁻² año⁻¹) y contribución de las diferentes fracciones y especies en el bosque de ribera del Ebro Medio durante 2007. SE±1 error estándar de la media. Las letras indican grupos homogéneos después de tests t (p < 0.05) entre las fracciones de hojarasca y entre las hojas caídas de cada especie, con parcelas (n = 12) como réplicas. |
| Total | 508 | 773 | 552 | 748 | 536 | 605 | 381 | 431 | 548 | 199 | 559 | 916 | 563 | 55 | 100 |
| Woody | 79 | 283 | 140 | 168 | 67 | 129 | 67 | 64 | 151 | 51 | 96 | 221 | 126 | b | 21 | 22 |
| Reproductive | 33 | 50 | 44 | 89 | 81 | 77 | 18 | 35 | 38 | 14 | 102 | 84 | 56 | c | 9 | 10 |
| Buds and scales | 52 | 40 | 43 | 51 | 27 | 31 | 14 | 40 | 13 | 14 | 77 | 42 | 37 | d | 6 | 7 |
| Debris | 34 | 43 | 26 | 35 | 26 | 21 | 16 | 24 | 9 | 18 | 31 | 25 | c | 3 | 4 |
| Leaves | 310 | 357 | 299 | 405 | 336 | 346 | 267 | 276 | 323 | 110 | 265 | 537 | 319 | e | 29 | 57 | 100 |
| Populus nigra | 304 | 133 | 292 | 358 | 197 | 121 | 159 | 216 | 56 | 98 | 1 | 11 | 162 | a | 33 | 51 |
| Tamarix spp. | 0 | 94 | 5 | 23 | 35 | 200 | 103 | 35 | 138 | 8 | 5 | 14 | 55 | b | 19 | 17 |
| Populus alba | 0 | 0 | 0 | 0 | 0 | 2 | 4 | 0 | 0 | 1 | 254 | 377 | 53 | ab | 36 | 17 |
| Ulmus minor | 0 | 0 | 1 | 2 | 47 | 8 | 0 | 16 | 108 | 1 | 0 | 130 | 26 | b | 13 | 8 |
| Salix alba | 0 | 127 | 0 | 6 | 1 | 10 | 0 | 0 | 16 | 1 | 1 | 0 | 13 | c | 10 | 4 |
| Fraxinus angustifolia | 0 | 1 | 0 | 12 | 53 | 0 | 0 | 0 | 0 | 2 | 0 | 6 | 4 | 2 |
| Other spp. | 5 | 2 | 1 | 4 | 2 | 6 | 1 | 9 | 5 | 2 | 3 | 4 | 4 | c | 1 | 1 |
Litterfall peaked in November in all plots (Fig. 1). Although most litter fell in autumn (42%), the material collected in spring and summer accounted for 25 and 20% of the total registered litterfall, respectively. The lowest litterfall rates were recorded in winter, comprising only 13% of the total annual collection. As shown by cross correlation analyses (Table 3), the litterfall time series were significantly correlated in 61 of 66 possible plot-to-plot comparisons at $m = 0$, indicating that the timing of total litterfall was approximately homogeneous between plots. Simultaneous correlation (i.e., at $m = 0$) in the timing leaf-fall curves was also significant between the 6 dominant tree species in the 15 possible species-to-species comparisons (Table 4), with

**Figure 1.** Temporal variation in monthly total litterfall rate (g of dry matter m$^{-2}$ month$^{-1}$) in 2007. In the upper graph, the 12 curves represent the 12 plots, and each point represents the monthly mean of 10 litter traps. Errors and a plot legend were not included in the figure to improve clarity. For the same reason, all plots but 2, 3, 10 and 11 were not labelled because their time series were not significantly different from any other plot in the floodplain, as shown by the cross correlation coefficients (Table 3). In the lower graph, each point represents the monthly mean of the 12 study plots. The error bars indicate the ±1 standard error of the mean. Variación temporal en la tasa de caída de hojarasca mensual (g peso seco m$^{-2}$ mes$^{-1}$) en 2007. En el gráfico de arriba, las 12 curvas representan las 12 parcelas y cada punto la media mensual de las 10 trampas de hojarasca. Los errores y la leyenda de las parcelas no se incluyeron en la figura para facilitar su legibilidad. Por la misma razón, todas las parcelas menos la 2, 3, 10 y 11 no se etiquetaron porque ninguna de sus series temporales resultó significativamente diferente de ninguna otra parcela en la llanura, como mostraron los coeficientes de correlación cruzados (Tabla 3). En el gráfico inferior, cada punto representa la media mensual de las 12 parcelas de estudio. Las barras de error indican ±1 error estándar de la media.

**Litterfall seasonal phenology**

**Figure 2.** Temporal variation in monthly leaf fall per species (g of dry matter m$^{-2}$ month$^{-1}$) in 2007. For each species, each point represents the monthly mean of 12 study plots. To improve graph clarity, errors are not shown. Variación temporal en la tasa de caída de hojas por especies (g peso seco m$^{-2}$ mes$^{-1}$) en 2007. Para cada especie, cada punto representa la media mensual de las 12 parcelas de estudio. Para mejorar la claridad de la gráfica, los errores no se muestran.

**Figure 3.** Temporal variation in the relative importance (by weight) of the 5 litter fractions in 2007. Variación temporal en la importancia relativa (en peso) de las cinco fracciones de hojarasca en 2007.
Litterfall phenology in the Middle Ebro

Table 3. Cross correlation coefficients for the litterfall time series of the 12 study plots at $k = 1$ month, $n = 12$ and $m = 0$ (no time-lag delay between each pair of time series under analysis) ***$p < 0.01$, *$p < 0.05$. Coeficientes de correlación cruzada para las series temporales de caída de hojarasca de las 12 parcelas a $k = 1$ mes, $n = 12$ y $m = 0$ (no desfase temporal entre cada par de series temporales analizadas) ***$p < 0.01$, *$p < 0.05$.

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all species peaking in November (Fig. 2). However, *P. nigra* and *P. alba* also had a secondary leaf-fall peak in the summer.

The relative importance of each litter category varied notably throughout the year (Fig. 3). Leaves represented more than 60% of the total litterfall from July to January, with a peak of 80-90% in the autumn. Litter composition from February to June was more diverse. The fall of buds and scales peaked in late-winter and early-spring (with approximately 30% of the total litterfall during the period of February-April) and preceded the spring peak of reproductive tissues, which represented 20-40% of the total litter production in the spring. The relative contribution of the woody fraction to total litterfall was more regular throughout the year (20-40%), aside from the autumn period when it rarely exceeded 10% due to the prevalence of leaf fall.

Nutrient content in litterfall

Almost one half of the total annual litterfall (563 g m$^{-2}$ y$^{-1}$) was C (255 g m$^{-2}$ y$^{-1}$), whereas the contribution of N (5.9 g m$^{-2}$ y$^{-1}$) and P (0.53 g m$^{-2}$ y$^{-1}$) was much smaller. C, N and P content varied significantly ($p < 0.001$) between litter fractions ($F_{4,55} = 163$; $F_{4,55} = 46$ and $F_{4,55} = 47$; respective ANOVAs with leaves, woody, reproductive, buds and scales and debris as the 5 fixed factors and % C, N and P as dependent variables). However, the highest differences among litter fractions were found within N and P, with reproductive tissues exhibiting outstanding levels of N and P compared to the other fractions (Fig. 4). This finding, in conjunction with the temporally changing relative contribution of the different fractions to total litterfall, caused the C:N, C:P and N:P ratios in litterfall to dif-

Table 4. Cross correlation coefficients for the leaf-fall time series of the 6 dominant species (averaged for 12 study plots) at $k = 1$ month, $n = 12$ and $m = 0$ (no time-lag delay between each pair of time series under analysis) ***$p < 0.01$, *$p < 0.05$. Coeficientes de correlación cruzada para las series temporales de caída de hoja de las 6 especies dominantes (mediadas para 12 parcelas de estudio) a $k = 1$ mes, $n = 12$ y $m = 0$ (no desfase temporal entre cada par de series temporales analizadas) ***$p < 0.01$, *$p < 0.05$.

<table>
<thead>
<tr>
<th>Fraxinus angustifolia</th>
<th>Populus alba</th>
<th>Populus nigra</th>
<th>Salix alba</th>
<th>Tamarix spp.</th>
<th>Ulmus minor</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>P. alba</em></td>
<td>0.78**</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>P. nigra</em></td>
<td>0.79**</td>
<td>0.95**</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Salix alba</em></td>
<td>0.67*</td>
<td>0.88**</td>
<td>0.89**</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td><em>Tamarix spp.</em></td>
<td>0.81**</td>
<td>0.96**</td>
<td>0.96**</td>
<td>0.94**</td>
<td>1</td>
</tr>
<tr>
<td><em>Ulmus minor</em></td>
<td>0.82**</td>
<td>0.98**</td>
<td>0.93**</td>
<td>0.94**</td>
<td>0.98**</td>
</tr>
</tbody>
</table>
fer throughout the course of the year (Fig. 5). The three ratios progressively decreased after the bulk of leaf fall in November, reached their minimum values in spring with the peak of reproductive tissues and then recovered their higher values in June and July, which were maintained during summer and autumn.

DISCUSSION

Annual litterfall

The total recorded litterfall at floodplain level (mean = 563 g m$^{-2}$ y$^{-1}$) was slightly higher than that found in other riparian forests in the Mediterranean and Iberian rivers (mean = 551 g m$^{-2}$ y$^{-1}$, see review by González et al., 2010c) but had a low proportion of leaves (57%) compared with the worldwide average of 70% in deciduous riparian forests (Bray & Gorham, 1964; Meentemeyer et al., 1982). Although some caution is warranted, as the woody fraction is not always computed in litterfall studies, the low relative percentage of leaves in the litterfall at floodplain level might be explained by the ongoing process of canopy dieback (i.e., generalised presence of dead and/or leafless branches in the canopy, sensu Rood et al., 2000) that is observed in the study area for pioneer trees (P. nigra, S. alba, Tamarix spp.) and, to a lesser extent, for P. alba. The canopy dieback is generally attributed to a lack of hydrogeomorphic dynamism, abrupt and long low-water periods in the drier sites and the lack of effective replacement by late-seral species (González et al., 2010a; 2012). Consistently, similar proportions of woody material that have been reported in the Ebro (> 20%) have been interpreted as evidence of senescence in other riparian forests (Muzika et al., 1987). However, at the patch level, we were unable to find significant relationships between the woody component (expressed as either absolute weight or percentage over the total litterfall and woody material/leaves ratio) and different descriptors of forest decline (dead basal area and mortality of pioneers) across the 12 plots. Alternate hypotheses to explain the high proportion of wood in litterfall compared to global means may be the thinning of the weakest trees and branches as a result of competition under a closed forest canopy and the strong winds that characterise the climate of the study area. Nevertheless, while the tendency toward forest decline is not likely to reverse in the near future, the effects of dieback on litter production and quality (and, in turn, on riparian-
Litterfall seasonal phenology

As in most of the temperate deciduous forests, the bulk of litterfall occurs in autumn, with leaf fall occurring over a relatively short period (Benfield, 1997; Pozo et al., 1997; Abelho, 2001) compared to other riparian ecosystems of different regions in the world (e.g., Neiff & De Neiff, 1990; Campbell et al., 1992; Aké-Castillo et al., 2006) and to other Mediterranean rivers. However, the frequent presence of evergreens (e.g., Nerium oleander in Morocco, Maamri et al., 1994) and sclerophyllous species (e.g., the Fynbos biome in South Africa, King et al., 1987; Steward & Davies, 1990) may extend the season of leaf fall or accelerate the onset of this process towards the summer, respectively. However, our results showed that the litterfall collected during the rest of the year and for the other litter fractions in addition to leaves are not negligible and must be considered in future studies; for example in those interested in organic matter and nutrient budgets. In fact, although the woody and reproductive compartments may be locally and seasonally important as sources that enter heterotrophic pathways in running waters, they have received little attention in comparison with the decomposition and breakdown of forest leaves (Abelho, 2001). In the Middle Ebro in particular, the fall of reproductive tissues occurs in the spring with the pulse of seed release from most of the dominant tree species: P. alba and U. minor peak in April and P. nigra, S. alba and Tamarix spp. in May (González, unpublished data). Prior to this, during the late-winter and early-spring, the highest amounts of buds and scales fall when inflorescences are blossoming and the leaves and new branches are sprouting. The abovementioned high number of dying branches observed in the canopy of most of the forest stand as well as other factors such as thinning and strong winds could underlie the continuous source of woody material (mostly bark and dead twigs) observed in litterfall throughout the year. The small summer leaf-
fall peaks could be the result of summer hydric stress, which may induce the precocious abscission of leaves. In fact, Rood et al. (2000) reported the precocious yellowing and death of leaves in some American species of riparian Populus (namely P. deltoides and P. fremontii) during the summer, coinciding with the lowest flow periods. They proposed that drought-induced xylem cavitation resulting in branch dieback was an adaptation to hydric stress. Similar processes might be occurring in the Middle Ebro floodplain forests, where the ideas suggested by Rood et al. (2000) could be tested for the European P. nigra and P. alba. However, this pattern of early leaf fall did not seem to follow any spatial pattern as was observed randomly in the 12 study plots; the leaf fall occasionally affected certain individuals with more intensity. In fact, the timing of litterfall and leaf fall was simultaneous across the floodplain, as shown by significant and positive cross correlation coefficients between plots and species in almost all paired comparisons. Contrary to our expectations, it seems that factors other than those that control the variability in litter production and quality within the floodplain and that differ between plots (essentially flood type, hydroperiod and forest structure) (González et al., 2010b; 2010c) drive litterfall seasonal phenomenology. Indeed, phenology drivers could be operating at a broader spatial scale than the 8 km study area and therefore might by climatic (e.g., photoperiod, wind, rainfall and, the most likely driver, sudden changes in temperature, such as the first autumn frost) and genetic (e.g., differing according to ecotypic species variability). However, some other hydrologic factors that were homogeneous within the study area but potentially variable at the catchment level (e.g., flow permanence or groundwater fluctuations) should also be considered as potential phenology controlling factors. Another limitation of our study in discerning litter and leaf fall seasonal phenomenology drivers is that, with only one year of observations, it is temporally unreplicated. In this sense, additional longer-term (> 1 year) research monitoring litterfall patterns and environmental factors would provide valuable information to clarify the mechanisms controlling litterfall timing.

**Nutrient content in litterfall and nutrient transfer to the ecosystem**

The C:N:P ratios provided evidence of the existence of seasonal nutrient imbalances in the litter input to riparian ecosystems in the Ebro, which may in turn affect nutrient cycling, decomposition and food webs. For example, previous studies have found evidence that variation in the quality of leaf litter could have effects on leaf breakdown rates, microbial metabolism and invertebrate detritivores elemental composition and growth (Cross et al., 2003; Greenwood et al., 2007). In the study area, C:N and particularly C:P ratios were well above the ratios necessary for the complete litter decay suggested by other authors (e.g., C:N = 16, C:P = 200, Brinson, 1977) during the whole year, which could indicate the existence of P and, to a lesser extent, N limitation on the ecosystem primary food sources. The N:P ratio fluctuated temporally below and above the reference value proposed by Lockaby & Conner (1999) for a balanced N:P supply in forested wetlands (N:P = 26.5). Thus, according to Lockaby & Conner’s index, from July to January (the dominance of leaf fall), the input of nutrients by litterfall would be P-limiting, whereas N-limitation would characterise the nutrient transfer from February to June (the period of heterogeneous litterfall morphology).

**CONCLUSIONS**

Litterfall peaked in November when all tree species reached their maximum values in leaf fall, the most abundant litterfall fraction. However, the amount of litter that fell during the rest of the year and the contribution of other litterfall components with different nutrient concentrations was not negligible. This variability resulted in seasonal imbalances in the litter quantity and C:N:P ratios, which may have important consequences for nutrient processing in the riparian ecosystem and for the structure of detritus-based communities. These consequences deserve further study. Litterfall phenology was not as controlled by the differences in forest structure and
hydrology observed across the floodplain gradient as litterfall quantity and quality. Therefore, as far as the new hydrology and forest composition induced by global change were maintained within the current range of variation, no dramatic changes in litterfall timing would be expected. However, more studies with larger spatial and longer temporal scales in relation to biotic (e.g., species ecotypes) and especially abiotic (e.g., climate, basin-scale hydrology) factors to potentially control litterfall could help us to foresee alterations in the timing of litter inputs that may have been undetected within the scope of this study, with cascading effects for their coupled terrestrial-aquatic ecosystems. This is especially important in the perspective of present and future changes in hydrology and tree species dominance.

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