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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*.

RESUMEN

Patrones estacionales de caída de hojarasca en el bosque de ribera de un gran río mediterráneo

La caída de hojarasca es un proceso clave controlador de la dinámica trófica y nutricional en los sistemas río-llanura aluvial asociada. La cantidad y calidad de la hojarasca y la fenología de su caída pueden estar parcialmente controladas por la hidrología y la estructura forestal local. En el río Ebro Medio (un gran río mediterráneo, NE España), la importancia de esos factores como controladores ha sido recientemente estudiada para la cantidad y la calidad de la hojarasca pero nunca para la fenología. En este estudio, los patrones estacionales de la caída de hojarasca (i.e., fenología intra-anual de la hojarasca caída total por vía vertical, contribución de las diferentes especies y fracciones en la hojarasca y su concentración de nutrientes) fueron descritos en el bosque de ribera del Ebro Medio durante 2007 para discutir el papel de sus factores controladores. Con este fin, la hojarasca caída fue recogida mensualmente en una serie de 12 parcelas que representaban la variedad (en términos de estructura forestal e hidroperíodo) existentes en la llanura aluvial. El material recogido fue clasificado por fracciones y especies y su concentración en C, N y P analizada. Los resultados evidenciaron que, como en la mayoría de bosques templados caducos, el grueso de la caída ocurrió en otoño (42 % del total) con la caída de la

hoja (57 % de entre todas las fracciones de la hojarasca) de las 6 especies arbóreas dominantes. Sin embargo, la cantidad de hojarasca recogida durante el resto el año (especialmente en primavera 25 % y verano 20 %, con unas concentraciones de N y P significativamente mayores) no fue despreciable, lo que conllevó desequilibrios en la cantidad y calidad del aporte de hojarasca al sistema ripario a lo largo del año que podrían controlar en última instancia la estructura de la comunidad basada en los detritus, las redes tróficas y el ciclado de nutrientes. Dos especies de Populus *(P. nigra y P. alba) exhibieron un segundo pico de caída de hoja en verano. Sin embargo, análisis de correlación cruzada mostraron que la fenología de caída de hojarasca y hojas era similar entre parcelas y especies arbóreas dominantes. Esto sugiere que, a diferencia de la cantidad y calidad de la hojarasca, la fenología no estaba tan controlada por las diferencias en estructura forestal e hidrología a escala de parche sino más bien por otros factores que pudieran operar a una escala espacial más amplia, como el clima regional.*

Palabras clave: *Fenología de la caída de hojarasca, bosque de ribera, aporte de hojarasca, materia orgánica,* 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 up-take, resorption, storage and loss, ultimately affecting litter quality (e.g., N_2-fixing vs. non N_2-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 m² 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 m² 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 ≤ 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.*

	Plot											
Forest structure	1	2	3	4	5	6	7	8	9	10	11	12
Live basal area (m²/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	22.5	25.4	28.1	10.9	11.8	0	0
Populus alba	0	0	0	0	0	0	0	0	0	0.2	66.5	55.1
Tamarix spp.	0	11.6	0	2.9	4.5	15.2	12.8	2.8	12.5	2	0.5	3.1
Salix alba	0	22.2	0	1.7	0	1.9	0	0	8.7	0	0	0
Ulmus minor	0	0	0	0.3	1.8	0.4	0	0.5	4.1	0	0	4
Fraxinus angustifolia	0	0	0	0.7	2.1	0	0	0	0	0	0.1	0
Other	0	0	0	0	0.1	0.1	0	0.3	0	0	0.1	0
Dead basal area (m²/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 · 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 ºC for 3 h followed by digestion in a 3.5 mol·L^{-1} HNO$_3$-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 absence of inflorescence) 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 correlation coefficients at a chosen maximum num-ber of time-lag delays between the two time series under analysis (m). In our case, n = 12, k = 1 month and m = 0 months (as we were only interested 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 general, 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, respectively, $p < 0.05$, n = 120). Leaves were the most abundant fraction, followed by woody and reproductive tissues. *Populus nigra* clearly dominated 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.*

	1	2	3	4	5	6	7	8	9	10	11	12	Mean	SE	% of litter	% of leaves
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	16	24	9	18	31	25^e	3	4	
Leaves	310	357	299	405	336	346	267	276	323	110	265	537	319^a	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^{abc}	36		17
Ulmus minor	0	0	1	2	47	8	0	16	108	1	0	130	26^{cb}	13		8
Salix alba	0	127	0	6	1	10	0	0	16	1	0	0	13^c	10		4
Fraxinus angustifolia	0	1	0	12	53	0	0	0	0	0	2	0	6^c	4		2
Other spp.	5	2	1	4	2	6	1	9	5	2	3	4	4^c	1		1

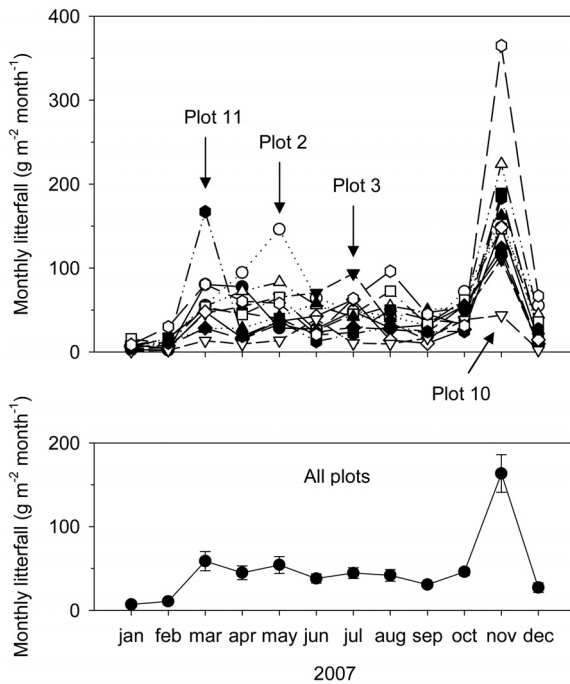**Figure 1.** Temporal variation in monthly total litterfall rate (g of dry matter m⁻² month⁻¹) in 2007. In the upper graph, the 12 curves represent the 12 plots, and each point represents the monthly mean of 10 litter traps. Errors and a plot legend were not included in the figure to improve clarity. 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

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
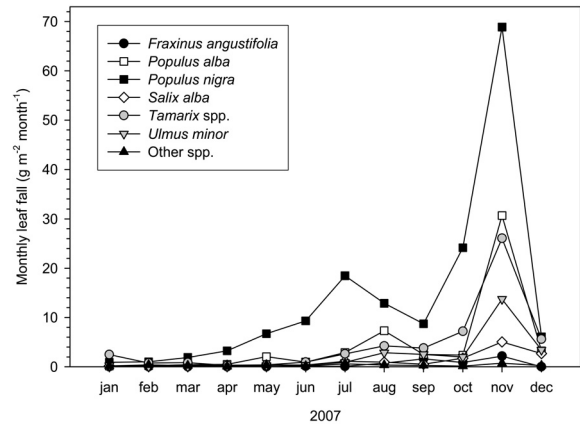

Figure 2. Temporal variation in monthly leaf fall per species (g of dry matter m⁻² month⁻¹) in 2007. For each species, each point represents the monthly mean of 12 study plots. To improve graph clarity, errors are not shown. *Variación temporal en la tasa de caída de hojas por especies (g peso seco m⁻² 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.*

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
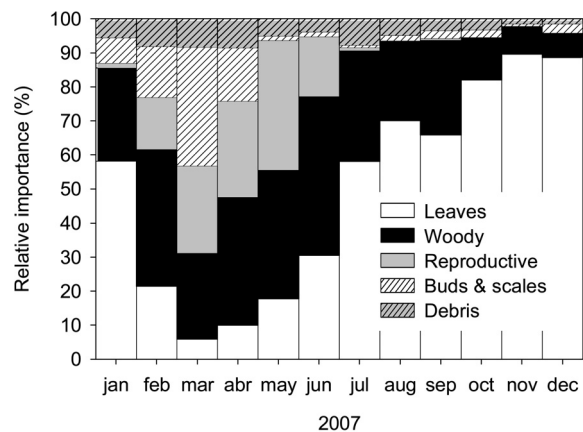

Figure 3. Temporal variation in the relative importance (by weight) of the 5 litter fractions in 2007. *Variación temporal en la importancia relativa (en peso) de las cinco fracciones de hojarasca en 2007.*

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.

	1	2	3	4	5	6	7	8	9	10	11	12
2	0.652*	1										
3	0.735**	0.734**	1									
4	0.790**	0.819**	0.728**	1								
5	0.800**	0.680*	0.628*	0.969**	1							
6	0.781**	0.765**	0.699*	0.933**	0.933**	1						
7	0.767**	0.691*	0.716**	0.926**	0.925**	0.931**	1					
8	0.768**	0.670*	0.844**	0.895**	0.875**	0.843**	0.907**	1				
9	0.716**	0.678*	0.729**	0.943**	0.920**	0.882**	0.958**	0.904**	1			
10	0.581*	0.543	0.652*	0.653*	0.578*	0.594*	0.763**	0.656*	0.794**	1		
11	0.777**	0.493	0.493	0.731**	0.802**	0.741**	0.720**	0.773**	0.649*	0.408	1	
12	0.733**	0.628*	0.617*	0.945**	0.982**	0.918**	0.897**	0.890**	0.898**	0.493	0.786**	1

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.

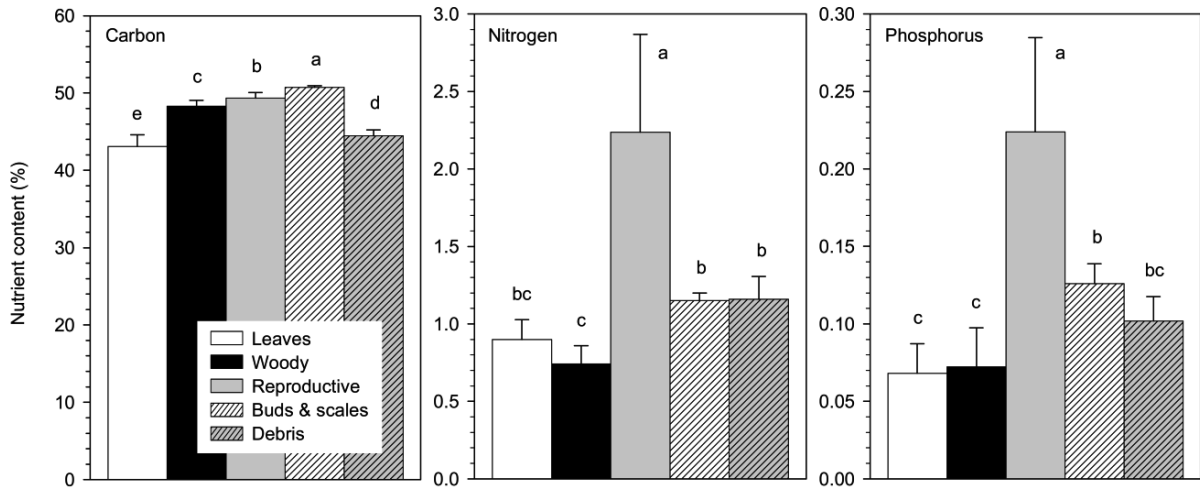|	Fraxinus angustifolia	Populus alba	Populus nigra	Salix alba	Tamarix spp.	Ulmus minor
Populus alba	0.78**	1				
Populus nigra	0.79**	0.95**	1			
Salix alba	0.67*	0.88**	0.89**	1		
Tamarix spp.	0.81**	0.96**	0.96**	0.94**	1	
Ulmus minor	0.82**	0.98**	0.93**	0.94**	0.98**	1

Figure 4. C, N and P concentration (%) of different litter fractions. Bars represent the mean of 12 plots. Error bars are ± 1 standard error of the mean. Letters indicate homogeneous post-hoc Tukey groups. *Concentración de C, N y P (%) de las diferentes fracciones de hojarasca. Las barras representan la media de 12 parcelas. Las barras de error son el ± 1 error estándar de la media. Las letras indican grupos homogéneos tras tests de Tukey.*

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-
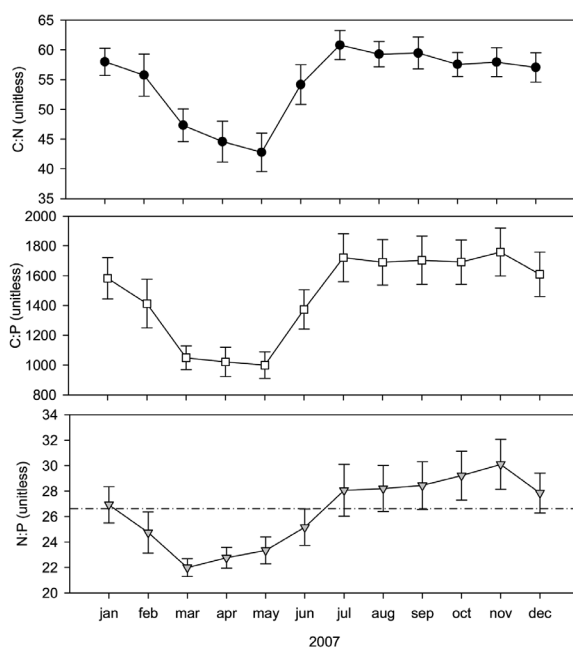
Figure 5. Temporal variation in monthly C:N, C:P and N:P molar ratios in litterfall (unitless) in 2007. Each point represents the monthly mean of 12 study plots. The error bars indicate the ± 1 standard error of the mean. The long dashed-dotted line denotes the optimum ratio for a balanced nutrient supply in forested wetlands (N:P = 26.5) as proposed by Lockaby & Conner (1999). *Variación temporal en los ratios molares mensuales C:N, C:P y N:P de la hojarasca (sin unidades) en 2007. Cada punto representa la media mensual de las 12 parcelas de estudio. Las barras de error indican el ± 1 error estándar de la media. La línea discontinua denota el ratio óptimo para un aporte equilibrado de nutrientes en bosques de ribera (N:P = 26.5) propuesto por Lockaby & Conner (1999).*

aquatic food webs and ecosystem function) merit further investigation. To date, studies assessing the ecological functions of the dead woody compartment have mainly focused on large woody material, especially debris jams and their effects on the river geomorphic dynamics (e.g., Gurnell *et al.*, 2000). In particular, it has been shown that dead wood contributes to the capacity of rivers to retain coarse particulate organic matter and provides habitat patchiness to the aquatic communities, which may even alter their structure (Abelho 2001). However, the majority of these studies have been performed in low-order streams (1 to 3), whereas fewer have been devoted to large rivers such as the Ebro (Tabacchi & Planty-Tabacchi, 2003; Seo *et al.*, 2010). In those systems, the importance of the woody material as a source of refractory material with slower de-

composition rates as a complementary function to decomposing leaf litter needs to be further explored (Tabacchi & Planty-Tabacchi, 2003).

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 phenology. 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 phenology 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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REFERENCES

ABELHO, M. 2001. From litterfall to breakdown in streams: A review. *The Scientific World*, 1: 656–680.

ABELHO, M. & M. A. S. GRAÇA. 1996. Effects of eucalyptus afforestation on leaf litter dynamics and macroinvertebrate community structure of streams in central Portugal. *Hydrobiologia*, 324: 195–204.

ACUÑA, V., A. GIORGI, I. MUÑOZ, F. SABATER & S. SABATER. 2007. Meteorological and riparian influences on organic matter dynamics in a forested Mediterranean streams. *Journal of the North American Benthological Society*, 26: 54–69.

AKÉ-CASTILLO, J. A., G. VÁZQUEZ & J. LÓPEZ-PORTILLO. 2006. Litterfall and decomposition of Rhizophora mangle L. in a coastal lagoon in the southern Gulf of Mexico. *Hydrobiologia*, 559: 101–111.

ALLEN, S. E., H. M. GRIMSBAN, J. A. PARKINSON, C. QUARMBY & J. D. ROBERTS. 1976. Chemical analysis. In: *Methods in plant ecology*. S. B. Chapman (ed.):411-466. Blackwell, Oxford, UK.

BAILEY, J. K., J. A. SCHWEITZER & T. G. WHITMAN. 2001. Salt cedar negatively affects biodiversity of aquatic macroinvertebrates. *Wetlands*, 21: 442–447.

BAKER III, T. T., B. G. LOCKABY, W. H. CONNER, C. E. MEIER, J. A. STANTURF & M. K. BURKE. 2001. Leaf litter decomposition and nutrient dynamics in four Southern forested floodplain communities. *Soil Science Society of America Journal*, 65: 1334–1347.

BENFIELD, E. F. 1997. Comparison of litterfall input to streams. *Journal of the North American Benthological Society*, 16: 104–108.

BOX, G. E .P. & G. M. JENKINS. 1976. *Time series analysis, forecasting and control.* Holden-Day, San Francisco, California. 575 pp.

BRAY, J. R. & E. GORHAM. 1964. Litter production in forests of the world. *Advances in Ecological Research*, 2: 101–157.

BRINSON, M. M. 1977. Decomposition and nutrient exchange of litter in an alluvial swamp forest. *Ecology*, 58: 601–609.

CABEZAS, A., F. A. COMÍN, S. BEGUERÍA & M. TRABUCCHI. 2009. Hydrologic and landscape changes in the middle Ebro River (NE Spain): implications for restoration and management. *Hydrology and Earth System Sciences*, 13: 273–284.

CAMPBELL, I. C., K. R. JAMES, B. T. HART & A. DEVEREAUX. 1992. Allochthonous coarse particulate organic material in forest and pasture reaches of two South-Eastern Australian streams. I. Litter accession. *Freshwater Biology*, 27: 341–352.

CROSS, W. F., J. P. BENSTEAD, A. D. ROSEMOND & J. B. WALLACE. 2003. Consumer-resource stoichiometry in detritus-based streams. *Ecology Letters*, 6: 721–732.

FISHER, S. G. & G. E. LIKENS. 1973. Energy flow in Bear Brook, New Hampshire: an integrative approach to stream ecosystem metabolism. *Ecological Monographs*, 43: 421–439.

FOLLSTAD SHAH, J. J. & C. N. DAHM. 2008. Flood regime and leaf fall determine soil inorganic nitrogen dynamics in semiarid riparian forests. *Ecological Applications*, 18: 771–788.

FOLLSTAD SHAH, J. J., M. J. HARNER & T. M. TIBBETS. 2010. Elaeagnus angustifolia elevates soil inorganic nitrogen pools in riparian ecosystems. *Ecosystems*, 13: 46–61.

GONZÁLEZ, E., M. GONZÁLEZ-SANCHIS, A. CABEZAS, F. A. COMÍN & E. MULLER. 2010a. Recent changes in the riparian forest of a large regulated Mediterranean river: Implications for management. *Environmental Management*, 45: 669–681.

GONZÁLEZ, E., E. MULLER, F. A. COMÍN & M. GONZÁLEZ-SANCHIS. 2010b. Leaf nutrient concentration as an indicator of Populus and Tamarix response to flooding. *Perspectives in Plant Ecology, Evolution and Systematics*, 12: 257–266.

GONZÁLEZ, E., E. MULLER, B. GALLARDO, F. A. COMÍN & M. GONZÁLEZ-SANCHIS. 2010c. Factors controlling litter production in a large Mediterranean river floodplain forest. *Canadian Journal of Forest Research*, 40: 1698–1709.

GONZÁLEZ, E., M. GONZÁLEZ-SANCHIS, F. A. COMÍN & E. MULLER. 2012. Hydrologic thresholds for riparian forest conservation in a regulated large Mediterranean river. *River Research and Applications*, 28: 71–80.

GREENWOOD, J. L., A. D. ROSEMOND, J. B. WALLACE, W. F. CROSS & H. S. WEYERS. 2007. Nutrients stimulate leaf breakdown rates and detritivore biomass: bottom-up effects via heterotrophic pathways. *Oecologia*, 151: 637–649.

GREGORY, S. V., F. J., SWANSON, A. MCKEE & K. W. CUMMINS. 1991. An ecosystem perspective of riparian zones. *BioScience*, 41: 540–551.

GURNELL, A. M., G. E. PETTS, D. M. HANNAH, B. P. G. SMITH, P. J. EDWARDS, J. KOLLMAN, J. V. WARD & K. TOCKNER. 2000. Wood storage within the active zone of a large European gravel-bed river. *Geomorphology*, 34: 55–72.

JENKINS, G. M. & D. G. WATTS. 1968. *Spectral analysis and its applications.* Holden-Day, San Francisco, California. 525 pp.

KING, J. M., J. A. DAY, B. R. DAVIES & M. P. HENSHALL-HOWARD. 1987. Particulate organic matter in a mountain stream in the southwestern Cape, South Africa. *Hydrobiologia*, 154: 165–187.

LAKE, P. S. 1995. Of floods and droughts: river and stream ecosystems of Australia. In: *River and Stream Ecosystems. Ecosystems of the World, Vol. 22.* C. E. Cushing, K. W. Cummins & G. W. Minshall (eds.): 659–694. Elsevier, Amsterdam, the Netherlands.

LAMB, R. J. 1985. Litter fall and nutrient turnover in two eucalypt woodlands. *Australian Journal of Botany*, 33: 1–14.

LOCKABY, B. G. & W. H. CONNER. 1999. N:P balance in wetland forests: productivity across a biogeochemical continuum. *The Botanical Review*, 65: 171–185.

MAAMRI, A., H. CHERGUI & E. PATTEE. 1994. Allochthonous input of coarse particulate organic-matter to a Moroccan Mountain Stream. *Acta Oecologica*, 15: 495–508.

MAGDALENO, F. & J. A. FERNÁNDEZ. 2011. Hydromorphological alteration of a large Mediterranean river: relative role of high and low flows on the evolution of riparian forests and channel morphology. *River Research and Applications*, 27: 374–387.

MCIVOR, J. G. 2001. Litterfall from trees in semi-arid woodlands of north-east Queensland. *Austral Ecology*, 26: 150–155.

MEENTEMEYER, V., E. O. BOX & R. THOMPSON. 1982. World patterns and amounts of terrestrial plant litter production. *BioScience*, 32: 125–128.

MEGONIGAL, J. P., W. H. CONNER, S. KROEGER & R. R. SHARITZ. 1997. Aboveground production in Southeastern Floodplain Forests: A test of the Subsidy-Stress Hypothesis. *Ecology*, 78: 370–384.

MEIER, C. E., J. A. STANTURF & E. S. GARDINER. 2006. Litterfall in the hardwood forest of a minor alluvial-floodplain. *Forest Ecology and Management*, 234: 60–77.

MUZIKA, R. M., J. B. GLADDEN & J. D. HADDOCK. 1987. Structural and functional aspects of succession in Southeastern floodplain forests following a major disturbance. *The American Midland Naturalist*, 117: 1–9.

NAIMAN, R. J., H. DÉCAMPS & M. E. McCLAIN. 2005. *Riparia. Ecology, conservation, and management of streamside communities.* Elsevier Academic Press. San Diego.

NEIFF, J. J. & A. P. DE NEIFF. 1990. Litterfall, leaf decomposition and litter colonization of Tessaria

integrifolia (compositae) in the Parana river flood-plain. *Hydrobiologia*, 203: 45–52.

OLLERO, A. 2007. Channel adjustments, floodplain changes and riparian ecosystems of the Middle Ebro River: assessment and management. *International Journal of Water Resources Development*, 23: 73–90.

POZO, J., E. GONZÁLEZ, J. R. DÍEZ, J. MOLINERO & A. ELÓSEGUI. 1997. Inputs of particulate organic matter to streams with different riparian vegetation. *Journal of the North American Benthological Society*, 16: 602–611.

ROOD, S. B., S. PATIÑO, K. COOMBS & M. T. TYREE. 2000. Branch sacrifice: cavitation-associated drought adaptation of riparian cottonwoods. *Trees*, 14: 248–257.

SEO, J. I., F. NAKAMURA & K. W. CHUN. 2010. Dynamic of large wood at the watershed scale: a perspective on current research limits and future directions. *Landscape and Ecological Engineering*, 6: 271–287.

STEWART, B. A. & B. R. DAVIES. 1990. Allochthonous input and retention in a small mountain stream, South Africa. *Hydrobiologia*, 202: 135–146.

TABACCHI, E. & A. M. PLANTY-TABACCHI. 2003. Recent changes in riparian vegetation: Possible consequences on dead wood processing along rivers. *River Research and Applications*, 19: 251–263.

TIBBETS, T. M., M. C. MOLLES JR. 2005. C:N:P stoichiometry of dominant riparian trees and arthropods along the Middle Rio Grande. *Freshwater Biology*, 50: 1882–1894.

TOCKNER, K. & J. A. STANFORD. 2002. Riverine flood plains: present state and future trends. *Environmental Conservation*, 29: 308–330.

VANNOTE, R. L., G. W. MINSHALL, K. W. CUMMINS, J. R. SEDELL & C. E. CUSHING. 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences*, 37: 130–137.

WALLACE, J. B., S. L. EGGERT, J. L. MEYER & J. R. WEBSTER. 1997. Multiple trophic levels of a forest stream linked to terrestrial litter inputs. *Science*, 277: 102–104.

WALLACE, J. B., S. L. EGGERT, J. L. MEYER & J. R. WEBSTER. 1999. Effects of resource limitation on a detrital-based ecosystem. *Ecological Monographs*, 69: 409–442.

WANTZEN, K. M. & R. WAGNER. 2006. Detritus processing by invertebrate shredders: a neotropical-temperate comparison. *Journal of the North American Benthological Society*, 25: 216–232.

XIONG, S. & C. NILSSON. 1997. Dynamics of litter accumulation and its effects on riparian vegetation: a review. *The Botanical Review*, 63: 240–264.