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Litter in a first-order stream of a temperate deciduous forest (Margaraça Forest, central Portugal)

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Abstract

To evaluate the importance and fate of organic matter inputs in forested streams, we determined the litterfall inputs and the benthic coarse particulate organic matter (CPOM) in one headwater stream flowing through a mixed deciduous forest, during one year. Both vertical traps and the stream bottom were sampled monthly. The material collected was sorted into four main categories: leaves, fruits and flowers, twigs and debris. Litter production was 715 g m^{-2} y^{-1} and seasonal, with 73% of the annual total during October–December (autumn). Leaves comprised the largest litter component. Benthic organic matter was 1880 g m^{-2} y^{-1}, and was also seasonal. Highest accumulation was attained in spring, and twigs and branches comprised the major component.

Introduction

Allochthonous organic matter is the major source of energy for woodland streams or streams with well developed riparian corridors of vegetation (e.g., Fisher & Likens, 1973). It may include leaves, floral parts, bark, wood (branches and twigs), fruits, other plant parts, and fragments. Litter may reach streams by vertical fall or lateral movement (blowing or sliding down the stream banks). The relative amounts of material reaching streams by these two routes vary considerably (Benfield, 1997), but vertical (direct) inputs are usually more important than lateral ones (e.g., Campbell et al., 1992; Benfield, 1997; Pozo et al., 1997).

The temporal and spatial distribution, the amount and quality of inputs, depend on the type of riparian vegetation (Webster & Meyer, 1997). In temperate deciduous forests, the bulk of litterfall occurs in autumn (Benfield, 1997) and leaves are the largest component of litterfall.

Since the mid-sixties there have been a number of papers focusing on the decomposition of terrestrial plant litter in streams (e.g., Triska et al., 1975; Webster & Benfield, 1986; Rowe et al., 1996). By comparison, there have been relatively few attempts to document the amount of allochthonous organic material entering and accumulating in streams, and such studies which have been published have largely been restricted to North America (e.g., Fisher & Likens 1973; Anderson & Sedell, 1979; Connors & Naiman, 1984). However, there have been some recent studies in the Iberian Peninsula. One study has measured litter input to streams of the Agüera basin (Pozo et al., 1997), and a few studies have measured litter production (vertical litterfall) in forests (Hernandez et al., 1992; Martín et al., 1996) and benthic organic matter in streams (González & Pozo, 1996; Mollá et al., 1996).

The objectives of the present work were to quantify and determine the temporal distribution and composition of: (1) litterfall in the riparian zone; and (2) benthic organic matter of a stream flowing through a mixed deciduous forest. A complementary objective was to describe the temporal patterns of biofilm development in the stream bed.

Material and methods

Study site

Margaraça Forest, an indigenous mixed deciduous forest covering an area of 50 ha, is located in Cen-

Table 1. Selected descriptive variables for Margaraça forest stream, measured during the study period

Variable	Mean (range)	Sample size
Basin drainage area (ha)	29	
Length of the study reach (m)	22.5	
Mean bankfull width at site (m)	1.4 (0.6 – 2.0)	6
Mean depth (cm)	3.4 (1.0 – 8.0)	57
Mean current velocity (m s^{-1})	0.23 (0.04 – 0.90)	32
Mean discharge (m^3 s^{-1})	0.023 (0.005 – 0.068)	12
pH	6.9 (6.4 – 7.7)	12
Alkalinity (mg CaCO3 L^{-1})	18.0 (14.5 – 20.5)	12
Conductivity (μS cm^{-1})	67.3 (59.4 – 73.6)	11
Water temperature (°C)	12.8 (9.3 – 16.9)	12
Dissolved oxygen (mg L^{-1})	10.4 (9.2 – 11.3)	12

Figure 1. Temporal variation in discharge of Margaraça forest stream.

tral Portugal. The forest is a national protected area, representing one of the last examples of the original vegetation of the schistous slopes in Central Portugal. The climate is temperate Atlantic/Mediterranean with mean annual rainfall of 1150 mm and mean annual air temperature of 11 °C. The work was conducted in a 1st order stream (catchment 29 ha) that drains a mature deciduous forest dominated by *Castanea sativa* Miller, *Quercus robur* L., and several species of *Prunus* (Paiva, 1981). The study site was an area of 360 m^2 including a stream reach of 22.5 m. Riparian vegetation at the reach was mainly large chestnut trees, which shaded the stream bed even when no leaves were present. The slope of the study reach was 5°. Along the study reach the stream formed a series of steps, with a typical pattern of small riffles and pools. The bed substrate was composed of boulders and pebbles with gravel accumulating in the pools. Mean annual conductivity of the stream water was 67 μS $cm^{-1}$and mean annual water temperature was 13 °C (Table 1). Mean annual discharge was 0.023 m^3 s^{-1} (Figure 1).

Methods

Vertical litterfall was determined from ten 0.152 m^2 traps randomly placed at ground level in the riparian forest. Each trap consisted of a circular plastic collector, pierced to allow rainwater to drain. Samples were collected monthly from March 1995 to March 1996.

Benthic organic matter was determined from six surber samples (area 0.09 m^2, mesh 0.5 mm) randomly taken from the stream bottom. Samples were taken monthly from February 1995 to February 1996.

Litter was sorted into categories: leaves, twigs and branches, fruit and flowers, and debris (unidentifiable fragments). Each category was oven-dried at 60 °C for 48 hours, weighed, and ashed at 500 °C for 5 hours to determine ash free dry mass (AFDM).

Standing crop of epilithic biofilm was determined from the upper surface of six stones randomly taken from the stream bottom. Samples were taken monthly from February 1995 to February 1996 by scraping the stone surface with a scalpel in two areas of 0.0013 m^2. The collected material was oven-dried at 60 °C for 48 hours, weighed, and ashed at 500 °C for 5 hours to determine ash free dry mass (AFDM).

Data analysis

A mean monthly value, expressed in g m^{-2} was calculated for each fraction per site. Seasonality of annual distributions was tested by chi-square goodness of fit (χ^2; Zar, 1996). A distribution was considered seasonal whenever the null hypothesis of equal seasonal distribution of organic matter was rejected. Turnover time of the system was calculated by dividing mean monthly benthic organic matter (g m^{-2}) by annual litterfall (g m^{-2} y^{-1}).

Results

Litterfall

Annual litterfall at the site was 715 g m^{-2} y^{-1} (Table 2). Leaves were the most important component, comprising 63% of annual litterfall. Temporal patterns of litter inputs were clearly seasonal (χ^2 = 885, DF = 3, $P<0.05$; Figure 2): 73% of the annual litterfall

Table 2. Litter production in Margaraça forest (g AFDM m^{-2} y^{-1})

	Litter composition		Winter (Jan–Mar)	Spring (Apr–Jun)	Summer (Jul–Sep)	Autumn (Oct–Dec)
	AFDM	% of annual AFDM	% of annual AFDM	% of annual AFDM	% of annual AFDM	% of annual AFDM
Total	715.3		6.1	13.3	7.7	72.9
Debris	2.8	0.4	0.0	100.0	0.0	0.0
Fruit and flowers	114.8	16.0	1.8	28.5	9.2	60.5
Twigs and branches	145.4	20.3	13.0	17.5	2.7	66.7
Leaves	452.3	63.2	4.9	7.6	8.9	78.6

Table 3. Benthic coarse particulate organic matter standing crop in Margaraça forest stream (g AFDM m^{-2} y^{-1})

	Litter composition		Winter (Jan–Mar)	Spring (Apr–Jun)	Summer (Jul–Sep)	Autumn (Oct–Dec)
	AFDM	% of annual AFDM	% of annual AFDM	% of annual AFDM	% of annual AFDM	% of annual AFDM
Total	1880.1		22.0	32.9	14.5	30.6
Debris	349.1	18.6	22.6	21.5	16.5	39.4
Fruit and flowers	130.7	7.0	9.3	27.7	10.6	57.4
Twigs and branches	1164.4	61.9	25.6	41.0	15.0	18.4
Leaves	235.9	12.5	10.5	15.4	11.0	63.1

Figure 2. Temporal variation in litter fall (mean ± 1 SE) at Margaraça forest.

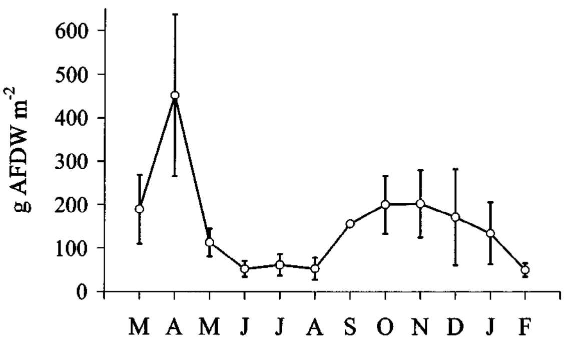

Figure 3. Temporal variation in benthic organic matter standing crop (mean ± 1 SE) in Margaraça forest stream.

occurred in autumn (October to December). Litter inputs in the other seasons were 13% in spring, 8% in summer, and 6% in winter of total annual litterfall (Table 2).

Litter composition also showed a seasonal trend ($\chi^2 > 94$, DF = 3, $P < 0.05$; Table 2). During the high peak period, approximately two thirds of annual organic matter inputs entered the forest: 79% of the annual amount of leaves; 67% of the annual amount of wood; and 61% of the annual amount of reproductive materials (Table 2).

Benthic organic matter

Annual benthic organic matter standing crop in the stream was 1880 g m^{-2} y^{-1} (Table 3). Twigs and branches were the most important component: 62% of annual standing crop. The temporal patterns of litter accumulation were seasonal ($\chi^2 = 161$, DF = 3, $P < 0.05$; Figure 3), although the differences between seasons were not very marked: 33% in spring, 31% in autumn, 22% in winter, and 15% in summer (Table 3).

Litter composition also showed a seasonal trend ($\chi^2 > 41$, DF = 3, $P < 0.05$; Table 3). Accumulation of leaves, fruit and flowers, and debris was highest in autumn (respectively 63, 57, and 39% of annual

Table 4. Epilithic biofilm in Margaraça forest stream (g AFDM m^{-2} y^{-1})

	AFDM	% of annual AFDM
Annual	34.4	
Winter (Jan–Mar)	8.5	24.6
Spring (Apr–Jun)	2.2	6.5
Summer (Jul–Sep)	7.8	22.5
Autumn (Oct–Dec)	15.9	46.4

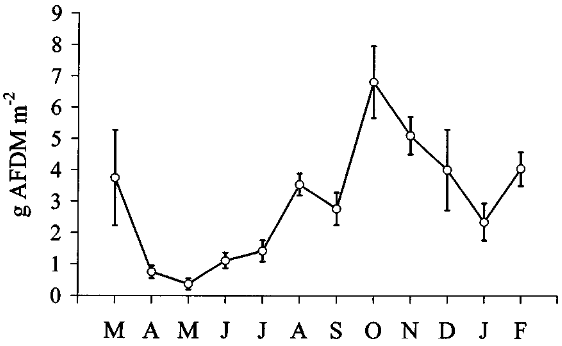

Figure 4. Temporal variation in the epilithic biofilm standing crop (mean ± 1 SE) in Margaraça forest stream.

amount). Wood accumulated mostly in spring: 41% of annual amount (Table 3).

Epilithic biofilm

Annual standing crop of epilithic biofilm was 34 g m^{-2} y^{-1} (Table 4). The temporal pattern of epilithic biofilm standing crop was clearly seasonal (χ^2 = 11, DF = 3, $P < 0.05$; Figure 4), with 46% in autumn, 25% in winter, 23% in summer, and only 7% in spring of annual standing crop (Table 4).

Discussion

An important aspect of stream ecology is the evaluation of the relative importance of external (allochthonous) versus internal (autochthonous) resources to stream biota. Production (at all trophic levels) depends on the exploitation of the available resources, and on the efficiency with which these resources are transformed into new biomass (Benke et al., 1988). The epilithic biofilm is a mixed community of bacteria, fungi, algae, and micrometazoans embeded in slime, and in an organic matrix secreted by the organisms (Rounick & Winterbourn, 1983; Bärlocher & Murdoch, 1989; Neu & Lawrence, 1997). The biofilm has therefore both heterotrophic and autotrophic activities. However, Rounick & Winterbourn (1983) showed that biofilms developing in a well shaded stream had lower diversity and abundance of algae than biofilms developing in a stream receiving direct sunlight. In our study, the mass of biofilm was very low, and the peaks coincided with the peaks of litterfall and benthic organic matter. In streams of deciduous forests, an autumn peak of algal growth is not uncommon. Although days are shorter and light intensity is lower, an increase in light availability to the streams may occur due to the opening canopy after leaf abscission. The interaction between light availability and the relatively high temperatures may lead to the development of algae communities. Although we did not study the biofilm composition, the stream was narrow and completely shaded by the riparian vegetation even when no leaves were present. Since there were no macrophytes in the stream, we assume that autochthonous production is unimportant when compared with allochthonous inputs to the stream. The biofilm seems, in this case, to act mainly as an organic matter trap, removing dissolved organic matter from the water column.

Direct inputs from European deciduous forests to streams and rivers range from 42 to 1719 g dry mass m^{-2} y^{-1} (Weigelhofer & Waringer, 1994). Our results (715 g AFDM m^{-2} y^{-1}) are within the reported range, and higher than the 611 g AFDM m^{-2} y^{-1} reported by Pozo et al. (1997) for a Spanish 1st order stream in a deciduous forest.

Benfield (1997) reported lateral movement contributions as 19, 22 and 82% of litterfall for North American low-order deciduous forest streams. Lateral inputs to European streams and rivers range from negligible (Chauvet & Jean-Louis, 1988) to 271 g dry mass m^{-2} y^{-1} (Weigelhofer & Waringer, 1994). Pozo et al. (1997) found lateral inputs to be 20% of the total litter entering the stream. On the other hand, Campbell et al. (1992) found litterfall in the riparian zone to be greater than in either the forest or over the streams, suggesting that riparian litterfall rates may overestimate litter input to streams.. Considering these two results, and considering that: (1) the channel of the studied stream is very narrow, (2) the stream is completely covered by the adjacent canopy, and (3) there have been no registered floods in the stream, we assume that the direct litterfall data is (in this case) a good estimate of the total allochthonous organic matter entering the stream.

It has been argued that, due to the highly seasonal patterns of litterfall, the availability of organic matter for the benthic community of deciduous forest streams is limited in winter (Campbell & Fuchshuber, 1994). Our results show that, although winter and summer had a limited supply of organic matter (6 and 8%, respectively), the standing crop of coarse benthic organic matter was high throughout the year, making organic matter available for the benthic community even in times when the litter inputs to the stream were low. Moreover, the seasonal quality of litter is highly variable in terms of energy. The spring peak, although quantitatively small, may be very important as an energy source in a time when leaf inputs are minimal, due to the high nutritive content of flowers (Fittkau, 1964; Winterbourn, 1976).

Differences in depth, substrate, discharge, and retentive structures such as wood may influence the retentive capacities of streams. The study stream had twice the amount of wood reported by González & Pozo (1996) for a 1st order deciduous stream in Spain. This may explain why standing crop of benthic organic matter in Margaraça forest stream was 5 times higher then that reported for the Spanish stream.

In temperate regions the highest CPOM standing crop occurs in late autumn following the period of highest annual litterfall (Bärlocher, 1983). In Margaraça forest stream, the autumn input of litter is reflected by the dynamics of benthic organic matter under changing discharge conditions (Abelho & Graça, 1996). The autumn peak of litterfall results in accumulation of organic matter in the stream bed, but the highest peak of standing crop was observed in April, when a second order peak of litterfall occurred. Thus, only when high inputs coincide with a period of low discharge, an increase of these materials on the stream bed are expected (Abelho & Graça, 1996). This was also found by González & Pozo (1996) for streams in the Agüera basin, although they could not find a discernible seasonal pattern in benthic organic matter. The timing of inputs and the hydrologic regime appear to act together influencing temporal dynamics of benthic CPOM (González & Pozo, 1996).

The unaltered riparian deciduous forest, the dense vegetation canopy, which ensures large inputs of particulate organic matter, the narrow channel and efficient structures of retention as debris dams, branches and roots (Bilby & Likens, 1980; Ehrman & Lamberti, 1992; Chergui & Pattee, 1993) would explain the high accumulation of CPOM in the stream.

Turnover time is an index of residence time of leaves, which is important in determining the influence of leaves on ecosystem processes (Shade & Fisher, 1997). Turnover time in Margaraça forest stream was more than 4 times slower than the values presented by Shade & Fisher (1997) for low-order deciduous streams of North America, but it was 2 times faster than the one calculated from the data of González & Pozo (1996) and Pozo et al. (1997). Because discharge strongly influences residence time of litter in streams, this fact may reveal that the Spanish stream may have stronger discharge rates than the Portuguese one. In fact, we never registered a strong flood event in this stream, which may be due to the vegetation and soil types (Abelho & Graça, 1996).

On a larger temporal scale, allochthonous organic matter, specially leaf material, plays a major role in energy and matter flow through this forest stream. Although litter inputs are patchy in time, the residence time of the litter is relatively high. Thus the stream contains a pool of organic matter to support the benthic communities throughout the year.

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