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Scientific Editors

Aquatic Ecology of the Mondego River Basin Global Importance of Local Experience

Coimbra • Imprensa da Universidade

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COORDENAÇÃO EDITORIAL
Imprensa da Universidade de Coimbra

CONCEPÇÃO GRÁFICA
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Estímulus [design] • Coimbra

EXECUÇÃO GRÁFICA
GRAFIASA

ILUSTRAÇÃO DA CAPA
P. P. Cunha e J. Dinis

ISBN
972-8704-04-6

DEPÓSITO LEGAL
175038/02

OBRA PUBLICADA COM O PATROCÍNIO DE:
IMAR – INSTITUTO DO MAR
IPIMAR – INSTITUTO DE INVESTIGAÇÃO DAS PESCAS E DO MAR

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SOURCES OF ENERGY IN LOW-ORDER STREAMS

Abstract

To quantify and characterise the sources of energy in low-order streams of the Mondego River Basin, data on the amounts and dynamics of litterfall, retention, decomposition and accumulation of allochthonous organic matter and on the standing stock of epilithic biofilm was collected on several years and streams. Our results showed that the deciduous forests of the Mondego River Basin produce abundant litter inputs, mainly in the form of leaves, and especially during late autumn. Leaves entering low-order streams tend to be rapidly retained especially by substrate structures such as debris dams. Therefore, at any given time, the organic matter transported by the streams is low when compared to benthic organic matter. Retained leaves decompose at different rates, depending on the stream and on leaf species. The different processing rates of several leaf species within a stream may provide a continuum of conditioned leaf litter available for the benthic invertebrate community throughout the year. Standing stock of benthic organic matter was 29-88 times higher in the deciduous and 5 times higher in the mixed forest stream than standing stock of epilithic biofilm. Allochthonous organic matter constitutes thus the main energy source to low-order streams of the Mondego River Basin.

Introduction

Organic matter in lotic systems comes from two main sources: (a) autochthonous matter from photosynthetic production within the stream and (b) allochthonous matter of terrestrial origin from the surrounding forest (Bunn 1986). Autochthonous sources of organic matter are considered to make only a minor contribution to the total energy pool of forest streams (Bunn 1986). Fisher and Likens (1973) found that less than 1% of the total energy inputs to a forested stream in New Hampshire (U.S.A.) was derived from photosynthesis within the stream.

Autotrophy may play an important role in the functioning in some streams, however, namely those that do not flow through dense canopy. Moreover, the relative importance of autochthonous sources of organic matter is also predicted to increase

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with stream order (Vannote et al. 1980). The wider channels of larger streams and rivers diminish the effect of shading by riparian vegetation and primary productivity is enhanced due to the increased solar radiation.

Allochthonous organic material entering streams from riparian vegetation depends on the amount of litter produced in the adjacent forest and on morphologic characteristics of the streams. The amount of litter produced in forests varies considerably and depend on factors such as climate, vegetation, type of soil, and age of the trees (Hernandez et al. 1992). For almost all kinds of wood, the massive litterfall occurs yearly during certain periods, depending on the phenology of the dominant species (Hernandez et al. 1992).

The continuous unidirectional flow through lotic ecosystems tends to transport matter to downstream reaches. After reaching a stream, allochthonous inputs will flow with the water being of little use to local biota, unless they are somehow retained. Retention removes matter from transport and makes it available for utilization by stream biota, providing a critical link between input and storage (Speaker et al. 1984). The process of retention includes both the immediate trapping of matter in transport and the sub-sequent longer-term storage of this material (Speaker et al. 1984).

Benthic detritus is an integral component of the functioning of headwater streams in forested areas; the knowledge of detritus storage is thus necessary to understand the structure and functioning of streams (Smock 1990). Accumulation of benthic organic matter depends on several factors, including litter inputs, discharge patterns and morphologic characteristics of the streams. After reaching a stream, CPOM is transformed to dissolved organic matter (DOM) through leaching (e.g. Petersen and Cummins 1974) or converted to fine particulate organic matter (FPOM) by physical abrasion or biological breakdown (Wallace et al. 1995). Litterfall, retention and breakdown are thus key processes in the energetics of low-order streams.

The objectives of this paper were to quantify and characterise the inputs and dynamics of detritus in several low-order streams of the Mondego River Basin, with special reference to litterfall, retention, decomposition and accumulation of allochthonous organic matter and to the standing stock of epilithic biofilm. The present paper is a synthesis of results included in the publications: Abelho 1994, Abelho 1999, Abelho and Graça 1996, Abelho and Graça 1998, Canhoto and Graça 1996, Canhoto and Graça 1998.

Material and methods

Study sites

The study was conducted in 6 streams of the Mondego River Basin, located at the Açor, Caramulo and Lousã Mountains. The sites were classified according to the surrounding vegetation into deciduous (streams flowing through mixed deciduous forests), "mixed" (streams flowing through eucalyptus plantations with a riparian corridor of deciduous trees: *Salix* spp., *Quercus* spp., etc.) and "agricultural" (streams draining agriculture fields and bordered by mixed deciduous riparian vegetation).

Table 1. Selected descriptive characteristics of the six study streams.

	Margaraça 1	Margaraça 2	Fraga da Pena	S. João	Laceiras	Sobral Cid
Location	Açor Mountain	Açor Mountain	Açor Mountain	Lousã Mountain	Caramulo	Coimbra
Riparian vegetation	Deciduous	Deciduous	Deciduous	Deciduous	Mountain Mixed	Agricultural
Stream order	1	3	3	5	3	1
Catchment area (ha)	29	182	559	1800	705	-
Discharge ($m^3 s^{-1}$)						
Mean	0.020 (N=15)	0.005 (N=3)	0.040 (N=3)	0.811 (N=18)	0.089 (N=3)	-
Range	0.005-0.068	0.003-0.009	0.021-0.071	0.140-1.526	0.067-0.131	-
Dissolved Oxygen (%)						
Mean	103 (N=15)	100 (N=3)	100 (N=3)	106 (N=17)	100 (N=5)	100
Range	97-113	97-104	94-104	100-112	93-107	-
mg O_2 L^{-1}						
Mean	11 (N=15)	11 (N=3)	11 (N=2)	12 (N=17)	12 (N=4)	-
Range	9-13	10-13	10-11	10-13	11-13	-
Temperature (°C)						
Mean	12 (N=16)	11 (N=4)	12 (N=4)	10 (N=17)	11 (N=5)	11
Range	9-17	9-14	9-16	7-12	9-13	-
Conductivity (µS cm^{-1})						
Mean	66 (N=12)	33 (N=3)	25 (N=3)	42 (N=18)	35 (N=2)	-
Range	55-74	10-58	10-45	38-47	30-40	-
pH						
Mean	6.8 (N=15)	6.4 (N=3)	6.7 (N=3)	6.4 (N=13)	5.8 (N=3)	7.0
Range	6.3-7.7	6.1-6.5	6.2-7.2	5.6-6.9	5.6-6.1	-
Alkalinity (mg $CaCO_3$ L^{-1})						
Mean	19 (N=15)	21 (N=3)	10 (N=3)	-	5 (N=3)	290
Range	15-24	17-23	9-11	-	4-6	-

Three deciduous streams were located at the Açor Mountain, two at Margaraça Forest (Margaraça 1 and Margaraça 2) and one at Fraga da Pena (Fraga da Pena). The other deciduous stream (S. João) was located at the Lousã Mountain. The "mixed" stream (Laceiras) was located at the Caramulo Mountain. The "agricultural" stream (Sobral Cid) was located near Sobral Cid Hospital, Coimbra. The study was conducted in riffle areas of the streams. The bed substrate was composed of boulders, pebbles and gravel. The streams were well oxygenated, circumneutral, with low conductivity and alkalinity values (Table 1). Discharge patterns were highly seasonal in all streams, with lowest flow during summer and highest flow during autumn and spring (Fig. 1).

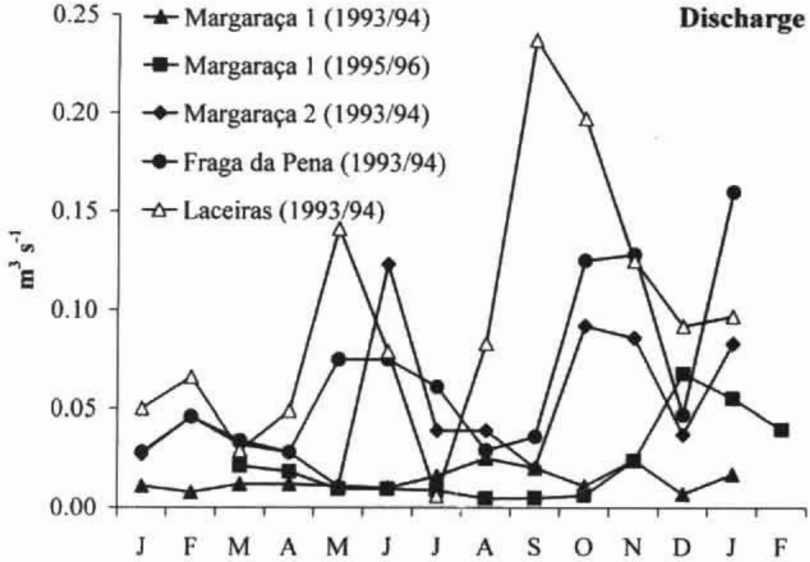

Figure 1. Temporal variation in discharge of three deciduous (Margaraça 1, Margaraça 2 and Fraga da Pena) and one mixed (Laceiras) forest streams during two non-consecutive years.

Litterfall

Litterfall was quantified during two non-consecutive years, in the riparian corridors of several streams. In the first year (February 1993 to February 1994), litterfall was determined at streams flowing through deciduous and mixed forests (Abelho 1994, Abelho and Graça 1996). The deciduous streams were Margaraça 1, Margaraça 2 and Fraga da Pena, and the mixed stream was Laceiras. In the second year (March 1995 to March 1996), litterfall was determined only at the site Margaraça 1 (Abelho and Graça 1998, Abelho 1999).

At each site, vertical litterfall was determined from 0.152 m^2 traps randomly placed at ground level in the riparian forest (four replicates during 1993/94 and 10 replicates during 1995/96). Each trap consisted of a circular plastic collector, pierced to allow rainwater to drain. Samples were collected every month during the study periods. Litter was sorted into three categories: leaves, twigs/branches, and fruit/flowers. 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). A mean monthly value expressed in g AFDM m^{-2} was calculated for each fraction per stream.

Short-term retention experiment

The experiment was carried out during the summer of 1995 in S. João stream, using leaves of *Alnus glutinosa*, *Castanea sativa*, *Quercus faginea* and *Eucalyptus globulus* as the experimental units (Canhoto & Graça 1998). Four to five hundred of each leaf species were released at one point of the stream and collected in 1-mm mesh nets stretched across the stream and placed at fixed distances from the releasing point (maximum 90-m). The leaves collected in each net were immediately counted and released. Leaves were considered retained when not arriving to the next net for longer than 3.5 h (Canhoto and Graça 1998).

Transported organic matter

Transported organic matter was determined during 1993/94, in the same streams described for the litterfall inputs (Abelho 1994). Every month, organic matter was collected in three drift nets (aperture 0.33 m x 0.33 m, 0.5 mm mesh size) during a period of 45 minutes. The water volume flowing through the nets during the exposure period was calculated from the width of the nets (m) and from measurements of current velocity (m s^{-1}) and depth (m) at the nets. Total trapped organic matter was dried and ashed as described above and final values were expressed in g AFDM m^{-3} per stream.

Benthic organic matter

Benthic organic matter was determined in the same streams and years described for the litterfall inputs (Abelho 1994, Abelho and Graça 1996, Abelho and Graça 1998, Abelho 1999). In each stream, six Surber samples (area 0.09 m^2, mesh 0.5 mm) were randomly taken from the stream bottom every month during the study periods. AFDM of litter was determined as described for the litterfall samples. A mean monthly value expressed in g AFDM m^{-2} was calculated for each fraction per stream.

Decomposition

Four independent decomposition experiments were carried out in several streams using different leaves and methodology (Abelho 1994, Abelho and Graça 1996, Canhoto and Graça 1996, Abelho 1999). One experiment was carried out during 84 days (February-April 1993) in Sobral Cid stream using oven-dried (50°C, 48 h) leaves of *Alnus glutinosa*, *Castanea sativa*, *Eucalyptus globulus* and *Quercus faginea* (Canhoto and Graça 1996). A second experiment was carried during 1993

(September-November) in the same streams described for the litterfall inputs, using oven-dried (50°C, 24 h) leaves of *Castanea sativa* and *Eucalyptus globulus* (Abelho 1994, Abelho and Graça 1996). The other two experiments were carried out during January 1997 and January-March 1998 in S. João stream using air-dried leaves of *Castanea sativa* (Abelho 1999).

Leaves (approximately 3 g) were enclosed in fine-mesh bags (0.5-1.0 mm), and exposed in the streams. In each sampling occasion, 3-7 replicate bags were randomly retrieved. In the laboratory, the leaves were gently washed to remove attached sediments and oven-dried (50-60°C, 24-72 h). Weight loss was expressed as percentage of initial weight.

Autochthonous standing stock

Autochthonous standing stock was estimated from the epilithic biofilm of the upper surface of stones randomly collected from the streambed in the same streams described for the litterfall inputs (Abelho 1994, Abelho and Graça 1998, Abelho 1999). Samples were taken twice (July/August and October) during 1993 (five stones) and monthly from February 1995 to February 1996 (six stones) by scraping the stone surface with a scalpel in two areas of 0.0013 m^2. The collected material was oven-dried (60°C, 48 h), weighed and ashed (500°C, 5 h) to determine ash free dry mass (AFDM). The mean value of the two areas scraped was converted to g AFDM m^{-2}.

Results

Litterfall

Annual litterfall was 250-765 g m^{-2} yr^{-1} in the deciduous streams and 463 g m^{-2} yr^{-1} in the mixed stream (Table 2). Leaves were the most abundant component, comprising 64-79% of total litterfall in all streams (Table 2). Temporal patterns of litter inputs were seasonal in the deciduous streams where litterfall peaked during the autumn-winter period (Fig. 2). In the mixed streams, litterfall showed no clear seasonal pattern (Fig. 2).

Table 2. Litter production and percent composition at the deciduous and mixed forest sites during the years 1993/94 and 1995/95.

	Annual total organic matter (g AFDM m^{-2} yr^{-1})	% of total		
		Fruit and flowers	Twigs and branches	Leaves
Deciduous				
Margaraça 1 (1993/94)	693.4	12.4	19.9	67.7
Margaraça 1 (1995/96)	715.3	16.0	20.4	63.5
Margaraça 2 (1993/94)	765.0	9.1	11.7	79.2
Fraga da Pena (1993/94)	249.7	17.2	11.0	71.8
Mixed				
Laceiras (1993/94)	463.2	5.5	18.5	76.0

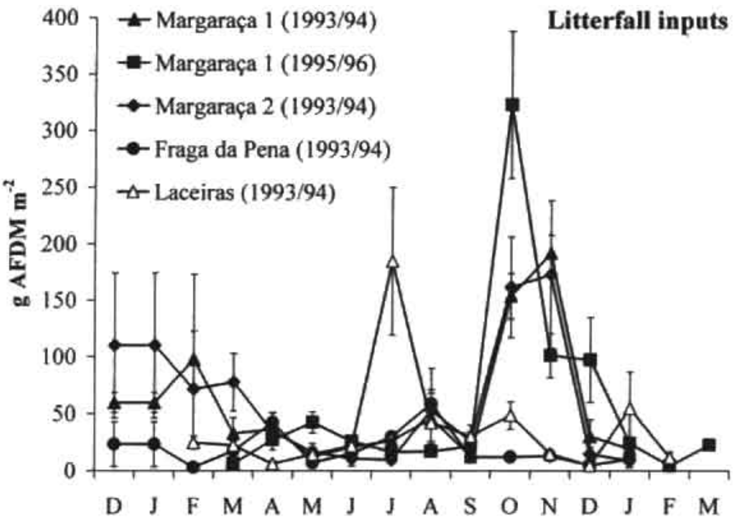

Figure 2. Temporal variation in litterfall at three deciduous (Margaraça 1, Margaraça 2 and Fraga da Pena) and one mixed (Laceiras) forest sites (mean ± 1 SE) during two non-consecutive years.

Short-term retention experiment

The stream was highly retentive trapping 90% of all leaves at short distances (mean 67 m) from the releasing point (Fig. 3). Leaves were more efficiently retained on substratum (i.e. debris dams) than on hydrological (i.e. margins and riffles) features of the stream (Canhoto and Graça 1998). Although no differences were found in the retention patterns of the four leaf species (ANCOVA, P>0.05), the substratum features retained

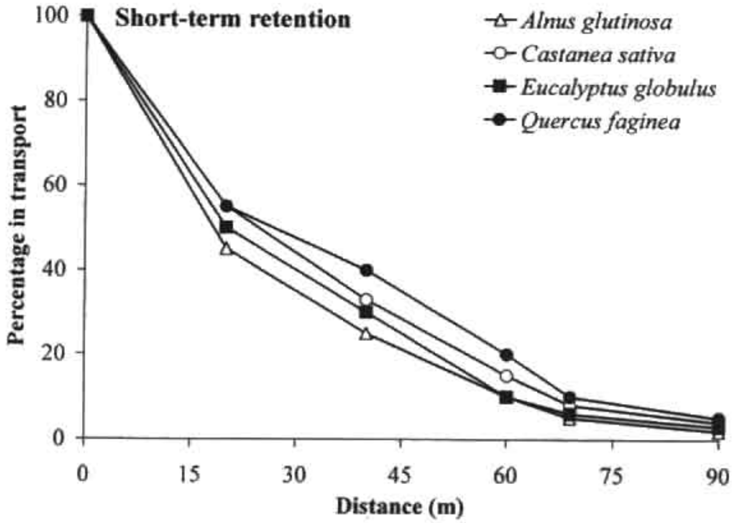

Figure 3. Percentage of released leaves remaining in transport along the experimental reach in S. João stream.

more efficiently the more flexible leaves of *Alnus glutinosa* and *Castanea sativa* than the harder leaves of *Quercus faginea* and *Eucalyptus globulus* (Canhoto and Graça 1998).

Transported organic matter

Transported organic matter was 0.9-1.8 g AFDM m^{-3} yr^{-1} in the deciduous and 0.3 g AFDM m^{-3} yr^{-1} in the mixed forest stream (Fig. 4). Transported organic matter was seasonal in the deciduous forest streams but showed no clear seasonal pattern in the mixed forest stream (Abelho 1994). In the deciduous forest streams, transported organic matter was negatively correlated with discharge ($r = -0.41$, $DF = 29$, $P<0.05$), but no correlation was found between transported organic matter and discharge in the mixed stream (Abelho 1994).

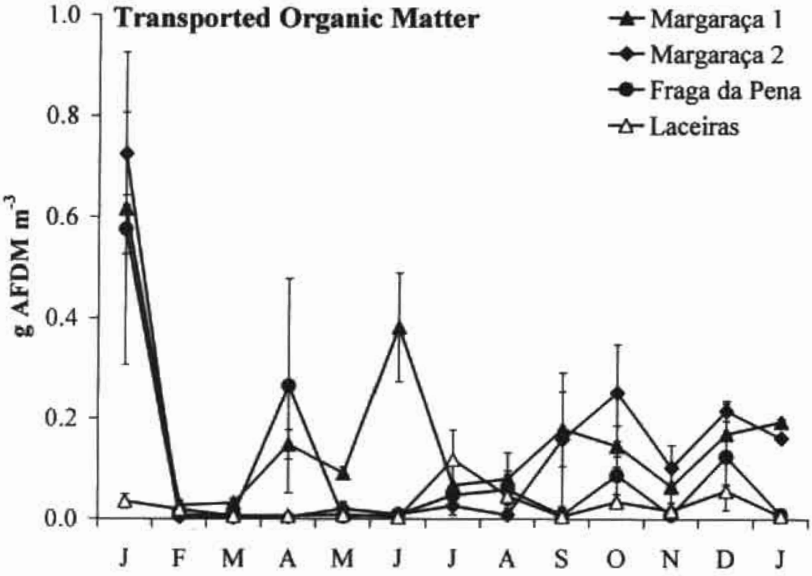

Figure 4. Temporal variation in transported organic matter of three deciduous (Margaraça 1, Margaraça 2 and Fraga da Pena) and one mixed (Laceiras) forest streams (mean ± 1 SE) during the year 1993/94.

Benthic organic matter and epilithic biofilm

Mean monthly benthic organic matter standing stock was 43-157 g m^{-2} in the deciduous and 24 g m^{-2} in the mixed stream (Fig. 5). The temporal patterns of benthic organic matter tended to be seasonal in all streams (Abelho and Graça 1996, Abelho and Graça 1998), with higher standing stock during spring and autumn (Fig. 5).

Standing stock of epilithic biofilm was 0.3-6.8 g AFDM m^{-2} in the deciduous and 1.3-5.5 g AFDM m^{-2} in the mixed forest stream (Fig. 6).

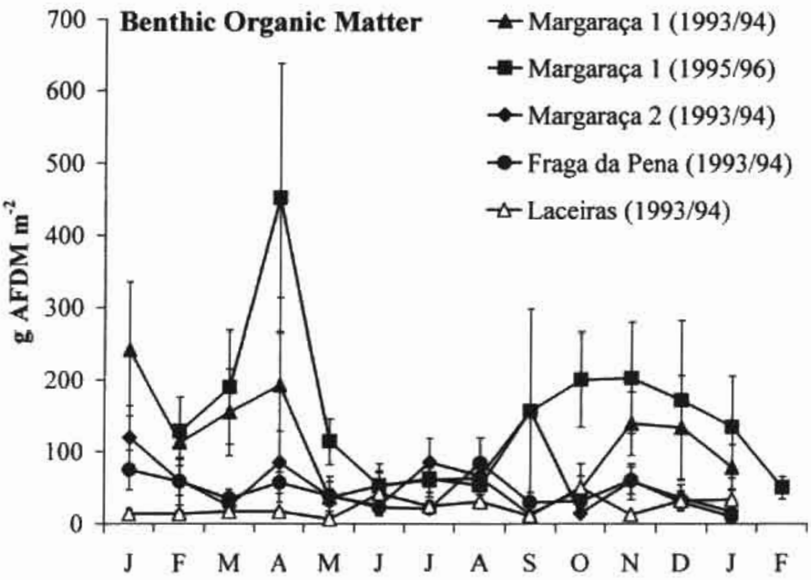

Figure 5. Temporal variation in standing stock of benthic organic matter in three deciduous (Margaraça 1, Margaraça 2 and Fraga da Pena) and one mixed (Laceiras) forest streams (mean ± 1 SE) during two non-consecutive years.

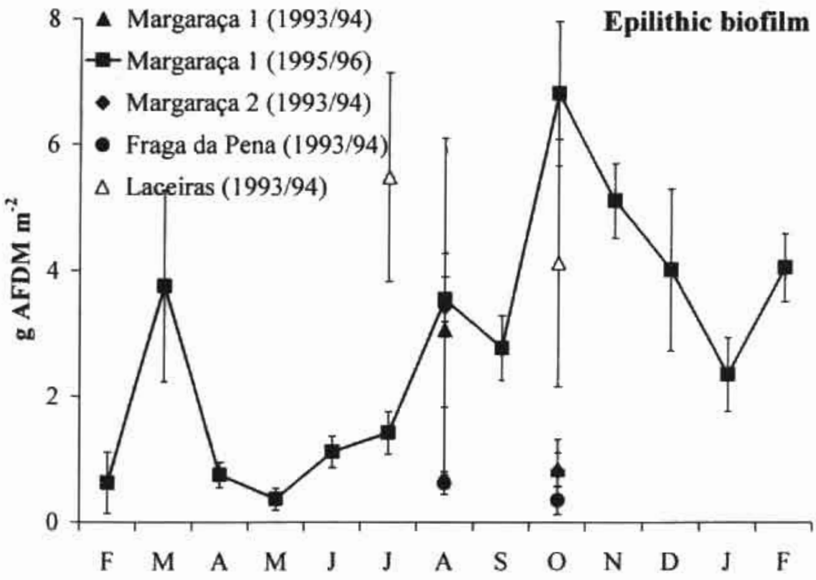

Figure 6. Temporal variation in standing stock of epilithic biofilm in three deciduous (Margaraça 1, Margaraça 2 and Fraga da Pena) and one mixed (Laceiras) forest streams (mean ± 1 SE) during two non-consecutive years.

Decomposition experiments

In Sobral Cid stream (Table 3), breakdown rates were fastest for the leaves of Alnus glutinosa (k = - 0.0161) and slowest for the leaves of *Quercus faginea* (k = - 0.0037). Decomposition rates of leaves of *Castanea sativa* (Table 3) varied between - 0.0066 and - 0.0079 day^{-1}. Decomposition in terms of mass remaining (Table 3) was faster for leaves of *Castanea sativa* (37-46%) than for leaves of *Eucalyptus globulus* (23-62%).

Table 3. Dry mass remaining at the end of the experimental periods and processing rates of different leaf species *(Alnus glutinosa, Castanea sativa, Eucalyptus globulus and Quercus faginea)* in one "agricultural" (Sobral Cid) and four deciduous streams (Margaraça 1, Margaraça 2, Fraga da Pena and S. João) of the Mondego River Basin.

Leaf species	Stream	Beginning	Experimental period (days)	Dry mass remaining (%)	Breakdown rate (*k* day^{-1})
Alnus glutinosa	Sobral Cid	February 1993	84	25	-0.0161
Castanea sativa	Sobral Cid	February 1993	84	50	-0.0079
Castanea sativa	Margaraça 1	September 1993	60	37	
Castanea sativa	Margaraça 2	September 1993	60	46	
Castanea sativa	Fraga da Pena	September 1993	60	42	
Castanea sativa	S. João	January 1997	31	78	-0.0066
Castanea sativa	S. João	January 1998	102	53	-0.0073
Eucalyptus globulus	Sobral Cid	February 1993	84	50	-0.0068
Eucalyptus globulus	Margaraça 1	September 1993	60	53	
Eucalyptus globulus	Margaraça 2	September 1993	60	62	
Eucalyptus globulus	Fraga da Pena	September 1993	60	23	
Quercus faginea	Sobral Cid	February 1993	84	70	-0.0037

Discussion

The litterfall inputs in the study sites (250-765 g AFDM m^{-2} yr^{-1}) are within the reported range for other European streams (Weigelhofer and Waringer 1994, Pozo et al. 1997). Litterfall had a seasonal distribution in the deciduous forests, with maximum inputs in autumn/winter primarily due to leaf abscission.

Due to their mixed nature, biofilms may have both heterotrophic and autotrophic activities. In our study, the standing stock of epilithic biofilm was very low. The source of energy it provides seems thus unimportant when compared with the allochthonous inputs and the standing stock of benthic organic matter, suggesting that the study streams are basically heterotrophic. The biofilm seems, in this case, to act mainly as an organic matter trap, removing dissolved organic matter from the water column (Abelho and Graça 1998, Abelho 1999).

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 and Fuchshuber 1994). In the deciduous study streams, the rapid trapping of the falling leaf litter, the different decomposition rates of different leaf species and the retention structures of the streams provide a high standing stock of benthic organic matter throughout the year (Abelho and Graça 1998, Abelho 1999). Moreover, the seasonal quality of litter is highly variable. The spring inputs, although quantitatively small, may be very important as an energy source on a time when leaf inputs are minimal, due to the high nutritive content of flowers (Fittkau 1964, Winterbourn 1976).

In temperate regions, the highest CPOM standing stock occurs in late autumn following the period of highest annual litterfall (Bärlocher 1983). In the study streams, the annual input of litter is reflected by the dynamics of benthic organic matter under changing discharge conditions (Abelho and Graça 1996). In the deciduous forest streams, the autumn peak of litterfall resulted in accumulation of organic matter in the streambed, but the highest peak of standing stock was observed in spring, coinciding with a smaller increase in litterfall. Thus, only when relatively high inputs coincide with a period of low discharge, an increase of these materials on the streambed is expected (Abelho and Graça 1996, Abelho and Graça 19989.

In summary, this study showed that the deciduous forests of the Mondego River Basin produce abundant litter inputs, mainly in the form of leaves, and especially during late autumn. Leaves entering low-order streams tend to be rapidly retained especially by substrate structures such as debris dams. Therefore, at any given time, the organic matter transported by the streams is low when compared to benthic organic matter.

Retained leaves decompose at different rates, depending on the stream and on leaf species. The different processing rates of several leaf species within a stream may provide a continuum of conditioned leaf litter available for the benthic invertebrate community throughout the year.

Standing stock of benthic organic matter was 29-88 times higher in the deciduous and 5 times higher in the mixed forest stream than standing stock of epilithic biofilm. Allochthonous organic matter constitutes thus the main energy source to low-order streams of the Mondego River Basin.

Acknowledgements

The work synthesised on this paper was financed by JNICT (projects PEAM/C/CNT/31/91 and PBIC/C/CEN 1131/92) and by the European Community (contract CI1*-CT94-0100). Manuela Abelho was financed by JNICT (BM/2265/91-RN), and by FCT (PRAXIS XXI/BD/2952/94). We wish to thank all colleagues who helped in fieldwork.

References

Abelho, M. 1994. Reflorestação com eucalipto: efeitos nos sistemas ribeirinhos baseados em detritos. M.Sc. thesis, University of Coimbra, Coimbra.

Abelho, M. 1999. Once upon a time a leaf: from litterfall to breakdown in streams. Ph.D. thesis, University of Coimbra, Coimbra.

Abelho, M. and Graça, M.A.S. 1996. Effects of eucalyptus afforestation on leaf litter dynamics and macroinvertebrate community structure of streams in Central Portugal. Hydrobiologia 324: 195-204.

Abelho, M. and Graça, M.A.S. 1998. Litter in a first-order stream of a temperate deciduous forest (Margaraça Forest, central Portugal). Hydrobiologia 386: 147-152.

Bärlocher, F. 1983. Seasonal variation of standing crop and digestibility of CPOM in a Swiss Jura stream. Ecology 64: 1266-1272.

Bunn, S.E. 1986. Origin and fate of organic matter in Australian upland streams. In Limnology in Australia. Edited by P. de Dekker and W.D. Williams. Monogr. Biol. Vol. 61, Junk Publishers, Dordrecht. pp 277-291.

Campbell, I.C. and Fuchshuber, L. 1994. Amount, composition and seasonality of terrestrial litter accession to an Australian cool temperate rainforest stream. Arch. Hydrobiol. 130: 499-512.

Canhoto, C. and Graça, M.A.S. 1996. Decomposition of *Eucalyptus globulus* leaves and three native leaf species (*Alnus glutinosa*, *Castanea sativa* and *Quercus faginea*) in a Portuguese low order stream. Hydrobiologia 333: 79-85.

Canhoto, C. and Graça, M.A.S. 1998. Leaf retention: a comparative study between two stream categories and leaf species. Verh. Internat. Verein. Limnol. 26: 990-993.

Fisher, S.G. and Likens, G.E. 1973. Energy flow in Bear Brook, New Hampshire: an integrative approach to stream ecosystem metabolism. Ecol. Monogr. 43: 421-439.

Fittkau, E.J. 1964. Remarks on limnology of central Amazon rainforest streams. Verh. Internat. Verein. Limnol. 15: 1092-1096.

Hernandez, I.M., Gallardo, J.F. and Santa Regina, I. 1992. Dynamic of organic matter in forests subject to a mediterranean semi-arid climate in the Duero basin (Spain): litter production. Acta Œcol. 13: 55-65.

Petersen, R.C. and Cummins, K.W. 1974. Leaf processing in a woodland stream. Freshwater Biol. 4: 343-368.

Pozo, J., González, E., Díez, J.R., Molinero, J. and Elosegi, A. 1997. Inputs of particulate organic matter to streams with different riparian vegetation. J. N. Am. Benthol. Soc. 16: 602-611.

Smock, L.A. 1990. Spatial and temporal variation in organic matter storage in low-gradient, headwater streams. Arch. Hydrobiol. 118: 169-184.

Speaker, R., Moore, K. and Gregory, S. 1984. Analysis of the process of retention of organic matter in stream ecosystems. Verh. Internat. Verein. Limnol. 22: 1835-1841.

Vannote, R.L., Minshall, G.W., Cummins, K.W., Sedell, J.R. and Cushing, C.E. 1980. The river continuum concept. Can. J. Fish. Aquat. Sci. 37: 130-137.

Wallace, J.B., Whiles, M.R., Eggert, S., Cuffney, T.F., Lugthart, G.J. and Chung, K. 1995. Long-term dynamics of coarse particulate organic matter in three Appalachian Mountain streams. J. N. Am. Benthol. Soc. 14: 217-232.

Weigelhofer, G. and Waringer, J.A. 1994. Allochthonous input of coarse particulate organic matter (CPOM) in a first to fourth order Austrian forest stream. Internat. Rev. Hydrobiol 79: 461-471.

Winterbourn, M.J. 1976. Fluxes of litter falling into a small beech forest stream. N. Z. J. Mar. Freshw. Res. 10: 399-416.

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