LEAF-LITTER BUDGETS IN TWO CONTRASTING FORESTED STREAMS

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SUMMARY

Leaf-litter budgets have been studied in two contrasting forested streams, one flowing under a deciduous forest and the other one flowing under an *Eucalyptus globulus* plantation. Inputs (vertical and lateral) of terrestrial CPOM to the streams, and CPOM storage in each stream bed were measured from September 93 to September 94. A model incorporating leaf-litter storage, terrestrial inputs and breakdown rates was applied to study leaf-litter dynamics in both streams. The relative importance of breakdown and transport as processes affecting the availability of leaf-litter in the stream bed was assessed. Our data suggest that 10-17 % of leaf litter entering these streams annually is processed in place. Significant relationships between organic matter storage and the rate of terrestrial input were found at both sites. However, because of the different timing of leaf fall between both forest types, relationships between stream flow and leaf-litter storage were site-dependent. Eucalyptus plantations, together with the hydrologic regime, modify the availability of benthic leaf-litter, the leaf-litter turnover and the ecosystem efficiency.

INTRODUCTION

Organic matter inputs from terrestrial ecosystemc are the main energy source for the communities in headwater streams draining forested catchments (e.g., FISHER & LIKENS, 1973; ANDERSON & SEDELL, 1979; VANNOTE *et al.*, 1980; BENKE *et al.*, 1988; CUMMINS *et al.*, 1989; RICHARDSON, 1991; BASAGUREN *et al.*, 1996; WALLACE & WEBSTER, 1996). The periodic (and thus, more or less predictable) inputs of allochthonous materials, reflecting the forest litter production, seem to be dominated by leaves, with wood and reproductive materials being less abundant, no matter the kind of the forest or the geographic area (BRAY & GORHAM, 1964; MEENTENMEYER *et al.*, 1982).

Allochthonous materials reach the stream vertically (sometimes referred to as direct inputs) or laterally. In the first case, litter enters the stream directly; in the second one, the material deposited on the ground is mobilised by different agents, a part of it entering the stream channel. Vertical inputs are usually most important, laterals being often only a slight portion of the total (usually less than 20 %; e.g., WINTERBOURN, 1976; COWAN & OSWOOD, 1983; CONNERS & NAIMAN, 1984; CAMPBELL *et al.*, 1992; BENSON & PEARSON, 1993; WEIGELHOFER & WARINGER, 1994).

The temporal and spatial distribution of inputs depends on the type of riparian vegetation, especially on its deciduous or evergreen characteristics. Thus, disturbances of the riparian vegetation (clear-cut, substitution...) affect the land-water relationships, as they modify the quantity, quality and temporal distribution of organic inputs and their fate in streams (e.g., GOLLADAY *et al.*, 1989; BRITTON, 1990; WEBSTER *et al.*, 1990; DELONG & BRUSVEN, 1994; MARIDET *et al.*, 1995; POZO *et al.*, 1997; WEBSTER & MEYER, 1997a).

Eucalyptus plantations are one of the most typical afforestation practices in northern Spain (ICONA, 1980), and the different quality and seasonality of eucalyptus litterfall could result in important modifications of the energetic resources for stream communities. The objective of this work was to evaluate the effects of the substitution of deciduous riparian forest by eucalyptus plantations on leaf-litter budgets in a stream system of northern Spain.

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STUDY SITE

The Agüera stream catchnient is in the North of Spain and drains an area of 144 km^2. Indigenous mixed forests cover **a** broad zone in the headwaters of the main channel. Other uplands are dominated by plantations of *Pinus radiata* D. Don and *Eucalyptus globulus* Labill, and the lowlands by meadows and crops.

This work has been carried out in two first-order tributaries of the Agüera stream: Saiderrey stream (UTM: 30T VN 784843) drains **a** catchment of 184 ha, and is currounded by **a** mature deciduous forest with *Quercus robur* L., *Castanea sativa* Miller and *Alnus glutinosa* Gaertner as dominant cpecies; and Jerguerón stream (UTM: 30T VN 769967) drains **a** catchment of 83 ha and flows through an *Eucalyptus globulus* plantation. One site was chosen in each of the streams. Site D (an area of 1,742 m^2 including **a** stream reach of 71 m) is located in the deciduous forest. Site E (an area of 393 m^2, including **a** stream reach of 31.5 m), in the eucalyptus plantation. Additional information on these cites can be found in POZO *et al.* (1997).

MATERIAL AND METHODS

Sampling and analysis

Vertical litterfall was determined from basket traps randomly placed in the riparian forest near the stream channel (15 traps at the deciduous site and 10 at the eucalyptus site): additional traps (10 at site D and 5 at site E) were uced to ectimate lateral inputs to the stream (see POZO *et al.,* 1997, for details).

Benthic CPOM wac sampled by using **a** modified Surber net (0.25 m^{-2}) with 1 mm mesh size. On each occasion, 5 random replicates were taken.

From 22 September 1993 to 22 September 1994, samples were collected monthly (twice a month in periods of heavy litterfall). Litter was air dried in the laboratory at room temperature and sorted into categories: leaves. twigs and bark, fruit and flowers, and unidentified fragments. Branches more than 1 cm in diameter were not considered. The leaf component was further sorted by species into oak, alder, chestnut, hazel, eucalyptus and other leaves. Each category was weighed, dried at 70 °C for 72 h, weighed, and ashed at 500 °C for 12 h to obtain ash free di-y mass (AFDM). Data were log-transformed before the statistical analysis (ZAR, 1984).

In each occasion, discrete measures (4 hours) of transported litter have been taken by using drift nets (1 mm mesh size) spanning the entire width of the channel at the end of each station. In the laboratory. material retained was processed in the same way that benthic CPOM.

Budget modelling

A first approach to the leaf-litter budget can be obtained from measures on benthic standing stocks and terrestrial inputs, and estimates of outputs (minimum outputs when, as in the present case, inputs by transport from upstream have not been measured). Minimum outputs are calculated by the difference between terrestrial inputs and the variation of storage in **a** given time:

$$O = I - \Delta S \qquad (1)$$

where O is output (g m^{-2})
I is terrestrial input (g m^{-2})
AS is the variation of the material standing stock in the stream bed (g m^{-2})

By using breakdown rates of oak, alder, chestnut and cucalyptus from previous studies in this catchment (POZO, 1993; MOLINERO *et al.*, 1996), and applying the model given beiow, we can measure how efficiently the stream system uses this type of resource. Thus, we estimated the outputs of leaf-litter by breakdown and those by transport downstream.

From the exponential equation by which breakdown rates have been calculated, in a given period we have:

$$S_t = S_o e^{-kt} \qquad (2)$$

where S, is the stock remaining at time t (g m^{-2})
S_o is the initial stock (g m^{-2})
k is the breakdown rate (d^{-1})
e is the natural log basis
t is time (d)

From equation (1) we have that

$$S_t = S_o - O_t + I_t \qquad (3)$$

where O, ic output between t_o and t (g m^{-2})
I_t is input between t_o and t (*g* m^{-2})

In each time unit (day), the standing crop decomposes and incorporates **a** new amount of leaf-litter (I_d) that will follow the process. Thus, considering outputs by decomposition (equation 2) and terrestrial inputs after one day,

$$S_1 = S_o e^{-k} + I_d \qquad (4),$$

in the second day we have:

$$S_2 = (S_o e^{-k} I_d)\, e^{-2k} + I_d \qquad (5)$$

Finally, in a given period of time, we have:

$$SE_t = S_o e^{-kt} + I_d(e^{kt} - 1)\,(e^{kt} - e^{k(t-1)})^{-1} \qquad (6)$$

where SE, is estimated benthic leaf-litter (g m^{-2}) at time t, as **a** function of S_o, of total inputs between t_o and t, and of the mass lost by decomposition in this period.

Following (1), outputs by decomposition can be determined by:

$$OD_t = S_o + tI_d - SE_t \qquad (7)$$

where OD, is output by decotnposition (g m^{-2}) during time t

And, finally,

$$OT_t = O_t - OD_t \tag{8}$$

where OT, is output by transport downstream during time t

Annual output by transport or decomposition can be calculated by summing up the respective outputs of all periods in a year.

Turnover time of leaf-litter was calculated dividing average standing stock of leaf-litter in the stream bed by annual inputs (FISHER & LIKENS, 1973).

From discrete transport data obtained by using drift nets at the end of each station, and from the breakdown rates of leaves, we calculated the distance the leaf-litter is transported downstream before its transformation to finer particles, dissolved organic matter, or CO_2.

NEWBOLD *et al.* (1982), defined a turnover length for organic carbon as:

$$S = F/R \tag{9}$$

where F is the downstream **flux** of organic carbon per meter width of stream (g m^{-1} s^{-1})
R is the **flux** of carbon lost to respiration (g m^{-2} s^{-1})

Similarly. we could define a turnover length for leaf-litter as:

$$L = F'/R' \tag{10}$$

where F' is the downstream flux of leaf-litter per unit of stream width (g m^{-1} s^{-1})
R' is the **flux** of benthic leaf-litter loss by breakdown (g m^{-2} s^{-1})

F' can be calculated by:

$$F' = M/tW \tag{11}$$

where M is leaf-litter mass retained by the drift net across the channel (g)
t is period of time of the drift net collecting leaf-litter (s)
W is the channel width (m).

R' was calculated applying the breakdown rate to the leaf-litter standing stock in the stream bed:

$$R' = k \times S \tag{12}$$

The leaf-litter turnover length here ic **a** measure of the rate at which the stream processes leaf-litter relative to the rate at which it is transported downstream.

RESULTS AND DISCUSSION

Leaf-litter inputs

Most of the CPOM inputs (vertical or lateral) to both streams were leaf-litter (table 1). Furthermore, 77% (deciduous stream) and 92% (eucalyptuc stream) of the total leaf-litter inputs entered the streams vertically.

Most of leaf-litter production (vertical inputs) occurred from September to December in the deciduous forest and from May to July in the eucalyptus plantation (fig. 1). This seasonality of inputs is usually shown for both types of forested streams (e.g., PRESSLAND, 1982; CONNERS & NAIMAN, 1984; WEBSTER *et al.*, 1990; CAMPBELL *et al.*, 1992; CAMPBELL & FUCHSHUBER, 1994; WEIGELGHOFER & WARINCER, 1994). At the deciduous stream, lateral inputs iagged slightly behind vertical ones; no clear seasonality was observed at the eucalyptus site (fig. 1). In the deciduous stream 98% of leaf-lit-

Table 1. Leaf-litter inputs (mean ± SD; g m^{-2} AFDM) to streams at sites D (deciduous) and E (eucalyptus) from 22 September 1993 to 22 September 1994. Columns headed by % represent the ratio leaf-litter/total CPOM in percentage.

INPUTS	SITE D g m^{-2}	%	SITE E g m^{-2}	%
VERTICAL	384.8 k78.4	62.9	288.3 ±82.6	60.3
LATERAL	113.9 ±59.5	76.9	24.3 ±14.7	61.7

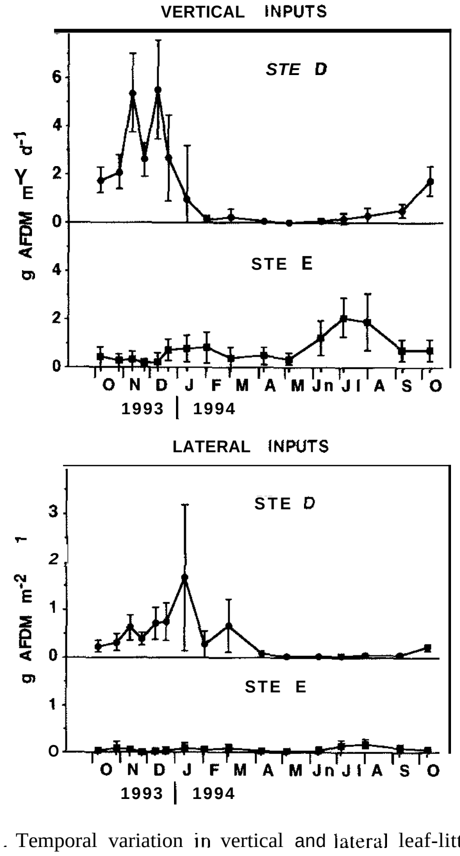

Figure 1. Temporal variation in vertical and lateral leaf-litter inputs (mean ± SD) to streams at sites D (deciduous) and E (eucalyptus).

ter inputs consisted of leaves from oak, alder, chestnut and hazel, whereas in the eucalyptus stream the same percentage was due to eucalyptus leaves only. Thus, the change of riparian vegetation produces a drastic change in the composition of leaf-litter inputs to streams. These results have been discussed elsewhere (POZO *et al.,* 1997).

Benthic leaf-litter

As reported in other studies (e.g., IVERSEN *et al.*, 1982; CONNERS & NAIMAN, 1984; CHAUVET & JEAN-LOUIS. 1988; WEIGELGHOFER & WARINGER, 1994), at both sites the highest stocks of benthic leaf-litter coincided with the period of maximum leaf fall: autumn for the deciduous stream and summer for the eucalyptus one (fig. 2). Mean values of benthic leaf-litter for the study period were lower in the deciduous stream (17.7 g AFDM m^{-2}) than in the eucalyptus stream (36.9 g AFDM m^{-2}).

As in the case of inputs, benthic leaf-litter was dominated by oak, chestnut, alder and hazel, altogether accounting for 99.3 % of leaf mass in the deciduous site, and by eucalyptus (97.6 %) in the plantation site (table 2). Thus, benthic leaf-litter in the Agüera channels was related to the ripanan vegetation, showing the strong influence of the terrestrial environment in the control of energetic resources in this type of ecosystems (CUMMINS *et al.*, 1984; BENKE *et al.,* 1988; GURTZ *et al.,* 1988; GONZALEZ & POZO, 1996). The deciduous environment contributes with a diverse but seasonally fluctuating leaf litter to the benthic community, while in the eucalyptus site, leaf-litter consumers have a low variety of food all along the year.

Leaf-litter budgets

To study leaf-litter budgets in these streams we have applied the model described to leaves of oak, alder and chestnut (representing 86 % of total leaf-litter entering site D) and eucalyptus (98 % of total leaf-litter entering site E).

Table *2.* Contribution (%) of the different leaf species to the benthic leaf-litter storage at sites D (deciduous) and E (eucalyptua).

SPECIES	SITE D	SITE E
Oak	37.73	0.49
Chestnut	28.26	0.05
Alder	20.19	1.79
Hazel	13.08	
Pine	0.39	0.03
Evergreen oak	0.06	
Eucalyptuc		97.61
Other	0.28	

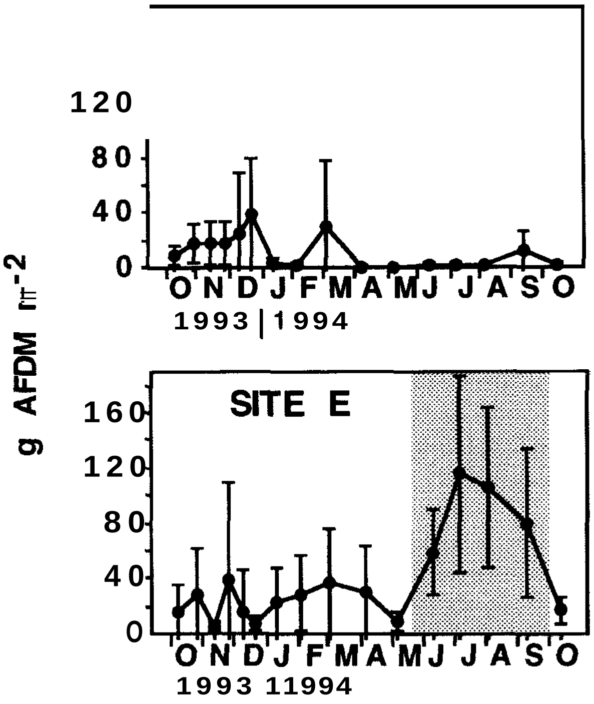

Figure *2.* Temporal variation in benthic leaf-litter standing stock (mean ± SD) at sites D (deciduous) and E (eucalyptus). Shaded area corresponds to a dry period at site E.

The temporal changes of terrestrial inputs, benthic storage, and breakdown and transport outputs of this leaf-litter are shown in fig. 3. Relationships between pairs of these variables are shown in fig. 4. In both streams, benthic leaf-litter is a function of terrestrial inputs. Furthermore, regression between standing stock of benthic leaf-litter and discharge was significant (inverse) only at site E, and that between outputs by transport and discharge only at site D (fig. 4). Discharge directly affects the stream retention capacity (PROCHAZKA *et al.,* 1991; SNADDON *et al.,* 1992; WEBSTER *et al.*, 1994) and can greatly influence organic matter budgets in streams (BILBY & LIKENS, 1980; CUMMINS *et al.,* 1983). Thus, periods of maximum terrestrial inputs contribute to high standing stocks of leaf-litter in the stream bed when discharges are low (BRETSCHKO, 1990). Accumulations of leaf-litter during summer are common to streams surrounded by eucalyptus due to the phenology of leaf fall (BOULTON & LAKE, 1992). On the other hand, accumulations of leaf-litter in the deciduous site during autumn were lower than expected, because of the coincidence with high flows (WALLACE *et al.,* 1995). When litter input peaks coincide with low flows, as usually occurs in Australian and South African streams (BOULTON & LAKE,

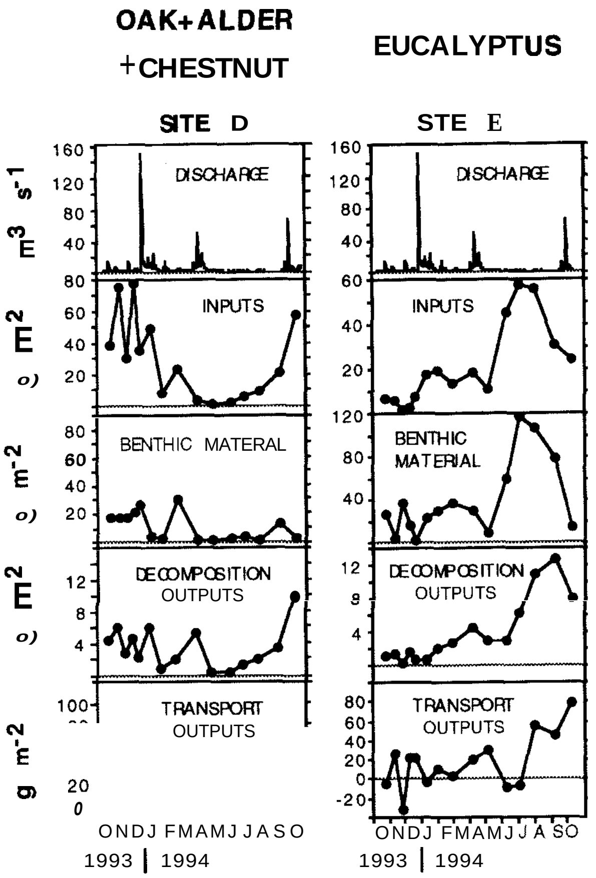

Figure 3. Temporal variation in leaf-litter storage and fluxes at sites D (deciduous) and E (eucalyptus).Terrestrial inputs and benthic materials are measures, breakdown outputs and transport outputs are caiculated from the model. For illustrative purposes, daily discharge in a gauge station near the river mouth is also shown at the top.

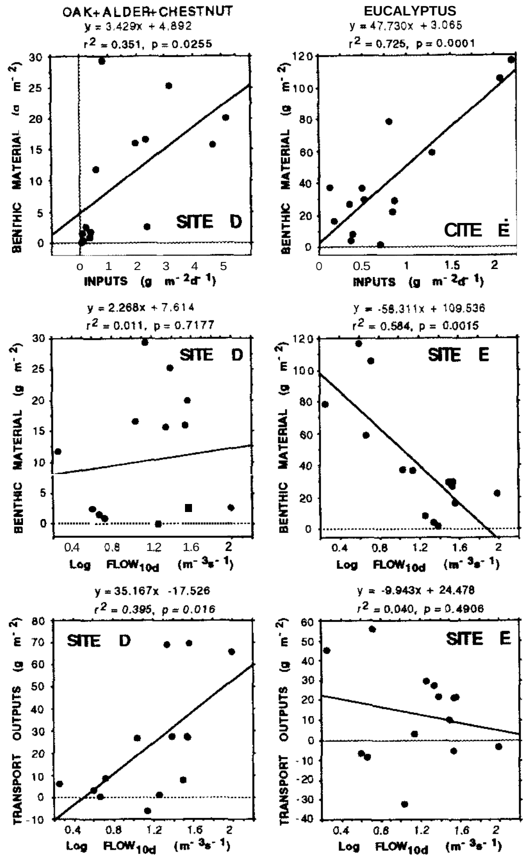

Figure 4. Linear regressions between different variables affecting leaf-litter budgets at sites D (deciduous) and E (eucalyptus).

1992; RACTLIFFE *et al.*, 1995), CPOM tends to accumulate in the stream bed. On the contrary, if litter inputs coincide with high flows, as in the deciduous forest streams from Europe, transport processes are favoured (MARIDET *et al.*, 1995). This seems to be the reason for the negative significant correlations between benthic leaf matter and flow at site E, and positive significant correlations between outputs by transport and flow at site D (fig. 4). The phenology **of** litter input and discharge regime are responsible for the temporal variation **of** benthic leaf-litter in Agüera streams.

The organic matter budgets constructed (fig. 5) show that between 10.5 % (deciduous stream) and 17.5 % (eucalyptus ctream) of leaf-litter inputs is processed. These efficiencies are similar to several examples reported by WEBSTER & MEYER (1997b) for streams from North America and Australia. Site E showed higher values, despite the slow breakdown of eucalyptus leaves. This is because, at this site, the benthic community have higher amount of available organic matter during longer periods of time, which favours its conditioning and breakdown. Given the scant importance of primary production in these headwater streams (ELOSEGUI, 1992; GONZALEZ, 1997), our efficiencies seem reasonable.

Leaf-litter turnover

Leaf-litter turnover times were calculated by dividing average standing stock of leaf-litter in the stream bed by annual inputs (WEBSTER & MEYER, 1997b). Turnover times were much lower at site D than at site E (9 and 47 days, respectively). This suggests that the eucalyptus stream is more retentive than the deciduous one. These turnover times are, however, lower than those of IVERSEN *et al.* (1982), who reported turnover times of 3.2 months for leaf-litter in an European stream surrounded by *Fagus sylvatica* with similar annual terrestrial

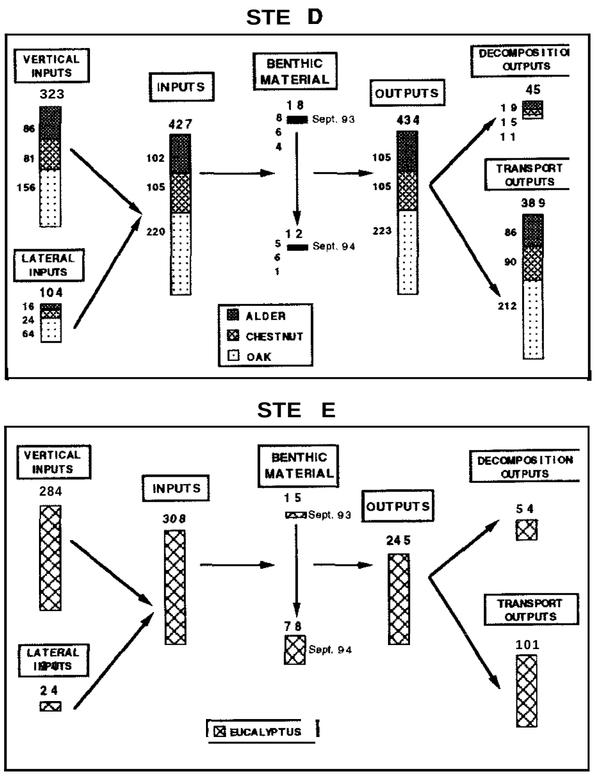

Figure 5. Leaf-litter budgets constructed with leaves of alder, chestnut ünd **oak,** at site D (deciduous)and with eucalyptus at site E (eucalyptus plantation). All the outputs are calculated frorn the model. Units are g **AFDM** m^{-2}.

inputs (510 g m^{-2}). Furthermore, in **a** set of papera included in the monograph by WEBSTER & MEYER (1997a), CPOM turnover times in 1st-order streams from North America were between 26 days and 3.8 years. From 10 cases presented, 5 were below 1 year and 4 were between 26 and 109 dayc. SCHADE & FISHER (1997) reported leaf-litter turnover times ranging from 113 days to 5.5 years. Thus. our results suggest **a** iow retentivity of the ctudied streams.

Turnover distances of leaf-litter depended on discharge, that affects transport, and ranged from 100 to 12,500 m at site D, and from 90 to 2,300 m at site E. Obviously, the highect values of both ranges would carry away leaf-litter out of the system. Differences in travel distance have been attributed to changes in discharge (WEBSTER & MEYER, 1997b) and to different size of streams (NEWBOLD *et al.,* 1982). In our case, although the stream under eucalyptus is smaller than the deciduous one (mean flows during the study period were 9.9 and 39.8 ls^{-1}, respectively), differencec in travel distances between both streams are clearly influenced, again, by input phenology and hydrologic regime: in the eucalyptus stream leaf-fall **peaks** in summer, when tlows are low, favouring leaf retention and therefore its use by the fluvial community.

Changes in terrestrial vegetation have important effects on the organic matter budgets of streams, as they modify storages and/or fluxes of organic matter (WEBSTER *et al.*, 1990; MINSHALL, 1996). The study of leaf-litter budgets in the Agüera stream system allows to discern impacts resulting from riparian vegetation disturbance on the strearn ecosystem function. Eucalyptus plantations directly result in changes of seasonality of litter inputs, peak-timing, and drastic reduction in leaf diversity; together with the hydrologic regirne, they modify the availability of benthic leaf-litter, the leaf-litter turnover and the ecosystem efficiency.

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