Aquat. Sci. 65 (2003) 158–166
1015-1621/03/020158-09
DOI 10.1007/s00027-003-0623-3

Aquatic Sciences

Research Article

Leaf retention in streams of the Agüera basin (northern Spain)

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Received: 10 July 2002; revised manuscript accepted: 18 March 2003

Abstract. The capacity of stream channels to retain leaf litter (retentiveness) was measured in 21 reaches of the Agüera basin (northern Spain) at different discharges, using plastic strips as leaf analogs. Strips were calibrated against seven local leaf species occurring in the area. Retention was highest for alder, followed by plastic strips, oak, beech, chestnut, eucalyptus, hazel, and sycamore. Inter-specific differences in retention were great, and not clearly related to leaf form or size. This result shows that a great deal of caution is necessary to compare results obtained by authors using different leaf species. The Agüera stream channels were highly retentive, especially in the headwaters. At baseflows, the average travel distance of strips was 3.6 m in 1st-order reaches, increasing to 16.6 m in 3rd-order streams. Travel distances of strips increased twofold in 3rd- and 2nd-order reaches and 5-fold in 1st-order streams during periods of high discharge. Leaf litter retentiveness was related to channel gradient, width, and substrate. Cobbles and wood showed high retention efficiencies, and the role of wood as a retention factor increased at high discharges. Retentiveness enhances storage and subsequent utilization of organic materials in forested streams, and thus should be taken into account when managing streams.

Key words. Leaves; plastic strips; retentiveness; retention; stream; coarse particulate organic matter.

Introduction

Forested streams are often heterotrophic systems, in that at least a portion of the available production is fuelled by allochthonous organic matter imported from the adjacent terrestrial community (Vannote et al., 1980; Bretschko and Moser, 1993). Thus, the amount, quality, and timing of organic inputs are important factors influencing lotic communities (Cummins et al., 1989). The dynamics of organic matter are also strongly influenced by the effectiveness of specific reaches in retaining material (retentiveness). Therefore, retentiveness is an important ecological characteristic of lotic ecosystems (Bilby and Likens, 1980).

Retention has been measured for various materials, e.g., hydrological retention (Morrice et al., 1997), nutrient retention (Martí and Sabater, 1996), and retention of organic matter in dissolved (Newbold et al., 1981), fine particulate (Minshall et al., 2000), and coarse particulate forms (Webster et al., 1994). The features in any reach that affect retentiveness differ for each of the materials above, but include characteristics of the hyporheic flow, substrate roughness, depth, discharge, and the abundance of woody debris dams. In this paper we compare the efficiency of stream channels with different retention characteristics in retaining coarse particulate organic matter (CPOM).

CPOM is an important form of organic material in streams that constitutes the base of complex food webs (Vannote et al., 1980), and is usually dominated by leaves from riparian trees (Meentmeyer et al., 1982). The retentiveness of CPOM is controlled by channel form; narrow, physically complex reaches often being the most retentive (Webster et al., 1994; Mathooko et al., 2001). In most reaches, retention of CPOM decreases with increasing discharge and the associated changes in water depth,

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Published on Web: July 3, 2003

velocity, shear stress, and stream power (Speaker et al., 1984; Ehrman and Lamberti, 1992). Wood, especially in the form of debris dams, increases CPOM retention capacity (e.g., Raikow et al., 1995; Díez et al., 2000), enhances standing stocks of leaf litter, and results in higher abundance of macroinvertebrate shredders (Prochazka et al., 1991; Chergui et al., 1993). Although factors controlling CPOM retention are relatively well known, there has been no analysis of spatial differences in retentiveness among streams, as most studies have been at a small number of sites.

Previous studies of CPOM in the Agüera stream assessed inputs, transport, storage, and breakdown of leaf material (Pozo et al., 1994; 1997a, b; 1998). One study also demonstrated the influence of forest management practices on litter budgets (Pozo et al., 1997a). Organic matter storage is a function of the interaction between inputs and retentiveness, but thus far little information exists on the relative ability of these streams to retain CPOM. The aim of this study was, therefore, to evaluate the retentiveness of stream channels in the Agüera watershed, to identify specific stream characteristics that control leaf retention, and to compare retention under different hydrological conditions.

Materials and methods

Study area

The Agüera is a 3rd-order stream located in northern Spain, draining a catchment of 145 km^2 (Fig. 1). The climate is temperate maritime. Total rainfall was 1381 mm and average temperature was 14.5 °C during the study period (September 1997 to August 1998), which approximated with the long-term averages (Elosegi et al., 2002). The highest discharges usually occur in winter, and the lowest in summer, although spates can occur at any time throughout the year. Underlying rocks are mainly siliceous, except in a broad calcareous belt in the centre of the catchment. The uplands are covered by mixed deciduous forests, plantations of *Eucalyptus globulus* (Labill) and *Pinus radiata* (D. Don), and heathland. Arable land and grassland meadows dominate the lowlands. The human population within the catchment is ca. 3000, and main activities include forestry, livestock grazing, and agriculture (Elosegi et al., 2002).

Reach characteristics

We selected 21 study reaches (Fig. 1), reflecting the range of environmental conditions occurring in the Agüera catchment. The reaches differed in geomorphology (channel width, gradient, bank slope, and substrate), and in the composition and structure of riparian forests. Thirteen reaches were 1st-order (Strahler, 1952), five 2nd-order, and three 3rd-order. Reach length was around 50 m in 1st-order reaches, and around 150 m in larger stream orders. The different lengths were selected to minimize within-reach physical heterogeneity.

Experimental reaches differed greatly in channel characteristics (Table 1), measured as described by Díez et al. (2001). Channel gradient ranged from 0.4% to 41.1%. In general, gradients were steeper in headwater reaches, although some headwaters were low gradient (e.g.,

Table 1. Morphometry, composition of inorganic substrate, and instream wood volume (cm^3 m^{-2}) in the study reaches. Grad = gradient; Sin = sinuosity; Area = drainage basin area. Data from Díez et al. (2001).

Study reach	Order	Grad (%)	Sin	Width (m)	Area (ha)	Bedrock (%)	Boulders (%)	Cobble (%)	Gravel (%)	Sand (%)	Wood
Antonilla	1	4.0	1.1	2.5	179	0	0	30	43	7	2,368
Baulajaia	1	22.4	1.0	3.2	65	58	16	6	17	2	4,489
Cabrerizas	1	15.7	1.2	3.3	152	0	36	30	29	4	22,926
Cuchillo C	1	5.7	1.7	3.5	160	4	22	12	46	16	23,552
Cuchillo E	1	14.3	1.2	3.9	179	5	44	16	28	6	0
Jerguerón	1	15.7	1.1	2.9	83	12	51	14	16	7	890
Laiseca 1	1	2.8	1.3	3.3	47	0	14	35	34	16	4,330
Laiseca 2	1	4.0	1.1	2.5	182	16	13	27	25	16	168
Peñalba	1	14.2	1.1	3.8	169	10	47	24	10	6	2,228
Perea 1	1	10.9	1.1	3.6	169	19	31	17	20	5	12,576
Perea 2	1	41.1	1.1	4.5	195	41	39	7	11	2	11,524
Salderrey C	1	9.0	1.0	3.8	184	29	23	20	17	7	13,760
Salderrey E	1	5.8	1.0	3.1	203	27	13	14	37	6	0
Adino	2	1.7	1.0	4.4	615	0	0	43	28	13	2,890
Agüera 2	2	3.1	1.2	5.1	825	45	17	16	18	3	481
Cuchillo 3	2	9.2	1.3	5.8	815	2	58	17	19	3	15,310
Remendón 1	2	2.7	1.0	6.9	408	13	46	20	18	2	167
Remendón 2	2	1.7	1.0	7.3	571	16	28	23	20	3	221
Agüera 5	3	1.1	1.2	8.2	4761	7	16	36	29	11	149
Agüera 7	3	0.8	1.2	13.6	6906	8	45	24	21	1	70
Agüera 9	3	0.4	1.0	15.1	11535	0	23	44	26	6	42

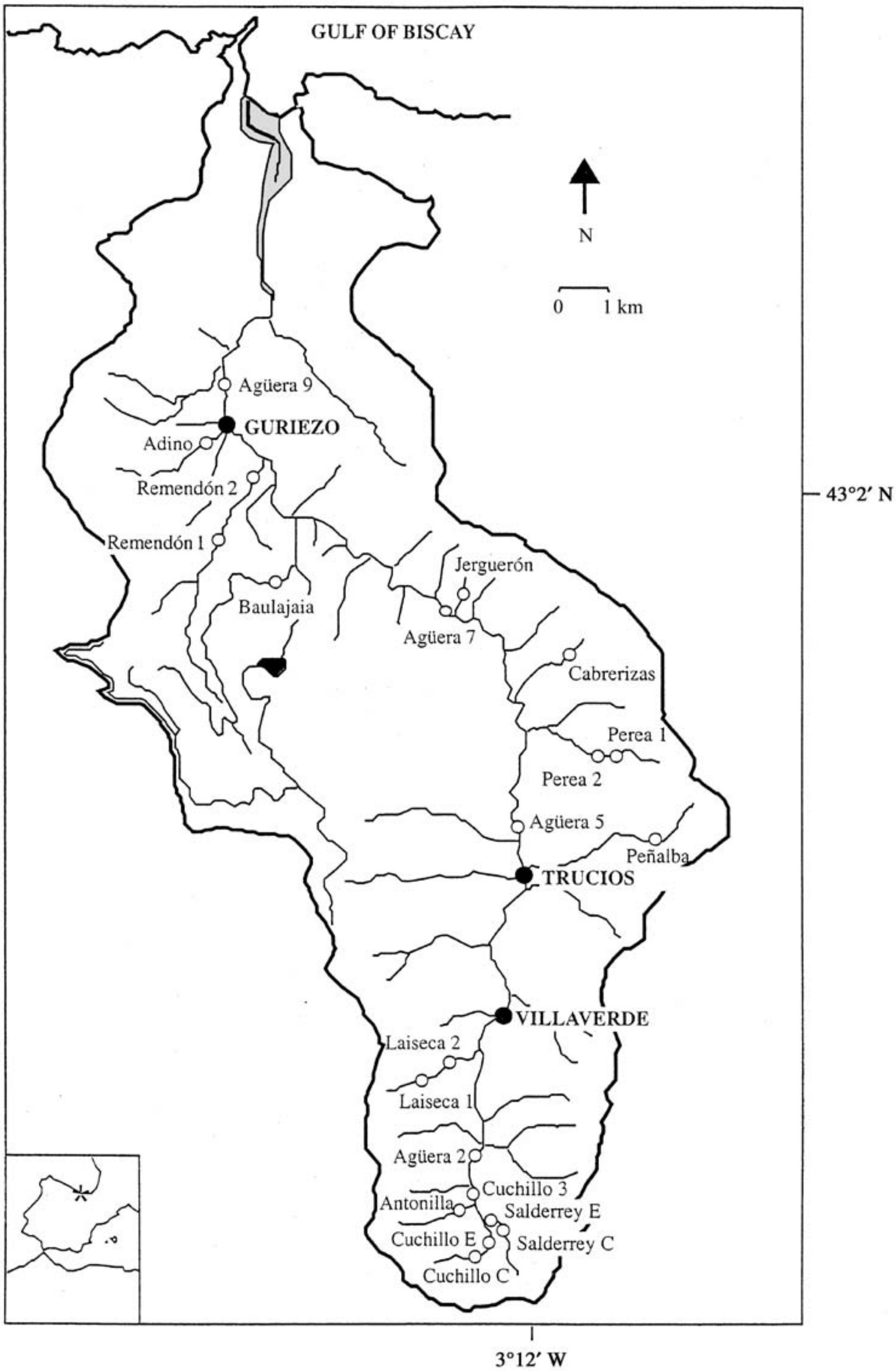

Figure 1. Location of the Agüera catchment (*), main villages (●) and study reaches (○).

Laiseca 1 and 2). Sinuosity ranged from 1.03 to 1.71, channel width from 2.5 m to 15.1 m, and drainage area (measured from 1 : 50000 maps) varied by more than two orders of magnitude (48 to 11,535 ha). The percentage cover by sand (< 0.2 cm), gravel (0.2 – 6.4 cm), cobbles (6.4 – 25.6 cm), boulders (> 25.6 cm), and bedrock in each stream reach were estimated visually every 0.5 m along transects across the stream channel. Transects were spaced at 5m intervals in 1st order reaches and at 20 m intervals in 2nd and 3rd order reaches. Boulders, cobbles, and gravel in different proportions dominated most reaches. Bedrock was the most variable substrate, ranging from 0 to 40 % of bed cover. Boulders tended to be most abundant in high-gradient reaches such as Cuchillo 3 or Jerguerón.

The volume of woody debris larger than 1 cm in diameter (Table 1) was quantified by measuring the length and diameter at both tips of each piece of wood within the channel, as described by Elosegi et al. (1999). There was no wood in Cuchillo E and Salderrey E after the first retention experiment, following removal by Díez et al. (2000). Elsewhere, wood volume ranged from 42 cm^3 m^{-2} to 23,552 cm^3 m^{-2}. Wood was usually most abundant in first-order reaches with mature riparian forests.

For each retention experiment, we calculated discharge (Q) from cross-sectional areas and velocities (General Oceanics flowmeter). In cases of very low discharge, Q was measured as the time necessary to fill a 1-L bottle just under a chute that channelized all water flow.

Retentiveness

We used plastic material to measure retentiveness because it is easy to prepare, store, manipulate and re-use. In a preliminary study, we compared different designs (circles, triangles, and rectangular pieces of plastic sheet, and plastic and fabric leaves of artificial plants), with the behaviour of natural leaves in streams. Based on the results, we decided to use yellow 3 × 10 cm flexible plastic strips, as they were easy to retrieve and behaved like alder leaves.

To compare retention of plastic strips with natural leaves, we collected and froze (– 20 °C) abscised eucalyptus (*Eucalyptus globulus*), chestnut (*Castanea sativa* Miller), alder (*Alnus glutinosa* Gaertner), oak (*Quercus robur* L.), hazel (*Corylus avellana* L.), beech (*Fagus sylvatica* L.), and sycamore (*Platanus hybrida* Brot) leaves. Two days before the experiment, we marked each leaf with a red line along each side, and soaked all leaves in water for 12 hours to standardise initial conditions (Speaker et al., 1984). We then simultaneously released 800 plastic strips, 170 leaves of *Eucalyptus*, 200 each of chestnut, alder, oak and hazel, 300 of beech, and 50 of sycamore in a 3rd-order reach (Agüera 7). Three hours after release, we located each strip and leaf and measured the distance travelled. We measured the area (LI-COR Portable Area Meter, LI-3000A), perimeter (curvimeter) and dry mass (3 days, 80 °C) of 50 additional leaves of each species to assess their influence on travel distance.

We measured retention at 21 selected reaches. To test the effect of discharge on retentiveness, we repeated the plastic strip experiments 3–5 times under different hydrological conditions within each reach from September 1997 to August 1998. Reaches in the same tributary were analysed simultaneously to contrast their behaviour under similar hydrological conditions. On each occasion, we released 400 strips in 1st-order reaches, 800 in 2nd-order, and 1200 in 3rd-order reaches individually in the middle of the channel at the upstream end of each reach. A gill net was placed at the downstream end of each reach to collect all strips that crossed the whole reach. Three hours after release we located each strip, measured the distance travelled, and identified the retaining structure (Speaker et al., 1984). For each strip, we noted the hydraulic feature (either riffle, pool, chute, or stream margin), and the substrate type (sand, gravel, etc.) that characterized its location. As strips could not have travelled further than the gill nets, strips not recovered were lost in the experimental reaches. Therefore, we assumed their distribution was similar to that of strips recovered, and the number of strips recovered was used for calculations. At extremely low discharges we released fewer strips to avoid clogging the stream; at very high discharges and at periods of high turbidity no experiment could be carried out.

We fitted the retention dynamics to a negative exponential model (Young et al., 1978):

$$T_d = T_0\, e^{-k\,d}$$

where T_d is the number of strips that travelled distance d (m), T_0 is the number of strips recovered, and k is the per metre retention rate, which is independent of the reach length or the number of strips released. The average distance travelled was calculated as 1/k (Newbold et al., 1981). The relative retention efficiency of each type of structure was calculated as the ratio of the percentage of strips trapped to the percentage of the streambed covered by that structure (Snaddon et al., 1992). The relative retention efficiency of wood could only be measured in Cuchillo C and Salderrey C, reaches where the areal cover of all woody debris had been measured for a separate project (Díez et al., 2000). The transect method used in this study was unreliable for assessing the cover of a substrate that occurred infrequently.

Results

Comparison of retention among materials

For all materials tested, transport was described by a negative exponential model (linear regression on log transformed data, $p < 0.05$). Retention was highest for alder leaves (average distance = 11.2 m), followed by plastic strips, oak, beech, chestnut, eucalyptus, hazel, and sycamore (average distance = 50 m). Tukey's test showed significant differences between some species ($p < 0.05$) (Table 2). Sycamore leaves were the largest, widest and heaviest, beech the smallest and lightest, and eucalyptus the narrowest (Table 3). Correlation showed a weak non-significant trend for materials to travel further as their surface, length, width, perimeter, or dry weight increased.

Channel retentiveness

Baseflow experiments showed the retentiveness of all reaches under similar hydrological conditions (Table 4). In Jerguerón, all strips were retained in the first metre, and thus the average travel distance was assessed as 0 m. Retentiveness was highest in 1st-order reaches (average travel distance = 3.6 m), where the majority of strips were often retained by the first obstacle encountered, resulting in average distances shorter than 2 m in Jerguerón, Baulajaia, Cabrerizas, Laiseca 1 and 2, and Perea 1 and 2. The least retentive 1st-order reach was Salderrey E, where strips travelled an average of 8.5 m. Travel distance for 2nd-order reaches averaged 9.0 m, and ranged from 3.4 m to 20.4 m. For 3rd-order reaches, it averaged 16.6 m, and ranged from 9.5 m to 23.8 m. At low flows, travel distance across all streams was positively correlated with discharge ($r^2 = 0.51$; $p < 0.001$), and negatively correlated with channel gradient ($r^2 = 0.41$; $p < 0.01$) and the percentage of the channel covered by bedrock ($r^2 = 0.28$; $p < 0.05$). A weak positive correlation was found between travel distance and channel width ($r^2 = 0.20$; $p < 0.05$). The remaining variables in Table 1 were not significantly correlated with baseflow travel distance.

In most reaches, retentiveness varied with discharge, showing a general inverse relationship (Fig. 2). Average

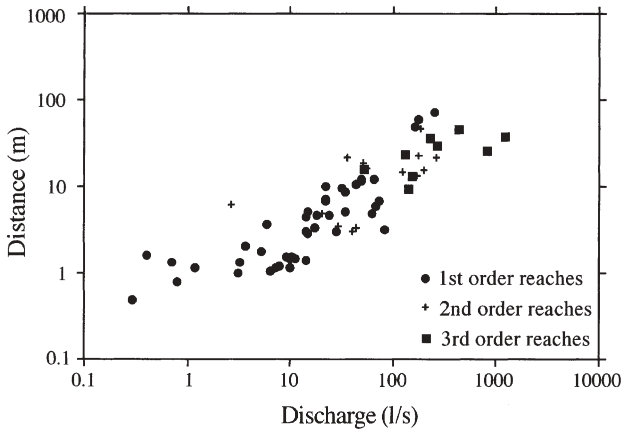

Figure 2. Changes in average travel distance of strips as discharge varied at the study reaches.

Table 2. Retention rates of different leaf species in the reach Agüera 7 during base flow. Rec = percentage of leaves recovered; D = average travel distance. Vertical lines indicate no significant differences (Tukey's test).

Leaf species	Rec (%)	D (m)
Alder	79.0	11.2
Plastic strips	94.0	13.3 |
Oak	86.0	13.9 |
Beech	75.3	22.2 |
Chestnut	89.0	24.4 |
Eucalyptus	92.4	29.4 |
Hazel	81.0	33.3 |
Sycamore	74.0	50.0

Table 4. Retentiveness of the study reaches at baseflow. Q = discharge; Rec = percentage of strips recovered; D = average travel distance.

Reach	Reach order	Q (l/s)	Rec (%)	D (m)
Jerguerón	1	0.1	100.0	0.0
Laiseca 1	1	0.4	100.0	1.6
Laiseca 2	1	0.7	100.0	1.3
Baulajaia	1	0.7	99.0	1.3
Perea 1	1	5.3	92.8	1.8
Peñalba	1	5.9	89.8	3.6
Perea 2	1	7.3	93.8	1.1
Cabrerizas	1	11.4	94.8	1.5
Antonilla	1	18.3	96.8	4.6
Cuchillo C	1	21.7	87.5	6.8
Cuchillo E	1	21.7	83.0	7.1
Salderrey C	1	34.3	81.3	5.0
Salderrey E	1	34.3	81.3	8.5
Adino	2	2.8	95.5	5.8
Remendón 1	2	21.5	94.1	4.6
Remendón 2	2	30.7	94.5	3.4
Agüera 2	2	37.7	90.0	20.4
Cuchillo 3	2	48.1	79.5	10.6
Agüera 5	3	52.0	94.3	16.4
Agüera 7	3	127.6	88.2	23.8
Agüera 9	3	137.6	95.3	9.5

Table 3. Average size of leaves (± SE, n = 50) from common tree species found along the Agüera stream. Max. length = maximum length; Max. width = maximum width.

Leaf species	Max. length (cm)	Max. width (cm)	Area (cm^2)	Perimeter (cm)	Dry weight (mg)
Beech	8.3 (0.2)	4.1 (0.2)	23.3 (0.8)	17.3 (0.3)	120 (12)
Alder	10.0 (0.3)	5.5 (0.1)	27.6 (1.1)	18.7 (0.4)	232 (22)
Strips	10.0 (0.0)	3.0 (0.0)	30.0 (0.0)	26.0 (0.0)	809 (6)
Hazel	10.6 (0.2)	7.8 (0.2)	52.3 (2.1)	27.2 (0.6)	267 (20)
Oak	12.8 (0.4)	4.7 (0.3)	38.1 (2.3)	30.1 (1.1)	242 (16)
Chestnut	18.1 (0.5)	6.5 (0.2)	68.5 (3.2)	40.0 (1.1)	481 (33)
Sycamore	18.6 (0.4)	17.5 (0.5)	152.5 (7.3)	74.1 (2.5)	1562 (94)
Eucalyptus	22.5 (0.7)	2.7 (0.1)	38.6 (1.9)	40.7 (1.2)	954 (56)

Table 5. Average percentage of strips retained by different hydraulic features and substrate structures, and relative retention efficiency of substrate structures at the lowest and highest discharge levels studied (average ± SE). Missing values correspond to features and structures whose areal cover was not measured.

	Percentage retained		Retention efficiency	
	Baseflow	High flow	Baseflow	High flow
Hydraulic feature				
Riffles	49.9 ± 6.3	79.8 ± 5.3		
Pools	47.9 ± 6.5	18.5 ± 5.3		
Chutes	0.2 ± 0.6	0.0 ± 0.0		
Margin	2.0 ± 4.3	1.8 ± 0.7		
Substrate structure				
Sand	0.4 ± 0.2	1.1 ± 0.5	0.083 ± 0.042	0.309 ± 0.176
Gravel	6.0 ± 2.1	16.0 ± 4.3	0.227 ± 0.057	0.781 ± 0.236
Cobbles	52.6 ± 5.7	35.2 ± 4.3	2.687 ± 0.407	1.552 ± 1.64
Boulders	24.0 ± 4.2	30.2 ± 18.9	0.967 ± 0.196	1.143 ± 0.164
Bedrock	9.1 ± 5.3	1.6 ± 0.8	0.554 ± 0.386	0.061 ± 0.028
Woody debris	5.8 ± 9.1	13.4 ± 3.0		
Live branches	1.5 ± 4.4	0.2 ± 0.1		
Roots	0.5 ± 0.9	1.7 ± 0.7		

travel distance during high flow was 18.3 m for 1st-order reaches, 20.7 for 2nd-order, and 32.9 for 3rd-order ones, thus reducing the differences between reaches. Using the pooled data, the correlation between discharge and average travel distance was highly significant ($r^2 = 0.342$, $p < 0.0001$). In all tributaries, except Remendón, the upstream reaches were more retentive than the downstream ones.

Retentive structures

The percentage of strips retained in riffles and pools was similar at baseflow (Table 5), but riffles retained far more strips than pools at high discharge. Chutes and stream margins retained very few strips at all discharges. Among substrate types, cobbles and boulders retained the most strips. Retention by wood increased at high discharge levels, reaching 13 %, whereas that of bedrock decreased markedly. Similarly, high flows resulted in increased retention by boulders and gravel, and decreased retention by cobbles. Sand, live branches, and roots retained few strips.

The data for percentage of strips retained must, however, be analysed with caution since the frequency of each feature or substrate type was highly site-dependent. Therefore, we calculated the relative retention efficiency of substrate types whose areal cover was known for all sites. At baseflows, cobbles were the most efficient structure, retaining 2.7 times greater proportion of strips than their relative areal cover might predict (Table 5). Boulder efficiency was a little less than 1 at base flow, and the other inorganic substrate types (especially sand) showed even lower efficiencies. At high discharges, cobble and bedrock retention efficiency decreased, and that of sand, gravel, and boulders increased slightly. The correlation between the retention efficiency of each inorganic substrate type and discharge was not significant for most reaches. Exceptions included a positive correlation with sand efficiency in Antonilla and Jerguerón, and with gravel in Agüera 7. Correlations were not significant when all data were pooled.

In Salderrey C and Cuchillo C, the areal cover of wood was known, and thus we calculated its retention efficiency (Fig. 3). In Salderrey C, the efficiency of cobbles was higher than that of wood, although they changed slightly with discharge. In contrast, in Cuchillo C, retention efficiency of wood at low flows was similar to that of cobbles, but cobble efficiency decreased and wood efficiency increased (values > 8) as discharge increased. All other substrate types had efficiencies < 1, indicating that they retained a smaller proportion of strips relative to their areal cover. Sand and bedrock were the most inefficient retention features in both reaches.

Discussion

The plastic strips used in the present study had a retention coefficient between those of alder and oak, the two main species in the headwaters of the Agüera basin (Pozo et al., 1997 b), and therefore were appropriate to estimate litter retention. Young et al. (1978), Prochazka et al. (1991), and Canhoto and Graça (1998) suggested that leaf form, size, or flexibility should explain inter-species differences in retention. However, we did not observe a significant relationship among leaf types and respective leaf

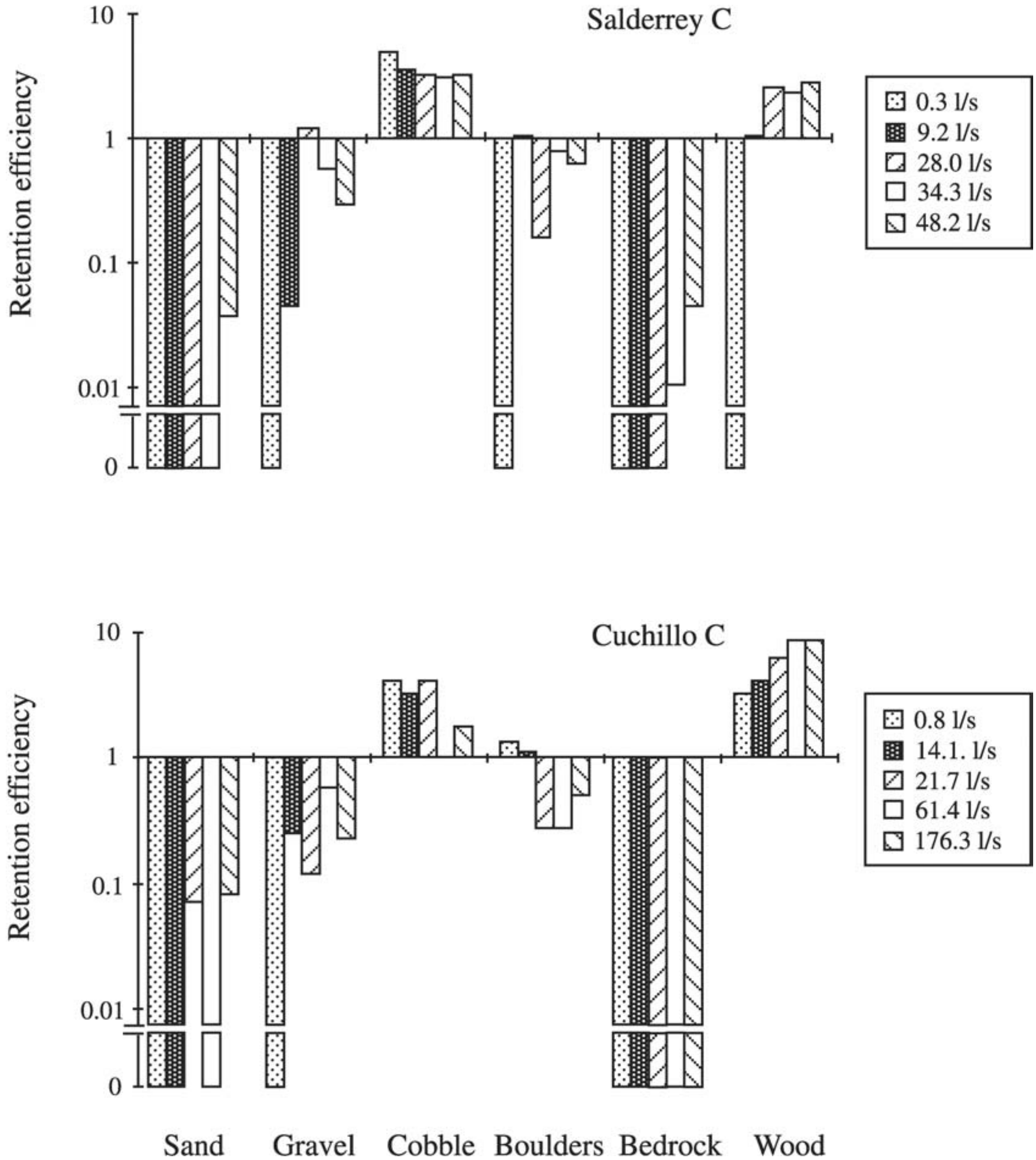

Figure 3. Relative retention efficiency (% of strips trapped/% of streambed covered) of inorganic substrate structures and wood at different discharges at Cuchillo C and Salderrey C. Logaritmic scale was used to show simetry of efficiency values. A relative retention efficiency of 1 indicates that a kind of substrate retains a fraction of the strips equal to the area of streambed it covers.

features measured in this study. Prochazka et al. (1991) suggested that flexible leaves are retained more readily, as they tend to wrap around stones. We did not measure flexibility, but oak leaves, which were most rigid, were among the most retained and hazel leaves, apparently the most flexible, were least retained. Similarly, sycamore leaves, which are large, irregular, and similar in shape to the highly retained maple leaves reported by Young et al. (1978), had the lowest retention. Clearly, more research is needed on this aspect, but it appears that differences in leaf morphology do not explain the results in the Agüera. Whatever the reasons for inter-specific differences, this experiment clearly shows that caution is necessary to compare results from different studies, as the material selected can greatly affect retention distances (also see Mathooko et al., 2001). Unfortunately, as our results showed no clear relationship between leaf morphology and retention, we can give no clues as how to standardise travel distances measured with different materials in the different studies.

Although differences in methods preclude clear-cut comparisons, the Agüera stream channels seem nevertheless highly retentive. Retentiveness in 1st-order streams in the Agüera was higher than in the Window stream, a

1st-order stream in South Africa (Prochazka et al., 1991), and similar to values reported by Jones and Smock (1991) in low-gradient streams. Furthermore, our 3rd-order reaches seemed to have higher retentiveness than Juday Creek, Indiana (Ehrman and Lamberti, 1992) or Deer Creek, Oregon (Speaker et al., 1988). Because discharge, width and gradient were similar in each of these 3rd-order streams, the observed differences seem to be related to the type of substrate: cobbles and boulders were dominant in the Agüera, versus gravel and sand in Juday Creek and gravel and cobble in Deer Creek. Nevertheless, as stated above, the materials selected in each study could affect travel distances, thus it is not possible to give comparable estimates of retentiveness.

At baseflow, there was a positive correlation between distance and discharge and width in the Agüera stream, confirming that small streams are more retentive than large ones (Wallace et al., 1995). Even the unexpected negative correlations between travel distance and gradient and bedrock abundance should be interpreted as an effect of stream size, as the small headwater streams tended to be steeper and flowed over extensive bedrock areas. Small steep streams have many shallow and narrow points, where at low discharge most leaves are retained. A stepwise regression model did not improve the information given by simple correlations. Although we did not measure stream depth, Webster et al. (1994) and Raikow et al. (1995) found it to be an important factor controlling retention. The importance of depth and width may explain why at the Agüera stream and elsewhere (e.g., Snaddon et al., 1992; Raikow et al., 1995), stream retentiveness is reduced in periods of high discharge. High flows result in greater depth and current velocity, thus increasing the distance travelled by particles before being retained by benthic structures (Cushing et al., 1993).

Channel retentiveness tends to increase with substrate roughness (Speaker et al., 1984; Lamberti et al., 1989; Mathooko et al., 2001; Oelbermann and Gordon, 2001). In the Agüera, cobbles had high retention efficiency at low flows. At higher discharges, cobbles and boulders were the most retentive inorganic substrata. Although the relationship between areal cover of substrate type and travel distance of leaves is complex, coarse materials like cobbles and boulders increase bottom roughness and thus promote retentiveness.

Several authors (Triska and Cromack, 1980; Winkler, 1991; Bretschko and Moser, 1993) reported that wood retained most of the leaf litter in headwater streams. In the Agüera, 6% of the strips were retained by wood at low discharge, and 13% at high discharge. These are relatively low values, probably because of the generally low amount of wood in the Agüera (Díez et al., 2001). Speaker et al. (1984) calculated the trapping efficiency of sticks to be one or two orders of magnitude greater than that of inorganic structures. Although differences among substrate types were not so marked in the Agüera, wood was one of the most efficient structures in the reaches where it was measured. In general, the percentage of strips retained by wood increased at high discharges, thus illustrating the potentially important role of wood in the retention of organic matter at high flows. For instance, the differences in the abundance of wood (much greater in Cuchillo C) could explain the differences in retention between Salderrey C and Cuchillo C.

Retention of leaf material is influenced by many factors (discharge, stream size, velocity, depth, substrate type, amount of wood), resulting in considerable interstream variability. Therefore, it is difficult to explain retention capacity using a single or even a few reach variables. In the Agüera stream, Pozo et al. (1997b) reported greater leaf-litter inputs in headwater streams adjacent to deciduous forests than in those surrounded by eucalyptus plantations. Nevertheless, these differences were not reflected in benthic storage of CPOM because peak inputs occurred at different times. Inputs from deciduous forests are highest in autumn when prevailing high discharges tend to transport litter downstream, whereas litter inputs from eucalyptus forests are highest in summer (Bunn, 1988; Campbell et al., 1992; Pozo et al., 1997b), a period of low flow and litter accumulation. Therefore, CPOM storage depends not only on channel characteristics and litter inputs, but also on timing of inputs relative to the hydrological regime.

Retentiveness is an important characteristic of streams that can influence the efficiency litter use by the fluvial community (Pozo et al., 1997a). However, it appears to have been greatly reduced by past management practices (Petersen and Petersen, 1991; Shields et al., 1998), and thus management policies that increase litter retentiveness should be encouraged. Particular care should be taken to conserve mature riparian forests in less retentive reaches, as these are primary sources of woody debris (Díez et al., 2001); a structure whose effect on leaf retention seems important at high flows when most litter is mobilised.

Acknowledgments

This research was supported by the General Bureau of Scientific and Technical Research, Central Government, Madrid (project DGICYT, PB 95-0498) and by the University of the Basque Country (project UPV 118.310-EC 232/97). J.R. Díez was supported by a grant from the Department of Education and Culture of the Central Government. We are very grateful to Terry Langford for checking the English.

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