

# THE MACROINVERTEBRATE COLONIZATION OF LEAF BAGS: IS THERE A PATTERN?

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## SUMMARY

There have been many studies of litter decomposition and the macroinvertebrates associated with litter. Nevertheless, the reasons why invertebrates colonize leaf bags are still a matter for discussion. Although invertebrates use leaves as food, it has been shown that they may use the leaf bags as a substrate. In this study, we investigate whether macroinvertebrates colonize leaf bags despite abundant natural leaf litter in the streams and whether they discriminate between leaves occurring naturally in the streams (*Alnus glutinosa*) and alien species (in this case, the South American *Hura crepitans*).

We found no differences in the relative abundance of shredders between *Alnus* and *Hura* leaf bags. In relation to the relative abundance of shredders in the leaf bags and in the streambed, we found all the possible combinations. In two streams there were no differences between the benthic samples and the leaf bags. In another stream, the relative abundance of shredders was higher in the benthic samples, and in a further stream, the relative abundance of shredders was higher in the leaf bags.

It seems therefore, that when there is an abundant supply of high quality food in the streams, there is no reason for the aggregation of shredders in the leaf bags.

## INTRODUCTION

Comparison of invertebrate colonization and breakdown rates between different leaf species is an essential procedure to obtain information about three relevant aspects: a) the preference of invertebrate taxa for a specific type of litter, b) the energetic supply to the aquatic community through the leaf-processing continuum, and c) the nutritional quality of allochthonous detritus. This approach has already been used in the Iberian stream systems (e.g., IMBERT & POZO, 1989; ESCUDERO *et al.*, 1991). The same methodology has also been applied in this geographical region to assess the ecological implications of extensive afforestations with the exotic species *Eucalyptus globulus*. Comparison of processing rates, colonization and consumption of eucalyptus and alder (*Alnus glutinosa*), one of the most common riparian species in northern low-order streams, may allow predictions on the impact of eucalyptus afforestations on the energetic budget of streams (POZO, 1993; BASAGUREN & POZO, 1994; CORTES *et al.*, 1994; CANHOTO & GRAÇA, 1995).

The difference in texture and litter quality between alder and

eucalyptus makes very predictable the distinction in decay rates, and also in the structure and composition of the invertebrate assemblages colonizing these leaves. A subject poorly investigated is the potential impact of an exotic species similar in leaf chemistry and decay rates to the natural occurring one.

The colonization of natural and artificial leaf packs by macroinvertebrates in streams has been a matter of extensive discussion (BUNN, 1988; DOBSON, 1991; BASAGUREN & POZO, 1994; MALMQVIST & OBERLE, 1995). Some authors suggest that, by colonizing artificial leaf packs, invertebrates seek an additional food source (e.g., ROWE *et al.*, 1996). Many of these studies focus only on the proportion of shredders present in the leaf packs, without reference to the stream invertebrates (but see MALMQVIST & OBERLE, 1995).

The objectives of the present study were: (1) to compare the dynamics of invertebrate colonization on *Hura crepitans*, a South American species not occurring in Europe, with the European *Alnus glutinosa*, and (2) to compare invertebrates in leaf bags with invertebrates sampled in the stream benthos.

Since in headwaters leaf processing can be highly dependent on stream typology (HORTON & BROWN, 1991; POZO,

1993; CORTES *et al.*, 1995), and even on stream patches (CASAS, 1996), this investigation was carried out simultaneously in four similar low-order streams.

## STUDY SITES

The study was carried out during autumn 1995 in 4 low-order streams (Tanha, Maíla, Azibais and Olo) located in the mountains of Vila Real, North Portugal (Douro watershed). The streams flow through woodlands of pine afforestations (*Pinus pinaster*) and natural oak stands (*Quercus pyrenaica*). Riparian vegetation was a relatively intact corridor of alder (*Alnus glutinosa*). The study area in each stream had relatively similar morphometry, substrate and water chemistry. Large boulders and cobbles with underlain gravel made the streambeds moderately retentive. Riffle areas dominated over shallow pools. In general, the water of the streams was poorly acidic and oligotrophic, although rivers Tanha and Maíla presented higher ion concentrations, probably as a consequence of short-scale agricultural practices (table 1).

## MATERIAL AND METHODS

Senescent leaves of *Alnus glutinosa* and *Hura crepitans* were collected just after abscission. Initial concentrations of nitrogen and phosphorus (mean  $\pm$  SD) for *Alnus* were respectively  $2.15 \pm 0.12$  and  $0.12 \pm 0.02$  ( $n = 6$ ), and for *Hura* were  $1.36 \pm 0.04$  and  $0.23 \pm 0.02$  ( $n = 5$ ). Groups of air-dried leaves were weighed ( $3 \pm 0.05$  g) and placed in 5 mm mesh plastic bags. Each bag was closed and tied to iron rod deeply introduced into the streambed. Three bags of *Alnus* and two of *Hura* were randomly retrieved after 1, 28 and 56 days.

Benthic invertebrates were sampled on days 0, 28 and 56 using a hand-net (qualitative sampling). Samples were taken along 4 transects, in order to represent the dominant habitats.

Due to the high current velocity and frequent flooding events, some of the bags were lost during the experiment, and sampling of the stream bottom was not possible in stream 4 on day 28.

Invertebrates removed from the leaf bags and collected in the stream bottom were identified to the lowest possible taxonomic level, counted and classified into 5 functional feeding groups: shredders, gathering-collectors, filtering-collectors, scrapers and predators (MERRITT & CUMMINS, 1996; TACHET *et al.*, 1987).

Because the number of individuals sampled in the streambed is not comparable to the number of individuals present in the leaf bags, data were transformed to species presence/absence. The Jaccard coefficient was used to determine similarity between samples and the resulting matrix was analyzed by cluster analysis (UPGMA). In order to compare the relative abundance of species, the Bray-Curtis coefficient was applied to a matrix of relative proportions (percentage similarity coefficient), and the resulting matrix analyzed as previously (BOESCH, 1977).

Statistical comparisons between the proportion of shredders present in the leaf bag and sampled in the streambed, and between the two leaf types were carried out by ANOVA (Zar, 1996).

## RESULTS

In streams Tanha and Olo there was no difference between the proportion of shredders present in the leaf bags and in the stream ( $F < 135$ ,  $p > 0.05$ ). In streams Maíla and Azibais, the proportion of shredders present in the leaf bags and in the stream was significantly different ( $F > 38$ ,  $p < 0.05$ ). However, in stream Maíla the relative abundance of shredders was higher in the benthic samples while in stream Azibais, the relative abundance of shredders was higher in the leaf bags (fig. 1). There was no statistical difference between the two leaf species in any of the streams ( $F < 135$ ,  $p > 0.05$ ).

Table 1. Physico-chemical characteristics of the stream water. Values are means with ranges in parentheses.

	Tanha	Maíla	Azibais	Olo
pH	6.8 (5.9 - 7.1)	6.7 (6.4 - 6.9)	6.3 (6.1 - 6.7)	5.5 (5.1 - 5.9)
Dissolved oxygen (%)	100 (92 - 107)	97 (92 - 106)	98 (91 - 112)	101 (94 - 115)
Temperature (°C)	9.6 (7.8 - 11.2)	10.2 (9.1 - 11.8)	9.7 (8.8 - 10.5)	7.8 (7.1 - 8.8)
Conductivity ( $\mu\text{S cm}^{-1}$ )	62 (44 - 72)	72 (58 - 83)	31 (30 - 32)	12 (11 - 13)
Nitrates ( $\text{mg l}^{-1}$ )	4.2 (2.7 - 5.9)	4.6 (4.1 - 5.4)	2.1 (1.8 - 2.4)	0.2 (0.1 - 0.4)
Ammonia ( $\text{mg l}^{-1}$ )	0.02 (0 - 0.10)	0.03 (0 - 0.10)	0.02 (0 - 0.09)	0.01 (0 - 0.03)
Phosphorus ( $\text{mg l}^{-1}$ )	0.02 (0 - 0.02)	0.01 (0 - 0.03)	0.01 (0 - 0.01)	0.01 (0 - 0.02)
Current velocity ( $\text{m s}^{-1}$ )	0.34 (0.08 - 0.74)	0.21 (0.07 - 0.49)	0.37 (0.07 - 2.06)	0.86 (0.06 - 3.26)
Discharge ( $\text{m}^3 \text{s}^{-1}$ )	0.96 (0.21 - 2.05)	0.39 (0.12 - 0.72)	0.93 (0.17 - 2.75)	0.86 (0.15 - 1.22)

Cluster analysis based on the Jaccard coefficient revealed 4 main groups (fig. 2). Samples from stream Azibais, excluding the benthic and the *Alnus* samples from day 56, and the *Hura* samples from day 28, form group 1. Group 3 is formed by benthic samples from day 56 (streams Maíla and Olo) and *Hura* samples from day 1 (streams Tanha and Olo) and from day 28 (stream Maíla). The other groups are a miscellaneous collection of samples. Cluster analysis based on the percentage similarity coefficient revealed 3 main groups (fig. 3). Group 1 is mainly formed by samples from day 28. Group 2 is mainly formed by samples from day 1, while group 3 is a miscellaneous collection of samples.

## DISCUSSION

GAZZERA *et al.* (1991) found that both total number of individuals and shredder biomass were not significantly different in decomposing litter of elm and maple. However, the same was not found in studies comparing processing of alder and eucalyptus in low order streams (BASAGUREN & POZO,

1994; CORTES *et al.*, 1994; CANHOTO & GRAÇA, 1995). This may be due to differences in processing rates, to different nutritional levels and to the content of refractory compounds.

Although no clear pattern arises from the performed cluster analyses, there is a tendency for highest similarity between samples from the same stream (fig. 2), probably meaning that the streams have distinct faunal compositions. Moreover, there seems to be a tendency for the difference between streams to be overcome by the difference between the temporal (sampling day) and the spatial (benthic/leaves) origin of the samples (fig. 3), when the relative percentage of invertebrates is taken into account.

In the present study, the relative percentage of invertebrates colonizing leaf species was similar, irrespective of the geographical origin of the leaves. It is possible that, when the exotic and indigenous species have similar nutritional quality (such as the case of *Alnus* and *Hura*), the differences between taxa colonizing both leaves are minimal. Many benthic taxa are food generalists that modify their diet according to food availability (e.g., HAWKINS, 1986; KING *et al.*, 1987; WARREN, 1995).

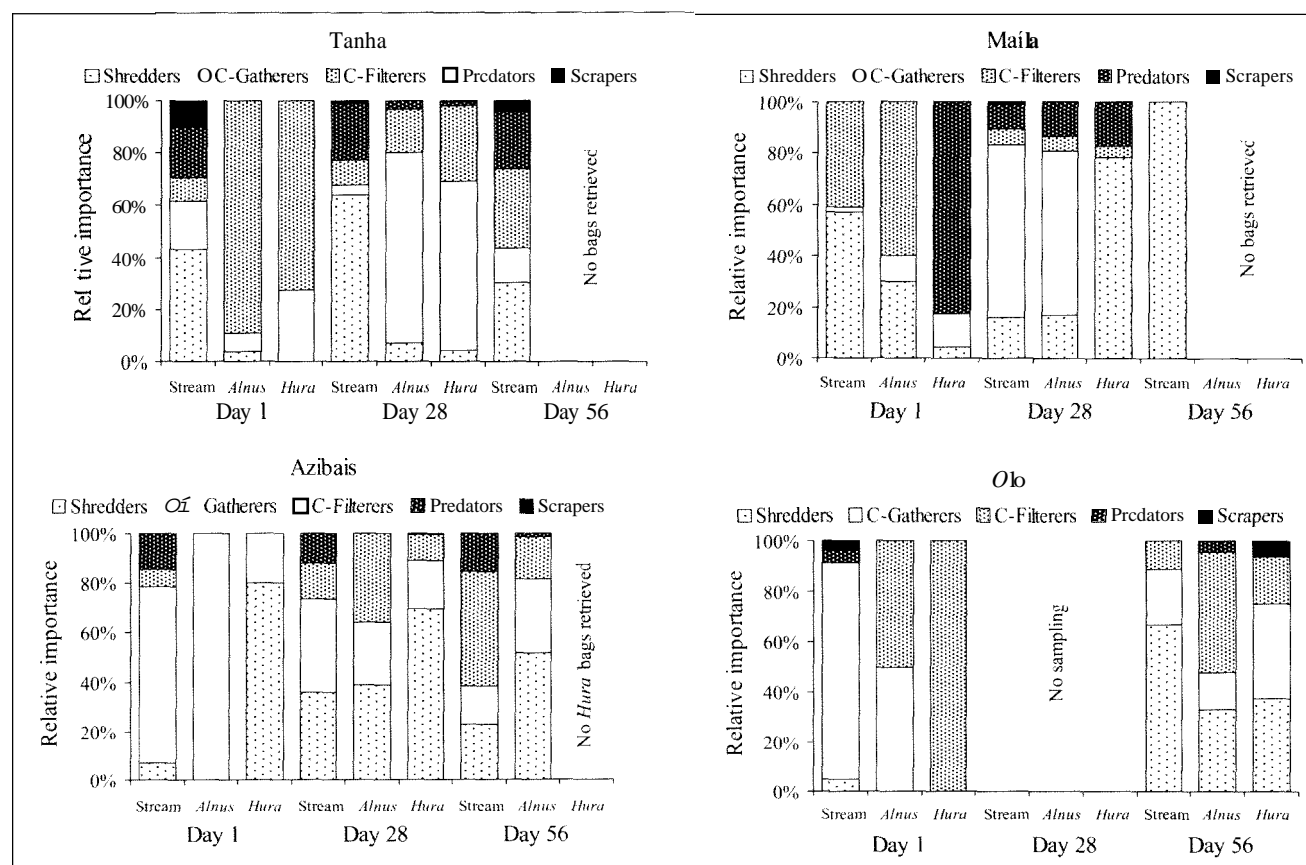


Figure 1. Percentage composition of the five functional feeding groups colonizing decaying *Hura* and *Alnus* leaves and in the stream bottom

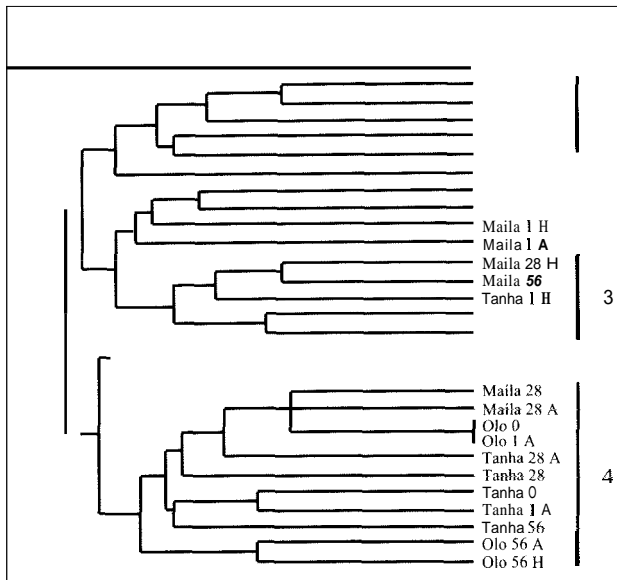


Figure 2. Cluster analysis based on the Jaccard coefficient (presence/absence data). Numbers refer to sampling dates. A and H stand for the leaf species. A date with no letter refers to the benthic samples.

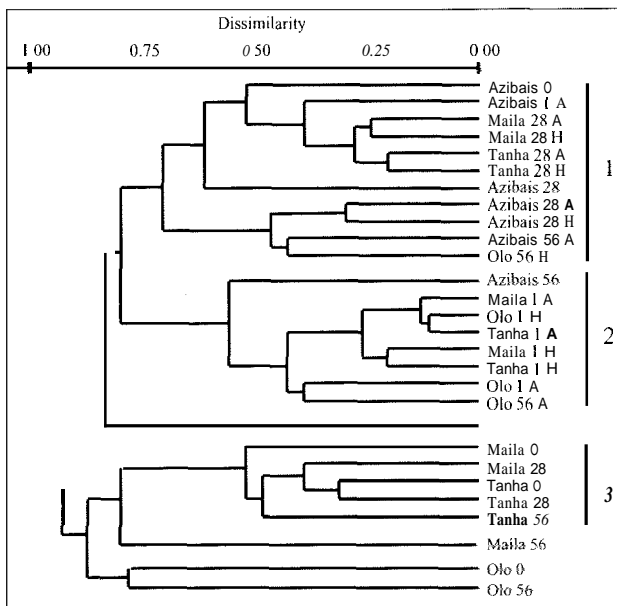


Figure 3. Cluster analysis based on the percentage similarity coefficient. Numbers refer to sampling dates. A and H stand for the leaf species. A date with no letter refers to the benthic samples.

Such generalist resource partitioning is particularly characteristic of taxa with similar mouthpart morphology, especially shredders (MIHUC & MIHUC, 1995).

The question why shredders choose or do not choose the leaf bags when they have an abundant natural supply of leaf litter in

the stream is not a simple one. Many factors can be involved in this choice. When comparing colonization of decomposing pine needles and plastic strips by macroinvertebrates, GRAÇA & PEREIRA (1995) found that the plastic strips were colonized first, although both numbers and biomass of macroinvertebrates became higher in the needles by day 40. However, shredders were no more abundant in the needles than in the plastic strips, suggesting that organic matter accumulations may have had an important role as shelter rather than as a food source in this case. REICE (1977) and DOBSON (1991) also reported that leaf packs provide food, attachment sites and refuge from direct current or extreme discharges.

In our study, shredders were proportionally more abundant in the leaves in just one case. This can be explained by the abundance of organic matter in the streams. Under these circumstances, invertebrates continuously feed and move between resource patches. According to the optimal foraging theory (BEGON *et al.*, 1996), a consumer is expected to remain in a food patch while its profitability is high. Consistent with this theory, GRAÇA (1992) found that the shredders *Asellus aquaticus* and *Gammarus pulex* were more abundant in stream patches with high food quality. The fact that shredders did not move from the stream to the leaf bags suggests that, when our experiment was carried out, food (both quality and quantity) was not a limiting factor in the streams.

In stream Azibais, shredders were more abundant in the leaf bags than in the stream. This may be related to the flooding events and high current velocity, that "cleaned" the streambed of naturally occurring litter. Moreover, the margins of this stream were very steep, which probably seduced the extent of shelter. In such a difficult environment, any additional supply of food and refuge is welcome.

In conclusion, our results suggest that when food availability in streams is high, there is no special reason for macroinvertebrates to aggregate in leaf bags.

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