

# LEAF LITTER DECOMPOSITION IN LARGE RIVERS: THE CASE OF THE RIVER GARONNE

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## SUMMARY

Recent investigations tend to demonstrate that the input of leaf litter from riparian vegetation, and its subsequent decomposition in water, are not only representative of small streams, but also of mid- to large-sized rivers. A review of different studies from the River Garonne (7th-order) points out the main traits of leaf litter decomposition, including the implication of microorganisms and invertebrates as well as the influence of environmental factors. When compared to a 3rd-order mountain stream, the River Garonne exhibited lower decomposition rates of the leaf species considered. Densities and biomass of invertebrates and the proportion of shredders associated with the decomposing leaf litter were higher in the large river. Likewise, microfungi appeared to play an important role in leaf litter decomposition in the River Garonne. Fungal biomass attained peaks of 5-10 % of detrital carbon and accounted on average for 96 % of the total microbial (fungal plus bacterial) biomass in leaf litter. Such a biomass was similar to those reported for leaf litter decomposing in headwaters. Therefore differences in breakdown capacities could not be attributed to differences in either invertebrate community structure or microbial activity. The limitation of abiotic fragmentation could instead be responsible for slower breakdown in the large river, although direct evidence to support the hypothesis is lacking. At a larger scale, the physical heterogeneity of the River Garonne floodplain appears to induce large discrepancies in breakdown rates, like observed both between and within aquatic and terrestrial habitats.

## INTRODUCTION

The importance of terrestrial leaf litter for the functioning of stream ecosystems has been documented by a number of studies over the last four decades (HYNES, 1963; CUMMINS *et al.*, 1989). The River Continuum Concept emphasizes the decreasing importance of leaf litter input as a carbon source for the stream food web as the stream channel gets larger and other sources produced within the stream are made available (VAN-NOTE *et al.*, 1980). It is not surprising, therefore, that the number of studies on leaf litter input to streams is inversely related to the size of the stream, namely the stream order, as shown by reviews of the literature on the subject (WEIGELHOFER & WARINGER, 1994; BENFIELD, 1997; and other references). For example, only five rivers of sixth order or higher are included in these reviews. These large rivers indeed tend to receive lower amounts of litterfall per unit surface area than headwaters, but inputs to large rivers can nevertheless be significant, as has been shown for two 7th-order rivers. The River McKenzie (Oregon, USA) received an annual leaf input of 218 g m<sup>-2</sup> (calculated from CUMMINS *et al.*, 1983, in WEBSTER & MEYER, 1997), and the direct, aerial, input of litter from the

riparian forest to the River Garonne (S-W France) was estimated to be 42 g m<sup>-2</sup> y<sup>-1</sup> (CHAUVET & JEAN-LOUIS, 1988) which corresponds to almost 10 % of the mean value for small woodland streams (BIRD & KAUSHIK, 1981). Moreover, the litter input to the River Garonne was calculated to exceed by three times the autochthonous production of aquatic macrophytes (CHAUVET, 1994). Like in streams, leaf litter entering a large river is expected to be subject to various abiotic and biotic processes causing its decomposition. However, large rivers and streams can differ in some traits, either related to their riparian leaf species, environment or biota, which are potentially determining for the fate of leaf litter. For instance, some observations suggest that the implication of macroinvertebrates in leaf decomposition tends to be less critical in large rivers than in headwater streams (MATHEWS & KOWALCZEWSKI, 1969; CHERGUI & PATTEE, 1988).

The objective of this paper is to review the studies on leaf litter decomposition conducted in the River Garonne over the last fifteen years, in order to highlight some particularities of the decomposition process when occurring in a large river system. This review doesn't aim to deal with studies on other large rivers. Although limited to the River Garonne and its flood-

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plain, this review however intends to tackle a number of factors which could also be relevant for most large rivers from temperate regions.

## LEAF SPECIES

Large rivers like the River Garonne typically flow in lowland areas while a major proportion of their headwaters is located in mountainous regions. In addition to physical discrepancies between both lotic habitats, this results in differences in the nature of leaf litter inputs originating from the riparian forests developed along these rivers. A shift in litter quality along the river continuum can be observed: softwood species tend to dominate in the riparian forests of large river systems and hardwood species like oaks and beech as well as conifers are generally more abundant along mountainous low-order streams. For instance, the three major species of the alluvial forest of the River Garonne are *Salix alba* L., *Populus nigra* L. and *Alnus glutinosa* Gaertn. (CHAUVET, 1987; CHAUVET & JEAN-LOUIS, 1988) while many mountainous streams of the River Garonne basin are typically influenced by a beech forest. The quality of leaf litter may be illustrated by its C:N ratio which ranges from about 20–40 for softwood species to 60 or more for hardwood species and conifers (fig. 1). Since decomposition rates have been demonstrated to be negatively related to the ini-

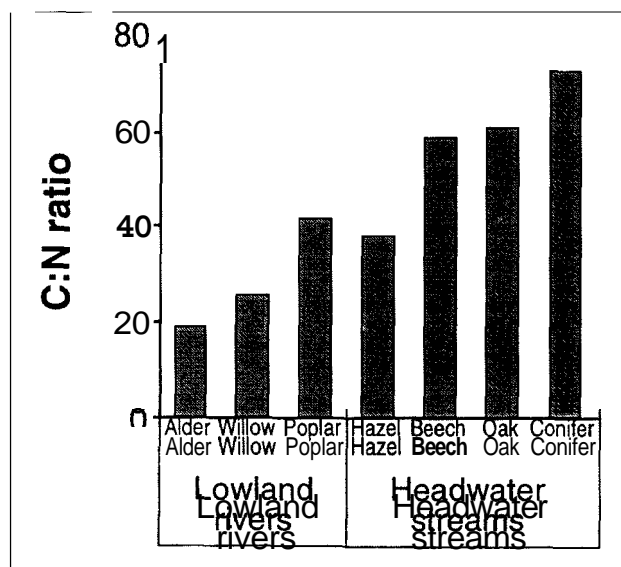


Figure 1. Initial C:N ratio of leaf litter of different tree species: alder (*Alnus glutinosa* Gaertn.), willow (*Salix Alba* L.), poplar (*Populus gr. nigra*), hazel (*Corylus avellana* L.), beech (*Fagus sylvatica* L.), oak (several sp. of *Quercus*), conifer (several sp.). Average values from CHAUVET (1987), GESSNER & CHAUVET (1994) and other literature sources

tial C:N ratio of leaf litter (TAYLOR *et al.*, 1989), the decomposition of softwood species is expected to be faster than that of the upstream species. Note that decomposition rates have also been shown to be correlated with other factors including lignin content of leaf litter (GESSNER & CHAUVET, 1994), and that rankings of species according to their C:N ratio or their lignin content are about consistent. The combination of these differences in decomposition rates and the contrasting distribution of tree species along the river continuum is probably crucial for the matter and energy budgets when the river functioning is examined at the river network level.

## PHYSICAL HETEROGENEITY OF RIVER SYSTEMS

River corridors are generally bound by transitional areas, or ecotones, between the aquatic and terrestrial ecosystems (NAIMAN & DÉCAMPS, 1990). Current theories (JUNK *et al.*, 1989; SEDELL *et al.*, 1989; THORP & DELONG, 1994) stressed the importance of these zones which, depending on the extent of the river floodplain, may provide a major portion of carbon to the aquatic food web through local autochthonous production and litterfall inputs. In addition to being highly productive and supplying considerable amounts of organic matter to the river system, these areas are influenced by flooding and are subject to substantial spatial and temporal fluctuations in such physical parameters as soil water content and oxygen concentration. A study was conducted on the river margins of the River Garonne to examine the influence of this heterogeneity on the fate of leaf litter during decomposition (CHAUVET, 1988). Willow leaves were exposed on five representative sites along a transect of the River Garonne: fast running water, slow flowing water, standing water, floodable soil and non-floodable soil. A striking result of this study was the strong overlap of the range of decomposition rates from the aquatic and "terrestrial" habitats, although this was partly due to a high variation within both environments (fig. 2). In both habitats, the oxygen level appeared to control the decomposition rate, with the most rapid decomposition occurring when oxygen was not limiting. The river bank which was subject to an 83 d-flooding period exhibited the slowest decomposition. At this site, the pattern of leaf mass loss revealed a marked slowing down as soon as leaf litter was buried by sediment deposits after the spring floods. Such a burial process, leading to a storage of organic matter in river margins, typically occurs in non regulated rivers whose natural flooding processes have been preserved (MAYACK *et al.*, 1989). A consequence of this spatial variability of physical parameters could be a patchy distribution of litter decomposi-

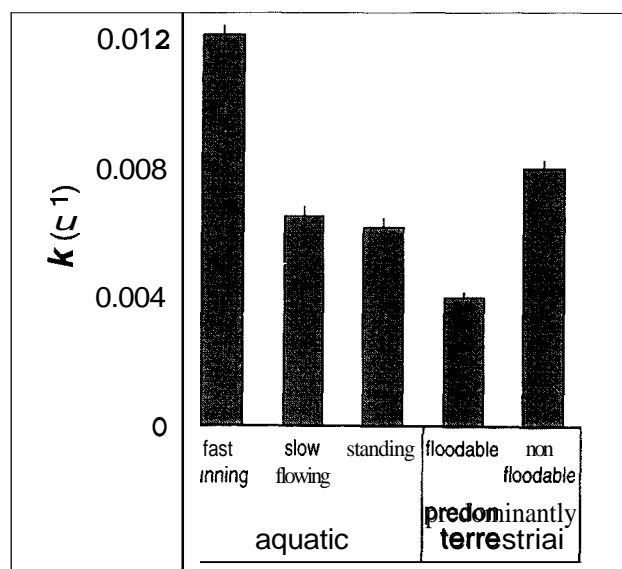


Figure 2. Decomposition rate ( $k$ ) of willow leaf litter in different locations along a transect of the River Garonne + 95% asymptotic confidence limit (from CHAUVET, 1988)

tion patterns and rates within large river floodplains

## ROLE OF INVERTEBRATES

According to current theory, the aquatic invertebrate community changes along the river continuum from one dominated by shredders and collectors in headwaters to one dominated by collectors in high-order reaches (MINSHALL *et al.*, 1983). Due to the implication of shredders in leaf litter decomposition, both decomposition rates and patterns are obviously expected to be affected by such a distribution. In order to document these changes, we compared the decomposition of leaf litter in two contrasting running waters located within the same river network, a 3rd-order mountain stream (The Touyre) and the 7th-order River Garonne (CHAUVET *et al.*, 1993). Beech (*Fagus sylvatica* L.) and willow (*Salix alba*) leaves, i.e. the dominant species indigenous to the Touyre and River Garonne, respectively, were incubated in both streams. The same methods were used for both sites, with 4-g portions of dried leaves being enclosed in mesh bags (4-mm mesh) and submerged in the streams. Both willow and beech decomposed at lower rates in the large river, but within both streams willow decomposed faster than beech and this leaf effect was stronger than the stream effect (fig. 3). Although characterized by slower leaf litter decomposition, the large river exhibited consistently higher total invertebrate densities and biomass associated with the decomposing leaves and a higher proportion of shredders (in

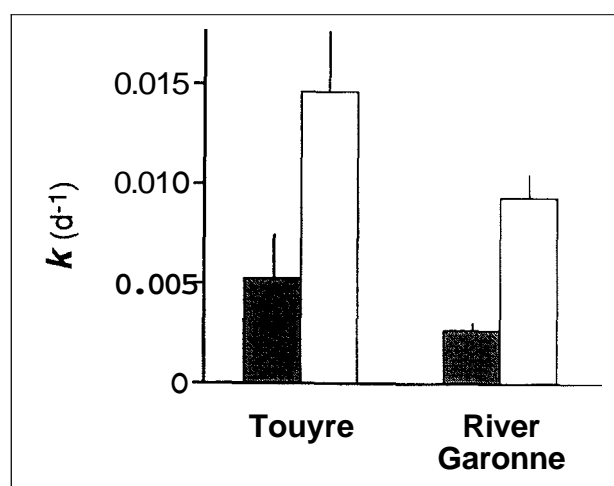


Figure 3. Decomposition rate of beech (■) and willow (□) leaves in a 3rd-order stream and a 7th-order river + 95% asymptotic confidence limit (from CHAUVET *et al.*, 1993).

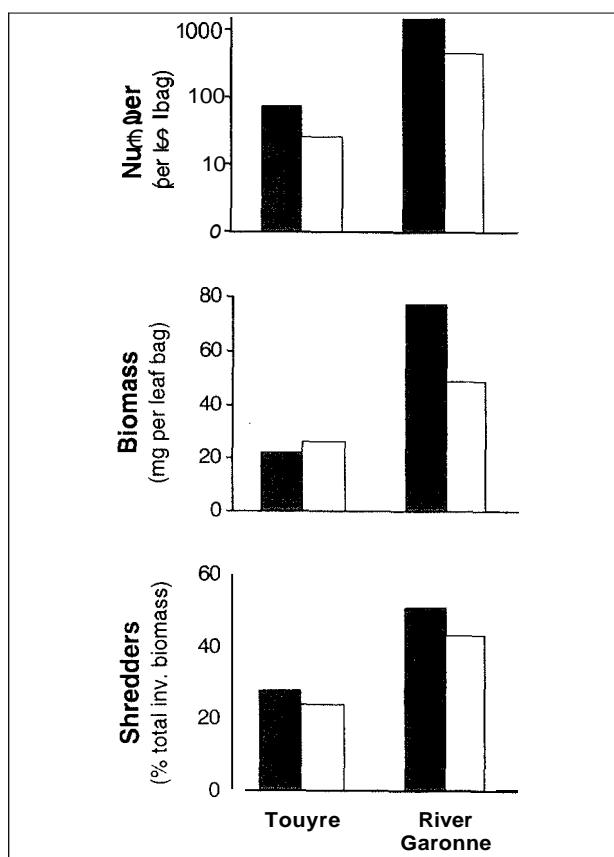


Figure 4. Number and biomass of invertebrates and percentage of shredders in the invertebrate assemblage associated with beech (■) and willow (□) leaves decomposing in a 3rd-order stream and a 7th-order river (average values over 6 months of decomposition; from CHAUVET *et al.* 1993)

terms of biomass) in these assemblages (fig. 4). The high numbers in the River Garonne were mainly due to the extremely numerous oligochaetes, particularly small naidids which feed on FPOM and probably used litter accumulations primarily as an habitat. In terms of biomass, unexpectedly, the major component of the invertebrate assemblages on leaves in the River Garonne were shredders, which represented about 50 % of the average total. The dominant taxa were the crustaceans *Asellus aquaticus* L. and *Gammarus* cf. *pulex* L., a feature also recorded in another large river in Southeastern France, the River Rhône (CHERGUI & PATTEE, 1988). In the 3rd-order stream investigated by CHAUVET *et al.* (1993), the shredders were represented by several plecopteran and trichopteran taxa and accounted for only 30 % of the invertebrate biomass, probably due to a high feeding pressure of invertebrate predators on the shredder community. However, in a similar study conducted in another year with alder leaf litter and only a few hundred meters upstream, shredders largely dominated the invertebrate community (GESSNER & DOBSON, 1993). Note that all these observations only concerned the assemblages on decomposing leaves, and not the whole invertebrate community from the river. While this denotes some possible variation in invertebrate assemblages between years and stretches within the same stream, all this suggests that the occurrence of shredders on leaves decomposing in a large river may be as high than that occurring in a low-order stream, a feature which contrasts with current observations or hypotheses on the distribution of macroinvertebrates along the river continuum. This finding is however consistent with recent theories which emphasize the importance of large particulate organic matter, including riparian leaf litter, in the functioning of large river ecosystems (e.g., THORP &

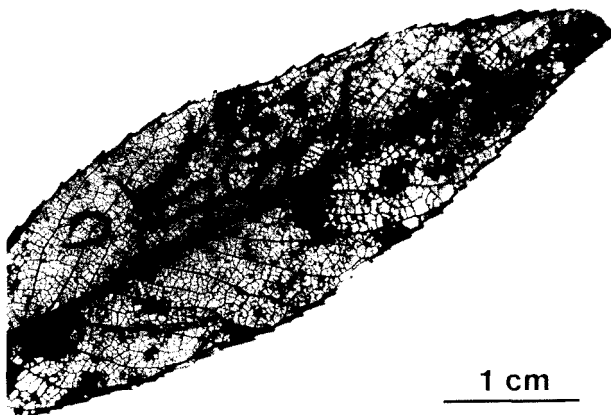


Figure 5. A willow leaf after 5 months of decomposition in the River Garonne. Note the presence of tubificid oligochaetes inside the leaf matrix.

DELONG, 1994). Whether or not this importance of shredders is typical of large rivers with unconstricted channel and extended floodplain, remains unknown; this question deserves further attention.

Another striking trait of the invertebrate assemblages on leaves in the River Garonne was the abundance of tubificid oligochaetes, which during late stages of decomposition represented up to 50 % of the total invertebrate biomass. Tubificids only occurred after 4-5 months of immersion on substantially degraded leaves, i.e. when the leaf epidermis peeled off and the leaf tissue was fragmented into several layers. These worms were regularly encountered even inside the leaf matrix, which suggests that they were feeding on leaf parenchyma cells and the bacteria associated with them (fig. 5). Consequently it was suggested that tubificids may enhance leaf fragmentation by their movement and feeding activity (as shown in a laboratory experiment; CHAUVET, unpublished data), thereby possibly increasing the incorporation of plant organic matter into the river sediment.

## MICROBIAL IMPLICATION

Although supporting a high biomass of shredders, leaf litter decomposed at slower rates in the River Garonne than in the headwater stream, suggesting a lower contribution of other agents, i.e. microorganisms, in the breakdown process or a limitation of abiotic fragmentation. Therefore, we attempted to evaluate directly the microbial biomass associated with three leaf species decomposing in the River Garonne: willow (*Salix alba*), poplar (*Populus nigra*) and plane (*Platanus hybrida* Brot) (BALDY *et al.*, 1995). Bacterial biomass was estimated from cell counts combined with measurements of bacterial cell biovolumes while fungal biomass was determined from leaf ergosterol contents, species-specific conversion factors and the relative abundance of species in the fungal community (GESSNER, 1997). In addition, sporulation rates of aquatic hyphomycetes were determined by short incubations conducted at different decomposition stages. Bacteria reached densities of almost  $10^8$  cells per mg of leaf ash free dry mass (AFDM) after 1-2 months of exposure in the river. Expressed relative to the initial amount of leaf carbon, the bacterial biomass represented a maximum of 0.3-0.5 % of the leaf detritus mass. The mycelial biomass attained peaks of 5 % (plane) to 10 % (poplar) of detrital carbon after 1-2 months, values quite consistent with those reported from leaf litter decomposing in headwaters (GESSNER, 1997). Peak sporulation rates on leaves in the River Garonne were in the range  $1.2-1.4$  conidia  $\mu\text{g}^{-1} \text{d}^{-1}$  with a value for plane leaf litter identical to that determined for the same leaf species in the

headwater of the River Garonne basin (GESSNER & CHAUVET, 1994). Fungi accounted for 88-100% (mean 96%) of the microbial (fungal plus bacterial) biomass in leaf litter decomposing in the large river. Such a dominance of fungal over bacterial biomass has been reported from small stream (FINDLAY & ARSUFFI, 1989; WEYERS & SUBERKROPP, 1996; BALDY & GESSNER, 1997) but was unexpected in large rivers. Given the amount of fungal biomass produced as mycelium and conidia, fungi have been calculated to contribute for about half of the overall carbon loss during periods of highest fungal activity in the River Garonne. Taken together, these results clearly demonstrate a pre-eminent role of fungi in the leaf decomposition process, which does not fundamentally differ from that reported from small streams. The slower decomposition observed in the River Garonne could then not be attributed to a lower microbial activity, but rather to a reduced loss of particles by mechanical breakage. The leaves decomposing in the deep and slow-flowing river were probably not subject to any shear stress while the physical abrasion and erosion may have accounted for a substantial leaf mass loss in the mountain stream, especially at later stages of decomposition and during periods of spate.

Although not the only fungi present, aquatic hyphomycetes appear to dominate the fungal assemblages on leaf litter in the River Garonne (CHAUVET *et al.*, 1986; BALDY, 1996). Species establishment is somewhat similar to that observed in the headwater mountain stream (GESSNER *et al.*, 1993) with early decomposition stages dominated by *Flagellospora curvula* Ingold and the latest stages characterized by *Clavariopsis aquatica* De Wild. Three other species, namely *Anguillospora longissima* (Sacc. et Sidow) Ingold, *Tetracladium marchalianum* De Wild. and *Lunulospora curvula* Ingold, were common colonizers during intermediate and late stages. The two latter species were not, or only very rarely, observed in the mountain stream while some species present there were not found in the River Garonne. This change in species assemblages, possibly due, in part, to different temperature regimes of the two streams (*see* CHAUVET & SUBERKROPP, 1998), constitutes the only major difference between communities developing in both streams.

## CONCLUSION

Leaf litter originated from the riparian vegetation can be an important source of organic matter even for large rivers like the River Garonne. As the riparian forest of such rivers is essentially composed of softwood tree species, decomposition of leaf litter tends to be enhanced when compared to that occurring in

headwater streams mostly influenced by inputs from hardwood and coniferous species. Due to their physical heterogeneity, large river systems are generally subject to a wide range of environmental conditions, inducing variable decomposition dynamics. For example, sediment deposition, a typical phenomenon occurring in large river systems, can slow down decomposition substantially. With regard to the biological activity in leaf decomposition, large rivers do not seem to function differently from low-order streams, since the implication of both microfungi and shredders was found to be similar in a headwater stream. The River Garonne was also characterized by the occurrence of tubificid worms which could enhance leaf fragmentation and the incorporation of organic matter into river sediments.

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