

## THE IMPORTANCE OF ORGANIC DETRITUS IN LOTIC ECOSYSTEMS: ASPECTS OF TROPHIC INTERACTIONS

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### Introduction

Ecological studies on lotic systems pay some lip-service to the importance of the micro-biota and their function within ecosystems, but experience tells me that this dimension is usually ignored in grand research schemes. I hope to make a convincing case for their inclusion in catchment ecosystem research. Others, more expert than I, will plead the importance of photosynthetic micro-organisms. In this short review, "microbiological aspects" cover the processing of organic detritus in lotic waters by heterotrophic micro-organisms.

I do not think it unfair or biased to observe that ecological studies are dominated by zoologists and that the larger or more attractive or more economically important the animal, the more attention it receives. Organisms that cannot readily be seen, sampled or identified can be safely ignored!

When, for example, an energy budget is drawn up for an ecosystem based on organic carbon transfers, the evaluations are based predominantly on ingestion of particulate organic matter by higher trophic levels, and the effects of consumption on population dynamics. But, as Wetzel (1995) has argued, in aquatic ecosystems, population fluxes are not representative of material or energy fluxes. These are dominated by the metabolism of particulate and, especially, dissolved organic detritus from autochthonous (internal) and allochthonous (external) sources. Because of the very large magnitudes and relative chemical recalcitrance of these detrital sources, the slow metabolism of detritus via micro-organisms provides a stability to the ecosystem that dampens the ephemeral, volatile fluctuations of higher trophic levels.

Very little research has been carried out on detrital energetics and pathways in lotic ecosystems. Most investigations have concentrated on the degradation of allochthonous plant litter by fungi, with a glance at heterotrophic bacteria associated with decaying litter.

### **Detritus in lotic waters**

The raw material for organic detritus in lotic waters is: allochthonous plant litter from riparian vegetation in the form of leaves and wood; dead material from aquatic macrophytes and bryophytes; dead algae and phytoplankton; dead zooplankton, other invertebrates and vertebrates; the faeces of living animals. This raw material is chemically complex, and for convenience it may be resolved into dissolved organic matter (DOM) and particulate organic matter (POM). The latter is designated as "coarse" if pieces are greater than 1 mm in diameter, and "fine" if they are less.

I shall describe what is known of the detrition of plant litter in lotic waters, which results from the degradative activities of colonising saprophytic fungi and bacteria, and go on to relate this process to those invertebrates that consume coarse and/or fine particulate detritus, or DOM that aggregates into colloidal exopolymer particles (CEPs). I shall confine myself to studies made in streams and rivers in temperate climatic zones.

All streams receive allochthonous plant litter of some sort. The leaves of deciduous trees provide a maximum pulse during autumn leaf fall. Estimates of annual input to streams in woodland indicate quantities ranging from 300 to 700 g per m<sup>2</sup> (Anderson & Sedell 1979). Of this, ca. 50% is woody debris in deciduous woodland and ca. 70% in coniferous woodland where needle-fall is less seasonal. In moorland and pastureland streams and rivers, litter is mainly in the form of dead grasses. Leaf litter either falls, freshly abscised, into the water, or dries along the riparian zone and is blown or washed into the watercourse.

The first process that occurs in a submerged leaf is abiotic leaching of soluble components: mainly reducing sugars, amino acids, phenolic substances, and nutrients such as nitrogen, phosphorous, sodium and potassium (Iversen 1974; Suberkropp et al. 1976). Leaching is more rapid in dried leaves than in fresh, senescent leaves where the cell walls retain their integrity longer. Most leaching occurs within 24 hours of submersion, accompanied by losses of up to 30% in mass, but it may continue for up to 2 weeks depending on leaf species (Petersen & Cummins 1974). Wood has very little soluble matter and rapid mass loss through leaching has not been observed, although a slow loss of soluble matter is believed to occur during decomposition.

The leachate enters the pool of DOM, which includes surface runoff and subsurface groundwater, and upwelling from the hyporheal zone. The ratio of dissolved organic carbon (DOC) to particulate organic carbon (POC) is between 6:1 and 10:1 (Wetzel 1984). Components of DOM that are labile are readily metabolised by micro-organisms - particularly those in benthic sediments, the hyporheal zone, and biofilms. Biofilms consist of bacteria, algae, fungi, protozoa, micrometazoa, exoenzymes and detritus particles enmeshed in a gelatinous polysaccharide matrix (Hax & Golladay 1993).

They cover solid substrata in streams.

DOM can be converted to fine particulate organic matter (FPOM) by physical flocculation and microbial assimilation, depending on the turbulence, temperature, pH and ionic concentration of the water. This is due to the aggregating nature of the colloidal particles included in DOM, which originate as mucopolysaccharide (exopolymer) exudates from living cells. These CEPs (<1  $\mu\text{m}$  in size) may be free in the water column, attached to each other or to surfaces of bubbles, or bound to each other to form aggregates. CEPs and their adsorbed coatings may be important in the nutrition of animals that capture and ingest them, such as suspension feeders (Wotton 1996).

Refractory compounds, such as aromatic humic substances, are metabolised more slowly, but at least 0.5% is hydrolysed per day (Wetzel 1995). The capacity of micro-organisms to degrade potentially toxic substances in flowing waters is an important feature of the ecosystem that is often overlooked.

The second process that occurs to submerged plant litter is colonisation by micro-organisms during transport or in surface films: cells and spores of bacteria, spores of aquatic fungi, and protozoans (Suberkropp & Klug 1974). Initial colonisers settle on substrata within a day, and dominant fungal species are established within a week or two (Chamier & Dixon 1982a). Although some terrestrial, phylloplane fungi persist for a time on leaves, the main group of aquatic fungi found on submerged litter are the aquatic hyphomycetes (Chamier et al. 1984). They are characterised by their conidia (spores) whose tetra- and sigmoidal forms are readily transported by flowing water, but enable them to take hold on a solid surface. Some 200 species have been described since C. T. Ingold first described them (Ingold 1942).

### **Degradation of leaves by aquatic fungi and bacteria**

The highest concentrations of aquatic hyphomycete conidia in streams are coincident with peaks of leaf litter fall. In the River Exe, Devon, up to 10,000 conidia per litre of water were counted in autumn. Between the end of March and the beginning of August there is a marked decline in the numbers of conidia and species (Iqbal & Webster 1973). The same seasonal pattern was observed in treeless moorland streams, but maximum concentrations were one-tenth those of the River Exe and there were fewer species, some of which are unique to the moorland streams (Iqbal & Webster 1977).

To establish whether aquatic hyphomycetes were merely using the leaf as a holdfast (substratum) and drawing their nutrients from the water, or whether they were active in degrading the leaf (i.e. using it as a substrate), I carried out extensive research into their enzymatic capabilities. Since the soluble components of leaves are lost swiftly by leaching, a colonising fungus would have to degrade leaf cell-wall polymers for its nutrition. The 14 species I

tested varied in their overall capabilities. All secrete an array of pectinases; some elaborate hemi-cellulases and all have some cellulolytic capability (Chamier 1985). A multi-species group of fungi colonising a leaf, as they do, degrades a leaf more quickly and completely than any individual species. Fungal consortia consist of about six dominant and ten occasional species (Chamier & Dixon 1982a,b; Chamier et al. 1984).

The physical effect of pectinase activity is to macerate the leaf tissue by separating cells from each other. Alder leaves are completely macerated by aquatic hyphomycetes in 10 to 12 days at 15°C (Chamier & Dixon 1982b). Alder leaves are skeletonised by microbial activity alone in 10 to 12 weeks in circumneutral streams at winter temperatures (Chamier 1987). The rate at which a particular species of leaf is degraded depends upon its initial lignin content; higher lignin means slower rates of degradation (Gessner & Chauvet 1994). Oak leaves, for example, take more than twice the time of alder to become skeletonised in circumneutral streams (Chamier 1987).

Aquatic hyphomycetes colonise conifer needles slowly and sparsely, partly due to their thick cuticle and epidermis which present a physical barrier to fungal penetration (Michaelides & Kendrick 1978), and partly due to the presence of polyphenolic compounds that depress growth of these fungi (Bairlocher & Oertli 1978).

Bacteria as well as fungi are present on decaying plant litter in flowing waters. Findlay & Arsuffi (1989) analysed the microbial biomass on three leaf species and found that microbial carbon never exceeded 5.2% of the total leaf-detritus complex. Of the total microbial biomass, on oak and elm, fungi accounted for 82 to 96%, and 63% on sycamore. Bacterial populations doubled about once per day. Gessner & Chauvet (1994) have estimated peak fungal biomass as 6 to 15.5% of detrital mass.

Little work has been done on the degradative capacity of bacteria associated with plant litter. But circumstantial evidence suggests that they play an active role. I found that in acid waters (pH 5.5 and below), microbial degradation of leaf litter is markedly lower than in circumneutral waters - in alder, degradation is six times slower and is accompanied by a precipitous decline in leaf calcium content, together with an accumulation of adsorbed aluminium. Counts of viable bacteria on the leaves in acid waters were about one-quarter of those in circumneutral waters (Chamier 1987; Chamier et al. 1989). Thinking that high levels of aluminium on the leaves might progressively depress fungal metabolism, I tested species of aquatic hyphomycetes colonising the leaves, for aluminium toxicity, but found little effect in species originating from acid waters (Chamier & Tipping 1997). Simon & Jones (1992) record that bacterial species which are common on decaying litter in circumneutral streams were absent from the acid streams. I concluded that slower degradation rates, in part at least, could be explained by the absence of degradative species of bacteria in acid waters.

### **Degradation of wood in lotic waters**

Few studies have been made on the decomposition of woody litter in flowing waters compared to leaves. Wood is an important resource because it influences channel morphology, increases habitat diversity, affects transport of other materials by creating debris dams, and serves as a carbon source, site of attachment and shelter for aquatic organisms. Shearer (1992) has done most of the experimental work in this area. Large numbers of aquatic hyphomycete species have been found on wood (Willoughby & Archer 1973) and there is evidence that some species are able to grow on wood, i.e. they have the necessary enzyme complement to use it as a substrate. But fewer species inhabit wood than leaves. Exudates from the bark of some tree species appear to inhibit early fungal colonisation. Removal of the bark results in the establishment of fungal species within a week.

Shearer (1992) investigated the wood-rotting ability of 22 species of aquatic hyphomycetes and found that one group caused extensive weight loss and soft-rot cavities. A second group caused moderate weight loss but no cavities. A third group caused little weight loss and no cavities. Most of the species in the first group have frequently been reported from surveys of submerged wood. But the persistence of woody substrates is of the greatest importance to the lotic ecosystem, because they are decomposed very slowly. Most leaf species are decomposed within a year. Fungi colonising wood have a site for sexual and asexual reproduction throughout the year, which serves as a source for fresh inocula. Of further interest is the finding that a number of aquatic hyphomycete species live as endophytes in the roots of typically riparian trees such as alder (Fisher et al 1991).

### **Relationships between organic detritus and invertebrates**

I have dealt so far with microbially-mediated cycles in the creation and processing of organic detritus in lotic ecosystems. Coupled to these is energy flow, derived from processed detritus, into higher organisms. Of these I shall limit myself to relationships between organic detritus and invertebrates. These animals I shall categorise by the functional feeding groups of Cummins (1994).

Many studies have noted the positive relationship between invertebrate abundance and the distribution of riparian vegetation and plant detritus in flowing waters (Egglisshaw 1964; Hildrew et al. 1980; Gee 1982; Dobson 1991). Recent studies indicate that both shredders and non-shredders are attracted to leaf packs for food rather than for shelter (Richardson 1992; Winterbourn 1978; Dobson et al. 1992). The relationship between the micro-habitats created by leaf packs and the diversity of macro-invertebrate colonisers is discussed by Dobson (1994).

Kaushik & Hynes (1971) noted that detritivores prefer leaves that have been subject to microbial colonisation and "conditioning". They observed that in the

early stages of decay, the nitrogen and/or protein content of such leaves increases, and assumed that the increase was due to microbial biomass developing on the leaves. Consumption of leaf plus microbes would therefore provide a more nutritious diet to an animal than a sterile leaf. Subsequent studies have confirmed this assumption - and have demonstrated further that animals choose to eat leaf patches that are colonised by fungi when these organisms are at the height of their metabolic activity (Arsuffi & Suberkropp 1984).

But not all fungal species are palatable to animals, and some leaf species such as beech and conifer needles are extremely unpalatable (Barlocher & Kendrick 1973a,b; Willoughby & Sutcliffe 1976). However, there is evidence that even unpalatable leaf species can be rendered palatable if they are colonised by a tasty species of fungus (Barlocher & Kendrick 1973a,b). I view these laboratory studies of feeding preferences with some scepticism, having found that at peak fungal colonisation of leaves in a stream there are very few discrete patches of individual species (Chamier et al. 1984), and therefore believe that a mixed mouthful is normally on the menu.

For a variety of invertebrate species, microbially-conditioned leaves have been shown to support better survival rates and promote faster growth than unconditioned leaves (Sinsabaugh et al. 1995; Findlay et al. 1986). These metabolic benefits apply to freshwater shrimps (*Gammarus*), which are important members of the shredder component of streams and rivers where pH is greater than 5.7 (Willoughby & Sutcliffe 1976; Sutcliffe et al. 1981; Barlocher & Kendrick 1973a,b, 1975). I conducted enzymatic studies on two species' of *Gammarus* to try to establish the role of fungi in their nutrition. I found that both species secreted a coupled cellulase system capable of degrading the native cellulose in primary plant cell walls. They also secrete 6-1,3-glucanase and chitinase capable of degrading fungal cell-walls, which would afford gut enzymes access to the cell contents of fungal mycelium. Secretion of cellulases was enhanced on a diet of leaves already partially degraded by fungal enzymes. Gut enzymes of *Gammarus* extracted 30% more reducing sugars from this substrate than from sterile leaves. Furthermore, specific enzyme secretion was enhanced by the presence of exposed, accessible substrates in the diet. Fungal enzymes did not appear to contribute directly to the digestive processes of gammarids (Chamier & Willoughby 1986; Chamier 1991).

For *Gammarus*, the improvement in nutritive value of a leaf partially degraded by fungus is cumulative and made up of a number of relatively small individual components. Unlike many detritivores in flowing waters, notably insect larvae which spend only part of their life cycles in water, *Gammarus* is permanently aquatic. By spring and summer the main foodstuff available is fine detritus in which only the more refractory cell-wall polymers will remain. Fine detritus has considerable nutritive value for gammarids (Sutcliffe et al.

1981); their capacity to degrade cellulose would help to explain this and must be an important feature of their ability to survive through the spring and summer (Chamier 1991). Insect larvae that spend the part of their life cycles in lotic waters when conditioned leaves are abundant, have low cellulolytic capacity compared to gammarids (Monk 1976; Bjarnov 1972; Martin 1987; Sinsabaugh et al. 1985).

Plant material that is finely comminuted by the action of microbial enzymes and/or passage through the guts of animals, enters the pool of FPOM in sediments or on surfaces where it becomes the foodstuff of collectors; or it is incorporated into the gelatinous matrix of biofilms on mineral and organic surfaces which are grazed by scrapers.

## Discussion

I hope I have made it clear that detritus is an important energy source for streams and rivers, and that little of its potential energy is unavailable to the ecosystem. However, actual availability depends on the extent to which it is retained within the system. The retentive capacity of a watercourse is governed by the structure of the channel, the nature of the substratum, flow rate and proneness to spates and disasters. Dobson & Hildrew (1992) manipulated the litter-retention characteristics of four low-order streams and found increased shredder populations associated not only with introduced litter traps, but in the streambed between traps. They concluded that resource limitation may be a decisive factor in controlling populations of invertebrates in low-order streams.

On the practical consequences of the trophic interactions I have discussed, which are based on organic detritus, I offer a few observations. In theory, all other parameters being equal, a watercourse lined with non-coniferous trees and shrubs should support a higher population of invertebrate-eating fish than one with sparse riparian vegetation. The greater the variety of tree and shrub species, the better. These need to be planted close to the bank to ensure that the majority of fallen wood and leaves enters the water, and that the plant roots help to retain the integrity of the bank. Roots also aid the retention of detritus and act as a home for species of aquatic hyphomycetes.

I have heard it argued that shade from riparian trees lowers the diversity of invertebrate species by reducing the number of scrapers. However, a study of invertebrate assemblages in forest and pastureland sites found that total biomass did not vary between sites. Predictably, there were more shredder species at the forest site and more scraper species at the pastureland site. Invertebrate assemblages were related to the stream itself rather than to land use, variation being greater between streams than between sites on the same stream (Reed et al. 1994). Species diversity may therefore be influenced by factors other than shading, and is an issue only if key prey species or species of critical value to the ecosystem are absent. From the point of view of predator

populations, it is total prey biomass that matters.

In surveying the literature for this short review I have been struck by the shift, in recent years, from studies of process to studies of function - largely in the service of rapid monitoring of some parameter of water quality. Whilst I appreciate the need for this, it is clear that many of the key processes involved in the relationships between the physical, the chemical, the biotic and the biochemical elements present in running waters are very complex and poorly understood. Simplistic correlations often miss the complex nature of a relationship. Those few aspects for which there are reliable models with predictive power have resulted from data collections made over periods of 20 years or more. Comprehensive research of single catchments would provide a fine opportunity to collect data over a long period. And a "bottom-to-top" approach towards processes in lotic ecosystems would be both rational and potentially fruitful.

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