

Edgardo Baldi Memorial Lecture

The stream and its valley

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With 4 figures and 2 tables in the text

These lectures were set up to honour the memory of Dr. EDGARDO BALDI, a man who regarded limnology as a science in its own right, one that deals with interrelationships and processes, and with transformations of energy and matter. In that approach he was somewhat ahead of many of us, as the ecosystem concept of ecology was fairly new at the time of his death. The lectures were also intended, as was noted by the late Dr. UMBERTO D'ANCONA who delivered the first of them, to discuss the most vital problems of hydrobiology in the light of their most recent developments. When, therefore, I was invited to address you here, I realized that I ought to attempt to present recent advances in running water ecology in the light of BALDI's concepts of limnology.

Fortunately now is an apposite time to do this, because, within the last few years, there has emerged a growing band of workers who are endeavouring to look at watercourses in a holistic way, rather than as conglomerations of processes, phenomena and taxa; or even, in the current jargon, as victims of "socio-economic problems". Our lacustrine colleagues have gone much further along this way, because in some respects their task was easier. It was possible at first for them to work with the idea of "the lake as a microcosm", and to produce at least a few theories and ideas before they realized that a lake is more than just a basinful of water. In running water there was no possibility of such a head start with a simple theory, so the early steps were more difficult, and we have really only begun to surge forward in this age of interdisciplinary contacts. Indeed, one could say that some of our most important recent discoveries have been of the existence of hydrologists, foresters and soil scientists; which perhaps says something of our innocence.

So my aim during this lecture will be to look at streams not as purely aquatic phenomena, as one can with lakes, but rather to view them as parts of the valleys that they drain. I shall probably fail in my endeavour as my eyes are always drawn to the water, and I like to paddle anyway. I also probably have nothing to say that will be new to my fellow workers in running water, from whom indeed come many of the ideas I shall put forward to-day, especially from my close associates Drs. N. KAUSHIK, M. LOCK and D. LUSH. However, perhaps the genuine limnologists among you, by whom I mean the lake folk, with their ancient Swiss lineage, will learn that we are just beginning to catch them up despite the rougher trail that we are following.

Early attempts to understand how streams differ from one another, and hence by implication how they function ecologically, concentrated on local phenomena, such as temperature and flow regime, water chemistry and substratum, to each of which the biota was shown to be clearly related. This led to classifications of watercourses for various purposes, but especially for fisheries. The most comprehensive attempt at such categorization was published by this Society, but it has been accepted in only very general terms. Recently PENNAK (1971) has returned to the topic, and suggests that streams should be described by 13 parameters in each of which he has 4 to 6 categories. In this way one could define over 180 million different types of stream, which is really little more useful than listing them by name. It would seem that, just as we have taken so long to appreciate about lakes, classification is not really the road to ecological

understanding. Dr. RIGLER has outlined the history of this process at this congress. One does better with processes, particularly those concerned with energetics. But they make a much less tidy classification, and as many of us are biologists by origin we expect the world to be classifiable. For most of us it requires almost a change of creed to admit that it is not — but surely God is no more a taxonomist than he is a mathematician, which is another ecological illusion.

Energy relationships in the water

One recent appreciation — we must not call it a discovery as it has been known since the early days of this Society, and one can find mention of it in the work of one of our founding fathers, Professor AUGUST THIENEMANN — is that streams are basically heterotrophic. They derive most, often nearly all, of their energy from uphill. This topic has been reviewed several times; a few pertinent recent references are EGGLESHAW (1968), FITTKAU (1970), KAUSHIK & HYNES (1971), FISHER & LIKENS (1973), and several papers given at this congress deal with this topic. A recently worked example is shown in Fig. 1, taken from HALL (1972).

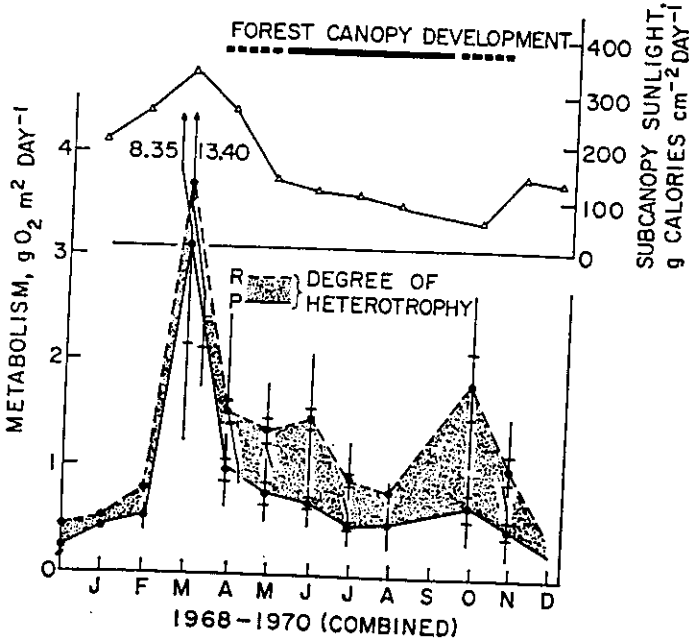


Fig. 1. The oxygen production (P), community respiration (R) and the sunlight recorded month by month at a station on New Hope Creek, North Carolina. The points are mean values, vertical bars are the range of values and horizontal bars are one standard error from the mean. Modified from HALL (1972).

Allochthonous material then undergoes a series of processes in the water that make it available as food for the benthic invertebrates that are so important a feature of all running waters. The significance of heterotrophic processes of this kind has long been appreciated by the soil biologists, and more recently

heterotrophy has figured prominently in work on estuaries (ODUM & DE LA CRUZ 1963; DARNELL 1967). It has even become the subject of an article in the popular scientific press (FLOODGATE 1973).

In estuaries, and also apparently in the sea (MANN 1973), much material produced by autochthonous photosynthesis enters the heterotrophic cycle directly, without being eaten in its live state. The same seems to apply to many macrophytes, such as *Rorippa*, *Potamogeton* and *Ranunculus*, which grow in streams and seem to be rather rarely attacked by herbivores (e. g. KOSLUCHER & MINSHALL 1973). Much then, of the biotic energy that drives stream communities begins in the form of dead material, some from within but, usually, most from outside the stream. In the water it is leached, and it also decays.

Decay of the dead plant material seems to be at least initiated by fungi (KAUSHIK & HYNES 1971), most probably because of their ability to penetrate the tissues and to attack cellulose and lignin. These may be geofungi or the aquatic hyphomycetes that we came to learn about through the work of INGOLD (1966 and earlier papers). It seems from a recent study at Waterloo (BÄRLOCHER & KENDRICK 1973) that the latter are the more important in cold water, and temperature seems to affect their abundance directly (CONWAY 1970). They also seem to be influenced by periods of high flow and to be controlled by the origin of the water, as DUDKA (1971) found their spores to be less abundant in streams arising from swamps on the Kola Peninsula than they were in montane streams.

There is also now good evidence that decaying litter, or more probably the organisms causing the decay, take up a great deal of ionic nitrogen from the water, and that they then convert it to protein. In this way the largely carbohydrate energy of the dead plant material is converted to more suitable food for animals, and the C/N ratio falls. There is now quite a body of literature on this general topic (ODUM & DE LA CRUZ 1963; DARNELL 1967; EHRLICH & SLACK 1969; MATHEWS & KOWALCZEWSKI 1969; KAUSHIK & HYNES 1971; IVERSEN 1973), but there are still many points about the process that need to be resolved. For instance, we still know little about the relative importance of fungi and bacteria, nor if there is a change in their status as decay proceeds. Perhaps a combination of the direct observational approaches of such workers as RODINA (1967), FENCHEL (1970) and MADSEN (1972) with experimental studies such as

Tab. 1. Summary of some comparative data from fast-flowing streams in Scotland. The cotton duck was left in the water for 17 weeks. From EGGLESHAW (1972).

Stream	Nitrate N, mg/l	Loss of tensile strength of cotton, %	Biomass of benthic fauna, g dry wt/m ²	Mean length of 0+ trout at end of season. mm
Buchanty	0.41	>95	1.03	67—76
Fincastle	0.40	77	1.06	—
Shelligan	0.26	95	1.17	59—64
Fender	0.20	71	1.59	69—71
Almond	0.15	20	0.54	52—55
Truim	0.11	15	0.41	48—51

those of KAUSHIK & HYNES (1971) will resolve these questions. But more important from the point of view of the ecology of streams is the finding that rates of decay, which are a crude measure of microbial activity, vary with the species from which the litter arose, the availability of ionic nitrogen, and probably that of phosphate also (NELSON et al. 1969). Other chemical properties of the water, amongst which the level of calcium, or something that varies with it, may also be important (EGGLISHAW 1968; HOFSTEN & EDBERG 1972). All of these characters are derived from the drainage area, and they are readily changed by alteration of the valley. How far-reaching are the implications of such factors in stream ecology is shown by Tab. 1, taken from EGGLISHAW (1972), who measured the loss of tensile strength of strips of cotton duck (in effect the rate of decay of cellulose) placed into several Scottish streams. Possibly, indeed probably, more than ionic nitrogen is involved, but the general message is clear — that the fertility of the valley rules that of the stream in many ways.

PARTICLE FORMATION IN FRESHWATER

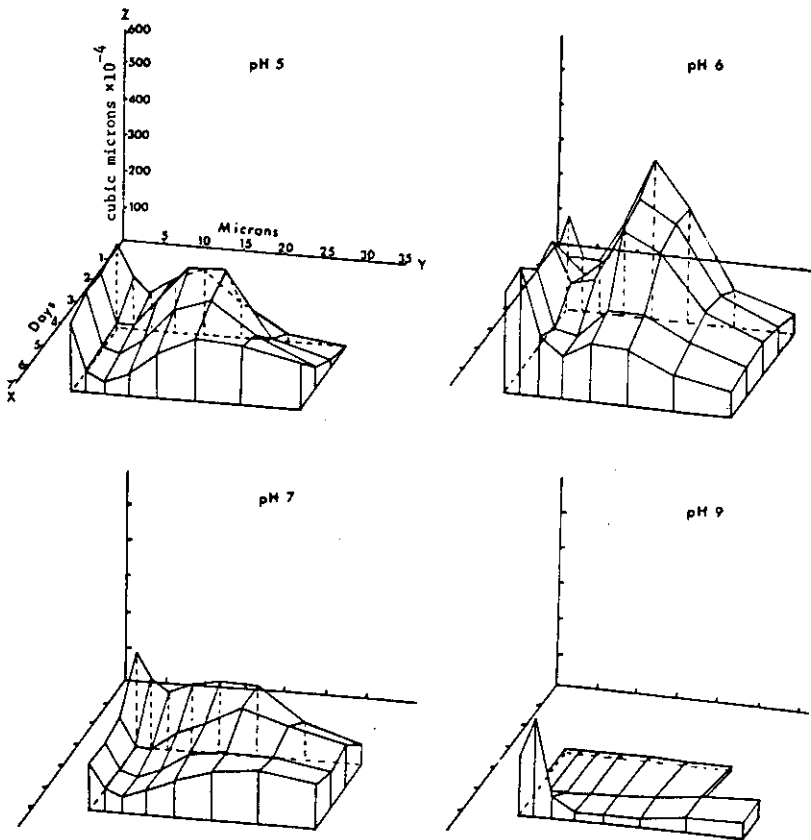


Fig. 2. The formation of particles in leachates of sugar maple leaves, and their changes in sizes and quantity during several days at different acidities. From LUSH & HYNES (1974).

The leaching of dead organic matter has also been subjected to much fairly recent study. It seems that in streams, as in the ocean (RILEY 1970), dissolved organic matter aggregates into small particles which form sites for microbial activity. Work in our laboratory has confirmed that leaf leachates in aerobic fresh water readily form particles under both sterile and nonsterile conditions, that turbulence enhances the process, and that it is much affected by pH (LUSH & HYNES 1974). Fig. 2 shows, as an example of this, the behaviour of leachates of sugar maple leaves at different levels of acidity. The leachate also acts as a buffer, in that its presence tends to bring the reaction of the water towards neutrality, and we have reason to believe that dissolved salts, and perhaps also nutrients, are important in the process of particle formation. This does not occur in distilled water, and addition of nutrients to coloured bog and fenn water is known to remove its colour presumably by precipitation and oxidation. Also WILLIAMS (1968) found that the C/N ratio of organic particles in the Amazon, which carries 20% of the world's river runoff, was much lower than that of the dissolved organic matter; which perhaps indicates the uptake of nitrogen from the water.

The amount that goes into solution from plant litter may be as high as 25–30% of the dry weight of leaves from deciduous trees, although it is less for conifers; and extracts from each species tend to behave differently. It has been shown by the Kellogg Laboratory group (CUMMINS et al. 1972; WETZEL & MANNY 1972), that most of a leaf leachate disappeared quite rapidly from the water in an experimental, recirculating, laboratory stream, and that both organic carbon and organic nitrogen were removed. They also noted an increase in fine particles, and in bacteria in suspension, which is in accord with our expectations from our own work. Many bacteria that occur in natural waters are floc formers which entangle small particles, and MADSEN (1972) has suggested that the microbiota that grow on stone surfaces in streams take up dissolved organic matter. Work in progress in our laboratory is showing this to be so. This is in effect, the same phenomenon as the trickling filter at the sewage works, and may indicate the original home of that useful, but empirical, engineering process.

Thus we can picture the dissolved organic matter in a stream as resulting in the first place from leaching, varying in its behaviour according to its specific origin and the chemical characteristics of the water, and perhaps achieving a more or less stable equilibrium between solution and precipitation or adsorption, as suggested by MANNY & WETZEL (1973) for a stream in Michigan. In that study, however, they showed that such features as a small lake and a swamp in the course of the stream caused changes in the water as it passed through them. Moreover, most of the dissolved organic matter goes into solution in or on the soil, which is where most of the litter falls rather than into the stream itself.

The source of the water

Prior to the last few years stream ecologists have been little concerned about the origins of the water. We distinguished between spring-fed and other streams, and between those that respond rapidly to rainfall and those that do not. But we

tended to think of basal-flow water as groundwater, and spates as being composed of runoff water. Recently, however, the hydrologists have been producing a whole series of new concepts and these have great implications for stream ecology.

For instance, studies by HEWLETT and his coworkers in the Coweeta Forest, North Carolina, (HEWLETT & NUTTER 1970) show that, in natural watersheds, overland flow is a rare phenomenon. Natural landscapes very rarely produce what hydrologists call "parking-lot hydrographs", and usually considerably less than half the precipitation of heavy storms goes off during the spate that follows. The soil of the valley in fact absorbs much of the water. It then goes on yielding it to the stream for a long period, and the water comes from unsaturated as well as from saturated soil. When rain falls onto a slope of which the soil is already partly drained, it therefore increases the flow from the lower part by displacement. So the yielding portion of the watershed shrinks and expands with drought and rain. and channels and wet spots in the valley get filled very largely from below, with only the rain that falls actually onto them getting into the watercourse without going through the soil. So, in effect, the channel reaches out to tap areas of low storage capacity, but they are mainly filled by water that has been long in the soil and has been displaced by recent rain or meltwater. This general "variable source area" concept has received considerable support among hydrologists, although some maintain that storms also add a fair amount of newly received water from slopes near the channel. Recent papers on this subject are those of DUNNE & BLACK (1970), who note that even when overland flow does occur it is often of old water forced up by displacement, CARSON & SUTTON (1971), who discuss recent ideas on stream flow, and FREEZE (1972), who stresses that the form of the valley slope and the permeability of the soil control the proportion of flood water that is new.

Clearly the hydrologists still have more work to do; but the implications for stream ecology of that which they have already done are, of course very great, because they indicate that most of the water that enters a stream has been for some time in contact with the soil, and that this applies even to at least a large proportion of floodwater. It is also clear that the slope of the valley, the depth and permeability of the soil, and the patterns of precipitation greatly affect the pattern of flow in the stream, which is a prime ecological factor; and more subtly, they effect the dissolved content of the water. As CURRY (1972) stresses, the activity of the water on the slopes, before it enters defined channels, is very important, and the dissolved and suspended load of a river is in large measure a function of the geologic, biologic, and meteorologic conditions within the entire watershed.

Another way in which conditions in a valley can affect stream discharge is, of course, through transpiration. This has been well documented by studies of experimental watersheds before and after felling (e. g. LIXENS et al. 1970). It is not, however, I believe, generally appreciated, at least among stream ecologists that vegetation can control discharge even during the non-growing season, because it dries out the soil during the summer, or dry season, and so makes storage space for winter, or wet-season, rain (HEWLETT & HELVEY 1970).

The source of the organic matter

In forested watersheds the annual amount of litterfall from the trees is well known to be several tons per hectare. Only some of this falls directly into the water, but more blows in from the land. For example, in forest near Hubbard Brook, New Hampshire, 49.1% of the organic matter that falls from the trees is leaves, but the leafy proportion of the litter that enters the streams is raised to 60% by blow-in (Gosz et al. 1972; FISHER & LIKENS 1973). Possibly, as this is fairly dense woodland, the amount that blows in is lower than normal. This material also falls seasonally from the trees; for example Gosz et al. (1972) recorded the distribution of litterfall as 49.7% in autumn, 21.2% in summer, 22.4% in winter, and 6.7% in spring. This is because forest debris is composed of branches, stems, bark, flowers, bud scales and insect frass, as well as leaves. So in the forests of the temperate zone there is a varying but more or less continual supply of coarse particulate matter, and in the tropics even the Amazonian forest has maxima and minima in the rates of litterfall (KLINGE & RODRIGUES 1968). Thus the type of vegetation in the valley very directly affects the supply of material to the stream, and in small streams where long dry seasons and heavy litterfall coincide, as in parts of North America, the litter may cause deoxygenation and be a major factor for living things in the water (SLACK & FELTZ 1968). In arid areas, as in the evergreen oak forest of Arizona, the dry spring-shed leaves may lie almost unleached, until summer rains sweep them into the water (McCONNELL 1968).

Fine material results from the break-up of litter actually in the water, but some is obviously produced by similar processes on the land. So when rainfall increases the area of the water surface, as described earlier, one would expect some of this matter to enter the stream. In fact, increases in the quantity of fine organic particles in the water at times of flooding have been observed (EGGLISHAW & SHACKLEY 1971), as have increases in bacteria, but one cannot be certain whether this extra material results from wash-in or from a mere increase in turbulence. However, HOBBIE & LIKENS (1973) noticed that the amounts rose after rain in Hubbard Brook tributaries even when there was little increase in flow, so one can assume that at least a considerable part of the increase is caused by the influx of new particles.

Perhaps though some of the extra particles which are found in the water arise from the increased dissolved organic matter that is brought in when the water rises. We have seen that rain water normally remains for some while in contact with the soil. There it clearly picks up leachates from the soil litter, thereby acquiring some dissolved organic matter from almost every dead leaf in the valley. It also acquires organic matter as it drips through the forest canopy, and once in the soil, evaporation and transpiration concentrate it. The result is that water reaching the stream is heavily loaded with dissolved organic matter. FISHER & LIKENS (1973), in their excellent study of a tributary of Hubbard Brook, record mean values of 2.5 to 3.2 mg/l, and state that about 47% of the total energy input into Bear Brook is in the form of dissolved organic matter. Similar values for concentrations of dissolved organic matter are reported from English chalk

streams (WESTLAKE et al. 1970) and somewhat higher ones from a stream in Michigan (MANNY & WETZEL 1973).

Now we know that different species of leaf give rise to different amounts of leachate, so the vegetation influences the total amounts that enter the stream. We can also expect that such compounds as amino-acids and sugars in leachates will be readily attacked in the soil and that tannins and lignins will probably be more persistent. There are also complex interactions between organic matter in soil and various cations, and with clays (SCHNITZER 1971; STEVENSON 1972). So the material that remains in that part of the soil water which is free to move into the stream depends to a great extent upon the nature of the soil, and it may be more or less labile according to the conditions in the valley.

The origin of the ions

It is obvious that the major minerals in the rocks of a valley dominate the inorganic chemistry of the water, but as JOHNSON et al. (1969) have so elegantly demonstrated, the rates at which various ions are delivered to the stream are to a large extent controlled by the terrestrial vegetation. This is illustrated in Tab. 2, taken from their work, which shows that certain elements, e. g. Ca, Mg, K and N, tend to be held up by the forest. Indeed K and N concentrations in the stream water were generally minimal in summer, presumably because of their use by vegetation, and the same has been found for N in English rivers (OWENS et al. 1972), and in North America (FETH 1966).

Tab. 2. The movement of certain nutrient elements through the ecosystem in the watershed at Hubbard Brook, New Hampshire. From JOHNSON et al. (1969).

Element	A Mean transport by stream kg/ha/yr	B Circulated through forest biota kg/ha/yr	% A/B × 100
Na	6.1	1.6	380
S	12.4	4.0	310
Cl	3.6	1.6	220
Al	1.9	1.6	120
Ca	10.6	32.0	33
Mg	2.5	16.0	16
K	1.5	32.0	5
N	1.9	44.0	4

It is clear also that the mere presence of vegetation in the valley gives rise to soil with all its complicated reactions between ions and humic and fulvic acids that were mentioned earlier. These must affect trace elements in the water as they do in soil, but this seems to be still quite unstudied in relation to streams. We may also note, as being very probably significant, that Ca/Na ratios in river water tend to be lower in warmer climates (CURRY 1972), and that groundwater from limestones almost always contains some nitrogen whereas that from granitic

rocks often does not (FETH 1966). Perhaps somewhere here lies a key to understanding why calcareous rivers and streams tend to be the most productive.

A further effect of vegetation, already seen in Tab. 2, is that it cycles the biologically important elements from soil to plant to soil. The data of Gosz et al. (1972), which are those used in the table, show that the forest litter moved 140.4 kg/ha/yr of such elements. This is, of course, to be expected, but of great interest to us is that the elemental composition of the litter of different species varies a great deal, even when the trees are growing in the same area (DAUBENMIRE 1953), and that the rate of loss of these elements from litter is faster in water than it is on the soil (THOMAS 1970). There seem also to be large regional differences. For instance, the orders of the rates of loss of elements from *Eucalyptus* litter from forests in southeast Australia is quite different from that reported from hardwood forest in Russia (ATTIWILL 1968). And, perhaps not surprisingly because of the preponderance of Leguminaceae, tropical forest litter tends to be more nitrogenous than temperate litter (KLINGE & RODRIGUES 1968).

Nitrate is known to be important in heterotrophic processes, and as we have seen it is taken up by decaying leaves, so that the C/N ratio of the material falls. Undoubtedly only a certain amount can be taken up by a given weight of litter. MATHEWS & KOWALCZEWSKI (1968) found that leaves placed in the Thames reached an asymptote when their N content had risen by about 150%; somewhat similar findings are reported by IVERSEN (1973) for beech leaves in a Danish stream. Similarly, rooted aquatic plants take up and store N (STAKE 1967). We know very little about its release back into the water, which may have considerable implications for running water ecology. Nor is it clear why, despite the increasing use of nitrogenous fertilizers on agricultural land, and its apparently continual loss from the soil, there seems to have been no comparable rise in the nitrate content of river waters in Britain (TOMLINSON 1970; OWENS et al. 1972). Perhaps nitrate is a limiting factor in most situations, but one wonders what becomes of it.

Similarly there are indications that phosphate is important, although EGGLESHAW (1972) did not find it to be so in his experiments with cotton fibres. It is undoubtedly held very tightly within the forest ecosystem where HOBBIÉ & LIKENS (1973) demonstrated a net gain, from rain, in New Hampshire. However, leaf litter from deciduous trees contains a great deal; so much so that it has been cited as a possible source of eutrophication of lakes (COWAN & LEE 1973). *Eucalyptus*, on the other hand, seems to shed less phosphate with its leaves (ATTIWILL 1968), so here again we find that the type of vegetation is important. Once in the stream, however, phosphate is readily taken up by higher plants (NORMANN 1967; STAKE 1968) and by the organisms growing on dead leaves — but not by the litter itself before it is attacked by microorganisms (NELSON et al. 1969; ELWOOD & NELSON 1972). And, as with nitrate, we know nothing about its release back into the water. Also with this ion, which is so tightly held in the soil and is not renewed there, there is the problem of its continued supply to running water. It has been suggested that fish may be important in carrying it upstream, a topic that is discussed by HALL (1972). It has even been suggested that one

ecological function of caimans in Amazonian waters is the release of nutrients at places in the river system where they are scarce (FITTKAU 1970). These are clearly topics that merit much more study.

Undoubtedly further research will show that other nutrients ions are withdrawn from the water by decaying litter. An indication of this is the demonstration by WOODALL (1972) that potassium, which is readily leached from alder leaves, is taken up from the water by such leaves as they decay. One is once more led back to thoughts about the soil and about the chelating properties of fulvic acid and its changing solubilities related to its iron and aluminium contents.

The organic matter in the stream

There is only time to give a very brief sketch of the fate of all this organic matter in the stream itself. It has, however, been clear for some time that where it accumulates on the stream bed it forms an attractive habitat for invertebrates, and one that changes with the season (EGGLISHAW 1968; MACKAY & KALFF 1969). It also forms a major foodstuff that is eaten by a great variety of invertebrates. Most species ingest some, and stream dwellers are opportunistic feeders; a recent paper that stresses this point is KOSLUCHER & MINSHALL (1973). Many fish species, especially in the tropics, are known feed directly on biodegradable matter, and at least one has been shown to select fine particles to eat, thereby probably increasing its take of microorganisms. However, this is a topic into which I must not digress here.

LEAF PREFERENCE BY GAMMARUS

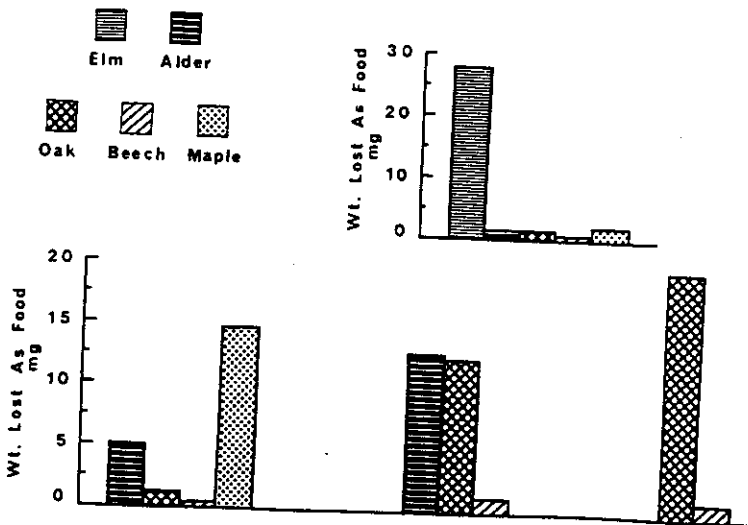


Fig. 3. Preferential feeding by *Gammarus* on autumn shed leaves from different tree species showing the succession of preference when the most favoured species is successively removed. From KAUSHIK & HYNES (1971).

CUMMINS in particular (1973; CUMMINS et al. 1973), has stressed that the first creatures to attack litter, which he calls shredders, reduce it to smaller particles that are available to collectors, and other workers have pointed out that shredders comminute much more than they eat (MCDIFFETT 1970). They also produce faeces that are eaten by other organisms or by other members of the same species (DÖLLING 1962; EGGLESHAW & SHACKLEY 1971; WOODALL 1972; LADLE 1972), and the importance of this type of coprophagy has also recently been stressed with respect to the marine environment (FRANKENBERG & SMITH 1967).

MICROBES AND LEAF PREFERENCE

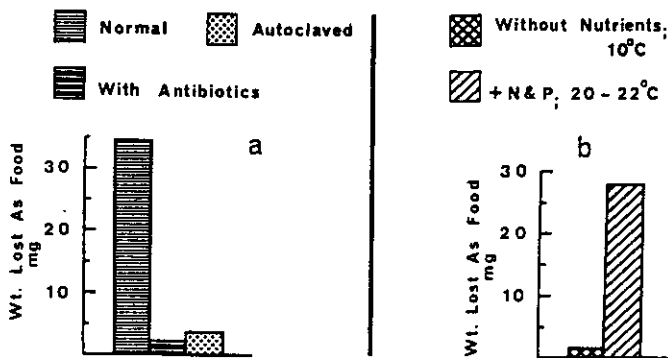


Fig. 4. Preferential feeding by *Gammarus* on elm leaves that had been variously treated to encourage or discourage growth of microorganisms. From KAUSHIK & HYNES (1971).

However, this whole process which lies at the base of almost all the biotic activity in the water, whether the debris is allochthonous or autochthonous, is subject to two conditions. First the debris must be acceptable as food by at least some shredders, and secondly it must be dietetically suitable for them.

There is now a growing body of literature showing that there are very definite preferences for different types of litter, that the leaves of some species are eaten before those of others, both in the laboratory and in the field (e.g. DÖLLING 1962; MATHEWS & KOWALCZEWSKI 1969; MCDIFFETT 1970; WALLACE et al. 1970; KAUSHIK & HYNES 1971; HAECKEL et al. 1973; BÄRLOCHER & KENDRICK 1973 b). An example is shown in Fig. 3, and others were reported at this congress. This results in a successional use of litter from different species, and one can anticipate that litter from mixed woodland produces a more continuously available food supply than does that from a forester's pure stand.

Also, to use CUMMINS' terminology, the litter must be "processed" before it is shredded, which means it must acquire its complement of microorganisms before it is edible, or even very attractive. Here again there is a new and growing literature showing that faster decaying litter is more attractive than that which decays slowly, and that at any rate a large part of the attraction is the microorganisms, mostly fungi, that grow on it (KAUSHIK & HYNES 1971; CUMMINS et al. 1973; BÄRLOCHER & KENDRICK 1973 a, 1973 b; IVERSON 1973). An example is shown in Fig. 4.

Here also the valley exerts its direct influence through the availability of nitrate, and possibly phosphate, potassium and other nutrients, not to mention such other factors as water temperature, liability to spate, and hence time of residence during which processing can occur, or even size of rock, stone, root or pool, in which the litter may lodge for a while. A smooth channel with few obstructions would allow the litter to leave before it had been processed.

Also, of course, the faeces of the shredders and the debris from their feeding, which are, presumably, still subject to microbial attack, are joined by the fine particles produced from the dissolved organic matter. These also depend fairly directly upon the valley, as leachates of litter from different species of tree behave differently, and the process of precipitation depends upon the chemistry of the water.

Such fine particles, either before they sink, or after resuspension, together with particles from other sources, such as plankton from a lake on the course of the stream, form food for filterers such as blackflies (MACIOLEK & TUNZI 1968; LADLE 1972; LADLE et al. 1972) and net-spinning caddisworms. On, and within, the substratum, they also form food for the collectors, and these also benefit from the faeces of the filterers.

Conclusion

We may conclude then that in every respect the valley rules the stream. Its rock determines the availability of ions, its soil, its clay, even its slope. The soil and climate determine the vegetation, and the vegetation rules the supply of organic matter. The organic matter reacts with the soil to control the release of ions, and the ions, particularly nitrate and phosphate, control the decay of the litter, and hence lie right at the root of the food cycle. One could go on and on, building up an edifice of complexity, all linked and cross-linked in the manner beloved by drawers of food nexes. These relationships are very important, and they are so complex that they will take much unravelling. They do, however, make it clear that every stream is likely to be an individual and thus not really very easily classifiable.

It is also clear that changes in the valley wrought by man may have large effects. Some are obvious and need not be stressed here; but others may be very subtle. For instance, even to replace mixed woodland with one species, or to fell one type of tree selectively, could affect the litter regime and the supply of ions. Even felling trees and leaving them where they lay produced enormous rises in N and P in the water of an experimental watershed (LIKENS et al. 1970; HOBBIIE & LIKENS 1973), which would have far reaching effects on litter decay.

WOODALL & WALLACE (1972) have recently shown that there are large biotic differences between streams draining valleys that have been variously altered by man. They attribute these very largely to differing inputs of allochthonous organic matter, and to its specific origin as well as its total amount.

FISHER & LIKENS (1973), in a very thoughtful discussion, suggest that within a stream the accumulated detritus possibly confers stability to the system, in the way that live vegetation may do on land, and they stress that the forest maintains the structural and functional integrity of the stream. MOTTEN & HALL (1972) also conclude that the forest probably dominates any ecological succession a stream might otherwise undergo. It is interesting therefore that English chalk streams, which have been largely deprived of their forests, should still store a great deal of energy as dead organic matter (WESTLAKE et al. 1970), especially as they are well known for their productivity. There the valleys have somehow avoided the consequences of human activity — or were they perhaps even more productive before?

We must, in fact, not divorce the stream from its valley in our thoughts at any time. If we do we lose touch with reality. The real lake is not a basin with two vertical sides as in the textbook. One that is like that, Loch Ness, is so out of line that it harbours monsters. Somewhere, in Australia; there must be a stream with a channel like a gutter, fed by runoff from a landscape paved like a parking lot. There, I predict, will be found the legendary river creature of the aboriginals — the Bunyip.

References

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