

The FUNGAL COMMUNITY

ITS ORGANIZATION AND ROLE IN THE ECOSYSTEM

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ROLE OF AQUATIC HYPHOMYCETES IN THE TROPHIC STRUCTURE OF STREAMS

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I. INTRODUCTORY REMARKS

Plants or plant parts that are eaten while still alive are said to enter the *grazing food chain*; if they die before being eaten they fuel the *detritus food chain* (Odum, 1971). The proportion of primary production eaten alive is usually small in terrestrial habitats (e.g., 1-20% in forests). It is often higher in aquatic environments, but even there detritus (dead organic material, including any attached microorganisms) supplies a substantial portion of the food web with energy. Valleys often support dense forests whose shade effectively curtails primary productivity in the streams that flow through them. However, the riparian vegetation sheds leaves, branches, and twigs which are trapped by the "sticky" water surface and thus become available to stream organisms (Hynes, 1963, 1970). The contribution made by this allochthonous detritus to the total energy budget of stream communities has been estimated to vary between 50 and 99% (Cummins et al., 1966; Fisher and Likens, 1973; Nelson and Scott, 1962; Teal, 1957).

The direct nutritional value of higher plant remains is usually poor. To begin with, much of the energy they contain is locked up in recalcitrant substances like cellulose and lignin, which together account for between 35 and 95% of leaves and wood (Daubenmire and Prusso, 1963; Hering, 1967; Käärik, 1974; Saitô, 1957). These substances are further protected by tannins, polyphenols, or even outright poisons (Levin, 1976; Swain, 1977) that actively depress the palatability and digestibility of the substrate. Undoubtedly, this simply means that the plant's chemical defenses against herbivores and pathogens persist beyond its death.

Very few animals indisputably produce enzymes active on native cellulose [the silverfish *Ctenolepisma*, the edible snail *Helix pomatia*, the marine isopod *Limnoria* (Dickinson and Pugh, 1974; Nielsen, 1962; Whitaker, 1971)], and none is known to decompose lignin. By contrast, a large number of bacteria and fungi can use cellulose, although many of them are less effective when substantial amounts of lignin are also present. Heavily lignified cellulose, such as occurs in wood, is usually attacked most successfully by fungi, particularly by basidiomycetes (Käärik, 1974). Therefore, if animals and microorganisms were to attack plant remains independently, one would

expect the microorganisms as a group to get much the larger share of the available energy. This is probably true in any case (for reviews see Dickinson and Pugh, 1974; Anderson and Macfadyen, 1976). But the natural decomposition of plant materials actually involves a complex series of interactions among many groups of organisms. Some of these interactions clearly benefit animals by giving them access to a larger proportion of the total plant material than their own enzymatic equipment would permit. An obvious way for the detritus feeder to accomplish this would be to enrich its diet with microorganisms that have used cellulose and lignin as food sources. An elegant solution has been evolved by some fungus-growing termites: they ingest plant material and presumably assimilate its less resistant fractions. The fecal leftovers are then deposited in a moist chamber where a fungus, tended by the termites, breaks them down further and uses them to increase its own biomass, which is subsequently harvested and eaten by the termites (Batra and Batra, 1967). Attine ants have gone a step further and no longer ingest the plant material they collect; instead, they use it as a substrate for a fungus which is their only source of food (Batra and Batra, 1967).

It was suggested at least as early as 1891 (H. Simroth; quoted by Baier, 1935) that a similar mechanism operates in the diet of less conspicuously specialized detritus-feeders in terrestrial environments; its significance for food webs in pond sediments was recognized by Baier (1935). Both authors assumed that detritus feeders primarily or exclusively assimilate microbial cells regardless of whether these are ingested with or without their substrate. This hypothesis has recently received new support from students of many detritus-dominated aquatic habitats, ranging from mangrove swamps (Heald and Odum, 1970), salt marshes (de la Cruz, 1975; de la Cruz and Gabriel, 1974; Fenchel, 1970, 1972; Harrison and Mann, 1975; Odum and de la Cruz, 1967), seaweed beds (Mann, 1972), reed swamps (Mason and Bryant, 1975), beaver ponds (Hodkinson, 1975a,b,c), caves (Dickson, 1975), temporary pools (Bärlocher et al., 1978b), to freshwater streams (Bärlocher and Kendrick, 1973a,b, 1974, 1976; Cummins, 1973, 1974; Cummins et al., 1973; Iversen, 1973; Kaushik and Hynes, 1971; Kostalos and Seymour, 1976; Mackay and Kalff, 1973; Madsen, 1974; Petersen and Cummins, 1974; Sedell et al., 1975; Suberkropp and Klug, 1976; Suberkropp et al., 1976; Triska, 1970; Triska et al., 1975).

It can often be observed that decomposing detritus initially undergoes increases in nitrogen or protein levels (de la Cruz, 1975; de la Cruz and Gabriel, 1974; Heald and Odum, 1970; Harrison and Mann, 1975; Hodkinson, 1975b; Mason and Bryant, 1975; Odum and de la Cruz, 1967), or in palatability to detritus feeders (Bärlocher et al., 1978a; Kostalos and Seymour, 1976; Mackay and Kalff, 1973; Madsen, 1974; Triska, 1970), or both (Bärlocher and Kendrick, 1974; Bärlocher et al., 1978b; Iversen, 1973; Kaushik and Hynes, 1971). These observations have been interpreted as meaning that microbial cells, whose growth may cause a protein increase, constitute the actual food of the animals. Cummins (1973) compared microbially conditioned detritus to peanut butter crackers in which the protein-rich peanut butter (microbial cells) is

embedded in a nutritionally poor cracker (plant remains). Obviously, only very small animals could ingest microbial cells exclusively and exclude the substrate; larger invertebrates ("shredders") are thought to digest the bacteria and fungi selectively while the remainder passes through their system virtually unchanged. It has indeed been observed that bacteria disappear during the passage of detritus through the intestines of invertebrates, while the substrate shows no visible changes (Fenchel, 1970, 1972). The fact that most detritus feeders pass food very rapidly through their guts (Baker and Bradnam, 1976; Berrie, 1976; Hynes, 1970) also makes extensive exploitation of recalcitrant substances unlikely.

Nevertheless, the problem of whether microbial colonization is in fact necessary for the growth and survival of detritus-feeding invertebrates was generally ignored for many years.

II. ECOLOGICAL STUDIES OF AQUATIC HYPHOMYCETES IN STREAM SYSTEMS

To return to stream systems: Kaushik and Hynes (1971) investigated the decay of autumn-shed leaves falling into streams and observed the rise in protein levels and palatability just described. The fresh leaves most preferred by several detritus feeders were also those which showed the highest protein increase and whose rate of weight loss was highest when invertebrates were excluded. By using bactericides and fungicides in laboratory experiments, Kaushik and Hynes showed that the fungi are mainly responsible for these phenomena, at least in the initial stages of decay. Triska (1970) reached similar conclusions by measuring respiration rates of leaf disks recovered from a stream and incubated with or without bactericides. Mackay and Kalff (1973) found that leaves inoculated with fungi were more palatable to caddis fly larvae (Trichoptera) than those inoculated with bacteria.

In these and many other cases fungi seem to be more important than bacteria in the early colonization of leaves. Their presence is therefore crucial to the unlocking of a major energy source in streams. Which are the dominant fungal forms? An obvious first step is to distinguish between the terrestrial fungi colonizing the phyllosphere of senescent leaves (*Aureobasidium*, *Cladosporium*, *Alternaria*, etc.), and the group of the aquatic hyphomycetes [or freshwater hyphomycetes (Nilsson, 1964) or amphibious hyphomycetes (Michaelides and Kendrick, 1978)] discovered by Ingold on dead leaves decaying in streams (see Ingold, 1942, 1975). But attempts at careful evaluation of the relative impact of the two groups are rare. From the outset, Triska (1970) restricted his study of the fungal flora on leaves to aquatic hyphomycetes, on the grounds that preliminary studies (which he did not specify) had shown their predominance. The same is true for Padgett's study (1976) of leaf decomposition in a tropical rainforest stream. The results of both investigators are based on the production of conidiophores on leaf disks kept under water, a procedure clearly favoring aquatic hyphomycetes. By contrast, Kaushik and Hynes (1971) plated leaf particles on a rich nutrient medium incubated at room temperature, a method just as

blatantly biased toward the fast-growing terrestrial genera they recovered. We repeated their study, but used both nutrient-rich (malt extract agar) and nutrient-poor (water agar, leaf agar) media, and incubated the plates either at room or at stream temperature (Bärlocher and Kendrick, 1974). Aquatic hyphomycetes proved to be consistently more common than terrestrial fungi on nutrient-poor agar incubated at the lower stream temperature (under these conditions aquatic forms were four to nine times more numerous than terrestrial species). In decomposition experiments with sterile leaves at low temperatures, significant weight losses could usually be achieved only when inoculum of an aquatic hyphomycete was used. When the leaves were sterilized before being introduced into the stream, terrestrial fungi could not be found in significant numbers until 4 to 5 months later, even on malt agar plates incubated at room temperature; nevertheless, such leaves lost weight and gained protein at the same rate as control leaves that had not been sterilized, and both groups had the same community of aquatic hyphomycetes. These results suggest that terrestrial fungi which are on the leaves before these fall into the stream have little influence on the subsequent direction or rate of leaf decay, at least during the colder seasons. These conclusions are corroborated by Suberkropp and Klug (1976). In their thorough study, direct examination and environment-simulating incubations showed that aquatic hyphomycetes were the dominant members of the mycoflora, whereas particle plating on nutrient medium at room temperature revealed the presence of terrestrial fungi. Willoughby and Archer (1973) showed that aquatic hyphomycetes are also the most common fungi colonizing presterilized twigs.

We have obtained additional evidence for the ecological importance of aquatic hyphomycetes from a recent study of conifer needles decaying in a stream (Bärlocher et al., 1978a). Needles are known to make poor food for invertebrates. Of four streams within a square mile, that running through a white pine plantation had the lowest standing crop of individuals and biomass of invertebrates (Woodall and Wallace, 1972). When areas originally covered with deciduous forests or heath were reafforested with spruce, there was a drastic reduction of the aquatic fauna in nearby streams (Huet, 1951). Sedell et al. (1975) found that needle packs of *Pseudotsuga menziesii* and *Tsuga heterophylla* had to be exposed to the stream environment for 140 days before any appreciable invasion by invertebrates took place. In addition Ingold (1966, 1975), who examined a large variety of substrates for the growth of these fungi, never observed them on conifer needles. A simple hypothesis linking these four observations is as follows: Aquatic hyphomycetes are the fungal group best adapted to the stream environment. If conifer needles, just like deciduous leaves, have to be colonized by fungi before they are accepted by invertebrates, their apparent resistance to attack by aquatic fungi will automatically protect them against animal consumers as well. Conversely, if it is possible to remove or destroy the factor inhibiting fungal growth, the needles should also become palatable to detritus feeders in a much shorter period of time. We found that the inhibition could be removed to some extent by treating needles with hot water. Hot alcohol was much more effec-

tive, but hot NaOH solution produced the most spectacular results of all. After 1 month of stream exposure, control needles had an average of less than 0.5 conidiophores of aquatic hyphomycetes per centimeter. Needles treated with NaOH carried almost 100 conidiophores per centimeter. As we expected, feeding started much earlier on the needles with heavy fungal colonization. After only 1 month, NaOH- or alcohol-treated needles showed unmistakable traces of animal feeding. After 4 months, about 80% of the dry weight of NaOH-treated needles had disappeared. By contrast, the control needles had lost only about 30% of their dry weight in the same period, and they did not show any traces of animal feeding until they had been in the stream for 5 months. During the last 4 months, the concentration of conidiophores on control needles had risen slowly from 0.5 to about 15 per centimeter. The stream in which we conducted this experiment flows through a mixed forest, so that detritus feeders presumably had plenty of alternative, more palatable food and could afford to ignore the unpalatable needles until they became fully "conditioned."

When the amphipod *Gammarus pseudolimnaeus* was given a choice between control needles and similar needles freshly treated with hot NaOH (needles never exposed to the stream and therefore carrying no aquatic hyphomycetes), the animals preferred the NaOH-treated needles over control needles at a ratio of about 2:1. But after the two needle types had been exposed to the stream for a month, NaOH-treated needles were preferred over control needles at a ratio of about 20:1. This is the same phenomenon we have mentioned before: those substrates which are preferred by *Gammarus* also allow best growth by fungi, and their conditioning proceeds fastest.

As a first approximation, we can assume that the food of leaf-eating stream invertebrates consists of two main components--the actual leaf material and fungal mycelium. In a series of experiments we compared their relative merits in the nutrition of *Gammarus pseudolimnaeus* (Bärlocher and Kendrick, 1973a,b, 1975b). When feeding on elm or maple leaves with negligible microbial populations, *Gammarus* assimilated 10-20% of dry weight, protein, or caloric content (assimilation = amount ingested minus amount defecated). This agrees well with data from other aquatic invertebrates, whose assimilation of detritus has been estimated to range between 7 and 35% (for review, see Berrie, 1976). By contrast, when *Gammarus* was feeding on fungal mycelium of one of 10 fungi, it could assimilate between 42.6 and 75.6% of the dry weight and 73.3 to 96.4% of the fungal protein. Hargrave (1970) estimated that *Hyalella azteca* (Amphipoda) assimilated 81-97% of its food when feeding on bacteria.

We also measured body weight increases and daily consumption for different sets of *Gammarus* which had as their sole food supply either maple or elm leaves or mycelium of one of 10 fungi. While the actual amounts consumed in all-leaf diets were roughly 10 times greater than in all-fungus diets, the highest weight increases were still found in those animals feeding on four of the fungi. Two other fungi not only failed to support growth, but appeared lethal, and the remaining four fell between these extremes. Cummins et al. (1973) could not observe any growth of *Stenonema* sp. (Ephemeroptera) on mycelium of *Lunulospora curvula*, whereas Willoughby and Sutcliffe

(1976) observed growth of *Gammarus pulex* on one of two fungi examined. An interesting practical application of such studies was tried by Newell and Fell (1975). Their approach was to use agricultural waste products (e.g., straw) as a substrate for fungi and then to feed the harvested mycelium to penaeid shrimps. Growth of these commercially important animals was described as ranging "from very poor to encouragingly high." The variability of these results is undoubtedly due in large measure to the natural variability of fungi. In an investigation of the suitability of many fungi as food for larvae of Cecidomyiidae (gall midges), Nikolei (1961) showed that such seemingly small changes in the cultivation of the fungus as a temperature increase of 4°C, an increased nutrient concentration in the medium, or the use of different strains of the same species could decide whether a fungus was nutritionally acceptable or toxic.

Results are more consistent when sterile leaves are compared with microbially conditioned leaves. Survival of *Gammarus minus* was highest on fungus-enriched leaves and lowest on sterile leaves (Kostalos and Seymour, 1976). Nilsson (1974) found that *Gammarus pulex* assimilated leaves microbially conditioned for 10 days in artificial stream water better than untreated leaves; also, chironomid larvae continued growth and hatched as adult winged insects when kept on a diet of decomposing cellulose (Park, 1974).

As one might expect, invertebrates have generally been shown to select the food which they use most efficiently. For example, in short-term experiments *Gammarus pseudolimnaeus* prefers fungal mycelium to unconditioned leaves (Bärlocher and Kendrick, 1973b) and *Gammarus minus* prefers fungus-enriched leaves to sterile leaves (Kostalos and Seymour, 1976). From these observations it appears that although these *Gammarus* species can survive and grow on freshly shed and perhaps even on sterile leaves, their food will be much improved, both in palatability and nutritional value, by prior microbial conditioning. The frequently observed preference for microbially conditioned leaves among other invertebrate taxa suggests that this is generally true. We know of only one study in which microbially conditioned leaves appeared to be less palatable than nonconditioned leaves. Otto (1974) found that green leaves of *Fagus* were preferred over leaves which had been in a stream for about 7 months. But beech leaves are known to become increasingly unpalatable during their development (Feeny, 1970), so dead leaves would be both less acceptable and less nutritious than living ones; in addition, Otto may have collected the stream-exposed leaves after their period of maximum palatability was over (cf. Iversen, 1973).

The aforementioned food selection experiments were done in the laboratory, where the invertebrates had ready access to good as well as poor food. This need not be the case in streams, where animals may be forced to search for conditioned food. The question arises as to whether the profit gained from higher food quality exceeds the extra cost involved in hunting for it (this includes the loss incurred by not using available, less palatable food). The available evidence indicates that the search generally pays off. The number of shredders colonizing leaf packets were distinctly

higher after a rise in microbial respiration, suggesting discrimination against unconditioned leaves (Anderson and Grafius, 1975; Sedell et al., 1975). A rise in invertebrate numbers with time was also found by Hart and Howmiller (1975). This lag period is generally longer and more distinct in nutritionally poor substrates (Peterson and Cummins, 1974). Selective feeding is also the basis for the staggered appearance of telltale signs of invertebrate feeding when the natural decay of several substrates is compared (Bärlocher et al., 1978a; Kaushik and Hynes, 1971). But food selection may take place on a much smaller scale: we found evidence (Bärlocher and Kendrick, 1974) that leaf areas with highest fungal biomass disappear fastest, again indicating preferential feeding by invertebrates. This possibility has also been suggested by Padgett (1976).

But some invertebrates may more profitably accept less-than-optimally conditioned food. This may be the case with relatively slow-moving shredders (such as some caddis fly larvae), whose chances of finding fully conditioned food are low when they are sharing their habitat with highly mobile competitors and who therefore cannot afford to turn down food that is only partly conditioned. *Gammarus* undoubtedly belongs to the more mobile class of shredders. Similar conditions may prevail for the whole community if the food supply is dominated by a strongly seasonal, nutritionally poor type of leaf whose conditioning requires several months. If no alternative food is available (e.g., algae), and unless they can fine-tune their life cycle to the point where their demand for food is highest a few months after leaf-fall, shredders may simply have to eat inadequately conditioned food. A possible consequence is that conditioning is of less consequence in those habitats where its effect would be most beneficial. In streams with a great variety of leaves, shredders can better afford to ignore poor substrates until they are considerably improved by microbial colonization, thus reaping the full benefits of conditioning. If this is the case, lag periods in the invasion of nutritionally poor leaf packets should be most distinct in streams running through mixed forests, or where leaf fall is spaced out evenly throughout the whole year. Some relevant observations are reported by Haeckel et al. (1973). In stream regions with alder, poplar, and beech trees, autumn-shed beech leaves were still largely untouched the following March, while most alder leaves were completely skeletonized. Poplar leaves were moderately decayed. But in a stream reach dominated by beech trees, the few poplar leaves were heavily damaged and the breakdown of beech leaves had progressed much farther.

How much of the food intake of detritus feeders in their natural habitat consists of microbial cells? This is a difficult question to answer, since the leaves we find in streams are often those which have been refused by the animals, presumably in favor of better-conditioned food. Microbial populations on such leaves may therefore be lower than those on the actual food. In addition, the biomass of microbial populations is notoriously difficult to estimate. A traditional approach is to measure mycelial length per unit of bleached leaves and, with the help of empirical ratios, convert it into fungal biomass per unit weight of decaying substrate. Visser and

Parkinson (1975) estimated that the highest densities of hyphae present in aspen poplar leaves decaying in a terrestrial habitat correspond to about 8% of the total dry weight. When the same ratios are applied to our data on maple leaves in a stream (Bärlocher and Kendrick, 1974), the highest average density would correspond to about 2%, but the maximum density found in small heavily colonized areas would be almost twice as high. Suberkropp et al. (1976) measured ATP concentrations in decaying hickory and oak leaves. ATP occurs only in living cells, and the ratio of ATP to total cell carbon is thought to be fairly constant (Ausmus, 1973; note, however, Greaves et al., 1973). When Suberkropp's values are converted into microbial biomass (using the average of bacterial and fungal values as given by Ausmus), the living microbial cells would generally vary between 5.9 and 11.8% of the dry weight of hickory leaves and between 1.6 and 3.3% of oak leaves.

Leaves unpalatable to invertebrates are apparently also more resistant to fungal colonization. Highest ATP levels coincided with highest activity of fungi observed by other methods (direct observations or plating out). Extremely low values were found by Iversen (1973) on decomposing beech leaves: fungal biomass (estimated by measuring hyphal length) would correspond to only 0.004% of the total substrate weight; bacteria were more common and contributed about 0.3%. Similar conclusions were reached by Davis and Winterbourn (1977) in a study on the breakdown of *Nothofagus* leaves: hyphae were seldom observed until about 4-5 months after immersion in the stream. These observations suggest that bacteria may be more active in the early colonization of very recalcitrant leaves; however, their biomass was very low (0.3% on beech leaves), and they may be simply existing on organic substances dissolved in the stream water and concentrated at the solid-liquid interfaces of submerged leaves. More detailed studies are certainly needed to examine the degradation of sterile leaves by selected bacteria and fungi. But despite the very low microbial biomass on beech or *Nothofagus* leaves, the palatability of the substrate still increased, as did nitrogen levels. Iversen estimates that only between 4 and 14% of the new nitrogen is actually bound to microbial cells, and he assumes that the remaining nitrogen is present in organic substances released by bacteria. A possible mechanism is suggested by Suberkropp et al. (1976). They found that a substantial fraction of the nitrogen is fixed in highly refractory complexes, presumably formed by leaf polyphenols and the microbial organic nitrogen compounds (possibly exoenzymes), which in conventional analytical methods show up as "lignin." The relative amount of total leaf nitrogen immobilized in such complexes was higher in the slow-decomposing oak (26-36%)--with higher initial levels of soluble polyphenols--than in the faster decomposing hickory (16-22%). Such complexes have been shown to be very resistant to enzymes, so that an invertebrate may derive little benefit from nitrogen levels increased in such ways. However, their stability is greatly influenced by the pH, and invertebrates with a high intestinal pH may be able to metabolize them at least in part (Davies et al., 1964; Feeny, 1970). Of equal importance to the detritus feeder may be the fact that the polyphenols in such leaves are saturated and no longer inter-

ferre with the animal's digestive enzymes. Protein may be precipitated directly from stream water, but at least in laboratory experiments protein increments have been strictly dependent on the presence of actively growing fungi.

If we accept the foregoing estimates of microbial biomass, their share of the total substrate weight would usually amount to some 2-10% (but below 1% in very recalcitrant leaves). If we further assume that microbial cells contain proportionally three times as much digestible material as the leaf, the average proportion of nutrients provided by microbial cells in the diet of leaf-eating invertebrates would vary between 6 and 25%, and be around 1% in the most refractory substrates. For comparison, Baker and Bradnam (1976) estimate that the filter-feeding blackfly *Simulium* derives about 2.1% of its food from ingested bacteria. These figures are quite substantial, and (taking into account the potential sources of error in their estimation) they may fully explain the observed improvement in the leaves' palatability and digestibility. But at least in some cases, additional mechanisms seem to be called for. For example, Nilsson (1974) reports that *Gammarus* assimilates virtually nothing of fresh beech leaves but can use 35% of fully conditioned leaves. If microbial biomass is indeed as low as that reported by Iversen (Nilsson offers no statement about it), the rise in digestibility cannot be due exclusively to enrichment with microbial cells.

It is possible that the leaf substrate itself becomes more digestible under the influence of microbial activity. We showed that, at least with maple leaves and with cellulose, palatability can be improved when the substrate is exposed to fungal exoenzymes or to hot HCl, a hydrolyzing agent (Bärlocher and Kendrick, 1975a). Nielsen (1962) and Bjarnov (1972) found that all detritus feeders they examined could use cellobiose, although most of them had little or no ability to degrade even modified cellulose. The presence of cellobiases in animals lacking cellulases has also been reported by Luxton (1972) and Kristensen (1972). Free cellobiose is very rare in nature (Pazur, 1970). Its most important occurrence is as a subunit of cellulose, and it is an intermediate product of cellulose degradation, a process which typically takes place in a series of steps (Whitaker, 1971). In aquatic detritus feeders cellulases, if present at all, are generally so weak that extensive degradation of native cellulose during its rapid passage through the gut appears unlikely (Monk, 1976). Kristensen (1972) suggested that, in noncellulolytic animals, enzymes able to degrade cellobiose were in fact nonspecific and acting on quite different substances in the animals' actual diet. This may well be the case. But the occurrence of enzymes active on cellobiose, and possibly on modified cellulose, would be an obvious advantage to detritus feeders if they had access to partly degraded cellulose. This would require that some microorganisms did not completely degrade and metabolize all the cellulose they attack. Some fungi behave like this, and it has already been established that other microorganisms can take advantage of it. For example, Tribe (1966) showed that a noncellulolytic oomycete, *Pythium oligandrum*, was able to grow on cellulose in association with the strongly cellulolytic hyphomycete *Botryotrichum piluliferum*, but

not without it. Similarly, Frankland (1966, 1969) observed many "sugar fungi" (fungi dependent on simple carbohydrates) late in the decay of *Pteridium aquilinum* petioles, even though soluble carbohydrates were less than 1%. Additional experiments with pure cultures demonstrated that the sugar fungi were dependent on the release of sugars from the substrate brought about by the activities of basidiomycete mycelium. The significance of such processes may well remain hidden when we use conventional analytical methods, which do not distinguish between stages in the stepwise degradation of cellulose and which rely on average values of large samples.

Decomposing leaves are mosaics made up of patches that range from virtually intact areas to heavily colonized ones. Even if areas with a high level of easily digestible substrate are constantly becoming available, the average overall value will not change perceptibly since these areas will quickly be removed by preferential feeding. Unless potential consumers are barred, the composition of the leaf at any particular time resembles the leftovers of a meal rather than the actual food of detritus feeders. This point is well illustrated by Saitô's (1965) experiments with two nutritionally different fungi. When sterile leaves were inoculated with a strongly cellulolytic basidiomycete, the content of soluble carbohydrates increased rapidly. But when a second fungus was introduced simultaneously, the increase was slower and only temporary. The soluble carbohydrates were now removed and used by the second species.

One factor which clearly regulates the amount of soluble substances produced during decomposition is oxygen. Under anaerobic conditions, cellulose is still degraded by various microorganisms, but only a small percentage is built into microbial cells. Most is converted into volatile fatty acids. Ruminants and some insects exploit this process by harboring in their own body microorganisms which break down inaccessible food sources such as cellulose into digestible subunits which are siphoned off by the animal (Blaxter, 1967; Buchner, 1965; Hungate, 1966). In this process, only a small percentage of the energy is lost through microbial respiration, and the advantage to the animal lies not in the production of microbial cells, as in the fungus-growing attine ants, but rather in microbial catalysis.

But most detritus feeders lack such far-reaching adaptations and have little control over the direction of microbial activity on plant remains. Of necessity, they must be more opportunistic and flexible in their feeding strategy. Besides directly digesting as much plant material as they can, they may enrich their diet with microbial cells and possibly profit from increased substrate digestibility brought about by previous microbial colonization. This argument may even be extended to some carnivorous stream insects. Cummins (1973) states that predators feeding on early instars take in food with little fat or protein, surrounded by an indigestible chitinous shell. The most nutritious portion of such prey may be the digestive tract, packed with food particles. At least to some extent, predators might be considered to feed on prey digestive tracts (Cummins, 1973). It is therefore not very surprising that cellobiases, or even weak cellulases, have been found in some carnivorous inverte-

brates (Kristensen, 1972; Monk, 1976). It remains to be seen whether or not microbial enzymes remain active, and for how long that activity might persist, when the substrate is chewed and bathed in the invertebrate's digestive fluids.

III. CONCLUSION

Much of the work on detritus processing has been done or inspired by zoologists. Not surprisingly, leaf conditioning has been described from an animal's point of view. But to an unbiased observer it is obvious that this process, so advantageous to invertebrates, has serious drawbacks for leaf-colonizing fungi. Their resources are depleted, and their biomass directly reduced, by animal consumption. The often-heard statement that shredding increases surface area and thereby stimulates microbial activity may be true, but this benefits primarily microorganisms specialized in growing on fine particles and there is no evidence to suggest that aquatic hyphomycetes belong to this group. To anybody who has ever observed the luxuriant growth of fungi on leaves from which all potential consumers are excluded and then contrasted that with the scarcity of visible mycelium on leaves just recovered from a stream, it seems obvious that predation on fungi in natural streams must be severe. One would therefore expect the fungi to have evolved some countermeasures, analogous to the plants' defenses against herbivores. The most obvious one would be for the fungus to produce unpalatable substances or poisons deterring leaf-eating animals. As we have already noted, some fungi appear to have adopted this mechanism. Alternatively, the fungus might spread its mycelium so thinly that the resulting increase in substrate palatability was unnoticeable. Predation would then be more or less accidental, and its effects on the fungus minimal. A third possibility and, to judge from the scant information available, the most likely is that the fungus also colonizes plant parts which are safe from consumers for a considerable length of time and thereby provide a refuge. This may be within wood (Willoughby and Archer, 1973), conifer needles (Bärlocher et al., 1978a), or the veins and petioles of deciduous leaves. Skeletonized leaves are often the most profitable source of aquatic hyphomycetes (Ingold, 1942, 1975). We found that, in early samples taken from sets of maple leaves exposed to a stream, *Tricladium angulatum* was much more common than *Heliscus lugdunensis* on lamina whereas *Heliscus* was slightly more common than *Tricladium* on veins and stalks. But after about 3 months in the stream, the frequency of occurrence of *Tricladium* declined drastically, while *Heliscus* continued to rise. At the same time skeletonization became more and more noticeable, so that the relative amount of veins increased. A simple explanation is that *Tricladium* grew much better on the softer leaf parts between the veins. Its rapid growth made these areas palatable, and they were removed by preferential feeding. As a result veins, which carried more *Heliscus* than *Tricladium*, became relatively more abundant. The seemingly paradoxical conclusion is that the fastest-growing fungus may also decline most rapidly because of its very success. *Tricladium* appeared to be better adapted to a good but dangerous substrate, and *Heliscus* to a poorer but safer habitat. In the first case, fast growth

and reproduction are crucial; in the second, efficient use of the substrate is probably more important. To translate this (under protest) into the jargon of evolutionary ecologists: *Tricladium* is probably more r selected, and *Heliscus* more K selected (MacArthur and Wilson, 1967).

Preferential removal of areas with high hyphal densities may have a quite different effect on the number of species coexisting on a leaf: density-dependent predation can allow inferior competitors of the prey population to exist in habitats where they would otherwise be outcompeted (MacArthur, 1972; Menge and Sutherland, 1976; Paine, 1966). The issue of whether such effects play any role at all or are overridden by the seasonality of leaf fall, or by the numbers and types of leaves falling into a stream, or other factors, cannot at present be resolved on firmly empirical grounds.

As we have already emphasized, the leaves which even before microbial colonization are most palatable to invertebrates are also those which lose weight fastest when attacked solely by microorganisms (Bärlocher and Kendrick, 1973b; Bärlocher et al., 1978a,b; Kaushik and Hynes, 1971). In other words, a source of food more nutritious to the detritus feeder is also more profitably exploited by the fungus (more nutritious probably means less cellulose, lignin, tannins, etc., and more proteins). Despite its ability to subsist on structural carbohydrates and dissolved inorganic nutrients, the average aquatic hyphomycete apparently grows better and faster when more easily digested substances are available. But the higher the original food quality, the greater the probability that it will reach a level where it is acceptable to animals without prior conditioning. For example, several *Gammarus* species are also carnivorous, and some ingest algae (Hynes, 1970; Moore, 1975). It is highly unlikely that this protein-rich food could be improved by fungal growth. But even if we restrict the argument to leaves, some of these are already so palatable that the improvement due to conditioning is slight. Nilsson (1974) estimated that *Gammarus pulex* assimilates 30% of freshly fallen alder leaves and 40% of microbially conditioned leaves. The gain might have been even lower or nonexistent had he used young, green alder leaves (cf. Otto, 1974). Not surprisingly, alder leaves are also a particularly good substrate for aquatic hyphomycetes (Nilsson, 1964): indeed, it was on decaying alder leaves that these organisms were originally observed by Ingold (1942). If certain leaves are indeed acceptable to animals without prior conditioning, the fungi and invertebrates will be in direct competition. Considering the ability of animal communities to shred and ingest vast amounts of materials in a short time, the outcome is hardly in doubt: unless there is a superabundance of this high-quality food, the share of the fungi would be limited to leftovers too small to be efficiently captured by the animals. But these particles might also be too small to permit an aquatic hyphomycete to develop from colonizing conidium to newly formed conidium. Thus the superior enzymatic equipment of the fungi may have evolved partly as compensation for their inability to compete with animals for the more easily exploitable substrates.

The relationships between fungi and invertebrates can be summarized as follows: In general an initially very unpalatable substrate will be improved only a little per unit time by fungal colonization, at least in the early stages of conditioning. As palatability increases, conditioning will also proceed more rapidly, until a maximum is reached, after which the speed of conditioning will start to decline, eventually reaching zero. Beyond that point, any further fungal colonization is likely to decrease the nutritive value, simply by depleting the substrate. The profit to the invertebrate of full leaf conditioning may actually be highest in the case of substrates which are initially so poor as to be virtually useless to the animal. This requires that the animal have alternative sources of food while the conditioning is going on and that the losses due to downstream transport during the long conditioning period are not too high (or are compensated for by gains from upstream). Depending on the position of a particular substrate in this spectrum, the relationships between fungus and invertebrate can be very different. On less palatable leaves the animal will prey on the fungus, while on palatable substrates they will be competitors. In the first case, the animal will try to ingest as much fungal biomass as possible; in the second case, to avoid it altogether by eating the leaf substrate as soon as it falls into the stream. This illustrates the inadequacy of certain terms common in ecological literature, such as *first* and *second trophic level*, and the distinction between *consumer* and *decomposer*. All heterotrophs consume organic substances; all of them have to decompose it at least partly to gain energy and assimilate or rearrange subunits. Microorganisms are simply able to use a wider range of natural substances, and they are more thorough in breaking down their substrates (e.g., they may produce inorganic nitrogen rather than the organic nitrogen excreted by terrestrial animals). In the context of detritus food chains, the significance of microorganisms may lie less in their ability to break down complex structures into organic substances than in the production of new microbial cells.

In assessing or rather predicting the significance of aquatic hyphomycetes in the trophic structure of natural streams, it is convenient to start with the trivial assumption that their impact is greatest where their activity and production are highest. With given chemical and physical characteristics of stream water, this seems to be the case when a wide range of substrates of different quality are available. This avoids a direct clash between fungi and invertebrates, thus reducing the likelihood of the substrate being reduced to fine particles before the fungi have had a chance to colonize it. It allows the fungi to stay one step ahead of their predators--colonizing substrates not yet attacked by invertebrates, building up their population, and producing propagules which will colonize the next substrate. A probable consequence is that a stream receiving leaves belonging to several species will support more shredders per unit weight of leaf than the same stream receiving the same total input of leaves of only one species. Nor is this likely to be restricted to shredders: the better the food, the more nutritious the feces derived

from it, and the better the supply for fine particle feeders. This amplifying effect is largely due to aquatic hyphomycetes.

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