MASTER

An Energy Budget Model
for Woodland Stream Ecosystems*

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The model has been structured to emphasize the fate and role of terrestrially produced organic matter once it enters the stream ecosystem. It is my contention that streams, like soil communities, are, in general, predominantly heterotrophic. This is in contrast to above ground terrestrial communities, lakes and oceans which are autotrophic. Probably the primary input of organic matter to streams enters in the form of leaves of terrestrial shrubs and trees. Even in grassland biomes, the distribution of trees and shrubs is essentially the distribution of running water courses. Also, I feel it is reasonable to include large rivers, particularly due to man's impounding activities, in an ecological category with lakes.

Seasonal and geographical differences in the balance between heterotrophy and autotrophy are standard features of streams, but heterotrophy usually dominates on an annual basis. In general, the autotrophic activities seem to be light limited; that is, maximum autotrophy occurs at seasonal light maxima or at locations where shading is naturally or artificially reduced. There is also a general relationship between stream width and the heterotrophy-autotrophy balance, the smaller streams often being the most heterotrophic. Shade adapted autotrophs, possibly with certain heterotrophic capabilities, that is diatoms, dominate most stream communities with normal unaltered light regimes. When light is increased, the dominance usually shifts to light adapted filamentous greens.

Vannote has data from his excellent experimental system showing that periodic flooding (flushing) in streams insures that autotrophy does not become the dominant process on an annual basis. Fisher has shown that

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80% or more of the particulate fraction that enters a small stream is processed in the stream. Triska's preliminary studies on "residence time" for leaves in streams also indicates that processing and not export is the dominant process.

The dimensions of the dissolved organic fraction and the utilization of that fraction still constitute a significant problem. The terrestrial literature as well as the work of Hynes and Kaushik and the group at Waterloo (especially Lush who is working specifically with the dissolved fraction) together with data from Triska's thesis, indicate that 10 to 25% of the dry weight of newly introduced leaves is leached away in the first one to three days. This, together with algal excretions and terrestrial input in dissolved form (which presently does not appear in the model) undoubtedly constitute quite a significant organic pool which turns over fairly rapidly, although a considerable number of rather refractive constituents might be expected. We have plans to monitor dissolved organic levels in both our natural and artificial streams, although most of our experiments will involve preleached leaves.

The microbial picture is also just beginning to be unraveled. The work of Kaushik and Triska has certainly led the way, together with the literature dealing with soil systems which in many cases seem to be, at least generally, analogous. The present impression is that the microbial decomposition of the leaf litter is dominated, particularly in the initial phase, by fungi--especially the aquatic hyphomycetes. The uniqueness of these fungi not only render them promising for investigation but their properties mesh well with the predominant stream functions, at least as I see them.

These fungi will only sporulate in the water, tend to be cool adapted (in contrast to many bacteria in stream systems) and have cellulase enzymes

(in contrast at least to the Bacillus bacterial species isolated which degrade intermediate compounds such as cellobiose). This means that the aquatic hyphomycetes are well adapted for infesting and initiating degradation of leaves entering the stream and that their adaptations, especially at higher latitudes, are such that they should dominate the process at times of maximum leaf input. The work of Kaushik and Triska, in which bacterial and fungal growth inhibitors were used, also implicate the fungi as the dominant functional group. In addition, Triska has shown that at least one large detritivore will not ingest the leaves unless they are infested with fungi.

Therefore, the sequence would seem to be fungal invasion of leached leaves followed by bacterial development when certain by-product substrate levels are sufficient. Once the leaves are "conditioned" by fungal infestation, the large detritivores (or "shredders") begin the process of fragmentation leading to the development of consumer populations which feed upon smaller particles. Again, however, we are faced with inputs the dimensions of which have yet to be accurately determined. The non-biological mechanical production of fine particles and the aggregation of colloidal material into discrete particles of sufficient size to serve as input for animal consumers are still essentially unknown inputs, obtained only by difference so far.

Whereas there is recycling of fine detrital particles through the consumers, including reingestion of feces, this is probably not a dominant feature of the feeding process of the "shredders". Vannote has estimated that Tipula (crane fly larvae) populations in woodland streams process, that is pass through their guts, a large proportion of the leaf litter that enters the system. Together with Pycnopsyche (caddisfly larvae), which we are working with, the estimate is that 40-60% of the introduced leaf litter would

pass through the digestive tracts of these two "shredders", and we know there are other "shredders" in the system.

I have indicated my impressions of the ranges in species numbers involved, on an annual basis, in the various animal macroconsumer compartments. The trophic compartments, detritivores (two categories), herbivores and carnivores, represent composites having been constructed by summing all the ingestion of a particular type attributable to each age class of each species in the system. A large portion of this work was done by Coffman. The rates of gut loading and unloading have been determined in the laboratory under semi-natural conditions at best. Mecom's suggestion should be followed and dye rapidly taken up by the fungi (vital) and or leaves (non-vital) should be introduced into a section of stream and the gut loading by members of the community followed by actual field sampling. The idea being that such dyes would produce less objectionable side effects than comparable tracer studies.

Obviously the model is still exceedingly rough and the general nature of most aspects of the design have yet to be tested. However, I feel that stream ecology is finally in a position to move from a strictly descriptive phase into a period in which theoretical generalizations can be tested and certainly more subtle, and probably much more successful, manipulations attempted.

Note: Triska's name does not appear in the directory since he has just been taken into the Army. As soon as his new address is available I will circulate it. In the meantime, I highly recommend his thesis: 1970. "Seasonal distribution of aquatic hyphomycetes in relation to the disappearance of leaf litter from a woodland stream". Univ. of Pittsburgh, Pittsburgh, Pennsylvania 15213 U.S.A. 189 pp. (can be obtained from University Microfilms, University Microfilms Ltd., High Wycomb, England or Ann Arbor, Michigan U.S.A.)

AVERAGE DAILY ENERGY BUDGET FOR A WOODLAND STREAM

An estimated energy budget for a typical woodland, that is heterotrophic, stream. Data and "impressions" from Cummins, Coffman, Roff, Vannote, Hynes, Kaushik, Triska, Wuycheck, Petersen, Howard, Fisher, Warren, Ulfstrand, Ross and Hall (see Directory).