

Factors affecting food utilization by a leaf shredding aquatic insect: leaf species and conditioning time

S. W. Golladay, J. R. Webster and E. F. Benfield

Golladay, S. W., Webster, J. R. and Benfield, E. F. 1983. Factors affecting food utilization by a leaf shredding aquatic insect: leaf species and conditioning time. — *Holarct. Ecol.* 6: 157-162.

Gravimetric feeding studies were used to examine the feeding strategy of *Pteronarcys proteus* (Plecoptera) using unconditioned, 1 month conditioned, and 2 month conditioned deciduous leaves of four species (white oak, red maple, black locust, dogwood). Assimilation efficiencies of *Pteronarcys* nymphs feeding on unconditioned and conditioned leaf material ranged from 13.4 to 21.9% AFDW of leaf material indicating that *Pteronarcys* was able to digest and assimilate leaf material. Assimilation efficiencies did not change as leaf material conditioned which suggests that assimilation efficiency does not accurately reflect changes in detrital food quality. However, as leaves conditioned, the ingestion rate of *Pteronarcys* nymphs accelerated. Rates at which dogwood and locust leaves were ingested peaked after 1 month, then declined with a second month of conditioning. Rates at which maple and oak leaves were ingested increased significantly with 2 months of conditioning. Assimilation rates of *Pteronarcys* nymphs varied in a pattern similar to ingestion rates. This reflects the importance of ingestion rate in the feeding response of *Pteronarcys*.

S. W. Golladay, J. R. Webster, E. F. Benfield, *Biology Dept. Virginia Polytechnic Inst. and State Univ., Blacksburg, VA 24061, USA.*

1. Introduction

Vascular plant detritus is usually considered to be a low quality food source, and there has been considerable discussion of how organisms which feed on this material fulfill their nutritional and energetic requirements. It has been proposed that the feeding strategies of detritivores are directed toward obtaining adequate levels of protein or nitrogen in their diet (Anderson 1976, Bowen 1979, Martin 1979, Martin et al. 1980). This may be accomplished through selective ingestion of protein rich algal or microbial cells (Hargrave 1970, Bärlocher and Kendrick 1973a, 1973b, 1975, Nilsson 1974, Calow 1975, Kostalos and Seymour 1976, Rossi and Fano 1979). These observations have led to the conclusion that aquatic detritivores rely mainly on microbial biomass for their nutritional and energetic requirements. However, other investigations have shown

that microbial biomass is not present in sufficient quantities to support the energy requirements of some detritivores. For example, Cummins and Klug (1979) reported that only 8.3% of the growth of *Tipula abdominalis* larvae in the laboratory could be attributed to microbial biomass on conditioned hickory leaves, and Baker and Bradnam (1976) found that bacteria alone were insufficient to supply the energy needs of species of *Simulium* and *Chironomus* from the River Frome. Reported assimilation efficiencies for detritivores feeding on plant detritus range from 1-40% (Vannote 1969, Hargrave 1971, Anderson and Grafius 1975, Bärlocher and Kendrick 1975, Prus 1976, Wotton 1978, Bowen 1979, Sinsabaugh 1980), indicating that some detritivores are able to obtain a considerable amount of energy directly from detrital material.

This study was designed to further examine the relationships among leaf species, leaf conditioning and

Accepted 19 February 1982

© HOLARCTIC ECOLOGY

detritivore feeding. In streams, the rate at which leaves become microbially conditioned and decay is species-specific (e.g. Kaushik and Hynes 1971, Petersen and Cummins 1974, Suberkropp and Klug 1976). Evidence of conditioning includes increases in observable microbial biomass (Suberkropp and Klug 1974), increases in protein content (Kaushik and Hynes 1968) and increases in microbial activity (Witcamp 1966, Triska 1970, Suberkropp and Klug 1976). These observations have led to the conclusion that leaves reach their nutritional peaks in a stepwise manner related to their suitability as a microbial substrate (Peterson and Cummins 1974). The specific objective of this study was to examine the feeding strategy of *Pteronarcys proteus* (Plecoptera: Pteronarcidae) using four leaf species at various stages of conditioning.

2. Materials and methods

Leaves of dogwood *Cornus florida*, red maple *Acer rubrum*, white oak *Quercus alba*, and black locust *Robinia pseudoacacia* were collected just prior to abscission. These species were selected because they are common in Appalachian deciduous forests and represent rapidly (dogwood), intermediate (maple), and slowly (oak) processed leaves (Petersen and Cummins 1974). Black locust was selected because it is a dominant early successional tree species in Appalachian forests. Leaves were air dried and stored in large ventilated bags until needed. Leaves used in the feeding studies were conditioned in the laboratory in trays of aerated stream water at 15°C. Water in the conditioning trays was changed at 2-day intervals. Conditioning was measured by changes in buffer soluble protein content (Sinsabaugh et al. 1981) and oxygen consumption of leaf tissue.

Gravimetric feeding studies were conducted to examine the feeding strategy of *Pteronarcys proteus* using unconditioned, 1 month, and 2 month conditioned leaves of each species. Ingestion rate, assimilation efficiency, and assimilation rate were determined for each leaf species at each conditioning time. Assimilation efficiencies were determined using a gravimetric method (Waldbauer 1968) and calculated as:

$$AE = (1 - E/I) \times 100$$

where I is the weight of food ingested and E is the weight of fecal material egested. Assimilation rate was calculated as the product of assimilation efficiency and ingestion rate.

Pteronarcys nymphs collected from Little Stony Creek (Giles County, Virginia) were returned to the laboratory where they were acclimated in plastic chambers containing aerated stream water at 15°C. After 1 week, two nymphs were placed in each of 6 plastic chambers (13 × 8 × 6 cm) containing aerated filtered

stream water. Nymphs were permitted to feed on pre-weighed discs of unconditioned, 1 month conditioned, or 2 month conditioned leaf material for several days. Concurrently, three chambers containing leaves but no nymphs were used to determine leaf weight loss due to handling, leaching, and microbial activity. Each day, nymphs and uningested leaf material were transferred to chambers containing freshly filtered stream water, and egested material was collected by filtration onto pre-weighed 0.45 µm Gelman A/E glass fiber filters. Nymphs were allowed to feed until significant ingestion occurred, but feeding periods never exceeded 8 d. At the end of the feeding period, uningested leaf material was removed from the chambers, dried at 50°C for 24 h, and weighed. Nymphs were permitted to clear their guts for 48 h, then egested material was filtered, dried, and weighed. Subsamples of leaf material and egested material were combusted (550°C, 20 min) to determine ash free dry weight. These values were corrected for changes in control chambers, and ingestion rates, assimilation efficiencies, and assimilation rates were computed. The entire procedure was performed four times for each set of 12 nymphs. Nymphs were then sacrificed and their dry weights were determined.

3. Results

Microbial respiration increased on all leaf species during the first 15–20 d of conditioning and remained relatively constant thereafter. Soluble protein content of dogwood leaves increased with conditioning time. The other leaf species exhibited initial net losses in soluble protein which were later offset by what was apparently increased microbial protein. These results indicate that our laboratory conditioning process was analogous to conditioning in streams.

3.1. Assimilation efficiency

Assimilation efficiencies of *Pteronarcys proteus* feeding on unconditioned leaves were 18.5%, 19.1%, and 13.4% for oak, maple, and dogwood, respectively (Fig. 1). Multiple comparisons were used to test for significant differences ($P < 0.05$) among means (Sokal and Rohlf 1969). Differences between assimilation efficiencies of the three species were not significant. Because ingestion rates of unconditioned oak, maple, and locust leaves were extremely low, collection of fecal material was difficult. For this reason, the number of samples used to determine the assimilation efficiency of unconditioned oak and maple leaves was low. Reliable collection of locust egesta was not possible.

With 1 month of conditioning, mean assimilation efficiencies were 19.1, 19.4, 11.7 and 17.4% for oak, maple, locust, and dogwood, respectively. Differences between oak, maple, and dogwood were not significant but values for these species were significantly

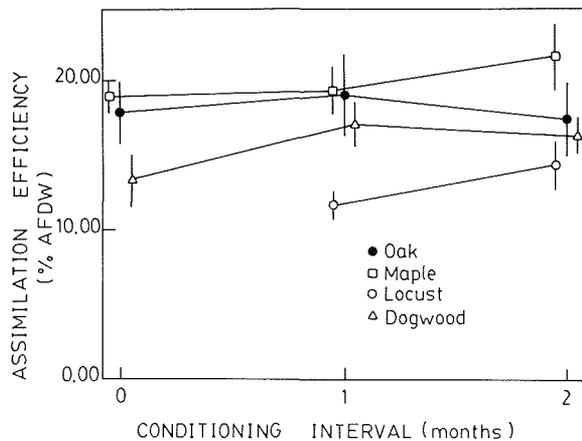


Fig. 1. Assimilation efficiencies of *Pteronarcys* feeding on unconditioned and conditioned leaves (mean \pm standard error).

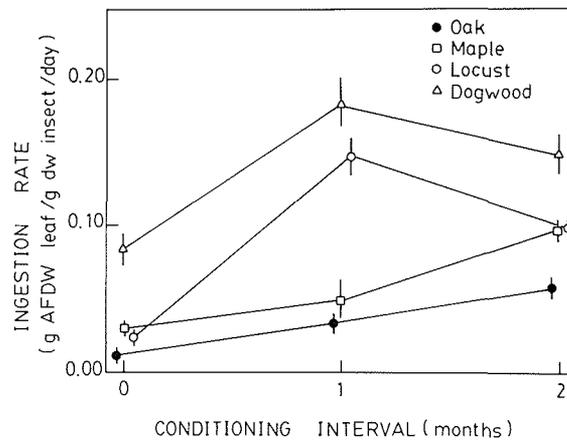


Fig. 2. Ingestion rates of *Pteronarcys* feeding on unconditioned and conditioned leaves (mean \pm standard error).

($P < 0.05$) higher than that of locust leaves. After two months of conditioning, mean assimilation efficiencies were 17.6, 21.9, 14.5, and 16.2% for oak, maple, locust, and dogwood, respectively. The assimilation efficiency of maple leaves was significantly ($P < 0.05$) higher than those of locust and dogwood leaves. No other differences were significant.

Assimilation efficiencies of dogwood and oak increased slightly after one month of conditioning, then declined slightly after two months. The assimilation efficiency of maple and locust leaves increased slightly after 2 months of conditioning. However, there were no statistically significant increases in the assimilation efficiencies of any leaf species with conditioning.

3.2. Ingestion rate

Ingestion rates of *Pteronarcys proteus* ranged from 0.013 to 0.086 g AFDW leaf/g DW insect/day (Fig. 2). As previously discussed, insects ingested unconditioned oak, maple, and locust leaves very slowly. The mean ingestion rate of unconditioned dogwood leaves was significantly higher ($P < 0.05$) than the other species. After 1 month of conditioning the mean ingestion rates of the 4 leaf species ranged from 0.037 to 0.185 g AFDW leaf/g DW insect/day. *Pteronarcys* ingested dogwood leaves at a significantly higher rate than the other leaf species ($P < 0.05$). Locust leaves were intermediate, i.e. they were ingested significantly ($P < 0.05$) slower than dogwood but much faster than oak and maple. After 2 months of conditioning, ingestion rates of the 4 leaf species ranged from 0.059 to 0.157 g AFDW leaf/g DW insect/day. Dogwood leaves were ingested more rapidly than any of the other species. Locust and maple were ingested at rates significantly lower than dogwood but greater than oak ($p < 0.05$).

Pteronarcys ingested all leaf species faster after 1

month of conditioning. The increases were significant for dogwood and locust leaves. Oak and maple ingestion rates increased with 2 months of conditioning. The increase was significant for maple ($P < 0.05$) but not for oak. The ingestion rate of 2 month conditioned oak leaves was significantly greater than the ingestion rate of unconditioned oak leaves. Ingestion rates of dogwood and locust leaves decreased with a second month of conditioning. This decline was significant for locust but not for dogwood. Based on ingestion rates, *Pteronarcys proteus* exhibited a distinct preference for dogwood leaves over any other species offered during the 2 month conditioning period.

3.3. Assimilation rates

Assimilation rates of the 4 leaf species by *Pteronarcys* varied in a pattern similar to ingestion rates. This reflects the importance of ingestion rate in the response of *Pteronarcys* to variations in food quality. Mean assimilation rates of unconditioned leaves were 2.3, 5.9, and 11.5 mg AFDW leaf/g DW insect/day for oak, maple, and dogwood, respectively (Fig. 3). The assimilation rate for dogwood leaves was significantly ($P < 0.05$) higher than for oak leaves. Differences between maple-oak, and maple-dogwood were not significant. Mean assimilation rates of 1 month conditioned leaves were 7.1, 9.6, 16.9, and 32.2 mg AFDW leaf/g DW insect/day for oak, maple, locust, and dogwood leaves, respectively. The assimilation rate of dogwood was significantly faster than the other leaf species ($P < 0.05$): locust was intermediate and was significantly greater than oak or maple leaves. Mean assimilation rates of 2 month conditioned leaves were 10.3, 21.5, 17.0, and 25.3 for oak, maple, locust, and dogwood leaves, respectively. The assimilation rate of oak was significantly slower than for the other species ($P < 0.05$).

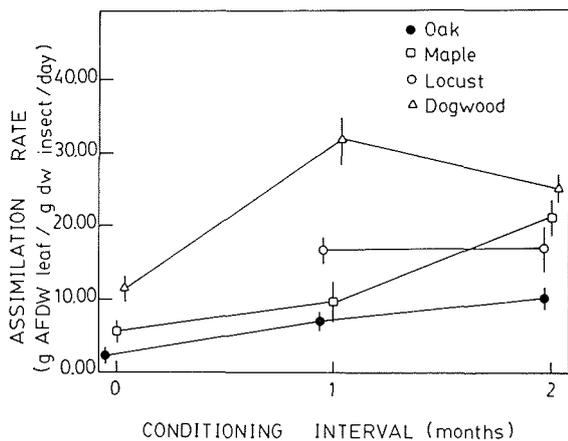


Fig. 3. Assimilation rates of *Pteronarcys* feeding on unconditioned and conditioned leaves (mean \pm standard error).

Oak and maple were assimilated at higher rates with longer conditioning periods. Assimilation rates of 2 month conditioned leaves were significantly faster than unconditioned leaves for both species. The assimilation rate of dogwood leaves increased sharply after one month of conditioning, but there was a significant decline ($P < 0.05$) after 2 months of conditioning. Assimilation data were not available for unconditioned locust, however, the assimilation rate of locust leaves was not significantly different between one and two months.

4. Discussion

Pteronarcys nymphs ate all of the leaf species offered as a food source, however, they preferred some species over others. Based on rates of ingestion and assimilation, dogwood leaves were preferred at all levels of conditioning. Assuming food quality is reflected by preference, dogwood leaves were highest in food quality among the four species tested. Of the remaining species, oak leaves were lowest in food quality, and maple and locust leaves were intermediate. In general, conditioning did not appear to influence assimilation efficiency of any of the four leaf species tested and we conclude that assimilation efficiency is a poor measure of food quality. Similar preferences for dogwood, red maple, and white oak leaves were exhibited by the nymphs of *Plecoptera* (Wallace et al. 1970).

Differences in food quality among the four leaf species as measured by ingestion rates and assimilation rates appear to be correlated with previously reported rates of leaf breakdown. Dogwood leaves breakdown rapidly, maple leaves breakdown at intermediate rates, and oak leaves breakdown slowly (Petersen and Cummins 1974). We found no studies reporting the rate of locust leaf breakdown. Differences in breakdown rates have been linked to differences in lignin content and

thus accessibility of leaf material as microbial substrate (Cromack and Monk 1975, Sedell et al. 1975, Triska et al. 1975, Suberkropp et al. 1976, Triska and Sedell 1976, Paul et al. 1978, Sinsabaugh et al. 1981). Dogwood leaves appear to condition rapidly (Golladay 1981), and based on the feeding responses of *Pteronarcys*, reach their nutritional optimum early; maple and locust are intermediate. Oak leaves condition slowly and appear to require prolonged conditioning before they represent a high quality food source.

Pteronarcys appears to react to differences in food quality by altering its feeding rate. The ingestion rates of dogwood and locust leaves increased greatly after 1 month of conditioning. This peak in feeding probably corresponded to peaks of microbial activity and biomass. The ingestion rates of maple and oak leaves increased less rapidly, apparently a result of their more refractory chemical composition and thus greater resistance to microbial colonization and conditioning.

As mentioned in the introduction, it has been suggested that detritivore feeding strategies have evolved to optimize protein intake. However, proteins in detritus, especially leaves of vascular plants, are often complexed with plant phenolics and structural polymers which reduce the availability of protein as a nitrogen source for insects (Feeney 1970). Several nutritional strategies have been proposed as ways in which detritivores circumvent this problem. One is the selective ingestion of protein rich elements from detrital material. This is often demonstrated as feeding preferred for detrital material with high quantities of microbial or algal cells (Hargrave 1970, Bärlocher and Kendrick 1973a, 1973b, 1975, Nilsson 1974, Calow 1975, Kostalos and Seymour 1976, Rossi and Fano 1979). A second proposed strategy is a partial dietary switch to carnivory in which calories obtained from detritus are supplemented by protein rich animal tissue (Anderson 1976, Fuller and Mackay 1980). While a nitrogen source is certainly important to consumers, a carbon source is also essential, and Bowen (1979) suggested that there is an optimum balance between nitrogen and carbon. Sinsabaugh (1980) and R. Sinsabaugh, E. Benfield and A. Linkins (unpubl. data) found that *Pteronarcys proteus* and other stream detritivores digest and assimilate leaf polysaccharides using either acquired microbial enzymes or enzymes produced by endosymbionts. These findings suggest that at least some detritivores have the ability to use leaves as an energy source.

Our investigation suggests that *Pteronarcys proteus* is probably not limited by an organic energy source. When confronted with a relatively unconditioned food source, nymphs ingested leaf material at low rates. Low ingestion rates tend to increase gut residence times of detrital material. Since microbes are absent or scarce on unconditioned detritus, long gut residence times present a greater opportunity for gut enzymes of some detritivores to degrade leaf structural material, (e.g. Hargrave 1970, Nilsson 1974, Bowen 1979). This strategy ap-

pears to enable detritivorous organisms to fulfill short term energy requirements on otherwise nutritionally inadequate food sources. When conditioned leaf material was available, *Pteronarcys* fed rapidly, as predicted by the models of Taghon (1981). Rapid ingestion permits large quantities of material to pass through the gut. Since conditioned material is composed of partially degraded plant material and microbial cells (Bärlocher and Kendrick 1975), it may be readily digested by the insects. As a result, assimilation efficiencies do not decrease significantly even though gut residence times are reduced. However, assimilation efficiencies do not increase with conditioning due to the rapid rate at which detrital material passes through the gut. This type of feeding strategy is advantageous for an organism not limited by an organic energy source because it maximizes ingestion of protein and other micronutrients essential for growth. Even though assimilation efficiency does not increase with leaf conditioning, the assimilation efficiency of protein and other microbial components is probably very high (Hargrave 1970, Bärlocher and Kendrick 1973a, 1973b, 1975, Kofoed 1975, Prus 1976).

This investigation is in agreement with previous studies in demonstrating that detritivorous organisms prefer well conditioned detritus (Bärlocher and Kendrick 1973a, 1973b, 1975). This conclusion along with information on leaf decay rates has led to the proposal of a leaf processing continuum (Petersen and Cummins 1974, Boling et al. 1975). In short, it states that leaves become conditioned in a stepwise manner related to their resistance to microbial metabolism. The effect of the continuum is to temporally partition detrital availability in streams. Any disturbance to deciduous forest systems which alters patterns of terrestrial vegetation could have a serious impact on stream consumers by reducing food resources (e.g. Benfield et al. 1977). For example logging, a common disturbance to deciduous forest systems, significantly alters leaf inputs to streams (Webster and Waide 1982). Dominant species are replaced by successional species like black locust. This study has demonstrated that locust leaves are palatable to stream consumers. However, they reach a nutritional optimum and decline in food quality relatively rapidly as compared to the leaves they replace. Since life cycle timing and growth of shredders is determined by food availability (Cummins and Klug 1979), and food quality (Otto 1974, 1981, Anderson and Cummins 1979, Ward and Cummins 1979), the absence of slowly conditioned leaf species in a disturbed system could seriously reduce the chances for successful completion of aquatic insect life cycles.

Acknowledgements – We thank Dr. J. Reese Voshell for his comments on early drafts of the manuscript. Financial support for this project came from the National Science Foundation and the U.S. Forest Service.

References

- Anderson, N. H. 1976. Carnivory by an aquatic detritivore, *Clistoronia magnifica* (Trichoptera: Limnephilidae). – *Ecology* 57: 1081–1085.
- and Grafius, E. 1975. Utilization and processing of allochthonous material by stream Trichoptera. – *Verh. Int. Verein. Limnol.* 19: 3083–3088.
- and Cummins, K. W. 1979. Influences of diet on the life histories of aquatic insects. – *J. Fish. Res. Bd Can.* 36: 335–342.
- Baker, J. H. and Bradnam, L. A. 1976. The role of bacteria in the nutrition of aquatic detritivores. – *Oecologia, Berl.* 24: 95–104.
- Bärlocher, F. and Kendrick, B. 1973a. Fungi in the diet of *Gammarus pseudolimnaeus* (Amphipoda). – *Oikos* 24: 295–300.
- and Kendrick, B. 1973b. Fungi and food preferences of *Gammarus pseudolimnaeus*. – *Arch. Hydrobiol.* 72: 501–516.
- and Kendrick, B. 1975. Assimilation efficiency of *Gammarus pseudolimnaeus* (Amphipoda) feeding on fungal mycelium or autumn-shed leaves. – *Oikos* 26: 55–59.
- Benfield, E. F., Jones, D. S. and Patterson, M. F. 1977. Leaf pack processing in a pastureland stream. – *Oikos* 29: 99–103.
- Boling, R. H., Goodman, E. D., Van Sickle, J. A., Cummins, K. W., Petersen, R. C. and Reice, S. R. 1975. Toward a model of detritus processing in a woodland stream. – *Ecology* 56: 141–151.
- Bowen, S. H. 1979. A nutritional constraint in detritivory by fishes: The stunted populations of *Sarotherodon mossambicus* in Lake Sibaya, South Africa. – *Ecol. Monogr.* 49: 17–31.
- Calow, P. 1975. The feeding strategies of two freshwater gastropods, *Ancylus fluviatilis* Mull. and *Planorbis contortus* Linn. (Pulmonata), in terms of ingestion rates and absorption efficiencies. – *Oecologia, Berl.* 20: 33–49.
- Cromack, K. Jr. and Monk, C. D. 1975. Litter production, decomposition, and nutrition cycling in a mixed hardwood watershed and a white pine watershed. – In: F. G. Howell, J. B. Gentry and M. H. Smith (eds.). *Mineral Cycling in Southeastern Ecosystems*. ERDA Symposium Series. (CONF-740513), pp. 609–624.
- Cummins, K. W. and Klug, M. J. 1979. Feeding ecology of stream invertebrates. – *Ann. Rev. Ecol. Syst.* 10: 147–172.
- Feeny, P. 1970. Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. – *Ecology* 51: 565–581.
- Fuller, R. L. and Mackay, R. J. 1980. Feeding ecology of three species of *Hydropsyche* (Trichoptera: Hydropsychidae) in southern Ontario. – *Can. J. Zool.* 58: 2239–2251.
- Golladay, S. W. 1981. The relationship between microbial conditioning of leaf litter and food utilization by an aquatic detritivore. – M.S. Thesis. Va. Polytech. Inst. and State Univ., Blacksburg.
- Hargrave, B. T. 1970. The utilization of benthic microflora by *Hyalella azteca* (Amphipoda). – *J. Anim. Ecol.* 39: 427–437.
- 1971. An energy budget for a deposit feeding amphipod. – *Limnol. Oceanogr.* 16: 99–103.
- Kaushik, N. K. and Hynes, H. B. N. 1978. Experimental study on the role of autumnshed leaves in aquatic environments. – *J. Ecology* 52: 222–243.
- and Hynes, H. B. N. 1971. The fate of dead leaves that fall into streams. – *Arch. Hydrobiol.* 68: 465–515.
- Kofoed, L. H. 1975. Feeding biology of *Hydrobia ventrosa* (Montagu). I. The assimilation of different components of the food. – *J. Exp. Mar. Biol. Ecol.* 19: 233–241.
- Kostalos, M. and Seymour, R. L. 1976. Role of microbial enriched detritus in the nutrition of *Gammarus minus* (Amphipoda). – *Oikos* 27: 512–516.

- Martin, M. M. 1979. Biochemical implications of insect mycophagy. – *Biol. Reviews* 54: 1–21.
- , Martin, J. S., Kukor, J. J. and Merritt, R. W. 1980. The digestion of protein and carbohydrate by the stream detritivore, *Tipula abdominalis* (Diptera: Tipulidae). – *Oecologia*, Berl. 46: 360–364.
- Nielsson, L. M. 1974. Energy budget of a laboratory population of *Gammarus pulex* (Amphipoda). – *Oikos* 25: 35–42.
- Otto, C. 1974. Growth and energetics in a larval population of *Potamophylax cingulatus* (Steph.) (Trichoptera) in a south Swedish stream. – *J. Anim. Ecol.* 43: 339–361.
- 1981. Food related adaptations in stream living caddisfly larvae feeding on leaves. – *Oikos* 37: 117–122.
- Paul, R. W., Benfield, E. F. and Cairns Jr., J. 1978. Effects of thermal discharge on leaf decomposition in a river ecosystem. – *Verh. Int. Verein. Limnol.* 20: 1759–1766.
- Prus, T. 1976. Experimental and field studies on the ecological energetics of *Asellus aquaticus* (Isopoda): I. Assimilability of lipids, proteins, and carbohydrates. – *Ekologia Polska*. 24: 461–472.
- Petersen, R. C. and Cummins, K. W. 1974. Leaf processing in a woodland stream. – *Freshwat. Biol.* 4: 343–368.
- Rossi, L. and Fano, A. E. 1979. Role of fungi in the trophic niche of the congeneric detritivores *Asellus aquaticus* and *A. coxalis*. – *Oikos* 32: 380–385.
- Sedell, J. R., Triska, F. J. and Triska, N. S. 1975. The processing of conifer and hardwood leaves in two coniferous forest streams: I. Weight loss and associated invertebrates. – *Verh. Int. Verein. Limnol.* 19: 1617–1627.
- Sinsabaugh, R. L. III. 1980. Distribution of microbial and macroinvertebrate cellulolytic activity in relation to leaf processing in a headwater stream. – M.S. Thesis. Va Polytech. Inst. and State Univ., Blacksburg.
- , Benfield, E. F. and Linkins III, A. E. 1981. Cellulase activity associated with decomposition of leaf litter in a woodland stream. – *Oikos* 36: 184–190.
- Sokal, R. R. and Rohlf, F. J. 1969. *Biometry*. – Freeman, San Francisco. 776 p.
- Suberkropp, K. F. and Klug, M. J. 1974. Decomposition of deciduous leaf litter in a woodland stream. I. A scanning electron microscope study. – *Microbial Ecol.* 1: 96–103.
- and Klug, M. J. 1976. Fungi and bacteria associated with leaves during processing in a woodland stream. – *Ecology* 57: 720–727.
- , Godshalk, G. L. and Klug, M. J. 1976. Changes in the chemical composition of leaves during processing in a woodland stream. – *Ecology* 57: 720–727.
- Taghon, G. L. 1981. Beyond selection: Optimal ingestion rate as a function of food value. – *Am. Nat.* 118: 202–214.
- Triska, F. J. 1970. Seasonal distribution of aquatic hyphomycetes in relation to the disappearance of leaf litter from a woodland stream. – Ph. D. Dissertation, Univ. of Pittsburg, Pittsburg.
- , Sedell, J. R. and Buckley, B. 1975. The processing of conifer and hardwood leaves in two coniferous forest streams: II. Biochemical and nutrient changes. – *Verh. Int. Verein. Limnol.* 19: 1628–1639.
- and Sedell, J. R. 1976. Decomposition of four species of leaf litter in response to nitrate manipulation. – *Ecology* 57: 783–792.
- Vannote, R. L. 1969. Detrital consumers in natural systems. – In: Cummins, K. W. (ed.). AAAS Symp. Tech. Rep. Michigan State Univ. Inst. Water Res. No. 7.
- Waldbauer, G. P. 1968. The consumption and utilization of food by insects. – *Adv. Insect Physiol.* 5: 229–288.
- Wallace, J. B., Woodall, W. R. and Sherberger, F. F. 1970. Breakdown of leaves by feeding of *Peltoperla maria* (Plecoptera: Peltoperlidae). – *Ann. Ent. Soc. Am.* 63: 563–567.
- Ward, G. M. and Cummins, K. W. 1979. Effects of food quality on growth of a stream detritivore *Paratendipes albimanus* (Meigen) (Diptera: Chironomidae). – *Ecology* 60: 57–64.
- Webster, J. R. and Waide, J. B. 1982. Effects of forest clear-cutting on leaf breakdown in a southern appalachian stream. – *Freshwat. Biol.* 12: 331–344.
- Witcamp, M. 1966. Decomposition of leaf litter in relation to environment, microflora, and microbial respiration. – *Ecology* 47: 194–201.
- Wotton, R. S. 1978. Growth, respiration, and assimilation of blackfly larvae in a lake-outlet in Finland. – *Oecologia*, Berl. 33: 279–290.