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# THERMAL REGULATION OF FUNCTIONAL GROUPS IN RUNNING WATER ECOSYSTEMS

Progress Report
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## DISCLAIMER

## 1.0. ABSTRACT

Upper and lower thermal limits and temperature dependent growth have been determined for a number of organisms (or populations) representing various functional groups of stream ecosystems (microconsumers, producers and macroconsumers - shredders, collectors, scrapers and predators). Although temperature functions as an overall control parameter, organic substrate (microconsumers) and inorganic nutrients (microconsumers and producers), light (producers) and food quality (macroconsumers) can modify thermal responses. Stream microorganisms typically grow below their thermal optima, community composition being determined by those that can manage the maximum growth at a given temperature utilizing a given organic substrate. Producers in first to third order streams are generally light limited (although nutrient availability is also important). Food quality, primarily a function of microbial biomass in the case of detritivores, can compensate for temperature dependent growth in non-predator macroinvertebrate functional groups.

## 2.0 INTRODUCTION

The research under contract E(11-1)-2002 encompassed two general objectives:

1) The establishment of lower and/or upper thermal limits, within the normal stream temperature range of 0-26°C, and degree-day (cumulative temperature) relationships for representatives of three broad functional groups - a) macroconsumers (shredders, collectors, scrapers [=grazers] and predators), b) producers (attached algae) and c) microconsumers (fungi and bacteria).

2) The determination of lability of the thermal control with respect to nutritional differences (macroconsumer food, producer nutrients N and P , microconsumer organic substrates).

Data were collected on all three major groups, macroconsumers, producers and microconsumers, a considerable portion of which has not been completely analyzed. Analyses are accomplished with the aid of a Hewlett-Packard mini-computer system. Since the mini-computer facility is presently taxed to its limit, data analysis and manipulation are running behind both field and laboratory data collection.

However, from preliminary inspection and analysis of data, it appears that organisms (or populations) representing the functional groups identified above can be defined as eurytherms (growth over essentially the entire range of stream temperatures) or stenotherms (growth, over a restricted thermal range), both types exhibit temperature-dependent growth, and that nutritional (and/or light in the case of producers) regimes can modify the basic temperature responses.

Two stream community bioassays (leaf packs, P/R) and one community analysis procedure (detritus standing crop; Fig. 1) have been developed and used extensively in recent years as an integral part of the lotic investigations conducted at the Kellogg Biological Station.

The processing of leaf litter, in the form of leaf packs designed and positioned in the streams to simulate natural accumulation of leaf litter, is taken as an integrated measure of community processing of coarse particulate organic matter (CPOM). As an integrator of the relationship of community photosynthesis (autotrophy) to total community respiration (heterotrophy) - P/R, or autotrophy/heterotrophy ratio - closed, circulating light and dark chambers are used to make in situ measures of changes in oxygen concentration. The standing crop of detritus is sampled seasonally from a given stream site (never less than 10 days after a major increase in discharge) and separated into six particle sizes. The ash free dry wt. (organic wt.) and respiration of each particle size (at ambient stream temperatures) provides an assessment of the rates of accumulation and decomposition of particulate detritus (particulate organic matter = POM, i.e. both coarse [CPOM] and fine [FPOM] particulate organic matter).

## 3.0 ORGANIC MATTER

As shown in Fig. 2, the stream organic matter derived primarily from the terrestrial environment (the watershed) can be partitioned into three pools. CPOM (particles generally>1-2 mm), FPOM (particles

generally <1-2 mm and >0.5 m) and dissolved organic matter (DOM, < 0.5 m). Primary attention has been directed toward POM; CPOM in leaf pack studies and CPOM-FPOM in standing crop assessments.

## 3.1. Coarse Particulate Organic Matter (CPOM)

The general thermal dependence of the processing of a given type of CPOM, hickory leaves in this case, by a given community structure is shown in Fig. 3. Thus, given the stream-site (community) and leaf litter species (CPOM type) temperature is the general control parameter. However, when different sites, that is different stream communities, are compared (Fig. 4) or when different leaf species at the same site are compared (Fig. 5) the temperature effect is seen to be somewhat less important than the biology. Particularly interesting is the inverse relationship between litter processing and temperature that is characteristic when lower reaches are compared to the headwaters. Although the greater abundance of certain microorganisms such as aquatic hyphomycete fungi in the headwaters is a significant factor in the faster rates of processing per unit of thermal input (degree days) in the headwaters, the dominance of shredders (large particle feeding detritivores) is possibly the most important difference.

The importance of the bioata is also apparent in the comparison of lotic and letic sites shown in Fig. 6. Although the lakes and pond were the warmest, accumulating the most degree-days, the processing rates for hickory leaves in the littoral zones were much slower than those measured in the running waters when compared on the basis of equal temperature intervals.

Therefore, by comparing leaf processing between sites over equal temperature intervals, i.e. % loss per degree day, the relative dominance of community function directed at CPOM utilization can be evaluated. As discussed below, the presence of shredders (which can be expressed as biomass per biomass of leaf litter) is considered to be a major determinant in the differing processing rates.

## 3.2. Fine Particulate (FPOM) and Dissolved (DOM) Organic Matter

Only FPOM was investigated during the contract period and primarily through analysis of standing crop data from a headwater site of Augusta Creek. As shown in Fig. 1, the characteristic autumnal pulses in the most coarse particulates (primarily leaf litter and large leaf fragments) were observed. However, the detrital biomass (ash free dry wt.) was dominated throughout the annual cycle by the finest particle size ( ≤75 µm >0.5 µm). Both the coarsest (>16 mm) and finest ( <75 µm > 0.5 µm) particle sizes exhibited the highest respiration rates. The heavily microbially colonized planar surfaces of leaves and leaf fragments as well as matrix penetration by fungi imparted the high rates to the coarsest size while surface to volume relationships accounted for the high respiration on the smallest particles, which were surface colonized by bacteria.

## 4.0 PRODUCERS

P/R ratios (gross community photosynthesis/total community respiration over a 24 hour period) have been measured at a variety of sites on Augusta Creek and in the experimental stream channels. The relationship to temperature (not fully analyzed yet) essentially reflects the light conditions prevalent at the different Strahler stream order sites. P/R values are less than one in the heavily shaded first order (headwater) streams - which have the coolest temperatures, and equal to or greater than one in the more open, warmer second and third order streams. In Augusta Creek, light saturation of photosynthesis occurs at approximately 1000 ft. candles.

However, temperature does exert a measure of control since blooms of filamentous green algae were produced in the KBS experimental streams by increasing the water temperature from 5 C to 10 C in one channel while light and nutrient concentrations (N and P) remained the same in both. The response was presumed to be due to increased rates of nutrient turnover at the higher temperature.

## 5.0. MICROCONSUMERS

### 5.1. Thermal Relationships of Fungal Species.

A definite seasonal occurrence of the dominant fungal species present on both hickory and oak leaves in Augusta Creek has been documented, and related to temperature. Fig. 7 and 8 indicate the dominant fungal species colonizing leaf material at four week intervals throughout an annual cycle in a third order reach of Augusta Creek. On hickory (Fig. 7), three species, Flagellospora curvula, Lemonniera aquatica and Alatospora acuminata predominated during the cooler months, i.e. when the mean temperature was below 15°C, while one species, Lunulospora curvulua, was present only in the summer when the temperature was above 15°C. Tetracladium marchalianum was present throughout the year and on hickory it was one of the dominant species over all temperature regimes. Similar results were obtained for oak leaves (Fig. 8), although T. marchalianum which was present throughout most of the year on oak, was not one of the dominant fungal species. On oak leaves, L. curvula was joined by Triscelophorus monosporus during the summer months.

As a test of the hypothesis that temperature constitutes the major environmental variable responsible for seasonal shifts in fungal species composition, oak leaf packs were placed at two sites on Augusta Creek which differed principally in their thermal regime. Table 1 indicates the mean temperature and composition of the fungal flora at each site. At site 1, where the mean weekly temperature remained between 10 and 13°C, the dominant fungal species included F. curvula, L. aquatica and A. acuminata, the same species which dominated on oak at site 2 during the fall, winter and spring (Fig. 8). At site 2, which had temperatures in excess of 15°C for most of the study period, the dominant fungal species included L. curvula, T. monosporus and F. penicillioides which were only present on oak during the summer months (Fig. 8). T. marchalianum was a minor species on leaf material

from both sites, as would be expected from the annual data on oak from site 2 (Fig. 8).

The temperature-growth response of isolate of the dominant fungi from Augusta Creek were characterized in cultures (Table 2). Based on temperature characteristics, these fungi can be placed into three groups: (1) species with optima near 20°C, maxima between 25 and 30°C and an ability to grow at 1°C; (2) species with optima of 25-30°C maxima between 30 and 40°C and an inability to grow below 5°C; and (3) one species, Clavariopsis aquatica, which exhibited high optimum (30°C) and maximum (30-35°C) temperatures for growth but could grow at 1°C. All species in group 1 with the exception of T. marchalianum were present on leaves primarily at stream temperatures below 15°C, while T. marchalianum was detected at the full range of environmental temperatures (0-25°C). Species in group 2 were found only in the summer when environmental temperatures exceeded 15°C. C. aquatica was also found throughout the year although it was generally a minor species on both oak and hickory. These data suggest that the environmental temperature is the major control factor influencing the seasonal occurrence of the fungal species in Augusta Creek. Species found during the summer have generally been reported from tropical areas, and inability to grow at temperatures below 5° would account for their absence during the fall and winter months. While the mean temperature of the water rarely exceeds the optimum for growth of group 1 species, maximum temperatures in the environment do approach the higher thermal limits for these species and might explain their decline in the summer.

## 5.2. Microbial Community Thermal Responses

Experiments are currently underway to assess the effect of temperature on the respiratory activity of the microbial community on leaf material colonized under different temperature regimes.. Respiratory activity of oak and hickory leaf discs cut randomly from leaf packs exposed to environmental temperatures of 5-10°C, and 0-5°C has been determined at 5°C intervals over the range of 5° to 40°C. Preliminary data from these experiments indicate broad maxima for microbial community respiration of 25-30°C with declining activity above 30°C. The temperature-respiration profiles from both the fall and winter experiments appear to be similar. Currently, similar determinations are being made on leaf material colonized by the summer microflora, with leaf material being exposed to environmental temperatures of 15-20°C.

# 6.0 MACROCONSUMERS

## 6.1. Size-Weight Relationships

A major effort was expended in collecting data on size-weight relationships of macroconsumers belonging to all four functional groups, in conjunction with leaf pack, detritus standing crop and P/R chamber sediment studies. These data will allow for a significant increase in the efficiency of handling macroconsumer information, allowing for results to be routinely expressed in biomass terms. Since regression techniques are inappropriate for analysis (because there is no true dependent and independent variable) correlation procedures are being used. One major advantage is the more realistic expression of

confidence intervals which are perpendicular to the major correlation axis rather than the x-axis. The majority of the computer programs required for the analysis have been developed for use on the Hewlett-Packard 2100A mini-computer system at KBS. The relationships developed will allow interconversion of body length, head capsule width (at the eyes), dry weight, ash free dry weight (and in some cases calories) for a given taxon. The practicability of the separation of various body form types within a functional group (i.e. shredders, collectors, scrapers and predators) for generalized size-weight relationships is being investigated.

6.2. Shredder-Collector Feeding and Growth

Data were collected on shredders (Brillia flavifrons, Tipula abdominalis, Kepidostoma costalis and Pycnopsyche guttifer, lepida and scrabripennis) and collectors (Stictochironomus annulicrus and Paratendipes albimanus) during the current contract period. Information related to Brillia is given in Table 3, Stictochironomus in Table 4 and Paratendipes in Table 5 and 6.

In all cases, temperature operated as a major control of annual growth rate (first column Tables 3-5). Measured growth rates, which ranged from about 1 to 16% of the body weight per day (considering only results in which there were weight gains), showed two to eight fold increases with one half to threefold elevations in temperature, when the best food substrates are compared.

Various methods were used to evaluate "food quality" under the assumption that higher microbial biomass associated with detritus constitutes higher food quality. In general, respiration associated with the detritus, ATP content and amount of nitrogen all correlated well with animal growth rates.

Leaf litter, colonized by microorganisms, consistently gave the highest growth rates; whole leaves in the case of the shredder Brillia, ground leaves for the collectors Stictochironomus and Paratendipes. Natural detritus was the poorest food substrate tested, as measured by animal growth. The fact that this is due to sparse microbial densities is corroborated by low respiration, ATP and nitrogen content, although the differences in the latter parameter are extremely small. Shredder (Tipula) feces produced better growth than natural detritus, demonstrating the importance of shredders to collector populations.

Reference to Tables 3-5 indicates that temperature differences between streams or stream reaches could, in fact, be compensated for by adjustments in food quality.

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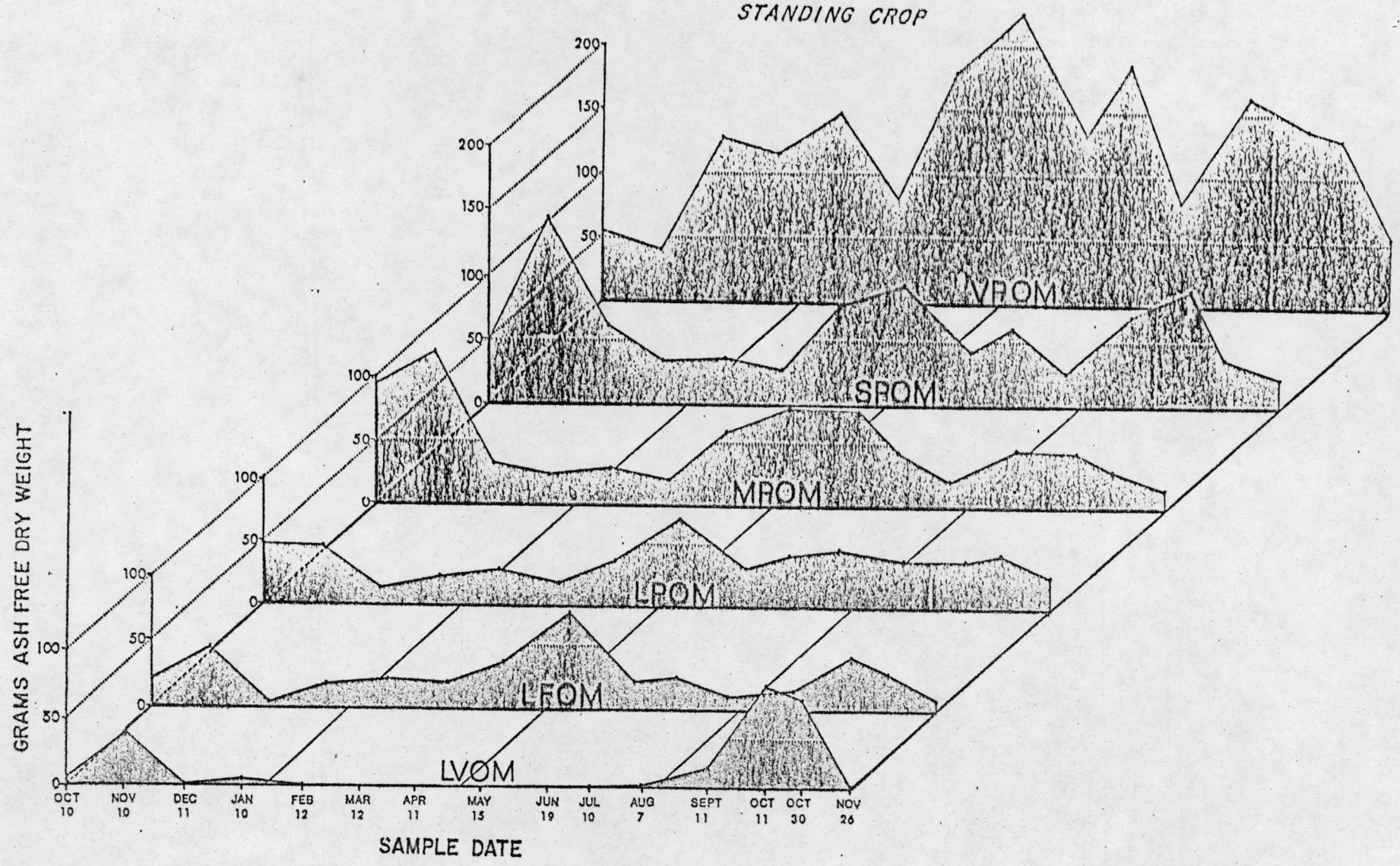


Fig. 1. Standing crop of detritus from the sediments in riffle sections of a headwater stream (Augusta Creek, B Ave., Strahler stream order 1) reported by particle size (LVOM = >16 mm, LFOM = <16>4 mm, LPOM = <4>1 mm, MPOM = <1>0.25, SPOM = <0.25>0.075, VPOM = <0.075>0.0005 mm).

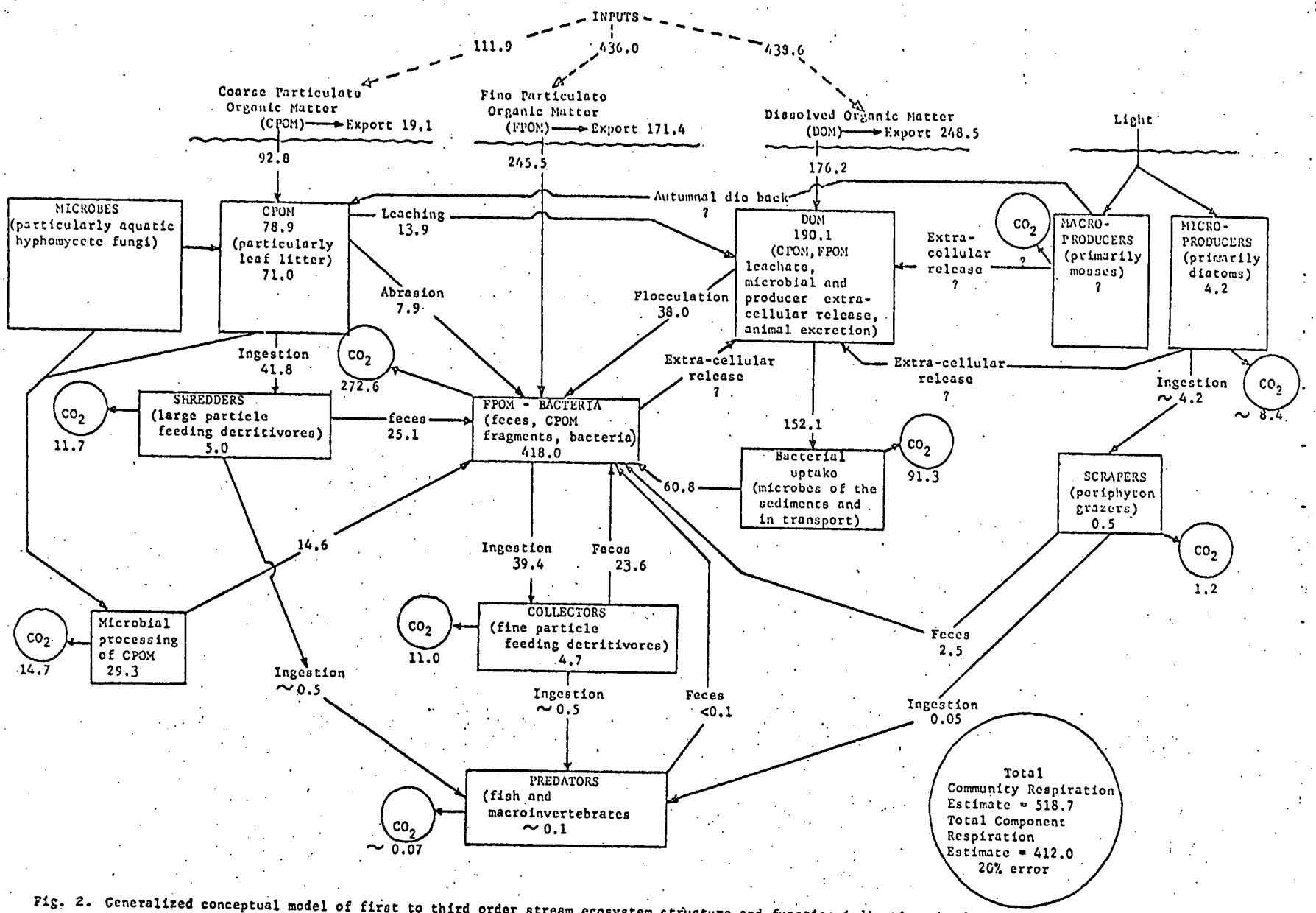


Fig. 2. Generalized conceptual model of first to third order stream ecosystem structure and function indicating the dependence upon particulate and dissolved organic matter inputs and the dominance of functional groups processing such allochthonous organics. Final processing to $CO_2$ by each functional category, export and total respiration are indicated. Values are in grams/$m^2$/yr. estimated for a first order stream in the Augusta Creek watershed (Kalamazoo and Barry Counties, Michigan).

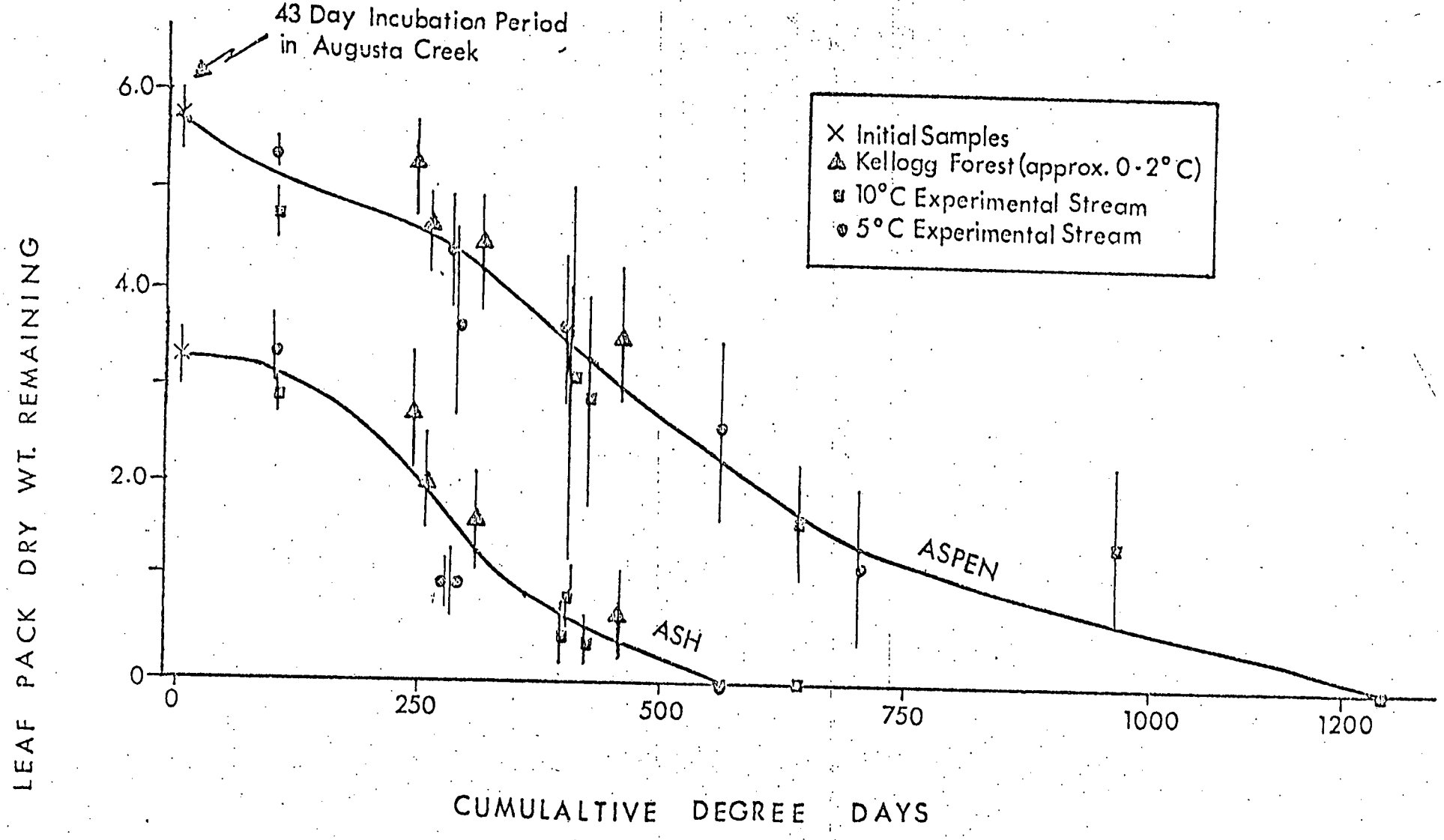


Fig. 3. Thermal dependence of leaf pack converstion rates in Augusta Creek and temperature controlled experimental channels.

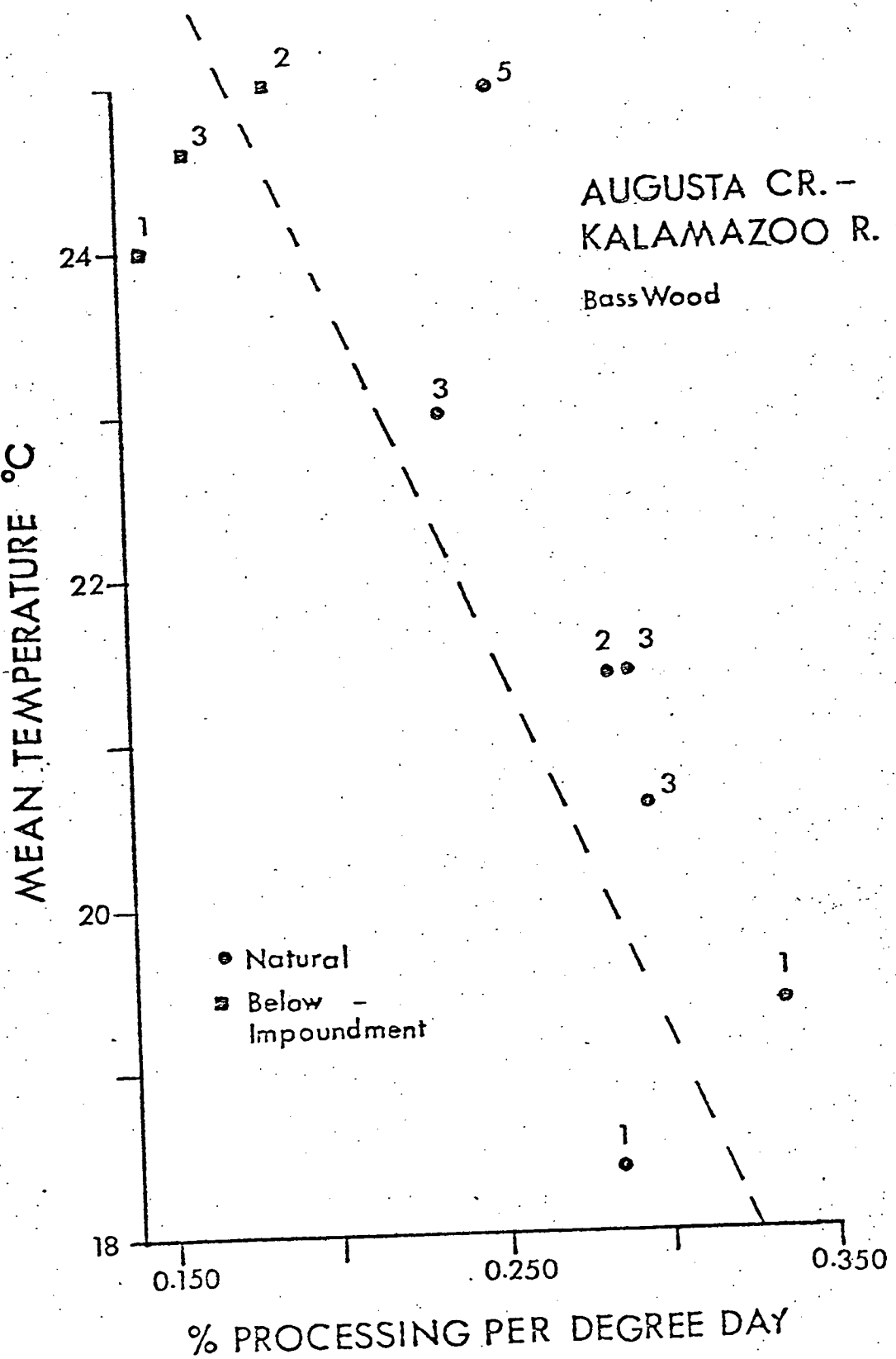


Fig. 4. Relationship of Leaf litter processing rates (as % loss per degree-day) to mean daily temperature over the processing period. The numbers indicate the Strahler stream order of the sites.

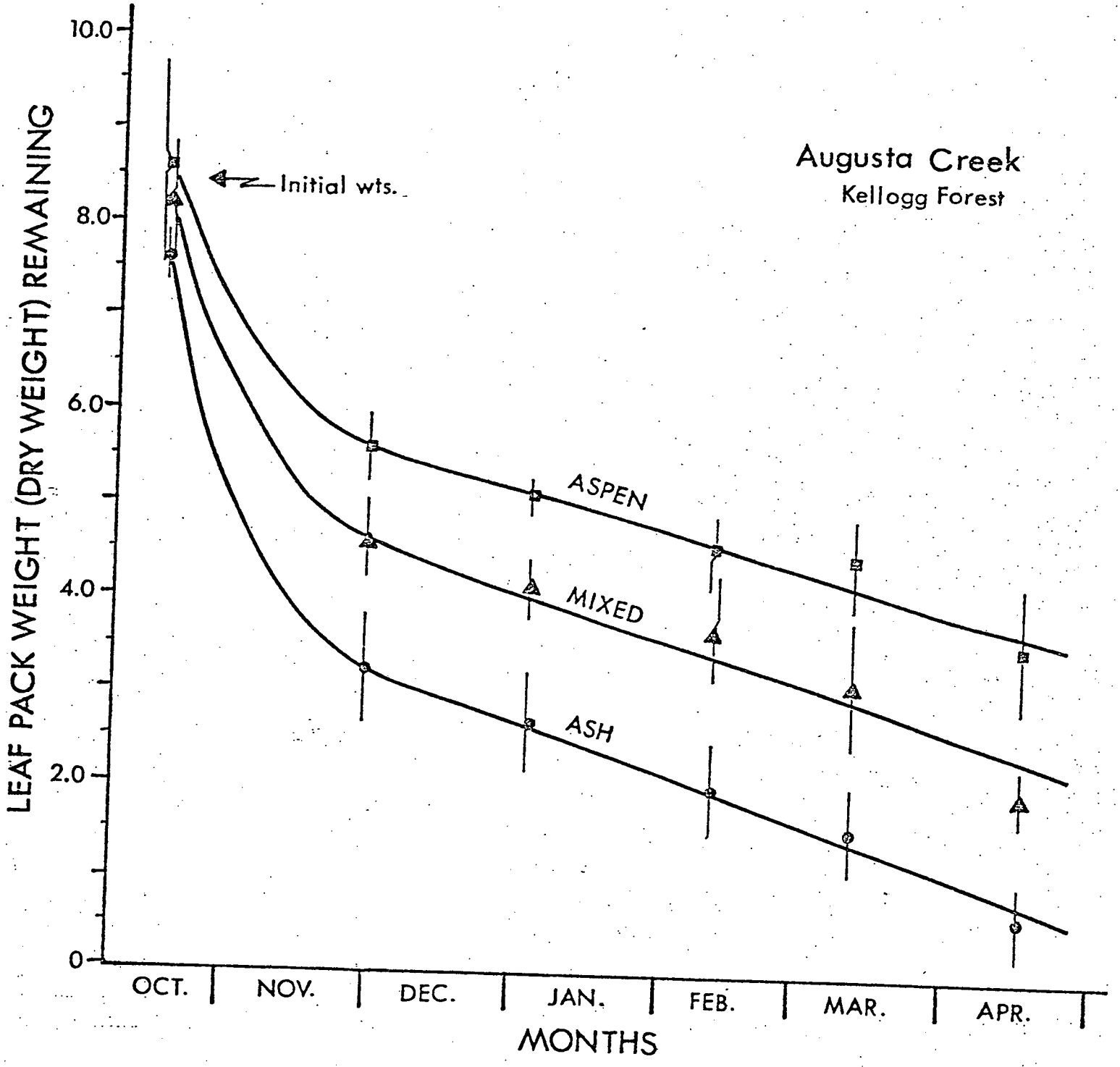


Fig. 5. Comparison of ash, aspen and mixed (50% each) leaf litter processing in the Kellogg Forest reach (Strahler stream order 3) of Augusta Creek.

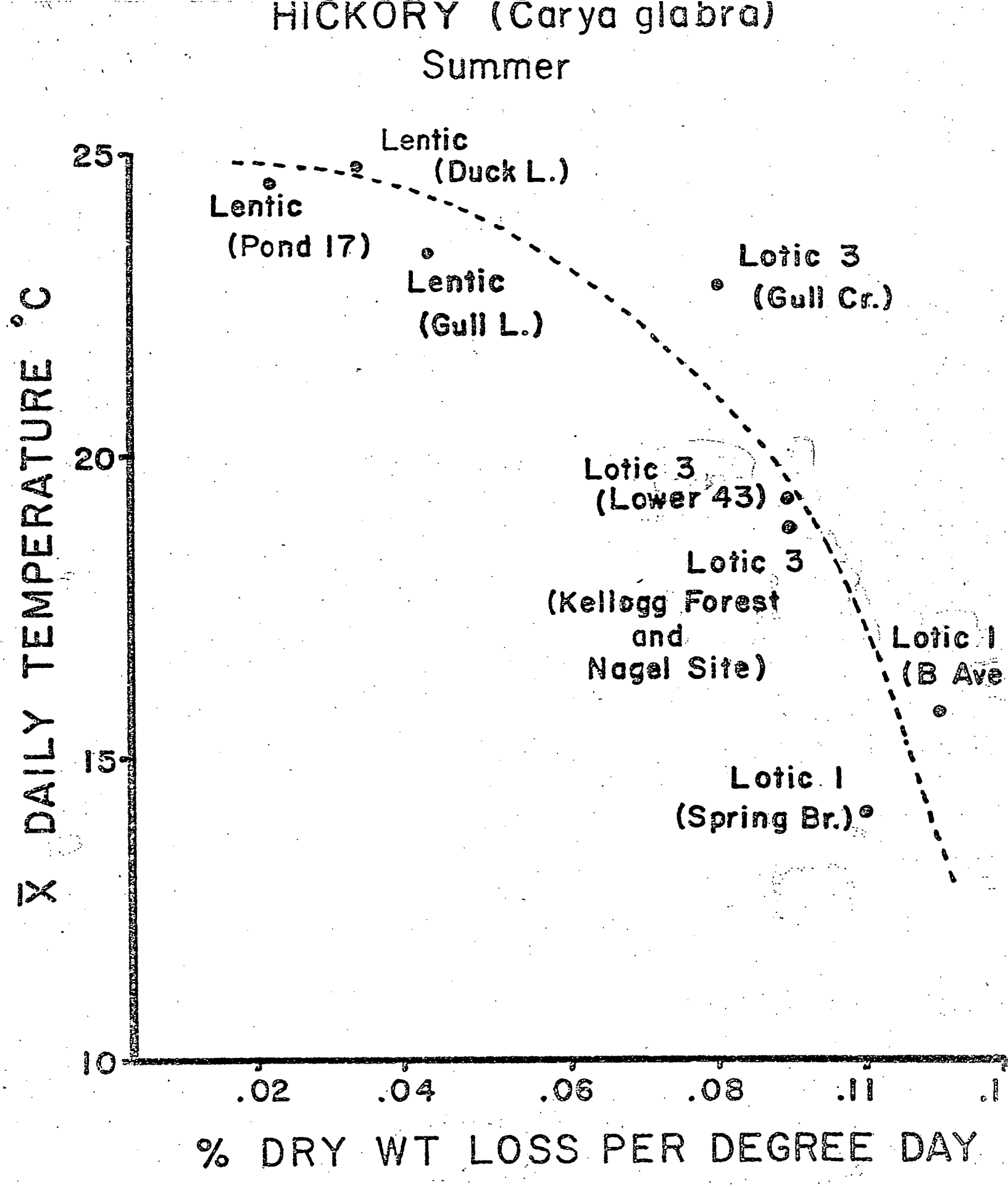


Fig. 6. Comparison of leaf processing rates at various lotic and lentic sites against mean daily temperature. Ten gram hickory leaf packs were followed over a 49 day period (June 17 - Aug. 8, 1975). The numbers indicated for the lotic sites are Strahler stream order. The lentic sites were all in shallow littoral zones (0.5 = 1m) and all packs remained aerobic.

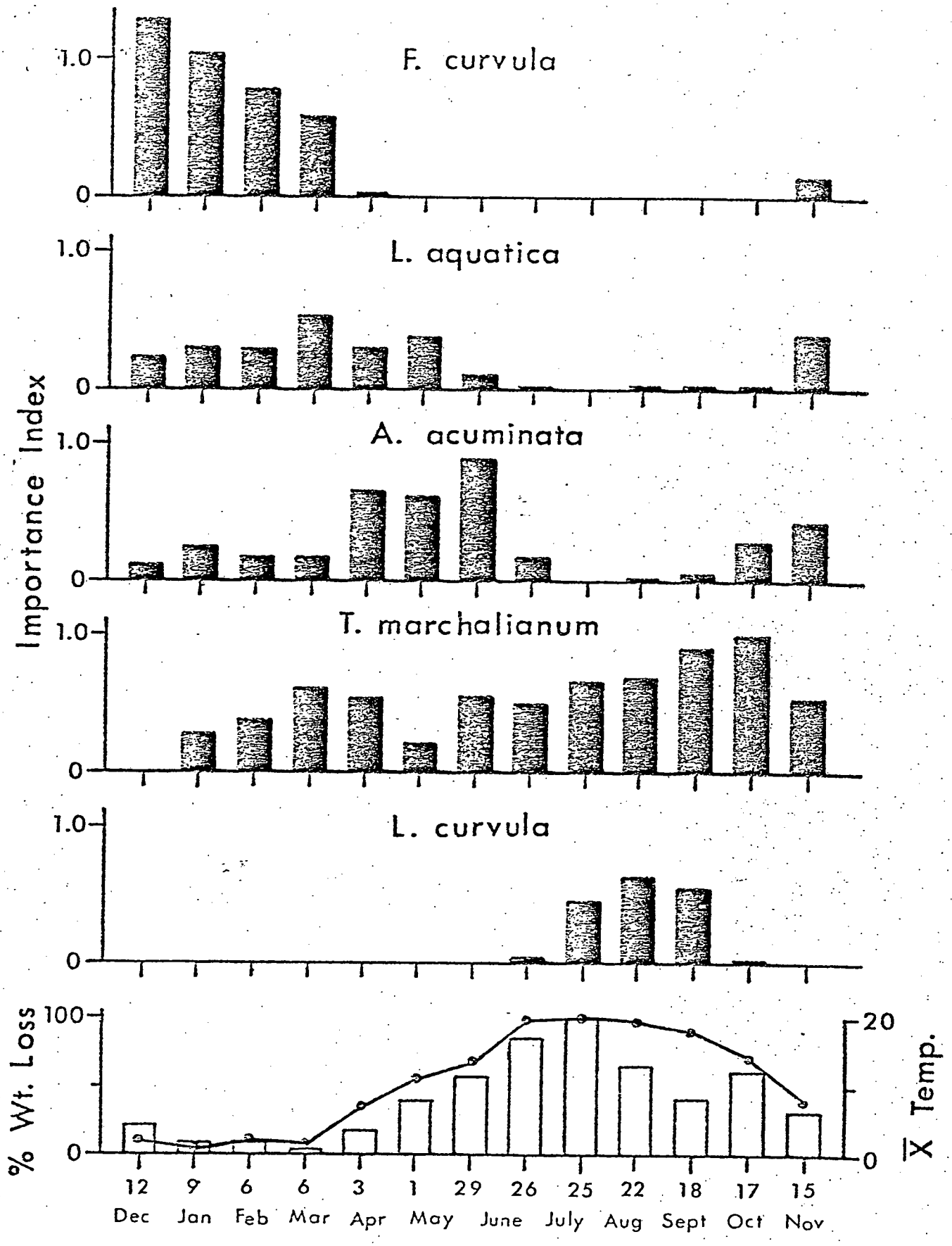


Fig. 7. Season occurrence of aquatic hyphomycetes species on hickory leaves. At each of 13 four week periods leaf packs were removed from Augusta Creek after a four week incubation period and analyzed for the composition of the fungal populations and dry weight. Black histograms represent importance indexes for fungal species, while histograms in bottom graph represent mean weight loss for the four week period. Dots connected with a solid line indicate the mean temperature for each four week period ending at the dates indicated along the x axis.

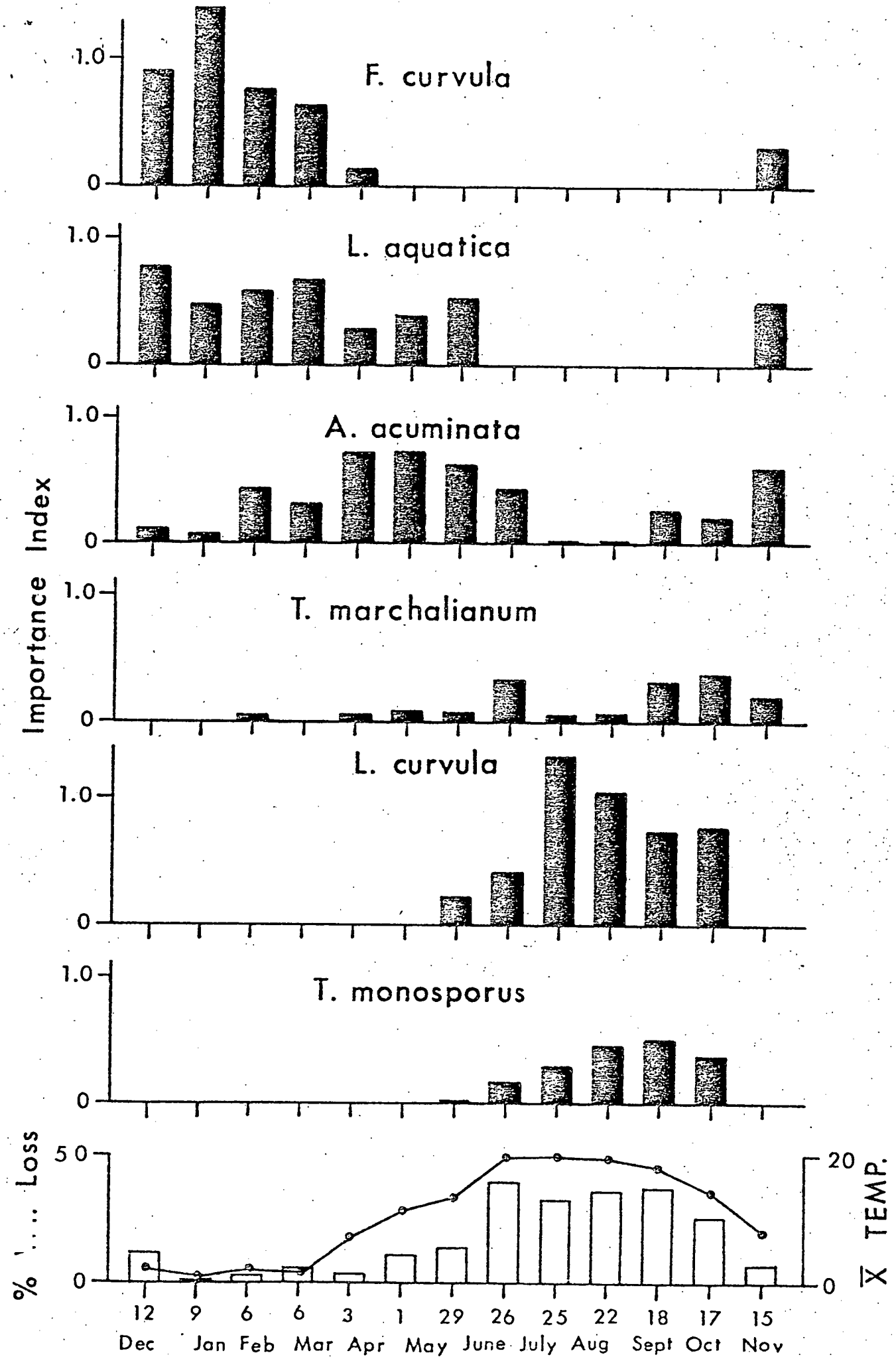


Fig. 8. Seasonal occurrence of aquatic hyphomycete species on oak leaves. For explanation see legend of Fig. 1.

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Table 1. Importance indices of fungal species on oak leaves placed at two sites on Augusta Creek having different temperature regimes.

| Date | | | | | | |
|---|---|---|---|---|---|---|
| Site 1 | 8/20 | 8/27 | 9/3 | 9/10 | 9/18 | 9/24 |
| $\bar{x}$ weekly temp ($^{o}$C) | 11.6 | 11.2 | 12.4 | | 10.8 | |
| Fungal species (importance index) | | | | | | |
| *F. curvula* | 0 | 1.185 | 1.025 | .993 | .438 | .438 |
| *L. aquatica* | 0 | .340 | .168 | .100 | 0 | 0 |
| *A. cuminata* | 0 | .350 | .648 | .716 | .963 | .939 |
| *T. marchalianum* | 0 | .100 | .091 | .054 | .383 | .457 |
| Other | 0 | .025 | .068 | .136 | .168 | .132 |
| Site 2 | | | | | | |
| $\bar{x}$ weekly temp ($^{o}$C) | 18.6 | 18.1 | 21.0 | 17.9 | 14.8 | 12.6 |
| Fungal species (importance index) | | | | | | |
| *L. curvula* | 1.426 | 1.273 | 1.230 | .708 | 1.279 | 1.161 |
| *F. penicillioides* | .196 | .260 | .231 | .216 | .081 | .042 |
| *T. monosporus* | .047 | .217 | .324 | .969 | .396 | .744 |
| *T. marchalianum* | .144 | .090 | .214 | .107 | .162 | 0 |
| Others | .163 | .132 | 0 | 0 | .081 | .042 |

Table 2. Temperature Characteristics of growth of species of Aquatic Hyphomycetes found in Augusta Creek.

| Group 1 | Optimum Temp. | Max. Temp. | Min. Temp. |
|---|---|---|---|
| Flagellospora curvula | 20 | 25-30 | <1 |
| Alatospora acuminata | 20 | 25-30 | <1 |
| Lemonniera aquatica | 20 | 25-30 | <1 |
| Angiullospora longissma | 15-20 | 25-30 | <1 |
| Tetracladium marchalianum | 20 | 25-30 | <1 |
| Group 2 | | | |
| Lumulospora curvula | 25 | 30-35 | 5-10 |
| Clavatospora tentacula | 25 | 30-35 | 10 |
| Flagellospora penicillioides | 30 | 35-40 | 5-10 |
| Group 3 | | | |
| Clavariopsis aquatica | 30 | 30-35 | <1 |

Table 3. Results of growth experiments with Brillia flavifrons (Joh.) at two temperatures on three food types.[1]

| TEMPERATURE and FOOD TYPE[2] | %GAIN/DAY | µl $O_2$/mg/hr[3] | nm ATP/gm[4] | %N[5] | %C | C:N | %ASH |
|---|---|---|---|---|---|---|---|
| 5°C | | | | | | | |
| Ash Leaves | 3.2 | 0.245 | 55.635 | 3.3 | 46.1 | 14.0 | 8.0 |
| Ground Ash | 2.8 | 0.118 | 34.197 | 2.8 | 46.6 | 16.7 | 8.0 |
| Natural Detritus | -0.9 | 0.065 | ------ | 2.1 | 29.8 | 14.4 | 34.0 |
| Natural Detritus (autoclaved) | -1.0 | 0.054 | 0.160 | 2.1 | 29.6 | 14.6 | 34.0 |
| 15°C | | | | | | | |
| Ash Leaves | 16.1 | 0.333 | 83.179 | 3.6 | 45.8 | 12.9 | 8.0 |
| Natural Detritus | -1.6 | 0.083 | 0.090 | 2.0 | 27.9 | 13.9 | 34.0 |

1. Feeding experiments of approximately 2 weeks each.
2. Food type included whole ash leaves (Fraxinus nigra). Remainder of food consisted of fine particulates, size = <1mm and >0.063mm.
3. Respiration with Gilson Respirometers. Data are means of means collected at beginning and end of experiments. Four to fifeteen replications for each mean.
4. ATP procedure of Suberkropp and Klug. Data are means of means collected at beginning and end of experiments. Three to six replications (2 subsamples ea.) for each mean.
5. N and C data with C. Erba CHN Analyzer, Model 1104. Data are means of means from data collected at beginning and end of experiments. Three replications (2 subsamples ea.) for each mean.

Table 4. Results of growth experiments with Stictochironomus annulicrus Townes at two temperatures on three food types.[1]

| TEMPERATURE and FOOD TYPE[2] | %GAIN/DAY | GAIN/DEGREE-DAY mg x $10^{-4}$ | µl $O_2$/mg/hr[3] | nm ATP/gm[4] | %N[5] | %C | C:N | %ASH |
|---|---|---|---|---|---|---|---|---|
| 5°C | | | | | | | | |
| Natural Detritus (no incubation) | -0.6 | -4.49 | 0.041 | 0.014 | 1.9 | 33.2 | 17.6 | 34.0 |
| Natural Detritus | -0.4 | -2.06 | 0.007 | 0.220 | 1.8 | 33.4 | 19.1 | 34.0 |
| Tipula Feces | 1.1 | 5.39 | 0.047 | 0.743 | 1.2 | 48.5 | 39.2 | 16.0 |
| Ground Ash Leaves | 1.3 | 11.56 | 0.064 | 27.859 | 2.6 | 43.1 | 16.6 | 8.0 |
| 15°C | | | | | | | | |
| Natural Detritus | 3.2 | 5.29 | 0.043 | 0.055 | 1.9 | 33.5 | 17.9 | 34.0 |
| Tipula Feces | 8.4 | 11.73 | 0.091 | 0.891 | 1.3 | 47.2 | 37.0 | 16.0 |
| Ground Ash Leaves | 16.3 | 34.48 | 0.187 | 12.516 | 3.3 | 48.4 | 14.3 | 8.0 |

1. Fourteen day feeding experiment with food changed on 7th day to fresh food of equivalent incubation period.
2. Food incubated in laboratory approx. 2 weeks prior to animal intro. Particle size = <1mm but>0.063mm.
3. Respiration with Gilson Respirometers. Data are means of means from data collected at beginning and end of each feeding period. Three to five replications for each mean.
4. ATP procedure of Suberkropp and Klug. Data are means of means from data collected at end of week 1 and 2 and beginning of week 2. Three replications (2 subsamples ea.) for each mean.
5. N and C data with C. Erba CHN Analyzer, Model 1104. Data are means of means from data collected at end of week 1 and 2 and beginning of week 2. Three reps. (2 subs. ea.) for each mean.

Table 5.

Tabular summary of temperature and food relationships in *Paratendipes albimanus* (Diptera: Chironomidae).

| TEMPERATURE | SUBSTRATE TYPE | ANIMAL GROWTH RATE [1] (mg/mg /day) | ATP CONTENT [2] (nM ATP/ g AFDW) | SUBSTRATE RESPIRATION [3] (ul $O_2$/ mg AFDW /hr) | TOTAL N [4] (% dry weight) |
|---|---|---|---|---|---|
| 10° | HICKORY | 0.0741 | 23.56 | 0.175 | 2.91 |
| | OAK | 0.0924 | 16.33 | 0.109 | 1.23 |
| | *TIPULA* FECES | 0.0295 | 2.47 | 0.076 | 1.26 |
| | NATIVE DETRITUS | 0.0247 | nd [5] | 0.030 | 2.10 |
| 15° | HICKORY | 0.1037 | 25.44 | 0.195 | 2.97 |
| | OAK | 0.0970 | 18.60 | 0.126 | 1.64 |
| | *TIPULA* FECES | - | 3.00 | 0.090 | 1.21 |
| | NATIVE DETRITUS | 0.0454 | nd [5] | 0.049 | 2.00 |
| 20° | HICKORY | 0.1113 | 29.83 | 0.252 | 2.85 |
| | OAK | 0.1058 | 17.60 | 0.235 | 1.19 |
| | *TIPULA* FECES | 0.0855 | 4.12 | 0.167 | 1.22 |
| | NATIVE DETRITUS | 0.0269 | nd [5] | 0.052 | 2.07 |

1. Waldbauer, 1968: Relative Growth Rate, mg growth/ mg body weight/day
2. Suberkropp and Klug,
3. Gilson Differential Respirometer
4. Carlo Erba Elemental Analyzer
5. Concentrations below detectible limits

TABLE 6.

Statistical summary of temperature and food relationships in *Paratendipes albimanus* (Diptera: Chironomidae)

| Comparisons Substrate | ATP Content | Substrate Respiration | Growth Rate |
|---|---|---|---|
| Hickory -vs-Oak | *** | * | * |
| Native Detritus-vs-*Tipula* Feces | - | *** | ** |
| Hickory + Oak-vs-*Tipula* Feces + Native Detritus | - | *** | *** |
| Hickory + Oak-vs-*Tipula* Feces | * | - | - |
| Temperature | ns | *** | *** |
| Interaction | ns | ns | * |

* $P < 0.05$
** $P < 0.01$
*** $P < 0.001$
ns not significant
\- not tested