Shifts In Aquatic Insect Populations In A First-Order Southern Appalachian Stream Following A Decade Of Old Field Succession

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Aquatic insects of two first-order southern Appalachian streams were sampled monthly during one year. Sawmill Branch Watershed was subjected to several disturbances before 1968, including clear-cutting. Since 1968 Sawmill Branch Watershed has undergone natural secondary succession from terrestrial vegetation dominated by Gramineae to a herbaceous/coppice hardwood dominated by black locust, Robinia pseudoacacia. Grady Branch, the control stream, drains an undisturbed hardwood watershed. Aquatic insect densities on Sawmill Branch were about twice those of Grady Branch, which represent a dramatic reversal from results obtained by a similar study in 1968. It is suggested that change in riparian vegetation is a major factor influencing long-term changes in aquatic insect populations, and these changes are manifested through a shift toward an allochthonous energy base. The most conspicuous changes in macrobenthos on the disturbed watershed between 1968 and 1978 were a reduction in grazer organisms and a corresponding increase in shredder organisms, especially Peltoperla (Plecoptera).

Key words: macrobenthos, secondary succession, watershed changes, clear-cutting, allochthonous detritus, food quality.


Nous avons prélevé mensuellement pendant un an des échantillons d'insectes aquatiques dans deux cours d'eau de premier ordre du sud des Appalaches. Le bassin hydrographique de la branche Sawmill a subi plusieurs perturbations avant 1968, y compris la coupe à blanc des bois. Depuis 1968, il y a dans ce bassin une succession secondaire naturelle, allant d'une végétation terrestre dominée par des graminées à un complexe herbacées/taillis de bois dur dominé par l'acacia blanc, Robinia pseudoacacia. La branche Grady, le cours d'eau témoin, draine un bassin de bois durs non perturbés. La densité des insectes aquatiques dans la branche Sawmill est environ le double de celle de la branche Grady. Ceci est tout à fait à l'opposé des résultats d'une étude semblable menée en 1968. Nous croyons qu'un changement dans la végétation riveraine est un facteur qui influe beaucoup sur les changements à long terme dans les populations d'insectes aquatiques, et que ces changements se manifestent par un glissement vers une base énergétique allochtonne. Les changements les plus remarquables, entre 1968 et 1978, dans le macrobenthos du bassin perturbé ont été une diminution des organismes brouteurs et une augmentation correspondante des organismes broyeurs, particulièrement Peltoperla (Plecoptera).

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ALLOCHTHONOUS inputs of leaf detritus are the major energy source for benthic invertebrates in most heavily shaded first-order streams (Hynes 1970; 1975; Cummins 1974). Because of dependence on leaf litter and its associated microflora as a food source (Cummins 1973), the distribution of many benthic invertebrates is correlated with that of leaf detritus (Egglishaw 1964; G. W. Minshall 1967; Woodall and Wallace 1972). Other factors including current velocity and substrate composition affect the distribution of benthic invertebrates and detritus (Ulfstrand 1967; Cummins and Lauff 1969; Minshall and Minshall 1977; Rabeni and Minshall 1977).

Woodall and Wallace (1972) investigated benthic insect
communities in four first-order southern Appalachian streams, including hardwood and old-field watersheds. They associated differences in species composition and abundance between the streams, with varying quantity and quality of allochthonous detrital inputs and primary production.

The present study investigates changes in benthic insect communities associated with old-field succession on the surrounding watershed, relying on the work of Woodall and Wallace (1972) on the same streams as baseline data. Current velocity and substrate composition were also investigated because of their effects on distribution of benthic insects (Hynes 1970).

**Study Site**

Grady Branch (Watershed 18) and Sawmill Branch (Watershed 6) are located at the Coweeta Hydrologic Laboratory, Macon Co., North Carolina. Both are first-order streams (~ 0.5—1.5 m in width) with mean depth about 15 cm. Substrate consists of pebbles and cobble (16 to <256 mm in diameter) and sand. Granitic boulder outcrops are prevalent on Sawmill Branch. Grady Branch drains an undisturbed hardwood watershed of 12.46 ha (1 ha = 10 000 m²), with a slope of 52%. Riparian vegetation consists of chestnut oak, red maple, northern red oak, tulip poplar, pignut hickory, and black oak, with a dense understory of rhododendron. Sawmill Branch drains a watershed of 8.86 ha with a slope of 54%.

This watershed was subjected to several perturbations from 1958 to 1968 including a clear-cutting, herbicide treatment, conversion to grass, and heavy fertilization (for a more complete description of watershed disturbances, see Webster and Patten 1979). Since 1968 this watershed has undergone natural secondary succession (cf. Fig 1a and b). Dominant riparian vegetation now includes various herbaceous plant species, black locust, and blackberry. Black locust is currently the dominant tree species with some specimens over 6 m in height. Sapling tulip poplar and oak are now apparent. Some grass species are still present along the stream banks.

Mean annual discharge measured by a V-notch weir is 5.64 L/s for Grady Branch and 3.38 L/s for Sawmill Branch. Water chemistry data (from Swank and Douglass 1975) are summarized in Table 1.

**Materials and Methods**

Each stream was sampled monthly for 1 yr beginning in November, 1977. Each month, six random 0.093 m² Surber samples (mesh size = 250 μm) were taken from six randomly selected sites on each stream. Samples were preserved in the field with 6% formalin containing Phloxine B dye to facilitate sorting (Mason and Yevich 1967). Current velocity measurements were made using a Gessner bag meter (Gessner 1950). The percentage of substrate was estimated visually for each sample and recorded in the field using Cummins' (1962) particle-size categories. These estimates were used to assign each sample to one of four substrate classifications: rock face (boulder or granite outcrop), cobble riffle, pebble—gravel riffle, and sandy reach.

In the laboratory, each sample was washed in a series of sieves, organic matter was decanted from inorganic matter, and insects were sorted at 7 x magnification with a binocular microscope. Detritus was grouped into four categories: aquatic moss, leaf, wood and twig, and fine particulate detritus. Detritus dry weights were obtained after drying in an oven at 60°C for 24 h.

The raw data were transformed into normal equivalent scores so parametric statistical tests could be used (Thorndike 1925). A series of two-way analyses of variance (ANOVA) (Gill 1978), using stream, season, and substrate as control variables, were done to investigate insect distributions.
Table 1. Average annual concentrations (mg/L) of ions in Grady Branch and Sawmill Branch.a

<table>
<thead>
<tr>
<th>Stream</th>
<th>NO₃-N</th>
<th>NH₄-N</th>
<th>PO₄-P</th>
<th>Cl</th>
<th>K</th>
<th>Na</th>
<th>Ca</th>
<th>Mg</th>
<th>SO₄</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grady Branch</td>
<td>0.003</td>
<td>0.004</td>
<td>0.002</td>
<td>0.538</td>
<td>0.461</td>
<td>0.883</td>
<td>0.626</td>
<td>0.296</td>
<td>0.298</td>
</tr>
<tr>
<td>Sawmill Branch</td>
<td>0.672</td>
<td>0.005</td>
<td>0.002</td>
<td>1.296</td>
<td>0.602</td>
<td>1.102</td>
<td>1.107</td>
<td>0.649</td>
<td>0.359</td>
</tr>
</tbody>
</table>

aData from Swank and Douglass (1975).

Table 2. Summary of substrate type, detritus standing crop (g dry wt/m²), and current velocity (cm/s) for Sawmill Branch and Grady Branch.

<table>
<thead>
<tr>
<th>Substrate Type</th>
<th>Sawmill Branch</th>
<th>Grady Branch</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aquatic moss</td>
<td>17</td>
<td>28</td>
</tr>
<tr>
<td>Leaf detritus</td>
<td>170.4</td>
<td>0</td>
</tr>
<tr>
<td>Wood and twig detritus</td>
<td>0</td>
<td>25.3</td>
</tr>
<tr>
<td>Fine detritus</td>
<td>0</td>
<td>57.4</td>
</tr>
<tr>
<td>Current velocity</td>
<td>60.03</td>
<td>53.05</td>
</tr>
</tbody>
</table>

C.R. = cobble riffle; P.G.R. = pebble—gravel riffle; S.R. = sandy reach; and R.F. = rock face. Substrate size-classes: boulder >256 mm; cobble = 64—256 mm; pebble = 16—63 mm; gravel = 2—15 mm; and sand = <2 mm.

Although a number of genera show significant differences between substrate types, these should be interpreted with caution, because detritus abundance varied significantly between substrates. No attempt was made to separate detritus and substrate effects. Therefore, some differences in substrate preference in the following discussion are undoubtedly due both to detritus abundance and/or substrate.

The data are summarized in Table 2 for substrate type, current velocity, and detritus. Because of the random sampling scheme, the number of samples of each substrate type reflects the relative abundances of the substrate types in the streams.

Results and Discussion

SUBSTRATE TYPE, CURRENT VELOCITY, DETRITUS

The random sampling method indicates that rock-face habitats are much more abundant in Sawmill Branch, but the remaining substrate types are similar for each stream.

Current velocity was highest in the rock-face habitats (Table 2), followed by cobble riffles, pebble—gravel riffles, and sandy reach habitats. There was no significant difference (α = 0.05) in current velocity for similar substrate types between the streams.

Moss was restricted to the rock-face habitat in both streams, and standing crops (g dry wt/m²) (Table 2) were 3 times higher on Sawmill Branch than on Grady Branch. High moss standing crops on Sawmill Branch may be due to: (1) potentially higher solar radiation on the large granite outcrop and in this stream, and (2) higher nutrient levels in Sawmill Branch (Table 1). Higher leaf and wood detritus in Grady Branch is attributed to the dense canopy of deciduous trees. Leaf detritus in Sawmill Branch consisted of grass, herbaceous plant leaves, and deciduous leaf detritus. There was no significant difference (α = 0.05) in the standing crop of fine detritus between the two streams.

Although leaf detritus standing crops were higher on Grady Branch, the food quality of leaf detritus must be considered. Black locust, the dominant riparian species along Sawmill Branch is a legume and fixes nitrogen by means of bacteria. High nitrogen levels in leaf litter of black locust (Harlow and Harrar 1958) may result in improved detritus food quality in Sawmill Branch. Iversen (1974) found that higher gross growth efficiency in Sericostoma personatum (Trichoptera: Sericostomatidae) was positively correlated with nitrogen content of detritus. Growth of heterotrophic microorganisms may also be enhanced by the 200X higher NO₃-N content of stream water in Sawmill Branch (Table 1). Concentrations of NO₃-N in Sawmill Branch were even higher than those reported in Table 1 during the November 1977, to October 1978, period of this study (W. Swank, Coweeta Hydrologic Laboratory, Franklin, N.C., personal communication and Coweeta Data Files). Fungi are known to extract soluble N compounds from stream water (Willoughby and Redhead 1973; Kaushik and Hynes 1971), and it has been shown that N and P additions accelerate fungal growth (Bärlocher and Kendrick 1973a). The above factors may potentially increase detritus food quality on Sawmill Branch and enhance larval growth (Cummins and Klug 1979).

Ephemeroptera — Baetis spp. (Baetidae) and Ephemerella spp. (Ephemerellidae) were significantly more abundant in Sawmill Branch than Grady Branch (Table 3). Both genera had significantly higher densities in the rock-face habitat. These genera are mainly fine particle feeders which seasonally ingest algae (Brown 1961; Chapman and Demory 1963; Gilpin and Brusven 1970; Woodall 1972). However, Jones (1949) reported that members of these genera may ingest large quantities of aquatic moss, which may account for higher densities of Baetis and Ephemerella in Sawmill Branch.

Paraleptophlebia sp. (Leptophlebiidae) was most common
TABLE 3. Results of ANOVA for dominant taxa showing stream and substrate preference.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Stream</th>
<th>Substrate</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ephemeroptera</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ephemeraella</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Baenis spp.</td>
<td>S.B.</td>
<td>R.F.</td>
</tr>
<tr>
<td>Paraleptophlebia sp.</td>
<td>G.B.</td>
<td>C.R. and P.G.R.</td>
</tr>
<tr>
<td>Steroneuma sp.</td>
<td>**</td>
<td>C.R.</td>
</tr>
<tr>
<td>Epeorus sp.</td>
<td>**</td>
<td>C.R.</td>
</tr>
<tr>
<td>Plecoptera</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Peltoperla maria</td>
<td>G.B.</td>
<td>**</td>
</tr>
<tr>
<td>Leuctra spp.</td>
<td>G.B.</td>
<td>C.R.</td>
</tr>
<tr>
<td>Alloperla sp.</td>
<td>G.B.</td>
<td>P.G.R. and S.R.</td>
</tr>
<tr>
<td>Nemoura sp.</td>
<td>S.B.</td>
<td>**</td>
</tr>
<tr>
<td>Odonata</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lanthus parvulus</td>
<td>S.B.</td>
<td>C.R. and P.G.R.</td>
</tr>
<tr>
<td>Cordulegaster erroneus</td>
<td>S.B.</td>
<td>S.R.</td>
</tr>
<tr>
<td>Trichoptera</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Parapsyche cardis</td>
<td>S.B.</td>
<td>R.F.</td>
</tr>
<tr>
<td>Diplectrona modesta</td>
<td>**</td>
<td>**</td>
</tr>
<tr>
<td>Dolophilodes distinctus</td>
<td>G.B.</td>
<td>C.R.</td>
</tr>
<tr>
<td>Rhacocphiida sp.</td>
<td>G.B.</td>
<td>**</td>
</tr>
<tr>
<td>Hydropila sp.</td>
<td>S.B.</td>
<td>R.F.</td>
</tr>
<tr>
<td>Neophylias</td>
<td>S.B.</td>
<td>**</td>
</tr>
<tr>
<td>Coleoptera</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ecdyra nervosa</td>
<td>**</td>
<td></td>
</tr>
<tr>
<td>Ancystus bicolor</td>
<td>S.B.</td>
<td>**</td>
</tr>
<tr>
<td>Elmidae (larvae)</td>
<td>S.B.</td>
<td>R.F.</td>
</tr>
<tr>
<td>Elmidae (adults)</td>
<td>**</td>
<td></td>
</tr>
<tr>
<td>Diptera</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nymphomyiidae</td>
<td>G.B.</td>
<td>**</td>
</tr>
<tr>
<td>Tipula spp.</td>
<td>S.B.</td>
<td>C.R.</td>
</tr>
<tr>
<td>Dicranota sp.</td>
<td>G.B.</td>
<td>**</td>
</tr>
<tr>
<td>Dicranota sp.</td>
<td>G.B.</td>
<td>**</td>
</tr>
<tr>
<td>Pericoma sp.</td>
<td>S.B.</td>
<td>R.F.</td>
</tr>
<tr>
<td>Ceratopogonidus</td>
<td>G.B.</td>
<td>**</td>
</tr>
<tr>
<td>Simuliidae</td>
<td>S.B.</td>
<td>**</td>
</tr>
<tr>
<td>Chironomidae</td>
<td>**</td>
<td>R.F.</td>
</tr>
</tbody>
</table>

* B.B.: significantly higher densities on Sawmill Branch (α = 0.05); G.B.: significantly higher densities on Grady Branch (α = 0.05); **: densities not significantly different.
* C.R.: cobble riffle; P.G.R.: pebble—gravel riffle; S.R., sandy reach; R.F.: rock face; and **: no significant substrate preference.

in cobble and pebble—gravel riffle areas and was significantly more abundant in Grady Branch (Table 3). Edmunds (1978) states that members of this genus are mainly shredders and detrital collectors, which agrees with gut content studies of Woodall (1972) on the Coweeta species. The correlation between Paraleptophlebia sp. densities and leaf detritus standing crop in Grady Branch was significant ($r = 0.37$, $\alpha = 0.003$). These facts suggest Paraleptophlebia sp. may have been more abundant on Grady Branch because of large quantities of deciduous leaf detritus.

Densities of Steroneuma sp. and Epeorus sp. (Heptageniidae) were not significantly different between the two streams (Table 3). Both genera are detrital collectors (Woodall 1972; J. N. Minshall 1967), although algal food may be important (J. N. Minshall 1967; Gilpin and Brusven 1970; Woodall 1972). These genera are apparently opportunistic feeders (Cummins 1973) and are not affected by differing food sources between the two streams. Densities of both genera were higher in cobble riffle areas.

Odonata — The gomphid, Lanthus parvulus Selys and Cordulegaster erroneus Hagen (Cordulegastridae) were significantly more abundant in Sawmill Branch (Table 3). Lanthus parvulus was more abundant in cobble and pebble—gravel riffle areas, while C. erroneus was more common in the sandy reach habitat. Needham and Westfall (1955) report similar habitats for these predators.

Plecoptera — Peltoperla maria Needham and Smith (Peltoperlidae) and Leuctra spp. (Leuctridae) had significantly higher densities in Grady Branch (Table 3), and were significantly correlated with leaf detritus standing crops (Peltoperla maria: $r = 0.66$, $\alpha = 0.001$; Leuctra sp.: $r = 0.45$, $\alpha = 0.0001$). Peltoperla maria and Leuctra spp. are both leaf shredders (Harper 1978) and Wallace et al. (1970) showed $P. maria$ had preferences for certain leaf species. Densities of $P. maria$ were not significantly different between substrate types, but Leuctra spp. were significantly higher in cobble riffle areas.

Alloperla sp. (Chloroperlidae) was significantly more abundant in Grady Branch (Table 3). Harper (1978) reports members of this genus are collector–gatherers and predators. The feeding habits of the Coweeta species are not known. Nemoura sp. (Neumouriidae) was significantly more abundant on Sawmill Branch and densities were not significantly different between substrate types (Table 3). Harper (1978) indicates that members of this genus are collector–gatherers or shredder–detritivores.

Trichoptera — Over 90% of the Rhyacophila sp. (Rhyacophilidae) in Sawmill Branch were collected from rock-face habitats. However, Rhyacophila in Grady Branch were more evenly distributed among all habitat types. Thus while Rhyacophila in rock-face habitats were significantly higher in Sawmill Branch overall stream densities were higher in Grady Branch. Dolophilodes distinctus (Philopotamidae) were significantly more abundant in Grady Branch (Table 3). Malas and Wallace (1977) reported $D. distinctus$ is generally restricted to the bottom of rocks in areas of lower current velocity. Low densities of $D. distinctus$ in Sawmill Branch may be related to large amounts of interstitial sand which may destroy potential microhabitats for the large, fine-meshed catchment constructed by this species.

Parapsyche cardis (Hydropsychidae), Hydropila sp. (Hydroptilidae), and Neophylias sp. (Limnephilidae) had significantly higher densities in Sawmill Branch (Table 3). This distribution is directly related to the abundance of the rock-face habitat for $P. cardis$ and $Hydropila sp.$, because both of these insects were largely restricted to this substrate (Table 3). Selection of the moss-covered rock face has been reported for these genera by Percival and Whitehead (1929) and Woodall and Wallace (1972). Parapsyche cardis was significantly correlated with moss standing crops ($r = 0.65$; $\alpha = 0.04$) and current velocity ($r = 0.24$; $\alpha = 0.04$) on Sawmill Branch, but neither correlation was significant on Grady Branch. This may be attributed to: (1) rarity of rock-face habitats in Grady Branch which were seldom sampled by
Diplectrona modesta Banks showed no significant preference for stream or habitat type (Table 3), although densities were much higher in moss-covered rock faces in Sawmill Branch. Diplectrona modesta was positively correlated with moss standing crop on Sawmill Branch (r = 0.51, α = 0.03), but not with current velocity (r = -0.03; α = 0.80); whereas, like P. cardis, D. modesta was not correlated with either moss standing crop or current velocity in Grady Branch. Malas and Wallace (1977) found the preferred microhabitat of D. modesta was the bottom of stones. Nevertheless, thick moss provides numerous microhabitats with respect to current velocity, while the interstitial sand in Sawmill Branch raffles may inhibit colonization by D. modesta.

Coleoptera — Densities of Ectopria nervosa (Psephenidae), a grazer (Pennak 1978), were not significantly different between the streams or substrate types (Table 3). Anchytarsus bicolor (Ptilodactylidae) had significantly higher densities in Sawmill Branch (Table 3). Anchytarsus bicolor is reported to feed on grass roots and leaf mold (Leech and Chandler 1963), and grasses are more abundant on stream banks and in the stream channel of Sawmill Branch. Most Elmidae collected were Optoservus spp. and Oulimnus spp. Promoresia sp. was occasionally collected from moss-covered rock faces in Sawmill Branch. Adult elmid densities were not significantly different between the streams or between substrate types (Table 3). Conversely, elmid larvae were significantly more abundant in Sawmill Branch and had highest densities on the rock-face habitat. Brown (1976) reports adults and larvae of the tribe Elmintae feed chiefly upon encrusted algae on solid substrates. The latter suggests that the higher larval elmid densities may be related to higher primary production in Sawmill Branch.

Diptera — Diptera which were significantly more abundant in Grady Branch include a new genus and species of Nymphomyiidae, the family Ceratopogonidae, and the tipulids Dicranota spp. and Hexatoma spp. Populations of the nymphomyiid were possibly destroyed by the earlier perturbations on Sawmill Branch, and the poor dispersal powers of this insect (Kevan and Cutten-Ali-Khan 1975) may account for the observed distribution. The psychodid Pericoma sp. and Simulidae had significantly higher densities in Sawmill Branch (Table 3). Egglishaw (1969) reports Pericoma sp. is restricted to moss, and although not confined to moss in this study, densities were 5 times higher in the moss-covered rock outcrops. Simulid densities were not significantly different between substrates. Tipula spp. (Tipulidae) were significantly more abundant in Sawmill Branch and had highest densities in cobble—riffle areas. Species within this large genus are regarded as shredders, collector—gatherers, scrapers, and engulfers (Byers 1978).

Chironomidae densities were not significantly different between the two streams. This family had significantly higher densities in the rock-face habitats, and their mean annual densities exceeded 23 000 m⁻² in the thick moss of the rock-face habitats of Sawmill Branch. Chironomids composed over 50% of the total aquatic insect densities in each stream.

BENTHOS COMPARISON 1977—78 VS. 1968—69

There are several problems when one compares the present data with those of Woodall and Wallace (1972): (1) the Surber sampler used in the earlier study had net mesh openings about 1.8x larger than that used in the present study; and (2) the 1968—69 samples of Woodall and Wallace were not picked under a binocular microscope. Consequently, many small insects (e.g. Nymphomyiidae) and early instars were possibly overlooked in the 1968—69 study. This supposition is supported by total abundances which are higher in the present study.

To minimize these problems, the ratio of abundances in Sawmill Branch to those in Grady Branch were determined for each study and then compared. This procedure assumes densities have not changed in Grady Branch. The Wilcoxon signed rank test (Hollander and Wolfe 1973) was used to test differences in ratios. The following are significant changes which occurred in the 10-yr period.

DETRITUS

The standing crop (g dry wt./m²) of total detritus (this included moss, as did Woodall and Wallace 1972) has increased significantly in Sawmill Branch since 1968—69 (Table 4). Various grass species and some herbaceous plants constituted most of the detritus in 1968—69 (Woodall and Wallace 1972). In addition to the preceding, deciduous tree leaves (black locust, tulip poplar, and oak), rhododendron leaves, and various herbaceous plant parts now comprise part of the detritus in Sawmill Branch. Changing riparian vegetation has undoubtedly affected Sawmill Branch in three ways: (1) increased food quality of allochthonous detritus; (2) increased food quantity through higher allochthonous inputs; and (3) reduced primary production associated with a denser canopy.

Ephemeroptera — Stenonema spp. have increased significantly in Sawmill Branch (Table 4), and were the only mayflies which showed significant change. Increased Stenonema spp. densities may be related to higher food quality of detritus on Sawmill Branch.

Odonata, Plecoptera, Trichoptera — Peltoperla maria was the only member of these three orders to change significantly (Table 4), and densities had increased significantly in Sawmill Branch in the present study. The increase is undoubtedly related to larger amounts of higher quality leaf detritus on Sawmill Branch, which is this insect’s preferred food (Wallace et al. 1970).

Coleoptera — Densities of all coleopterans, A. nervosa, A. bicolor, elmid larvae and adults, were significantly lower in Sawmill Branch in the 1977—78 study than in 1968—69 (Table 4). These reductions are potentially related to lower
levels of primary production through shading since these groups are grazers. Anchytarsus bicolor density decrease may be related to the decrease in its food source, which is reported as grass roots (Leech and Chandler 1963).

**Diptera** — Ceratopogonidae and Chironomidae are now significantly lower on Sawmill Branch (Table 4). Generic and species analyses were not conducted; thus, conclusions cannot be drawn from these observations. The tipulid Dicranota sp. had significantly lower densities in the present study. This genus is carnivorous (Byers 1978) and the reasons for its decline are unknown.

**Conclusions**

Ward (1975) compared benthos in a Colorado creek with those results obtained in a similar study of the same creek 29 years earlier. Ward concluded that despite differences in flow, riparian vegetation, and temperature, macroinvertebrate composition was similar to that of the study conducted 29 years earlier. Our study differs from that of Ward’s in several respects: (1) Based on Fig. 1 in Ward’s (1975) study, both the magnitude and rate of changes in riparian vegetation are much greater in the southern Appalachians; (2) the stream studied by Ward is much larger, with an average discharge about 3000× that of Sawmill Branch; and (3) small woodland streams are more closely linked to terrestrial environments (Cummins 1974; Hynes 1975; Vannote et al. 1980), and one would expect such streams to be much more influenced by terrestrial succession than larger streams.

Hynes (1975) concluded that the stream is ruled by its valley. Surrounding forests exert very important influences on headwater stream ecosystems. High allochthonous organic inputs and lower solar radiation reaching the stream are two of the most obvious of these influences. The terrestrial ecosystem also influences stability characteristics of stream ecosystems. Headwater streams of forested regions have been characterized as having low resistance to perturbation and high resilience following perturbation (Webster et al. 1975; O’Neill et al. 1975; Webster and Patten 1979). However, recent studies suggest that recovery of small southern Appalachian streams from watershed disturbance is controlled by the rate of recovery of the surrounding terrestrial vegetation (Gurtz et al. 1980). That is, recovery is related to the restoration of the quality, quantity and timing of allochthonous organic inputs. Likewise, this study suggests that recovery of stream benthos trophic structure and function is related to the recovery of surrounding vegetation. Although we have documented significant changes in certain benthic taxa on Sawmill Branch over a 10-yr period, there are still significant differences between this disturbed watershed and an adjacent hardwood stream. Some of the differences between these streams can be attributed to differences in substrate availability, e.g., rock-face habitat. Major differences on Sawmill Branch since 1968 are manifested through both reduced abundances of grazer organisms and increased abundances of dominant shredders such as Peltoperla. This suggests: (1) terrestrial successional vegetation influences sequential changes in stream macrobenthos; and (2) restoration of the stream benthos community with respect to trophic structure and function is a long-term process dependent on recovery of terrestrial vegetation.

**Acknowledgments**

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