

## Effects of Streamside Vegetation on Macroinvertebrate Communities of White Clay Creek in Eastern North America

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**ABSTRACT.** — The presence or absence of trees on land adjacent to stream channels is shown to significantly affect the structure and function of macroinvertebrate communities in White Clay Creek, a Piedmont stream in southeastern Pennsylvania. Low order forested tributaries are about 2.5x wider than deforested streams and have more benthic surface area in the form of inorganic (sand, gravel, cobble) and organic (tree roots, leaf litter, wood, etc.) substrates for macroinvertebrate colonization. Streamside forests affect food quality and quantity for macroinvertebrates directly through inputs of particulate food (leaf litter, soils, wood, etc.) and indirectly by affecting the structure and productivity of the microbial (algae, bacteria) food web through shading and modifying the levels of dissolved organic carbon and nutrients. Deforestation eliminates shading and can result in a 2-5°C warming of small streams which is shown to greatly affect important life history characteristics of macroinvertebrates (e.g. growth rate, survivorship, adult size and fecundity, timing of reproduction). The effect of native versus foreign tree species in streamside areas is discussed within the context of stream recovery and restoration. A spatial protocol for planting streamside forests as buffers for mitigating non-point pollution is reviewed and recommendations concerning the details (site preparation, seedling size and species, weed abatement, use of tree shelters, etc.) of streamside reforestation are given.

For most of the 10,000 years since the last glacial period, the land between the Mississippi River and the Atlantic Ocean was a vast expanse of forest (Williams 1989) broken only by occasional patches of meadow and prairie (Trautman 1981). Thus, stream and river systems flowed through mostly forested landscapes and the many stream species of macroinvertebrates that evolved and/or continued to evolve as they expanded their geographic range during this period did so in this environment. Stream ecologists have clearly shown a strong link between the dynamics of stream ecosystems and the characteristics of the landscape through which they flow (Hynes 1975; Vannote et al. 1980).

The forest composition of watersheds in eastern North America has slowly but continuously changed during the past 10,000 years due to a gradual warming trend in climate following glaciation (Custer 1984). During this period there

were also periodic disturbances of the forest in specific regions by a variety of natural factors (e.g. forest fires due to lightning, wind throws from tornadoes and hurricanes, outbreaks of forest pests and disease, etc.). However, the relative amount of disturbed forest for a given time interval was probably minimal, and the general condition of most of the watersheds of the region could probably be considered natural, even pristine during most of the post-glacial period.

It has only been in recent history (last 1000 years) that watersheds have been altered extensively and frequently enough by human activities to be considered non-pristine or disturbed. The extent of this forest disturbance, and concomitant impact on stream ecosystems, has increased steadily during recent history in parallel with increased population levels of native Americans and foreign settlers. The process of

forest clearing and the use of fire to alter the structure of forests (especially the undergrowth) was developed and refined by the natives of North America as their population grew to an estimated peak of between 9.8 and 12.2 million by the 15th century (Williams 1989). The arrival and rapid population increase of Europeans only accelerated and intensified an already established process.

To the early settlers, the vastness of the forests in eastern North America gave the impression of an endless resource and was generally viewed as an impediment to the development of agriculture. Exploitation intensified and by the mid-1800's 75% of the area had been completely deforested from the streams to the mountain tops (Trefethen 1976). Those areas where soils were shallow and unproductive, or where local relief was so steep that soils quickly eroded, were abandoned after a few years by the settlers and gradually returned to forest. Estimates of soil loss from upland areas range from 7.6 to 30.5 cm or more since the initial clearing of forest (Costa 1975). Today, a substantial amount of this forest occurs as small tracts or woodlots. Contemporary streams in eastern North America, therefore, flow through an environmental mosaic of forested and deforested areas.

This paper focuses on how the presence or absence of streamside forests affect the structure and function of aquatic macroinvertebrate communities. The paper will be based largely on quantitative and qualitative data gathered over a number of years from a small watershed and stream system, White Clay Creek (hereafter WCC), in the Piedmont Physiographic region of southeastern Pennsylvania. I also will include

original data from other stream systems, even some that are not in the Piedmont region, in order to emphasize certain points that pertain to many regions but where data from WCC are unavailable or incomplete. Although many of these studies were not performed with streamside ecology per se in mind, the results have been focused towards that topic. These data will illustrate both the obvious and subtle ways that the vegetation adjacent to stream channels can affect macroinvertebrate communities.

### RELATIONSHIP BETWEEN STREAMSIDE VEGETATION AND AQUATIC MACROINVERTEBRATES

The main point of this paper is that the presence or absence of trees adjacent to stream channels may be the single most important factor altered by humans that affect the structure and function of stream macroinvertebrate communities, especially in streams like WCC of the Piedmont Physiographic region of eastern North America. I also explore the possibility that restoring streamside forests to the most recent historical steady-state condition may be a necessary prerequisite to restoring a disturbed stream system to a natural or quasi-natural state. A conceptual model (Fig. 1) illustrates that the presence of streamside forests can significantly affect the quality and quantity of light (shading) striking the stream channel and banks, the chemistry of groundwater flowing through the riparian zone towards the stream (groundwater biochemistry), and the availability of leaf litter and other forest products for consumption. These factors in turn affect the amount of primary production (light for photosynthesis), the amount of benthic surface area or habitat for macroinvertebrates (channel width), seasonal temperature regime, levels of dissolved nutrients (dissolved organic carbon, nitrate, etc.), and the availability of particulate organic matter. Finally, these factors all interact to influence the survivorship, growth, relative abundance, and, ultimately, the productivity of each macroinvertebrate species in the community. It is within this conceptual framework that the remainder of this paper is developed.

### DRAINAGE BASIN AND SOILS OF THE WHITE CLAY CREEK WATERSHED

In WCC, a 158 km<sup>2</sup> drainage basin in Chester

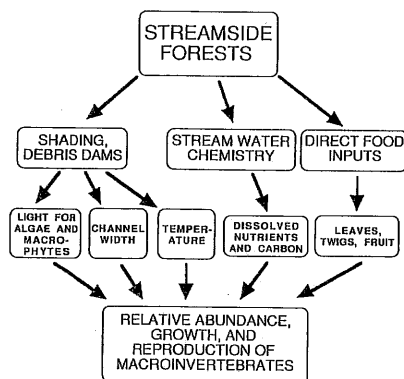


Fig. 1. A conceptual model showing the potential pathways that streamside forests can affect the relative abundance, growth, and reproduction of macroinvertebrates.

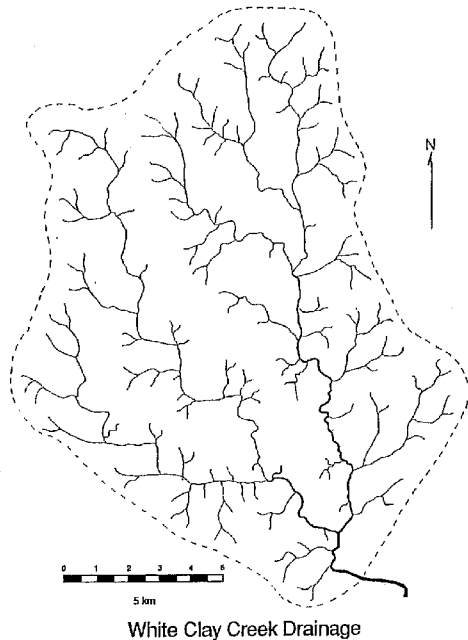


Fig. 2. Map showing the location of first through fifth order tributaries of the White Clay Creek drainage basin in Chester County, Pennsylvania and New Castle County, Delaware.

County, Pennsylvania (Fig. 2), some 203 individual stream channels comprise a total stream length of 268 kilometers. About 95.1% of the total number of channels in the WCC drainage is represented by first and second order streams (Fig. 3), where stream order refers to Strahler's (1957) modification of Horton's (1945) classification system (e.g. headwater streams with no tributaries are first order, two first orders join to form a second order, etc.). These data are probably typical of most watersheds in eastern North America as well as elsewhere because they compare favorably with the estimate by Leopold et al. (1964) that 94.9% of the total stream channels in the United States was represented by first and second order streams. In WCC, only 1.5% of the total number of channels are greater than third order. Thus, available stream habitat in WCC, as well as other Piedmont streams, consists mainly of a large number of very small channels (first and second order).

The soils of the drainage basin, especially from areas where most of the data in this paper were gathered, are mainly Glenilg channery silt

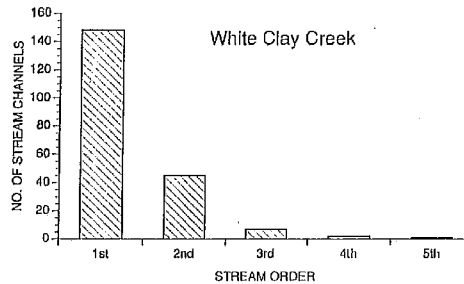


Fig. 3. Showing the total number of stream channels for each of the five stream order categories within the White Clay Creek drainage basin.

loam of variable depth. The soils overlay a schist-gneiss parent material and are easily erodable. The soils near the stream in the principal study area are mainly Wehadkee silt loam and Guthrie silt loam with some Worsham silt loam. The stream's name, White Clay Creek, reflects the seams of white kaolinite clay that are common in the drainage basin.

#### PHYSICAL EFFECTS OF STREAMSIDE VEGETATION

The preponderance of small streams in watersheds like WCC means that the canopy of streamside trees growing on opposite banks of a channel will touch and form a complete vegetative bridge over the stream. This overhead canopy shades the stream during certain seasons and the trees provide woody debris and roots to the channel which are readily colonized by macroinvertebrates. In this section I show that the presence of heavy shade, woody debris, and root structures result in forested streams with significantly more physical habitat for macroinvertebrates than deforested channels. Moreover, the presence or absence of trees is shown to greatly modify the quality and quantity of light striking the stream surface as well as the seasonal pattern and magnitude of water temperature.

*Availability of Benthic Habitat: Channel Width and Exposure of Inorganic Substrates for Macroinvertebrate Colonization.* Unlike lakes, where the planktonic food web predominates,

most of the biological activity in stream ecosystems takes place on inorganic and organic substrates on the surface of or within the benthic or bottom area of the channel (sand, gravel, cobble, leaves, woody debris, etc.). This means that factors affecting the availability and overall surface area of benthic substrates can directly affect the amount of space or habitat available for stream organisms such as macroinvertebrates. In the WCC drainage basin, the width of the stream channel changes significantly in response to changes in the type of vegetation bordering the stream. Forested streams are consistently much wider than streams bordered by grassy meadows (Table 1). For small streams (e.g. first and second order), forested streams are on the average 2.5 times wider than meadow streams. The narrowing of meadow streams becomes relatively less pronounced in the larger tributaries (third and fourth order) but is still significant. Even fourth order channels are 35% wider in the forested areas, and thus have at least 35% more exposed inorganic substrate area available for colonization by stream organisms.

The process of stream narrowing in meadows involves the formation of sod by grassy vegetation along the stream margin that eventually encroaches on the stream channel itself and causes the channel to narrow gradually (Zimmerman et al. 1967). As the channel narrows, it degrades or cuts down in order to accommodate the discharge. Thus, meadow channels are narrower and deeper at base flow conditions than forested streams.

It is not known how the present width of forested channels in the WCC basin compares to

their width prior to recent (past 300 years) episodes of watershed disturbance. Forest clearing and intense agriculture during the 18th and 19th centuries certainly released large amounts of sediment into WCC as well as other streams of eastern North America (Trautman 1981). In some areas, the paleosol or top soil layer of the original floodplain can be clearly seen buried under nearly one meter of silt and other fine sediments undoubtedly released during recent history (Costa 1975). It is known that streams carrying a high suspended sediment load have high silt-clay contents along their streamside perimeter or margin, while bedload streams tend to have high sand contents in these areas (Richards 1982). Moreover, channels with silty banks tend to be narrower and deeper in cross section than channels with sandy banks. Thus, it seems possible that low order forested channels preceding major watershed disturbance may have been even wider than the reforested contemporary channels that have more silt on their floodplain.

The presence or absence of a forest along a channel of WCC affects the amount of exposed benthic surfaces available for colonization by benthic plants and animals. By combining present day estimates of channel width for forested and deforested channels and the total length of stream channel for first through fourth order streams in the WCC basin, the amount of habitat loss associated with deforestation can be estimated. It appears that the 158 km<sup>2</sup> basin would have 1.01 × 10<sup>6</sup> m<sup>2</sup> of benthic habitat if riparian zones were entirely forested. In contrast, benthic habitat would be reduced 54% (to 0.47 × 10<sup>6</sup> m<sup>2</sup>) if streamside trees were completely

Table 1. Average and standard error of ten stream width (wetted channel width) measurements taken on various tributaries of White Clay Creek differing in size (order) and discharge in Chester County, Pennsylvania. In all cases, the forested and meadow reaches were more or less immediately upstream or downstream from one another. Width measurements were made at baseflow conditions in either November or March. Discharge (m<sup>3</sup>/s) was measured in January.

	Stream Width (meters)					
	First Order	First Order	Second Order	Third Order	Fourth Order	Fourth Order
Streamside	(0.0056 m <sup>3</sup> /s)	(0.059 m <sup>3</sup> /s)	(0.0379 m <sup>3</sup> /s)	(0.08 m <sup>3</sup> /s)	(0.63 m <sup>3</sup> /s)	(0.81 m <sup>3</sup> /s)
Condition	Mean (SE)	Mean (SE)	Mean (SE)	Mean (SE)	Mean (SE)	Mean (SE)
Forested	3.14 (0.29)	2.83 (0.28)	2.99 (0.25)	4.82 (0.47)	11.70 (0.63)	17.75 (0.91)
Meadow	1.19 (0.25)	1.66 (0.11)	1.39 (0.13)	2.85 (0.19)	8.63 (0.42)	11.16 (0.68)

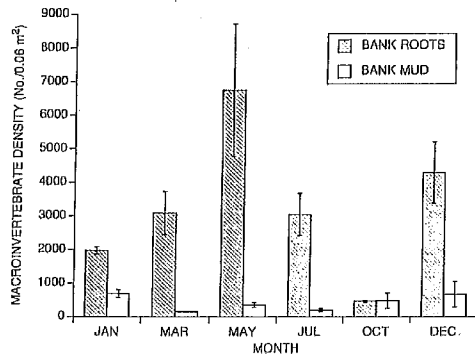


Fig. 4. Average macroinvertebrate density (all taxa) in six replicate bank mud samples and on six replicate bundles of tree roots suspended for eight weeks at mid-depth along the stream margin of Upper Three Runs Creek, Aiken County, South Carolina during different times of the year. Each of the six sections of bank mud taken as a sample per date was about 20 x 30 x 5 cm deep. Each of the six replicate tree root bundles was 17 x 35 x 17 cm thick, about 600-700 g wet weight, and was a mixture of roots from oak, birch, and gum trees. Vertical bars are  $\pm$  one standard error.

eliminated.

*Benthic Habitat: Tree Roots and Woody Debris.*

Historical accounts of pristine streams in eastern North America often noted how the banks were "thickly clothed" with large trees whose roots "acted as so many ligatures and fillets of net-work in protecting the earth from the wash of the waters" (Hildreth 1848 cited in Trautman 1981). The woody roots of trees growing close to the stream also provide additional surface for macroinvertebrate colonization (Rhodes and Hubert 1991). Tree roots have an extremely high surface area to volume ratio, can persist for a long time, and provide habitat for a variety of macroinvertebrate species. In contrast, the roots of herbaceous plants such as grasses along meadow streams are very fine and do not provide good habitat because they either quickly collect silt particles to form sod or are readily broken off by the current.

In portions of the WCC basin, native tree species such as American sycamore (*Plantanus occidentalis*) and black willow (*Salix nigra*) have root structures forming a tight network over the soil of banks that keep them from sloughing into the river (especially during spates) and provide habitat for macroinvertebrates. In certain reaches of WCC, roots are prime substrata for collecting

a variety of aquatic insects in large numbers. We have not quantified the amount of surface area provided by roots per unit length of forested stream channel in WCC nor estimated the standing stock of macroinvertebrates supported by the roots. However, we have observed significant colonization of tree roots in streams flowing through the Coastal Plain Physiographic region of eastern North America. For example, bundles of natural tree roots placed along stream bank habitat of Upper Three Runs in Aiken County, South Carolina contained 2,000 or more macroinvertebrates per 0.06 m<sup>2</sup> of root mat throughout most of the year (except October; Fig. 4). In contrast, densities of macro invertebrates on the mudflat areas of bare stream banks was always less than 1000 per 0.06 m<sup>2</sup>. The large difference between macroinvertebrate densities on rooted and bare bank habitat means that streamside trees can substantially increase the standing stock (and productivity) of macroinvertebrates per unit length of stream channel. Rhodes & Hubert (1991) describe streams in Wyoming where exposed root filaments of banks represent only 8.5% of the total habitat but contain an estimated 44% of the total aquatic insect fauna in July and 30% in August. In some small coastal plain streams, the roots from streamside trees have been shown to create the majority of debris dam sites for organic matter accumulation along the channel length and these debris dams support 10 and 5 times the density and biomass respectively of macroinvertebrates relative to sites without debris (Smock et al. 1989).

Additional surface area for macro invertebrates is continuously added to streams in the form of woody debris shed from the streamside forest (tree twigs, branches, whole trunks). This debris provides additional surface area of a very different texture (than roots or rocks) and with an additional dimension (interior) for benthic organisms to use for various stages of their life histories. The woody debris also tends to accumulate and form small dams at periodic intervals which not only adds local habitat variety (depth, flow, etc.) but also plays a role in retention and stabilization (i.e., the ability of the channel to retain organic matter and inorganic sediments and for the bed of the channel to resist degradation or downcutting; Triska & Cromack 1981).

In WCC, a forested second order channel contained substantially more woody debris, in

Table 2. The average number of pieces and volume (m<sup>3</sup>) of large woody debris occurring in four 25 m long reaches of a second order stream channel of White Clay Creek flowing through a forest and a grassy meadow.

Streamside Condition	No. Woody Pieces/25 m reach			Snag Volume/25 m reach		
	Mean	(SE)	Forest/Meadow ratio	Mean	(SE)	Forest/Meadow ratio
Forested	3.75	1.10	7.5	0.54	0.44	27.0
Meadow	0.5	0.5		0.02	0.02	

terms of both number and volume of woody pieces, than a contiguous meadow reach (Table 2). Because the data from the meadow reach were taken immediately downstream (about 50 m) of the forested reach, there seems little, if any, tendency for forested stream sections to provide woody debris to downstream meadow reaches. Thus, macroinvertebrates requiring woody debris for all or part of their life history may be precluded from meadow stream channels. In terms of adding physical surface area, this will certainly vary according to the nature and extent of the streamside forest. For the second order tributary of WCC, an average of about 4.73 m<sup>2</sup> of surface area was added in the form of woody debris per 25 meters of channel length. For a coastal plain stream in Georgia, Benke et al. (1984) estimated that woody debris supported an annual mean macroinvertebrate density of 26,043 m<sup>-2</sup> of woody surface area and an annual macroinvertebrate production level of 51,891 mg m<sup>-2</sup>. Moreover, Smock et al. (1989) has shown for a coastal plain stream in Virginia that benthic areas covered with woody debris dams contained an annual average of about 22,302 macroinvertebrates per m<sup>2</sup>. Although these data may not be directly transferable to WCC (a Piedmont stream), they demonstrate the relevance of woody debris as habitat for macroinvertebrates in stream systems.

In addition to providing habitat for benthic macroinvertebrates, the presence of woody debris changes stream morphology and creates depositional areas for storage and processing (Nilson & Larimore 1973; Keller & Swanson 1979; Benke et al. 1985; Sedell et al. 1988; Trotter 1990). Numerous other studies have shown that streams with woody debris are generally more retentive of particulate organic matter than streams without wood (Bilby & Likens 1980; Bilby 1981; Speaker et al. 1984; Golladay et al.

1987; Bilby & Ward 1989; Webster et al. 1988; Bilby & Ward 1991). Thus, macroinvertebrates specializing in either eating woody debris or using it as a substrate for attaching larval retreats or nets, building larval cases, laying eggs, etc. will be severely limited in meadow reaches of streams because of: (1) the lack of direct particulate woody input; (2) the limited amount of input from upstream forested reaches; and (3) the possibility that narrow meadow channels have less retention capacity for particulate organic material if or when it might enter the channel.

*Light quality and quantity.* The presence of a forest canopy over small stream channels not only sheds organic debris into the channel but greatly affects the intensity of light striking the surface of the stream (Hill & Harvey 1990). Measurements on a third order tributary of WCC indicate that average light intensity for a meadow channel increased gradually through the spring, peaking in mid-summer at about 400-500 G Cal cm<sup>-2</sup> day<sup>-1</sup> and declined gradually to about 100 G Cal cm<sup>-2</sup> day<sup>-1</sup> in late December (Fig. 5; T. L. Bott pers. comm.). In contrast, average light intensity for a forested channel peaked in mid-April at 300 to 400 G Cal cm<sup>-2</sup> day<sup>-1</sup> and then declined following canopy leaf-out to mid-summer levels of less than 100 G Cal cm<sup>-2</sup> day<sup>-1</sup>. Thus, on clear days along WCC, radiation in a shaded reach during the summer ranges from 6-30% (avg. = 17%) of that received by a meadow reach. On a clear winter day, radiation in a shaded reach ranges from 30-60% (avg. = 42%) of the meadow reach. These very different seasonal patterns of light for forested and meadow streams in WCC are important because levels of both gross and net algal productivity seem to be closely tied to them (see below).

In addition to visible light and infrared radiation, streams are exposed to ultraviolet radia-

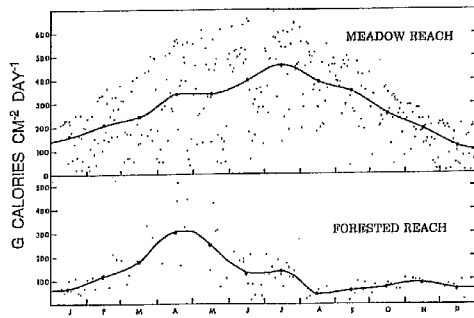


Fig. 5. Seasonal pattern of solar input (G calories  $\text{cm}^{-2} \text{day}^{-1}$ ) for forested and deforested (meadow) reaches of a third order tributary of White Clay Creek. The line was drawn by eye through monthly mean data points. Data collected using pyranometers (Model 5-3850 A Pyrheliograph, Belfort Co., in the forested reach; Model 8-48 Pyranometer, Eppley Co., in the meadow reach). Note that each G calorie equals 4.19 Joules of solar radiation.

tion (UV) in the 290-400 nm region. Approximately 4% of the total sunlight energy occurs in the UV band. Recently, two classes of UV light have been differentiated: UV-A (320-400 nm) and UV-B (290-320 nm). Both classes of UV radiation have the potential for directly damaging the biochemically important molecules that absorb them. However, the UV-B band contains more energy and its radiation is more strongly absorbed by biomolecules. UV radiation can also affect the structure of natural and man-made chemicals which in turn affects their toxicity (see review by Larson & Berenbaum 1988).

Unfortunately, human activities such as the production and use of chlorofluorocarbons has reduced the concentration of ozone in the stratosphere which, in turn, has resulted in an increased flux of UV-B radiation to the surface of the earth. Further reduction of ozone and hence increased levels of UV radiation are predicted over the next century. Moreover, there now is direct evidence from Antarctic marine ecosystems (Smith et al. 1992) that as the ozone layer thins out during austral spring, both the sea surface- and depth-dependent ratios of UV-B irradiance (280-320 nm) to total irradiance (280-700 nm) and UV-B inhibition of algal photosynthesis increases. Although there are no data for streams, the Smith et al. (1992) study clearly shows that UV radiation penetrates water to sufficient depths to expose benthic organ-

isms. We presently do not know whether the negative effects observed for a variety of other plants and animals will also be observed for benthic macroinvertebrates or the microbial food web to which they are intimately tied.

It is possible that streamside trees can help protect benthos from the effects of increasing UV radiation. For example, it is known that UV light is absorbed fairly well by the epidermis of certain plants (DeLucia et al. 1991). However, a plant canopy also tends to diffuse incident light and UV light represents a greater proportion of diffuse light than other wavelengths. It appears, therefore, that two opposing tendencies may be operating within riparian forest canopies: a high efficiency for absorbing UV light and a high tendency to diffuse it, allowing it to pass through. Few published measurements have been made underneath a forest canopy to determine its effectiveness in filtering out UV radiation. However, preliminary findings suggest that the effects of a forest canopy on the transmittance of UV light may be similar to the observed effects for visible light (E. H. DeLucia pers. comm.).

**Temperature.** The modification of solar inputs by streamside vegetation also plays a major role in the diel and seasonal pattern of water temperatures (Barton et al. 1985). The extent of the riparian influence at a given site depends on a number of factors (Gregory et al. 1991): the upstream length of forested channel, the width and density of streamside canopy, the width of the stream relative to the lateral and vertical dimensions of the streamside vegetation (hence, the size of the canopy opening above the stream), and the season (angle of incident solar radiation and presence or absence of leaves on deciduous plants).

The thermal regime of a small stream like WCC is usually dominated by the temperature of groundwater outflow, which in the continental United States is generally within  $1^{\circ}\text{C}$  of mean annual air temperature (see Fig. 1 of Vannote & Sweeney 1980). Thermal variation within the WCC basin, as well as most other streams in eastern North America, largely reflects alteration of the temperature of groundwater once it surfaces as streamwater. This alteration occurs mainly by the interaction of climate, channel geometry, streamside vegetation, and other watershed characteristics (see Fig. 2 Vannote & Sweeney 1980 for temperature patterns of first through third order tributaries of WCC).

In the headwaters of WCC, a forested second

order stream is on the average cooler from April through October and warmer from November to March than a meadow stream (Fig. 6). On an annual basis, the meadow reach accumulated about 228 more degree days than the forested reach. Other studies have also shown meadow streams to be 3-5°C warmer throughout significant portions of the year (see data in Welsch 1991). A recent analysis of thermal regimes in the Piedmont region of eastern North America has revealed that a 4°C increase in water temperature on an annual basis is equivalent thermally to shifting the latitude (geographic location) of the stream about 680 km south (Sweeney et al. 1992). Thus, the removal of trees along small streams in this region has already warmed the streamwater by about the same magnitude as predicted from global warming in the next 50 years (Hansen et al. 1987). If the combined effect of deforestation of riparian areas and global warming increases stream temperatures 6-10°C, it is likely that a significant number of aquatic taxa in each stream system will be affected (see below for discussion of direct and indirect effects of temperature on macroinvertebrates). Clearly, reforestation of all small stream channels over the next decade would not only help remove carbon dioxide from the atmosphere (as tree biomass) but would help reduce water temperatures at a time when increased air temperatures are tending to drive them higher.

#### CHEMICAL EFFECTS OF STREAMSIDE VEGETATION

It has long been recognized that the location of the stream in a drainage network and the nature of the surrounding terrestrial ecosystem are major determinants of stream ecosystem structure and function (Hynes 1975; Vannote et al. 1980). The chemistry of water exiting a given watershed as streamflow reflects the chemistry of rainfall for the region and the addition, removal, and modifications of chemical substances, both organic and inorganic, in the water at a variety of contact zones within the watershed. Principal contact zones are at the watershed surface (type and structure of surface vegetation, quality and quantity of dead plant debris, etc.), subsurface (soil type, condition, compaction, texture), and deeper geologic strata (rock type, degree of fracturing, etc.). Streamside vegetation probably affects the chemistry of streams in a number of ways: (1) through inputs of

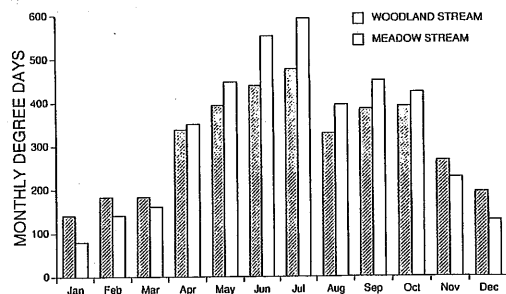


Fig. 6. Seasonal pattern of monthly degree day (>0°C) accumulations for forested and deforested (meadow) reaches of a second order tributary of White Clay Creek. Total annual degree day accumulation was 3951 for the meadow reach and 3723 for the forest reach. Data were collected using continuous recording thermographs.

particulate plant structures (leaves, fruits, woody parts) into the stream channel or onto the forest floor which later release dissolved nutrients (organic and inorganic compounds) directly into the stream water or into shallow groundwater which subsequently moves into the stream; (2) by intercepting shallow groundwater with their roots and removing nutrients just before the groundwater moves laterally into the stream channel; (3) by modifying the underlying soil structure, allowing greater infiltration and more contact time with subsurface sites of biogeochemical processing; and (4) by modifying the extent and perhaps rate of photooxidation reactions and aerobic processing of dissolved organic and inorganic compounds in streamwater through shading.

It is difficult to pinpoint, let alone quantify, direct chemical effects on macroinvertebrates from any of these processes. It is known, however, that the range of tolerance (or preference) for various chemical parameters differs from species to species among macroinvertebrates. In some instances, these data form the basis for using macroinvertebrate community structure for assessing chemical pollution of streams and rivers (Hynes 1960; Johnson et al. 1992). For many small stream systems like WCC, changes in stream chemistry (other than the point discharge of toxins) is probably a subtle process (e.g. changes in nutrient chemistry, quality and quantity of dissolved organic matter, alkalinity, etc.). This process gradually affects important ecosystem properties that, in turn, affects the



food base for many macroinvertebrate populations (e.g. levels of nutrients and primary production, levels of DOC and bacterial production, etc.). It is from this latter perspective that the link between streamside vegetation, water chemistry, and the macroinvertebrate community is discussed below.

*Streamside Forests as a Source of Dissolved Organic Carbon Compounds.* Although dissolved organic compounds (DOC) have been known to contribute a substantial amount (possibly 30 to 50% or more) of the total carbon flux into stream ecosystems (Fisher & Likens 1973; McDowell & Fisher 1976; Fisher 1977; Mulholland 1981), few data are available that quantify the relative amount of DOC that enters from the various sources, how it is actually utilized, and what biological pathways are involved in its incorporation into the food web of these systems. Furthermore, the role of streamside forests on DOC dynamics has not been well documented. Meyer & Tate (1983) studied streams draining forested and deforested watersheds and showed that annual DOC export and DOC concentrations in streamwater were reduced in deforested streams. They attributed this reduction largely to: (1) reduced inputs of DOC from the streamside zone (e.g. lower litter inputs and subsequent leaching; lower throughfall inputs during storms); (2) reduced DOC input from subsurface water sources (which they in turn attribute to lower litter fall and slower litter decomposition on the deforested watershed); and (3) reduced in-stream generation of DOC (e.g. DOC leached from algae, DOC leached from organic matter - leaves and woody debris - in the channel, and DOC generated by consumers shredding leaves—see also Meyer & O'Hop 1983). More data clearly are needed to quantify the link between streamside forests and levels of DOC.

In the WCC drainage, the quality and quantity of DOC inputs to the stream has been characterized (Larson 1978a; Kaplan et al. 1980; Kuserk et al. 1984), some of its sources have been investigated (Kaplan & Bott 1982), its actual uptake by bacteria has been quantified (Kaplan & Bott 1983, 1985, 1989; Bott et al. 1984; Bott & Kaplan 1985; Kaplan et al. 1992), and the subsequent utilization of bacteria by meiofauna (especially protozoa and nematodes) has been quantified (Bott & Kaplan 1989, 1990). Research is currently underway to further assess the relationships within the DOC-bacteria-meiofauna food web as well as its importance to higher

consumer levels (viz. macroinvertebrates) in the WCC ecosystem (Bott & Borchardt pers. comm.). In addition, studies have been initiated to determine the ultimate source of streamwater DOC within the watershed, including its pattern of movement from source areas to the stream (Kaplan, Newbold, & Standley pers. comm.).

*Nutrient Uptake by the Root Systems of Streamside Trees.* In contrast to the general paucity of data on DOC dynamics, there have been a number of studies, especially in coastal plain watersheds, showing that mature streamside forests can reduce non-point chemical pollution, especially the flux of nutrients to streams and rivers (Asmussen et al. 1979; Lowrance et al. 1984; Peterjohn & Correll 1984; Jacobs & Gilliam 1985). The streamside forests of coastal plain watersheds seem to be especially effective at removing nitrogen, with removal levels of 65% (Lowrance et al. 1984) and 75% (Peterjohn & Correll 1984) being reported. In some instances, however, the presence of nitrogen-fixing trees such as alder in streamside areas can actually add nitrogen to the soil or groundwater (Gregory et al. 1991).

In WCC, low N levels (<0.1 ppm) have also been observed in shallow (<3 m) groundwater monitoring wells along riparian zones. In contrast, local surface springs and deeper groundwater wells (>25 m) within the WCC watershed contain relatively high N levels (averaging >7 ppm). The streamwater contains N levels that are intermediate (averaging  $\approx$  3 ppm) between wells and springs from deeper groundwater sources and the shallow groundwater sources near the channel. Although these data can be interpreted many ways, they suggest that streamside areas or wetlands may be important sites for nitrogen removal within the WCC watershed.

In an adjacent watershed (Brandywine Creek) to WCC, we have been monitoring the chemistry of two first order streams draining agricultural fields (sub-watersheds) located next to one another. These data show consistently higher levels of nitrate nitrogen in the stream without a streamside forest (Morris Run) relative to the stream with an extensive (i.e. wide) buffer of mature forest along most of its length (Fig. 7). We have now established a network of lysimeters and shallow (<25 m) groundwater monitoring wells to determine the pathway of nitrogen flux from the agriculture fields to the streams and more precisely define the effect of a stream-

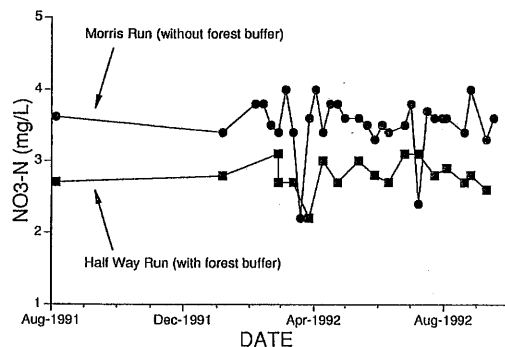


Fig. 7. Seasonal variation in nitrate nitrogen ( $\text{NO}_3\text{-N}$ ) levels in two adjacent first order streams differing mainly by the presence (Half Way Run) or absence (Morris Run) of a wide forest buffer.

side forest on these pathways.

For WCC and other Piedmont streams, it is obvious that the role of streamside vegetation in the nutrient dynamics of groundwater and surface water is presently not well understood. To some extent, the answer may depend on the structure and function of the root system and the degree of maturity of the forest. For example, Dawson & Ehleringer (1991) have shown that mature deciduous trees growing in or directly next to (within 2 m) a perennial stream use little or none of the surface stream water. Their work clearly shows that: (1) although mature trees located both streamside and non-streamside may have roots distributed throughout a soil profile, the active sites of water absorption (and hence nutrients) were mostly limited to deeper soil and bedrock layers; and (2) small streamside trees (within 2 m of stream) used streamwater and small non-streamside trees (about 25–45 m of stream) used recent precipitation stored in upper soil layers as their primary water source. In addition, more data concerning the effect of subcanopy shading on the translocation of compounds within individual trees (Schleser 1992) will also greatly improve our ability to understand the role that forest maturity may play in water and nutrient flux through streamside trees.

In addition to the type, age distribution, and density of streamside trees, another factor affecting the ability of streamside forests to alter the chemistry of streamwater is the rate and spatial pattern of water movement through the streamside zone before entering the stream channel. Any evaluation of streamside forests as regulators of nutrient flux must involve a careful assessment of hydrology to determine the

proportion of the total water budget for the drainage basin that actually passes through the root zone and how long it remains in contact with the tree roots. Recent developments in watershed hydrology suggests that the dynamics of water movement underneath and through streamside forests is complex. For example, it now appears that most of the stormflow in streams consists of water that was stored in the watershed prior to the onset of the storm (i.e. not from rainfall associated with the current storm, Wallis et al. 1981; Hooper & Shoemaker 1986; Kennedy et al. 1986; Pearce et al. 1986; Sklash et al. 1986). This implies that water exchange in streamside areas may be rapid during storms but quite slow between storms. In WCC, there is some evidence of this phenomenon. Larson (1978) showed that the concentration of DOC in WCC water declined more slowly than discharge following a storm event and continued to decline gradually until the next storm. Similar patterns have been observed in other streams (Comiskey 1978; McDowell & Likens 1988). Kaplan & Newbold (1992) point out that this less than proportionate decline would be predicted if most of the stormflow were to originate from soil water with higher concentrations of DOC than the groundwater, which dominates at baseflow. Moreover, they further note that the extended period of decline indicates that soilwater may contribute substantially to the DOC (even as its contribution to flow becomes small) and that mixing of soilwater DOC with groundwater may occur in streamside areas rather than in the stream itself.

*Photooxidation.* The shading by streamside vegetation can also affect stream water chemistry via the photooxidation of dissolved organic compounds (see review by Larson 1978b). However, most work in this area has focused on the fate of aquatic pollutants following exposure to sunlight (Larson & Berenbaum 1988). Few data are available concerning the photooxidation of naturally occurring organic compounds in streamwater, and the potential influence of shading from streamside trees on this phenomenon has not been explored to date (Larson pers. comm.).

#### BIOLOGICAL EFFECTS OF STREAMSIDE VEGETATION

As shown above, the presence of a streamside forest can greatly modify the physical and chemi-

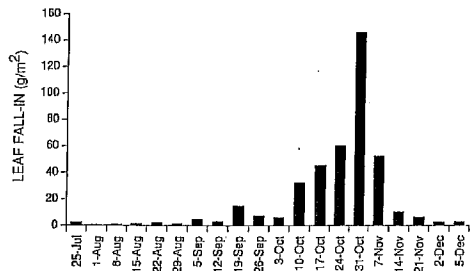


Fig. 8. Seasonal pattern of average weekly fall-in (dry mass) of leaf litter to Half Way Run, a forested tributary of Brandywine Creek, Chester County, PA. Leaves were collected in 10 traps (0.067 m<sup>2</sup> each) spaced at about 10-m intervals along the length of the study reach.

cal habitat characteristics of a given stream reach. Some of these modifications directly affect the biological activity of macroinvertebrate organisms (e.g. temperature effects on bioenergetics, developmental dynamics, etc.). Others exert indirect effects by changing the food base or by altering, in a more subtle fashion, factors that affect survivorship of the various life stages and thus overall reproductive success. The discussion below focuses on how macroinvertebrate life history characteristics respond to changes in their physical, chemical, and biological habitat induced, either directly or indirectly, by streamside vegetation.

*Particulate Detritus as Food for Macroinvertebrates.* Leaves and other coarse particulate detritus from streamside forests are readily used as food by macroinvertebrates (see Cummins et al. 1989 for review). Tributaries

flowing through forested areas or having well developed riparian canopies, continuously receive organic detritus throughout the year. Standing crop of detritus (particle size: 0.45 μm to 16.0 mm) in small forested streams averages 248 g of organic matter per square meter for the year, with leaf litter detritus (particle size >16.0 mm) rarely falling below 40 g m<sup>-2</sup> during the year (Vannote & Sweeney 1980).

In WCC, organic detritus enters the stream all year but a substantial proportion of the annual input from streamside forests occurs during October and November (Fig. 8). Because streams are depressions in the land that trap terrestrial detritus blowing across the forest floor, they can accumulate high standing stocks of leaf litter, especially during the fall. For example, a forested second order tributary of WCC in November 1991, just after peak leaf fall, had an average of 748 g m<sup>-2</sup> dry mass of leaf litter and another 312 g m<sup>-2</sup> dry mass of woody debris (Table 3). In contrast, when the stream flowed out of this woodlot and into a grassy pasture, the standing stock of leaf litter and woody debris decreased to about 14 and 15 g m<sup>-2</sup>, respectively. This strongly suggests that leaf litter and woody debris do not travel far in small forested channels (and hence forested reaches do not seem to subsidize downstream meadow reaches) and/or meadow channels do not retain much of the coarse particulate matter that washes into them.

Deciduous leaves are clearly a major food input to forested reaches of WCC. The rate at which these leaves decompose and enter the food web depends on a number of factors and processes: resistance to physical abrasion (by flow, sand and silt particles in transport, etc.), chemical composition and susceptibility to chemical leaching, ambient stream temperature

Table 3. Standing stock of leaf litter and woody debris for adjacent forest and meadow stream reaches of a second order tributary of White Clay Creek. Data are means (standard error) for all parameters.\*

Streamside condition	n	Stream width(m)	g/m <sup>2</sup> dry mass		
			Leaf litter, grass	Wood	Total
Forested	11	2.99 (0.25)	748 (306)	312 (164)	1061 (449)
Meadow	6	1.39 (0.13)	14 (6)	15 (8)	28 (10)

\* all measurements were taken as transects at 25 m intervals in the forested and meadow reach; all leaf litter, grass, and wood data were obtained by collecting these materials from 27 cm wide transects spaced evenly along the study reach; stream width represents the wetted channel width at baseflow conditions in October 1991.

Table 4. Mean percent (%) composition per unit mass of tulip poplar and American beech leaves collected from the WCC watershed.\*

Leaf Component	Tulip Poplar		American Beech	
	Mean	SD	Mean	SD
Lipid	11.96	1.23	9.13	0.46
Carbohydrate	9.26	2.17	9.96	1.01
Protein	11.36	0.28	8.10	0.72
Hemicellulose	15.77	0.55	25.44	0.60
Lignin	16.66	0.34	23.62	1.78
Cellulose	17.36	0.51	23.55	2.04
Other (Non-Structural)	13.24	0.24	5.23	0.25
Ash	8.20	0.73	6.42	0.59

\* Methods include: Lipid (Ethanol extraction), Carbohydrate (Dubois et al. 1956), Protein (Lowry et al. 1951), Hemicellulose (Acid Detergent extraction, Van Soest 1963), Lignin (Permanganate oxidation, Van Soest & Wine 1968), Cellulose (incineration following Lignin extraction).

following inundation, microbial activity, and the feeding activity of aquatic macroinvertebrates. In WCC, the various species of leaves that fall into the channel can differ significantly in chemical composition (Table 4; T. L. Bott pers. comm.). For example, American beech (*Fagus grandifolia*) leaves have 42% more lignin, 61% more hemicellulose, and 36% more cellulose than tulip poplar (*Liriodendron tulipifera*) leaves while tulip poplar leaves have 40% more protein and 31% more lipids available per unit mass as food for aquatic detritivores than American beech. Thus, American beech leaves contain a high percentage of very refractory compounds (such as lignin and cellulose) and a low percentage of nutritionally relevant compounds (such as nitrogen and lipids), two factors that could make them a poor food resource for aquatic detritivores (a point corroborated by feeding studies discussed below).

There is also considerable variability among species in the rate at which leaves leach and decompose once they have fallen into WCC. For example, Tulip Poplar leaves lost about 75% of their mass after being submerged for 150 days in stream water (temperatures between 8 and 16°C), whereas American beech leaves only lost about 50% of their mass during the same time period (Fig. 9; T. L. Bott pers. comm.). Most of the weight loss during this experiment was probably due to microbial activity because leaves kept in sterile stream water for control purposes only lost about 10-20% of their mass during the same period.

In WCC, the decomposition process of some leaf species can be accelerated by introducing aquatic macroinvertebrates into submerged leaf packs. Thus, the presence of crane fly larvae (*Tipula abdominalis*) greatly reduced the decom-

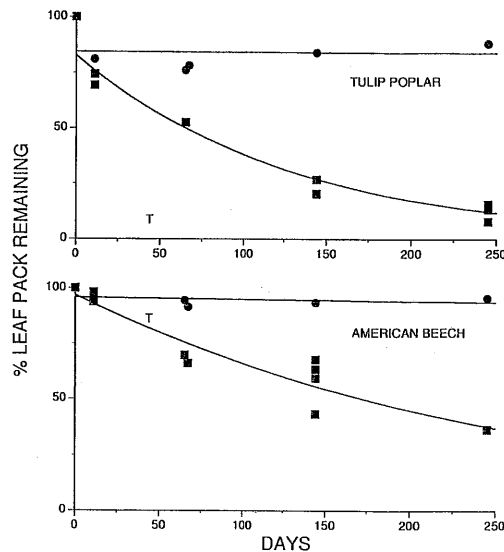


Fig. 9. Showing the temporal decline in mass for leaf packs (tulip poplar and American beech) incubated in stream water and exposed to the natural microbial flora of White Clay Creek (squares), as compared to leaf packs incubated in sterilized stream water (circles). The data point labeled "T" shows the percent leaf pack remaining after 48 days for packs kept in stream water with natural microbes but where insect larvae (Tipulidae) were added. Lines are fitted exponential functions. Each data point represents one leaf pack.

position time of tulip poplar leaves by ingesting almost all of the leaves by the end of six weeks (Fig. 9). In contrast, the larvae had little or no measurable effect on the rate of decomposition of American beech leaves because they were not readily ingested.

For macroinvertebrates, the importance of the leaf itself relative to the microbial biomass associated with the leaf has been the subject of much investigation and discussion over the years (see Cummins & Klug 1979 for review). In WCC, we have observed that leaves with high nitrogen and ATP levels (presumably from microbial biomass) tend to be more palatable and result in better growth for aquatic detritivores. At least some of this growth is due to microbial biomass. Thus, experiments have shown that when tulip poplar leaves containing about  $19.6 \times 10^6$  bacteria per mg and  $6.4 \times 10^2$  fungi per mg are fed to crane fly larvae (*T. abdominalis*), they produced fecal pellets containing 74% fewer bacteria and 77% fewer fungi (T. L. Bott pers. comm.). This suggests that bacteria and fungi are removed from the detritus during passage through the digestive tract. However, the amount of microbial biomass ingested per day by this species is generally not sufficient to account for more than 8% of the observed growth in biomass (Cummins & Klug 1979). Even if most of the larval biomass is produced directly from the leaves, microbes may supply certain fatty acids and other compounds that the insects cannot produce themselves (S. Kilham pers. comm.).

Differences in the physical and nutritional (chemical and microbial qualities) characteristics of the various deciduous leaves that fall into WCC and other streams in eastern North America often result in marked differences in the feeding rate and growth rate of macroinvertebrates that use them as food. For example, larvae of the crane fly *T. abdominalis*, when fed a variety of species of deciduous leaves, feed preferentially on species that maximize their rate of growth and avoid eating species that result in poor growth (Fig. 10). It is presently unclear exactly how these larvae can discriminate among the various species of leaves in a mixed diet.

The difference in larval growth rate observed for *T. abdominalis* when fed a variety of leaf types has also been observed for other species of macroinvertebrates in WCC. These data suggest that the leaves of all deciduous species are not equal in terms of supporting larval growth of

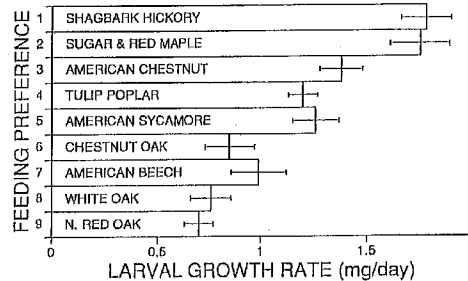


Fig. 10. Showing the order of feeding preference (1 = highest preferred, 2 = second highest, etc.) and growth rate (mean  $\pm$  one standard error) of crane fly larvae (*Tipula abdominalis*) fed various species of deciduous leaves. Actual tabular data have been presented elsewhere (Vannote and Sweeney 1985).

macroinvertebrates (Table 5). For example, white ash (*Fraxinus americana*) and hickory (*Carya ovata*) consistently result in the best growth performance of the macroinvertebrates tested and American beech consistently resulted in poor growth performance for a given experiment. The nutritional value of some leaves [e.g. red oak (*Quercus rubra*)] varied substantially depending on the species of macroinvertebrate feeding on it. Although more species of leaves need to be tested, available data seem to indicate that a mixed species composition of trees growing in streamside areas will probably support a wider variety of macroinvertebrate species than a monoculture of trees.

*Particulate Detritus from Non-Native Streamside Plants as Food for Macroinvertebrates.* In the WCC watershed, as well as most other watersheds in eastern North America, most if not all streamside areas have been disturbed by anthropogenic practices either: (1) directly, by clear cutting, thinning, monoculture reforestation, etc. or (2) indirectly, by changes in forest communities resulting from man's presence and activities in the watershed [forest fires, introduction of foreign plant species, or disease driven changes [e.g. American chestnut (*Castanea dentata*) blight, American elm (*Ulmus americana*) disease, gypsy moth infestation, woolly adelgid fly infestations of eastern hemlock (*Tsuga canadensis*), etc.]. Smock & MacGregor (1988) have speculated on some of the ways that the above changes in streamside plant communities could affect the overall productivity of stream ecosystems. In this regard, it is helpful for stream ecologists to

Table 5. Showing the relative value of various leaf diets to overall larval growth performance of four species of aquatic insects collected from White Clay Creek and reared at various temperature regimes in the laboratory. Larval growth rate or adult female biomass were used as a measure of growth performance. For a given temperature regime, the diet producing the highest growth rate or largest average adult female was assigned a 100% growth performance value; all other diets within that temperature regime were scaled as a percentage of this top rated diet (e.g. a 50% rating indicates that adult females were about 50% of the size observed on the top diet).

Growth Performance (%)	<i>Soyedina carolinensis</i> *			<i>Tipula abdominalis</i> **				<i>Leptophlebia intermedia</i> †				<i>L. cupida</i> ‡	
	10°C	WCC	18°C	WCC	WCC + 4°C	WCC + 8°C	WCC	WCC ± 3°C	WCC ± 6°C	WCC	WCC ± 3°C	WCC ± 6°C	10°C
90-100	hickory	tulip poplar hickory sugar maple red maple white ash	hickory sugar maple	hickory	hickory	white ash hickory	hickory	hickory	white ash	hickory	white ash	white ash	hickory white ash
80-89	white ash	white oak red oak Am. sycamore chestnut oak			white ash		white ash		hickory				
70-79			Am. chestnut	white ash red oak		red oak		chestnut oak	red oak				
60-69	chestnut oak red oak		tulip poplar Am. beech	chestnut oak Am. beech	red oak Am. beech		Am. beech	chestnut oak hickory					
50-59			chestnut oak		chestnut oak	chestnut oak Am. beech							
40-49			white oak red oak				chestnut oak red oak Am. beech		red oak	Am. beech	Am. beech	Am. beech	
30-39	Am. beech												
0		smooth alder Am. beech											

\* data from Sweeney et al. 1986b.

\*\* data from Varro and Sweeney 1985.

† data from Sweeney et al. 1986a.

‡ data from Sweeney et al. 1992.

reconstruct, as near as possible, how the forest composition has naturally changed historically in each region, especially the period following the last glaciation and prior to major human influence. It is not unreasonable to assume that some macroinvertebrate species inhabiting streams have evolved mechanisms for improving their ability to exploit the organic detritus (leaves, twigs, seeds, etc.) shed into their habitat by the native streamside vegetation, even though the vegetative characteristics of a given region are known to have changed during this period. The key issue is whether the most recent (historically) steady-state streamside forest condition for a given location (i.e. species composition and stand structure) must be restored in order to enable the stream macroinvertebrate communities of a disturbed stream to recover to a quasi-natural or natural state.

For the WCC watershed, the work of Custer (1984) and Carbone (1976) provide the greatest insight into historical changes in climate and forest species composition. In this regard, Carbone (1976) divides the mid-Atlantic region into subareas, with the WCC watershed located in the "transitional area of the Middle Atlantic" composed of Pennsylvania, New Jersey, Maryland, and Delaware. The term transitional means that this area contains floral, fauna, and geomorphological characteristics of both glaciated and non-glaciated regions. Wendland & Bryson (1974) provide the theoretical basis for interpreting the data. Their "episodic model" of environmental change fits well for this region. This model notes that climatic change in this region involved a series of time periods (episodes) of reasonably stable climate interrupted at various times by abrupt changes in climate. These

changes in climate are inferred from changes in plant communities as reflected by temporal changes in pollen data from cores taken throughout the region. Table 6 shows a few of the more pertinent pollen data for the WCC region during the various historical episodes. In general, these data show that the plant communities of the region during the past 10,000 years have gradually changed from one dominated by grasses, sedges, and pines (10,000-8,000 B.C.), to a mix of pine and oak (8,000-6,500 B.C.), to a mix of oak/hemlock/pine (6,500-800 B.C.), and finally to a forest dominated by oak and chestnut in recent history (800 B.C.-present).

Although it may not be necessary (or possible) to restore the full complement of plant species that were present in recent history, (e.g. American chestnut and American elm are presently non-viable) there currently are insufficient data to rank species as to their importance to the stream ecosystem. For example, species that have root structures capable of providing much needed stability to stream banks may have leaves that are not palatable or nutritious for macroinvertebrates or vice versa. Species that have nutritious leaves [e.g. alder (*Alnus serrulata*) or black locust (*Robinia pseudo-acacia*)] may be nitrogen fixers and therefore undesirable in watersheds where streamside forests are managed to help reduce nutrient flux to the stream. Again, we do not know whether the most recent steady-state forest condition needs to be restored in the streamside areas of a region in order to enable disturbed stream communities to recover to a natural state. Moreover, we know even less about how extensive (wide) the streamside forest needs to be and whether a forest dominated by foreign species will suffice.

Table 6. Historical comparison of the dominant plant communities occurring near the White Clay Creek watershed as determined by pollen analysis of material from three excavation sites.

Episode	Date	Marsh Creek* Chester Co., PA	Delaware Park** New Castle Co., DE	Mitchell site† Hockessin, DE
Sub-Atlantic	recent - 800 B.C.	Oak/Chestnut		
Sub-Boreal	800 B.C. - 3100 B.C.		Grasses/Oak/Pine	
Atlantic	3100 B.C. - 6500 B.C.	Hemlock/Oak		Oak/Hemlock
Pre-Boreal/Boreal	6500 B.C. - 8000 B.C.	Pine		Pine/Oak
Late Glacial	8000 B.C. - 10000 B.C.	Grasses/Sedges/Pine		Pine/Spruce/Burnet

\* Martin 1958.

\*\* Thomas 1981.

† Custer 1981.

In the WCC watershed, streamside areas that have been historically clear cut for agriculture generally become immediately dominated by foreign plant species [multiflora rose (*Rosa multiflora*), Asiatic bittersweet (*Celastrus orbiculatus*), Japanese honeysuckle (*Lonicera japonica*), among others] when left fallow. This dominance is known to last for >30 years and, in some instances, even after 40 years there is no indication of further succession. The effect of foreign plants in streamside areas on the ecology of stream communities has been little studied (Sweeney et al. 1992). For the mayfly *L. cupida* in WCC, laboratory experiments show that the replacement of native species of trees (e.g. white ash, hickory, American beech) with foreign species [e.g. mul-

tiflora rose, Asiatic bittersweet, princess tree (*Paulownia tomentosa*)] has a significant effect on larval survivorship (Table 7). Survivorship was consistently lower for *L. cupida* on foreign as compared to native plant species, even if the foreign species seemed to provide adequate nutrition (as judged by growth performance). On multiflora rose leaves, all *L. cupida* larvae died. Thus, stream reaches where this plant dominates would probably not support viable populations of *L. cupida* unless other sources of leaf litter were available. However, the response of growth and survivorship to leaf litter from foreign plant species seems to be depend on the species of macroinvertebrate. For example, the stonefly *S. carolinensis* exhibited larval growth

Table 7. Comparison of survivorship and adult size for individuals of *S. carolinensis* and *L. cupida* reared in the laboratory at 10°C while fed leaves from various native and foreign plant species known to grow along stream channels of White Clay Creek.\*

Leaf type	<i>Soyedina carolinensis</i>				<i>Leptophlebia cupida</i>			
	Sex	Survivorship	Adult Size		Sex	Survivorship	Adult Size	
			Mean	SE			Mean	SE
Native species								
White ash	F	10.5%	1.22	0.12	F	85.0%	10.76	0.29
	M		1.39	0.06	M		7.04	0.14
Shagbark hickory	F	14.5%	2.04	0.06	F	80.7%	11.87	0.33
	M		1.32	0.03	M		7.03	0.12
American beech	F	6.0%	1.58	0.06	F	83.5%	5.48	0.24
	M		1.12	0.04	M		4.16	0.11
Foreign species								
Multiflora rose	F	15.0%	2.24	0.05	F	0.0%	—	—
	M		1.43	0.04	M		—	—
Bittersweet	F	15.5%	2.15	0.04	F	69.2%	10.71	0.33
	M		1.30	0.04	M		6.63	0.14
Princess tree	F	16.5%	2.08	0.06	F	38.5%	6.41	0.50
	M		1.32	0.03	M		5.10	0.18

\* All larvae were reared in flow-through polypropylene trays (45 x 24 x 20 cm deep) supplied continuously with streamwater from a large reservoir. About 18 g of leaves of a given type were placed in each tray; there were two replicate trays for each diet. The outflow of each tray was screened with nitex® netting to prevent larvae from escaping. The top of each tray was fitted with nylon netting to capture emerging adults. Trays were checked daily for emerging adults. For *S. carolinensis*, the experiment was started October 30 by placing 100 larvae into each tray; initial larval size was: avg. dry mass = 0.27 mg per larva (S.E. = 0.007; n = 108). For *L. cupida*, the experiment was started November 15 by placing 70 larvae into each tray; initial larval size was: avg. dry mass = 0.71 mg per



and survivorship on foreign species that was equal to or greater than that observed on native species (Table 7).

At the present time, the data are too sparse to make any general statements concerning the potential effect of foreign plant species on stream ecosystems. It is clear that the comparative chemistry of native and foreign plant species (especially their leaves) needs to be studied. Furthermore, we obviously need more laboratory and field studies comparing the palatability and nutritional value of the exotic plant species growing along our streams. Many of the field experiments have already been established by landowners who have allowed deforested streamside areas to lay fallow and be colonized by foreign plants. Stream ecologists need only take notice and start monitoring.

*Algal Community Structure and Productivity.* Regardless of whether a streamside forest consists of native or non-native tree species, the shading from their canopy can affect factors that are known to greatly influence the amount and type of algal production available as food for macroinvertebrates [viz. total photon density and the spectral quality (favoring green) of light incident on streams]. Engelmann (1883, cited in Raven 1992) hypothesized long ago that exposure of a water body to a green-enriched shade could favor algal species with pigments such as phycobilin, chlorophyll c, or certain carotenoids that have increased absorption in the 500-700 nm range of light. This long-standing hypothesis concerning light quality has not been substantiated by actual data on algal communities from either streams or the marine environment (see review by Raven 1992) because: (1) carefully designed laboratory experiments to isolate the effects of light quality from light quantity have been lacking; and (2) field data are usually confounded by variation in both light quality and quantity as well as other factors. For example, Bilby & Bisson (1992) showed that the algal community of a stream heavily shaded by old growth forest was dominated all year by diatoms, while a nearby deforested stream was consistently dominated by filamentous green algae in the spring and diatoms at other times. Lowe et al. (1986) showed that open sites were dominated by upright filamentous algae while more shaded sites were dominated by epilithic diatoms. Also, in Big Sulphur Creek, California, open sites frequently have higher levels of filamentous algae (e.g. *Cladophora*) as compared to

diatoms which predominate under moderate to high canopy cover (Feminella et al. 1989). For each study mentioned above, both light quality and quantity differ significantly among test sites during the year. In addition, the kind and relative abundance of invertebrate grazers, which also affect the structure of algal communities, usually differed. Thus, it is presently difficult to evaluate the relative importance of spectral quality to the structure and productivity of benthic algal communities in small streams.

In contrast, light quantity (photon density) is generally considered to be one of the main physical factors affecting benthic algal communities of streams and rivers (Raven 1992). Existing data show that high light levels typical of deforested stream channels can greatly affect the dynamics of stream algal assemblages, especially with respect to nutrient limitation. For example, phosphorous limitation of periphyton growth often occurs when both nitrogen:phosphorous (N:P) ratios and light availability are high (Elwood et al. 1981; Newbold et al. 1983; Pringle et al. 1986). Similarly, enrichment of a stream with phosphorus can induce nitrogen limitation of the algal community if N:P ratios and light inputs are both high (Pringle & Bowers 1984). Also, Grimm & Fisher (1986) and Hill & Knight (1988) have observed N limitation in a number of streams with low N:P ratios and high light availability. In general, responses of the algal community to nutrient enrichment are greater in unshaded than in artificially or naturally shaded streams that are otherwise identical with regard to the original nutrient conditions (Lowe et al. 1986; Hill & Knight 1988).

Although adequate light is obviously necessary to sustain autotrophic productivity, studies providing experimental or correlative evidence of light limitation are scarce in stream ecology (but see Triska et al. 1983; Hill & Knight 1988; Feminella et al. 1989). Hill & Harvey (1990) have shown that in Ish Creek, which is in an undisturbed watershed and has a fully developed canopy during late spring and summer, light is likely to be the principal abiotic factor limiting benthic primary productivity. Photosynthetically active radiation was generally below  $50 \mu\text{E m}^{-2} \text{s}^{-1}$  and photosynthesis by periphyton in shaded streams of that vicinity was saturated above  $100 \mu\text{E m}^{-2} \text{s}^{-1}$ . Few other studies have been published on the relationship between photosynthetic activity and levels of irradiance for stream benthic algae (in contrast to phytoplank-

ton). In a third order tributary of WCC, net algal productivity in a meadow reach was about 5-20 times greater than in a shaded reach during the September-October period and about 3-6 times greater in the November-December period (T.L. Bott pers. comm.). Moreover, annual net primary productivity, as estimated from intensive data collected over a six month period from January to June, was about 2.3 times higher in the open meadow reach than in the forested reach. It was also observed that the seasonal pattern of productivity in both forested and meadow reaches of WCC was closely tied to the pattern of irradiation. For example, a peak of primary production was consistently observed in mid-April for forested reaches, a time of the year when peak light levels are observed (just prior to canopy leaf out) but also when stream temperatures are rising.

Consistent with the observation that light plays an important role in periphyton production of WCC, Hornberger et al. 1976 found that algal photosynthesis was a linear function of light intensity and was not light saturated for deforested sections of a small river. For streams in general, very little is known about how shading affects the response of algae to light (Boston & Hill 1991). Recently, Hill & Harvey (1990) reported a strong correlation between primary production and light level in a shaded stream in Tennessee, and Hill & Boston (1991) inferred that periphyton production was primarily light limited in several shady streams. However, results showing high saturation irradiation levels are somewhat confusing because they suggest that stream algae cannot adapt to low light conditions to the same extent that has been observed in other plant communities. Hill & Boston (1991) offer two possible hypotheses: (1) that photosynthesis in shaded rivers is geared toward the temporary high light levels provided by sunflecks (produced by small openings in the canopy) moving across the streambed during the day; and (2) that photosynthesis may be generally adapted or set for an average yearly light level (i.e. a level that would incorporate both low levels during the summer and higher light levels when the canopy is missing). No data are presently available to test these hypotheses.

*Algal Availability and Consumption by Macroinvertebrates.* Numerous studies have implicated the streamside forest canopy, and its effects on incident levels of light that reach

streams, as a major factor influencing benthic macroinvertebrate communities (Cummins 1974; Minshall 1978; Murphy et al. 1981; Hawkins et al. 1982; Feminella et al. 1989). In general, stream sections with open canopies have been shown to have higher periphyton standing crops and primary production than more shaded sections (Lyford & Gregory 1975; Hawkins et al. 1982; Murphy 1984; Power 1984; Fuller et al. 1986). Other studies have shown that macroinvertebrate grazers benefit from improved food resources when more sunlight reaches the stream channel and algal growth is stimulated (Weber 1981; Kirchofer 1984; Murphy 1984; Wallace & Gurtz 1986; Perrin et al. 1987; Bilby & Bisson 1991). In WCC, for example, two species of algal grazing caddisflies, *Neophylax nacatus* and *N. oligius*, both grew to a significantly greater size (i.e. pupal biomass) in artificially de-canopied (sunny) reaches of a second and third order tributary, respectively, relative to nearby (within 100 m) heavily forested (shaded) reaches (Fig. 11). Hawkins et al. (1982) also found higher biomass of grazers in open versus shaded areas of a stream but found the densities of grazers to actually be lower in open streams. In contrast, Behmer & Hawkins (1986) found both higher biomass and densities for most grazers in the open sites.

Although the relationship between the density and biomass of grazers and the degree of shading has been studied, only a few studies have measured macroinvertebrate production in relation to shading. To date, these studies (Allen 1951; Hopkins 1976; Wallace & Gurtz 1986; Behmer & Hawkins 1986) have all re-

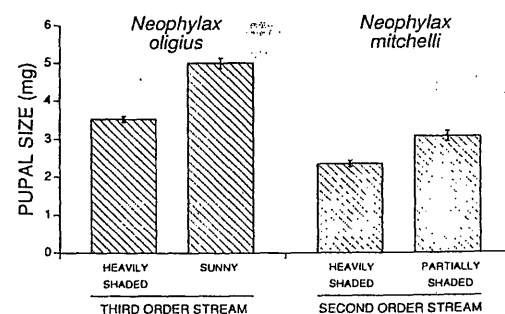


Fig. 11. Average dry mass of *Neophylax oligius* and *N. mitchelli* pupae collected from heavily shaded and sunny reaches of White Clay Creek. Vertical bars are  $\pm$  one standard error of the mean.

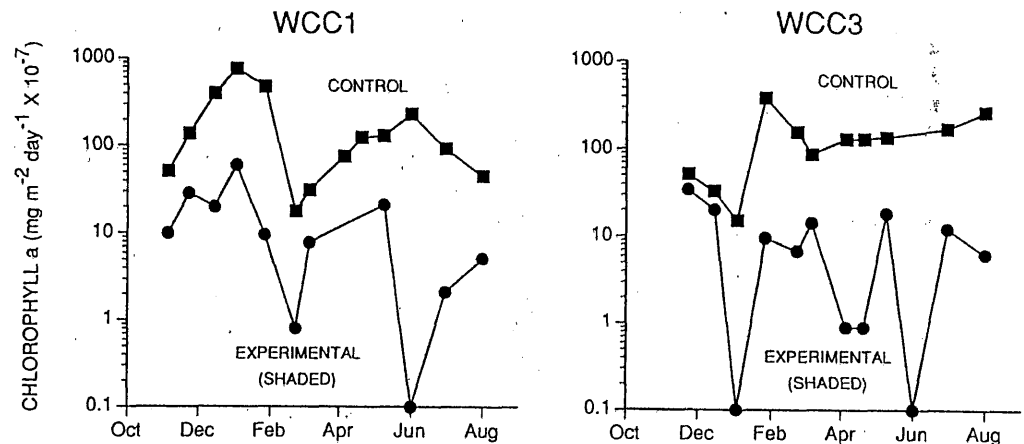


Fig. 12. Seasonal pattern of chlorophyll a accumulation on glass microscope slides incubated in riffle areas receiving natural shading from streamside trees (control) and in riffles where light levels were artificially reduced by shading with black plastic (experimental). Slides were incubated for three weeks prior to measurement.

ported greater levels of secondary production in open versus shaded sites. Behmer & Hawkins (1986) further report that, for all species studied, the higher production was always a reflection of greater standing stock rather than faster growth.

It has been suggested that removal of streamside vegetation can change the composition of the macroinvertebrate community from predominantly univoltine detritivores to multivoltine grazers and collector-gatherers (Gregory et al. 1987). In WCC, the physical characteristics (width, depth, flow pattern, turbulence, etc.) of deforested reaches differs so much from forested reaches that it is difficult to separate the physical effects from the trophic effects in terms of differences in community structure. One potential approach would be to experimentally remove the canopy of a forested reach and observe the response of the entire community (as above for *Neophylax* caddisflies) for a one or two year period.

Although a light enhancement experiment has not been done in WCC, we have artificially reduced the light intensity to negligible levels over riffles in forested reaches of first and third order tributaries and were able to reduce the standing stock of algae by an order of magnitude throughout an eight month (November-June) period (Fig. 12). An analysis of the Ephemeroptera-Plecoptera-Trichoptera (EPT) community of the experimental (heavily shaded) and control riffles indicates that, although shading reduced the average density of

EPT macroinvertebrates by 44.5% and 26.5% in first and third order tributaries, respectively, the overall species composition changed only slightly (see Table 8 for summary). When rare taxa are eliminated from the analysis (i.e. those represented by less than 15 individuals during the entire study), then only two taxa seemed to be completely eliminated by the increased shading (*Agapetus minutus* in the first order stream; *Serratella serrata* in the third order stream). Other common species, although not eliminated altogether, exhibited substantial declines in population densities in response to the shading. For example, *Ephemerella dorothea*, *Ameletus ludens*, and *Neophylax nacatus* in the first order tributary and *Baetis* sp., *Glossosoma nigrior*, *Neophylax oligius*, and *Goera calcarata* in the third order stream. All of these species are known to specialize in grazing epilithic periphyton. The only common species to exhibit relative abundance in the heavily shaded area equal to or greater than the control areas were filter-feeding caddisflies (*Diplectrona modesta*, *Hydropsyche slossonae*, *Hydropsyche sparna*, *Dolophilodes distinctus*), the predaceous caddisfly *Rhyacophila* sp., the wood-dwelling mayfly *Habrophlebiodes americana*, and the leaf shredding stonefly *Allopnia recta*. Even though these data are somewhat confounded because we could not control for upstream drift into the experimental reaches, it is notable that the main outcome of lowering light levels (hence algal availability) was a decline in abundance of grazing species

Table 8. Summary of the total number of taxa and larvae collected from either the stream bottom (riffle data) or from artificial leaf packs in a first (WCC1) and third (WCC3) order tributary of White Clay Creek. Con = control reach (natural shading from a streamside forest); Exp = experimental reach (natural shading supplemented by shading from black plastic or aluminum covers). The total abundance values for riffles can be converted to no./m<sup>2</sup> per collection date by multiplying by 0.5574. The total abundance values for each leaf pack can be converted to number per leaf pack by multiplying by 0.2 for the WCC1 data and 0.055 for the WCC3 data.\*

Taxonomic group	Riffle				Leaf Pack			
	WCC 1		WCC 3		WCC 1		WCC 3	
	Con	Exp	Con	Exp	Con	Exp	Con	Exp
Plecoptera (stoneflies)								
no. taxa	6	6	6	6	3	3	4	3
no. larvae	342	202	186	215	23	13	5	4
Ephemeroptera (mayflies)								
no. taxa	7	9	19	16	4	3	12	11
no. larvae	720	195	6072	4241	28	73	1999	852
Trichoptera (caddisflies)								
no. taxa	18	13	19	16	2	3	9	8
no. larvae	408	418	4940	3777	6	10	132	157
Total no. taxa	31	28	44	38	9	9	25	22
Total no. larvae	408	418	4940	3777	6	10	132	57

\*The experimental riffle in the first order tributary (WCC1) was shaded with sheets of black polyethylene (6 ml thick) fastened in tent-like fashion over the stream. Experimental shading at the third order site (WCC3) was provided by corrugated aluminum roofing fastened as a flat roof over the stream. Additional black polyethylene was draped over the upstream and downstream openings. Control riffles were located downstream of the experimental riffles. Chlorophyll a levels at all sites were monitored by suspending microscope slides (2.5 x 7.6 cm) in the water for three week periods. Macroinvertebrates were sampled using a petite (0.023 m<sup>2</sup>) Hess sampler; six samples were taken at random from each riffle per month from November through June. In addition, leaf packs (dried Sugar Maple, *Acer saccharum* leaves) were placed in each riffle in November (5 packs/riffle in WCC1, 9 packs/riffle in WCC3) and collected 10 weeks later. All insect larvae from the Hess and leaf pack samples were removed, identified to the lowest possible taxon, counted, dried (at least 48h at 60°C), and weighed.

and an increase in abundance of filter feeding species. One interpretation is that the grazing species needed to expand their territory in order to meet their individual nutrient requirements under reduced algal conditions, resulting in lower densities of grazers and hence more space available for filter feeding species.

The above data from WCC and elsewhere (see Fuller et al. 1986 for results from another shading experiment) show, as expected, that quantity and quality of algae greatly affect the density and biomass of macroinvertebrates that specialize in eating periphyton. Minshall (1978) long ago suggested that periphyton probably

also plays a significant role in the bioenergetics of species that are generally considered to be detritivores or omnivores. In WCC, some species that are generally considered to be detritivores often exhibit equal or better growth and/or survivorship when fed algal diets relative to diets consisting entirely of whole or ground up leaf detritus. For example, the mayfly *Eurylophella funeralis*, which generally feeds on leaves in first order streams of WCC, can grow equally well on algae or leaves at 10 and 20°C in the laboratory, although growth is depressed at the higher temperatures regardless of diet (Table 9). The importance of algae to

Table 9. Effects of temperature on larval survivorship, time to complete larval development (from date of collection), and adult size of the stonefly *Soyedina carolinensis* and the mayfly *Eurylophella funeralsis* when fed various species of deciduous leaves or algae.†

Species	Temperature	Food	Survivorship*		No. days to**		Adult dry mass (mg)				Fecundity						
			Survivorship*	Mean	S.D.	first adult	median adult	Male		Female		Mean	S.D.				
								Mean	S.D.	Mean	S.D.						
<i>Soyedina carolinensis</i>	5°C	hickory white ash red oak chestnut oak American beech	0.0%	—	—	—	—	—	—	—	—	—	—	—	—	—	
			25.0%	126.0	11.3	—	144.0	12.7	0.69	0.10	—	—	0.80	0.15	ND	ND	
			18.5%	123.0	4.2	133.5	3.5	0.64	0.13	0.86	0.17	—	—	—	—	—	—
			2.0%	175.0	35.3	162.0	—	0.67	0.12	0.84	—	—	—	—	—	—	—
	10°C	hickory white oak red oak chestnut oak American beech	53.5%	91.0	1.4	105.5	0.7	1.42	0.23	—	—	2.24	0.30	ND	ND		
			61.0%	98.5	0.7	106.0	1.4	1.23	0.18	1.93	0.31	—	—	—	—		
15°C	hickory white oak red oak chestnut oak American beech	48.5%	92.0	7.1	113.0	8.4	1.00	0.20	—	—	1.38	0.21	ND	ND			
		53.5%	98.5	4.9	107.5	3.5	1.01	0.13	1.45	0.24	—	—	—	—			
		1.0%	126.0	—	—	—	—	—	—	—	0.80	0.08	—	—			
		2.0%	117.5	0.7	132.0	—	1.15	—	—	—	2.03	0.40	—	—			
10°C	hickory† algaet††	1.0%	122.0	—	122.0	—	—	—	—	—	1.28	0.09	ND	ND			
		6.5%	97.5	0.7	111.5	2.1	0.83	0.14	1.39	0.33	—	—	—	—			
		4.5%	106.5	0.7	108.5	2.1	0.91	0.04	1.37	0.08	—	—	—	—			
		0.0%	—	—	—	—	—	—	—	—	—	—	—	—			
<i>Eurylophella funeralsis</i>	10°C	hickory† algaet††	74.0%	59.5	13.4	64.0	7.1	1.64	0.40	—	—	2.74	0.72	1992	762		
			68.0%	37.0	1.4	50.5	4.9	1.75	0.31	2.93	0.52	—	—	2073	474		
20°C	hickory† algaet††	43.0%	13.5	0.7	18.5	0.7	1.25	0.24	—	—	2.19	0.53	1436	500			
		32.0%	10.5	3.5	12.0	2.8	1.60	0.23	1.79	0.17	—	—	1047	172			

\* overall male and female survivorship.

\*\* average development time for males and females combined.

† initial larval mass was: Mean = 0.71 S.D. = 0.41.

†† initial larval mass was: Mean = 1.46 S.D. = 0.79.

*S. E. funeralsis* larvae were reared in flow-through trays (38 x 7.5 x 5 cm). Food consisted of algae (diatoms from WCC) or pre-leached hickory leaves. Initial larval size was: hickory diet: Mean = 1.60; S.D. = 1.04; algae diet: Mean = 1.46; S.D. = 0.79. Adults were collected daily as they emerged and then dried and weighed. Methods for *S. carolinensis* are given in Sweeney et al. 1986b.

detritivores, however, can vary from species to species. Thus, supplementing a leaf diet with algae does little to improve larval growth of the leaf shredding caddisfly *Heteroplectron americanum* (Fig. 13). For some omnivorous species that feed on small organic particles, the relative importance of algae seems to depend on temperature. For example, algae are the only food that can sustain successful survivorship, growth, and fecundity of the omnivorous mayflies *Eurylophella prudentialis* and *Eurylophella macdunnoughii* at 20°C, even though larvae can do equally well on pure detritus at certain lower temperatures (Table 10).

*Thermal Effects on Macroinvertebrate Populations: Laboratory Results.* Aside from altering the food base of a given stream reach for macroinvertebrate consumers, removal of riparian vegetation can significantly alter the annual pattern and magnitude of water temperature in the reach (see earlier discussion). Thus, a deforested reach of WCC can be as much as 3-5°C warmer or cooler than a nearby or contiguous forested reach, depending on the season. A 3-5°C difference in temperature almost seems trivial given that most aquatic macroinvertebrate species experience a thermal range of 20°C or more while completing their life cycle in temperate streams such as WCC. However, many important life history characteristics of both the egg and larval stages of these species can be greatly altered by small changes in temperature.

For example, experiments involving the egg stage of some widespread and common mayflies in WCC have shown that a 5°C change in temperature can cause as much as a 2-4 fold change in embryonic development time (Table 11). Moreover, a 5°C change near the lower or upper range of stream temperatures can often create a lethal situation or reduce hatch success to levels that would probably be insufficient to maintain viable populations. These data suggest that, based on thermal characteristics alone, it is possible for eggs of certain species to be deposited or transported into two contiguous reaches of stream, one forested and the other deforested, and to: (1) have complete recruitment in one reach but little if any recruitment in the other reach; or (2) to have eggs hatching in one reach completely out of synchrony with those in the adjacent reach. It is presently impossible to assess the degree to which population synchrony of the various stages affects the over-

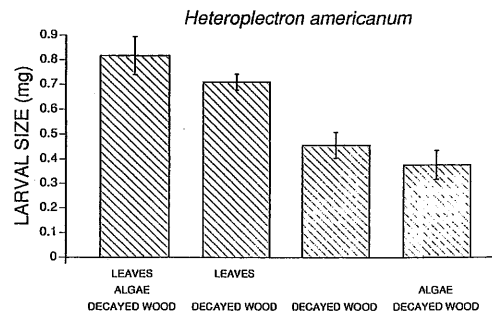


Fig. 13. Average larval size (dry mass) of the caddisfly *Heteroplectron americanum* after being fed four distinct diets for 46 days in the laboratory at about 21.5°C. Initial dry mass of first instar larvae for all experimental treatments was: Mean = 0.008, S.D. = 0.0008. Vertical bars indicate  $\pm$  one standard error.

all life table (survivorship, recruitment, etc.) of these species. However, it seems unlikely that synchrony is a neutral characteristic or maladaptive because many, if not most, of these species have evolved physiological/developmental mechanisms that synchronize various aspects of their life history.

Similarly, experiments on the larval stage of widespread and common macroinvertebrates in WCC have shown that small changes in temperature can greatly alter the length of time spent in the larval stage as well as the magnitude of growth that can be achieved on a given diet during the larval growth period. The results, however, are highly species dependent. For example, we compared four species of mayflies that feed on fine particles of organic matter in WCC (Table 10). Each species exhibited a highly significant response to small changes in rearing temperature but the response varied greatly across species depending on the diet. Thus, individual survivorship, adult size, and fecundity of *E. macdunnoughii* was similar at 10 and 15°C for an algal diet but decreased significantly at the higher temperature on the detritus diet. At 20°C, either all individuals died (detritus diet) or adults were significantly smaller and less fecund than at lower temperatures. In contrast, results for a closely related species, *E. prudentialis*, show that individual survivorship, adult size, and fecundity declined with increased temperature on the detritus diet (with 100% mortality at 20°C). On the algal diet, however, these parameters tended to actually increase with increased temperature (albeit survivorship was generally low even at

Table 10. A comparison of the effects of temperature on larval development time, individual survivorship, and adult size and fecundity of four species of mayflies (Ephemeroptera) fed various diets of fine particulate organic matter (FPOM). See also Swenceny and Vannote (1984) for additional data on *C. triangulifer*.<sup>‡</sup>

Species	Temp.	FPOM Diet	Median Development time (d)		Survivorship (%)	Adult male size (mg)		Adult female size (mg)		Fecundity	
			Mean*	SD		Mean	SD	Mean	SD	Mean	SD
<i>Eurylophella macdunnoughi</i>	10°C	Mixed Detritus	74.0	2.8	62	2.05	0.21	3.05	0.45	1545	532
	10°C	Algae	82.5	0.7	74	2.81	0.45	3.67	0.38	1627	396
	15°C	Mixed Detritus	50.0	1.4	39	0.96	0.20	1.15	0.31	367	446
	15°C	Algae	45.0	0	56	2.44	0.38	3.23	0.82	1617	550
	20°C	Mixed Detritus	—	—	0	—	—	—	—	—	—
	20°C	Algae	27.0	1.4	65	1.88	0.26	2.68	0.37	1051	258
	WCC	Mixed Detritus	62.5	2.1	25	0.94	0.27	1.21	0.23	340	173
	WCC	Algae	57.0	0	48	1.94	0.42	3.02	0.69	1506	550
<i>Eurylophella prudentialis</i>	10°C	Mixed Detritus	115.5	2.1	21	1.12	0.59	1.53	0.53	825	354
	10°C	Algae	—	—	0	—	—	—	—	—	—
	15°C	Mixed Detritus	66.5	2.1	11	0.60	0.06	0.92	0.09	448	111
	15°C	Algae	41.0	2.8	12	1.27	0.12	1.74	0.67	1310	630
	20°C	Mixed Detritus	—	—	0	—	—	—	—	—	—
	20°C	Algae	40.5	12.0	9	1.25	0.34	2.00	0.12	1387	232
	WCC	Mixed Detritus	123.0	2.8	11	1.01	0.14	1.39	0.18	921	217
	WCC	Algae	126.0	—	1	0.86	—	—	—	—	—
<i>Ameletus ludens</i> **	5°C	Mixed Detritus	—	—	0	—	—	—	—	—	—
	5°C	Algae	—	—	0	—	—	—	—	—	—
	10°C	Mixed Detritus	—	—	0	—	—	—	—	—	—
	10°C	Algae	56	—	74	—	—	4.95	0.80	1088	255
	15°C	Mixed Detritus	—	—	0	—	—	—	—	—	—
	15°C	Algae	35	—	45	—	—	2.12	0.75	364	244
	20°C	Mixed Detritus	—	—	0	—	—	—	—	—	—
	20°C	Algae	—	—	0	—	—	—	—	—	—
<i>Centroptilum triangulifer</i> **	10°C	Leaf microbes	—	—	0	—	—	—	—	—	—
	10°C	Algae	179†	—	16.5	—	—	1.8	0.4	1275	485
	20°C	Leaf microbes	—	—	0	—	—	—	—	—	—
	20°C	Algae	45†	—	25	—	—	1.0	0.1	937	180
	25°C	Leaf microbes	30†	—	10	—	—	0.5	0.1	456	87
	25°C	Algae	27†	—	36.5	—	—	0.6	0.1	574	142

<sup>‡</sup> *E. macdunnoughi* and *E. prudentialis* larvae were reared in flow-through polypropylene trays (38 x 75 x 5 cm deep) provided with either algae (mixed culture of WCC diatoms) or finely ground hickory and white ash leaves which were soaked in stream water for 7 days. Stream water was recirculated continuously into the trays from various waterbaths depending on temperature and diet. Each treatment of diet and temperature had two replicate trays. The *E. macdunnoughi* experiment was started with 35 larvae per tray; initial larval mass was: mean = 0.27, S.D. = 0.12. The *E. prudentialis* experiment was started with 45 larvae per tray; initial larval mass was: mean = 0.09, S.D. = 0.03. Maximum, minimum, average temperature for WCC was: *E. macdunnoughi* = 17.0, 5.5, 12.1°C and for *E. prudentialis* = 20.5, 3.0, 11.6°C. *A. ludens* were reared in flow-through plastic trays (38 x 7.5 x 5 cm deep). Twenty-five larvae were placed in each tray; food and temperature control were as described above. Initial size range of larvae was: 10°C = 0.19 - 0.91 mg; 15°C = 0.13 - 1.03 mg (dry mass). *C. triangulifer* were reared in static, aerated plastic trays (37 x 7 x 5 cm deep). One hundred first instar larvae (dry mass about 0.001 mg) were placed in each tray, with replicate trays at each temperature - food combination. The algal diet (diatoms) was as described above; the detritus diet consisted of Hickory leaves colonized with bacteria and fungi.

\* average of male and female median development times.

\*\* parthenogenetic species.

† days to first adult instead of median.

— no data because all larvae died or no males in populations or only one data point.

Table 11. Development time (as estimated by "days" to first hatch) and hatch success of eggs for five species of mayflies that inhabit White Clay Creek at various constant temperatures as well as at ambient WCC temperatures.

	WCC			5°C			10°C			15°C			20°C			25°C			30°C									
	Days		% Hatch	Days		% Hatch	Days		% Hatch	Days		% Hatch	Days		% Hatch	Days		% Hatch	Days		% Hatch							
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD						
<i>Centroptilium triangulifer</i>	9.2	0.4	ND	ND	—	—	0	0	0	4.2	56	47	28.0	6.8	40.1	27.4	10.5	1.2	49.2	23.1	6.9	1.5	18.3	11.8	5**	—	<0.1	—
<i>Ephemera varia</i>	44	15.1	82.0	8.5	—	—	0	0	68**	0	66.0	19.8	28**	0	69.5	26.1	18**	0	79.3	3.2	24**	—	49.0	15.5	—	—	0	0
<i>Ephemera varia</i>	15.5	0.5	76.2	17.0	ND	ND	ND	46*	—	<0.5	—	20*	—	90	—	16.5	0.7	59.6	0.7	10.6	2.0	40.4	48.1	11*	—	—	0.5	—
<i>Eurylophella funeralis</i>	44.0	13.3	ND	ND	—	—	0	0	64.5	8.3	66.1	15.4	32.8	4.9	71.6	22.5	20.1	1.2	76.9	22.7	18.8	2.8	62.4	27.3	—	—	0	0
<i>Ametatus ludensis</i>	171.2	2.8	ND	ND	590	—	ND	ND	165	20.5	ND	145.0	7.0	ND	ND	188.6	2.3	ND	ND	—	—	0	0	0	ND	ND	ND	ND

— no hatching time because all eggs died at the given temperature.  
 ND "no data" because the measurement or treatment was not part of the study.  
 \* unreplicated experiment.  
 \*\* all replicates began hatching the same day.  
 † For each species, eggs were placed in glass jars (5.5 cm O.D.; 6.5 cm deep) with 100 ml filtered (0.45 µm) stream water. Usually one clutch of eggs (between 500-2000 eggs depending on the species) was placed in each jar. The number of replicate clutches per experimental temperature varied between 4 and 10 depending on the species. Each jar was inspected daily for hatching. Hatch success was a direct count of hatched versus unhatched eggs. Maximum, minimum, and average temperature, respectively, for WCC during the developmental period of each species are as follows: *C. triangulifer* (21.4, 17.8, 19.6°C), *E. subvaria* (21.3, 8.2, 14.7°C), *E. varia* (21.4, 13.1, 17.9°C), *E. funeralis* (21.6, 10.4, 16.2°C), *A. ludensis* (22.4, 4.0, 15.8°C).



high temperatures). The point is that small changes in temperature greatly affects life history parameters, although food quantity and quality can modify the direction and magnitude of the response.

The other two fine particle feeding species, *Ameletus ludens* and *Centroptilum triangulifer*, that we studied are clearly obligate algal grazers. Neither species was able to survive on a detritus diet under most temperature regimes. On an algal diet, however, both species exhibited a highly significant decline in survivorship, adult size, and fecundity when rearing temperatures were raised above 10°C. The only consistent result across all four species was for development time, which always decreased significantly with every 5°C increase in rearing temperature. This pattern of shorter development time at higher temperature has also been observed for the pupal stage (non-feeding developmental stage) of the algal grazing caddisfly, *Glossosoma nigrrior*, in WCC (Table 12). In this case, survivorship and adult size did not show any consistent or significant relationship with incubation temperature but developmental time declined significantly with each 5°C increase in temperature between 5 and 20°C.

Results similar to those above for fine particle feeders have also been observed for leaf shredding species. Two leaf shredding species, *E. funeralis* and *H. americanum*, were each reared at two or more temperatures on leaf and algal diets (Tables 9, 13). As expected, overall survivorship and individual growth performance was generally highest on the leaf diet and, within a diet (leaf or algae), these parameters declined significantly with increased temperatures above 10°C.

Because a variety of trees occur along streamside areas in the WCC drainage, we also assessed the relative effect of temperature on survivorship, growth, etc. when a leaf shredder was fed different species of leaves. For the stonefly, *S. carolinensis*, survivorship and adult size was highest at 10°C for all diets and declined significantly with both a 5°C increase and decrease in temperature (Table 9). Similarly, overall development time was shortest at 10°C and increased at warmer and cooler temperatures. As discussed earlier, most individuals failed to complete growth and development when fed American beech leaves at all temperatures.

These laboratory data for a variety of species

Table 12. Pupal size, development time and overall survivorship to the adult stage, and size of adults for *Glossosoma nigrrior* when pre-pupae collected from White Clay Creek were reared to the pupal and adult stage at various constant temperatures. N.D. = no data.\*

Temp	Development time (d)			Survivorship	Pupal mass				Adult mass			
	First adult	Median adult	Duration of Emergence (d)		Male		Female		Male		Female	
					Mean	SD	Mean	SD	Mean	SD	Mean	SD
5°C	71	89	31	50%	3.62	0.75	3.85	0.24	2.60	0.67	3.32	0.6
10°C	30	42	33	84%	3.39	0.95	4.01	1.09	2.38	0.64	3.07	0.74
15°C	23	28	28	75%	3.42	0.58	3.36	1.13	2.75	0.60	3.30	0.66
20°C	19	25	12	78%	3.11	0.64	3.59	0.60	2.84	0.66	3.00	0.79
25°C	19	22	13	60%	3.40	0.94	3.76	0.67	2.60	0.75	3.07	0.72
WCC*	56	70	24	93%	ND	ND	ND	ND	2.72	0.91	2.61	0.65

† Pre-pupae were collected in early February from WCC. Five replicate groups of 25 specimens were reared at each of the six thermal regimes. For a given treatment, each group of 25 pre-pupae were kept in a separate container (piece of 7.5 cm OD plastic pipe with 1 mm Nitex® netting glued to the bottom) which was submerged in a plastic tray (12 x 60 x 6 cm deep) provided continuously with stream water kept at a specific temperature. For each temperature, one of the five replicate groups was sacrificed to determine average size at the onset of pupation. All specimens were weighed as soon as they pupated. Individuals in the remaining four replicate groups were reared to the adult stage, dried, and weighed.

\* WCC temperatures (daily mean, range) for the experimental period from collection of pre-pupae until adult emergence were as follow: First adult (6.9, 3.4-11.6°C), Median adult (7.3, 3.4-12.6°C).

Table 13. The effect of temperature on larval survivorship and growth of the caddisfly *Heteroplectron americanum* when fed various diets.

Temperature	Food	70 day performance*		
		Survivorship	Larval mass (mg)	
			Mean	S.D.
10°C	hickory	66.7%	8.19	4.05
	hickory + algae	68.8%	7.12	3.09
	algae	45.9%	4.49	2.39
15°C	hickory	79.2%	7.65	2.75
	hickory + algae	70.9%	6.15	2.22
	algae	29.2%	3.64	1.94
20°C	hickory	ND	ND	ND
	hickory + algae	60.5%	6.26	2.47
	algae	10.5%	5.04	2.84
25°C	hickory	58.4%	4.87	1.53
	hickory + algae	68.8%	5.50	2.23
	algae	10.5%	2.36	0.73

\* Larvae were collected on September 10 and reared in flow-through trays (23 x 45 x 22 cm deep). Fifty larvae were placed in each of 24 trays; there were two replicate trays for each temperature-food treatment. The algal diet was a mixed culture of diatoms from WCC; hickory diet consisted of pre-leached, whole hickory leaves; hickory + algae diet was a mixture of both diatoms and leaves. Rearing trays were supplied continuously with recirculated stream water from reservoirs. Initial larval size for all trays was: Mean = 3.16, S.D. = 1.32 mg dry mass. On day 70 of the experiment, all larvae in one of the replicate trays were removed, counted, dried, and weighed. The remaining larvae were continued to be reared with limited success: On day 307 of the experiment, no larvae were alive at 10, 20, or 25°C; survivorship at 15°C was low: hickory (12.5%), hickory + algae (31.3%), algae (16.7%); average (S.D.) dry mass (mg) of larvae was: hickory - 14.2 (4.5), hickory + algae - 11.26 (4.7), algae - 4.60 (2.50). ND = no data due to mechanical failure.

in WCC clearly suggest that most, if not all, macroinvertebrate species are quite sensitive to small changes in temperature during all stages of their life cycle. This sensitivity, as reflected by significant changes in key life history characteristics such as survivorship, developmental time, adult fecundity, etc., is scaled such that the observed changes in temperature in deforested streams is of sufficient magnitude to be highly relevant to the ecology of the resident macroinvertebrates.

Although experimental data based on constant temperatures provide the most effective way of evaluating the effect of a given temperature on specific life history characteristics, its applicability to natural streams with fluctuating temperature regimes has been questioned

(Sweeney 1976, 1978, 1984; Sweeney & Schnack 1977). This is because most temperate streams like WCC fluctuate thermally on both a diel and seasonal basis, even in headwater areas where the thermal regime is dominated by the temperature of local groundwater that remains more or less constant annually. For species in WCC, this aspect has been tested in the laboratory by comparing their life history characteristics at natural WCC temperatures to those measured when the natural temperature regime was modified by adding various amounts of heat (2, 3, 5, or 6°C) to it constantly. For the leaf shredding test species, overall development time consistently decreased with temperature (regardless of leaf type) for the mayfly *L. cupida* and the crane fly *T. abdominalis*, and decreased with

temperature for the stonefly *S. carolinensis* on most diets (except hickory at WCC + 3°C and red oak at WCC + 6°C; Table 14). In terms of overall survivorship, the only clear pattern was for significantly lower survivorship (on most diets) at the WCC + 6°C for all three species relative to the WCC + 3°C regime [exceptions include data on red oak and chestnut oak (*Quercus prinus*) for *T. abdominalis*]. The response of adult size was highly species and diet specific. Adults were generally larger for *L. cupida* on most diets at the warmest regime but slightly smaller for *T. abdominalis*. Most *S. carolinensis* larvae died at the warmest regime prior to metamorphosing to the adult.

For species fed mostly algal diets, development time also generally decreased with a 2 or a 5°C warming of the WCC regime for all species (except at WCC + 5°C for *E. subvaria*). Survivorship, however, was actually higher for *A. ludens* and *E. funeralis* with a 2°C warming relative to both warmer and cooler regimes. Adult size declined with increased temperature for *A. ludens* and *E. subvaria*, but was greatest at the warmest regime for *E. funeralis* (Table 15).

In general, thermal effect data gathered under laboratory conditions were fairly consistent within a species whether they were gathered at constant or variable temperature regimes. The high variability from species to species in response pattern probably reflects differences in the evolutionary history of each species. For example, one would not a priori expect two species in WCC to respond identically to a given change in temperature if, in fact, one species had evolved in more northern habitats under colder conditions and the other had evolved south of WCC under much warmer conditions (see Ross 1956 for discussion of cold and warm adapted species). Thus, the effect of a given change in temperature on the structure of macroinvertebrate communities in streams like WCC probably will depend, in part, on the evolutionary history of the component species. One point that is clearly supported by the laboratory results presented above is that a small change in temperature (2 - 6°C) can and undoubtedly will alter key life history characteristics of most, if not all, macroinvertebrate species in a stream community.

*Thermal Effects on Macroinvertebrate Populations: Field Results.* The above laboratory data concerning thermal effects on macroinvertebrate life histories have been further corroborated by

field observations. For example, extensive field experiments on the stonefly *S. carolinensis* in a variety of headwater spring areas of WCC have shown that most of the variation in the rate and magnitude of larval growth among study sites could be explained by small differences in temperature from site to site (Sweeney & Vannote 1986). Thus, for this species, a decrease of 600 degree days (about a 6°C change) during the period when larvae are accumulating 80% of their biomass (i.e. December-February) results, on the average, in a 32% decrease in final size.

The impact of altered thermal regime on the species composition of the macroinvertebrate community and life history characteristics of resident species is best exemplified by field data from the mainstem of the Delaware River, the master drainage system of WCC. These data were collected along the East and West branches of the Delaware River in areas where the natural thermal regime has been altered by the hypolimnetic discharge of the Pepacton and Cannonsville reservoirs, respectively (Fig. 14). Thus, the thermal regime for more than 70 km below each of these reservoirs is characterized by reduced diel and seasonal temperatures relative to unaffected reaches (viz. warmer winter and cooler summer conditions). The unusual temperature regime below reservoirs have often been implicated as the primary factor underlying observed downstream changes on the species composition of aquatic macroinvertebrate communities (Spence & Hynes 1971; Lehmkuhl 1972; Ward 1974). The potential mechanisms for selective elimination of these benthic species by unusual thermal regimes have been reviewed (Ward & Stanford 1979, 1982). Although the effects of temperature on the rate and magnitude of larval growth and development have been included in the list of potential mechanisms, only recently have field studies below dams focused on this interrelationship (Perry et al. 1986, 1987).

Our study of about 120 taxa of three main groups of macroinvertebrates (stoneflies, mayflies, caddisflies) in the Delaware River (Table 16) indicated that sites with a thermal regime at or near the normal magnitude and pattern for the region (sites 1,2) had on the average about 22% more taxa than the four sites where the natural thermal regime had been altered significantly (avg. = 78.5 for stations 1,2 versus 61.2 for stations 3,4,5,6). The most thermally altered sites (sites 5,6) averaged 32% fewer taxa than the

Table 14. Effects of warming the temperature regime of White Clay Creek on various life history characteristics of the stonefly *Soyedina carolinensis*, the mayfly *Leptophlebia cupida*, and the crane fly *Tipula abdominalis* when fed five types of deciduous leaves (see also Sweeney et al. 1986a, b, and Vannote and Sweeney 1985 for additional data).\*

Species	Temperature	Food	Survivorship	No. days to first adult		No. days to median adult		Adult dry mass (mg)				Fecundity	
				Mean	S.D.	Mean	S.D.	Male		Female		Mean	S.D.
								Mean	S.D.	Mean	S.D.		
<i>Soyedina carolinensis</i>	WCC	hickory	19.5%	105.5	0.7	131.5	4.9	1.31	0.19	1.92	0.28	ND	ND
		white ash	4.5%	125.5	4.9	141.5	0.7	1.41	0.29	1.86	0.72	ND	ND
		red oak	44.5%	108.5	6.4	133.0	7.1	1.28	0.14	1.93	0.31	ND	ND
	WCC+3°C	chestnut oak	5.0%	136.0	16.9	140.5	10.6	1.25	0.14	1.71	0.23	ND	ND
		American beech	7.0%	123.0	5.6	141.0	5.6	0.99	0.12	1.10	0.48	ND	ND
		hickory	7.0%	122.0	2.8	133.0	9.8	1.09	0.15	1.60	0.24	ND	ND
	WCC+6°C	white ash	5.0%	119.5	3.5	135.5	13.4	1.14	0.16	1.84	0.31	ND	ND
		red oak	20.5%	102.0	1.4	122.0	2.8	1.08	0.15	1.53	0.19	ND	ND
		chestnut oak	3.0%	123.0	4.2	141.5	14.8	1.02	0.02	1.20	0.13	ND	ND
<i>Leptophlebia cupida</i>	WCC	American beech	16.5%	99.0	2.8	123.5	2.1	0.94	0.21	1.17	0.20	ND	ND
		hickory	1.0%	106.0	-	106.0	-	1.13	0.04	-	-	ND	ND
		white ash	2.0%	95.0	33.9	114.5	6.3	1.10	0.04	1.84	-	ND	ND
	WCC+3°C	red oak	1.0%	114.0	-	114.0	-	1.16	0.08	-	-	ND	ND
		chestnut oak	0.5%	112.0	-	112.0	-	1.10	-	-	-	ND	ND
		American beech	2.0%	96.0	-	100.0	-	1.06	0.18	-	-	ND	ND
	WCC	hickory	20.0%	80.0	4.2	94.5	3.5	1.90	0.47	3.70	1.14	1064	471
		white ash	19.0%	75.0	24.1	94.5	3.5	2.51	0.42	3.27	0.90	831	480
		red oak	12.0%	90.0	9.8	118.0	-	1.37	0.17	1.69	0.51	272	470
WCC+3°C	chestnut oak	77.0%	94.5	3.5	113.5	2.1	1.48	0.34	1.82	0.50	223	188	
	American beech	85.0%	94.5	3.5	116.5	2.1	1.36	0.14	1.63	0.41	212	156	
	hickory	50.0%	54.5	0.7	74.0	4.2	2.01	0.34	3.23	0.90	939	474	
WCC+6°C	white ash	46.0%	52.0	2.8	71.5	2.1	2.30	0.63	3.91	1.09	1079	588	
	red oak	12.0%	85.5	6.4	102.5	0.7	1.55	0.37	1.92	0.96	732	312	
	chestnut oak	16.0%	81.0	5.6	93.5	4.9	1.73	0.36	3.11	1.14	787	613	
WCC+6°C	American beech	8.0%	70.0	21.2	91.0	1.4	1.66	0.35	2.67	1.31	641	733	

Table 14. (continued)

Tipula <i>abdominalis</i>	WCC	Species	%	Terminal Larval Wet Mass (g)										
				Mean	S.D.	44.0	1.41	55.0	—	2.06	0.40	2.61	0.52	479
WCC+6°C		hickory	39.0%	44.0	1.41	55.0	—	2.06	0.40	2.61	0.52	479	349	
		white ash	25.0%	43.0	—	50.0	—	2.31	0.45	3.80	1.16	1329	643	
		red oak	7.0%	51.5	10.6	64.0	7.1	1.47	0.13	2.84	1.18	865	742	
		chestnut oak	7.0%	49.5	9.2	66.0	4.2	1.66	0.39	2.65	1.28	774	775	
		American beech	3.0%	56.0	18.3	56.0	18.4	1.17	0.23	2.04	0.57	307	—	
		hickory	100.0%											
		white ash	95.0%											
		red oak	95.0%											
		chestnut oak	73.6%											
		American beech	93.7%											
WCC+3°C		hickory	88.8%		1.17	0.23								
		white ash	ND		ND	ND								
		red oak	36.8%		1.05	0.33								
		chestnut oak	60.0%		0.82	0.16								
		American beech	65.0%		0.70	0.18								
WCC+6°C		hickory	25.0%		1.13	0.27								
		white ash	13.3%		0.99	0.13								
		red oak	52.6%		0.89	0.13								
		chestnut oak	62.5%		0.96	0.20								
		American beech	55.0%		0.66	0.18								

\* All larvae were collected from WCC and reared in flow through polypropylene trays (23 x 45 x 22 cm deep), with replicate trays at each specific temperature - food combination. Leaves were collected in September and soaked in stream water for two weeks. Water was kept at or near ambient WCC temperatures by continuously pumping fresh stream water through heat exchangers submerged in the reservoir used to supply the trays. The WCC+3°C and WCC+6°C regimes were obtained by varying the numbers of heat exchangers and adding a constant amount of heat with aquarium heaters. For *S. carolinensis*, 100 larvae (initial mass: Mean = 0.31, S.D. = 0.08) were placed in each rearing tray at the start of the experiment on October 24. For *L. capida*, 150 larvae (initial mass: Mean = 2.61, S.D. 1.03) were placed in each rearing tray at the start of the experiment on January 2. For *T. abdominalis* larvae collected from WCC were divided into small and large size groups and 50 larvae of each size class were placed in separate rearing trays as described above. Data for the small size class were reported in Vannote and Sweeney (1985). The data in this Table are for the large size class which had an average wet biomass of 0.211 g (S.D. = 0.086) at the start of the experiment.

reference sites (53.5 versus 78.5). There were 23 taxa present at the reference sites that were missing from the stream reaches immediately below the reservoirs. Nine taxa were conspicuously missing at all four sites in the thermal gradient below the reservoirs (sites 3,4,5,6). In addition, five taxa were missing from the three coldest sites (sites 4,5,6) while nine taxa were missing from the two coldest sites (sites 5,6).

We also studied the pattern of larval development and adult emergence of the 20 most widespread and common macroinvertebrate species at the study sites (Table 17). The seasonal pattern of emergence seems consistent with the unusual temperature relationship among sites as well as the significant thermal effect on developmental times observed in laboratory experiments (see above). For example, species that normally emerge in late spring or during the summer emerged substantially later in the year at the sites that were cooled during this period by the hypolimnetic discharge. Species that normally emerge in early spring (i.e. before the period of greatest thermal difference between study sites) emerged more or less at the same time at all sites. The close relationship between seasonal emer-

gence time and local thermal regime is further demonstrated by examining taxa at site 5, which had temperatures similar to sites 1 and 2 during early to mid-spring but site 6 during the summer. Species at site 5 that normally emerged during early to mid-spring exhibited emergence times closely aligned with those observed at sites 1 and 2, whereas species that normally emerge during the summer exhibited a pattern more closely aligned with those observed at site 6.

The effect of the altered thermal regimes on the seasonal pattern and magnitude of larval growth was highly species dependent (Fig. 14). For example, although the larval growth period was consistently longer at the colder sites for most species, the magnitude of larval growth (i.e. maximum larval size at maturity) of some species seem to be retarded by the colder temperatures (e.g. *Ephemerella subvaria*) but enhanced for other species (e.g. *Eurylophella verisimilis*).

These data from the Delaware River show convincingly that thermal modification along the length of a river system, whether it be due to a discharge from the bottom of a reservoir, a power plant discharge, differential shading because of deforestation, etc., can greatly affect

Table 15. Effect of warming the White Clay Creek temperature regime on larval survivorship, time to complete larval development (from date of collection), and adult size and fecundity of three mayfly species fed diets dominated by fine particulate algae. ND = no data. See also Sweeney and Vannote (1978) for additional data. †

Species	Temperature	Food	Survivorship	No. days to first adult		No. days to median adult		Adult dry mass (mg)				Fecundity*
				Mean	SD	Mean	SD	Male		Female		
<i>Ameletus ludens</i>	WCC	algae	25.0%	71.0	—	76.0	—	unisexual		3.85	0.54	797
	WCC + 2°C	algae	41.6%	54.0	—	56.0	—	unisexual		3.51	1.09	712
	WCC + 5°C	algae	12.5%	54.0	—	55.0	—	unisexual		3.31	0.46	662
<i>Eurylophella funeralis</i>	WCC	algae (leaves)**	26.1%	87.0	—	93.0	—	unisexual		3.52	0.68	2408
	WCC + 2°C	algae (leaves)**	61.5%	68.0	—	77.0	—	unisexual		3.53	1.00	2417
	WCC + 5°C	algae (leaves)**	18.4%	56.0	—	61.0	—	unisexual		3.92	0.61	2741
<i>Ephemerella subvaria</i>	WCC	algae	ND	93.5	0.7	100.5	3.5	4.31	0.29	6.57	0.50	533
	WCC + 2°C	algae	ND	63.0	0	67.0	0	2.77	0.61	4.84	0.59	430
	WCC + 5°C	algae	ND	90.0	0	96.0	0	2.79	0.25	3.98	0.29	375

\* fecundity estimated by the following equations describing fecundity (F) as a function of adult dry mass (DM): *A. ludens*,  $F = 251.3 \text{ DW} - 169.7$ ,  $r^2 = 0.75$ ; *E. subvaria*,  $F = 59.3 \text{ DW} + 143.4$ ,  $r^2 = 0.44$ ; *E. funeralis*,  $F = 830.4 \text{ NW} - 514.1$ ,  $r^2 = 0.75$ .

\*\* rearing trays also provided with some deciduous leaves.

† all larvae were collected from WCC on January 13 or 14. For each species, 40 leaves were reared in flow through polypropylene trays (45 x 24 x 20 cm deep). Water temperatures were maintained as described for Table 14. Algae were mainly diatoms cultured from WCC. Hickory leaves were added as a thin coating in the bottom of the tray. Average (S.D.) dry biomass of larvae at the start of the experiment were as follows: *A. ludens*: 0.660 (0.175), *E. funeralis*: 0.87 (0.41), *E. subvaria*: 1.278 (0.78).

important life history characteristics. For example, how temperature affects the length of the larval period as related to the duration of exposure to mortality factors, the timing of adult emergence as related to suitability of air temperatures for adult mating and reproductive flights and availability of terrestrial food for appropriate species, the synchrony of adult emergence as related to susceptibility to predators, ability to find a mate, the size of adults as

related to fecundity and reproductive effort for females, etc. The critical point is that thermal effects in river systems have been historically evaluated in terms of upper and lower lethal limits as judged by short term laboratory exposures in constant temperature environments. These types of data often greatly underestimate the potential impact of a few degrees centigrade change in temperature when experienced over a significant portion of the entire life cycle of a

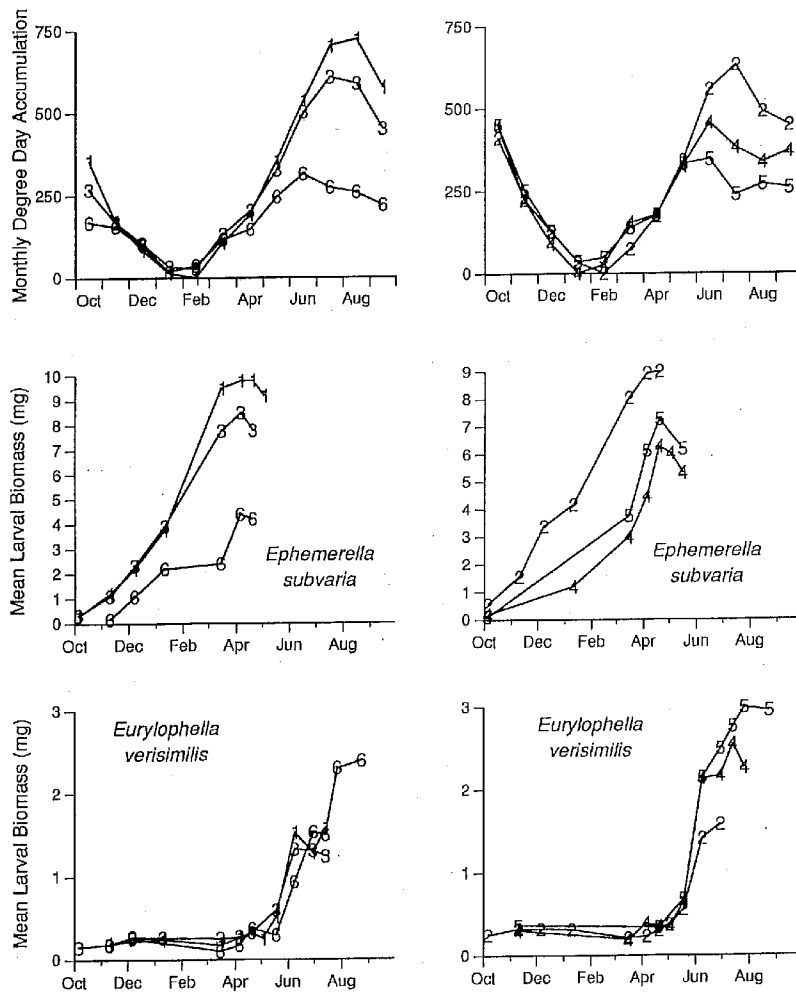


Fig. 14. The seasonal pattern of water temperature and larval growth of two mayfly species (*Ephemera subvaria* and *Eurylophella verisimilis*) at six sampling stations in the upper Delaware River drainage in the vicinity of the Cannonsville and Pepacton reservoirs. Stations 1 and 2 are the mainstem of the Delaware River and Beaverkill Creek, respectively, which were unaffected by the cold water release from the reservoir and served as control sites. Stations 3 and 6 are on the East Branch of the Delaware River about 22 and 7 km below the Pepacton reservoir, respectively. Stations 4 and 5 are on the West Branch of the Delaware River about 14 and 7 km below the Cannonsville reservoir, respectively. Temperatures were measured by continuous recording thermographs. Data points indicating larval growth were mean dry mass of larvae collected from each site on a given date.

stream macroinvertebrate.

*Macroinvertebrate Reproduction (adult emergence, feeding, oviposition, and survivorship).* For most insects, which are the predominant macroinvertebrates in streams, the transition from the aquatic larval stage to the winged, terrestrial adult stage is a physiologically demanding and risky (predation) period. Although many species have evolved mechanisms for completing metamorphosis and emerging (flying) from streams while floating on the water surface, many others, especially hemimetabolous species, need to crawl as larvae from the stream bottom out of the water current and complete metamorphosis on a dry surface [e.g. many mayflies (Ephemeroptera), stoneflies (Plecoptera), dragonflies and damselflies (Odonata)]. For such species that inhabit areas near the margin of streams, larvae typically emerge by crawling up the bank on roots, soil, grassy vegetation, etc. For those species inhabiting non-marginal habitat, preference is given to protruding rocks and twigs in mid-channel.

In first through fourth order forested streams of WCC, the channel is typically wide and shallow, with numerous cobbles protruding through the water surface (especially in riffle areas) providing both a substantial number of individual sites and a large collective area for adult emergence (Table 18). Unfortunately, deforestation of riparian areas causes the stream channel to narrow and deepen and most, if not all, of these potential sites are inundated. Moreover, the loss of streamside trees eliminates protruding logs, twigs, etc. as alternate emergence sites. This means that all benthic larvae requiring dry substrata for emergence must migrate to the stream edge to emerge, rather than crawling to the top of the rock or piece of woody debris that they inhabit. Although few, if any, data are available, it seems reasonable to suggest that the increased distance should increase susceptibility to predation by both fish and other aquatic invertebrates.

Further risk for newly emerged adults is the migration from the water surface to terrestrial substrata. In WCC, adults of a variety of species actively select streamside trees as the preferred site to complete their metamorphosis (e.g. molt from subimago to adult for mayflies), to rest while awaiting the proper swarming time, to feed in order to produce eggs, or to mate. Whether this behavior reflects an evolutionary history involving streams flowing through forested landscapes is unknown but intriguing. Regardless,

the probability of surviving the migration from the benthic feeding ground of the larva to the forest canopy habitat of the adult depends on, among other things, the density of predators, the density of prey (predator satiation), and the time of exposure to predation (function of migration distance). For example, individual survivorship on a given day of emergence for the mayfly *Dolania americana* from a coastal plain stream is inversely related to the density of conspecific prey (Fig. 15a) as well as inversely related to the density of predators (Fig. 15b). Although there are no data relating migration distance from the benthic feeding ground to the adult swarming or mating site of *D. americana* (or any other stream insect), one reasonable hypothesis is that fewer emergence sites within the stream channel coupled with a longer flight distance from the water surface to a forest canopy would greatly increase adult mortality relative to that in a forested reach (assuming of course that all other factors are equal which might not be the case). This would mean, for example, that phenomena such as predator satiation (shown in Fig. 15a) would effectively occur only at the highest densities of prey and probably only result in a small reduction in adult mortality.

For some species, adult emergence must also be synchronized with the flowering of streamside trees because adults need to feed on flowers in order to successfully mate, mature ovaries, and produce eggs. For example, female adults of the stonefly *Taenionema atlanticum* (Fig. 16a) collected during the first two weeks in April refused to mate and their ovaries remained undeveloped (Fig. 16b) when presented with lichens, tree bark, algae, etc. However, after about three days of feeding on maple flowers, females mated and eggs began to mature in the ovaries (Fig. 16c). A full clutch of eggs was completed (Fig. 16d) within about 20 days from the start of feeding (D. H. Funk pers. comm.). Because feeding on flowering plants is mandatory, deforestation of streamside areas of WCC (which also eliminates the understory plant communities) would, at a minimum, greatly increase adult migration distance to and from feeding grounds. Moreover, deforestation could, if adult behavior is such as to exclude long distance flight, preclude reproduction completely for adults emerging from the reach.

Deforestation of stream channels and loss of woody debris can also limit the number of egg deposition sites for many insect species. For



Table 16. Presence (X) or absence ( ) of various stonefly, mayfly, and caddisfly taxa at six study sites on the Delaware River. Study sites are listed in order from warmest (1) to coolest (6) on an annual basis. The thermal regime of the six study sites is given in Fig. 14.

Taxa	Study Sites*					
	1 (BYK5)	2 (DEL8)	3 (EBH5)	4 (WBH7)	5 (WBD6)	6 (EBD5)
<b>Plecoptera</b>						
<i>Pteronarcys</i>		X				
<i>Allonarcys biloba</i>						X
<i>Strophopteryx</i>	X			X		X
<i>Strophopteryx fasciata</i>	X		X	X	X	X
<i>Taenionema</i>	X					
<i>Taenionema atlanticum</i>	X	X	X	X	X	X
<i>Taeniopteryx</i>					X	
<i>Taeniopteryx metequi</i>	X					X
<i>Taeniopteryx nivalis</i>	X	X	X	X	X	X
<i>Taeniopteryx burksi/maura</i>	X	X	X			X
<i>Taeniopteryx</i> sp. A			X			
<i>Taeniopteryx</i> sp. B			X			
<i>Brachyptera</i>	X	X	X	X	X	X
<i>Nemoura perfecta</i>						X
<i>Prostoia</i>	X	X	X			
<i>Soyedina</i>	X					
<i>Acroneuria</i>		X				
<i>Acroneuria abnormis</i>	X	X	X			
<i>Acroneuria internata</i>	X					
<i>Acroneuria lycorias</i>	X	X				
<i>Acroneuria carolinensis</i>			X			X
<i>Phasganophora capitata</i>	X					X
<i>Paragnetina media</i>	X	X	X			
<i>Paragnetina immarginata</i>	X					X
<b>Ephemeroptera</b>						
<i>Ephemera</i>	X	X				
<i>Ephemera guttulata</i>	X	X	X			
<i>Ephemera varia</i>	X	X	X			
<i>Tricorythodes</i>	X	X	X	X		
<i>Caenis</i>	X	X				
<i>Attenella</i>		X				
<i>Attenella attenuata</i>	X	X	X	X		
<i>Attenella margarita</i>			X			
<i>Ephemerella</i>		X				X
<i>Ephemerella dorothea</i>	X	X	X	X	X	X
<i>Ephemerella needhami</i>	X	X	X	X	X	X
<i>Ephemerella septentrionalis</i>	X	X	X	X	X	X
<i>Ephemerella excrucians</i>		X	X			
<i>Ephemerella invaria</i>		X			X	X
<i>Ephemerella subvaria</i>	X	X	X	X	X	X
<i>Ephemerella invaria</i> grp.	X	X	X	X	X	X
<i>Dannella simplex</i>	X	X	X	X	X	X
<i>Drunella cornuta</i>	X	X	X	X	X	X
<i>Drunella tuberculata</i>	X	X	X			

Continued on next page

Table 16 continued

Taxa	1 (BVK5)	2 (DEL8)	3 (EBH5)	4 (WBH7)	5 (WBD6)	6 (EBD5)
<i>Drunella walkeri</i>	X	X	X			
<i>Drunella lata</i>	X	X	X		X	X
<i>Drunella cornutella</i>	X	X	X	X	X	X
<i>Drunella</i> sp. 2	X					
<i>Eurylophella</i>			X		X	
<i>Eurylophella bicolor</i>			X			
<i>Eurylophella funeralis</i>			X	X	X	X
<i>Eurylophella verisimilis</i>	X	X	X	X	X	X
<i>Eurylophella aestiva</i>	X	X	X		X	
<i>Eurylophella verisim/aestiva</i>			X			
<i>Serratella</i>		X	X			
<i>Serratella deficiens</i>	X	X	X	X	X	X
<i>Serratella serrata</i>	X	X	X	X	X	
<i>Serratella sordida</i>	X	X				
<i>Serratella serratoides</i>	X	X	X	X		
<i>Leptophlebia cupida</i>	X	X	X	X	X	X
<i>Paraleptophlebia</i>	X					
<i>Paraleptophlebia adoptiva</i>	X	X	X	X	X	X
<i>Paraleptophlebia mollis</i>	X	X	X	X	X	X
<i>Paraleptophlebia</i> sp. 2	X					
<i>Paraleptophlebia</i> sp. A	X					
<i>Paraleptophlebia</i> sp. B	X					
<i>Paraleptophlebia</i> sp. 3	X	X	X			
<i>Paraleptophlebia</i> sp. 4	X					X
<i>Epeorus pleuralis</i>	X	X	X	X	X	X
<i>Epeorus vitreus</i>	X	X	X	X	X	X
<i>Heptagenia</i>	X			X		
<i>Heptagenia hebe</i>	X	X	X	X	X	X
<i>Heptagenia juno</i>						X
<i>Heptagenia pulla</i>	X	X	X	X	X	X
<i>Heptagenia</i> sp. 4	X					
<i>Rhithrogena</i>	X					X
<i>Stenonema</i>	X	X	X	X	X	
<i>Stenonema femoratum</i>			X			
<i>Stenonema modestum</i>	X	X	X			X
<i>Stenonema mediopunctatum</i>	X	X	X	X		
<i>Stenonema vicarium</i>	X	X	X	X	X	X
<i>Stenonema ithaca</i>	X	X	X	X	X	X
<i>Cinygmula subaequalis</i>	X	X	X	X	X	X
<i>Stenacron</i>		X	X	X		X
<i>Stenacron carolina</i>			X			
<i>Stenacron interpunctatum</i>	X	X	X	X		X
<i>Siphonurus quebecensis</i>		X	X	X	X	X
<i>Isonychia</i>	X	X	X	X	X	X
<i>Isonychia bicolor</i>			X			X
<i>Ameletus</i>			X	X		X
<i>Ameletus ludens</i>	X	X	X	X		X
<i>Potomanthus myops</i>	X					
<b>Trichoptera</b>						
<i>Glossosoma</i>		X	X	X	X	X

Continues on next page

Table 16 continued

Taxa	1 (BVK5)	2 (DEL8)	3 (EBH5)	4 (WBH7)	5 (WBD6)	6 (EBD5)
<i>Dolophilodes</i>	X					
<i>Cheumatopsyche</i>	X	X	X	X	X	X
<i>Hydropsyche</i>	X	X	X	X		X
<i>Hydropsyche bifida</i>	X	X	X	X	X	X
<i>Hydropsyche slossonae</i>	X		X	X	X	X
<i>Hydropsyche bronta</i>	X	X	X	X	X	
<i>Hydropsyche morosa</i>	X	X	X	X	X	X
<i>Hydropsyche sparna</i>	X	X	X	X	X	X
<i>Hydropsyche</i> sp. C	X	X		X		X
<i>Hydropsyche</i> sp. D		X				
<i>Hydropsyche</i> ( <i>Symphitopsyche</i> )			X			X
<i>Hydropsyche bifida</i> grp.	X	X	X	X	X	X
<i>Macronema</i>			X			
<i>Macronema zebratum</i>	X	X				
<i>Ptilostomis</i>		X	X	X	X	X
<i>Apatania</i>		X				X
<i>Hydatophylax</i>	X		X	X		X
<i>Neophylax</i>		X	X	X		
<i>Neophylax</i> sp. A				X		
<i>Platycentropus</i>		X	X	X		X
<i>Pycnopsyche</i>	X	X	X	X		X
<i>Lepidostoma</i>				X		
<i>Brachycentrus</i>	X	X	X	X	X	X
<i>Helicopsyche borealis</i>	X		X			
<i>Psilotreta</i>	X	X	X			X
<i>Psilotreta labida</i>	X					
<i>Rhyacophila</i>			X			
<i>Polycentropus maculatus</i>			X			

\* The six study sites were located on the Mainstem and the East and West Branches of the Delaware River in New York. Reference sites (unimpacted by thermal discharge) were located on the mainstem of the Delaware River (site 2; DEL8) about 13.8 km downstream of the confluence of the East and West Branches and on a tributary of the East Branch (Beaverkill River, site 1; BVK5) about 8 km downstream of the Pepacton Reservoir. The two coldest sites were each located about 7 km downstream from the Pepacton (EBD5; site 6) and Cannonsville (WBD6; site 5) reservoirs. Intermediate cold sites were about 14 km below the Cannonsville reservoir (WBH7; site 4) and 22 km below the Pepacton Reservoir (EBH5; site 3).

example, many species of insects in WCC and nearby watersheds oviposit gelatinous egg masses out of the water on overhanging tree limbs and dead tree trunks as well as just above the water line on protruding woody snags, tree roots, etc. (e.g. *Pycnopsyche* and *Hydatophylax* caddisflies, *Sialis* and *Corydalus* dobsonflies, tabanid Diptera). Some species in WCC actually have sclerotized ovipositors, allowing eggs to be deposited directly into the soft tissue of submerged wood (e.g. the mayfly *Habrophlebiodes*, the dragonfly *Boyeria*, the caddisfly *Lype*).

Another factor that can limit the availability of oviposition sites is the increased depth associated with channel narrowing in deforested reaches. As noted above, this greatly reduces the number of protruding rocks which serve as sites where adults can land and crawl under water to oviposit. The limited number of protruding rocks could reduce the probability for successful reproduction by increasing the flight time for adults in search of suitable oviposition sites and concentrating recruitment into a few areas of the channel (thus increasing the competition for

Table 17. Seasonal timing of adult emergence for selected aquatic insect species in the Delaware River. For each species, the numbers indicate the approximate time period when mature larvae (i.e. with black wing pads and ready to undergo metamorphosis) were last collected from the six study sites. The thermal regime and geographic location of the six study sites are given in Fig. 14 and Table 16, respectively.

	April			May			June			July			August				
	1-7	8-14	15-21	22-30	1-7	8-14	15-21	22-31	1-7	8-14	15-21	22-31	1-7	8-14	15-21	22-31	
<i>Taenionema atlanticum</i>			1,3,4,5,6														
<i>Ephemera subvaria</i>			3,6,2	1	4,5												
<i>Paraleptophlebia adolptiva</i>			3,6,4	1,2		5											
<i>Epeorus pleuratis</i>				2,3	1,4,5		6										
<i>Cinygmula subaequalis</i>				2	3,5		4,6										
<i>Stenonema vicarium</i>							1,3,6										
<i>Drunella cornuta</i>							1-5	6									
<i>Ephemera needhami</i>							1,2,3	4									
<i>Ephemera septentrionalis</i>							1,2,3,5		4								
<i>Ephemera dorothea</i>							1,2		3				4				5,6
<i>Siphonurus quebecensis</i>							2,3,5,6	2,5	4				6				
<i>Paraleptophlebia mollis</i>									1,3				6				
<i>Damella simplex</i>									1,2,3,4				6				
<i>Eurylophella verisimilis</i>										1,2,3			4				5,6
<i>Stenonema ihaca</i>													1,3,5,6				4
<i>Epeorus vitreus</i>										2			3				1,4,5,6
<i>Drunella lata</i>										1			2,3				
<i>Drunella cornutella</i>										3			1,4				5,6
<i>Serratella deficiens</i>										1,4			3,6				2,5
<i>Serratella serrata</i>													1,2,3				4

Table 18. The average number of rocks protruding above the water surface and total wetted perimeter of protruding rocks in four riffle areas of a second order tributary of White Clay Creek in forested and meadow areas.

	No. Protruding Rocks			Total Wetted Rock Perimeter (m)		
	Mean	(SE)	Forest/Meadow ratio	Mean	(SE)	Forest/Meadow ratio
Forested	17.8	(8.1)	17.8	10.1	(4.7)	16.8
Meadow	1.0	(0.7)		0.6	(0.4)	

oviposition sites among adults and for resources among the resulting offspring). The importance of protruding substrates in WCC as oviposition sites is readily shown by floating artificial substrates in areas where protruding rocks are rare. In a few days, the underside of the substrates often become covered with egg masses of Baetid mayflies, hydropsychid and philopotamid caddisflies, gerrid waterstriders, etc. It is obviously not the substrate per se that the adults find attractive (a rubber inner tube will do nicely). They are seeking out any reasonably solid object that protrudes above the water surface in the stream channel.

**STREAMSIDE REFORESTATION**

After carefully examining the physical, chemical, and biological effects of altering the quantity and quality of streamside vegetation, it is clear that a diverse and intact riparian forest is one of the most important factors in either maintaining the structure and function of a macroinvertebrate community in a natural state or restoring it to a natural or quasi-natural state following stream/watershed disturbance. Recently, Welsch (1991) in cooperation with the Forest Service of the United States Department of Agriculture (U.S.D.A.), has further advocated the restoration of streamside forests on "open lands" citing some of the factors discussed in detail above. This protocol for a streamside forest buffer has now been adopted as an "Interim Standard and Specification" for the eastern region of the United States by the South and Northeast National Technical Centers of the U.S.D.A.'s Soil Conservation Service. Although adequate data are not presently available to support or refute the validity of the Welsch (1991) protocol, it does represent a starting point that can be refined as more information becomes available. The protocol is well thought out but contains many untested

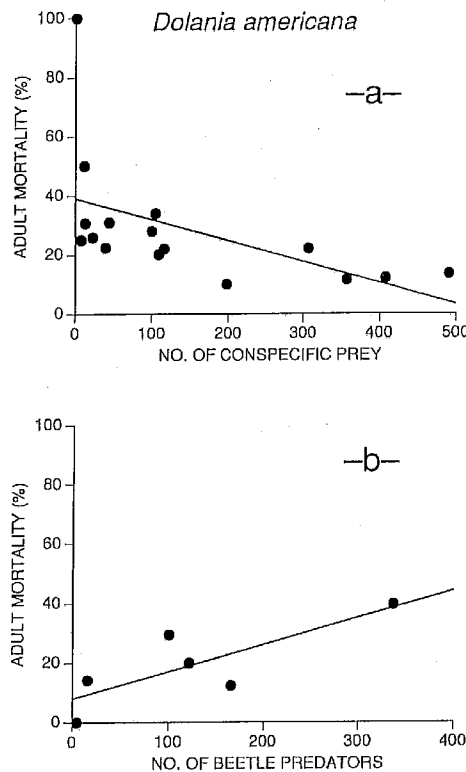


Fig. 15. Adult mortality for the mayfly *Dolania americana* as a function of the number of conspecific prey emerging from the study reach on a given day (a) as well as the number of surface predators present (b). All mortality data refer to adult death due to predation by the surface feeding beetle *Dineutes discolor*. Variation in the number of conspecific prey per day (a) was natural; the data were collected from the same 50m long study reach of Upper Three Runs, Aiken County, South Carolina over a three year period. Variation in the number of predators was created artificially by adding and removing beetles from the study reach during the emergence period of one year. Lines represent linear regressions.

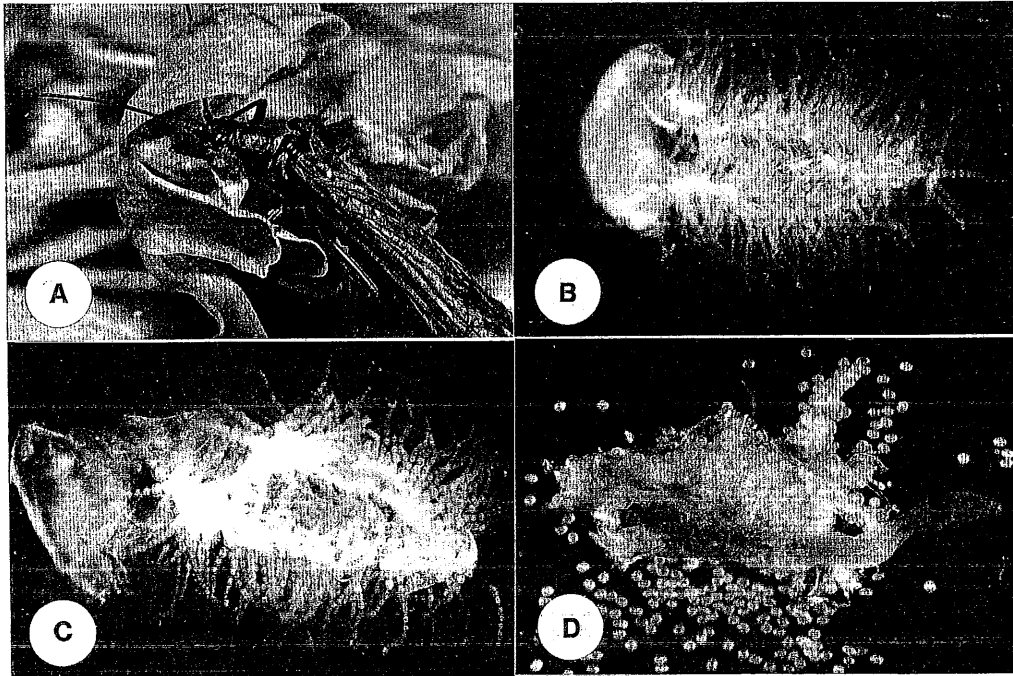


Fig. 16. An adult stonefly, *Taenionema atlanticum*, feeding on a maple flower (a), and the gradual change in the condition of the female ovaries of the adult from an undifferentiated state (b) prior to feeding, to an intermediate state of maturity (c) about one week after feeding, to a fully developed state (d) in about two weeks.

ideas. It is presented here because it is a "state-of-the-art" protocol whose uncertainties should help scientists focus their research. In general, Welsch's model (1991) divides the streamside area into three zones (Fig. 17):

Zone 1 begins at the top of the stream bank and occupies a strip of land with a fixed width of about 4.6 m (15 ft) measured horizontally on a line perpendicular to the streambank. The primary function of the Zone 1 forest is to stabilize the streambank, to moderate water temperature and promote the growth of desirable algae via shading, maximize stream width (benthic surface area) by shading out grasses that tend to narrow stream channels, to provide soil/water contact area for biogeochemical processing of nutrients, and to contribute necessary organic detritus and large woody debris to the stream ecosystem.

Zone 2 begins at the edge of Zone 1 and occupies an additional strip of land with a minimum width of about 18.3 m (60 ft). The purpose of Zone 2 is to provide "necessary contact time and carbon energy source for buffering processes to take place and to provide for long term

sequestering of nutrients in the form of forest trees" (Welsch 1992). In addition, a portion of the forest detritus (leaves, fruits, seeds, etc) from Zone 2 will be transported by wind through Zone 1 and enter the stream. The presence of forest and lack of farming (soil compaction) in Zone 2 will improve soil structure and its capacity for infiltration of overland flow of rainwater.

Zone 3 begins at the edge of Zone 2 and has a minimum width of 6.1 m (20 ft). This zone is intended to be an unforested, grassy area (grazed or ungrazed) separating the streamside forest from other upland landuses such as agriculture. Its function is to "provide sediment filtering, nutrient uptake, and the spacing necessary to convert concentrated flow to uniform, shallow, sheet flow" (Welsch 1991).

Welsch (1991) also provides numerous suggestions for the long-term maintenance/management of the forest that develops in these various zones next to the stream. However, aside from advocating the use of native riparian tree and shrub species representing a variety of species, factors such as site preparation, type and size of tree to plant, and maintenance during the

early stages of forest regrowth are not addressed. Given the highly disturbed nature of streamside areas, especially with regard to the presence of foreign species, there also needs to be a prescription or working protocol with regard to the design and implementation of actual streamside reforestation projects. I will use field experience in the WCC watershed and surrounding watersheds in southeastern Pennsylvania to give some rudimentary guidelines.

As noted earlier, streamside areas in the Piedmont region of the mid-Atlantic (especially in southeastern Pennsylvania) that have been deforested for agriculture and then abandoned in the last forty years have not undergone natural succession to the forested state. For example, Fig. 18a shows how the banks of a cattle pasture along a third order tributary of WCC becomes completely dominated after 10 years by non-woody foreign plants (multiflora rose, Asiatic bittersweet, Japanese honeysuckle) if it is left fallow. Careful removal of this non-woody vegetation reveals little or no regeneration of native North American trees along this reach, a condition that may persist for 40 years or longer. Thus, landowners wishing to establish a "native" forest along stream channels on their property may be faced with considerable site preparation. Not only do these foreign species have to be removed prior to planting trees, but they have to be controlled following planting or they will out-compete many of the native tree species.

Because the widespread use of herbicides in riparian areas should be avoided, mechanical removal is advocated. In our experience, the most efficient and cost effective method is to mow or cut off by hand the stem of each undesired plant at ground level during the spring just after the plants have leafed out (i.e. after a substantial amount of stored energy has been expended by the plant). Although most plants will sprout stems from the cut off root stump, mow-

ing or cutting once or twice again during the subsequent summer can weaken and kill many of the plants.

As noted in Welsch (1991), plant species for Zones 1 and 2 should consist of native streamside (wetland) tree species on soils of Hydrologic Groups D and C and native upland tree species on soils of Hydrologic Groups A and B. Therefore, species recommendations for streamside plantings must, by necessity, be very site specific. In the WCC area, we have successfully planted the following native species in areas near stream channels: red maple (*Acer rubrum*), sugar maple (*Acer saccharum*), sweet birch (*Betula lenta*), river birch (*Betula nigra*), black gum (*Nyssa sylvatica*), black willow (*Salix nigra*), pin oak (*Quercus palustris*), American sycamore (*Platanus occidentalis*), big toothed aspen (*Populus grandidentata*), tulip poplar, red oak, black walnut (*Juglans nigra*), American elm, and white ash. Other tree species that have been recommended for streambank areas include: American basswood (*Tilia americana*), ironwood (*Carpinus caroliniana*), silver maple (*Acer saccharinum*), swamp white oak (*Quercus bicolor*), black cherry (*Prunus serotina*), among others. Recommended native shrubs include: red-osier dogwood (*Cornus stolonifera*), spicebush (*Lindera benzoin*), arrowwood (*Viburnum dentatum*), white swamp azalea (*Rhododendron viscosum*), pinxterbloom azalea (*Rhododendron periclymenoides*), and elderberry (*Sambucus canadensis*), among others. As noted earlier, species that are known to be nitrogen-fixing plants (e.g. alder, black locust) should be avoided in areas where streamside plantings are being implemented for reducing the flux of nutrients to stream systems.

Because transplanting large trees is not feasible (either economically or physically) for most landowners, streamside plantings usually involve small (<0.5m) to intermediate (1.0-1.5 m)

Table 19. The effect of tree shelters on growth of black walnut and red oak seedlings after two years.

Tree species	Treatment	Tree Height After Two Years (mm)		
		Mean	(SE)	ratio*
Black walnut	tree shelter	86.8	(3.6)	2.36
	natural	36.7	(3.1)	
Red oak	tree shelter	54.7	(4.7)	1.63
	natural	33.5	(5.7)	

\* ratio of height measurements (tree shelter/natural)

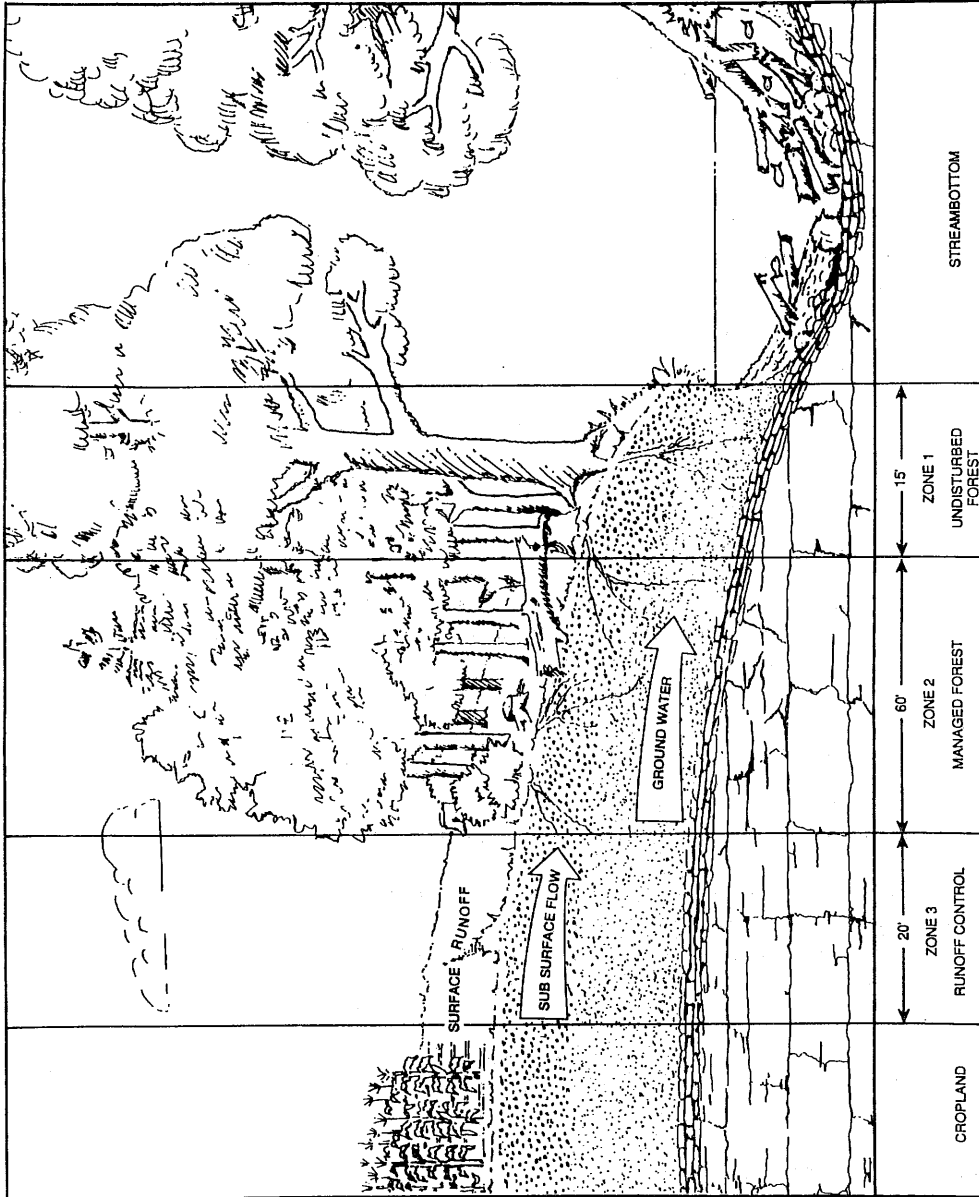


Fig. 17. Schematic diagram modified from Welsch (1991) showing a streamside forest buffer protocol for the eastern region of the United States that has been adopted as an "Interim Standard and Specification" by the South and Northeast National Technical Centers of the U.S.D.A.'s Soil Conservation Service.



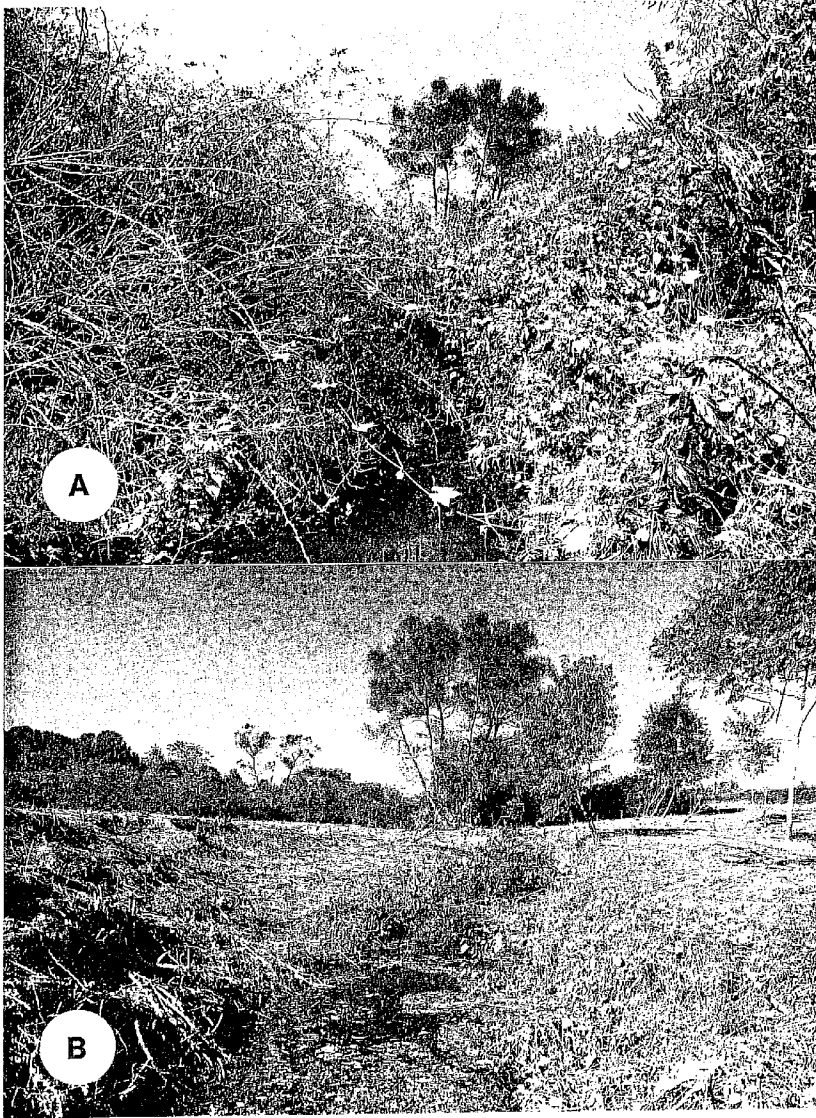


Fig. 18. (a) streamside vegetation dominated by foreign plant species (mainly multiflora rose, Asiatic bitter-sweet, and Japanese honeysuckle) adjacent to a stream channel that had been left fallow from agriculture for 10 years, and (b) the same streamside area following the removal of the foreign plants (n.b. the limited number of small black walnut trees were probably present when the field was abandoned).

size seedlings. We have used both sizes in streamside plantings along WCC. Small seedlings are more desirable because they can usually be purchased from the state or federal government at about one-tenth the cost of the intermediate size plants. However, survivorship of small seedlings is often low when they are stressed by factors such as soil moisture, competition with other plants (native and exotic), and

predation by herbivores. Since the importance of each of these mortality factors greatly diminishes as the tree gets larger, it behooves the landowner to either start with an intermediate size seedling (if economically possible) or to start with a small seedling and try to promote the fastest possible vertical growth.

Competition (space, light, nutrients, moisture, etc.) with other plants and density of herbi-

vores (e.g. rabbits, whitetail deer, etc.) during the first two to five years following planting are probably the most important factors that affect seedling survivorship and growth. Mechanical weed abatement (mowing and hand weeding) and mulching can greatly reduce plant competition and improve seedling growth. Seedlings planted in rows with about a 3 m spacing has worked well in the WCC watershed both in terms of accommodating quick and effective mowing of large areas with tractors and as proper spacing between seedlings to minimize strong competition among neighboring plants during their first 6-8 years of life. Herbiciding the area immediately around seedlings is also effective but must be done with caution in riparian areas because of their proximity to both the stream and to shallow groundwater sources providing a portion of the streamflow.

In the headwater areas of WCC, mowing areas planted with seedlings at least twice per year (May and August) for the first three to five years is the minimum necessary treatment in order to avoid almost complete mortality in the plantation. For example, in 1981 a five acre field near the creek was plowed, disked, and deciduous tree seedlings were machine planted in rows at about 7.3 m (8 ft) intervals. One portion of the field received no weed abatement during the first few years, while the remaining portions were mowed and sometimes herbicided. After eleven years, average survivorship among rows

was about 73.0% (S.E. = 5.4%) in areas receiving weed abatement and it presently consists of a young, canopied forest that requires selective thinning to reduce tree densities. In contrast, average survivorship among rows in the untreated areas was only 8.4% (S.E. = 3.1%) and the area is dominated by foreign, non-woody plants, resembling other abandoned fields in the area. Most of the mortality in the untreated plot occurred during the first 2-3 years when the area was invaded and taken over by the foreign plants.

Mowing probably increases survivorship because it keeps light levels non-limiting and prevents the seedlings from being physically overgrown by competing herbaceous plants and vines. However, mowing probably does little to reduce competition for nutrients and moisture because seedlings are still surrounded with low lying plants and their root systems. One method of optimizing vertical seedling growth for a given level of nutrients and moisture is to install "tree shelters" on them when they are planted. Tree shelters, which were originally developed in England, are tall plastic tubes installed around seedlings in order to protect them from vertebrate herbivores (e.g. deer, rabbits, mice, etc.) and improve growth by creating a "greenhouse-like" effect around each tree (Tuley 1985).

Numerous studies from Europe have demonstrated the effectiveness of tree shelters for improving seedling growth and survivorship [see the recent review of the history and use of tree shelters by Windell (1991)]. Their utility is further indicated by the increase in use from about 80 in 1979 in Great Britain to about 10 million per year worldwide in 1991 (Potter 1991). Lantagne et al. (1990), in one of the few published studies in North America, showed that northern red oak seedlings planted in tree shelters were 1.40 times taller than unsheltered seedlings after one growing season and 1.42 times taller after two growing seasons. In the WCC watershed, red oak and black walnut seedlings planted in tree shelters (122 cm tall; Tubex Co., St. Paul, MN) were 1.63 and 2.36 times taller, respectively, after two growing seasons than those not planted in shelters (Table 19). Studies in England indicate that trees grown in shelters retain their height advantage in succeeding years (Potter 1986). These results are very important because current silviculture practices, especially shelterwood methods, usually do not promote the development of slow growing species such

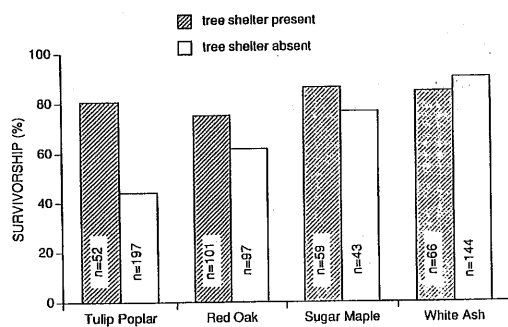


Fig. 19. Showing the effect of tree shelters on seedling survivorship for four species of deciduous trees after the first growing season. n = the number of seedlings monitored for the study.

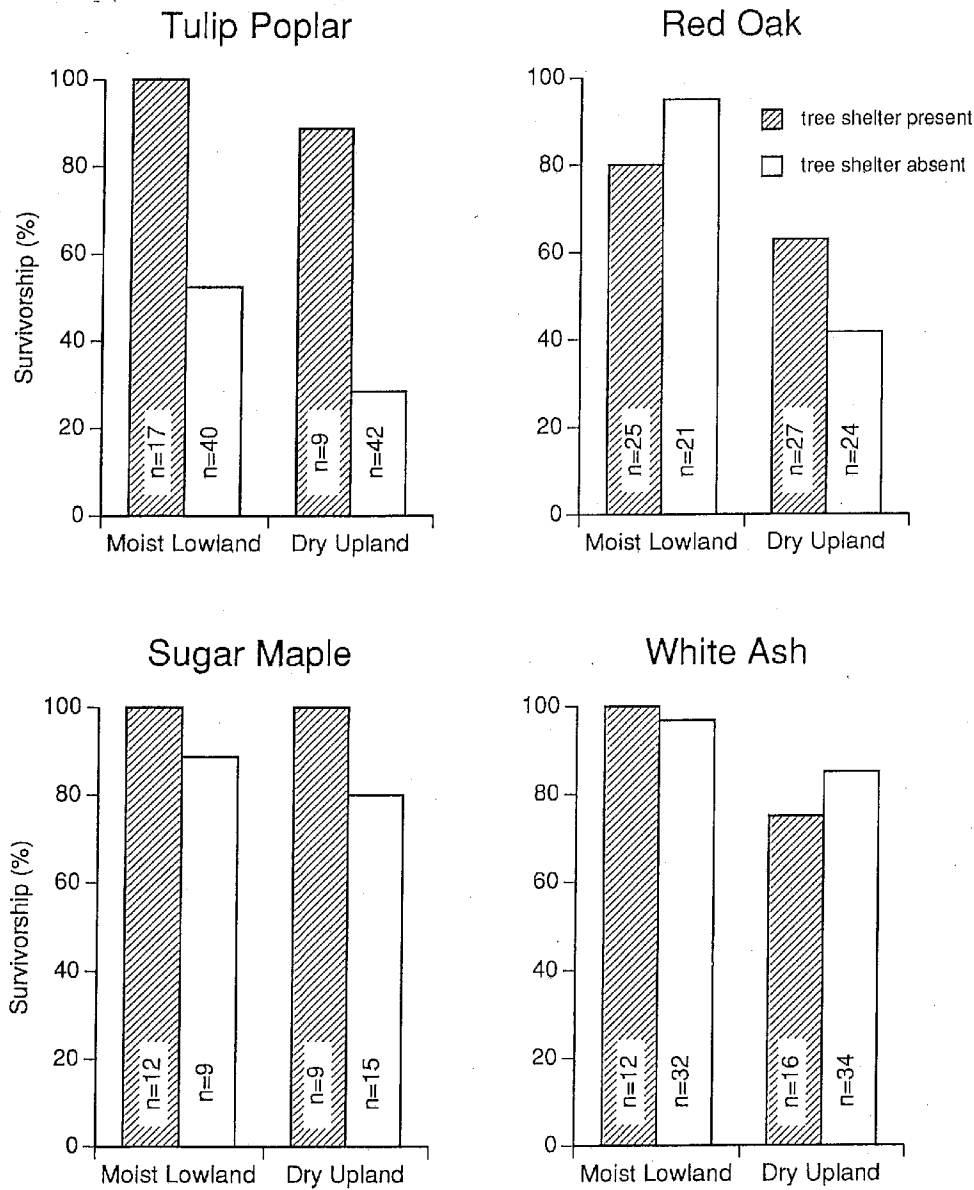


Fig. 20. Showing the effect of tree shelters on seedling survivorship for four species of deciduous trees planted in dry upland and moist lowland areas of a small watershed. Survivorship was measured after one growing season.

as red oak and black walnut (Sander 1979; Lantagne et al. 1990), which are out competed by faster growing species [such as red maple, black cherry, sassafras (*Sassafras albidum*), etc.; see also Rudolph & Lemmien 1976]. Thus, the increased height of the sheltered red oak and black walnut seedlings places them in a dominant position in the understory relative to other species of

seedlings (Lantagne et al. 1990).

For streamside plantings in the WCC watershed and elsewhere, shelters may be the only satisfactory method to assure adequate representation in the mature forest of slow growing species (e.g. pin oak, black gum, hickory, etc.) relative to fast growing species such as red maple, American sycamore, river birch, and black wil-

low. Moreover, the availability of shelters in different heights (up to 1.8m) allow successful forest regeneration in streamside areas where high densities of deer, voles, rabbits, etc have heretofore made it impossible. We are presently attempting to quantify the level of predation of seedlings by herbivores on sheltered and non-sheltered plants.

We have also observed in our experimental watersheds that shelters increase seedling survivorship during drought. For example, in late April 1991 we planted 759 seedlings representing four species (tulip poplar, red oak, sugar maple, white ash) at the very headwater tip of a small watershed that had been in hay production for the previous 10 years. The period following planting was extremely dry (rainfall during May 1991 was only 3.0 cm compared to an average of 11.5 cm for the month during the previous decade). There was considerable mortality in the plantation but it varied substantially with tree species, the presence or absence of tree shelters, and the location of each seedling (the 0.75 ha site had a steep relief, grading gradually from a moist lowland area to a dry hilltop area). In general, overall survivorship was 16.5% higher for seedlings planted in shelters (80.9% versus 64.4%). However, differences in survivorship was highly variable among species, ranging from 36.5% higher in shelters for tulip poplar to actually being 5.4% lower for sheltered white ash (Fig. 19). There was also considerable difference in the pattern of mortality for the four species between the moist low elevation areas and the drier upland zone. Fig. 20 shows that in lowland sites survivorship was fairly high in three of the four species (red oak, sugar maple, white ash) regardless of the presence of shelters. The fourth species, tulip poplar, exhibited 100% survivorship in the shelters but only 52.5% survivorship without shelters, a notable difference. In contrast, at the drier upland sites, where seedling survivorship was generally reduced relative to the moist lowland sites, survivorship was 20-60% higher with shelters for three of the four species (tulip poplar, red oak, sugar maple). The pattern for white ash was different, with survivorship actually being 10% lower. Low survivorship of white ash in tree shelters may be due to a higher susceptibility of blight under moist conditions within the shelter (P. Johnson pers. comm.).

Although these data suffer from lack of replication among sites, they strongly suggest that,

for three of the four species, tree shelters reduced the overall water requirements of the seedlings in our plantation and promoted increased survivorship when moisture became limiting due to drought and/or competition with surrounding plants. Since the seedlings were planted at random and shelters were assigned to individual seedlings at random, the effectiveness of the shelters was often immediately visible by mid-summer when comparing neighboring plants of the same species. For example, sheltered tulip poplar seedlings were generally larger and had green succulent leaves whereas its unsheltered conspecific neighbor (within 3m) was dead, dying (wilted), or stunted and characterized by dry leather-like leaves.

These preliminary findings from the WCC and surrounding watersheds show that reforestation of streamside areas can be accomplished within a reasonable time frame (about 10 years). The use of new experimental techniques (tree shelters) on selected tree species may reduce this time period further as well as assure a mixed species composition in the final canopy. More research is clearly needed in this important area of stream ecology.

#### SUMMARY AND CONCLUSIONS

Although stream ecosystems in eastern North America have been subjected by humans to a vast array of perturbations (altered physical, chemical, and biological characteristics) during the past 300 years, the most severe perturbation may have been the earliest—viz. the extensive removal of virgin forest from streamside and upland areas of their watershed. Unfortunately, there are few, if any, rigorous data concerning the nature of stream ecosystems when the forests of eastern North America were intact. We can only try to reconstruct their previous status based on recent observations from streams flowing through deforested and reforested areas of eastern North America. This task is difficult because we have no "reference" to gauge the current status of these ecosystems. In many ways it is like trying to describe the dynamics of a steady-state forest with only data from early successional stages. Thus, data from early successional stages can provide useful insights, but not a precise definition of the actual steady-state forest.

In this paper, I have tried to piece together the relative importance of streamside vegetation to

aquatic macroinvertebrates using data from stream and river communities at various, poorly defined stages of recovery from major perturbation. It will be fortuitous if insights based on these data precisely define the actual relationship that existed between the structure and function of macroinvertebrate communities and the primary forest that bordered streams historically. Regardless, existing data from WCC and elsewhere strongly suggest that streamside forests greatly increase the amount and complexity of benthic habitat available to macroinvertebrates. The estimate that deforested reaches of WCC have about 50% less habitat may, in fact, be conservative. Channels bordered by primary forest may have been even wider than today's channels bordered by secondary growth and the estimate does not take into account the additional surface area provided by other aspects of a streamside forest such as woody debris, leaf packs, root mats, etc. Although 50% more space may not necessarily translate into 50% greater macroinvertebrate production or ecosystem efficiency per unit length of channel, it would be foolish to argue status quo. One could easily advocate the maintenance and/or restoration of streamside forests based solely on preserving existing habitat and/or mitigating lost stream habitat, respectively.

I have shown in this paper, however, that space is not the only issue supporting the proposal that streamside forests greatly affect the life history characteristics of lotic macroinvertebrates. Additional support comes from: (1) field studies showing how deforestation along stream channels alters the natural temperature regime of the stream and can affect the food base of macroinvertebrates either directly (through inputs of DOC, leaf litter, woody debris) or indirectly (shading effects on the quality and quantity of algal production); and (2) laboratory studies that demonstrate how changes in temperature, food quality, etc. can significantly affect important life history characteristics of a variety of species (e.g. survivorship, growth, adult size, fecundity). The data are presently too limited to speculate as to what extent (if any) streamside forests helped shape the evolution of life history characteristics of lotic macroinvertebrates. It may be that most species have been evolutionarily stable over a much longer time frame than for forest stability. However, some influence is suspected especially in

view of certain patterns that have been observed in contemporary streams. For example, small deforested tributaries of WCC often have large standing crops of blue-green or filamentous green algae in the middle of the summer. These algal forms have obviously been able to outcompete other algae, especially diatoms, under the prevailing conditions of high light, nutrient, and temperature. However, the high standing crop of algae persists because nothing consumes it. Where are the macroinvertebrate species that specialize in eating this type of algae? Should we expect a wide variety of such species if indeed these algal forms were probably a very rare food type when WCC and other Piedmont streams flowed through heavily shaded primary forest?

Finally, I have tried to discuss all aspects of streamside forests in terms of maintaining a rich and productive macroinvertebrate community in streams of eastern North America. This review has also presented numerous reasons why reforestation of denuded streamside should proceed in earnest. For example, streamside forests may help mitigate the flux of nutrients and sediments from upland agricultural activities, counteract the impact of global warming on stream ecosystems, and reduce the exposure of stream organisms to UV radiation as our protective ozone layer diminishes. Whatever the reason, the evidence supports the widespread reforestation of these areas to help stream ecosystems return to a more natural condition.

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### BIBLIOGRAPHY

- Allen, K. R. 1951. The Horokiwi stream: A study of a trout population. New Zealand Marine Department Fisheries Bulletin 10: 1-238.
- Asmussen, L. E., J. M. Sheridan, and C. V. Booram, Jr. 1979. Nutrient movement in streamflow from agriculture watersheds in the Georgia coastal plain. *Transactions of the Society of Agricultural Engineering* 22: 809-815.
- Barton, D. R., W. D Taylor, and R. M. Biette. 1985. Dimensions of riparian buffer strips required to maintain trout habitat in southern Ontario streams. *North American Journal of Fishery Management* 5: 364-378.
- Behmer, D. J. and C. P. Hawkins. 1986. Effects of overhead canopy on macroinvertebrate production in a Utah stream. *Freshwater Biology* 16: 287-300.
- Benke, A. C., T. C. Van Arsdall, Jr., and D. M. Gillespie. 1984. Invertebrate productivity in a subtropical blackwater river: The importance of habitat and life history. *Ecological Monographs* 54(1): 25-63.
- Benke, A. C., R. L. Henry III, D.M. Gillespie, and R. H. Hunter. 1985. Importance of snag habitat for animal production in southeastern streams. *Fisheries* 10: 8-13.
- Bilby, R. E. 1981. Role of organic debris dams in regulating the export of dissolved and particulate matter from a forested watershed. *Ecology* 62: 1134-1143.
- Bilby, R. E. and P. A. Bisson. 1992. Allochthonous versus autochthonous organic matter contributions to the trophic support of fish populations in clear-cut and old-growth forested streams. *Canadian Journal of Fisheries and Aquatic Sciences* 49: 540-551.
- Bilby, R. E. and G. E. Likens. 1980. Importance of organic debris dams in the structure and function of stream ecosystems. *Ecology* 60: 1107-1113.
- Bilby, R. E. and J. W. Ward. 1989. Changes in the characteristics and function of woody debris with increasing size of streams in western Washington. *Transaction of the American Fisheries Society* 118: 368-378.
- Bilby, R. E. and J. W. Ward. 1991. Characteristics and function of large woody debris in streams draining old-growth, clear-cut, and second-growth forests in southwestern Washington. *Canadian Journal of Fisheries and Aquatic Sciences* 48: 2499-2508.
- Boston, H. L. and W. R. Hill. 1991. Photosynthesis-light relations of stream periphyton communities. *Limnology and Oceanography* 36(4): 644-656.
- Bott, T. L., L. A. Kaplan, and F. T. Kuserk. 1984. Benthic bacterial biomass supported by streamwater dissolved organic matter. *Microbial Ecology* 10: 335-344.
- Bott, T. L. and L. A. Kaplan. 1985. Bacterial biomass, metabolic state, and activity in streambed sediments: Relation to environmental variables and multiple assay comparisons. *Applied Environmental Microbiology* 50: 508-522.
- Bott, T. L. and L. A. Kaplan. 1989. Densities of benthic protozoa and nematodes in a piedmont stream. *Journal of the North American Benthological Society* 8: 187-196.
- Bott, T. L. and L. A. Kaplan. 1990. Potential for protozoan grazing of bacteria in streambed sediments. *Journal of the North American Benthological Society* 9: 336-345.
- Carbone, V. A. 1976. Environment and prehistory in the Shenandoah Valley. Ann Arbor, Michigan: University Microfilms.
- Comiskey, C. E. 1978. Aspects of the organic carbon cycle on Walker Branch watershed: A study of land/water interaction. Ph.D. thesis, The University of Tennessee.
- Costa, J. E. 1975. Effects of agriculture on erosion and sedimentation in the Piedmont Province, Maryland. *Geological Society of America Bulletin* 86: 1281-1286.
- Cummins, K. W. 1974. Structure and function of stream ecosystems. *Bioscience* 24: 631-641.
- Cummins, K. W. and M. J. Klug. 1979. Feeding ecology of stream invertebrates. *Annual Review of Ecology and Systematics* 10: 147-172.
- Cummins, K. W., M. A. Wilzbach, D. M. Gates, J. B. Perry, and W. B. Taliaferro. 1989. Shredders and riparian vegetation. *Bioscience*. 39: 24-30.
- Custer, J. F. 1981. Report on archaeological research in Delaware FY 1981 by the Department of Anthropology, University of Delaware. Bureau of Archaeology and Historic Preservation, Division of Historical and Cultural Affairs, Dover. MS on file.
- Custer, J. F. 1984. Delaware prehistoric archeology: An ecological approach. University of Delaware Press, Newark.
- Dawson, T. E. and J. R. Ehleringer. 1991. Streamside trees that do not use stream water. *Nature* 350: 335-337.
- De Lucia, E. H., T. A. Day, and T. C. Vogelmann. 1991. Ultraviolet-B radiation and the rocky mountain environment: Measurement of incident light and penetration into foliage. *Current Topics in Plant Biochemistry and Physiology* 10: 32-48.
- Dubois, M., K. Gilles, J. Hamilton, P. Rebers, and F. Smith. 1956. Colorimetric method for determination of sugars and related substances. *Analytical Chemistry* 28: 350-356.

- Elwood, J. W., J. D. Newbold, A. F. Trimble, and R. W. Stark. 1981. The limiting role of phosphorous in a woodland stream ecosystem: Effects of P enrichment on leaf decomposition and primary production. *Ecology* 62: 146-158.
- Feminella, J. W., M. E. Power, and V. W. Resh. 1989. Periphyton responses to invertebrate grazing and riparian canopy in three northern California coastal streams. *Freshwater Biology* 22: 445-457.
- Fisher, S. G. 1977. Organic matter processing by a stream-segment ecosystem: Fort River, Massachusetts, U.S.A. *Internationale Revue der Gesamten Hydrobiologie* 62: 701-727.
- Fisher, S. G. and G. E. Likens. 1973. Energy flow in Bear Brook, New Hampshire: An integrative approach to stream ecosystem metabolism. *Ecological Monographs* 43: 421-439.
- Fuller, R. L., J. L. Roelofs, and T. J. Fry. 1986. The importance of algae to stream invertebrates. *Journal of the North American Benthological Society* 5: 290-296.
- Golladay, S. W., J. R. Webster, and E. F. Benfield. 1987. Changes in stream morphology and storm transport of seston following watershed disturbance. *Journal of the North American Benthological Society* 6: 1-11.
- Gregory, S. V., G. A. Lamberti, D. C. Erman, K. V. Koski, M. L. Murphy, and J. R. Sedell. 1987. Influence of forest practices on aquatic production. Pages 233-255 in E. O. Salo and T. W. Cundy, eds. *Streamside management: Forestry and fishery interactions*. Institute of Forest Resources, Contribution 57, University of Washington AR-10, Seattle.
- Gregory, S. V., F. J. Swanson, W. A. McKee, and K. W. Cummins. 1991. An ecosystem perspective of riparian zones. *Bioscience* 4 (8): 540-551.
- Grimm, N. B. and S. G. Fisher. 1986. Nitrogen limitation in a Sonoran desert stream. *Journal of the North American Benthological Society* 5: 2-15.
- Hansen, J., A. Lacias, D. Rind, G. Russell, I. Fung, and S. Lebedeff. 1987. Evidence for future warming: How large and when? Pages 57-75 in Shands, W. E., J.S. Hoffma, eds. *The greenhouse effect, climate change, and U.S. forests*. The Conservation Foundation, Washington.
- Hawkins, C. P., M. L. Murphy, and N. H. Anderson. 1982. Effects of canopy, substrate composition, and gradient on the structure of macroinvertebrate communities in Cascade Range streams of Oregon. *Ecology* 63: 1840-1856.
- Hill, W. R. and H. L. Boston. 1991. Community development alters photosynthesis-irradiance relations in stream periphyton. *Limnology and Oceanography* 36(7): 1375-1389.
- Hill, W. R. and B. C. Harvey. 1990. Periphyton responses to higher trophic levels and light in a shaded stream. *Canadian Journal of Fisheries and Aquatic Sciences* 47: 2307-2314.
- Hill, W. R. and A. W. Knight. 1988. Nutrient and light limitation of algae in two northern California streams. *Journal of Phycology* 24: 125-132.
- Hooper, R. P. and C. A. Shoemaker. 1986. A comparison of chemical and isotopic hydrograph separation. *Water Resources Research* 22: 1444-1454.
- Hopkins, C. L. 1976. Estimate of biological production in some stream invertebrates. *New Zealand Journal of Marine and Freshwater Research* 10: 629-640.
- Horton, R. E. 1945. Erosional development of streams and their drainage basins: hydrophysical approach to quantitative morphology. *Bulletin of the Geological Society of America* 56: 275-370.
- Hornberger, G. M., M. G. Kelly, and R. M. Eller. 1976. The relationship between light and photosynthetic rate in a river community and implications for water quality modeling. *Water Resources Research* 12: 723-730.
- Jacobs, T. C. and J. W. Gilliam. 1985. Riparian losses of nitrate from agricultural drainage waters. *Journal of Environmental Quality* 14: 472-478.
- Johnson, R. K., T. Wiederholm, and D. M. Rosenberg. 1992. Freshwater biomonitoring using individual organisms, populations, and species assemblages of benthic macroinvertebrates. Pages 40-158 in D. M. Rosenberg and V. H. Resh, eds. *Freshwater biomonitoring and benthic macroinvertebrates*. Chapman and Hall, New York.
- Kaplan, L. A., R. A. Larson, and T. L. Bott. 1980. Patterns of dissolved organic carbon in transport. *Limnology and Oceanography* 25: 1034-1043.
- Kaplan, L. A. and T. L. Bott. 1982. Diel fluctuations of DOC generated by algae in a piedmont stream. *Limnology and Oceanography* 27: 1091-1100.
- Kaplan, L. A. and T. L. Bott. 1983. Microbial heterotrophic utilization of dissolved organic matter in a piedmont stream. *Freshwater Biology* 13: 363-377.
- Kaplan, L. A. and T. L. Bott. 1985. Acclimation of streambed microflora: Metabolic responses to dissolved organic matter. *Freshwater Biology* 15: 479-492.
- Kaplan, L. A. and T. L. Bott. 1989. Diel fluctuations in bacterial activity on streambed substrata during vernal algal blooms: Effects of temperature, water chemistry, and habitat. *Limnology and Oceanography* 34: 718-733.
- Kaplan, L. A., T. L. Bott, and J. K. Bielicki. 1992. Assessment of [3H]thymidine incorporation into DNA as a method to determine bacterial productivity in streambed sediments. *Applied and Environmental Microbiology* 58: 3614-3621.
- Kaplan, L. A. and J. D. Newbold. 1992. Sources

- and biogeochemistry of terrestrial dissolved organic carbon entering streams. Pages 139-165 in T. E. Ford, ed. *Aquatic microbiology: an ecological approach*. Blackwell Scientific Publications Inc., Cambridge, Massachusetts.
- Keller, E. A. and F. H. Swanson. 1979. Effects of large organic material on channel form and fluvial processes. *Earth Surface Processes* 4: 361-380.
- Kennedy, V. C., C. Kendal, G. W. Zelweger, T. A. Weyerman, and R. J. Avanzino. 1986. Determination of the components of stormflow using water chemistry and environmental isotopes, Mattole River basin, California. *Journal of Hydrology* 84: 107-140.
- Kuserk, F. T., L. A. Kaplan, and T. L. Bott. 1984. In situ measures of dissolved organic carbon flux in a rural stream. *Canadian Journal of Fisheries and Aquatic Sciences* 41: 964-973.
- Lantagne, D. O., C. W. Ram, and D. H. Dickmann. 1990. Tree shelters increase height of planted oaks in a Michigan clearcut. *Michigan State Northern Journal of Applied Forestry* 7(1): 24-26.
- Larson, R. A. 1978a. Dissolved organic matter of a low-coloured stream. *Freshwater Biology* 8: 91-104.
- Larson, R. A. 1978b. Environmental chemistry of reactive oxygen species. *CRT Critical Reviews of Environmental Control* 8: 197-246.
- Larson, R. A. and M. R. Berenbaum. 1988. Environmental phototoxicity. *Environmental Science and Technology* 22(4): 354-360.
- Lehmkuhl, D. M. 1972. Change in the thermal regime as a cause of reduction of benthic fauna downstream of a reservoir. *Journal of the Fisheries Research Board of Canada* 29: 1329-1332.
- Leopold, L. B., M. G. Wolman, and J. P. Miller. 1964. *Fluvial processes in geomorphology*. W. H. Freeman and Company, San Francisco.
- Lowe, R. L., S. Golladay, and J. R. Webster. 1986. Periphyton response to nutrient manipulation in streams draining clear-cut and forested watersheds. *Journal of the North American Benthological Society* 5: 221-229.
- Lowrance, R. R., R. L. Todd, and L. E. Asmussen. 1984. Nutrient cycling in an agricultural watershed. I. Phreatic movement. *Journal of Environmental Quality* 13: 22-27.
- Lowry, O. H., N. J. Rosebrough, A. L. Farr, and R. J. Randall. 1951. Protein measurement with the folin phenol reagent. *Journal of Biological Chemistry* 193: 265-275.
- Lyford, J. H., Jr. and S. V. Gregory. 1975. The dynamics and structure of periphyton communities in three Cascade Mountain streams. *Internationale Vereinigung fur Theoretische und Angewandte Limnologie. Verhandlungen* 19: 1610-1616.
- Martin, D. S. 1958. Taiga-tundra and the full glacial period in Chester County, Pennsylvania. *American Journal of Science* 256: 470-502.
- McDowell, W. H. and S. G. Fisher. 1976. Autumnal processing of dissolved organic matter in a small woodland stream ecosystem. *Ecology* 57: 561-569.
- McDowell, W. H. and G. E. Likens. 1988. Origin, composition, and flux of dissolved organic carbon in the Hubbard Brook Valley. *Ecological Monographs* 58: 177-195.
- Meyer, J. L. and J. O'Hop. 1983. Leaf-shredding insects as a source of dissolved organic carbon in headwater streams. *American Midland Naturalist* 109: 175-183.
- Meyer, J. L. and C. M. Tate. 1983. The effects of watershed disturbance on dissolved organic carbon dynamics of a stream. *Ecology* 64: 33-44.
- Minshall, G. W. 1978. Autotrophy in stream ecosystems. *Bioscience* 28: 767-771.
- Mulholland, P. J. 1981. Organic carbon flow in a swamp-stream ecosystem. *Ecological Monographs* 51: 307-322.
- Murphy, M. L. 1984. Primary production and grazing in freshwater and intertidal reaches of a coastal stream, Southeast Alaska. *Limnology and Oceanography* 29: 805-815.
- Murphy, M. L., C. P. Hawkins, and N. H. Anderson. 1981. Effects of canopy modification and accumulated sediment on stream communities. *Transactions of the American Fisheries Society* 110: 469-478.
- Newbold, J. D., J. W. Elwood, R. V. O'Neill, and A. L. Sheldon. 1983. Phosphorous dynamics in a woodland stream ecosystem: A study of nutrient spiralling. *Ecology* 64: 1249-1265.
- Nilson, H. C. and R. W. Larimore. 1973. Establishment of invertebrate communities on log substrates in the Kaskaskia River, Illinois. *Ecology* 54: 366-374.
- Pearce, A. J., M. K. Stewart, and M. B. Sklash. 1986. Storm runoff generation in humid headwater catchments. 1. Where does the water come from? *Water Resources Research* 22: 1263-1272.
- Perrin, C. J., M. L. Bothwell, and P. A. Slaney. 1987. Experimental enrichment of a coastal stream in British Columbia: Effects of organic and inorganic additions on autotrophic periphyton production. *Canadian Journal of Fisheries and Aquatic Sciences* 44: 1247-1256.
- Perry, S. A., W. B. Perry, and J. A. Stanford. 1986. Effects of stream regulation on density, growth, and emergence of two mayflies (Ephemeroptera: Ephemerellidae) and a caddisfly (Trichoptera: Hydropsychidae) in two Rocky Mountain rivers (U.S.A.). *Canadian Journal of Zoology* 64: 656-666.
- Perry, S. A., W. B. Perry, and J. A. Stanford. 1987. Effects of thermal regime on size, growth rates, and emergence of two species of stoneflies



- (Plecoptera: Taeniopterygidae, Pteronarcyidae) in the Flathead River, Montana. *The American Midland Naturalist* 117: 83-93.
- Peterjohn, W. T. and D. L. Correll. 1984. Nutrient dynamics in an agricultural watershed: observations on the role of a riparian forest. *Ecology* 65: 1466-1475.
- Potter, M. J. 1986. Major innovations mark the 1986 tree shelter scene. *Forestry and British Timber* 15 (10) October 1986.
- Potter, M. J. 1991. Tree shelters. *Handbook 7, Forestry Commission, HMSO, London.*
- Power, M. E. 1984. Habitat quality and the distribution of algae-grazing catfish in a Panamanian stream. *Journal of Animal Ecology* 53: 357-374.
- Pringle, C. M. and J. A. Bowers. 1984. An in situ substratum fertilization technique: Diatom colonization on nutrient enriched, sand substrata. *Canadian Journal of Fisheries and Aquatic Sciences* 41: 1247-1251.
- Pringle, C. M., P. Paaby-Hansen, P. D. Vaux and C. R. Goldman. 1986. In situ nutrient assays of periphyton growth in a lowland Costa Rican stream. *Hydrobiologia* 134: 207-213.
- Raven, J. A. 1992. How benthic macroalgae cope with flowing freshwater: Resource acquisition and retention. *Journal of Phycology* 28: 133-146.
- Rhodes, H. A. and W. A. Hubert. 1991. Submerged undercut banks as macroinvertebrate habitat in a subalpine stream. *Hydrobiologia* 213: 149-153.
- Richards, K. 1982. *Rivers: Form and process in alluvial channels.* Methuen, New York.
- Ross, H. H. 1956. *Evolution and classification of the mountain caddisflies.* The University of Illinois Press, Urbana.
- Rudolph, V. J. and W. A. Lemmien. 1976. Silvercultural cuttings in an oak-hickory stand in Michigan: 21 year results. Pages 431-452 in *Proceedings of the First Central Hardwood Forest Conference.* Southern Illinois University, Carbondale.
- Sander, I. L. 1979. Regenerating oaks with the shelterwood system. Pages 54-60 in *Regenerating oaks in upland hardwood forests.* John S. Wright Forestry Conference Proceedings. Purdue University, West Lafayette.
- Schleser, G. H. 1992. s13 pattern in a forest tree as an indicator of carbon transfer in trees. *Ecology* 73 (5): 1922-1925.
- Sedell, J. R., P. A. Bisson, F. J. Swanson, and S. V. Gregory. 1988. What we know about large trees that fall into streams and rivers. Pages 47-79 in C. Maser, R. F. Tarrant, J. M. Trappe, and J. F. Franklin, eds. *From the forest to the sea: a story of fallen trees.* USDA Forest Service General Technical Report PNW-GTR-229. Pacific Northwest Research Station, Portland.
- Sklash, M. B., M. K. Stewart, and A. J. Pearce. 1986. Storm runoff generation in humid headwater catchments. 2. A case study of hillside and low-order stream response. *Water Resources Research* 22: 1273-1282.
- Smith, R. C., B. B. Prezelin, K. S. Baker, R. R. Bidigare, N. P. Boucher, T. Coley, D. Karentz, S. MacIntyre, H. A. Matlick, D. Menzies, M. Ondrusek, Z. Wan, and K. J. Waters. 1992. Ozone depletion: Ultraviolet radiation and phytoplankton biology in Antarctic waters. *Science* 255: 952-959.
- Smock, L. A. and C. M. MacGregor. 1988. Impact of the American chestnut blight on aquatic shredding macroinvertebrates. *Journal of the North American Benthological Society* 7(3): 212-221.
- Smock, L. A., G. M. Metzler, and J. E. Gladden. 1989. Role of debris dams in the structure and functioning of low-gradient headwater streams. *Ecology* 70: 764-775.
- Speaker, R., K. Moore, and S. Gregory. 1984. Analysis of the process of retention of organic matter in stream ecosystems. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie* 22: 1835-1841.
- Spence, J. A. and H. B. N. Hynes. 1971. Differences in benthos upstream and downstream of an impoundment. *Journal of the Fisheries Research Board of Canada* 28: 35-43.
- Sweeney, B. W. 1976. A diurnally fluctuating thermal system for studying the effect of temperature on aquatic organisms. *Limnology and Oceanography* 21(5): 758-763.
- Sweeney, B. W. 1978. Bioenergetic and developmental response of a mayfly to thermal variation. *Limnology and Oceanography* 23(3): 461-477.
- Sweeney, B. W. 1984. Factors influencing life history patterns of aquatic insects, Pages 56-100 in V. H. Resh and D. Rosenberg, eds. *Ecology of aquatic insects.* Praeger Scientific Publishers, New York.
- Sweeney, B. W. and J. A. Schnack. 1977. Egg development, growth and metabolism of *Sigara alternata* (Say) (Hemiptera: Corixidae) in fluctuating thermal environments. *Ecology* 58(2): 265-277.
- Sweeney, B. W. and R. L. Vannote. 1978. Size variation and the distribution of hemimetabolous aquatic insects: Two thermal equilibrium hypotheses. *Science* 200 (4340): 444-446.
- Sweeney, B. W. and R. L. Vannote. 1982. Population synchrony in mayflies: A predator satiation hypothesis. *Evolution* 36: 810-821.
- Sweeney, B. W. and R. L. Vannote. 1984. Influence of food quality and temperature on life history characteristics of the parthenogenetic mayfly *Cloeon triangulifer*. *Freshwater Biology* 14: 621-630.
- Sweeney, B. W. and R. L. Vannote. 1986. Growth and production of a stream stonefly: Influences of diet and temperature. *Ecology* 67: 1396-1410.
- Sweeney, B. W., R. L. Vannote, and P. J. Dodds.

- 1986a. Effects of temperature and food quality on growth and development of a mayfly, *Leptophlebia intermedia*. *Canadian Journal of Fisheries and Aquatic Sciences* 43: 12-18.
- Sweeney, B. W., R. L. Vannote, and P. J. Dodds. 1986b. The relative importance of temperature and diet to larval development and adult size of the winter stonefly *Soyedina carolinensis* (Plecoptera: Nemouridae). *Freshwater Biology* 16: 39-48.
- Sweeney, B. W., J. K. Jackson, J. D. Newbold, and D. H. Funk. 1992. Temperature change and the life histories and biogeography of aquatic insects. Pages 143-176 in P. Firth and S. Fisher, eds. *Global warming and freshwater ecosystems*. Springer-Verlag Inc. New York.
- Thomas, R. A. 1981. Excavations at the Delaware Park site (7NC-E-71). MS on file, Department of Transportation, Dover.
- Trautman, M. B. 1981. *The fishes of Ohio*. Ohio State University Press, Columbus, Ohio.
- Trefethen, J. B. 1976. *The American Landscape: 1776-1976 Two centuries of change*. K. J. Sabol, ed. *The Wildlife Management Institute*, Washington.
- Triska, F. J. and K. Cromack, Jr. 1981. The role of wood debris in forests and streams. Pages 181-190. in R. H. Waring, ed. *Forests: Fresh perspectives from ecosystems analysis*. Oregon State University Press, Corvallis.
- Triska, F. J., V. C. Kennedy, R. J. Avanzino, and B. N. Reilly. 1983. Effect of simulated canopy cover on regulation of nitrate uptake and primary production by natural periphyton assemblages. Pages 129-159 in T. D. Fontaine III and S. M. Bartell, eds. *Dynamics of Lotic Ecosystems*. Ann Arbor Science, Ann Arbor.
- Trotter, E. H. 1990. Woody debris, forest-stream succession, and catchment geomorphology. *Journal of the North American Benthological Society* 9(2): 141-156.
- Tuley, G. 1985. The growth of young oak trees in shelters. *Forestry* 58: 181-95.
- Vannote, R. L. and B. W. Sweeney 1980. Geographic Analysis of Thermal Equilibria: A conceptual model for evaluating the effect of natural and modified thermal regimes on aquatic insect communities. *American Naturalist* 115(5): 667-695.
- Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* 37: 130-137.
- Vannote, R. L. and B. W. Sweeney. 1985. Larval feeding and growth rate of the stream crane fly *Tipula abdominalis* in gradients of temperature and nutrition. *Proceedings of the Academy of Natural Sciences of Philadelphia* 137: 119-128.
- van Soest, P. J. 1963. Use of detergents in the analysis of fibrous feeds. II. A rapid method for the determination of fiber and lignin. *Journal of the Association of Official Agricultural Chemists* 46: 829-835.
- van Soest, P. J. and R. H. Wine. 1968. Determination of lignin and cellulose in acid-detergent fiber with permanganate. *Journal of the Association of Official Agricultural Chemists* 51: 780-785.
- Walace, J. B. and M. E. Gurtz. 1986. Response of *Baetis* mayflies (Ephemeroptera) to catchment logging. *American Midland Naturalist* 115: 25-41.
- Wallis, P. M., H. B. N. Hynes, and S. A. Telang. 1981. The importance of groundwater in the transportation of allochthonous dissolved organic matter to the streams draining a small mountain basin. *Hydrobiologia* 79: 77-90.
- Ward, J. V. 1974. A temperature-stressed stream ecosystem below a hypolimnial release mountain reservoir. *Archiv fur Hydrobiologie* 74: 247-275.
- Ward, J. V. and J. A. Stanford. 1979. Ecological factors controlling stream zoobenthos with emphasis on thermal modification of regulated streams. Pages 35-55 in J. V. Ward and J. A. Stanford, eds. *The ecology of regulated streams*. Plenum Press, New York.
- Ward, J. V. and J. A. Stanford. 1982. Thermal responses in the evolutionary ecology of aquatic insects. *Annual Review of Entomology* 27: 97-117.
- Weber, P. K. 1981. Comparisons of the lower trophic levels of small stream communities in forest and clearcut sites, southeast Alaska. Ph. D. thesis, University of Washington, Seattle.
- Webster, J. R., E. F. Benfield, S. W. Golladay, R. F. Kazmierczak, Jr., W. B. Perry, and G. T. Peters. 1988. Effects of watershed disturbance on stream seston characteristics. Pages 279-296 in W. T. Swank and D. A. Crossley, Jr., eds. *Forest hydrology and ecology at Coweeta*. Springer-Verlag, New York.
- Welsch, D. 1991. Riparian forest buffers: Function and design for protection and enhancement of water resources. United States Department of Agriculture Forest Service Report No. NA-PR-07-91.
- Wendland, W. and R. A. Bryson. 1974. Dating climatic episodes during the Holocene. *Quaternary Research* 4: 9-24.
- Williams, M. 1989. *Americans and their forests: A historical geography*. Cambridge University Press, Cambridge.
- Windell, K. 1991. Tree shelters for seedling protection. United States Department of Agriculture Forest Service Report No. 9124-2834-MTDC.
- Zimmerman, R. C., J. C. Goodlett, and G. H. Comer. 1967. The influence of vegetation on channel form of small streams. Pages 255-275 in *Symposium on river morphology*. International Association of Scientific hydrology. Publication no. 75.