

STREAMSIDE FORESTS AND THE PHYSICAL, CHEMICAL, AND TROPHIC CHARACTERISTICS OF PIEDMONT STREAMS IN EASTERN NORTH AMERICA

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ABSTRACT

It is now clear that water and habitat quality in the coastal embayments, of eastern North America are greatly affected by the quality of water and habitat in the thousands of feeder streams and rivers comprising their watershed. In this paper I suggest that the quality of streamside forests may be the single most important factor altered by humans that affects the structure and function, and ultimately water quality, of the streams providing water to the coastal embayments. I use comparative data from forested and deforested reaches of streams in a small Piedmont watershed (White Clay Creek) to illustrate the actual and/or potential effects of streamside forests on: (i) availability of habitat; (ii) the nutrient chemistry of the water; and (iii) the quantitative and qualitative nature of the primary food base (organic detritus and algae) supporting higher trophic levels in streams. Also discussed are the potential role of streamside forests in partially mitigating the flux of sediment and nutrients into aquatic ecosystems, the effects of global warming on stream temperatures, and the deleterious effects on stream organisms of the increased levels of UV radiation associated with global ozone depletion. Current methods and approaches for streamside forest restoration are presented.

KEYWORDS

Streamside; riparian; forest; stream ecology; deforestation; piedmont; macroinvertebrates; algae; nutrients; temperature.

INTRODUCTION

It has now been well established that eastern North America was an almost unbroken expanse of forest during most of the past 10,000 years (Williams, 1989). Although these forested watersheds were disturbed periodically during this period by a variety of natural processes (e.g. forest fires due to lightning, wind throws from tornadoes and hurricanes, outbreaks of forests pests and disease, etc.), the relative amount of disturbed landscape for a given time interval was probably minimal. Thus, most of the watersheds of the region as well as their associated stream and river ecosystems, could be considered natural, even pristine during most of the post-glacial period. Unfortunately, there are no factual data that clearly document the quality of water in the numerous streams, rivers, and estuaries draining the forested landscape of eastern North America prior to and during the early years of European settlement. However, anecdotal biological information from historians concerning fishery yield (both fish and shellfish) from these ecosystems clearly suggests that they were characterized by levels of biodiversity and productivity much higher than we observe today (Sage and Pilling, 1988).

The coincidence of a high structural and functional level of integrity for both the aquatic ecosystems (streams, rivers, estuaries) and the forests that they drained along the Atlantic Piedmont and Coastal Plain region is probably not accidental. Similarly, most contemporary scientists agree that the recent (last 300 years) decline in water quality and biological productivity of our coastal estuaries is related in part to non-point pollution associated with aquatic and terrestrial ecosystems throughout the surrounding watershed of these embayments.

Here I argue that one of the biggest factors contributing to the decline in water and habitat quality of aquatic ecosystems (freshwater and estuarine) in eastern North America was the removal of forest ecosystems adjacent to the streams and rivers comprising the Atlantic drainage. Although the process of forest clearing was developed and practiced by native Americans prior to the 15th Century, it was greatly accelerated and intensified following European colonization (Williams, 1989). To these 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 sustainable agriculture. Exploitation intensified and by the mid-1800s 75% of the area had been completely deforested (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 soils range from 7.6 to 30.5 cm or more since the initial clearing of forest (Costa, 1975). Today, much of this forest occurs as small tracts or woodlots. Contemporary Piedmont streams, therefore, flow through an environmental mosaic of forested and deforested areas, which greatly affects the dynamics of key ecosystem properties (Cummins, 1974; Hynes, 1975; Vannote *et al.*, 1980).

This paper briefly outlines how streamside forests can affect the physical, chemical, and trophic characteristics of Piedmont streams in eastern North America. The paper is 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 region of southeastern Pennsylvania. I also will discuss restoration of streamside forests as a way of improving the structure and function of stream ecosystems. This summary will illustrate both the obvious and subtle ways that streamside forests (or lack thereof) can affect the thousands of waterways in the Piedmont region that ultimately provide the freshwater to our coastal embayments.

CONCEPTUAL MODEL

The two main points of this paper are: (i) that the presence or absence of trees adjacent to stream channels is one of the single most important factors altered by humans that affects the structure and function of stream ecosystems providing water to estuaries of the Atlantic drainage of eastern North America; and (ii) that restoring streamside forests to a natural state is requisite to restoring a disturbed stream system to a natural or quasi-natural state and hence improving overall water quality within a given watershed. A conceptual model (Fig. 1) illustrates how 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 (hence stream water chemistry), and the availability of leaf litter and other forest products for consumption. These factors in turn affect the amount of primary production (light for algae and aquatic macrophytes), 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, all these factors interact to affect the survivorship, growth, and relative abundance of the primary producers and consumers (mainly bacteria, algae, and macroinvertebrates) of the ecosystem, which, in turn, ultimately affect the structure and productivity of higher trophic levels, especially fish.

DRAINAGE BASIN CHARACTERISTICS OF WHITE CLAY CREEK

In WCC, a 158 km² drainage basin in Chester County, Pennsylvania, there are a total of 203 individual stream channels comprising a total stream length of 268 kilometres. About 77.6% of the total stream length in the WCC drainage is represented by first and second order streams (Fig. 2), 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 Piedmont watersheds as well as elsewhere because they compare favorably with the estimate by Leopold et al. (1964) that 73.2% of the total stream length in the United States is represented by first and second order streams, respectively. In WCC, only 11.2% of the total length of channels are greater than third order. Thus, available stream habitat in WCC, as well as other Piedmont and Coastal Plain streams, consists mainly of a large number of very small channels. The preponderance of small streams in watersheds like WCC means that the canopy of trees growing on opposite banks of a channel touch and form a complete vegetative bridge over most of the stream network. As shown below, this phenomenon greatly affects several basic characteristics of the individual streams.

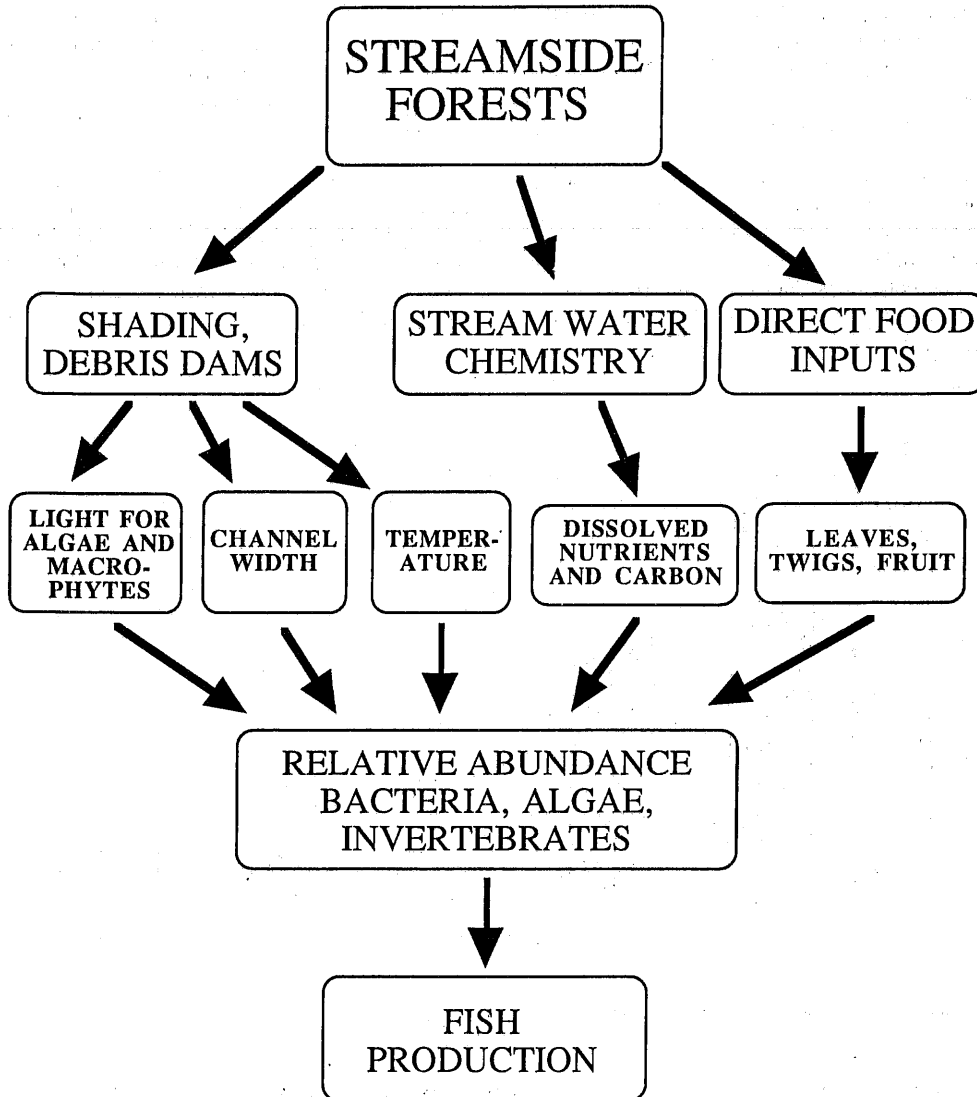


Fig. 1. A conceptual model showing the potential pathways by which streamside forests can affect the primary and secondary consumer organisms of a stream ecosystem.

PHYSICAL EFFECTS OF STREAMSIDE VEGETATION

Availability of Benthic Habitat

Since most of the biological activity in stream ecosystems takes place on inorganic (sand, gravel, cobble, etc.) and organic (leaves, woody debris, etc.) substrates on the bottom of the channel, any factor affecting the availability and overall surface area of benthic substrates can directly affect the amount of space or habitat available for most stream organisms. In the WCC drainage basin, the width of the stream channel (hence bottom surface area per unit length of 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 (Fig. 3). For small streams (e.g. first and second order), forested streams are about 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 on the bottom available for colonization by stream organisms.

Stream narrowing in grassy meadows has been described elsewhere (Zimmerman *et al.*, 1967) and seems to involve the formation of sod by grassy vegetation along the stream margin. The sod eventually encroaches on the stream channel itself and causes the channel to narrow gradually. 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 located immediately upstream or downstream from them. It appears that shading by streamside forests discourages the growth of grassy vegetation, keeping stream channels wide and shallow.

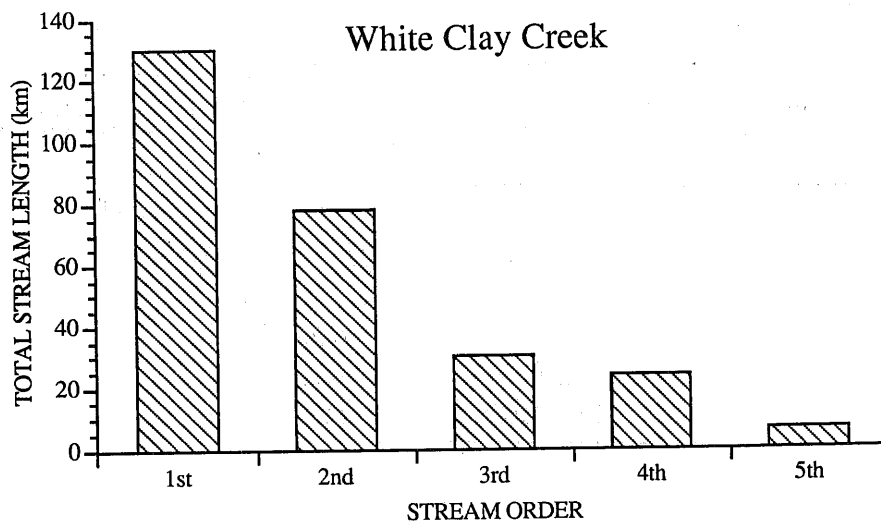


Fig. 2. Showing the total length of stream for each of the five stream order categories within the White Clay Creek drainage basin.

It is unclear how the present width of forested channels in the WCC basin compares with 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 the WCC channels. In some areas, the paleosol or top soil layer of the original floodplain can be clearly seen buried under nearly one metre 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 perimeter silt-clay contents", while bedload streams tend to have high sand contents along their streamside perimeter or margin (Richards, 1982). Moreover, Richards (1982) points out that channels with silty banks tend to be narrow and deeper in cross section than channels with sandy banks. Thus, it seems possible that forested channels prior to major watershed disturbance may have been even wider than the reforested contemporary channels that have a high content of sand and silt in their floodplain.

The presence or absence of trees along a channel of WCC certainly 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 evaluated. It appears that $1.01 \times 10^6 \text{ m}^2$ of benthic habitat would occur in the 158 km^2 basin if streamside areas were entirely forested. In contrast, benthic habitat would be reduced about 54% (to $0.47 \times 10^6 \text{ m}^2$) if streamside trees were completely eliminated.

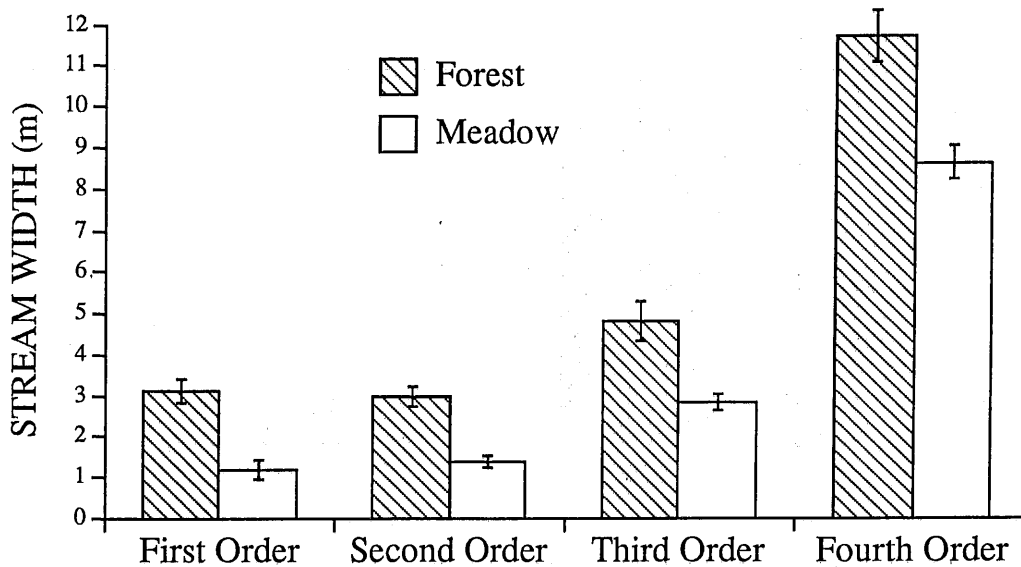


Fig. 3. Average stream width of various size (order) tributaries of White Clay Creek flowing through forested and meadow areas of Chester County, Pennsylvania. Vertical bars are \pm one standard error.

In the WCC basin, the woody roots of native tree species such as American Sycamore (*Plantanus occidentalis*), Black Willow (*Salix nigra*), Alder (*Alnus serrulata*), River Birch (*Betula nigra*), can form a tight network over the bank surface, helping to stabilize the bank and providing additional surface area (habitat) for aquatic species, especially macroinvertebrates. In certain reaches of WCC, roots are prime substrata for collecting, a variety of aquatic insects in large numbers. Rhodes and Hubert (1991) have reported a similar phenomenon 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.

Streamside forests also provide additional surface area for aquatic species by continuously shedding woody debris (tree twigs, branches, whole trunks) into stream channels. This debris provides additional surface area of a very different texture (than roots or rocks). The woody debris also tends to accumulate and form small dams at periodic intervals that not only add local habitat variety (depth, flow, etc.) but also play a role

in channel 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 and Cromack, 1981).

As expected, a forested second order channel of WCC contained substantially more pieces of large (> 0.3 m long) woody debris, than a contiguous meadow reach (Fig. 4). In this case, the data from the meadow reach were taken immediately downstream (about 50 m) of the forested reach. This suggests little, if any, tendency for forested stream sections to provide woody debris to downstream meadow reaches. Thus, species requiring woody debris for all or part of their life history (e.g. certain caddisflies) 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 m² of surface area was added in the form of woody debris per 25 meters of channel length. In a coastal plain stream, Benke *et al.*, (1984) estimated that woody snag habitat supported an annual mean macroinvertebrate density of 26,043 m⁻² and an annual macroinvertebrate production level of 51,891 mg m⁻². Although these data may not be directly transferable to WCC, they demonstrate the relevance of woody debris as habitat for macroinvertebrates in streams.

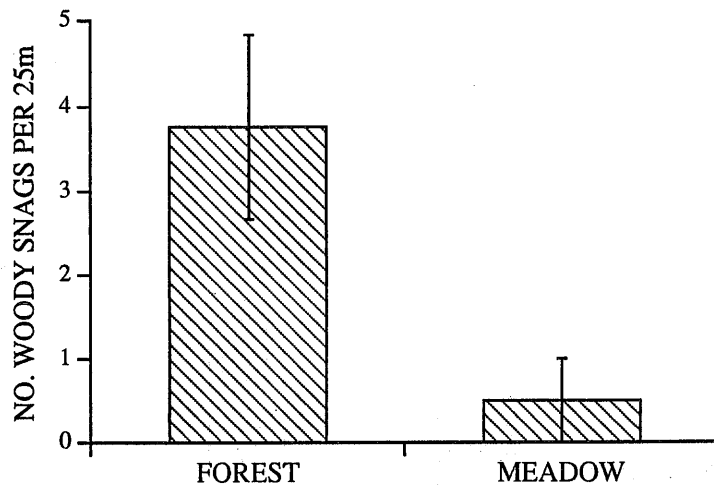


Fig. 4. Average number of pieces of large (> 0.3 m long) woody debris occurring in four replicate 25 m long reaches of a second order tributary of White Clay Creek flowing through a forested and a meadow region of the watershed. Vertical bars are one standard error.

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 and Harvey, 1990). Measurements on a third order tributary of WCC indicate that average light intensity for an "open" meadow channel increased gradually through the spring, peaking in mid-summer at about 1885 J cm⁻² day⁻¹ and declined gradually to about 420 J cm⁻² day⁻¹ in late December (Fig. 5; T. L. Bott, personal communication). In contrast, average light intensity for a "shaded" forest channel peaked in mid-April at about 1250 J cm⁻² day⁻¹ and then declined following canopy leaf-out to mid-summer levels of about 200 J cm⁻² day⁻¹. Thus, on clear days along WCC, radiation in a shaded reach ranges from 6-30% (avg. = 17%) and 30-60% (avg. = 42%) of levels received by a meadow reach during the summer and winter, respectively. The different seasonal patterns of light for forested and meadow streams in WCC are important because they affect both gross and net algal productivity (see below).

In addition to visible light and infrared (IR) radiation, streams are exposed to ultraviolet (UV) radiation in the 290-400 nm region. Approximately 4% of the total sunlight energy occurs in the UV band. Human activities such as the production and use of chlorofluorocarbons has resulted in an increased flux of UV radiation to the surface of the earth. 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 irradiance (280 - 320 nm) to total irradiance (280 - 700 nm) and UV 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 organisms. We presently do not know whether the negative effects observed for a variety of terrestrial plants and animals will also be observed for aquatic organisms. We do know, however, that UV radiation can affect the structure of natural and man-made chemicals dissolved in streamwater, which in turn affects their toxicity (see review by Larson and Berenbaum 1988).

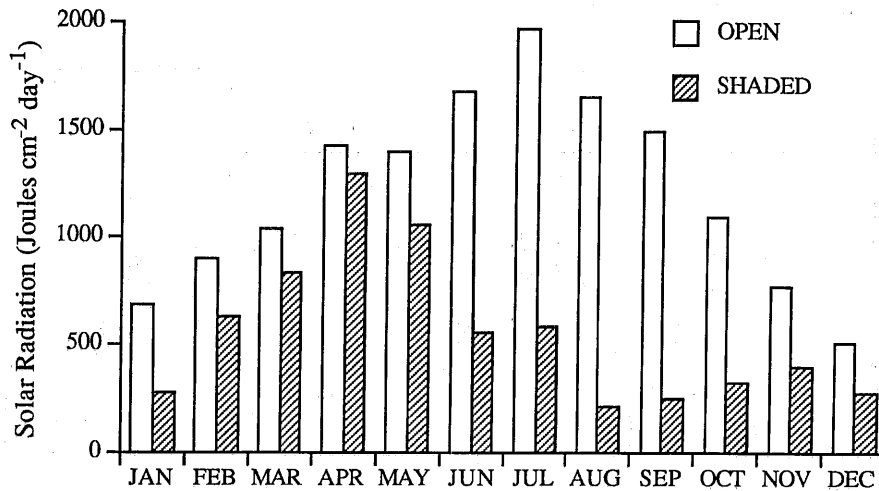


Fig. 5. Seasonal pattern of mean monthly solar input ($\text{J cm}^{-2} \text{ day}^{-1}$) for shaded forest and open meadow reaches of a fourth order tributary of White Clay Creek. Data were collected using pyranometers (Model 5-3850 A Pyrheliograph, Belfort Co., in the forested reach; Model 8-48 Pyranometer, Eppley Co., in the meadow reach).

It is possible that streamside trees can help protect stream organisms 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 incipient light. The fact that UV light represents a greater proportion of diffuse light than other wavelengths suggests that two opposing tendencies could 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 transmittance of UV light may scale about the same as for visible light (E. H. DeLucia, personal communication).

Temperature

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), the season (angle of incipient solar radiation and presence or absence of leaves on deciduous plants), and geographic location. In WCC, a forested second-order stream is cooler

from April through September and warmer from late fall to early winter than a deforested stream (Fig. 6). Other studies have also shown deforested streams to be 3-5°C warmer throughout the late spring-summer-early fall portions of the year (Welsch, 1991).

A recent analysis of stream 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 historical removal of trees from along small streams in the Atlantic Piedmont has already warmed these streams 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 will be affected. 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.

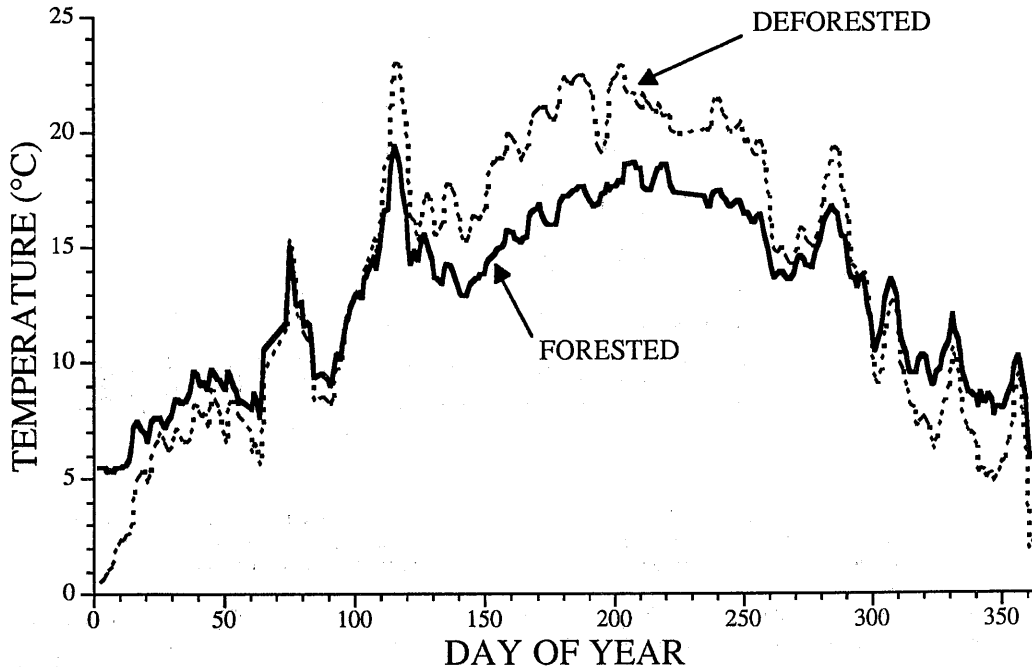


Fig. 6. Seasonal pattern of average daily temperature for forested (woodland) and deforested (meadow) reaches of a third order tributary of White Clay Creek. Data collected using continuous recording thermographs.

CHEMICAL EFFECTS OF STREAMSIDE VEGETATION

Introduction

Streamside vegetation probably affects the chemistry of streams in a number of ways: (i) through inputs of particulate plant structures (leaves, fruits, woody parts) into the stream channel or onto the forest floor that later release dissolved nutrients (organic and inorganic compounds) directly into the stream water or into shallow groundwater, which subsequently move into the stream; (ii) by intercepting shallow groundwater with their roots and removing nutrients just before the groundwater moves laterally into the stream channel;

(iii) by modifying the underlying soil structure, allowing greater infiltration and more contact time with subsurface sites of biogeochemical processing; and (iv) by modifying the extent and perhaps rate of photooxidation reactions and aerobic processing of dissolved organic and inorganic compounds in streamwater through shading.

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, etc.). This process gradually affects important ecosystem properties that, in turn, affect the food base for primary and secondary consumer 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 stream ecosystem can best be made.

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 energy input into stream ecosystems (Fisher and Likens, 1973; McDowell and 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 and Tate (1983) studied streams draining forested and deforested watersheds and showed that annual DOC export and DOC concentrations in streamwater were reduced in the deforested stream. They attributed this reduction largely to: (i) reduced inputs of DOC from the streamside zone (e.g. lower litter inputs and subsequent leaching; lower throughfall inputs during storms); (ii) 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 (iii) 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 and O'Hop, 1983).

In WCC, 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 and Bott, 1982), its actual uptake by bacteria has been quantified (Kaplan and Bott, 1983, 1985, 1989; Bott *et al.*, 1984; Bott and Kaplan, 1985; Kaplan *et al.*, 1992), and the subsequent utilization of bacteria by meiofauna (especially protozoa and nematodes) has been quantified (Bott and Kaplan, 1989, 1990). Important areas of future research for WCC and other Piedmont streams include: (i) the relationships within the DOC-bacteria-meiofauna food web as well as its importance to higher consumer levels (*viz.* macroinvertebrates); (ii) studies to determine the ultimate source of streamwater DOC within the watershed, including the role of streamside forests as a source area for DOC; and (iii) the effect of these forests on the pattern of movement of DOC from source areas to the stream (T.L. Bott, M.A. Borchardt, L.A. Kaplan, J.D. Newbold, and L.J. Standley, personal communication).

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 and Correll, 1984; Jacobs and Gilliam, 1985). The streamside forests of coastal plain watersheds seem to be especially effective at removing nitrogen (N), with removal levels of 65% (Lowrance *et al.*, 1984) and 75% (Peterjohn and Correll, 1984) being reported. Furthermore, it has been shown that streams draining forested watersheds export significantly less nitrogen than those draining deforested basins (Omernik, 1977). 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 nitrate-N levels (< 0.1 ppm) have also been observed in shallow (< 3 m) groundwater monitoring wells along riparian zones (Fig. 7). In contrast, local surface springs and deeper groundwater

wells (> 25 m) elsewhere within the WCC watershed contain relatively high nitrate-N levels (averaging > 7 ppm). The streamwater contains nitrate-N levels that are intermediate 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.

For WCC and other Piedmont streams, the role that streamside vegetation plays 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 streamside trees. For example, Dawson and 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. This work clearly shows that: (i) 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 (ii) 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.

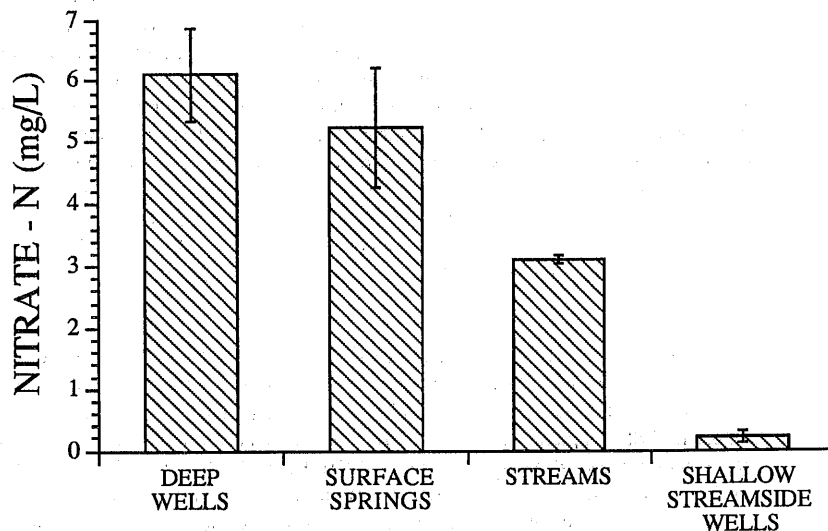


Fig. 7. Average nitrate nitrogen concentration in water collected from deep (>25 m) wells, the discharge of surface springs, the surface water from a fourth order tributary, and shallow (<3 m) streamside wells in the headwater region of the east Branch of White Clay Creek. Vertical bars are one standard error.

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, by necessity, 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 suggest 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 and 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 (Kaplan and

Newbold, 1992), allowing sufficient time for processes such as denitrification to significantly affect the chemistry of the water.

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 and 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 personal communication).

TROPHIC EFFECTS OF STREAMSIDE VEGETATION

Introduction

As shown above, the presence of a streamside forest can greatly modify the physical and chemical habitat characteristics of a given stream reach. Some of these modifications directly affect the biological activity of stream 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 of primary consumer organisms. The following discussion focuses on how streamside vegetation may affect the food base for primary consumers of WCC and other Piedmont streams.

Availability of Particulate Detritus as Food

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 WCC averages 248 g m^{-2} of organic matter for the year, with leaf litter detritus (particle size > 16.0 mm) rarely falling below 40 g m^{-2} during the year (Vannote and Sweeney, 1980). On an annual basis, the total input of organic detritus greatly exceeds the level of net primary productivity for the same study reach in WCC (about 78 - 84 $\text{g C m}^{-2} \text{y}^{-1}$; T. L. Bott, personal communication).

In WCC, a substantial proportion of the annual input of organic detritus from streamside forests occurs during October and November, even though inputs continue at a much lower scale during other months. Because streams are depressions in the landscape, they act as traps for terrestrial detritus blowing across the forest floor and hence can accumulate standing stocks of leaf litter, especially during the fall, that exceed normal levels for the adjacent forest floor. For example, a forested second-order tributary of WCC in November 1991, just after peak leaf fall, had an average of 748 g m^{-2} dry mass of leaf litter (Fig. 8) and another 312 g m^{-2} dry mass of woody debris. In contrast, when the stream flowed out of this woodlot and into a grassy meadow, the standing stock of leaf litter and woody debris immediately decreased to about 14 and 15 g m^{-2} , 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.

In the WCC watershed, as well as most other watersheds in the Atlantic Piedmont, most if not all streamside forests have been disturbed by anthropogenic practices either: (i) directly, by clear cutting, thinning, monoculture reforestation, etc.; or (ii) 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.]. Moreover, 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 a long time (>30 years) and, in some instances, even after 40 years there is no indication of natural plant succession beyond this state. The effect of foreign plants in streamside areas on the ecology of stream communities has been little studied. For the leaf eating mayfly *Leptophlebia cupida* in WCC, laboratory experiments have shown that the replacement of leaves from native species of trees (e.g. White Ash, Hickory, American Beech) with leaves from foreign species [e.g. Multiflora Rose, Asiatic Bittersweet, Paulownia (*Paulownia tomentosa*)] had a significant effect on larval survivorship (Sweeney *et al.*, 1992). 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.

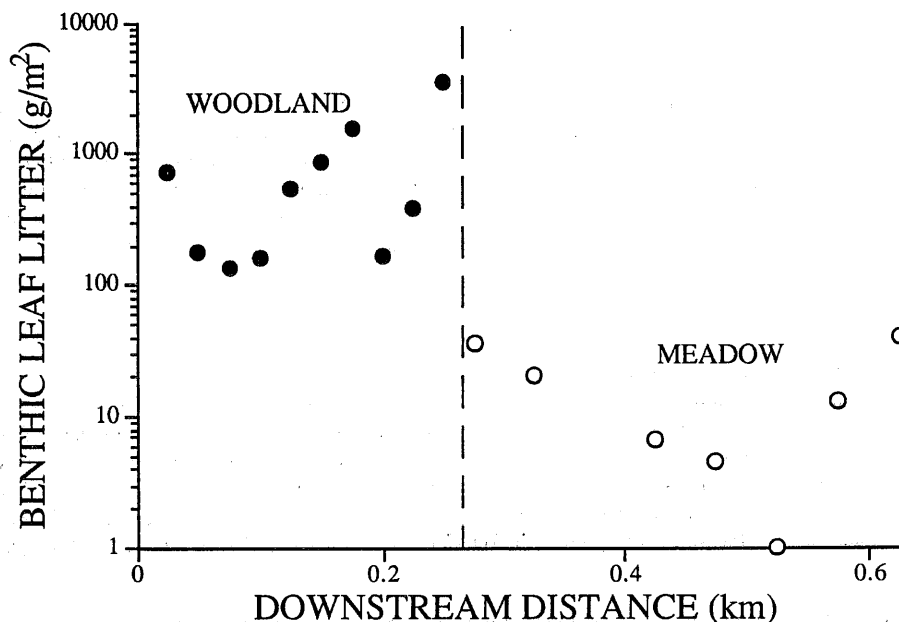


Fig. 8. Standing stock of leaf litter measured in late November at various points along a third order tributary of White Clay Creek. All measurements were taken as transects across the stream bottom at 25 m intervals in the forested reach and 50 m intervals in the contiguous, downstream meadow reach. For each transect, all leaf litter occurring in a 27 cm wide area across the channel was collected, dried (50°C), and weighed.

At the present time, the data are too sparse to make any general statements concerning the potential effect of foreign plant species on food availability for stream ecosystems. It is clear that the comparative chemistry of native and foreign plant species (especially their leaves) needs to be studied. Furthermore, more laboratory and field studies are needed 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 let deforested streamside areas lie fallow and allowed them to 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]. For example, Bilby and 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). Unfortunately, it is not possible to differentiate between the effects of light quantity and quality in these studies because both parameters differed significantly among test sites during the year, and the kind and relative abundance of invertebrate herbivores feeding on the algal communities also differed. Regardless, the modification of light regime by streamside forests clearly affects the autotrophic characteristics of a stream reach, which in turn, greatly affects primary consumers in the ecosystem (Minshall, 1978).

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 and Knight, 1988; Feminella et al., 1989). Hill and 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 phytoplankton). 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 (Bott, personal communication). 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 and Hill, 1991). Recently, Hill and Harvey (1990) reported a strong correlation between primary production and light level in a shaded stream in Tennessee, and Hill and 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 and Boston (1991) offer two possible hypotheses: (i) 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 (ii) 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.

STREAMSIDE REFORESTATION

After carefully examining the physical, chemical, and trophic effects of altering the quantity and quality of streamside vegetation, it is clear that a diverse and intact streamside forest is an important requisite for maintaining the structure and function of a stream ecosystem in a natural or quasi-natural state. This is not a new revelation, for example Newbold et al. (1980) and others have shown that a wide strip of forest along streams can buffer them from 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 mentioned in detail above. This spatial 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. In general, Welsch's model (1991) divides the streamside area into three zones (Fig. 9).

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, 1991). 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.

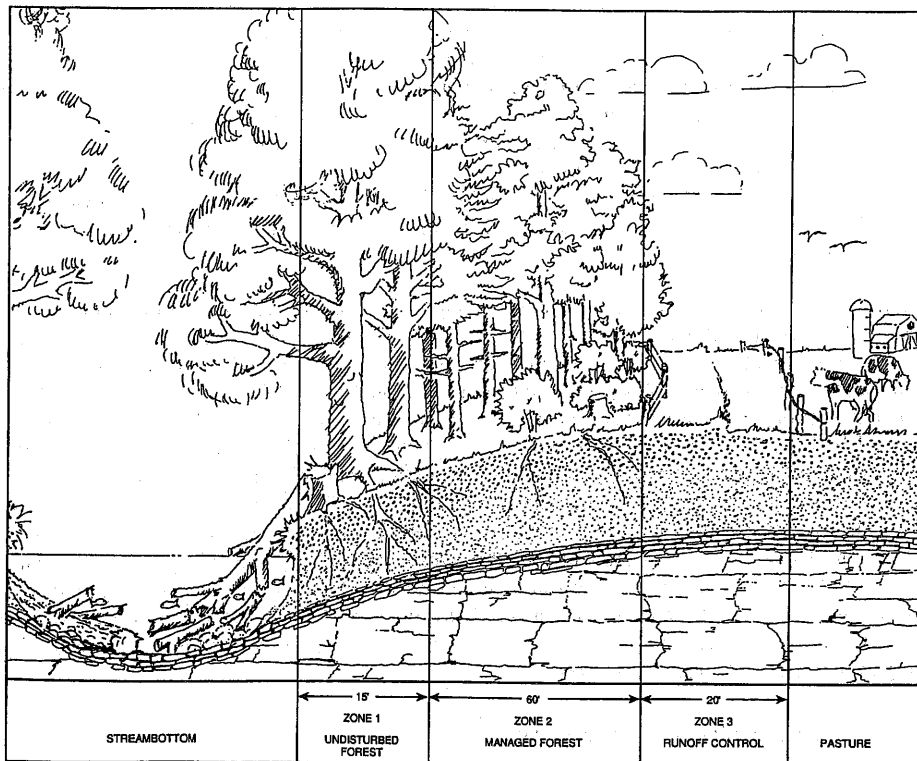


Fig. 9. Schematic diagram modified from Welsch (1991) showing the streamside forest buffer protocol of the United States Department of Agriculture Forest Service that is presently being implemented in the Piedmont region of eastern North America.

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 some field experience in the WCC watershed and surrounding watersheds in southeastern Pennsylvania to give some rudimentary guidelines.

As noted earlier many streamside areas in the Piedmont region of eastern North America 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. 10a 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 (Fig. 10b) 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 an ecologically suitable 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.

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 rubra*), 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) size seedlings. We have used both sizes in streamside plantings along WCC. Small seedlings are more desirable because in the United States they can 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.



Fig. 10. (a) streamside vegetation dominated by foreign plant species (mainly Multiflora Rose, Asiatic Bittersweet, 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).

Competition (space, light, nutrients, moisture, etc.) with other plants and density of herbivores (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 seedling-planted areas 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. 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 40% taller than unsheltered seedlings after one growing season and 42% 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 63% and 136% taller, respectively, after two growing seasons than those not planted in shelters (Fig. 11). 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 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 and 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 Red Maple, American Sycamore, River Birch, and Black Willow. Moreover, the availability of shelters in different heights (up to 1.8 m) allow successful forest regeneration in streamside areas where high densities of deer, voles, rabbits, etc. have heretofore made it impossible.

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.

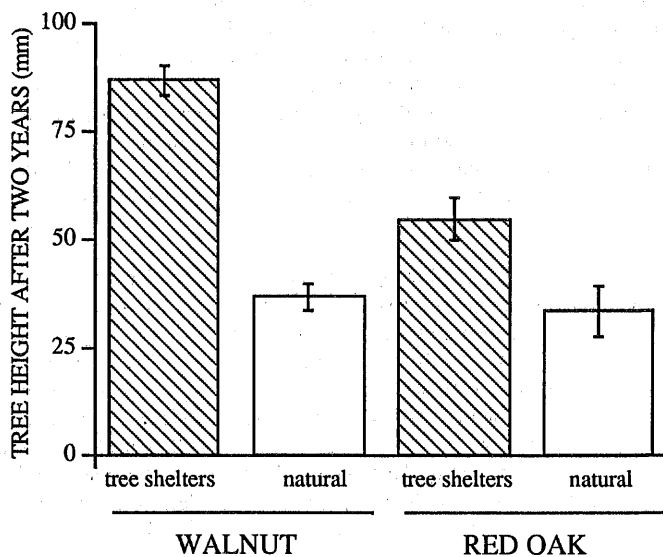


Fig. 11. The effect of tree shelters on average height of Black Walnut and Red Oak seedlings after two years of growth. Vertical bars are one standard error.

SUMMARY AND CONCLUSIONS

Although stream ecosystems in eastern North America have been subjected by man to a vast array of perturbations 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 the Piedmont. This task is difficult because we have no "reference" to gauge the current status of these ecosystems.

In this paper, I have tried to describe the relative importance of streamside vegetation to the physical, chemical, and trophic characteristics of streams using data from tributaries of White Clay Creek flowing through landscapes in various stages of recovery from major perturbation. It will be fortuitous if insights based on these data precisely define the actual relationship that existed historically between streamside forests and the characteristics of stream ecosystems in watersheds bordered by primary forest. Regardless, existing data from WCC and elsewhere strongly suggest that streamside forests greatly increase the amount and complexity of benthic habitat available to stream organisms. 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. Moreover, 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, roots, etc. Although 50% more space may not necessarily translate into 50% greater macroinvertebrate or fish production or higher 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 characteristics of lotic ecosystems. Additional support comes from field studies showing how deforestation along stream channels can alter the natural temperature regime of the stream and

the chemical composition of its water. Furthermore, streamside forests affect the food base of streams both directly (through inputs of DOC, leaf litter, woody debris) or indirectly (shading effects on the quality and quantity of algal production). Finally, I have tried to present numerous reasons why reforestation of denuded streamside areas 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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REFERENCES

- Asmussen, L.E., Sheridan, J.M., and Booram, C.V. Jr. (1979). Nutrient movement in streamflow from agriculture watersheds in the Georgia coastal plain. *Trans. Soc. Agri. Eng.*, **22**, 809-815.
- Barton, D.R., Taylor, W.D., and Biette, R.M. (1985). Dimensions of riparian buffer strips required to maintain trout habitat in southern Ontario streams. *N. Am. J. Fish. Man.*, **5**, 364-378.
- Benke, A.C., Van Arsdall, T.C., Jr. and Gillespie, D.M. (1984). Invertebrate productivity in a subtropical blackwater river: The importance of habitat and life history. *Ecol. Monogr.*, **54**, 25-63.
- Bilby, R.E. and Bisson, P.A. (1992). Allochthonous versus autochthonous organic matter contributions to the trophic support of fish populations in clear-cut and old-growth forested streams. *Can. J. Fish. Aquat. Sci.*, **49**, 540-551.
- Boston, H.L. and Hill, W.R. (1991). Photosynthesis-light relations of stream periphyton communities. *Limnol. Oceanogr.*, **36**, 644-656.
- Bott, T.L., Kaplan, L.A., and Kuserk, F.T. (1984). Benthic bacterial biomass supported by streamwater dissolved organic matter. *Microb. Ecol.*, **10**, 335-344.
- Bott, T.L. and Kaplan, L.A. (1985). Bacterial biomass, metabolic state, and activity in streambed sediments: Relation to environmental variables and multiple assay comparisons. *Appl. Environ. Microbiol.*, **50**, 508-522.
- Bott, T.L. and Kaplan, L.A. (1989). Densities of benthic protozoa and nematodes in a piedmont stream. *J. N. Am. Benthol. Soc.*, **8**, 187-196.
- Bott, T.L. and Kaplan, L.A. (1990). Potential for protozoan grazing of bacteria in streambed sediments. *J. N. Am. Benthol. Soc.*, **9**, 336-345.
- Costa, J.E. (1975). Effects of agriculture on erosion and sedimentation in the Piedmont Province, Maryland. *Geol. Soc. Am. Bull.*, **86**, 1281-1286.
- Cummins, K.W. (1974). Structure and function of stream ecosystems. *Bioscience*, **24**, 631-641.
- Cummins, K.W., Wilzbach, M.A., Gates, D.M., Perry, J.B., and Taliaferro, W.B. (1989). Shredders and riparian vegetation. *Bioscience*, **39**, 24-30.
- Dawson, T.E. and Ehleringer, J.R. (1991). Streamside trees that do not use stream water. *Nature*, **350**, 335-337.
- De Lucia, E.H., Day, T. A., and Vogelmann, T. C. (1991). Ultraviolet-B radiation and the rocky mountain environment: Measurement of incident light and penetration into foliage. *Curr. Top. Plant Biochem. Physiol.*, **10**, 2-48.
- Feminella, J.W., Power, M.E., and Resh, V.W. (1989). Periphyton responses to invertebrate grazing and riparian canopy in three northern California coastal streams. *Freshwater Biol.*, **22**, 445-457.
- Fisher, S.G. (1977). Organic matter processing by a stream-segment ecosystem: Fort River, Massachusetts, U.S.A. *Inter. Rev. Ges. Hydrobiol.*, **62**, 701-727.
- Fisher, S.G. and Likens, G.E. (1973). Energy flow in Bear Brook, New Hampshire: An integrative approach to stream ecosystem metabolism. *Ecol. Monogr.*, **43**, 421-439.
- Gregory, S.V., Swanson, F. J., McKee, W. A., and Cummins, K.W. (1991). An ecosystem perspective of riparian zones. *Bioscience*, **4**, 540-551.

- Hansen, J., Lacias, A., Rind, D., Russell, G., Fung, I., and Lebedeff, S. (1987). Evidence for future warming: How large and when? In: *The Greenhouse Effect, Climate Change, and U.S. Forests*. W. E. Shands and J.S. Hoffma, (Eds.). The Conservation Foundation, Washington, D.C. pp. 57-75.
- Hill, W.R. and Boston, H.L. (1991). Community development alters photosynthesis-irradiance relations in stream periphyton. *Limnol. Oceanogr.*, **36**, 1375-1389.
- Hill, W.R. and Harvey, B.C. (1990). Periphyton responses to higher trophic levels and light in a shaded stream. *Can. J. Fish. Aquat. Sci.*, **47**, 2307-2314.
- Hill, W.R. and Knight, A.W. (1988). Nutrient and light limitation of algae in two northern California streams. *J. Phycol.*, **24**, 125-132.
- Hooper, R.P. and Shoemaker, C.A. (1986). A comparison of chemical and isotopic hydrograph separation. *Water Resour. Res.*, **22**, 1444-1454.
- Hornberger, G.M., Kelly, M.G., and Eller, R.M. (1976). The relationship between light and photosynthetic rate in a river community and implications for water quality modeling. *Water Resour. Res.*, **12**, 723-730.
- Horton, R.E. (1945). Erosional development of streams and their drainage basins: hydrophysical approach to quantitative morphology. *Bull. Geol. Soc. Amer.*, **56**, 275-370.
- Hynes, H.B.N. (1975). The stream and its valley. *Verh. Int. Verein. Theor. Angew. Limnol.*, **19**, 1-5.
- Jacobs, T.C. and Gilliam, J.W. (1985). Riparian losses of nitrate from agricultural drainage waters. *J. Environ. Qual.*, **14**, 472-478.
- Kaplan, L.A., Larson, R.A., and Bott, T.L. (1980). Patterns of dissolved organic carbon in transport. *Limnol. Oceanogr.*, **25**, 1034-1043.
- Kaplan, L.A. and Bott, T.L. (1982). Diel fluctuations of DOC generated by algae in a piedmont stream. *Limnol. Oceanogr.*, **27**, 1091-1100.
- Kaplan, L.A. and Bott, T.L. (1983). Microbial heterotrophic utilization of dissolved organic matter in a piedmont stream. *Freshwater Biol.*, **13**, 363-377.
- Kaplan, L.A. and Bott, T.L. (1985). Acclimation of streambed microflora: Metabolic responses to dissolved organic matter. *Freshwater Biol.*, **15**, 479-492.
- Kaplan, L.A. and Bott, T.L. (1989). Diel fluctuations in bacterial activity on streambed substrata during vernal algal blooms: Effects of temperature, water chemistry, and habitat. *Limnol. Oceanogr.*, **34**, 718-733.
- Kaplan, L.A., Bott, T.L., and Bielicki, J. K. (1992). Assessment of [³H]thymidine incorporation into DNA as a method to determine bacterial productivity in streambed sediments. *Appl. Environ. Microbiol.*, (in press).
- Kaplan, L.A. and Newbold, J.D. (1992). Sources and biogeochemistry of terrestrial dissolved organic carbon entering streams. In: *Aquatic Microbiology: An Ecological Approach*. T. E. Ford (Ed.). Blackwell Scientific Publications Inc. pp.000-000 (in press).
- Kennedy, V.C., Kendal, C., Zelweger, G.W., Weyerman, T.A., and Avanzino, R.J. (1986). Determination of the components of stormflow using water chemistry and environmental isotopes, Mattole River basin, California. *J. Hydrol.*, **84**, 107-140.
- Kuserk, F.T., Kaplan, L.A., and Bott, T.L. (1984). *In situ* measures of dissolved organic carbon flux in a rural stream. *Can. J. Fish. Aquat. Sci.*, **41**, 964-973.
- Lantagne, D.O., Ram, C.W., and Dickmann, D.H. (1990). Tree shelters increase height of planted oaks in a Michigan clearcut. *Mich. St. North. J. Appl. For.*, **7**, 24-26.
- Larson, R.A. (1978a). Dissolved organic matter of a low-coloured stream. *Freshwater Biol.*, **8**, 91-104.
- Larson, R.A. (1978b). Environmental chemistry of reactive oxygen species. *CRT Crit. Rev. Environ. Contr.*, **8**, 197-246.
- Larson, R.A. and Berenbaum, M.R. (1988). Environmental phototoxicity. *Environ. Sci. Technol.*, **22**, 354-360.
- Leopold, L.B., Wolman, M.G., and Miller, J.P. (1964) *Fluvial processes in geomorphology*. W. H. Freeman and Company, San Francisco.
- Lowe, R.L., Golladay, S.W., and Webster, J.R. (1986). Periphyton response to nutrient manipulation in streams draining clear-cut and forested watersheds. *J. N. Amer. Benthol. Soc.*, **5**, 221-229.
- Lowrance, R.R., Todd, R.L., and Asmussen, L.E. (1984). Nutrient cycling in an agricultural watershed. I. Phreatic movement. *J. Environ. Qual.*, **13**, 22-27.
- McDowell, W.H. and Fisher, S.G. (1976). Autumnal processing of dissolved organic matter in a small woodland stream ecosystem. *Ecology*, **57**, 561-569.
- Meyer, J.L. and O'Hop, J. (1983). Leaf-shredding insects as a source of dissolved organic carbon in headwater streams. *Amer. Mid. Naturalist*, **109**, 175-183.
- Meyer, J.L. and Tate, C.M. (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. *Ecol. Monogr.*, **51**, 307-322.
- Newbold, J.D., Erman, D.C., and Roby, K.B. (1980). Effects of logging on macroinvertebrates in streams with and without buffer strips. *Can. J. Fish. Aquat. Sci.*, **37**, 1076-1085.
- Omernik, J.M. (1977). Nonpoint source-stream nutrient level relationships: A nationwide survey. EPA-600/3-77-105. Ecol. Res. Ser. U.S. Environmental Protection Agency, Washington, D.C.
- Pearce, A.J., Stewart, M.K., and Sklash, M.B. (1986). Storm runoff generation in humid headwater catchments. 1. Where does the water come from? *Water Resour. Res.*, **22**, 1263-1272.

- Peterjohn, W.T. and Correll, D.L. (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, London:HMSO.
- Rhodes, H.A. and Hubert, W.A. (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.
- Rudolph, V.J. and Lemmien, W.A. (1976). Silvicultural cuttings in an oak-hickory stand in Michigan: 21 year results. In: *Proceedings of the First Central Hardwood Forest Conference*. Southern Illinois University, Carbondale, IL. pp.431-452.
- Sage, L. E. and Pilling, F.B. (1988). The development of a nation: The Delaware River. In: *Ecology and restoration of the Delaware River Basin*. S.K. Majumdar, E.W. Miller, and L.E. Sage (Eds.). The Pennsylvania Academy of Science.
- Sander, I.L. (1979). Regenerating oaks with the shelterwood system. In: *Regenerating oaks in upland hardwood forests*. John S. Wright Forestry Conference Proceedings. Purdue University, West Lafayette, IN. pp.54-60.
- Sklash, M.B., Stewart, M.K., and Pearce, A.J. (1986). Storm runoff generation in humid headwater catchments. 2. A case study of hillside and low-order stream response. *Water Resour. Res.*, **22**, 1273-1282.
- Smith, R. C., Prezelin, B.B., Baker, K.S., Bidigare, R.R., Boucher, N. P., Coley, T., Karentz, D., MacIntyre, S., Matlick, H.A., Menzies, D., Ondrusek, M., Wan, Z., and Waters, K. J. (1992). Ozone depletion: Ultraviolet radiation and phytoplankton biology in antarctic waters. *Science*, **255**, 952-959.
- Sweeney, B.W., Jackson, J.K., Newbold, J.D., and Funk, D.H. (1992). Temperature change and the life histories and biogeography of aquatic insects. In: *Global warming and freshwater ecosystems*. P. Firth, and S. Fisher (Eds.). Springer-Verlag Inc. New York, pp. 143-176
- Trefethen, J.B (1976). *The American Landscape: 1776-1976 Two Centuries of Change*. K.J. Sabol (Ed). The Wildlife Management Institute, Washington, D.C. 91 pp.
- Triska, F.J. and Cromack, K. Jr. (1981). The role of wood debris in forests and streams. In: *Forests: Fresh perspectives from ecosystems analysis*. R. H. Waring (Ed.), Oregon State University Press, Corvallis, OR. pp. 181-190.
- Triska, F.J., Kennedy, V.C., Avanzino, R.J., and Reilly, B.N. (1983). Effect of simulated canopy cover on regulation of nitrate uptake and primary production by natural periphyton assemblages. In: *Dynamics of Lotic Ecosystems*. T.D. Fontaine III and S.M. Bartell (Eds.). Ann Arbor Science, Ann Arbor, MI. pp.129-159.
- Tuley, G. (1985). The growth of young oak trees in shelters. *Forestry*, **58**, 181-95.
- Vannote, R.L. and Sweeney, B.W. (1980). Geographic Analysis of Thermal Equilibria: A conceptual model for evaluating the effect of natural and modified thermal regimes on aquatic insect communities. *Amer. Naturalist* **115**, 667-695.
- Vannote, R.L., Minshall, G.W., Cummins, K.W., Sedell, J.R., and Cushing, C.E. (1980). The river continuum concept. *Can. J. Fish. Aquat. Sci.*, **37**, 130-137.
- Wallis, P.M., Hynes, H.B.N., and Telang, S.A. (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.
- Welsch, D. (1991). Riparian forest buffers: Function and design for protection and enhancement of water resources. U.S. Department of Agriculture Forest Serv. Rep. No. NA-PR-07-91.
- Williams, M. (1989). Americans and their forests: A historical geography. Cambridge University Press, Cambridge.
- Windell, K. 1991. Tree shelters for seedling protection. U.S. Department of Agriculture Forest Serv. Rep. No.9124-2834-MTDC.
- Zimmerman, R.C., Goodlett, J.C., and Comer, G.H. (1967). The influence of vegetation on channel form of small streams. In: *Symposium on river morphology*. International Association of Scientific Hydrology, Publication no. 75 pp. 255-275

