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STABILITY OF STREAM ECOSYSTEMS

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INTRODUCTION

The ability of ecosystems to recover from external disturbances, that is, their stability, is a fundamental property of these systems. Quantification of the ability for various ecosystems to recover and understanding of the mechanisms behind stability are currently areas of major ecological research. In this paper we present an overview of how the stability concept has been used in ecology and a more specific discussion of the application of these ideas to stream ecosystems. This is followed by a case study in which we have been observing the stability of small streams in response to watershed logging and comparing stream stability to stability of the adjacent forest ecosystem.

THE CONCEPT OF ECOLOGICAL STABILITY

Discussions of ecological stability began with and have been primarily focused around a relationship between stability and system complexity (e.g., Odum, 1953). MacArthur (1955) formalized this idea by providing a measure of pathway complexity, and Margalef (1957, 1963) suggested using species diversity as a measure of stability. The diversity-stability relationship has been supported with a variety of lines of evidence (e.g., Elton, 1958; Dunbar, 1960; Pimentel, 1961), but experimental studies have generally failed to demonstrate an obligate relationship between diversity and stability (e.g., Watt, 1964; Patten and Witkamp, 1967; Hairston et al., 1968; Hurd et al., 1971; Murdoch et al., 1972; Larson, 1974; Goodman, 1975), though they also have not invalidated such a relationship (McNaughton, 1977). Lack of support for a causal relationship between diversity and stability also has come from theoretical (model) studies, most of which suggested that the more complex the model, the less likely it was to be stable (e.g., Gardner and Ashby, 1970; May, 1971a, 1971b, 1972; Smith, 1972; Hubbell, 1973). However, model studies also have suggested that there are situations where increasing the complexity of ecological models may lead to greater probability of stability (e.g., Smith, 1972; Roberts, 1974; Webber, 1974; DeAngelis, 1975; Waide and Webster, 1975). Also Van Voris et al. (1980) demonstrated experimentally a correlation between functional diversity and stability.

Discussions of ecological stability have been hampered by diverse and poorly stated definitions. Two concepts predominate (e.g., Margalef, 1968). First is the notion of constancy or lack of variability. Ecosystems (or communities) which show little temporal change--for example, show year-to-year constancy in population sizes and community composition--are considered stable; whereas ecosystems with large temporal variability, such as tundra ecosystems, are considered unstable. The other notion of ecological stability involves the ability of an ecosystem to respond to disturbance, that is, its ability to exhibit secondary succession (Connell and Slatyer, 1977; McIntosh, 1980). An ecosystem is considered stable if its response to a disturbance is small and its return to its original state is relatively rapid. An ecosystem is unstable if it is greatly changed by disturbance, returns slowly to its original state, or if it never recovers to the original state.

These two notions of stability are related since the constancy or lack of constancy shown by an ecosystem is a reflection of its ability to respond to the almost continuous disturbances to which it is subjected (Lewontin, 1969). Ecosystems which show the greatest constancy should be those with the greatest ability to respond to disturbance. However, it may

also be argued that the ability to dampen small "normal" disturbances may not contribute to the ability to respond to large disturbances. An ecosystem which experiences only small normal environmental variability may appear stable when in fact it is poorly adapted to respond to an unusual disturbance. Ecosystems with highly fluctuating environments become "desensitized" to exogenous perturbations (Watt, 1968; Copeland, 1970; Peterman, 1980).

Attempts to quantify ecological stability have been based mostly on engineering concepts of stability (e.g., Lewontin, 1969; May, 1973). Stability in the sense of Liapunov (or neighborhood stability) concerns the ability of a system to return to steady state if disturbed an infinitesimal distance from steady state. It has been argued that this stability concept is not applicable to ecosystems (Lewontin, 1969; Preston, 1969; Holling, 1973, 1974; Botkin and Sobel, 1975). However, it also has been argued that by their existence ecosystems demonstrate stability in the sense of Liapunov (Webster et al., 1975). This stability then becomes a starting point for more relevant discussions which allow comparisons of the relative stability of various types of ecosystems. Several authors have suggested that relative stability can be divided into various components (Patten and Witkamp, 1967; Child and Shugart, 1972; Waide et al., 1974; Hurd and Wolf, 1974). Two aspects of disturbance response seem most important. One involves the ability of the ecosystem to exhibit minimal response to disturbance. The other aspect relates to the rapidity with which an ecosystem responds once it has been displaced by a disturbance. These two aspects of relative stability have been given a variety of names (cf. Orians, 1974; Cairns and Dickson, 1977; Connell and Slatyer, 1977). We will use the terms resistance and resilience respectively (Webster et al., 1975).

Only a few workers have quantified resistance and resilience of ecosystems or ecosystem models and they used several techniques (e.g., Patten and Witkamp, 1967; Webster, 1975; Webster et al., 1975; Stauffer et al., 1978; Swank and Waide, 1980). While no clearly applicable method exists for evaluating relative ecosystem stability, these studies indicate several important points. Ecosystem resistance is related to a large, slow ecosystem component which damps or buffers disturbances (Golley, 1974; O'Neill et al., 1975; O'Neill and Reichle, 1980). This component of the ecosystem, which is usually soil organic matter, sediment, or detritus, provides an inertia which makes it difficult to displace the system from steady state. Resilience is related to rapid turnover of ecosystem components. Ecosystems in which the autotrophs are phytoplankton are much more resilient than ecosystems dominated by trees. Generally, the two aspects of relative stability are inversely correlated (Webster et al.,

1975). However, there are exceptions. The arctic tundra is an ecosystem with relatively slow turnover compared to other terrestrial ecosystems, perhaps because of the harsh environment and short growing season, and therefore has relatively low resilience. This ecosystem also has a low accumulation of biomass and thus low resistance. On the other hand, Watson and Loucks (1979) suggested that Lake Wingra, as represented by their models, has both large, slow components which confer resistance and rapid turnover pools which provide resilience.

Because most studies of ecological stability have been based on traditional engineering stability concepts, there has been little consideration of the type or magnitude of disturbance. Such considerations are obviously needed in ecosystem studies.

APPLICATION OF ECOSYSTEM STABILITY CONCEPTS TO STREAMS

In 1960, Margalef noted that running waters had failed to attract the interest of general ecologists. This has continued to be especially true with respect to studies of stream ecosystem stability. Further, the few attempts to apply traditional approaches of ecosystem stability (diversity, stability, maturity) and more recent stability concepts (relative stability) to streams have often led to contradictions.

Traditional Stability Concepts

Traditional indicators of ecosystem stability (diversity, maturity) show considerable disagreement when applied to streams (Table 1). Species diversity or number of stream fish species has been found to generally increase with stream order (Kuehne, 1962; Harrell et al., 1967; Sheldon, 1968; Platts, 1979), though streams larger than 6th-order were not included in any of these studies. Whiteside and McNatt (1972) found that fish species diversity increased through the first four stream orders but decreased in the 5th-order stream. Harrell and Dorris (1968) found a downstream increase in macroinvertebrate diversity through 5th-order and a decrease in the number of macroinvertebrate species in the highest order (6th) reach. Headwater streams usually are considered to have moderate or low biotic diversity, mid-order reaches have higher diversity, and in very large streams diversity is fairly low (Vannote et al., 1980). According to Margalef (1963), stability and maturity should follow this same trend. However, Margalef (1960) suggested that there is a general downstream trend from low to high maturity (and thus low to high diversity). We might speculate that the low observed diversity in large rivers is the result of several factors. First, large rivers have not been widely studied. Second, organisms of large rivers (e.g., oligochaetes and

Table 1. Indicators of stream ecosystem stability. ***, high; **, intermediate; *, low.

	Low Order Stream (headwater)	Middle Order Stream	High Order Stream	Reference
Biotic Diversity	**	***	*	Vannote et al., 1980
Functional Group Diversity	**	**	*	Cummins, 1975
Maturity	*	**	***	Margalef, 1960
Geologic Age	*	**	***	Cummins, 1975
Exploit Other Subsystems	*	**	***	Hall, 1972
Pigment Ratio	**	*	-	Motten and Hall, 1972
P:R and/or P:B Ratio	**	*	-	Motten and Hall, 1972
Detritus Base	***	*	**	Fisher and Likens, 1973
Stored Detritus	***	**	*	Naiman and Sedell, 1979

chironomids) are seldom identified to species and diversity estimates are based on higher taxonomic categories. Finally, and perhaps most importantly, most studies of large rivers have been done on polluted ecosystems, since few large pristine rivers still exist. As documented by Wilhm (1972) and many others, pollution decreases stream diversity and may cancel normal trends in diversity (Tramer and Rogers, 1973). In a pristine condition, large rivers were characterized by large floodplains and backwater areas, many woody snags, and often very clear water with light reaching the bottom (Bartram, 1791; Bates, 1863;

Bakeless, 1961). Because of the diversity of habitats in such a river, one might expect to find a highly diverse community.

Headwater streams commonly are regarded as immature (e.g., Margalef, 1960; Hall, 1972; Fisher and Likens, 1973). Survival strategies of benthic stream communities in general are typical of pioneer communities: small body size, short generation time, high reproductive rate, and resting stages resistant to unfavorable conditions (Patrick, 1970). Fisher (this volume) stated that in typical streams of mesic areas which experience frequent flooding, succession is truncated, and these streams are dominated by pioneer type species. Nelson and Scott (1962) suggested that river communities are in a frequent disclimax condition as a consequence of periodic high water.

Geologically, headwater streams are younger than the streams into which they drain (e.g., Leopold et al., 1964). However, the most primitive representations of most orders of aquatic insects are found in headwater streams (Cummins, 1975). This is not surprising if, as it is currently believed, insects evolved terrestrially and invaded freshwater from land, since headwater streams represent the maximum interface between land and water (Vannote et al., 1980). Also, one might argue that while a specific stream is younger than the stream it drains into, the headwater stream ecosystem predates the large river type of ecosystem. In an evolutionary sense, then, the headwater type of stream ecosystem is more mature.

A number of other factors do not support Margalef's (1960) suggestion of a downstream increase in maturity. Margalef (1960, 1963) suggested that immature ecosystems should be exploited by mature ecosystems, and, as Hall (1972) noted, small streams export energy to large streams. However, physical factors (e.g., gravity) are so important, it is questionable whether this criterion should be applied. Headwater streams receive large amounts of energy from forests, but we probably wouldn't consider a stream more mature than a forest.

Motten and Hall (1972) found that two other factors, pigment ratio and P/R (production/respiration) ratio, indicated greater maturity at their upstream station, and suggested that in small streams, internal organizing mechanisms were so overridden by external factors that analysis of developmental strategies is spurious.

Finally, Odum (1969) suggested that a detritus base is typical of mature ecosystems. Fisher and Likens (1973) pointed out that, on this basis, headwater streams are very mature ecosystems. Middle-order streams where autotrophic production is highest (Vannote et al., 1980) would be the least mature.

Further, if organic detritus can substitute for living biomass as suggested by Fisher and Likens (1973), and we bring in Margalef's (1963) idea that biomass is the "keeper of organization" in ecosystems, then maturity clearly decreases downstream. Naiman and Sedell (1979) documented a downstream decrease in the benthic standing crop of detritus in streams and pointed out that the large accumulation of detritus, primarily logs, in headwater streams contributes to the resistance of these ecosystems. They further suggested that as stream order increases, the pathway for obtaining stability changes from one of resistance to resilience.

In general, there is no weight of evidence supporting a downstream increase in stream ecosystem stability. In fact, if maturity, geologic age, and exploitation are ruled out of Table 1 as inappropriate or reversed, as discussed above, then the weight of evidence would seem to support a greater stability in the headwaters. Probably the best indicator of stream ecosystem maturity and perhaps stability would be estimates of energy utilization efficiency (Fisher and Likens, 1973). However, estimates of small stream efficiency are few (e.g., Fisher and Likens, 1973; Webster and Patten, 1979; Mulholland, 1981), and estimates for larger streams are almost non-existent (Fisher, 1977) (But see also Cummins et al., this volume).

Assimilative Capacity

Assimilative capacity is another way of viewing stream ecosystem stability, especially concerning its response to man-induced stress or pollution. Assimilative capacity has been widely used--in a narrow sense related to the response to a decrease in dissolved oxygen due to organic waste and more broadly as the ability of a stream to purify itself when subject to inputs of various types of wastes (Velz, 1976). Cairns (1977a, b) said that assimilative capacity should be defined as the ability of an aquatic ecosystem to assimilate a substance without degrading or damaging the system's ability to maintain its community structure and functional characteristics.

There is considerable debate as to whether streams have any assimilative capacity, that is, whether there is a threshold below which pollution does not change the ecosystem (Woodwell, 1975). Campbell (1981) stated that addition of a very small quantity of a pollutant to a stream may result in an extremely small change--perhaps the death of a few bacteria--but because the stream has responded, it can not be said to have an assimilative capacity. On the other hand, Cairns (personal communication) argues that the ability of the stream to respond to disturbance without change in the basic functional capabilities of the stream ecosystem is evidence of its assimilative capacity even if this response involves the loss of

a few organisms or even a few species. Perhaps we should speak of assimilative capacity as the bounds within which a stream ecosystem has the ability to return (in time or distance) to its original state at least in terms of its function. This region has been referred to as a domain of attraction (Holling, 1973; Peterman, 1980).

In general, the bounds of the domain of attraction of a stream appear to be large. Because of the ability of rivers to cleanse themselves of impurities (Cairns and Dickson, 1977), rivers are one of the main recipients of anthropogenic wastes. Two major factors contribute to this form of stream ecosystem stability. First is the ability of the stream to biologically transform the pollution. The second, but possibly more important, factor is streamflow. In contrast to other types of ecosystems into which wastes might be dumped, discharges into streams "are immediately carried away from the doorstep of the discharger" (Cairns and Dickson, 1977). For this latter reason, streams have a much greater assimilative capacity than any other type of ecosystems. Cline et al. (1979), for example, found that stream runoff and spates ameliorated short-term construction impacts on a Colorado stream resulting in higher stability than had been predicted.

Relative Stability

As discussed above, a number of authors have suggested that we look for relative measures of the ability of ecosystems to minimize response to disturbance. Based on its rapid turnover and small autotrophic component, O'Neill et al. (1975) ranked a small headwater spring as the most sensitive to environmental changes of the various ecosystems they studied. In a later comparison of relative stability, O'Neill (1976) found that a model of this spring ecosystem had the next to smallest stability of the six ecosystems he examined. Webster et al. (1975) ranked their stream model lowest in both resistance and resilience among their eight ecosystem models; however, it should be noted that the stream model was unique among the models in their study because it lacked nutrient cycling. Based partly on these same eight models, but using different techniques to estimate resistance and resilience, Webster (1975) suggested that though streams have low resistance to disturbance, they have very high resilience. This high resilience has been borne out by studies showing rapid recovery of disturbed streams relative to terrestrial ecosystems (e.g., Webster and Patten, 1979). Factors which contribute to the high resilience of stream ecosystems include the short life cycles of the organisms in the community, rapid recolonization mechanisms (drift, flying adults), recolonization from the hyporheic zone, annual renewal of allochthonous inputs (Fisher and Likens, 1973), and, probably

most important, the continual flushing by the current (Webster and Patten, 1979).

Unidirectional flow of water in streams is the primary factor which has made it difficult to get a theoretical grasp on stream ecosystems (Hutchinson, 1963). Margalef (1968) suggested that stream ecosystems should be conceptualized as processes rather than as stable organizations. O'Neill et al. (1979) concluded that the spatial dimension, which is necessary when modeling streams, can significantly alter conclusions about the dynamic behavior of the system in its response to perturbation. Current is an important mechanism of stream stability because it removes or at least displaces effects of disturbance; however, from the standpoint of resistance, current is a force of instability as it continually removes accumulated biomass and detritus, especially during storms. This instability is countered by instream mechanisms which act to retain materials within the stream (Vannote et al., 1980; Minshall et al., 1983), such as debris dams (Bormann et al., 1969; Fisher and Likens, 1973; Sedell et al., 1978; Bilby and Likens, 1980), filter feeders (Wallace et al., 1977), and rapid nutrient uptake (Ball and Hooper, 1963; Elwood and Nelson, 1972; Meyer, 1979; Newbold et al., 1981).

AN EXPERIMENTAL STUDY OF STREAM ECOSYSTEM STABILITY: BIG HURRICANE BRANCH

In 1974 we began a study to evaluate the stability of a stream ecosystem in response to commercial logging (Monk et al., 1977). A primary objective was to compare the stability of the stream with the stability of the forest. Defining stability as the ability of an ecosystem to maintain primary and secondary production following disturbance, we predicted prior to this study that the stream would be less resistant but more resilient than the forest. The forest was cut in 1977 and in this paper we present an overview of some of our observations on the response of the stream.

Site Description

This study was conducted on Watershed (WS) 7 at Coweeta Hydrolic Laboratory in the southern Appalachian Mountains of North Carolina. Prior to logging in 1977, the only experimental manipulation to this watershed since the U.S. Forest Service began management in 1924 was a woodland grazing experiment. Six cattle grazed the watershed from 1941 through 1949 but had little long-term impact on the vegetation (Johnson, 1952; Williams, 1954). Twenty-five years later there were no discernible effects of grazing on water chemistry or stream flow (Swank and Douglass,

1977). Pre-clearcut vegetation on the watershed was separated into four main types. A pine-hardwood association occurred at higher elevations and along ridges. An oak-hickory association at intermediate elevations occurred in two distinct types based on dominant tree species, litter depth and decay rate, and soil moisture and temperature: mesic on east-facing slopes and xeric on west-facing slopes. At lower elevations along streams, the vegetation was a typical cove hardwood association.

Watershed 7 is drained by a second-order stream, Big Hurricane Branch. The substrate of this stream varies from sections of steep exposed bedrock to short sandy reaches of low gradient and infrequent small pools. Prior to logging, dissolved nutrient levels in Big Hurricane Branch were quite low (Table 2).

Hugh White Creek, which drains Coweeta Watershed 14, was used as a reference stream for biological research on Big Hurricane Branch. Vegetation on WS 14 is similar to that on WS 7 prior to logging, although WS 14 has a northwestern aspect and WS 7 has a southern aspect. Hugh White Creek was selected as a reference stream because of its similarity in size and discharge to Big Hurricane Branch. Comparisons of physical and chemical characteristics of the two streams and their watersheds are given in Table 2.

During April-June, 1976, three roads with a total length of 3 km were built on WS 7 for logging access. Two of the roads crossed the main stream. Approximately 5% of the watershed area was disturbed by road building. Logging began in January 1977 and was completed in June. Site preparation--i.e., clearfelling trees that remained after logging--was completed in October 1977. A mobile cable system was used for most logging; however, tractor skidding was used on more gentle slopes (about 8.9 ha). A total of 15.9 ha was not logged (but was site prepared) due to insufficient volume of marketable timber. Mineral soil was exposed on less than 10% of the total watershed area. Following logging, most of the logging debris which fell in or over the stream was removed from the main channel. Neither debris dams that existed prior to logging nor debris in tributary channels were removed.

Abiotic Factors

Streamflow. Both Big Hurricane Branch and Hugh White Creek are equipped with sharp-crested V-notch weirs for continuous stream flow measurement (Fig. 1). Hugh White Creek has had a slightly higher annual discharge than Big Hurricane Branch (Table 2), and prior to logging WS 7 there was a consistent linear relationship between annual discharge in the two streams. However, due to decreased summer transpiration loss following

Table 2. Physical and chemical characteristics of Hugh White Creek (WS 14) and Big Hurricane Branch (WS 7) prior to logging WS 7.

	WS 14 Hugh White Creek	WS 7 Big Hurricane Branch
Watershed area (ha)	61.1	59.5
Maximum elevation of WS (m)	996	1060
Minimum elevation of WS (m)	708	724
Main stream channel length (m)	1077	1225
Mean bank-full width ^a (cm)	406	256
Mean mid-stream depth ^a (cm)	6.4	10.5
Main channel gradient (m.m ⁻¹)	0.16	0.19
Mean annual discharge ^b (l.sec ⁻¹)	19.5	17.7
Maximum discharge during study period (l.sec ⁻¹)	-	1281.2
Mean annual elemental concentrations ^c (mg l ⁻¹)		
NO ₃ -N	0.004	0.002
NH ₄ -N	0.004	0.004
PO ₄ -P	0.002	0.002
Cl ₄	0.540	0.699
SO ₄ -S	0.362	0.475
K	0.350	0.492
Na	0.739	0.946
Ca	0.460	0.846
Mg	0.280	0.372
pH	6.61	6.82

^aMeasurements taken every 5 m for the first 500 m above the weir pond.

^bBased on 40 and 26 years of record, respectively. Data from Coweeta Hydrological Laboratory.

^cData from Swank and Douglass, 1977.

logging (e.g., Swift et al., 1975; Bormann and Likens, 1979), annual discharge in Big Hurricane Branch has increased relative to Hugh White Creek (Fig. 2). The monthly distribution of increase occurs primarily in summer but continues through fall, and early winter, a timing pattern similar to many other cutting experiments conducted at Coweeta (Douglass and Swank, 1975).

Rainfall has had a significant effect on the response of Big Hurricane Branch to logging operations. In May 1976, when logging roads were under construction, there were two large storms, with precipitation amounts of 17 and 21 cm, the second having a recurrence interval of 100 years. Some of the effects of these storms are described below. The effects of a severe drought during 1980 have not yet been fully evaluated. Streamflows during this period reached previously unrecorded lows.

Stream temperatures. As has been found in other studies (e.g., Swift and Messer, 1971), summer water temperatures increased in Big Hurricane Branch following logging (Fig. 3). After removal of the canopy which shaded the stream, water temperatures during summer months were several degrees higher than temperatures predicted from a pre-logging regression against water temperatures in a stream draining an adjacent, forested watershed. The most recent data suggest that with canopy regrowth, water temperatures are decreasing.

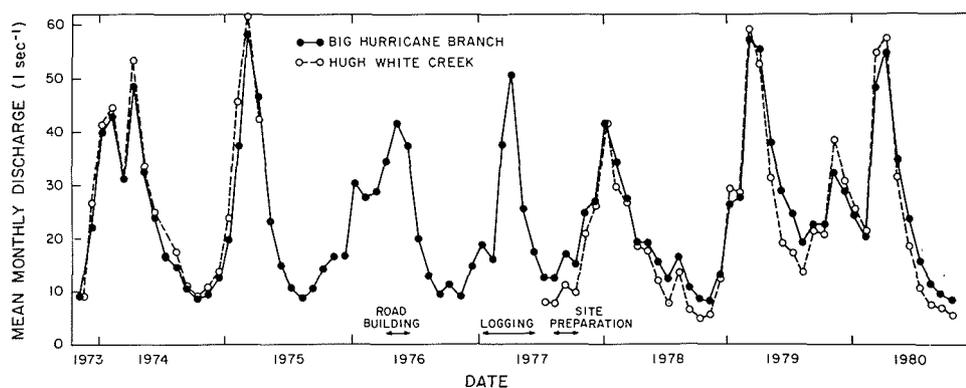


Fig. 1. Mean monthly discharge in Big Hurricane Branch (WS 7) and Hugh White Creek (WS 14) during the study period. Periods of disturbance on WS 7 are also indicated.

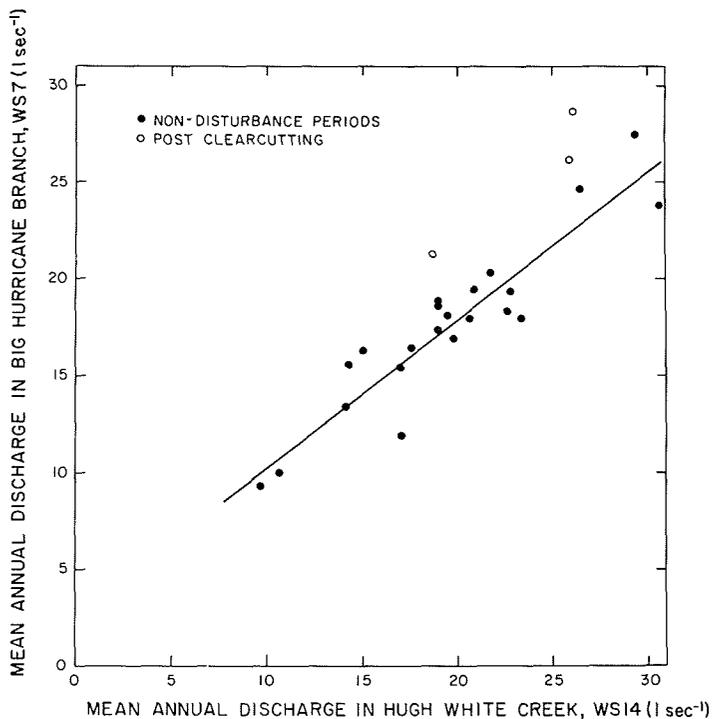


Fig. 2. Comparison of mean annual discharge in Big Hurricane Branch before and after logging with mean annual discharge from an undisturbed watershed, WS 14, drained by Hugh White Creek. The regression line fits the points for non-disturbance periods.

Dissolved nutrient levels. Small but detectable changes in concentrations of dissolved ions occurred in Big Hurricane Branch following logging. During and following road-building (1976), but prior to logging, increases were found in concentrations of Ca, $\text{SO}_4\text{-S}$, K, Cl, Mg, Na, and SiO_2 . However, $\text{NO}_3\text{-N}$, $\text{NH}_4\text{-N}$, and $\text{PO}_4\text{-P}$ showed no response during the following year (1977). In the next year (1978), the most conspicuous change was a large increase in the concentration of dissolved $\text{NO}_3\text{-N}$, beginning in August 1977. The concentration of $\text{NO}_3\text{-N}$ subsequently increased from pre-disturbance levels of $0.002 \text{ mg}\cdot\text{l}^{-1}$ to $0.04 \text{ mg}\cdot\text{l}^{-1}$ or higher. The concentration of $\text{PO}_4\text{-P}$ remained near pre-disturbance levels.

Sediment. Suspended inorganic sediments in Big Hurricane Branch showed large increases, principally during road building

and logging, when use of roads was greatest (Fig. 4). The highest suspended sediment concentration was recorded in June 1976, following the two large storms mentioned previously. Suspended sediment concentrations then declined until they again rose in the period of logging and site preparation (March–October 1977). Concentrations generally declined thereafter.

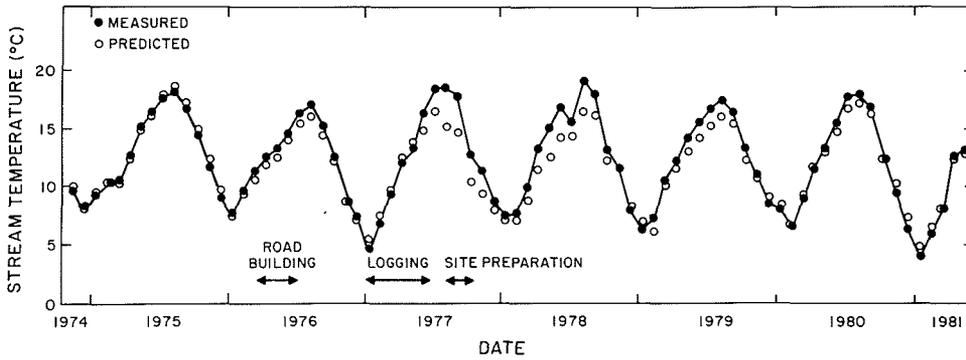


Fig. 3. Measured mean monthly water temperatures in Big Hurricane Branch compared with temperatures predicted from regression on water temperatures in a stream draining an adjacent, undisturbed watershed, WS 10.

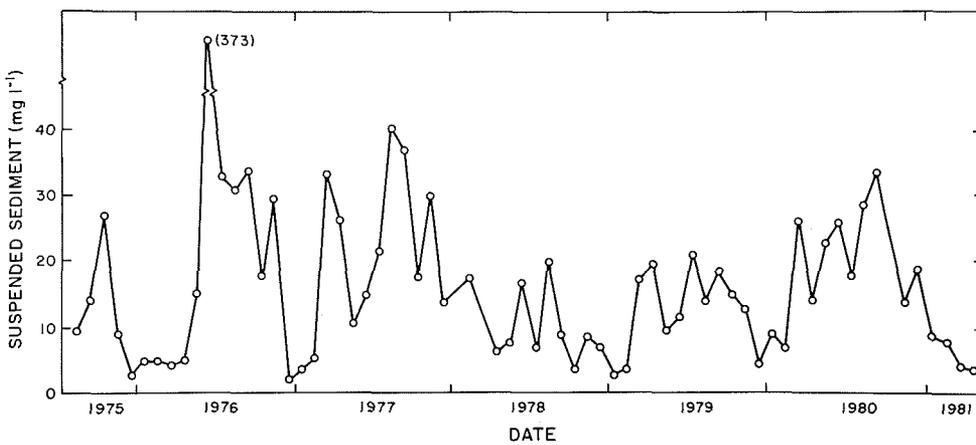


Fig. 4. Mean monthly suspended sediment concentrations in Big Hurricane Branch.

Sediment which accumulated in the weir pond, primarily bed load, averaged $32 \text{ kg}\cdot\text{d}^{-1}$ prior to disturbance. During road construction, this fraction of the sediment load increased to $765 \text{ kg}\cdot\text{d}^{-1}$. Much of this increase can be attributed to the effects of the two large storms which occurred as the roads were being built. These storms washed large amounts of material from roadbeds into the stream channel. In the subsequent period of road stabilization, sediment load decreased to $47 \text{ kg}\cdot\text{d}^{-1}$. During logging this fraction of the sediment load increased to $80 \text{ kg}\cdot\text{d}^{-1}$, and it further increased to $188 \text{ kg}\cdot\text{d}^{-1}$ during early 1978. There has been some subsequent decrease in sediment accumulation in the weir pond, though it still continues much above pre-disturbance levels. Much of the post-logging sediment has been fairly large particles ($>0.05 \text{ mm}$), and we think that most of this material entered the stream during the 1976 storms and is continuing to be washed out of the streams, mainly during storms. Except for a brief period including the spring 1976 storms, sediment transport in undisturbed streams at Coweeta has remained low (c.f. Gurtz et al., 1980).

Leaf Fall and Blow-in

Leaf fall into Big Hurricane Branch was measured with six 0.4045-m^2 litter traps located over or adjacent to the main channel. Two traps were placed at each of three sites located on lower, middle, and upper reaches of the stream. Four 40-cm wide blow-in traps were also placed at each of these three sites, two traps on each bank. Material accumulated in the litter traps was collected approximately bi-weekly in the fall, separated to species if possible, oven dried, and weighed.

Prior to disturbance, leaf fall was estimated to be $259.2 \text{ g DW}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$, a fairly typical value for eastern deciduous forests (Table 3). The species composition was dominated by oaks, hickories, yellow poplar, and rhododendron. One year after logging, leaf fall dropped to nearly zero, but two years later was up to about half the pre-logging input. Post-logging leaf fall was dominated by herbaceous material (e.g., Aster curtisii), woody shrubs such as blackberry (Rubus sp.) and green briar (Smilax sp.), and rapidly sprouting tree species (yellow poplar, black locust, sourwood, sassafras).

Blow-in, material that moves laterally from the stream bank into the stream, was measured as $174.8 \text{ g DW}\cdot\text{m}^{-1}\cdot\text{y}^{-1}$ prior to logging. Based on an average channel width of 1.65 m (from measurements made on the entire WS 7 stream network), blow-in represented 45% of the total allochthonous input. From fall 1978

Table 3. Leaf fall to Big Hurricane Branch before and after clearcutting. The "other" category includes all leaf species comprising less than 2% of the total and all unrecognizable leaf fragments.

	Percent Composition			
	1974	1978	1979	1980
White Oak <u>Quercus alba</u>	14.2	-	-	-
Red Oak <u>Quercus rubra</u>	13.4	-	-	-
Rhododendron <u>Rhododendron maximum</u>	11.6	26.5	-	-
Hickories <u>Carya spp.</u>	11.4	-	-	-
Yellow Poplar <u>Liriodendron tulipifera</u>	9.1	10.8	-	5.0
Birches <u>Betula spp.</u>	5.4	15.7	11.8	-
Chestnut Oak <u>Quercus prinus</u>	4.8	-	-	-
Red Maple <u>Acer rubrum</u>	4.8	-	-	-
Basswood <u>Tilia americana</u>	4.2	-	-	-
Beech <u>Fagus grandifolia</u>	-	-	-	-
Dogwood <u>Cornus florida</u>	-	3.9	5.2	2.0
Sourwood <u>Oxydendrum arboreum</u>	-	-	4.9	4.2
Black Locust <u>Robinia pseudoacacia</u>	-	-	4.1	2.3
Sassafras <u>Sassafras albidum</u>	-	-	-	2.4
Other	21.1	43.1	74.0	84.1
Total annual leaf fall (g DW·m ⁻²)	259.2	4.2	43.3	124.9

through summer 1979, blow-in was $38.6 \text{ g DW} \cdot \text{m}^{-1} \cdot \text{y}^{-1}$ (92% of total input), and the next year it was $41.0 \text{ g DW} \cdot \text{m}^{-1} \cdot \text{y}^{-1}$ (53% of total input). Initially, blow-in was not as greatly affected by logging as leaf fall, since much of the blow-in may have been from litter accumulated on the ground in previous years. However, blow-in is apparently not recovering as rapidly as direct leaf fall, perhaps due in part to the thick undergrowth.

Periphyton Primary Production

Measurements of periphyton primary production were made in both Big Hurricane Branch and Hugh White Creek following logging of WS 7. Approximately monthly measurements were made from October 1977 through February 1979, and an additional seven measurements were made between June 1980 and May 1981. All primary production measurements were made using ^{14}C uptake on natural substrates exposed in circulating water chambers similar to those used by Rodgers et al. (1978) and Hornick et al. (1981).

Periphyton primary production in Hugh White Creek averaged $0.3 \text{ mg C} \cdot \text{m}^{-2} \cdot \text{hr}^{-1}$ (Fig. 5). This rate of carbon fixation is similar though somewhat smaller than rates reported for other small, forested eastern streams (Minshall, 1967; Elwood and Nelson, 1972; Hornick et al., 1981). Applying this rate to Big Hurricane Branch prior to logging (assuming that rates were similar in the two streams prior to disturbance and that measurements taken from small areas of rocks can be expanded to stream area, carbon is 45% of dry weight, production occurs 12 hr per day, and ^{14}C fixation approximates net primary production) periphyton primary production accounted for $2.9 \text{ g DW} \cdot \text{m}^{-2} \cdot \text{y}^{-1}$, approximately 0.6% of that provided by allochthonous inputs.

Following logging, primary production in Big Hurricane Branch was significantly ($p < 0.05$) greater than in Hugh White Creek (average 1977-1978 = $8.9 \text{ mg C} \cdot \text{m}^{-2} \cdot \text{hr}^{-1}$). Using the assumptions above, autochthonous input in 1977-78 was $86.6 \text{ g DW} \cdot \text{m}^{-2} \cdot \text{y}^{-1}$, slightly larger than total allochthonous inputs and much larger than direct leaf fall during the same period. However, two years later periphyton primary production had decreased to $0.9 \text{ mg C} \cdot \text{m}^{-2} \cdot \text{hr}^{-1}$ and accounted for only about 5% of that provided by allochthonous inputs. A similar increase in periphyton primary production following logging was reported by Gregory (1979).

The high level of periphyton primary production in 1977-78 may be attributed to opening of the canopy, increased dissolved

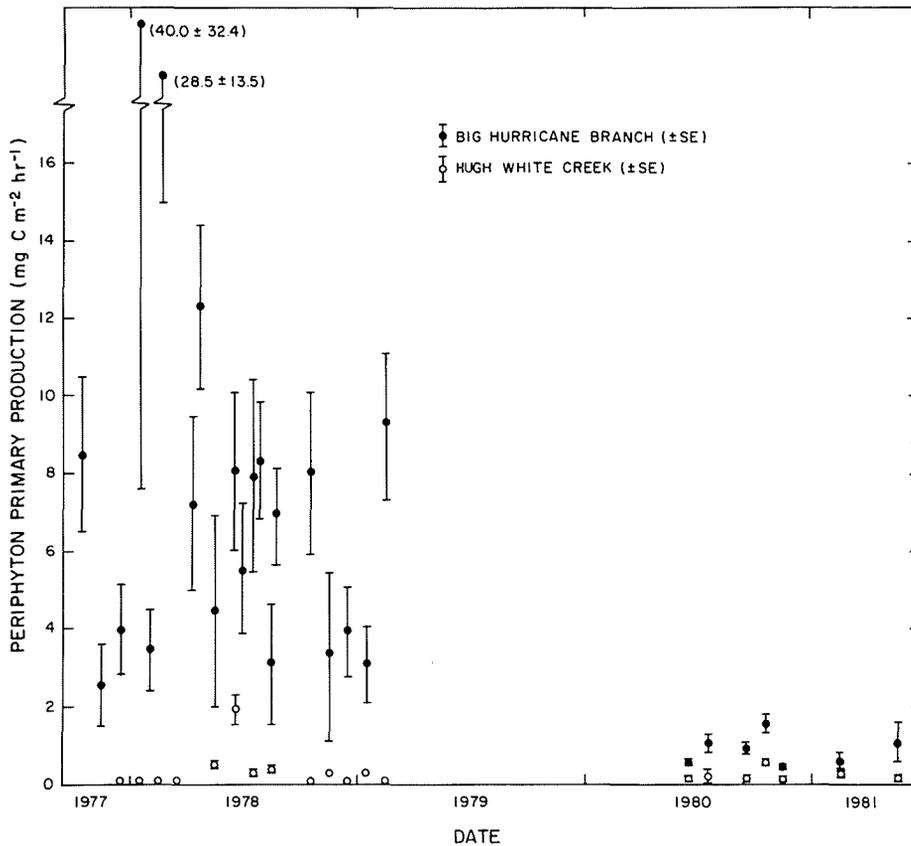


Fig. 5. Periphyton primary production in Big Hurricane Branch and Hugh White Creek. Error bars are \pm SE.

nutrient concentrations, and possibly a sparse grazer fauna (see below). Several factors may have been involved in the subsequent decrease in primary production including increased shading, increased number of grazers, and scouring by the large sediment particles in transport beginning in early 1978. Further details on primary production of both algae and moss in Big Hurricane Branch and Hugh White Creek were reported by Hains (1981).

Dissolved Organic Carbon

Water samples for dissolved organic carbon (DOC) analysis were collected biweekly from both Big Hurricane Branch and Hugh White Creek from July 1979 through June 1980. Estimates for DOC budgets for the two streams were based on samples collected from the main streams just above the weir ponds, precipitation (throughfall), tributaries, and subsurface water seeps. Eleven

storms were intensively sampled to develop concentration-discharge regressions. All samples were analyzed on a Dohrmann DC-54 Carbon Analyser, which used UV-catalyzed oxidation in the presence of persulfate.

DOC concentrations in the reference stream, Hugh White Creek, were highest during the growing season, averaging about $1 \text{ mg C} \cdot \text{l}^{-1}$ during spring and summer (Fig. 6). Concentrations in biweekly samples from the disturbed stream, Big Hurricane Branch, stayed at about $0.5 \text{ mg C} \cdot \text{l}^{-1}$ throughout the study. During baseflow conditions in the growing season, the reference stream showed a consistent increase in DOC concentration from the headwaters to the base of the watershed. This increase was not observed during dormancy, nor was it observed at any time in Big Hurricane Branch. DOC concentration increased to as high as $5 \text{ mg C} \cdot \text{l}^{-1}$ during storms on both watersheds, and there was no difference in concentration-discharge regressions between the two streams or between rising and falling limbs of the hydrograph. This is in marked contrast to observations on fine particulate organic matter in these streams (Gurtz et al., 1980).

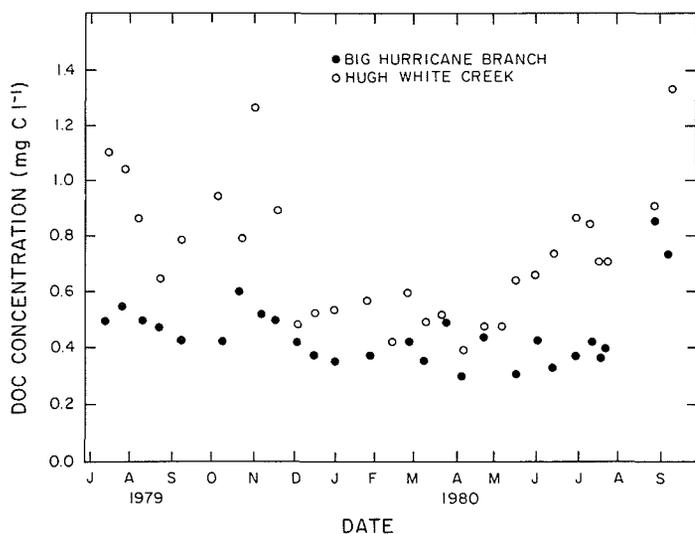


Fig. 6. Dissolved organic carbon concentrations in Big Hurricane Branch and Hugh White Creek.

Decreased DOC concentrations in Big Hurricane Branch cannot be attributed entirely to dilution because of higher discharge. During the period beginning two years after logging, annual DOC export was substantially less from the logged watershed ($10.6 \text{ kg C}\cdot\text{ha}^{-1}$ vs. $14.8 \text{ kg C}\cdot\text{ha}^{-1}$ from WS 14). Three factors appear to be responsible for the lower export from Big Hurricane Branch: (1) The rate at which DOC was taken up by the biota was greater in Big Hurricane Branch. Experimentally added sucrose and leaf leachate was removed from the water column more rapidly than in the reference stream (J. Meyer, unpubl. data). This was due in part to warmer water temperatures and greater microbial biomass (as ATP, J. Meyer, unpubl. data). During storms, the uptake capacity of the stream was exceeded, DOC moved downstream faster than it could be taken up, and more similar concentrations were observed in the two streams. (2) Within stream production of DOC due to leaching of leaf and other litter was lower in Big Hurricane Branch due to lower standing stock of this material. The lack of a consistent downstream increase in DOC concentration in this stream supports this observation. (3) Less DOC was entering Big Hurricane Branch. Budget calculations showed DOC inputs in Big Hurricane Branch were about 70% of the inputs to the reference stream. The difference was primarily due to decreased inputs from tributaries and subsurface water.

During the year studied, both streams showed a net loss of DOC. This may be due to an underestimation of the within stream sources of DOC and the extraordinarily wet year; annual runoff was 52% greater than the 44 year average. Further details of DOC dynamics in Big Hurricane Branch and Hugh White Creek are being prepared for publication (Meyer and Tate, in press).

Benthic Particulate Organic Matter

Prior to logging WS 7, samples of benthic particulate organic matter (BPOM) were collected for two years from Big Hurricane Branch. Ten random samples (one sample every 100 m starting at a random point in the first 100 m) were taken with a square foot Surber sampler (0.57-mm mesh opening) each month. Collected material was separated into woody and non-woody (primarily leaves and moss), dried, and weighed. Monthly samples were taken from January 1977 through September 1978 using a somewhat different sampling scheme. Four samples (Surber, 0.30-mm mesh openings) were taken from each of four different habitat types: moss (moss covered boulders and outcrops), cobble riffle (riffles dominated by cobble-sized rocks, i.e., 64-256 mm), pebble riffle, and sand (predominantly sand and gravel substrate). To make these data comparable with the pre-logging samples, we used weighted means based on the percent of stream bottom area occupied by each habitat type.

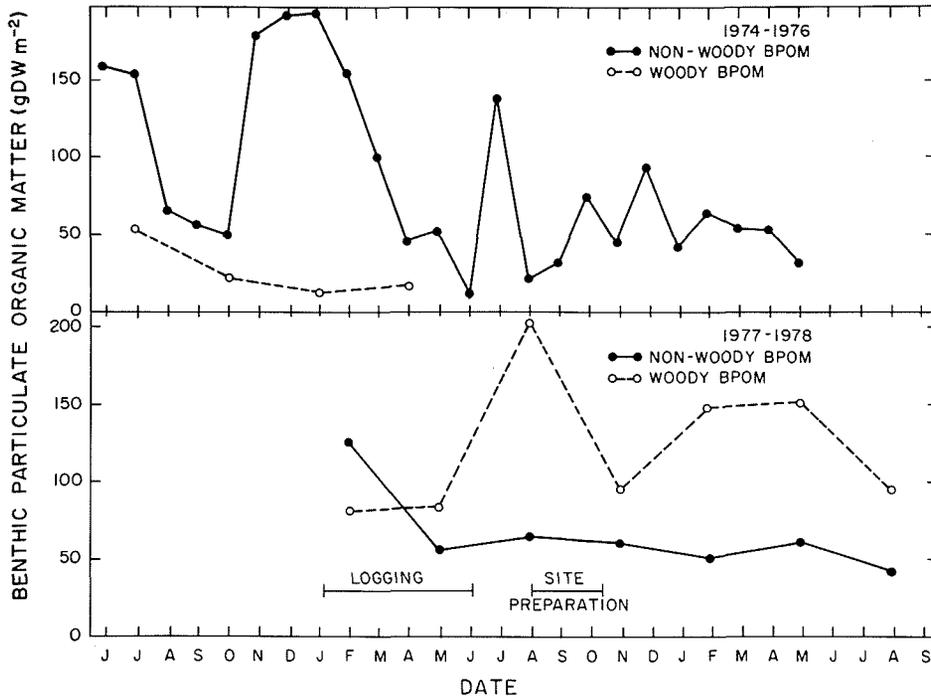


Fig. 7. Benthic particulate organic matter (BPOM) in Big Hurricane Branch. Woody BPOM and 1977-1978 non-woody BPOM are quarterly means of monthly samples.

In the two years prior to logging, non-woody BPOM in Big Hurricane Branch averaged 86.2 g DW·m⁻² and woody BPOM was 27.0 g DW·m⁻² (Fig. 7). In comparison, non-woody BPOM in the year following logging (October 1977 through September 1978) was down to 54.7 g DW m⁻², but woody material had increased to 120.6 g DW·m⁻². Though slash was removed from some parts of the main stream during site preparation, it is evident that large amounts of woody material entered Big Hurricane Branch as a result of logging. In the first fall following logging, the usual pulse of leaf detritus was absent. However, there was a considerable amount of leaf detritus which entered the stream primarily from rhododendron slash over and adjacent to the stream.

Leaf Breakdown Rates

Breakdown rates in Big Hurricane Branch of three leaf species, dogwood, white oak, and rhododendron, were measured before (1974-1975), during (1976-1977), and after (1977-1978)

logging. Prior to logging, senescent leaves were collected just prior to abscission from trees on WS 7 or adjacent undisturbed watersheds. After logging, leaves were collected only from the adjacent watersheds so that changes in breakdown rates would not be caused by altered quality of successional vegetation. Two to four grams of air dried leaves were placed in nylon mesh bags (10 x 10 cm, 3-mm mesh openings). These bags were placed in the stream in autumn and retrieved periodically until most leaf material had disappeared. In the laboratory, leaves were rinsed to remove attached sediment, air dried, and weighed. Subsamples were ashed to determine ash-free dry weights (AFDW). Exponential breakdown rates were calculated as the slopes of semi-log regressions of AFDW remaining against time (Jenny et al., 1949; Olson, 1963; Petersen and Cummins, 1974). All regression slopes were significantly different from zero ($p < 0.05$). Breakdown rates were compared using analysis of covariance (Sokal and Rohlf, 1969).

In both the before-logging and during-logging studies, dogwood leaves broke down significantly ($p < 0.05$) faster, and rhododendron broke down significantly slower than the other two leaf species (Table 4). Although dogwood breakdown was still significantly faster after logging, rates for rhododendron and white oak were not significantly different. Breakdown rates of all three species were significantly slower during logging than before logging. Dogwood and white oak were affected similarly, declining to about 60% of their original rate, while rhododendron was more strongly affected, slowing to about 30% of its original rate. In contrast, white oak and rhododendron breakdown rates increased after logging as compared to before logging. Dogwood broke down at the same rate in both study periods, white oak increased 40%, and rhododendron was again most affected, increasing about 180% over its before-logging rate.

We analyzed in detail various factors which might have affected these results, including water temperature, dissolved nutrient concentrations, stream flow, sediment transport, and faunal abundance (Webster and Waide, in press). We have concluded that sediment and fauna are probably the two most important factors. In the study conducted during logging, burial of leaves in the sediment and decline of the dominant shredder decreased rates of leaf breakdown. The next year sedimentation was much less, but the shredder fauna remained low. However, because of the very low allochthonous leaf input that year (Table 3), our bags of leaves represented islands of a scarce food source. Dogwood leaf breakdown was not greatly affected since it is a rapidly conditioned and preferred shredder food (Wallace et al., 1970). However, rhododendron leaves, which are normally ignored by shredders at least during the first half year of conditioning, were eaten because of the scarcity of preferred

Table 4. Breakdown rates (d^{-1}) of three leaf species measured before, during, and after logging. Each rate is given with its 95% confidence interval. Numbers in parentheses are the number of samples and the coefficient of determination, r^2 , of the semi-log regression.

	Before Logging 1974-1975	During Logging 1976-1977	After Logging 1977-1978
Dogwood	0.0219 ± 0.0025 (104, 0.74)	0.0134 ± 0.0023 (45, 0.77)	0.0219 ± 0.0024 (84, 0.81)
White Oak	0.0064 ± 0.0006 (143, 0.78)	0.0038 ± 0.0004 (44, 0.91)	0.0090 ± 0.0010 (84, 0.79)
Rhododendron	0.0037 ± 0.0007 (156, 0.37)	0.0011 ± 0.0003 (45, 0.65)	0.0105 ± 0.0020 (82, 0.59)

food. White oak leaves were affected at an intermediate level. Results of this study are discussed more fully by Webster and Waide (in press).

Particulate Organic Matter Transport

Transport of particulate organic matter (POM) was measured by two techniques. Large particulate organic matter (LPOM) in Big Hurricane Branch was measured using a 1-mm mesh drift net placed in the stream a few meters above the weir pond where a wooden flume directed all flow into the net. Samples were collected at approximately weekly intervals over 4 or 24-hour periods for 18 months prior to logging and 14 months following logging. Collected material was dried, washed to remove inorganic sediment, re-dried, and weighed.

Periodic samples of total POM were collected from Big Hurricane Branch and Hugh White Creek from 1977 through 1981. These samples were processed by filtering measured volumes of water through a series of stainless steel screens (Gurtz et al., 1980). Material collected on the screens and aliquots of material passing the finest screen were collected on ashed and preweighed glass fiber filters. The filters were dried (50°C), weighed, ashed (500°C), and reweighed.

Monthly averages of LPOM concentrations in Big Hurricane Branch during non-storm periods showed a substantial increase in

the year following logging (Fig. 8). We suspect that most of this increase was due to logging debris that fell in the stream. Total POM concentration showed a pattern very similar to LPOM (Fig. 9). POM concentrations in Big Hurricane Branch have been significantly (t -test, $p < 0.05$) greater than Hugh White Creek since WS 7 was logged. This has resulted in substantially greater export of POM from Big Hurricane Branch than Hugh White Creek (Fig. 10). However, comparison of summer 1981 samples with summer 1978 samples suggests that the elevated POM transport in Big Hurricane Branch may be declining.

In addition to elevated transport during low flows, samples taken during storms in 1977 and 1978 (Gurtz et al., 1980) and in June 1981 (Fig. 11) indicate greatly increased storm transport. The most recent storm samples were taken during a thunderstorm on 30 June - 1 July 1981. The storm lasted about two hours and was very intense during the first hour. Flows returned to near

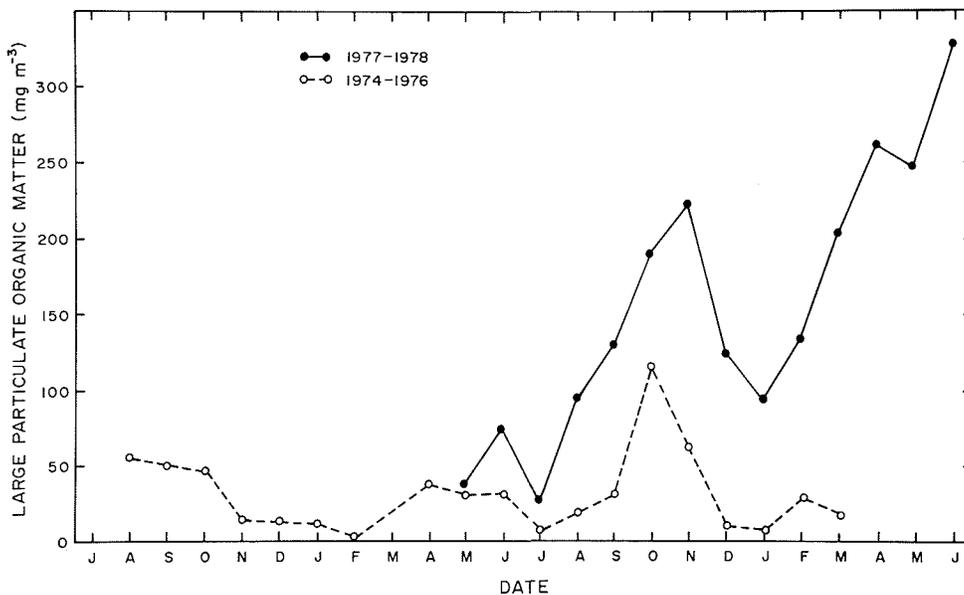


Fig. 8. Mean monthly estimates of large particulate organic matter (> 1 mm) concentrations in Big Hurricane Branch before (1974-1975) and after (1977-1978) logging. All samples included in this figure were taken during non-storm periods.

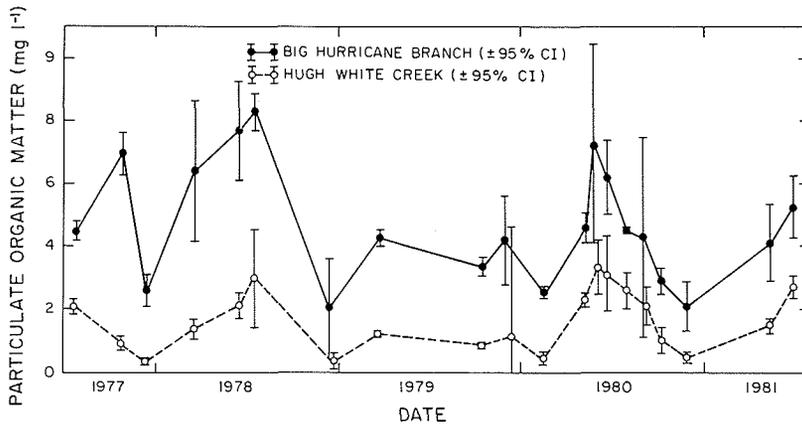


Fig. 9. Total particulate organic matter (POM) concentrations in Big Hurricane Branch and Hugh White Creek following logging WS 7. Only samples taken during non-storm periods are included. In all sampling periods, the POM concentration in Big Hurricane Branch was significantly ($p < 0.05$, t-test) higher than the POM concentration in Hugh White Creek.

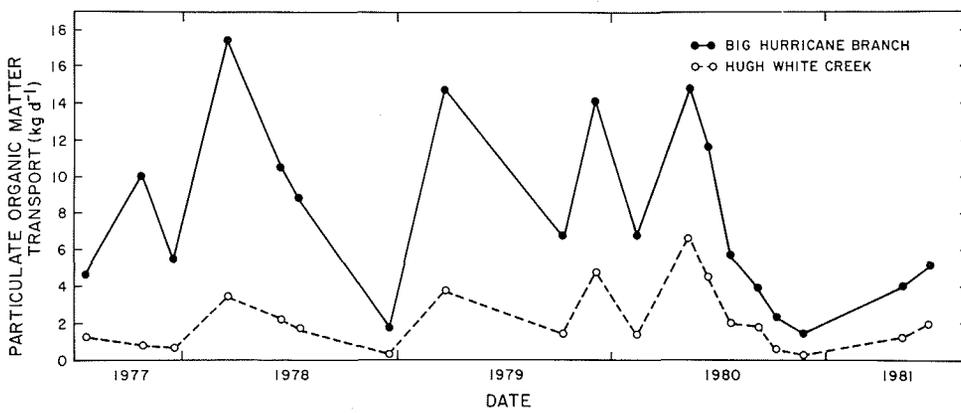


Fig. 10. Particulate organic matter transport in Big Hurricane Branch and Hugh White Creek following logging WS 7. Only non-storm periods are included.

baseflow two hours after the rain ended. The concentration of POM in Big Hurricane Branch peaked at the very beginning of the storm (Fig. 11). Bilby and Likens (1979) also noticed this peak in POM concentration which occurs prior to the discharge peak and attributed it to entrainment of materials in the streambed. This phenomenon was magnified in Big Hurricane Branch where, with the absence of a tree canopy, direct impact of rain drops on the stream bed helped initiate particle movement.

Based on the particle size fraction analysis, there was little difference between the particle size distributions in Big Hurricane Branch following clearcutting and Hugh White Creek. The median particle size ranged from 0.041 to 0.093 mm and 0.037 to 0.101 mm in the two streams, respectively. However from October 1977 through June 1978, the median POM particle size in Big Hurricane Branch was consistently and significantly (t-test, $p < 0.05$) larger than in Hugh White Creek. This was a period when we also observed elevated transport of large (> 1 mm) inorganic particles (Gurtz et al., 1980).

Benthic Macroinvertebrates

Collections of benthic macroinvertebrates were made in both Big Hurricane Branch and Hugh White Creek for a 21-month period beginning in January 1977 with the onset of logging. A Surber sampler (mesh opening 0.3 mm) was used to collect four samples monthly (three in Hugh White Creek) in each of four common substrates: moss, cobble riffle, pebble riffle, and sand. Samples were preserved in the field with approximately 10% formalin solution, and invertebrates were picked from the samples with the aid of a microscope at 7X magnification. Further details of this study were given by Gurtz (1981); our concern here is with faunal changes that occurred in response to logging. Changes in the invertebrate fauna were compared between the streams using two-way analysis of variance on log-transformed data. The overall abundance estimates in Figure 12 were calculated by weighting habitats according to their occurrence in each stream. In the discussion below, functional feeding groups for each taxon are those assigned by Merritt and Cummins (1978).

Among the statistically significant changes that occurred in Big Hurricane Branch relative to Hugh White Creek following logging, the greatest change occurred in the collector-gatherer (and possibly scraper) mayflies (Baetis spp. and Ephemerella spp.). Initial abundances were similar in the two streams, but within several months of logging, abundances in Big Hurricane Branch were much higher than in the reference stream. These increases occurred in all habitats for Baetis with the most pronounced increases in the moss habitat. Species in the genus Ephemerella increased in all habitats except sand.

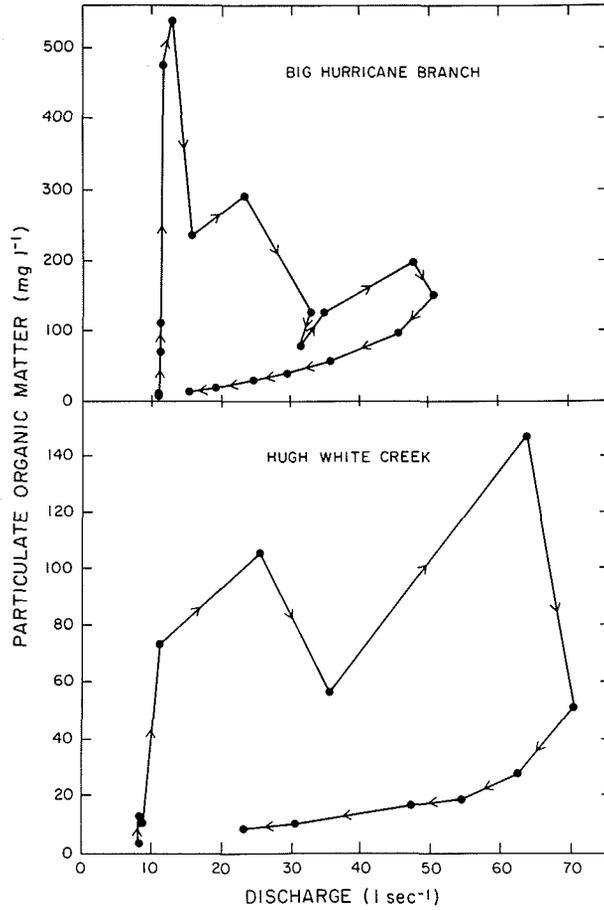


Fig. 11. Particulate organic matter concentrations in Big Hurricane Branch and Hugh White Creek during a storm on 30 June - 1 July 1981. Arrows indicate the time sequence of samples. The total sampling period was about four hours. Samples from Hugh White Creek were taken every 15 min. Samples from Big Hurricane Branch were taken even more frequently when the stream was rising. The time between the onset of the storm and peak discharge was 50 min. in Big Hurricane Branch and 65 min. in Hugh White Creek.

The dominant shredder in low-order Coweeta streams, Peltoperla (Tallaperla) maria declined in all habitats in Big Hurricane Branch relative to Hugh White Creek throughout the study period. Much of the decrease in Peltoperla was due to significant declines in the smallest size classes. Samples collected for an additional year after the study period reported here indicate that Peltoperla was nearly eliminated from Big Hurricane Branch within three years after logging.

Caddisflies represent a variety of functional groups and responded accordingly. Grazing caddisflies, including Glossosoma nigrrior, Micrasema sp., and Neophylax spp., increased in moss samples and in pebble riffles as well as overall. Lype diversa, a caddisfly which constructs its retreat in grooves of decaying wood, was more abundant in Big Hurricane Branch than in Hugh White Creek; it increased over time in Big Hurricane Branch in each habitat in which it was commonly found, perhaps in response to decay of wood which entered the stream channel during logging. Hydatophylax argus and Pycnopsyche spp., relatively common shredding caddisflies in the study stream, decreased significantly in Big Hurricane Branch in moss and sand substrates as well as overall. No significant trends were found in abundance of the net-spinning hydropsychids Diplectrona modesta and Parapsyche cardis. Abundances of predaceous caddisflies, including Rhyacophila spp. and Polycentropus sp., did not change in response to logging.

All aquatic Coleoptera in the present study, including the psephenid Ectopria nervosa and the elmids Optioservus immunis, O. ovalis, and Oulimnius spp., can be considered scrapers. Elmids increased in the moss habitat as well as overall. This increase was much slower to develop than the increase in mayflies, in part because of the longer life cycle of the elmids.

Chironomidae was the most abundant taxon in both streams overall, in all habitats in Big Hurricane Branch, and in all habitats except moss in Hugh White Creek, where it was second to Parapsyche. Chironomidae increased in the moss habitat and decreased in sand, with little overall difference between the streams; increases in moss were largely due to Orthoclaadiinae, especially Eukiefferiella spp.

Summaries of insect abundance data by functional feeding group are presented in Figure 12. Chironomids were excluded from this analysis since they were identified below family level for only a subset of the samples and since this family represents a wide variety of functional groups.

A decline in shredder abundance as a response to the decreased BPOM food resource did not occur overall, despite the

decline in *Peltoperla* (Fig. 12). In fact, total shredder abundance increased in the moss habitat, where FPOM accumulates and LPOM is scarce. This suggests that taxa categorized as shredders (e.g., *Amphinemura wui*) may in fact be feeding on FPOM.

The mayflies that increased were categorized as collector-gatherers, although some may be scrapers. Thus it is unclear whether the increase in collector-gatherers (Fig. 12) was in response to elevated amounts of FPOM in Big Hurricane Branch or to increased availability of algae. Largest increases occurred in moss, which serves both as a trap for FPOM and as a substrate for growth of attached algae.

Scraper taxa increased near the end of the study period (Fig. 12), with a temporal lag similar to that observed with

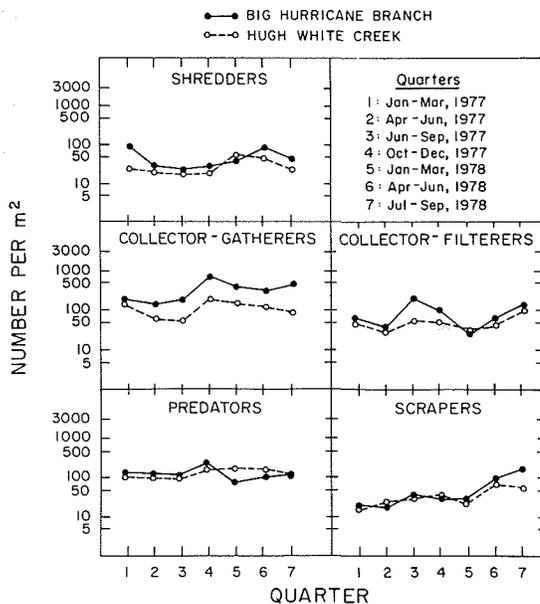


Fig. 12. Densities of benthic macroinvertebrate functional feeding groups in Big Hurricane Branch and Hugh White Creek. Data points are quarterly means of monthly abundance estimates. Big Hurricane Branch and Hugh White Creek densities were significantly different ($p < 0.05$) for shredders, quarter 1; collector-gatherers, quarters 4-7; and collector-filterers, quarter 3.

Elimidae alone. Significantly higher abundances in Big Hurricane Branch compared to the reference stream occurred only in moss and cobble substrate, while lower abundances were found in sand. This latter finding suggests that siltation may have inhibited establishment of periphytic algae in depositional substrates. The increase in scrapers can probably be attributed to the increase in periphyton production (Fig. 5). Also some insects have been observed to feed on moss (e.g., *Micrasema*, Chapman and Demory, 1963), and their increase may reflect an increase in moss production.

No significant trends were apparent among the filter feeders (Fig. 12). Predators apparently responded to increases in potential prey organisms. Though they changed little overall (Fig. 12), they increased in moss and decreased in sand, reflecting similar trends observed for total organisms.

Thus, the stream invertebrate community responded to logging in a direction corresponding to changes in food availability. A differential response by the invertebrates depending on habitat was also observed. For example, more taxa increased in moss compared to other habitats. For many taxa the pattern was highest increase in moss, progressively less increase in cobble and pebble, and least increase or a decrease in sand. Of those taxa which declined in any habitat, more did so in sand. Explanation of these trends includes the probable increase in food availability (FPOM and periphytic algae) in the moss habitat, while this habitat was probably least affected by sediment. Depositional areas, characterized by slower current velocity and smaller substrate particle size, may have been most adversely affected by sediments which entered the stream during road building. This added sediment increased the physical instability of these low-gradient reaches.

CONCLUSIONS

In our study of the response of Big Hurricane Branch to logging of WS 7, we found the following changes:

(1) Abiotic changes included increased streamflow during the growing season, higher summer water temperatures, increased levels of some nutrients, and increased sediment load. There was also an obvious increase in light to the stream bed. After four years, most of these changes were showing significant return toward pre-logging levels.

(2) Allochthonous inputs to Big Hurricane Branch were greatly reduced by logging. These inputs increased significantly within three years after logging with the regrowth of terrestrial vegetation.

(3) Periphyton primary production is generally a small portion of the energy base of Coweeta streams. However, following logging, periphyton primary production increased to levels greater than allochthonous inputs. Three years after logging, periphyton production was again fairly low, though still higher than reference levels.

(4) Two years after logging, DOC levels were significantly lower than reference levels due primarily to more rapid uptake, less instream production, and less watershed input.

(5) With reduced leaf fall and blow-in, BPOM decreased following logging. At the same time there was an increase in woody material which remained from the logging operation.

(6) Leaf breakdown rates were initially slowed and later accelerated. A variety of factors were probably involved, but sediment and fauna appear most important.

(7) Concentration and transport of POM were significantly increased by logging. Recent samples suggest that POM levels are returning toward reference levels.

(8) Stream invertebrates responded to logging in a direction corresponding to changes in food availability. While previously dominant shredder species declined, collectors and scrapers increased, as did taxa associated with wood. These changes were modified by substrate stability.

Interpreting these results in the context of stream ecosystem stability, we focus on attributes which reflect ecosystem function. One measure of stream stability is the response of the stream ecosystem to changes in the quantity and quality of energy inputs. This response should be reflected in the flora and fauna of the recovering stream, as well as in the quantity and quality of materials in transport (i.e., export). The concepts of resistance and resilience, while difficult to quantify, provide a useful framework for discussing the mechanisms involved in ecosystem stability.

The annual energy subsidy of allochthonous inputs is especially important to ecosystem function in headwater streams of forested watersheds. Its removal was directly related to the observed decline in storage of benthic particulate organic matter, a parameter associated with the resistance component of stability. The decrease in BPOM and the elevated levels of POM in transport point toward decreased efficiency of utilizing this energy resource. The change in energy base of the stream ecosystem suggests low resistance.

Resistance of a headwater stream in a forested watershed to disturbances associated with logging is low because of the near total dependence of the stream ecosystem on allochthonous inputs. Higher order streams have a greater diversity of energy sources (Vannote et al., 1980); hence, removal of streamside vegetation would have less impact in such a stream. In addition, sediment additions to Big Hurricane Branch had a greater effect (e.g., on macroinvertebrates) than might occur in a larger stream. The headwater study stream had low power and therefore, low ability to move large grain sediments. In fact, the greatest impact of sediment on the invertebrate fauna appeared to be in the slower current reaches of sandy substrate. In a larger stream, with greater power, a much greater fraction of the sediment would have been immediately washed away from the area of disturbance.

On the other hand, low stream power may also be viewed as a mechanism contributing to resistance. Debris dams trap and stabilize sediment (Bilby and Likens, 1980). Organic inputs from logging slash were also trapped in debris dams where they could be utilized rather than washed out of the system. Another factor which contributed to resistance in Big Hurricane Branch was the presence of moss-covered bedrock outcrops. These areas of stable substrate apparently provided refuges for many stream organisms. They served as traps for POM as well as substrates for growth of periphytic algae.

Resistance of the stream may not differ greatly from that of the surrounding forest. The energy base was changed in both ecosystems. While the stream shifted from allochthonous to a more autochthonous energy base, the terrestrial system energy base went from trees to primarily herbaceous plants (Boring et al., 1981). Further, consumers in both ecosystems underwent changes in response to the changed energy base and physical conditions (Seastedt and Crossley, 1981; Schowalter et al., 1981).

Resilience of the stream ecosystem cannot be adequately evaluated within the time frame of the present study. Return to pre-disturbance conditions requires recovery of the terrestrial ecosystem, i.e., canopy regrowth and renewal of allochthonous inputs. However, certain of the observed changes in Big Hurricane Branch can be attributed to the resilience component of stability.

While algal densities are typically low in undisturbed Coweeta streams, a rapid increase in algal growth in Big Hurricane Branch followed removal of the canopy. This increase in autochthonous production compensated in part for the reduction of allochthonous inputs. With this energy base shift, there was a corresponding shift in the invertebrate fauna. Reduced

abundance of the dominant shredder, Peltoperla, was offset by numerical increases in taxa probably functioning as scrapers and more dependent on an autochthonous energy base. Invertebrates categorized as collector-gatherers increased in abundance, utilizing the FPOM resource or perhaps algae. There were also indications that some taxa which typically feed as shredders switched to a collector-gatherer feeding mode. The ability of the stream consumers as a group to quickly shift in response to a modified energy base clearly contributed to the resilience of the stream ecosystem.

It is clear from our study that the ability of the stream to recover from this particular disturbance was not entirely a function of the resilience mechanisms of the stream itself. Because of the dependence of the stream ecosystem on allochthonous inputs, complete recovery cannot occur until the quantity and quality of inputs have returned to predisturbance levels (Gurtz et al., 1980; Haefner and Wallace, 1981). We do not feel, however, that the resilience of the stream is exactly equal to that of the surrounding forest. Rather, the stream ecosystem has a much higher potential resilience that is not realized because of the continuing effects of the disturbance (Webster and Patten, 1979). Our study further reinforces the observation that the dynamics of a stream are very closely tied to characteristics of its watershed (e.g., Hynes, 1975), illustrating in another way the nature of some of these linkages.

In this study we attempted to evaluate some of the factors affecting the stability of a stream ecosystem in response to logging, both resistance to disturbance and resilience following disturbance. We emphasized functional characteristics of the ecosystem rather than the more traditional use of community structure as an indicator of stability. Logging caused a multifarious disturbance to Big Hurricane Branch, including physical alteration of habitat, changes in chemical and thermal characteristics of the water, and changes in food resources. While Big Hurricane Branch or another stream might respond in quite different ways to other types or combinations of disturbances, many of the factors investigated in this study would operate in a similar manner to ameliorate disturbance. Stauffer et al. (1978) attempted to evaluate the resistance and resilience (inertia and elasticity in their terminology) of a series of streams affected by coal mining using a largely subjective rating system (Cairns and Dickson, 1979) and data on fish community structure. It would be extremely useful to make a similar but objective evaluation of the functional characteristics considered in this study for different types of streams in a wide geographical area. From such a classification it would be possible to initiate a meaningful management program. As suggested by Stauffer et al. (1978), certain streams, perhaps

those with high resistance but low resilience, would be given maximum protection. Other streams, those with higher resilience, could sustain short term disturbance, while others could be used for long term disturbance. Such a classification and an understanding of the differences in functional response induced by disturbance should be an important long term objective of lotic ecology.

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