

**Legacies of Early 20th Century Logging in Southern Appalachian
Streams**

by

Paul F. Wagner

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Committee:

E. F. Benfield, Chair

J. R. Webster

C. A. Dolloff

R.H. Jones

R. H. Wynne

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(ABSTRACT)

I examined streams in the Joyce Kilmer-Slickrock wilderness to determine if streams responded to logging following 75 y of recovery. Joyce Kilmer was never logged and the Slickrock wilderness was logged from 1917 until 1922. Wood was common in unlogged streams and averaged 417 m³ of wood/ha of streambed. Logged streams had significantly less wood (1.1 m³ of wood/ha of stream), probably because of the construction of railroads in streambeds used to remove timber. Fine substrates (<5.6 mm diameter) were less abundant in logged streams and the retention of fines decreased as wood volume decreased. Species diversity was similar between streams in unlogged and logged catchments; however, the abundance of several taxa and functional feeding groups did differ. Streams in unlogged catchments had significantly greater proportions of shredders while streams in logged catchments had significantly greater proportions of scrapers. Ecosystem parameters showed that the linkages between streams and the forests they drain were weaker in logged

than unlogged streams and that unlogged streams derived a greater proportion of fixed carbon from riparian vegetation. Stream-forest linkage strength increased as debris dam abundance increased, while the use of riparian vegetation inputs increased as moss increased. Contrary to predictions, solute storage was significantly greatest in logged catchments and negatively related to debris dam abundance that decreased streambed permeability. Additionally, phosphorus retention, instead of being enhanced by solute storage, was negatively related to transient storage. Uptake velocity was significantly greater in unlogged than logged streams and significantly related to debris dam abundance. Mean breakdown rate of experimental leaf packs and wood veneers was not significantly different between unlogged and logged streams. Leaf breakdown was strongly related to shredder colonization, while wood breakdown was unrelated to variables measured. Much of the persisting disturbance to streams by past logging was directly or indirectly related to differences in wood volume, debris dam frequency, and streambed substrate composition. Results support the hypothesis that logging results in a downstream shift from the headwaters in ecosystem function and that logging disturbance to streams likely persists for centuries.

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General Introduction

Most southern Appalachian forests are second or third growth reflecting the extensive regional deforestation that occurred following European settlement and catchments without logging history are very uncommon (Davis 1996). Landscape scale disturbances such as logging can alter stream ecosystem structure and function, and logging disturbance in streams is well documented (see review by Campbell and Doeg 1989). Most studies of logging disturbance in streams have focused on short-term recovery (months to years) to as long as 45 years (Silsbee and Larson 1983). Consequently, it is not clear if disturbance from logging persists for longer periods and by what.

Effects of logging on streams

Wood and debris dams

Southern Appalachian streams typically drain densely forested catchments and are heavily shaded. Wood is typically abundant in undisturbed low-order southern Appalachian streams, but streams in logged catchments often contain much less wood (Silsbee and Larson 1983, Fleebe and Dolloff 1995) and removal of mature trees eliminates the primary input source of large wood capable of forming debris dams

(Likens and Bilby 1982). Consequently, logging can decrease wood input rates for centuries and can be a long-term disturbance.

Wood is important in stream geomorphology and ecosystem function (Bormann and Likens 1974, Sedell et al. 1978, Bilby and Likens 1980, Cummins et al. 1983, Silsbee and Larson 1983, Speaker et al. 1984, Harmon et al 1986, Fleebe and Dolloff 1995, Wallace et al. 1995, Wallace et al. 1997) and wood also influences nutrient dynamics (Munn and Meyer 1990, Wallace et al. 1995). Logging often reduces the amount of wood in streams (Silsbee and Larson 1983, Bilby and Ward 1991, Fleebe and Dolloff 1995) and eliminates the primary input source of logs and large pieces of wood capable of forming debris dams (Likens and Bilby 1982). Several studies have shown wood can be important in sediment retention (Bilby 1981, Smith et al. 1993, Wallace et al 1995) and removal of wood can cause increased bed load transport (Smith et al. 1993) or scouring of stored sediment (Beschta 1979). Addition of wood decreases average water velocity (Trotter 1990) and increases depositional areas in streams (Wallace et al 1995).

Removal of trees eliminates the source of log input into streams and immature forests contribute far fewer and much smaller logs to streams (Hedin et al. 1998). Large pieces of wood are particularly important in mountain streams because they strongly shape the

characteristics of aquatic habitats (Swanson and Lienkaemper 1978). Comparisons between logged and unlogged catchments show that differences can persist in excess of 45 years (Silsbee and Larson 1983). Researchers speculate that log inputs may be reduced for up to 400 years (Golladay et al. 1987).

Water and sediment

Forest vegetation is important in regulating the amount of water that drains into streams. Evapotranspiration accounts for 40-60% of annual water loss in forests (Kovner, 1956). Removal of forest vegetation decreases evapotranspiration and increases runoff and stream flow (Bosch and Hewlett 1982; Swank et al. 1988). Overland flow is normally uncommon in Southeastern deciduous forests but can result from the destruction of protective vegetation associated with many forms of timber removal (Hornbeck 1973). Surface runoff in such forests is often highly erosive and carries considerable amounts of surface sediment. Sediment input associated with runoff is often a greater disturbance to stream ecosystems than the increased stream flow. High overland flow and associated sediment input diminish as vegetation recovers, but may take 20-30 years to return to pre-disturbance levels (Swift and Swank 1981).

Numerous studies have examined the impact of sedimentation on benthic insects (e.g., Tebo 1955; Newbold 1977; Newbold et al. 1980; Lemly 1982; Culp and Davies 1983; Silsbee and Larson 1983). Sediment may reduce density or diversity in aquatic insect assemblages in several ways. Less habitat heterogeneity from sedimentation reduces diversity and production of benthic organisms (Grenney and Porcella 1976). Localized elimination of filter-feeding taxa and taxa not adapted to habitats with high levels of fine particulate materials have been documented in streams that have high sediments (Lemly 1982, Mayack and Waterhouse 1983). Increased invertebrate drift in logged areas is thought to cause lower density in localized areas of streams (Tebo 1955). Aquatic insects not normally resident in the hyporheos may use the hyporheos as a refugium during disturbance (Bishop 1973). Absence of hyporheic refugia due to sedimentation could exacerbate the effects of episodic disturbances on aquatic insects, especially disturbances such as flooding. The extent of faunal disturbance depends on whether fine sediments penetrate the streambed, how long the sediment remains, and whether organisms are dependent on interstitial spaces during all or part of their life history (Halse and Blyth 1992).

Increased overland flow and associated sediment due to logging diminishes as vegetation recovers, but may take 20-30 years to return to

pre-disturbance levels (Swift and Swank 1981). The effects of sediment input often persist for much longer due to the redistribution of sediments deposited shortly after logging (Golladay et al. 1987, Brown and Krygier 1971).

Nutrients

Forests absorb and use soil nutrients allowing forest ecosystems to trap nutrients (Likens et al. 1977). Logging removes vegetation and causes forests to “leak” nutrients because nutrients are no longer absorbed by vegetation (Campbell 1978). Decomposition of debris left after logging can further elevate nutrient levels (Webster et al. 1992). These nutrients are leached from soils via subsurface water flows and ultimately elevate stream nutrient levels. Additional elevation of stream nutrient concentrations occurs when inorganic materials that have absorbed terrestrial nutrients are washed into streams (Fredricksen 1971). Logging also causes increased stream nutrient levels by disturbing stream biota responsible for normal nutrient processing (Campbell and Doeg 1989). Growth of recovering forest vegetation can reduce nutrient concentrations to pre-logging levels. In fact, stream nutrient levels may be lower in recovering forests than in mature forests because of greater nutrient absorption rates by recovering vegetation (Johnson and Swank

1973; Vitousek and Reiners 1975). Nutrient levels may be altered in excess of 45 years following logging (Silsbee and Larson 1983).

Changes in stream nutrient concentration can cause changes in the diversity and productivity in stream organisms. One study attributes the presence and absence of particular species in benthic assemblages to variations in nutrient concentrations (Minshall and Minshall 1978).

Nutrient manipulations can change both primary and secondary productivity in streams (Hall et al. 1970). Habitat complexity and substrate characteristics can be altered due to high nutrient levels (e.g. macrophyte, algal blooms etc.) that cause subsequent changes in insect diversity or productivity (Benke 1984). Nutrient increases can also increase leaf decomposition rates (Elwood et al. 1983). Functional feeding groups that are dependent on leaves may decrease in density because higher leaf decomposition rates reduce the amount of leaf material available late in the growing season (Cummins et al. 1989).

Organic material

Logging changes both the quality and quantity of organic material entering streams. Organic material inputs generally increase immediately following logging (Beschta 1979) resulting primarily from twigs, branches, leaves, and needles that are left behind following logging (Webster and

Waide 1982). Much of this debris is washed into streams by elevated surface flows. Additional changes in organic input occur as forest vegetation recovers. Allochthonous input to streams are greatly reduced in recovering forests (Webster et al. 1988) and differences in nutritional value and palatability may occur in leaf material entering streams due to changes in species composition of vegetation following logging. Removal of trees and other streamside vegetation reduces shading and changes seasonal stream temperatures. Generally, shading reduces summer temperatures, while winter temperatures are often higher (Campbell and Doeg 1989).

Headwater streams in undisturbed forests typically have well-developed riparian vegetation with dense overhanging canopies and are heavily shaded, resulting in little autochthonous production (Vannote et al. 1980, Minshall 1983). Energy in forested streams comes primarily from terrestrially fixed carbon and enters largely as autumnally shed leaves and wood that enters year-round. Thus, forested headwater streams are tightly linked to the forests they drain by the processing of allochthonous inputs (Fisher and Likens 1972) and depend particularly on the processing of leaves, and to a lesser extent, wood.

In summary, stream response to logging can include elevated nutrient concentration (Likens et al. 1970, Silsbee and Larson 1983,

Campbell and Doeg 1989), increased sedimentation (Tebo 1955, Crickmay 1974, Lemly 1982), decreased organic matter retention, changes in relative abundances of macroinvertebrate functional feeding groups (Haefner and Wallace 1981, Hawkins et al 1982, Silsbee and Larson 1983, Chapter II) and higher water temperatures (Webster and Waide 1982, Culp and Davies 1983). Changes in the aforementioned can alter organic matter processing rates (Sedell et al. 1975, Short et al. 1980, Webster and Waide 1982, Benfield and Webster 1985, Webster and Benfield 1986, Golladay and Webster 1988, Campbell and Doeg 1989, Griffith and Perry 1991, D'Angelo and Webster 1992, Tank and Webster 1998) and ecosystem function.

Research

I was interested in exploring whether logging disturbance persists in catchments following 75 y of recovery. I examined wood standing stocks, total suspended sediment (collected at base flow), and streambed substrate composition to determine if there were physical differences between unlogged and logged streams (chapter I). These data were also used with data from subsequent chapters (chapter II-IV) to examine how logging disturbs ecosystem structure and function. In chapter II, I examined macroinvertebrate assemblages and used these data to

examine ecosystem parameters including production to respiration ratios, linkage strength between streams and riparian vegetation, streambed stability, and top-down control. Chapter III was a team project that involved Virginia Tech Stream Team members Dr. H. M. Valett and Chelsea Crenshaw. We examined nutrient uptake and transient storage to determine if logging affected nutrient spiraling and, if so, why. Finally, I examined wood and leaf breakdown (Chapter IV) to determine if organic matter breakdown rates respond to logging disturbance after 75 y of recovery.

Study Site

This study was conducted in the Joyce Kilmer-Slickrock wilderness (Figure 1), which lies southwest of the Great Smoky Mountains National Park in the Nantahala National Forest. The Joyce Kilmer-Slickrock wilderness consists of two adjacent wilderness areas. Joyce Kilmer is one of the few remaining southern Appalachian forests that was never logged. The Slickrock wilderness was logged once and then allowed to recover. Slickrock wilderness borders the northwest boundary of Joyce Kilmer with portions of the forest residing in Graham Co., North Carolina and Monroe Co., Tennessee. Joyce Kilmer Memorial Forest is approximately 1540 ha and the Slickrock wilderness is approximately 4500 ha. Elevation ranges

are from 670 m to 1585 m in Joyce Kilmer and from 330 m to 1585 m in Slickrock. Annual precipitation is normally > 200 cm per year (Daniels 1985). Joyce Kilmer is underlain primarily by arkosic metasandstone, muscovite phyllite and mica schist. Geology in Slickrock is similar and underlain by arkosic metasandstone, graphitic metagreywacke, and slate.

Vegetation types in the Joyce Kilmer-Slickrock wilderness include mixed mesophytic cove hardwood associations in moist lowlands and north facing slopes, mixed oak-hickory (Quercus spp.-Carya spp.) stands on steep side slopes, oak-pine (Quercus spp.-Pinus spp.) stands on southern slopes, and rhododendron-laurel-azalea slicks on exposed ridges (Daniels et al. 1987). Eastern hemlock (Tsuga canadensis) is common throughout the Joyce Kilmer-Slickrock wilderness and is particularly abundant along streamsides, often with thick Rhododendron maximum understory. South facing slopes generally have thinner understory than north facing slopes.

Joyce Kilmer and Slickrock are similar geologically but differ in land use history. Joyce Kilmer was never logged and Slickrock was logged from 1917 until 1922. The area now designated as the Joyce Kilmer wilderness was examined for potential timber production at least as early as 1910 (Anon. 1910). The Joyce Kilmer wilderness was never logged due to several changes in ownership that repeatedly delayed logging and a

flood around 1930 resulting from construction of Calderwood Lake Dam, which destroyed the only railroad access to the area.

The Babcock Land and Timber Company purchased the Slickrock portion of the Joyce Kilmer-Slickrock wilderness in the 1915. Babcock Land and Timber began logging in 1917 and logging ended in 1922 with the construction of Calderwood Dam. The area that presently composes the Joyce Kilmer-Slickrock wilderness was purchased by the U.S. Forest Service in 1936 and designated wilderness in 1975.

Study streams in the Joyce Kilmer-Slickrock wilderness (Chapter I- Figure 1) were selected based on land use history (streams in unlogged Joyce Kilmer catchments versus logged Slickrock catchments), similarity in size range between treatments, and similarity in slope. Five replicate unlogged catchments in Joyce Kilmer (U1-U5) and five replicate catchments logged ca. 75 y ago (L1-L5) were studied for comparison. Catchment area is the total area within each watershed upstream of each sampling site and slope was estimated from USGS topographical maps. Streams in unlogged forests drained catchments ranging from 47 to 151 ha and stream gradients ranged from 8.8 to 21.8%. Logged catchments ranged from 35 to 227 ha and stream slopes ranging from 9.1 to 23.6 %, respectively.

Although forest composition is similar between Joyce Kilmer and Slickrock, there are clear indications of past land-use in streams. Railroads were often constructed in streambeds because stream channels made the best roadbeds (Dolloff 1993) and logs were carried out of the forests on rail carts. Such railroads were constructed in many Slickrock streams (Homan 1990). In other instances, logs were simply pulled by Oxen or other animals downstream with out assistance of railroads. Although Babcock Land and Timber Company removed most of the rails, many streams still contain sections of track, pieces of cable, and other debris that was used in logging and later abandoned. Long sections of rail remain in stream L5 and long lengths of cable remain along the banks of L4. Old railroad grades are evident through other parts of the Slickrock wilderness and pieces of metal refuse are not uncommon.

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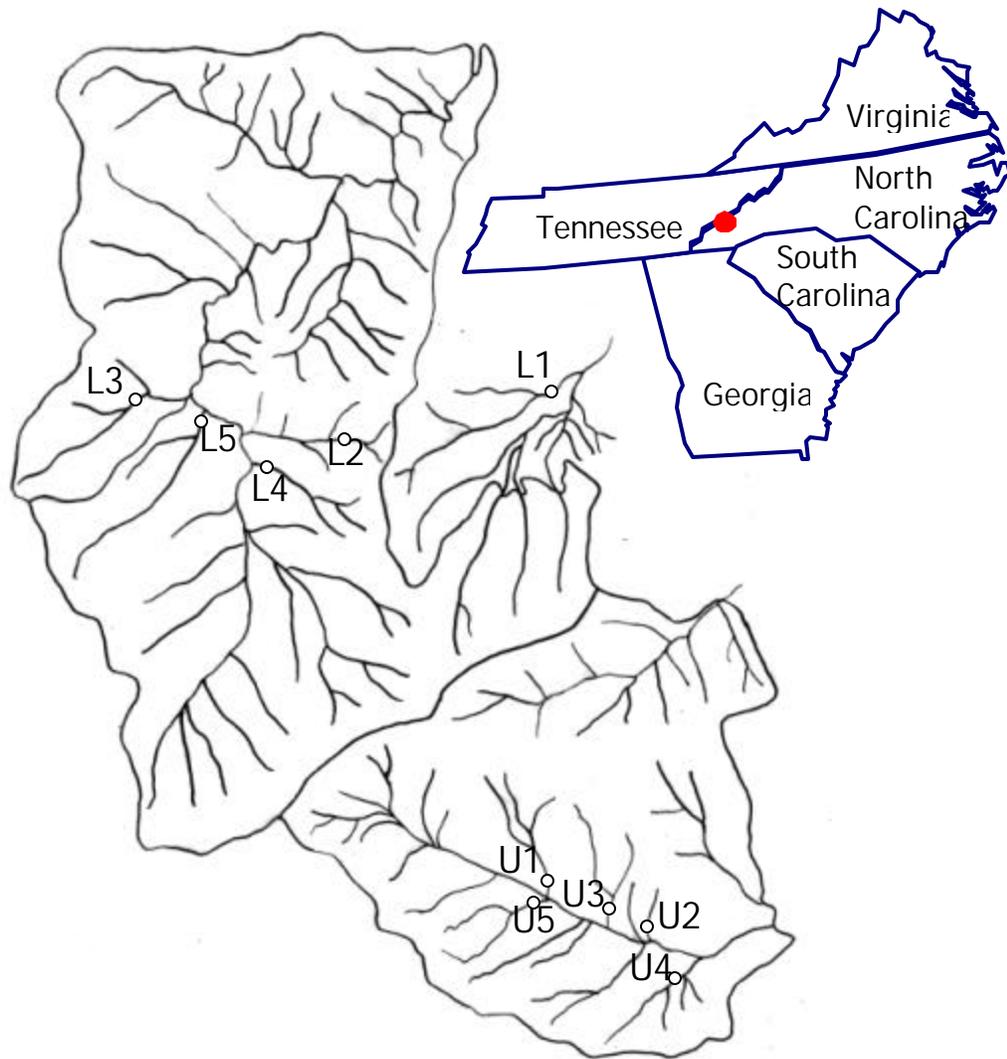
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Table 1. Catchment area and slope for streams studied in the Joyce Kilmer-Slickrock wilderness.

| | Unlogged | | Logged | | |
|----|------------------------|--------------|------------------------|--------------|-------|
| | Catchment Area (ha) | Slope (%) | Catchment Area (ha) | Slope (%) | |
| U1 | 146.7 | 12.8 | L1 | 126.3 | 11.6 |
| U2 | 41.1 | 12.5 | L2 | 35.0 | 23.64 |
| U3 | 151.8 | 11.1 | L3 | 158.0 | 9.1 |
| U4 | 89.0 | 21.9 | L4 | 114.0 | 18.2 |
| U5 | 100.1 | 8.8 | L5 | 227.2 | 10.85 |

Figure 1. Map of Southeastern United States showing location of the Joyce Kilmer-Slickrock Wilderness (JKSRW). Detailed map shows study sections of unlogged (U1-U5) and logged (L1-L5) streams.



Chapter I

The long-term effects of early 20th century logging on wood and benthic habitat in southern Appalachian streams.

Abstract

I compared wood volume (m^3/ha streambed) and substrate size (relative abundance in 7 size classes) in unlogged and second growth forested streams to determine if logging disturbance persisted after 75 y of recovery. Unlogged streams had an average of 417 m^3 of wood/ha of streambed and were significantly different from logged streams that had an average of 1.1 m^3 of wood/ha of streambed. Sand, fine gravel, medium gravel, small cobble, coarse gravel, and large cobble were significantly different between unlogged and logged streams. Retention of fine substrate ($<5.6 \text{ mm}$ diameter) was related to wood volume while the relative abundance of large cobble was related to catchment size in logged streams. My data suggest recovery time from late 19th and early 20th century logging in southern Appalachian streams is on the order of centuries rather than decades.

Introduction

Undisturbed low-order southern Appalachian streams often contain large amounts of wood, particularly large pieces of wood (LW) (Silsbee and Larson 1983, Fleebe and Dolloff 1995). Numerous studies have shown the importance of wood in structuring low order forested stream ecosystems (Sedell et al. 1978, Bilby and Likens 1980, Cummins et al. 1983, Harmon et al 1986). LW retains particulate organic matter (Bilby and Likens 1980), provides habitat for stream organisms (Angermeier 1984), and influences nutrient dynamics (Munn and Meyer 1990, Wallace et al 1995). Logging often reduces the amount of LW in streams (Silsbee and Larson 1983, Bilbee and Ward 1991, Fleebe and Dolloff 1995) and eliminates the primary input source of LW capable of forming debris dams (Likens and Bilby 1982). Most southern Appalachian forests are second or third growth and streams in them are affected by logging history.

Several studies have shown wood can be important in sediment retention (Bilby 1981, Smith et al. 1993, Wallace et al 1995). Removal of wood can cause increased bed load transport (Smith et al. 1993) or scouring of stored sediment (Beschta 1979). Addition of wood decreases average water velocity (Trotter 1990) and increases depositional areas in streams (Wallace et al 1995). Many studies have described changes for sediment stored behind debris dams but not the changes in reach-long

substrate characteristics. Additionally, most of the experimental studies examined short-term changes (months to several years). Consequently, little is known about the long-term effects of logging on wood abundance and substrate composition.

Erosion often occurs following logging and primarily results from the construction of logging roads, skidding of logs across land, and the loss of protective riparian vegetation. Water quality and ecosystem integrity are often affected by increased sedimentation and particles <6 mm (henceforth referred to as fines) which are considered most detrimental to fish (Stock 1996). Impacted streams are often compared to reference streams to assess the type or severity of disturbance. Reference streams are generally in catchments with little or no current disturbance, but probably continue to respond to past disturbance (Webster et al 1992, Harding et al 1998).

Most southern Appalachian forests were commercially logged between the 1880s and 1920s. Patches of unlogged forest are still present in the southern Appalachians but entire catchments of unlogged forests are rare. Assessment of streams draining 75 y-old forests are of particular interest because they are often used as reference streams in comparative studies of more recent disturbance.

I examined streams in logged and unlogged forests to assess the persistence of logging disturbance following 75 y of recovery. This research addressed three questions: 1) Is wood volume significantly different in unlogged versus 75 y-old forested streams; 2) is size distribution of inorganic substrates in unlogged forested streams significantly different than 75 y-old second growth forested streams; and (3) are differences in substrate size distributions related to wood volume?

Study Site

This study was conducted in the Joyce Kilmer-Slickrock wilderness (Figure 1), which lies southwest of the Great Smoky Mountains National Park in the Nantahala National Forest. The Joyce Kilmer-Slickrock wilderness consists of two adjacent wilderness areas. Joyce Kilmer is in Graham Co. North Carolina and is one of the few remaining southern Appalachian forests that was never logged. The Slickrock wilderness was logged once and then allowed to recover. Slickrock wilderness borders the northwest boundary of Joyce Kilmer with portions of the forest residing in Graham Co., North Carolina and Monroe Co., Tennessee. Joyce Kilmer Memorial Forest is approximately 1540 ha and the Slickrock wilderness is approximately 4500 ha. Elevation ranges are from 670 m to 1585 m in Joyce Kilmer and from 330 m to 1585 m in Slickrock. Annual

precipitation is normally > 200 cm per year (Daniels 1985). Joyce Kilmer is underlain primarily by arkosic metasandstone, muscovite phyllite and mica schist. Geology in Slickrock is similar and underlain by arkosic metasandstone, graphitic metagreywacke, and slate.

Vegetation types in the Joyce Kilmer-Slickrock wilderness include mixed mesophytic cove hardwood associations in moist lowlands and north facing slopes, mixed oak-hickory (Quercus spp.-Carya spp.) stands on steep side slopes, oak-pine (Quercus spp.-Pinus spp.) stands on southern slopes, and rhododendron-laurel-azalea slicks on exposed ridges (Daniels et al. 1987). Eastern hemlock (Tsuga canadensis) is common throughout the Joyce Kilmer-Slickrock wilderness and is particularly abundant along streamsides, often with thick Rhododendron maximum understory. South facing slopes generally have thinner understory than north facing slopes.

Joyce Kilmer and Slickrock are similar geologically but differ in land use history. Joyce Kilmer was never logged and Slickrock was logged from 1917 until 1922. The area now designated as the Joyce Kilmer wilderness was examined for potential timber production at least as early as 1910 (Anon. 1910). The Joyce Kilmer wilderness was never logged due to several changes in ownership that repeatedly delayed logging and a flood around 1930 resulting from construction of Calderwood Lake Dam,

which destroyed the only railroad access to the area. (personal communication, Cheoa Ranger Station, Graham Co., North Carolina).

The Babcock Land and Timber Company purchased the Slickrock portion of the Joyce Kilmer-Slickrock wilderness in the 1915. Babcock Land and Timber began logging in 1917 and logging ended in 1922 with the construction of Calderwood Dam. The area that presently composes the Joyce Kilmer-Slickrock wilderness was purchased by the U.S. Forest Service in 1936 and designated wilderness in 1975 (personal communication, Cheoa Ranger Station, Graham Co., North Carolina).

Study streams in the Joyce Kilmer-Slickrock wilderness (Figure 1) were selected based on land use history (streams in unlogged Joyce Kilmer catchments versus logged Slickrock catchments), similarity in size range between treatments, and similarity in slope. Five replicate unlogged catchments in Joyce Kilmer (U1-U5) and five replicate catchments logged ca. 75 y ago (L1-L5) were studied for comparison. Catchment area is the total area within each watershed upstream of each sampling site and slope was estimated from USGS topographical maps. Streams in unlogged forests drained catchments ranging from 47 to 151 ha and stream gradients ranged from 8.8 to 21.8%. Logged catchments ranged from 35 to 227 ha and stream slopes ranging from 9.1 to 23.6 %, respectively.

Although forest composition is similar between Joyce Kilmer and Slickrock, evidence of past land-use in streams is present. Railroads were often constructed in streambeds because stream channels made the best roadbeds (Dolloff 1993) and logs were carried out of the forests on rail carts. Such railroads were constructed in many Slickrock streams (Homan 1990). In other instances, logs were simply pulled by Oxen or other animals downstream with out assistance of railroads. Although Babcock Land and Timber Company removed most of the rails, many streams still contain sections of track, pieces of cable, and other debris that was used in logging and later abandoned. Long sections of rail remain in stream L5 and long lengths of cable remain along the banks of L4. Old railroad grades are evident through other parts of the Slickrock wilderness and pieces of metal refuse are not uncommon.

Materials and Methods

I measured wood along a 100 m midstream transect in five streams from each forest type (unlogged and logged 75 y ago) (Table 2). Wood <100 mm in diameter was measured using verneer calipers and wood >100 mm dia. was measured with a meter tape. Wood volume per square meter of streambed was calculated using the line intersect method

(De Vries 1974; Wallace and Benke 1984) and expressed as m³ of wood per hectare of streambed.

Total suspended solids (TSS) were collected by three 1 L grab samples of water from each stream on six occasions at base flow. Water was filtered in the field on ashed and weighed Gelman 25 mm A/E glass fiber filters (1 μ m nominal pore size) using a hand-operated vacuum pump. Filters were returned to the lab, dried (40°C, 48 hr), weighed, ashed (550°C, 1 hr), wetted, re-dried (40°C, 24 hr) and reweighed.

A minimum of 100 substrate particles were measured along a bank full to bank full (zigzag) transect except where debris dams prevented measurement. The zigzag transect allowed for a variety of habitats (riffles, pools, bends) to be covered which gave us an integrated measure of differences in substrate composition between logged and unlogged streams (Bevenger and King 1995). I used a gravelometer to group particles based on intermediate axis length (Yuzyk 1986). Substrate particles were defined as follows: sand (> 2mm), fine gravel (2 – 5.6 mm), medium gravel (5.6 – 16 mm), coarse gravel (16 – 32 mm), small cobble (32 – 90 mm), medium cobble (90 – 180 mm), and large cobble (>180 mm).

Results

Wood

Wood volume was significantly different between unlogged and logged streams (t-test, $p < 0.05$) and ranged from 140 to 927 m³/ha and 0.4 to 3.2 m³/ha, respectively (Figure. 2). Most wood in unlogged streams was LW (> 10 cm) and located in debris dams, while much of the wood found in second growth streams was not LW and some streams had no wood >10 cm. Wood in unlogged streams ranged from small twigs (< 5 mm) to large logs 1 m+ in diameter. Large logs (up to 1.5 m in diameter) spanned some streams but fell high on the hill slopes due to their length and were above the stream.

Substrate and TSS

Sand, fine gravel, small cobble, coarse gravel, and large cobble (Figure 3) were significantly different between U and L streams (chi square contingency test with Bonferroni correction, $p < 0.05$) (Table 3). Cluster analysis (SYSSTAT 8.0, SPSS inc.) (Figure 4) showed two main groups, the first (U2, U3, U4, U5) had relatively high proportions of sand and gravel and the second (L1, L2, L3, L4, L5, U1) was characterized by cobble. The first division in the cobble group separated streams into cobble-sand and cobble gravel streams. The cobble-sand group was the only instance where U and L streams were joined on a common branch.

No significant difference was found for TSS in U and L streams at base flow (paired t-test) (Table 2). Mean values in U and L were 1.8 and 2.3 mg/L respectively.

Wood and substrate composition

A scatter plot of wood versus fines separated sites into two groups (Figure 5); L streams had small amounts of wood and fines and U streams had much more wood and fines. I examined logged and unlogged streams separately to look for relationships between wood volume and substrate composition. A significant relationship between wood and substrate \leq fines was found in unlogged streams (linear regression of \log_{10} transformed data, $r^2 = 0.85$, $p < 0.05$) (Figure 6). No significant relationship was found between wood and fines in logged streams probably because there is not enough wood to create debris dams that retain particles.

Physical gradients, including stream size, are important in structuring lotic ecosystems (Vannote et al 1980). I examined the relationship between catchment area (an estimate of stream size) and each substrate class to determine if any relationships existed. Only large cobble was related to catchment area in both unlogged and logged streams. Large cobble was significantly more abundant in larger

catchments (Figure 7) in logged (linear regression of \log_{10} transformed data, $r^2 = 0.77$, $p < 0.05$) and unlogged streams (linear regression of \log_{10} transformed data, $r^2 = 0.95$, $p < 0.05$) and was almost twice as abundant in logged than unlogged streams.

Discussion

Old growth forests contribute fallen boles, broken branches, or whole trees to streams whereas early successional forests primarily contribute twigs and small branches (Harmon et al 1986). Not surprisingly, previous studies have shown significant differences in wood between streams draining uncut and logged forests (Silsbee and Larson 1983, Bilby and Ward 1991, Fleebe and Dolloff 1995). Silsbee and Larson (1983) studied unlogged and 45 y-old second growth forested streams in the Great Smoky Mountains National Park. Comparison of their data with ours shows some consistent effects of logging on streams, although the magnitude of difference is variable. Mean wood volume in unlogged Joyce Kilmer-Slickrock wilderness streams was comparable to unlogged GSMNP streams (mean = 417 versus 338 m^3 per hectare, respectively). Differences in mean wood volume among second growth streams (logged Joyce Kilmer-Slickrock wilderness versus logged GSMNP) was much

greater. Logged GSMNP streams had 77 times more wood than logged Joyce Kilmer-Slickrock wilderness streams. Reasons for the disparity are unclear. Stochastic factors such as storm damage or disease outbreak could have caused higher tree mortality in GSMNP. Wood could have been introduced during or following logging in GSMNP or some mature streamside trees could have been left uncut and later fell into streams. Another possible explanation is the manner in which the Slickrock wilderness was logged. Railroads were often constructed in headwater streambeds to aid in timber removal (Dolloff 1993) and would have required the removal of all or most LW. Silsbee and Larson do not mention whether such railroads were used in GSMNP streams they studied. Portions of old railroad tract are still present in some logged Slickrock wilderness streams so it is likely that most wood was removed from streams during logging. Thus, differences in LW could be due to differences in logging practices. Finally, logged Slickrock wilderness catchments are approximately 30 y older than were second growth GSMNP forests when studied and wood in logged Slickrock wilderness catchments might be more decayed and weakened enough that it broke apart and was transported downstream.

Only 30-100 mm dia. streambed substrate was significantly different in logged and unlogged GSMNP streams (18.3 vs. 10.2%

respectively), whereas I found differences in all size classes except medium gravel and medium cobble in unlogged and logged Joyce Kilmer-Slickrock wilderness streams. Differences in 30-100 mm substrates in GSMNP streams were attributed to material washed into streams following logging (Silsbee and Larson 1983). I also found a significant difference in small cobble (32-90 mm) but cannot be certain if the difference is due to material washed into logged streams or because smaller substrates were flushed from the stream and increased the relative abundance of small cobble. GSMNP streams had relatively low abundance of sand (1.5 and 0.6 % for unlogged and logged, respectively) compared to unlogged (26.4%) and logged (1.2%) streams. Unlogged and logged Joyce Kilmer-Slickrock wilderness stream gradients ranged from 8.8 to 21.9% and 9.1 to 23.6% respectively, while streams in GSMNP ranged from 8 to 20%. Consequently, I cannot attribute substrate difference to gradient differences. The difference in sand between GSMNP and Joyce Kilmer-Slickrock wilderness streams is unlikely due to geologic differences, but because all watersheds are underlain by metaconglomerate bedrock. A more likely explanation is the method of assessment. I collected substrates along a bank to bank transect (a downstream zigzag pattern). Silsbee and Larson (1983) collected substrates along a mid-stream transect where stream competence is greater, likely leaving fewer fines.

Unlogged Joyce Kilmer wilderness streams had an average of 22 times more sand than logged Slickrock wilderness streams (26.4 vs. 1.2% respectively), whereas unlogged and logged GSMNP streams differed by 2.1 fold. I attribute the relative difference in sand retention in logged Slickrock wilderness and logged GSMNP streams to the almost 2 orders of magnitude differences in wood. Logged GSMNP streams had an average of 84.5 m³ wood/ha, which might also be enough to retain small substrate, including sand. Consequently, I believe logged GSMNP streams probably had sufficient wood to retain sand, whereas logged Slickrock wilderness streams did not.

No pre-logging sedimentation data exist for Joyce Kilmer-Slickrock wilderness streams nor were sediment data collected immediately after logging, however it is well known that sedimentation increases dramatically during and for several years following logging (Hedin et al 1988, Webster et al 1992). Loggers in Slickrock located catchments that were being logged by the color of the water (W. Lee Daniels, Crop and Soil Environmental Sciences, Virginia Tech, personal communication.). Streams in catchments being logged had brown to black water, presumably due to erosion of the organic layers of soil. Consequently, it is highly likely that Slickrock wilderness streams suffered substantial sediment input during and after logging.

The positive relationship between catchment size and large cobble in both unlogged and logged Joyce Kilmer-Slickrock wilderness streams suggests that stream flow is important in structuring substrate composition, particularly large substrate. Because large cobble is the largest size class, it increases in abundance only if another size class decreases in abundance. Consequently, I interpret the positive relationship between catchment area and large cobble as a cumulative measure of the scouring of smaller substrate (i.e., any substrate <180 mm). Sediment concentration in transport generally increases with velocity (Leopold et al 1964) and velocity increases as debris dams decreases (Trotter 1990). Lack of fines in logged catchments probably results from scouring of the streambed and scouring increases as catchment size increased because discharge and storm runoff are positively related to catchment area (Dunne and Leopold 1978; Leopold 1994). Thus, storm flows and stream competence increase with catchment size and probably causes scouring of stored sediment (Wolman and Miller 1960, Leopold et al. 1964; Crickmay 1974, Mosley 1981). I believe that storm flow is more important than base flow in structuring large substrate abundance because: 1) Logged and unlogged TSS were similar suggesting no differential base flow export of very small substrate; and 2) seston export during storm flows from logged streams is

significantly greater than reference streams, while base flow export is not (Golladay et al. 1987). The relationship between wood and fines suggests wood increases stream resistance to scouring.

Changes in natural flow regimes can have important and long-lasting effects on aquatic ecosystems (Poff et al. 1997). Ecosystems may take years to centuries to recover from disturbance. Most ecosystems, including streams, have not been continually monitored since being disturbed. Consequently, studies of ecosystem recovery are generally based on measurements made at various points along a temporal gradient. Models of recovery are often based on two points: a reference point (an undisturbed or less disturbed system); and an experimental point (a site more recently disturbed). Models of similar disturbances can generate different predictions if the method or magnitude of the disturbances differs. Two models of small stream recovery from logging differ in predictions of wood accumulation and sediment dynamics (Hedin et al 1998, Webster et al. 1992). The Hubbard Brook Model (Hedin et al 1988) suggests that sediment export is reduced below pre-disturbance levels after 25 y when debris dams form that act as sediment sinks. The Coweeta model (Webster et al 1992) suggests sediment export is above pre-disturbance levels for 50-200 y because the streambed is the major source of transported sediment after logging and LW inputs are low until

mature trees begin to die and fall into streams. My data suggest that wood inputs are depressed for at least 75 y, 3 times longer than predicted by the Hubbard Brook model. Furthermore, sediment accumulation seemingly does not occur for at least an equal length of time. The Hubbard Brook model suggests sediment transport in logged catchments is no longer elevated after 25 Y although few data support that prediction. The ratio of sediment yield between logged and reference catchments in HB had decreased from a peak of 18:1 three y after logging to < 1:1 by year 14. However, after 15 y the ratio was approximately 4:1 and sediment transport in logged catchments was still elevated after 20 y of recovery. The Hubbard Brook model prediction that sediment export recovers after 25 y might be based on the trend of decreased sediment transport and the assumption that streambeds would stabilize after 25 y when debris dams were estimated to begin to recover. Predictions of debris dam recovery for the Hubbard Brook model were based on forest floor wood input rates (Bormann and Likens 1979). However, it is likely that the relatively small pieces of wood that 25 y-old forests contribute to streams will not form debris dams (Likens and Bilby 1982).

Evidence from logged Slickrock wilderness streams suggests no attempts were made to reduce stream disturbance during logging and is likely why these streams have such small amounts of wood. Stream

protection was not a priority in the southern Appalachians in the late 19th and early 20th centuries and many streams in logged forests probably suffered similar disturbance. Protective measures were used in Hubbard Brook streams and the Hubbard Brook model is more a measure of recovery from tree removal than the effects of historic logging. Consequently, the Coweeta model is probably more applicable than the Hubbard Brook model to forest streams recovering from late 19th and early 20th century logging.

Physical changes from logging and the River Continuum Concept

The river continuum concept (RCC) proposes that streams are structured along longitudinal gradients and reflect the mean state of the physical conditions (Vannote et al 1980). The model proposes that wood and leaf inputs are highest in small (1st-3rd) order streams and decrease in abundance and importance in higher order streams. Several studies have shown that LW decreases as stream order increases (Lienkamper and Swanson 1982, Robison and Beschta 1990). Additionally, fine sediment abundance has been shown to decrease as stream order increases from 2nd to 5th order in both logged and unlogged streams in similar physical settings (Bilby and Ward 1991). A potential effect of stream disturbance is to shift the position of streams structurally and/or functionally on the

river continuum. I found that logged catchments had less wood, which caused substrate composition of logged streams to be similar to larger streams in undisturbed catchments. Notably, substrate in the largest unlogged stream (U1) was most similar to the smallest logged stream (L2); the remaining streams were different enough that a common branch did not join any other logged and unlogged streams. Consequently, logged streams are similar to larger streams that are downstream on the continuum.

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Table 1. Catchment area and slope for streams studied in the Joyce Kilmer-Slickrock wilderness.

| | Unlogged | | Logged | | |
|----|------------------------|--------------|------------------------|--------------|-------|
| | Catchment Area (ha) | Slope (%) | Catchment Area (ha) | Slope (%) | |
| U1 | 146.7 | 12.8 | L1 | 126.3 | 11.6 |
| U2 | 41.1 | 12.5 | L2 | 35.0 | 23.64 |
| U3 | 151.8 | 11.1 | L3 | 158.0 | 9.1 |
| U4 | 89.0 | 21.9 | L4 | 114.0 | 18.2 |
| U5 | 100.1 | 8.8 | L5 | 227.2 | 10.85 |

Table 2. Mean values (\pm 1 SD) of wood volume (m^3 of wood per ha of streambed), % sand, and total suspended solids (mg/L). Joyce Kilmer-Slickrock wilderness data were collected for this study; GSMNP data are from Silsbee and Larson (1983).

| | Unlogged | | Logged | |
|---------------------------------------|-----------------|-------|---------------|-------|
| | JKSRW | GSMNP | JKSRW | GSMNP |
| Wood Volume (m^3 /ha streambed) | 417 (398) | 338.7 | 1.1 (1.2) | 84.5 |
| % Sand | 26.4 (12.1) | 1.5 | 1.2 (1.0) | 0.8 |
| TSS (mg/L) | 1.8 (1.1) | 1 | 2.3 (1.9) | 1.75 |

Table 3. Substrate counts from logged and unlogged Joyce Kilmer-Slickrock wilderness streams. *Bonferroni correction applied (individual probabilities were multiplied by 8, the number of tests conducted).

| | Logged | Unlogged | Chi square probability* |
|---------------------------|---------------|-----------------|--------------------------------|
| Abundance of fines | | | |
| < 5.6 mm | 43 | 221 | p < 0.008 |
| > 5.6 mm | 575 | 370 | |
| By diameter class | | | |
| Sand | 8 | 149 | p < 0.008 |
| Fine Gravel | 35 | 72 | p < 0.008 |
| Medium Gravel | 69 | 87 | NS |
| Coarse Gravel | 43 | 12 | p < 0.008 |
| Small Cobble | 115 | 66 | p < 0.05 |
| Medium Cobble | 106 | 74 | NS |
| Large Cobble | 242 | 131 | p < 0.008 |
| Total Observations | 618 | 591 | |

Figure 1. Map of Southeastern United States showing location of the Joyce Kilmer-Slickrock Wilderness (JKSRW). Detailed map shows study sections of unlogged (U1-U5) and logged (L1-L5) streams.

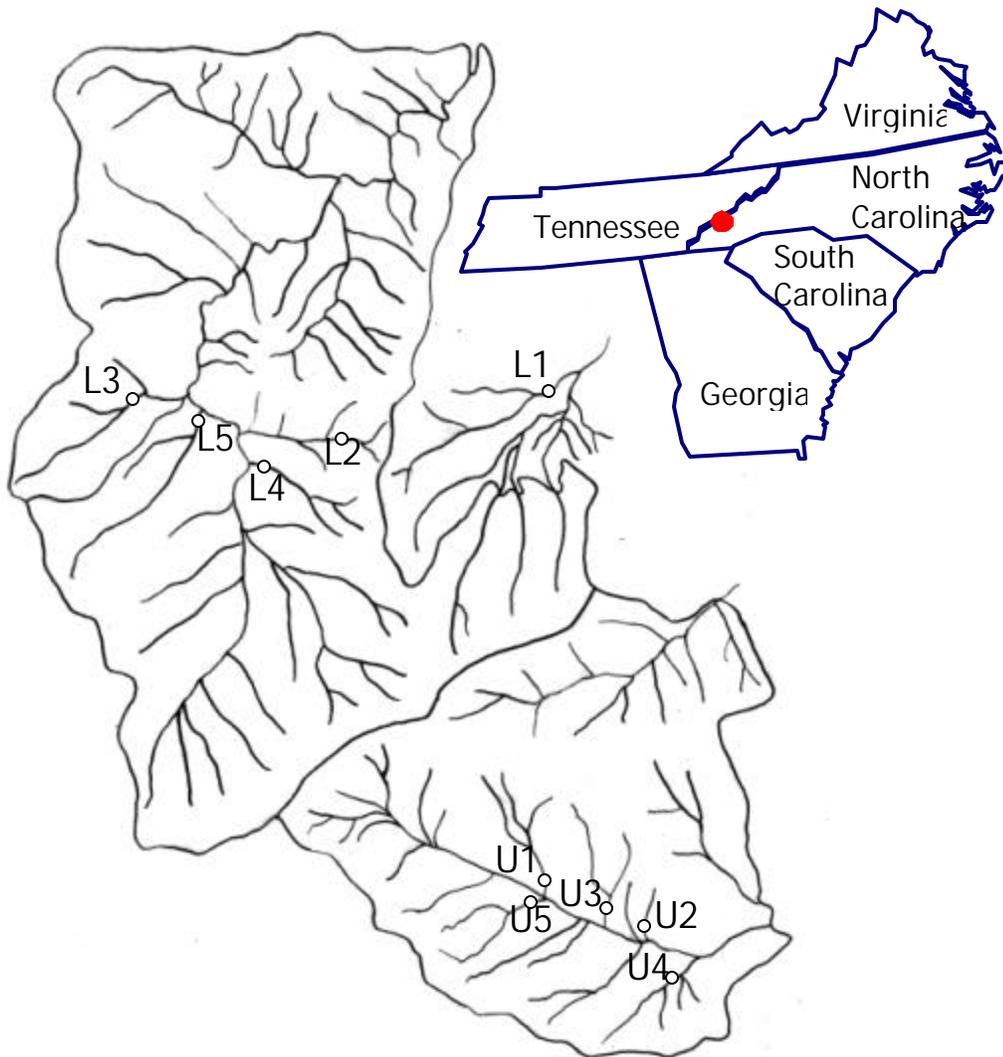


Figure 2. Woody debris volume (m³ of wood per ha of streambed) collected from unlogged (JK1-JK5) and logged (SR1-SR5) JKSW streams.

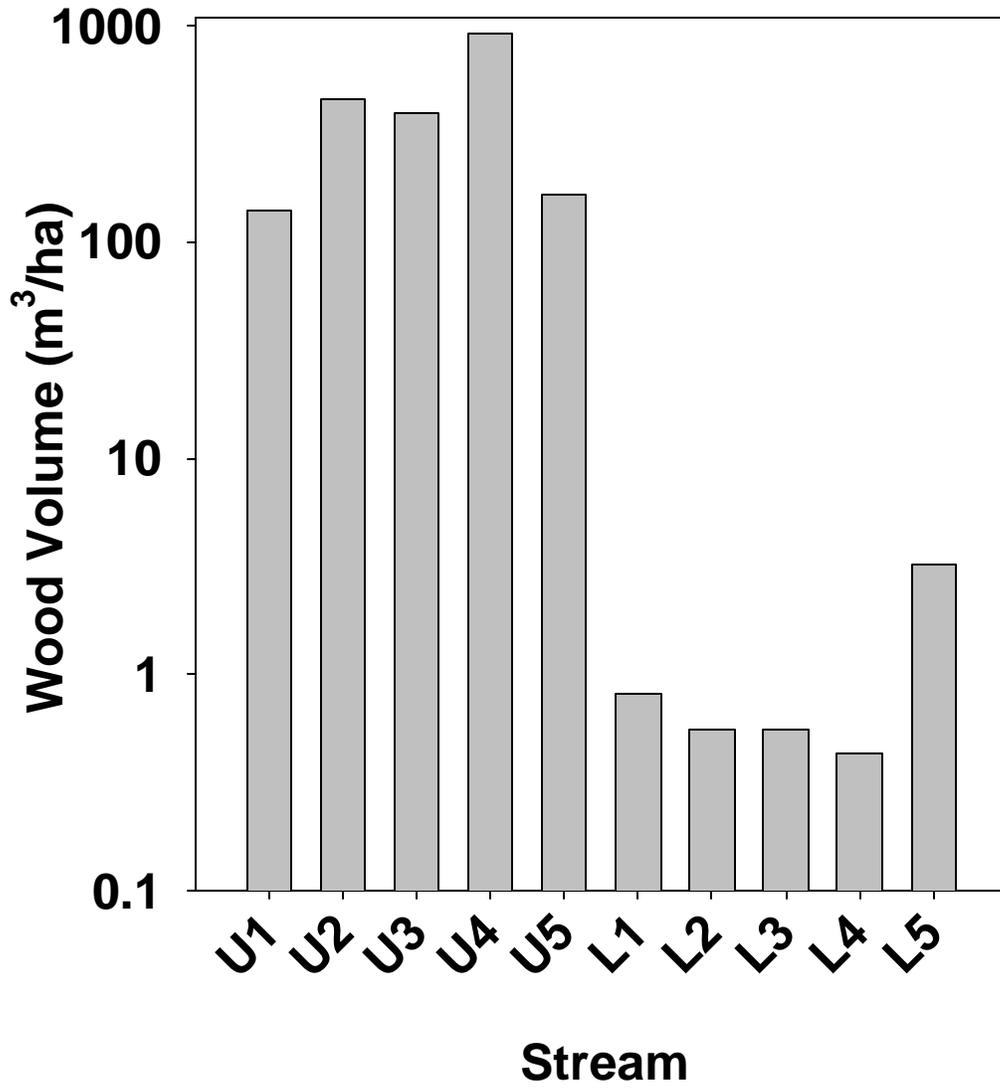


Figure 3. Percent composition of substrate in unlogged (U1-U5) and logged (L1-L5) streams.

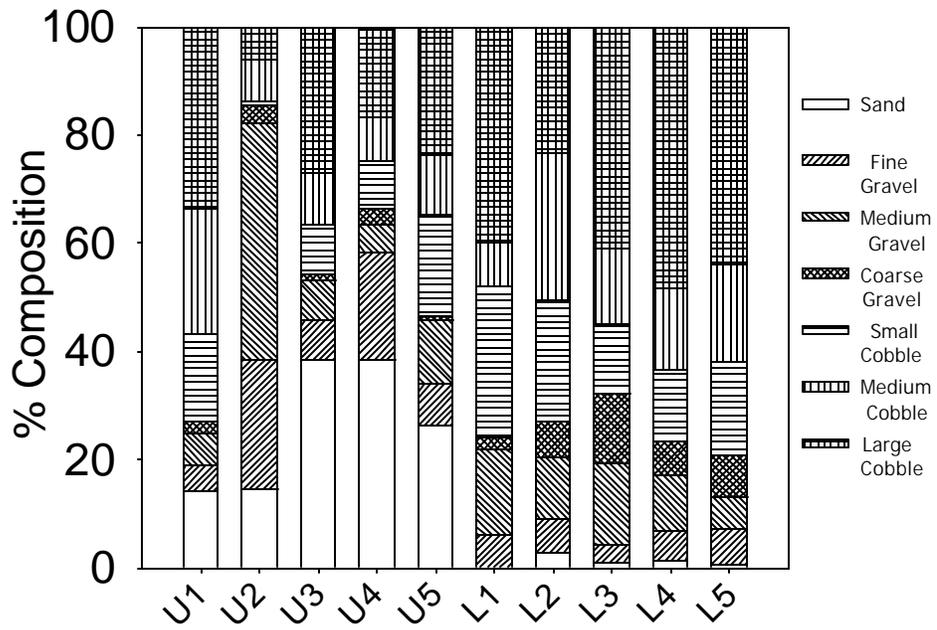


Figure 4. Cluster analysis (Euclidian distance, Ward minimum variance method) of substrate composition for Joyce Kilmer-Slickrock wilderness streams. Labels indicate substrate characteristics of corresponding branch.

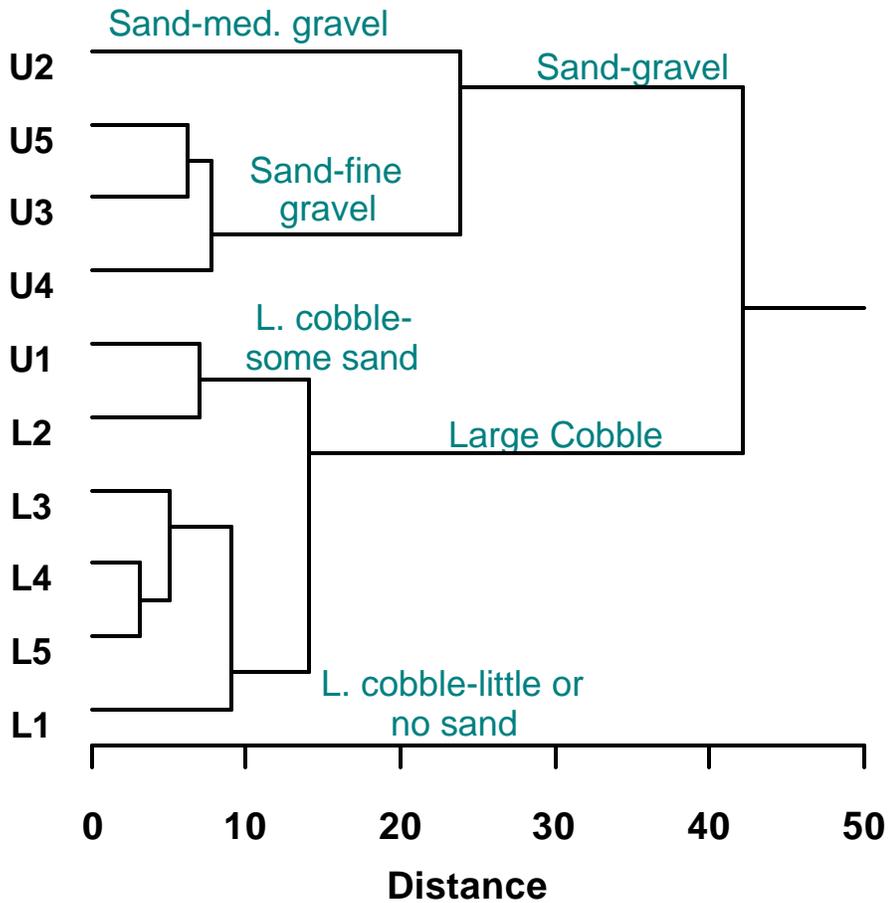


Figure 5. Scatter plot of woody debris volume (m^3 of wood per ha of stream) versus the percent abundance of fine substrates (diameter < 5.6 mm) in unlogged (U1-U5) and logged (L1-L5) JKSRW streams.

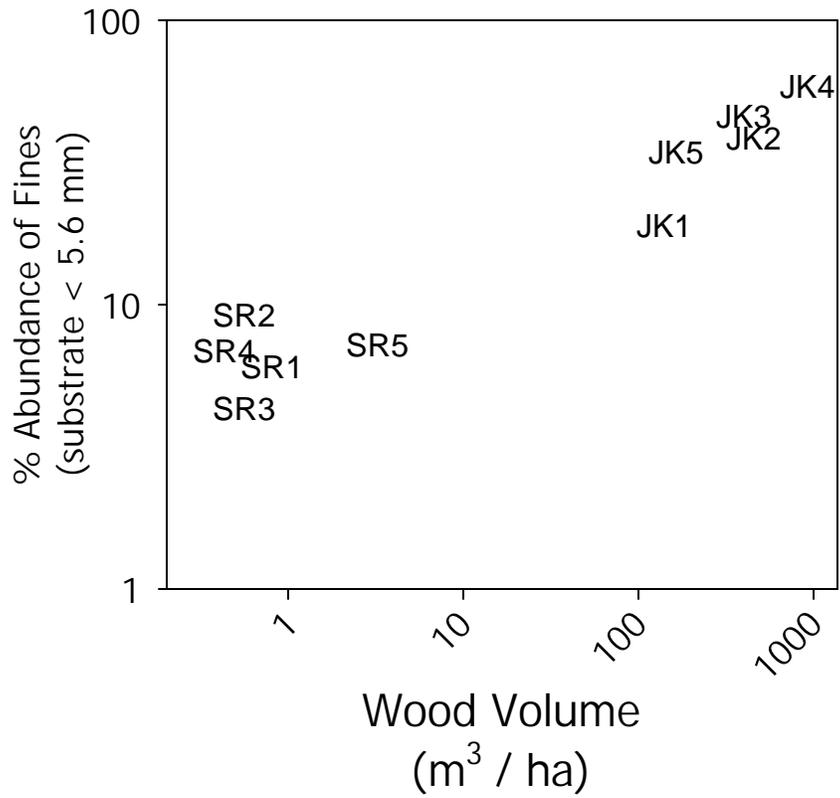


Figure 6. Relationship between woody debris volume (m^3 of wood per ha of streambed) and the percent abundance of fine substrate (diameter <5.6 mm) in unlogged streams.

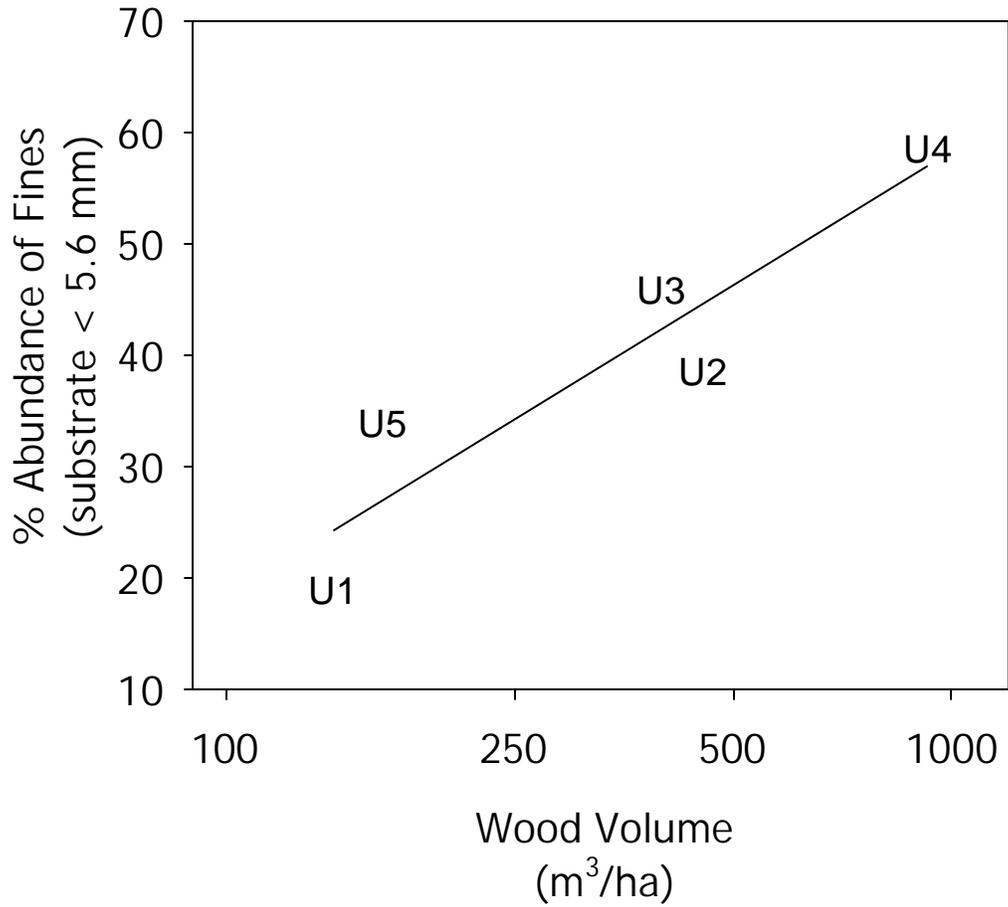
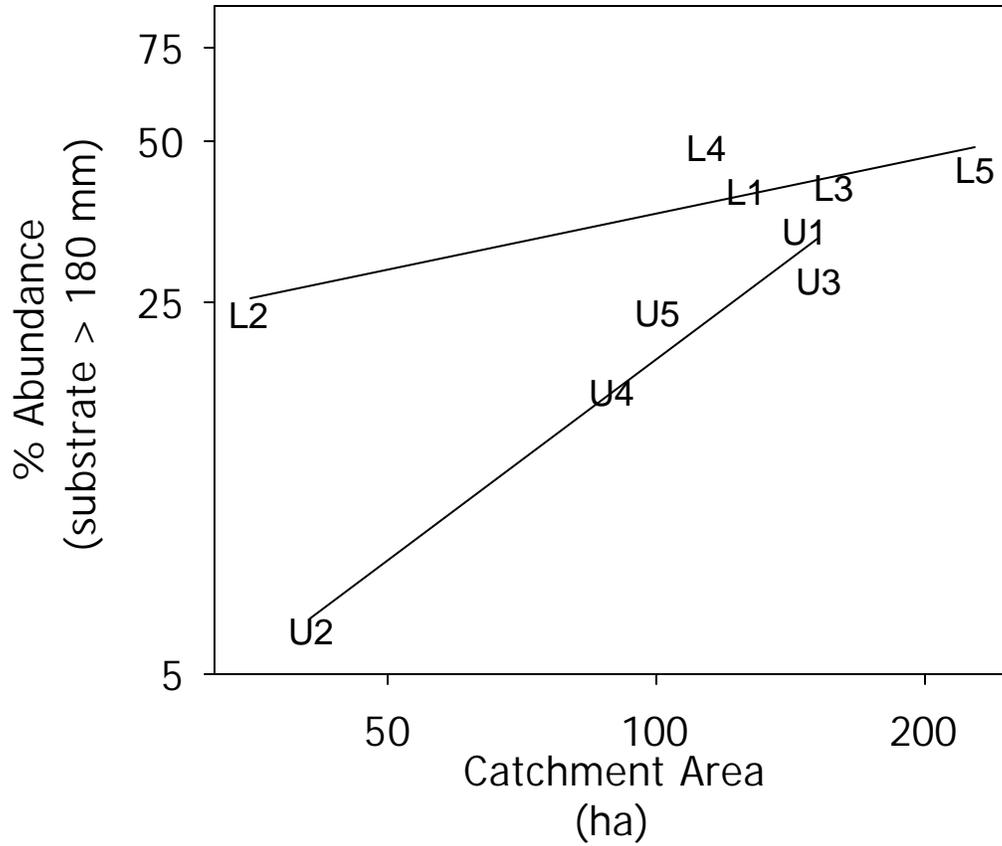


Figure 7. Relationship between catchment area and abundance of large cobble (diameter > 180 mm) in logged (L1-L5) and unlogged (U1-U5) JKSRW streams.



Chapter II

The persistence of disturbance from early 20th century logging in mountain streams following 75 years of recovery: macroinvertebrate and ecosystem response.

Abstract

I studied streams in catchments that were never logged (n=5) and catchments that were logged once (n=5) to determine if logging disturbance persists after 75+ y of recovery. Wood volume in streams draining unlogged catchments was several orders of magnitude greater than in logged catchments, and streams in logged catchments had few or no debris dams in study reaches. Species diversity did not differ significantly between streams in unlogged and logged catchments; however, the abundance of several taxa and functional feeding groups did differ. Taxa differing in relative abundance between stream types included two filterers (Parapsyche cardis and Diplectrona modesta), one gatherer (Stenonema spp.), two predators (Isoperla spp. and Acroneuria abnormis), two scrapers (Epeorus spp. and Neophylax sp.), and three shredders (Fattigia pele, Tallaperla sp., and Pycnopsyche spp.). Streams in unlogged catchments had significantly greater proportions of shredders while streams in logged catchments had significantly greater proportions of scrapers. Ecosystem parameters derived from functional feed group analysis showed that linkages between streams and riparian vegetation were weaker in logged catchments and that linkage strength increased as debris dam frequency increased. P/R indices indicated significantly more

heterotrophy in streams draining unlogged catchments and increased heterotrophy was associated with increased moss abundance. A streambed substrate stability index showed less bed stability in unlogged streams that were dominated by fine substrates. Much of the persisting disturbance to streams by past logging was directly or indirectly related to differences in wood volume, debris dam frequency, and streambed substrate composition. Results support the hypothesis that logging results in a downstream shift from the headwaters in ecosystem function. Furthermore, this downstream shift will likely persist for centuries because wood input rates do not return to natural levels for several centuries following logging.

Introduction

Undisturbed southern Appalachian headwater streams generally drain forested catchments that are heavily shaded and depend primarily on allochthonous inputs for their energy base (Webster and Meyer 1997). Consequently, these streams have comparatively large proportions of invertebrate shredders and gatherers that depend on autumnal leaf inputs, and ecosystem function is strongly linked to the surrounding forest (Vannote et al. 1980, Cummins et al. 1989).

Forested streams often contain large amounts of wood that is important in geomorphology and ecosystem function (Sedell et al. 1978, Bilby and Likens 1980, Cummins et al. 1983, Silsbee and Larson 1983, Speaker et al. 1984, Harmon et al 1986, Fleebe and Dolloff 1995, Wallace et al. 1995, Wallace et al. 1997). Logs and other large pieces of wood increase particulate organic matter retention (Bilby and Likens 1980), provide habitat for stream organisms (Angermeier 1984), and influence nutrient dynamics (Munn and Meyer 1990, Wallace et al. 1995).

Most southern Appalachian forests were logged following the arrival of European settlers and only a few patches of catchment-wide uncut forest remain in the Eastern United States (Davis 1996). Logging can change wood standing stocks and other forms of allochthonous organic

matter (OM) (Ponce 1974, Silsbee and Larson 1983, Golladay and Webster 1988, Hedin et al. 1988, Bilbee and Ward 1991, Hicks et al. 1991, Ralph et al. 1994, Fleebe and Dolloff 1995). Furthermore, logging eliminates the primary input source of logs and other large pieces of wood capable of forming debris dams (Likens and Bilby 1982). Such disturbances can alter community or ecosystem structure and function and can shift the biotic energy base from allochthonous to autochthonous (Hansmann and Phinney 1973, Vannote et al. 1980, Webster et al. 1983, Ulrich et al. 1993, Stone and Wallace 1998). The effects of extremely large reductions in leaf retention can extend beyond primary consumers and reduce predator abundance through bottom-up control (Wallace et al. 1999).

Aquatic insect assemblages reflect the geological and terrestrial characteristics of the catchments they inhabit and are important links in energy dynamics, particularly in the transfer of primary production to higher trophic levels (Cummins 1973, Cummins and Klug 1979, Vannote et al. 1980). Shredders convert allochthonous inputs into secondary production by consuming riparian vegetation that enters the stream. Scrapers convert autochthonous primary production into secondary production by consuming periphyton in addition to other sources of fixed carbon. Shredders and scrapers contribute to fine particulate organic matter (FPOM) production (Wallace et al. 1982, Cuffney et al. 1984) that

is food for gatherers and filterers by comminuting coarse particulate organic matter (CPOM). Shredder abundance tends to decrease and scraper abundance tends to increase downstream as streams become wider, shading decreases, and allochthonous inputs are replaced by autochthonous production (Vannote et al. 1980, Gurtz and Wallace 1984, Cummins et al. 1989).

Macroinvertebrates are adapted to using specific feeding modes (e.g., filtering, scraping, shredding etc.) or are limited to the particle size they can consume (Cummins 1973, Cummins 1974, Cummins and Klug 1979, Lamberti and Moore 1984). Specialization limits many invertebrates to use specific foods (e.g., periphyton, FPOM, CPOM, heterotrophic prey) although they may meet their caloric needs from multiple sources (Cummins and Klug 1979, Merritt and Cummins 1996a). The functional role of stream macroinvertebrates can be characterized because the food they consume can be identified as autochthonous or allochthonous (or from secondary producers in the case of predators) and functional feeding group abundance can be strongly linked to the abundance of food such as CPOM and FPOM (Minshall et al. 1982). Shifts in a stream's energy base from or to allochthonous or autochthonous sources are reflected in shifts in functional feeding group (FFGs) proportions (Vannote et al. 1980, Merritt and Cummins 1996b).

Studies of ecosystem disturbance and recovery generally involve assessment of one or many ecosystem attributes. It can be difficult, time consuming, and expensive to make such measurements directly and can be impractical when multiple streams are studied. Aquatic insects and other benthic macroinvertebrates are widely used to monitor disturbance and recovery (Loeb and Spacie 1994, Rosenberg and Resh 1993, Williams and Feltmate 1992, Merritt and Cummins 1996b).

Food specialization (e.g. leaf shredders and algal scrapers) allows FFG ratios to be used as surrogates for measuring ecosystem attributes such as P/R ratios, stream-riparian vegetation linkage strength, fine particulate organic matter dynamics (FPOM), and top-down versus bottom-up control (Merritt and Cummins 1996b, Merritt et al. 1996, Cummins and Merritt 1999) (see Table 1 for derivations). Stone and Wallace (1998) found that shredder to scraper ratios were particularly sensitive to the effects of logging on recovering mountain streams in Coweeta, NC. Additionally, stream substrate stability can be estimated from taxa that need physically stable substrates for attachment or stable substrates that can accumulate epilithon that they feed on (Merritt and Cummins 1996).

Biomonitoring and other stream studies often use an experimental stream (the stream of interest) and a control or reference stream used for

comparison. Although many forested reference streams lack contemporary disturbance, most have some history of past disturbance including disturbance from logging. Webster et al. (1992) suggested that many reference streams are still responding to past disturbance and recovery may take centuries. Streams draining 75 y-old forests are of interest because they are often used as reference streams and remaining catchment-wide uncut forests allow assessment of the persistence of logging disturbance to streams that are often used as reference streams.

I was interested in determining if logging disturbance persists in catchments following 75 y of recovery. My examination of wood (Table 2) and substrate composition (Table 3) in streams in unlogged and logged catchments showed wood standing stocks and debris dam frequency were significantly lower in streams in logged catchments. I expected that lower standing stocks of wood in logged catchments resulted in less OM retention (Bormann and Likens 1974, Sedell et al. 1978, Bilby and Likens 1980, Cummins et al. 1983, Speaker et al. 1984, Harmon et al 1986,) and also in structural and functional differences between streams in unlogged and logged catchments (Silsbee and Larson 1983, Wallace et al. 1988, Wallace et al. 1995, Wallace et al. 1997). I examined macroinvertebrate assemblages to determine if they continue to respond to disturbance from logging. These data were used to estimate ecosystem parameters

including production to respiration ratios (P/R), stream-riparian vegetation linkage strength, substrate stability, and top-down control (Merritt and Cummins 1996b). The habitat variables wood volume, debris dam frequency, moss coverage, and the size class distribution of inorganic substrates were measured for each stream. Species data and ecosystem attributes were regressed against habitat variables to determine if differences in habitat influenced structure and function and how past logging disturbance continues to influence recovering streams.

Study Site

This study was conducted in the Joyce Kilmer-Slickrock wilderness (Figure 1), which lies southwest of the Great Smoky Mountains National Park in the Nantahala National Forest. The Joyce Kilmer-Slickrock wilderness consists of two adjacent wilderness areas. Joyce Kilmer is in Graham Co. North Carolina and is one of the few remaining southern Appalachian forests that was never logged. The Slickrock wilderness was logged once and then allowed to recover. Slickrock wilderness borders the northwest boundary of Joyce Kilmer with portions of the forest residing in Graham Co., North Carolina and Monroe Co., Tennessee. Joyce Kilmer Memorial Forest is approximately 1540 ha and the Slickrock wilderness is approximately 4500 ha. Elevation ranges are from 670 m to

1585 m in Joyce Kilmer and from 330 m to 1585 m in Slickrock. Annual precipitation is normally > 200 cm per year (Daniels 1985). Joyce Kilmer is underlain primarily by arkosic metasandstone, muscovite phyllite and mica schist. Geology in Slickrock is similar and underlain by arkosic metasandstone, graphitic metagreywacke, and slate.

Vegetation types in the Joyce Kilmer-Slickrock wilderness include mixed mesophytic cove hardwood associations in moist lowlands and north facing slopes, mixed oak-hickory (Quercus spp.-Carya spp.) stands on steep side slopes, oak-pine (Quercus spp.-Pinus spp.) stands on southern slopes, and rhododendron-laurel-azalea slicks on exposed ridges (Daniels et al. 1987). Eastern hemlock (Tsuga canadensis) is common throughout the Joyce Kilmer-Slickrock wilderness and is particularly abundant along streamsides, often with thick Rhododendron maximum understory. South facing slopes generally have thinner understory than north facing slopes.

Joyce Kilmer and Slickrock are similar geologically but differ in land use history. Joyce Kilmer was never logged and Slickrock was logged from 1917 until 1922. The area now designated as the Joyce Kilmer wilderness was examined for potential timber production at least as early as 1910 (Anon. 1910). The Joyce Kilmer wilderness was never logged due to several changes in ownership that repeatedly delayed logging and a

flood around 1930 resulting from construction of Calderwood Lake Dam, which destroyed the only railroad access to the area. (personal communication, Cheoa Ranger Station, Graham Co., North Carolina).

The Babcock Land and Timber Company purchased the Slickrock portion of the Joyce Kilmer-Slickrock wilderness in the 1915. Babcock Land and Timber began logging in 1917 and logging ended in 1922 with the construction of Calderwood Dam. The area that presently composes the Joyce Kilmer-Slickrock wilderness was purchased by the U.S. Forest Service in 1936 and designated wilderness in 1975 (personal communication, Cheoa Ranger Station, Graham Co., North Carolina).

Study streams in the Joyce Kilmer-Slickrock wilderness (Figure 1) were selected based on land use history (streams in unlogged Joyce Kilmer catchments versus logged Slickrock catchments), similarity in size range between treatments, and similarity in slope. Five replicate unlogged catchments in Joyce Kilmer (U1-U5) and five replicate catchments logged ca. 75 y ago (L1-L5) were studied for comparison. Catchment area is the total area within each watershed upstream of each sampling site and slope was estimated from USGS topographical maps. Streams in unlogged forests drained catchments ranging from 47 to 151 ha and stream gradients ranged from 8.8 to 21.8%. Logged catchments

ranged from 35 to 227 ha and stream slopes ranging from 9.1 to 23.6 %, respectively.

Although forest composition is similar between Joyce Kilmer and Slickrock, evidence of past land-use in streams is present. Railroads were often constructed in streambeds because stream channels made the best roadbeds (Dolloff 1993) and logs were carried out of the forests on rail carts. Such railroads were constructed in many Slickrock streams (Homan 1990). In other instances, logs were simply pulled by Oxen or other animals downstream with out assistance of railroads. Although Babcock Land and Timber Company removed most of the rails, many streams still contain sections of track, pieces of cable, and other debris that was used in logging and later abandoned. Long sections of rail remain in stream L5 and long lengths of cable remain along the banks of L4. Old railroad grades are evident through other parts of the Slickrock wilderness and pieces of metal refuse are not uncommon.

Materials and Methods

Aquatic insects, inorganic streambed substrates, wood volume (m^3/ha streambed), debris dam frequency and relative moss coverage were measured in a typical 100-m reach in each stream. Functional feeding group ratios were used to estimate ecosystem parameters (Table 1) including the amount of autotrophy versus heterotrophy (P/R), the strength of the linkage between streams and riparian vegetation (Riparian Linkage Index), transported versus stored fine benthic organic matter (T/BFPOM Index), streambed stability (Stability Index), and the degree of top-down control (Top-down Control Index). Ecosystem attributes (Merritt and Cummins 1996b) were estimated using functional feeding group ratios (Merritt and Cummins 1996a; modified for southern Appalachian mountain streams according to Wallace et al. 1999).

Aquatic Insects and Ecosystem Attributes

Aquatic insects were sampled using a 500-micron mesh dip net. Streambed substrate composition was highly variable and ranged from streambeds dominated by sand to streambeds dominated by large cobble and boulders. A variety of microhabitats that included riffles, runs, and pools were measured and standard quantitative sampling devices such as

a Surber or Hess sampler could not be used consistently across all streams. I used a qualitative/time per sample design to sample insects. Six 1.0-m long sampling reaches in mixed substrate reaches (free of bedrock outcrops) were randomly selected along a transect and were sampled on six occasions over 1 year. The streambed was agitated for five minutes in accessible microhabitats and dislodged insects washed into the net. Insects were preserved in the field using Kahle's fluid, transported to the lab, sorted, identified to the lowest practical taxonomic level using a Wild™ dissecting microscope, and classified into FFGs. Insect data are expressed as relative abundance (i.e., the % a given taxon composes of the total number of individuals collected in a given stream). I used FFG ratios to provide a relative estimate of P/R, stream-riparian vegetation linkage strength, substrate stability, and top-down control.

Traditional diversity indices such as the Shannon Index can be biased by uncommon species (Magurran 1988). Diversity was calculated using the Q statistic, which is a measure of the inter-quartile slope of the cumulative species area curve and was used because it is unaffected by very uncommon species (Magurran 1988). I used the Q statistic as a measure of diversity because numerous species in my study were very uncommon or represented as a single individual and the Q statistic is

relatively unaffected in such situations. Furthermore, the Q statistic is comparatively discriminant and advocated by some authors (e.g., Kempton and Wedderburn 1978, Magurran 1988).

Wood, Moss, and Inorganic Substrate

Wood volume per square meter of streambed was calculated using the line intersect method (De Vries 1974, Wallace and Benke 1984) and expressed as m³ of wood per hectare of streambed. Other researchers have used the same method to assess wood in flood plains by using a transect perpendicular to the stream (e.g. Wallace and Benke 1984). I was interested in quantifying only the wood that was likely to divert flow and/or increase retention in the study reach of each stream and was not concerned with wood deposited above the stream bank. Consequently, I measured each piece of wood along a 100 m midstream transect.

Diameter of wood <100 mm was measured using vernier calipers. Wood greater than 100 mm in diameter was measured using a meter tape.

Debris dam frequency was also recorded (Bilby 1984, Hedin et al. 1988) and is expressed as the number of debris dams per 100 m.

Moss abundance was estimated based on methods developed by (Pfankuch 1975) with a few modifications. Moss coverage on submerged substrates was scored as follows: moss abundant throughout the reach

from bank to bank (3 points); moss common in slower portions of the stream but decrease in abundance or are absent in swift flowing portions (2 points), moss almost totally absent from swifter portions of stream reach and may also be absent from some slow or still areas (1 point), and moss rare or absent in all portions of the reach (0 points). Fractional values were estimated for abundance between categories (e.g. some sections scored 0.25 points or 2.67 points). I evaluated ten 3-m long reaches in each stream and scored streams based on the sum of all ten reaches.

Streambed substrate composition was estimated from pebble counts (Bevenger and King 1995). A minimum of 100 substrate particles were measured along a bank to bank (zigzag) transect except where debris dams prevented collection. I used a zigzag transect to cover a variety of habitats (riffles, pools, bends) giving an integrated measure of differences in substrate composition between logged and unlogged streams (Bevenger and King 1995). I used a gravelometer described by Yuzyk (1986) and characterized streambed particles based on the smallest aperture through which they could pass. The gravelometer had the following sized openings: 2, 2.8, 4, 5.6, 8, 11, 16, 22.6, 32, 45, 64, 128, and 180 mm. Data were grouped into the following size classes: fines (< 5.6 mm), medium gravel (5.6 – 16 mm), coarse gravel (16 – 32 mm),

small cobble (32 – 90 mm), medium cobble (90 – 180 mm), and large cobble (>180 mm).

Data Analysis

Data were analyzed using Minitab 12.1 and an alpha level of 0.05 was used for all comparisons. Abundance data for taxa and streambed substrate are expressed as percent of total (relative abundance). T-tests were used to compare biotic variables (taxa and ecosystem parameters) and habitat variables (wood, substrate size classes, moss abundance, stream gradient, and catchment area) between stream types. Indices (P/R, riparian linkage, FPOM, top-down, stability) were square root transformed and percentages (streambed substrate, taxa) were arcsine square root transformed to meet assumptions of normality as needed. I used stepwise regression analysis (alpha = 0.1 for inclusion) to relate habitat variables to biotic variables.

Results

Diversity

Diversity scores ranged from 7.98 to 19.84 and from 11.48 to 15.84 in unlogged and logged streams, respectively and means were not significantly different (Table 4). No relationship was found between diversity and habitat variables measured. Most taxa were found in all streams, although there were some exceptions. Fattigia pele was uncommon (0.17 to 1.14 % relative abundance) but was collected in all unlogged streams and in only one logged stream. Neophylax sp. was also uncommon (0.35 to 0.42%) and occurred in four of five logged streams, but in only one unlogged stream.

Functional Feeding Groups

Filterers averaged 13.52 and 14.80 % of taxa collected in unlogged and logged streams, respectively, and mean abundance did not differ significantly between stream types (Table 5). Parapsyche sp. was the dominant filterer in unlogged catchments and Diplectrona modesta was the dominant filterer in logged catchments and the abundance of both differed significantly between stream types. Parapsyche sp. abundance was positively related to moss (Figure 2). Diplectrona

modesta was more abundant in logged than unlogged catchments, but D. modesta abundance was not significantly related to habitat variables measured.

Gatherers did not differ significantly between streams in logged and unlogged catchments ($p=0.34$) and averaged 14.08 and 13.52% of the population, respectively. Gatherers were not significantly related to habitat variables measured in unlogged or logged streams. Stenonema spp. was significantly more abundant in unlogged (mean = 3.09%) than logged streams (mean = 1.35%).

Predators were 19.84 and 16.20 % of taxa collected and did not differ significantly between unlogged and logged streams as a group, although three genera were significantly different. Acroneuria sp. were almost six times more abundant in logged versus unlogged streams (1.9 vs. 0.3%, $p = 0.004$). Isoperla spp. was four times more abundant in unlogged than logged streams (1.92 vs. 0.47 % abundance, $p = 0.007$). Cordulagaster was significantly more abundant in unlogged than logged streams (0.48 vs. 0.16 %, $p = 0.05$) and was negatively related to large cobble abundance in unlogged streams (Figure 3).

Scrapers were significantly more abundant in streams in logged versus unlogged catchments (24.13 versus 13.97 % respectively, $p = 0.026$) and their abundance was negatively related to moss (Figure 4).

Taxa significantly different between stream types included Epeorus spp, Leucrocuta sp., and Neophylax sp., and all were more abundant in logged catchments. None of these scrapers were strongly related to habitat variables measured, however, Epeorus spp. was observed on top of large cobbles free of moss and Neophylax sp. cases were commonly found attached to moss free surfaces of small to large cobbles.

Shredders were 27.36 and 14.47 % of taxa collected in unlogged and logged streams, respectively, and were highly significantly different ($p = 0.002$). Shredders abundance was positively related to moss in unlogged catchments and to large cobble (positively) and catchment area (negatively) in logged catchments (Figure 5).

Three of the six dominant shredders (Tallaperla sp., Pycnopsyche spp., and Fattigia pele) differed significantly between unlogged and logged streams. Tallaperla sp. was the most abundant shredder in unlogged and logged catchments (17.62 and 5.08 % respectively, $p < 0.001$) and was the most abundant taxon in unlogged forests. Tallaperla sp. abundance was positively related to moss in unlogged catchments (Figure 6), but not significantly related to habitat variables measured in logged catchments. Pycnopsyche spp. was the second most abundant shredder in unlogged catchments (2.68%) and the fifth most abundant (1.39%) in logged catchments. Pycnopsyche spp. abundance was related

to coarse gravel in unlogged catchments and to medium gravel in logged catchments (Figure 7). Fattigia pele was present in all unlogged catchments, but in only one stream in a logged catchment, and its abundance was related to fines (Figure 8).

Ecosystem Attributes

P/R Index

Production to respiration estimates were based on the ratio of scrapers to shredders and gatherers. Streams with P/R scores < 0.75 are considered heterotrophic and all streams in this study were heterotrophic according to this index (Table 6). Streams in unlogged catchments were significantly more heterotrophic (i.e. lower P/R scores) than were streams in logged catchments ($p = 0.044$). Mean P/R scores for streams in unlogged and logged catchments were 0.215 and 0.428, respectively, and ranged from 0.112 to 0.296 in unlogged catchments to 0.276 to 0.734 in logged catchments. P/R scores were related to moss abundance (Figure 9).

Riparian linkages

Riparian linkage scores in unlogged streams ranged from 0.511 to 1.00 and from 0.201 to 0.416 in logged streams and means were highly significantly different ($p = 0.004$). Riparian linkages increased in strength (higher scores) as the number of debris dams increased across both unlogged and logged streams (Figure 10). All streams except L2 had linkages above 0.25, which is considered normal for forested streams.

T/BFPOM Index

T/BFPOM scores ranged from 0.354 to 0.756 (mean = 0.564) in unlogged forests and from 0.300 to 0.874 (mean = 0.532) in logged streams. Scores for streams in unlogged catchments were not significantly different from scores for streams in logged catchments. Additionally, T/BFPOM scores were not significantly related to habitat variables measured.

Channel Stability Index

Based on the ratio of scrapers and filterers to shredders and gatherers, channels in logged streams were significantly more stable (mean = 0.933) than unlogged streams (mean = 0.530) ($p = 0.04$). Stability was unrelated to habitat variables measured. Stability scores

greater than 0.50 indicate a stable channel. Three of five unlogged (U1-U2, U4) and all logged streams had stable channels.

Discussion

Changes in species richness, diversity, and production often occur in streams after logging (Tebo 1955, Haefner and Wallace 1981, Murphy and Hall 1981, Murphy et al. 1981, Lemly 1982, Silsbee and Larson 1983) and such catchment scale disturbances can persist for many decades (Harding et al. 1998). While some faunal differences existed between streams in unlogged and logged Joyce Kilmer-Slickrock wilderness catchments, overall diversity between the two catchments was not different. Other researchers (Stone and Wallace 1998) also noted shifts in abundance, but with few taxa lost entirely from insect assemblages following logging. Comparisons to other southern Appalachian streams are difficult due to variability in taxonomic resolution. Species identified in our study are typical of regional fauna and no new species or range extensions were observed.

Although diversity scores provide a numerical value for assessment, they do not convey taxonomic composition. Fauna in southern Appalachian streams has a high incidence of endemism and numerous

endemic species are considered vulnerable to extirpation (Morse et al. 1993). *E. pele* is endemic to the southeastern United States and is generally found in cool, sandy bottomed, streams (Wiggins 1998). Its absence in all but one logged catchment suggests that species composition continues to be altered in some southern Appalachian streams for many decades even though overall diversity recovers.

Aquatic insect assemblages in forested basins depend primarily on terrestrially fixed carbon for their energy (Fisher and Likens 1973) and accumulations of organic matter inputs strongly govern community and ecosystem structure in headwater Appalachian streams (Wallace et al. 1988, Wallace 1999). I expected FFGs and ecosystem attributes in logged and unlogged streams to differ significantly due differences in wood standing stocks and debris dam frequency that strongly influence habitat and OM retention (Sedell et al. 1978, Bilby and Likens 1980, Vannote et al. 1980, Cummins et al. 1983, Harmon et al 1986). In particular, I expected to find a similar pattern of shredder-scraeper abundance shifts associated with decreased retention in streams recovering from more recent logging (Silsbee and Larson 1983, Wallace et al. 1988).

Organic particles larger than 1 mm are considered coarse particulate organic matter (CPOM) (Cummins 1974) and are a major source of fixed carbon for shredders in small, forested streams (Cummins

et al 1983). CPOM must enter and then be retained streams shredders can consume it. CPOM retention may be enhanced by streambed roughness, wood dams, pools and backwaters, and decreases as water velocity increases (Minshall 1982, Speaker et al. 1984, Jones and Smock 1991, Trotter 1990, Raikow et al. 1995). Evidence suggests that shredder abundance is related to the availability of CPOM (Townsend and Hildrew 1988) and shredder abundance increases as retention increases (Wallace et al. 1988). I expected shredders to be more abundant in streams in unlogged catchments because there was significantly more wood and greater frequency of debris dams that increase CPOM retention, but not all shredders were more abundant in unlogged than logged streams. The shredding stonefly, Tallaperla sp. showed the largest difference in relative abundance between streams of any taxa in our study. Tallaperla sp. abundance has been correlated with leaf packs (Woodall and Wallace 1972, Elwood and Cushman 1975, Haefner and Wallace 1981, Angradi 1996), particularly those that accumulate in flowing areas rather than in pools (Elwood and Cushman 1975). Furthermore, Tallaperla feeds directly on leaves rather than only on surface biofilms (Harper 1978). These observations suggest that leaf packs are more important in structuring unlogged than logged streams. Pycnopsyche spp. was also more abundant in unlogged streams (2.64%) than logged streams (1.36%) and

was related to gravel abundance. Pycnopsyche is known to be more abundant in depositional areas with accumulations of OM (Wiggins 1998) and differences in abundance are consistent with higher standing stocks of wood in unlogged streams. Neophylax is known to be more abundant in disturbed streams (Haefner and Wallace 1980) and in streams where leaves are excluded (Wallace et al. 1999). Neophylax was more abundant in logged streams in my study suggesting that logged streams derived less energy from leaves. Shredders are important links between stream ecosystem function and riparian vegetation (Cummins et al. 1989) and much of the difference in riparian linkage scores were most strongly correlated with differences in shredder abundance ($p < 0.001$, $r = 0.970$).

The riparian linkage index estimates the strength of the linkage between streams and surrounding riparian vegetation and was the most sensitive index used in our study. Merritt and Cummins (1996b) characterized riparian linkage scores of >0.25 as normal for forested streams. Riparian linkages in unlogged streams were well above 0.25, ranging from 0.51 to 1.00. Logged streams also had normal riparian linkages except L2, but none of the logged streams had riparian linkages equal to or greater than unlogged streams. A similar index based on the ratio of shredders to scrapers (shredder-scrapers index) used by Stone and Wallace (1998) was also particularly sensitive in their study of logging

disturbance. The strongly positive relationship between the riparian linkages and debris dam frequency underscores the importance of wood and debris dams in connecting streams to the catchments they drain.

Debris dams are important in leaf retention, but cobbles and boulders can also be important in trapping leaves and other forms of CPOM in the absence of wood (Minshall et al. 1982, Gurtz and Wallace 1984, Speaker et al. 1984, Lamberti et al. 1988). Wood and debris dams were uncommon or absent in logged streams and the significant positive relationship between large cobble and shredders in logged streams suggests that cobble is important in CPOM retention in logged streams in this study.

Logging often results in functional shifts that increase the abundance of epilithon and/or scrapers (Lyford and Gregory 1975, Murphy et al. 1981, Wallace et al. 1988, Stone and Wallace 1998). Scrapers tend to be most abundant on intermediate sized substrates free of moss (Wallace et al. 1988). Moss coverage was significantly greater in unlogged catchments and would have reduced the available area for epilithic algal production that supports scrapers. Furthermore, larger, more stable substrates that are resistant to movement often have more attached algae (Steinmann and McIntire 1990) and these substrates were less abundant in unlogged catchments. Moss has been shown to retain

FPOM and CPOM and support greater numbers of gatherers (Wallace et al. 1988), shredders (Percival and Whitehead 1929, Gurtz and Wallace 1984), and filterers (Haefner and Wallace 1980) than other habitats. Our field observations and observations by Percival and Whitehead (1929) show some predators such as Rhyacophilia spp. are also more abundant in moss-covered substrate than non-moss covered substrate.

Consequently, the relationship between the relative abundance of scrapers and moss is probably due to the combination of scrapers displaced by moss-covered substrates and increased use of those same habitats by non-scrapers. Shifts in scraper abundance were most strongly correlated with P/R scores ($p < 0.001$, $r = 0.978$).

Both unlogged and logged streams in my study drained mature forests and, not surprisingly, P/R scores indicate all streams are heterotrophic. I expected unlogged streams would have lower P/R scores (indicating greater heterotrophy) due to the presence of more wood and debris dams that increase CPOM retention and stream heterotrophy.

Although P/R scores were greater in logged catchments, P/R scores were most strongly (negatively) related to moss. It is seemingly contradictory for lower autotrophy to be related to higher moss abundance since moss is autotrophic. P/R scores are derived in part from scrapers that obtain most of their energy from epilithon scraped from mineral surfaces

(Wallace and Webster 1996). Scrapers were less abundant where moss was more abundant probably because moss displaced epilithon. Moss also probably contributed to lower P/R scores through organic matter retention as evidenced by the positive relationship of shredders in unlogged catchments and gatherers in logged catchments to moss abundance.

Filterers were not significantly different between stream types, although two filtering taxa did differ significantly. Diplectrona modesta was 3.25 times more abundant in logged than unlogged streams. Woodall and Wallace (1972) found D. modesta was inversely related to detritus standing crops, and Wallace et al. (1999) found D. modesta more abundant in streams where litter was excluded. These data further suggest standing stocks of leaves are greater in unlogged streams in the Joyce Kilmer-Slickrock wilderness. Parapsyche sp. was the dominant filterer in unlogged streams and increased in abundance as moss abundance increased. Other researchers (Haefner and Wallace 1980) showed correlation between moss and Parapsyche sp. in disturbed catchments but not in reference catchments. The absence of a significant relationship in the reference streams of their study was attributed to low frequency of rock face habitat and low standing crops of moss. I sampled mixed substrates and moss was more abundant in unlogged streams

despite cobble and boulders being less common. Cobbles in unlogged streams might support more moss because they are less prone to movement due to the presence of wood that reduces stream power (Trotter 1990).

Gatherers feed on FPOM deposited in sediments or as surface films (Cummins and Klug 1979). Differences in the amount or quality of FPOM should result in changes in the abundance of gatherers (Vannote et al. 1980). The absence of a response by gatherers in our study suggests the relative contribution of FPOM in the study streams (quantity or quality) is proportionately similar following 75 y of recovery. Stenonema spp. was the only gatherer significantly different between treatments. Although I found Stenonema abundance to be negatively related to small cobble and moss, others found its abundance was positively related to the occurrence of pools (Silsbee and Larson 1983). We did not measure the number or size of pools in study streams, but our data are not necessarily inconsistent with the findings of Silsbee and Larson (1983). There were more debris dams capable of forming pools in unlogged catchments and more small substrates associated with these debris dams. It is possible that Stenonema spp. responds to pool size or abundance and small cobble is a covariate. I observed Stenonema spp. active on the streambed in pools in unlogged streams after sunset, lending anecdotal support to this

hypothesis. The positive relationship between Stenonema spp. and moss is probably due to Stenonema feeding on FPOM trapped in moss and supports the characterization of Stenonema spp. as a gatherer rather than a scraper.

Stability scores and other observations from our study streams suggest that there is an important temporal component in channel stability in unlogged and logged catchments. Stream channels in logged catchments are probably more stable at base flow because of the abundance of large substrates that resist movement. During high flows large cobbles in logged catchments might be more prone to movement because of the absence of wood that reduces stream power (Trotter 1990). This is supported by the presence of more moss in unlogged catchments despite their being less cobble on which moss tends to grow. Channel stability is estimated from the ratio of scrapers + filterers / shredders + collector gatherers. Large substrates require greater stream power to move them and are more physically stable. Filterers need relatively stable substrates to affix their bodies (e.g. Simuliidae) or their nets (e.g. Hydropsychidae). Scrapers also need stable substrates that can accumulate epilithon. Streams in unlogged catchments were probably less stable than streams in logged catchments because fine substrates that were more abundant in unlogged catchments are moved more easily than

cobbles and boulders. The negative relationship between Parapsyche and fine gravel lends some support to this hypothesis. Moss also requires stable substrates and was more abundant in unlogged catchments, which seems to contradict the previous suggestion.

Although predators did not differ as a group and top-down control scores were within values considered normal (Merritt and Cummins 1996b), several predators differed between stream type. Acroneuria abnormis was 6 times more abundant in logged streams, but no relationship between Acroneuria abundance and habitat variables was found. Acroneuria abnormis was present in all logged streams, but was not collected in three of five unlogged streams. Isoperla spp. was 4 times more abundant in unlogged streams. I found Cordulagaster sp. was negatively related to large cobble while Haefner and Wallace (1980) found its abundance was positively related to sand. Life history studies have shown that this species buries itself in fine sediment (Brigham et al. 1982) and unlogged streams with less large cobble have more fine sediments of varying sizes and could account for the relationship I found.

Higher trophic levels are resistant to small to moderate reductions in OM standing crops in detritus based ecosystems, but there is a threshold beyond which energy flow from primary consumers (shredders, scrapers, gathers, filterers) is insufficient to maintain secondary

consumers (Wallace et al. 1999). Bottom-up effects of very large litter inputs reductions can lead to food limitation for predators (Wallace et al. 1999). I found no significant difference in predator abundance and top-down scores indicated that there was no difference in the amount of top down control between stream types and that bottom-up energy flow was sufficient to maintain predators.

The river continuum concept (Vannote et al. 1980) predicts that anthropogenic disturbances including logging can shift headwater streams down stream on the continuum. Undisturbed forested headwater streams are heavily shaded and contain comparatively large amounts of wood making them highly heterotrophic and tightly coupled to the catchments. Moving downstream on the continuum autotrophy increases, stream-riparian linkages weaken and scrapers replace shredders (Vannote et al. 1980). Streams in logged catchments in our study showed lower proportions of shredders and greater proportions of scrapers compared to unlogged streams and P/R indices also showed more autotrophy. Logged streams had weaker linkages to the riparian vegetation in the catchments they drain than did unlogged streams. Functional shifts were strongly related to the absence of wood in logged catchments and debris dams and to decreased moss abundance in streams draining logged catchments. Logged streams in our study drained ca. 75 y-old forests and

show little or no long-term accumulation of wood and debris dams. Consequently, streams in logged catchments might not show additional recovery for several centuries when forests begin to senesce and wood input rates are restored to pre-disturbance levels. Many reference streams, particularly those that were logged, probably continue to respond to land-use history and studies that use reference streams should be cognizant of this.

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Table 1. Ecosystem attributes and formulae used for their derivation (Merritt and Cummins 1996b).

| Ecosystem parameter (Abbreviation) | Functional Feeding group ratio | General criteria ratio level | Evaluation |
|---|--|---|--|
| Production to respiration (P/R). An estimate of the relative contribution of allochthonous versus autochthonous energy sources. | $\frac{\text{Scrapers}}{\text{Shredders} + \text{Collectors}}$ | < 0.75 | Heterotrophic stream, dependent primarily on allochthonous energy. |
| Coarse to fine particulate organic matter (Riparian linkage). A measure of the linkage between riparian vegetation and shredders. | $\frac{\text{Shredders}}{\text{Collectors}}$ | > 0.25 | Normal shredder association linked to a functioning riparian system. |
| Transported to stored fine particulate organic matter (T/BFPOM). | $\frac{\text{Filterers}}{\text{Gatherers}}$ | > 0.50 | FPOM transport (in suspension) greater than normal particulate load in suspension. |
| Substrate stability (Stability). A measure of the abundance of stable substrates. | $\frac{\text{Scrapers} + \text{Filterers}}{\text{Shredders} + \text{Gatherers}}$ | > 0.50 | Stable substrate (e.g. LWD, boulders, cobble) plentiful. |
| Top-down control. A measure of top-down control by predators. | $\frac{\text{Predators}}{\text{All other groups}}$ | < 0.15 | Typical predator to prey balance. |

Table 2. Physical characteristics of study catchments in JKSRW.

| | Catchment area (ha) | Aspect (°) | Mean Gradient (°) | # of Debris Dams (/100m) | Woody debris volume (m³/ha) | Moss abundance index | |
|---------------------|------------------------------------|-----------------------|----------------------------------|-------------------------------------|---|-------------------------------------|------|
| Unlogged Catchments | | | | | | | |
| U1 | 146.6 | 170 | 12.8 | 3 | 140.3 | 7.5 | |
| U2 | 41.0 | 194 | 12.5 | 6 | 454.6 | 11.7 | |
| U3 | 151.7 | 206 | 11.1 | 10 | 398.3 | 16.0 | |
| U4 | 89.0 | 80 | 21.9 | 12 | 926.5 | 15.5 | |
| U5 | 100.1 | 52 | 8.8 | 5 | 164.1 | 18 | |
| Logged Catchments | | | | | | | |
| L1 | 126.3 | 59 | 11.6 | 1 | 0.8 | 5.0 | |
| L2 | 34.9 | 275 | 23.6 | 0 | 0.6 | 6.0 | |
| L3 | 158.0 | 56 | 9.1 | 2 | 0.6 | 4.0 | |
| L4 | 114.0 | 300 | 18.2 | 1 | 0.4 | 9.5 | |
| L5 | 227.2 | 45 | 10.8 | 0 | 3.2 | 8.0 | |
| t-test (p) | | NS | NA | NS | 0.005 | <0.001 | 0.01 |

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Table 3. Substrate composition of streambeds in unlogged (U1-U5) and logged (L1-L5) catchments in JKSRW.

| | Fines < 5.6 mm | Medium Gravel 5.6 -16 mm | Coarse Gravel 16-32 mm | Small Cobble 32-90 mm | Medium Cobble 90-180 mm | Large Cobble and Boulders >180 mm |
|------|-------------------|--------------------------------|---------------------------|--------------------------|-------------------------------|---|
| U1 | 18.92 | 6.08 | 2.03 | 16.22 | 22.97 | 33.78 |
| U2 | 38.46 | 43.59 | 3.42 | 0.85 | 7.69 | 5.98 |
| U3 | 45.79 | 7.48 | 0.93 | 9.35 | 9.35 | 27.10 |
| U4 | 58.42 | 4.95 | 2.97 | 8.91 | 7.92 | 16.83 |
| U5 | 33.90 | 11.86 | 0.85 | 18.64 | 11.02 | 23.73 |
| mean | 39.10 | 14.79 | 2.04 | 10.79 | 11.79 | 21.49 |
| L1 | 6.00 | 16.00 | 2.00 | 28.00 | 8.00 | 40.00 |
| L2 | 9.22 | 11.35 | 6.38 | 22.70 | 26.95 | 23.40 |
| L3 | 4.30 | 15.05 | 12.90 | 12.90 | 13.98 | 40.86 |
| L4 | 6.90 | 10.34 | 6.21 | 13.10 | 15.17 | 48.28 |
| L5 | 7.19 | 5.76 | 7.91 | 17.27 | 17.99 | 43.88 |
| mean | 6.72 | 11.70 | 7.08 | 18.79 | 16.42 | 39.29 |

Table 4. Diversity (Q statistic) and taxonomic composition of aquatic insects from JKSRW streams. Taxa shown include species comprising at least 92% of the total rank abundance for all taxa collected in each stream. Abundances are expressed as percent of total taxa collected in each stream.

| | U1 | U2 | U3 | U4 | U5 | Mean | L1 | L2 | L3 | L4 | L5 | Mean | t-test (p) |
|--------------------------------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|------------|
| Diversity (Q statistic) | 19.84 | 12.81 | 14.10 | 16.38 | 7.98 | 14.22 | 15.84 | 15.20 | 11.48 | 15.41 | 14.90 | 14.56 | NS |
| Filterers | | | | | | | | | | | | | |
| <u>Parapsyche cardis</u> | 6.59 | 4.84 | 6.74 | 5.44 | 7.06 | 6.14 | 1.07 | 3.06 | 0.14 | 2.15 | 2.68 | 1.82 | < 0.001 |
| <u>Diplectrona modesta</u> | 2.20 | 3.19 | 0.39 | 3.72 | 3.70 | 2.64 | 5.15 | 9.26 | 10.06 | 9.93 | 8.33 | 8.55 | < 0.001 |
| Tanytarsinii | 0.00 | 3.52 | 0.58 | 1.72 | 1.51 | 1.47 | 2.66 | 4.80 | 2.64 | 0.10 | 0.36 | 2.11 | NS |
| <u>Prosimulium</u> spp. | 1.61 | 0.33 | 2.50 | 0.57 | 1.51 | 1.31 | 3.02 | 0.35 | 0.57 | 1.13 | 0.14 | 1.04 | NS |
| <u>Dolophilodes</u> sp. | 2.05 | 0.88 | 0.19 | 1.15 | 1.34 | 1.12 | 0.53 | 0.63 | 1.21 | 0.72 | 0.94 | 0.81 | NS |
| Gatherers | | | | | | | | | | | | | |
| <u>Ephemerella</u> spp. | 7.91 | 17.05 | 17.73 | 4.87 | 8.40 | 11.19 | 11.01 | 15.80 | 1.36 | 20.16 | 33.74 | 16.41 | NS |
| Orthoclaadiinae | 6.30 | 3.85 | 7.51 | 4.58 | 2.35 | 4.92 | 11.19 | 2.16 | 6.92 | 3.38 | 5.21 | 5.77 | NS |
| <u>Paraleptophlebia</u> sp. | 3.22 | 3.85 | 0.39 | 4.58 | 6.55 | 3.72 | 0.71 | 8.49 | 6.71 | 0.92 | 1.45 | 3.66 | NS |
| <u>Stenonema</u> spp. | 2.05 | 4.29 | 3.28 | 3.15 | 2.69 | 3.09 | 1.24 | 1.60 | 1.50 | 1.13 | 1.30 | 1.35 | < 0.001 |
| <u>Ameletus</u> sp. | 3.51 | 2.20 | 0.96 | 0.86 | 0.67 | 1.64 | 0.71 | 1.39 | 0.93 | 4.50 | 0.87 | 1.68 | NS |
| Predators | | | | | | | | | | | | | |
| <u>Rhyacophila</u> spp. | 6.88 | 2.53 | 5.39 | 1.72 | 3.36 | 3.98 | 3.55 | 2.51 | 2.21 | 3.89 | 2.03 | 2.84 | NS |
| <u>Hexatoma</u> spp. | 2.05 | 3.08 | 1.73 | 8.02 | 3.36 | 3.65 | 1.95 | 2.78 | 3.00 | 1.02 | 0.58 | 1.87 | NS |
| <u>Malirekus hastatus</u> | 2.05 | 1.54 | 4.05 | 0.57 | 6.55 | 2.95 | 3.55 | 2.02 | 1.00 | 1.02 | 0.22 | 1.56 | NS |
| Tanypodinae | 1.61 | 2.20 | 0.96 | 1.72 | 1.01 | 1.50 | 0.00 | 6.40 | 3.57 | 3.68 | 0.36 | 2.80 | NS |
| <u>Isoperla</u> spp. | 3.37 | 1.21 | 0.77 | 2.58 | 1.68 | 1.92 | 0.53 | 0.77 | 0.21 | 0.31 | 0.51 | 0.47 | 0.006 |
| <u>Acroneuria abnormis</u> | 1.32 | 0.22 | 0.00 | 0.00 | 0.00 | 0.31 | 1.60 | 1.04 | 2.86 | 1.84 | 2.17 | 1.90 | 0.001 |
| <u>Yugus</u> sp. | 1.02 | 0.11 | 1.73 | 0.29 | 1.01 | 0.83 | 0.18 | 0.97 | 2.43 | 1.02 | 1.74 | 1.27 | NS |
| <u>Lanthus vernalis</u> | 0.88 | 1.54 | 0.77 | 1.43 | 1.01 | 1.13 | 0.36 | 0.28 | 1.64 | 1.64 | 0.87 | 0.96 | NS |
| <u>Dicranota</u> spp. | 1.61 | 0.55 | 0.58 | 1.15 | 1.51 | 1.08 | 0.18 | 0.49 | 0.43 | 1.43 | 0.07 | 0.52 | NS |
| Scrapers | | | | | | | | | | | | | |
| <u>Epeorus</u> spp. | 4.39 | 9.46 | 5.78 | 8.02 | 4.03 | 6.34 | 17.23 | 9.60 | 21.34 | 7.16 | 10.28 | 13.12 | 0.034 |
| Baetidae | 7.91 | 6.60 | 6.74 | 1.72 | 1.68 | 4.93 | 5.68 | 4.52 | 11.21 | 7.37 | 7.53 | 7.26 | NS |
| Elmidae | 1.02 | 0.00 | 0.58 | 1.15 | 1.68 | 0.89 | 2.49 | 2.02 | 0.50 | 0.20 | 0.29 | 1.10 | NS |
| <u>Psilotreta</u> sp. | 0.59 | 0.44 | 0.00 | 1.15 | 0.17 | 0.47 | 0.18 | 0.14 | 0.29 | 0.20 | 0.22 | 0.20 | NS |
| <u>Leucrocuta</u> sp. | 0.00 | 0.22 | 0.19 | 0.00 | 0.17 | 0.12 | 0.53 | 0.90 | 0.21 | 1.33 | 0.00 | 0.60 | NS |
| <u>Ectopria</u> sp. | 1.17 | 0.22 | 0.19 | 0.57 | 0.00 | 0.43 | 0.36 | 0.28 | 0.21 | 0.10 | 0.14 | 0.22 | NS |
| <u>Neophylax</u> sp. | 0.00 | 0.00 | 0.39 | 0.00 | 0.00 | 0.08 | 0.00 | 0.42 | 0.36 | 0.72 | 0.51 | 0.40 | 0.004 |
| Shredders | | | | | | | | | | | | | |
| <u>Tallaperla</u> sp. | 11.86 | 15.40 | 16.76 | 20.06 | 24.03 | 17.62 | 1.95 | 5.43 | 3.43 | 9.11 | 5.50 | 5.08 | < 0.001 |
| <u>Leuctra</u> sp. | 2.64 | 0.88 | 3.47 | 4.30 | 2.02 | 2.66 | 0.71 | 1.95 | 4.50 | 1.33 | 2.53 | 2.20 | NS |
| <u>Pycnopsyche</u> spp. | 2.93 | 3.63 | 2.12 | 3.72 | 1.01 | 2.68 | 2.31 | 1.11 | 2.36 | 0.82 | 0.36 | 1.39 | 0.046 |
| <u>Amphinemura wui</u> | 1.32 | 0.99 | 2.50 | 2.58 | 0.67 | 1.61 | 0.18 | 0.84 | 1.78 | 2.66 | 3.62 | 1.82 | NS |
| <u>Tipula</u> spp. | 0.44 | 0.55 | 0.19 | 0.86 | 0.67 | 0.54 | 8.88 | 0.56 | 0.43 | 0.92 | 0.80 | 2.32 | NS |
| <u>Lepidostoma</u> sp. | 1.02 | 0.33 | 0.19 | 0.29 | 1.01 | 0.57 | 0.89 | 0.00 | 0.93 | 0.61 | 0.80 | 0.65 | NS |
| <u>Fattigia pele</u> | 0.44 | 0.33 | 0.39 | 1.15 | 0.17 | 0.49 | 0.18 | 0.00 | 0.00 | 0.00 | 0.00 | 0.04 | 0.003 |

Table 5. Proportions (% abundance) of functional feeding groups collected in JKSRW.

| | Filterers | Gatherers | Predators | Scrapers | Shredders |
|---------------------|------------------|------------------|------------------|-----------------|------------------|
| Unlogged Catchments | | | | | |
| U1 | 13.03 | 23.72 | 25.62 | 16.98 | 20.64 |
| U2 | 13.31 | 30.36 | 16.39 | 17.6 | 22.33 |
| U3 | 10.98 | 31.02 | 17.15 | 14.45 | 26.4 |
| U4 | 14.33 | 19.48 | 19.48 | 12.89 | 33.81 |
| U5 | 15.97 | 21.18 | 21.34 | 7.9 | 33.61 |
| Mean (± 1 SD) | 13.52 (2.78) | 25.15 (5.72) | 20 (3.60) | 13.97 (8.59) | 27.36 (10.77) |
| Logged Catchments | | | | | |
| L1 | 12.97 | 28.06 | 12.97 | 30.73 | 15.28 |
| L2 | 18.23 | 32.01 | 21.71 | 17.95 | 10.09 |
| L3 | 15.06 | 17.77 | 19.41 | 34.12 | 13.63 |
| L4 | 14.84 | 30.71 | 17.71 | 17.81 | 18.94 |
| L5 | 12.89 | 42.94 | 9.7 | 20.06 | 14.41 |
| Mean (± 1 SD) | 14.8 (2.85) | 30.3 (11.77) | 16.3 (3.74) | 24.13 (7.06) | 14.47 (8.64) |
| t-test (p) | NS | NS | NS | 0.026 | 0.002 |

Table 6. Ecosystem parameters for Joyce Kilmer-Slickrock wilderness streams derived from functional feeding group analysis.

| | P/R | Riparian Linkage | T/BFPOM | Channel Stability | Top-Down Control |
|---------------------|--------------|-------------------------|----------------|--------------------------|-------------------------|
| Unlogged Catchments | | | | | |
| U1 | 0.296 | 0.562 | 0.549 | 0.677 | 0.344 |
| U2 | 0.267 | 0.511 | 0.438 | 0.587 | 0.196 |
| U3 | 0.211 | 0.628 | 0.354 | 0.443 | 0.207 |
| U4 | 0.191 | 1.00 | 0.735 | 0.511 | 0.242 |
| U5 | 0.112 | 0.905 | 0.754 | 0.436 | 0.271 |
| Mean (± 1 SD) | 0.215 (0.17) | 0.721 (0.34) | 0.566 (0.17) | 0.53 (0.26) | 0.252 (0.05) |
| Logged Catchments | | | | | |
| L1 | 0.546 | 0.372 | 0.462 | 1.008 | 0.149 |
| L2 | 0.298 | 0.201 | 0.57 | 0.86 | 0.277 |
| L3 | 0.734 | 0.415 | 0.847 | 1.566 | 0.241 |
| L4 | 0.276 | 0.416 | 0.483 | 0.658 | 0.215 |
| L5 | 0.286 | 0.258 | 0.3 | 0.574 | 0.107 |
| Mean (± 1 SD) | 0.428 (0.20) | 0.332 (0.54) | 0.532 (0.22) | 0.933 (0.41) | 0.198 (0.05) |
| t-test | 0.044 | 0.004 | NS | 0.041 | NS |

Figure 1. Map of Southeastern United States showing location of the Joyce Kilmer-Slickrock wilderness (JKSRW). Detailed map shows study sections of unlogged (U1-U5) and logged (L1-L5) streams.

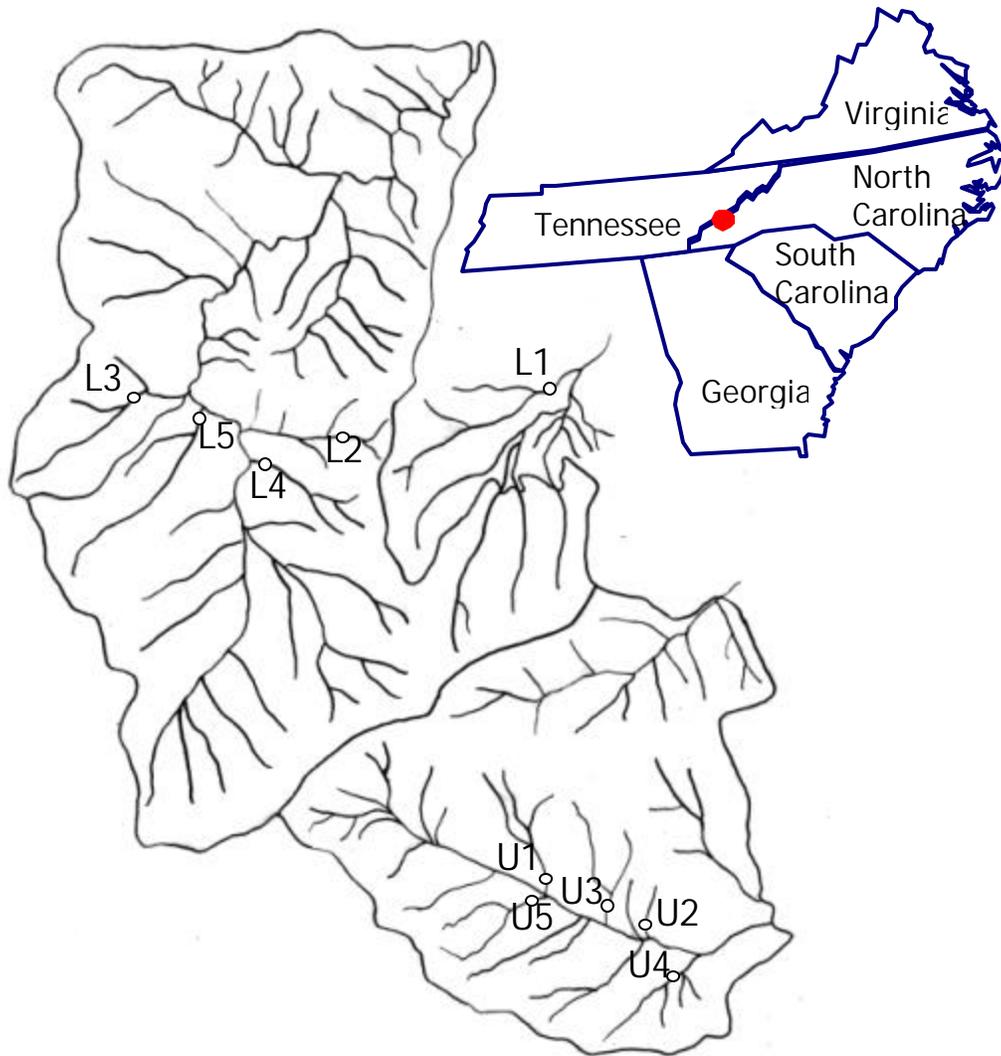


Figure 2. Parapsyche abundance versus moss in unlogged (U1-U5) and logged (L1-L5) JKSRW streams.

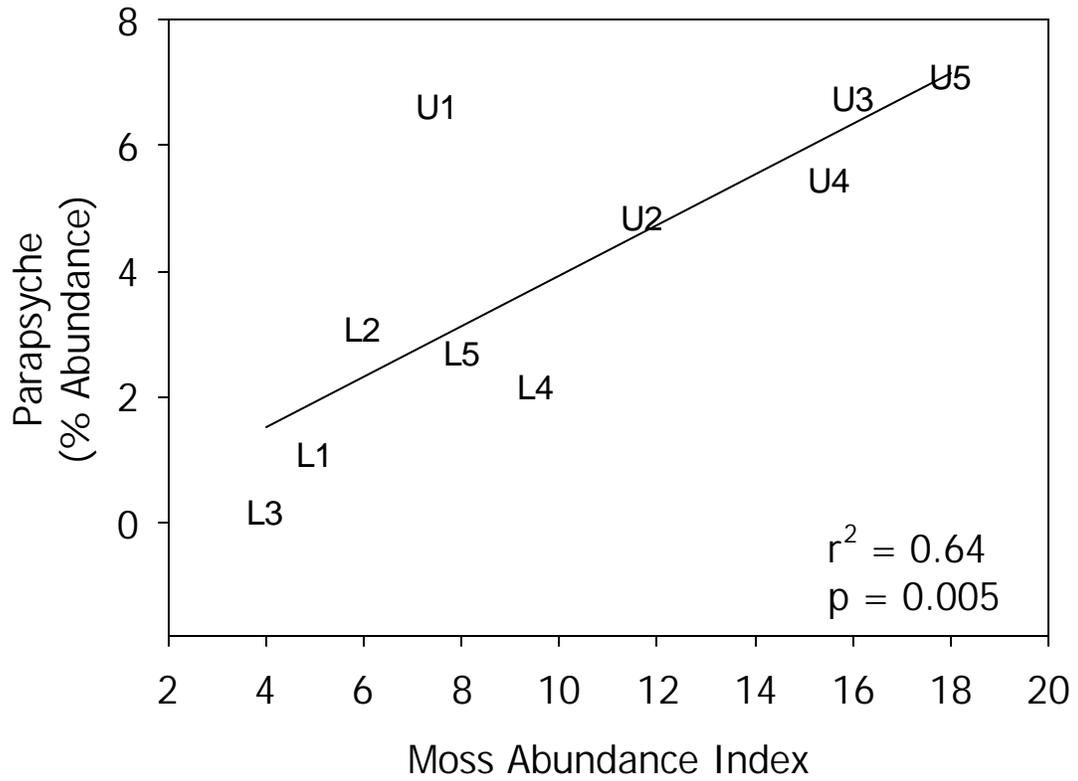


Figure 3. Cordulagaster abundance (% of total taxa collected) versus large cobble abundance in unlogged (U1-U5) JKSRW streams.

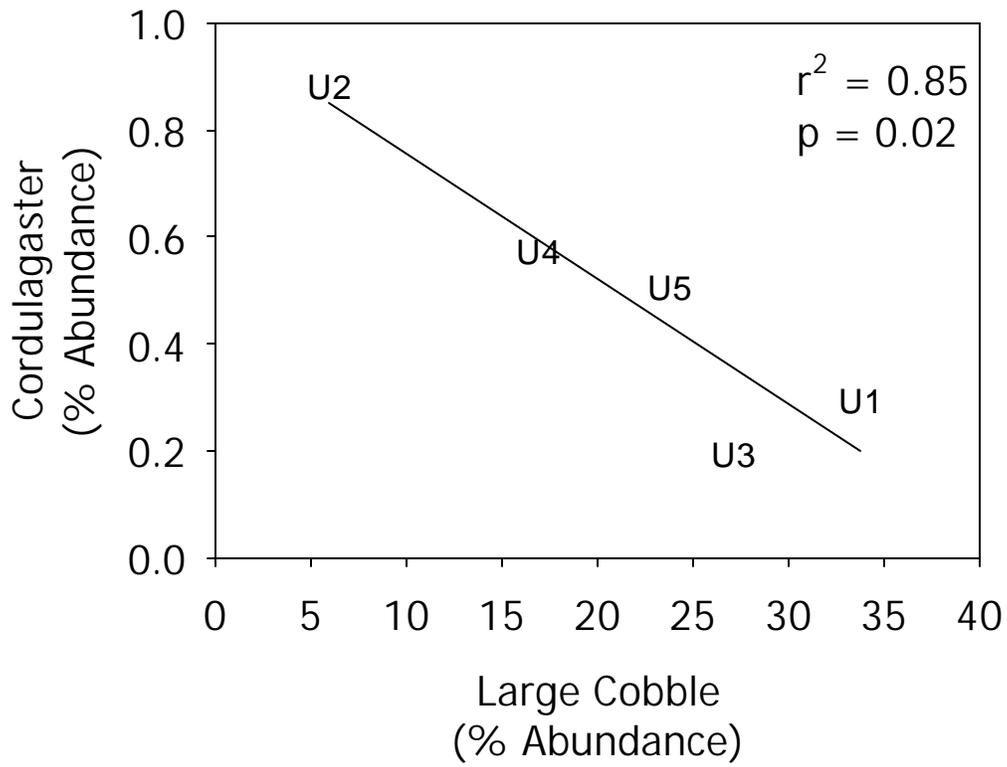


Figure 4. Scraper abundance (% of total taxa collected) versus moss abundance in unlogged (U1-U5) and logged (L1-L5) JKSRW streams.

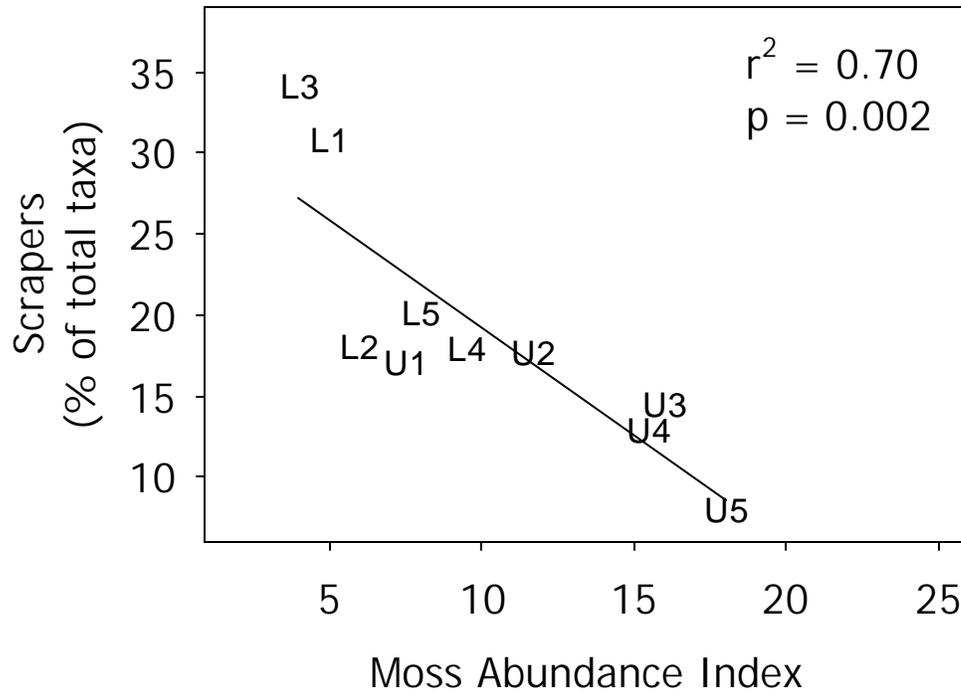


Figure 5. Shredder abundance (% of total taxa collected) versus moss abundance (index) in unlogged streams (U1-U5) and versus large cobble abundance in logged streams (L1-L5) in JKSRW.

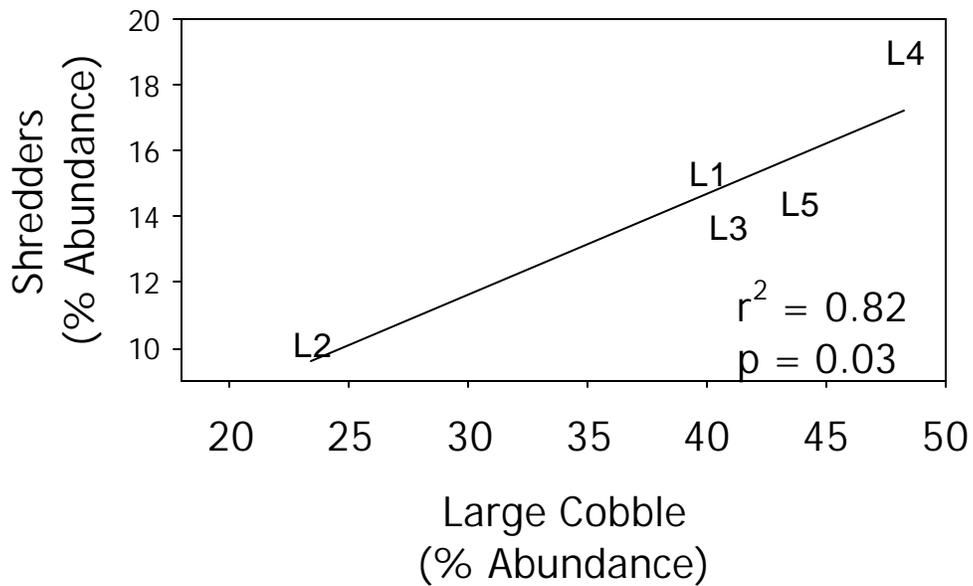
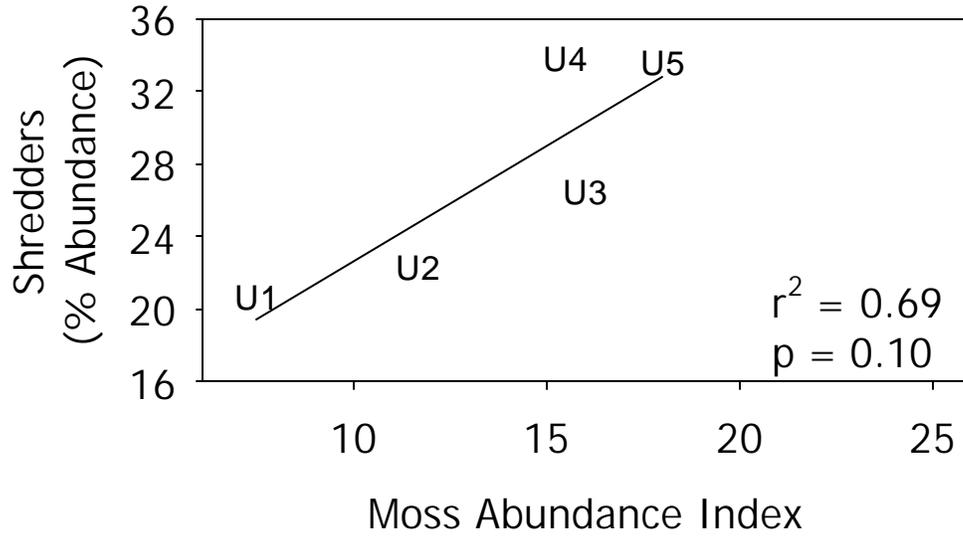


Figure 6. Tallaperla (% of total taxa collected) versus moss abundance index in unlogged streams (U1-U5) in JKSRW.

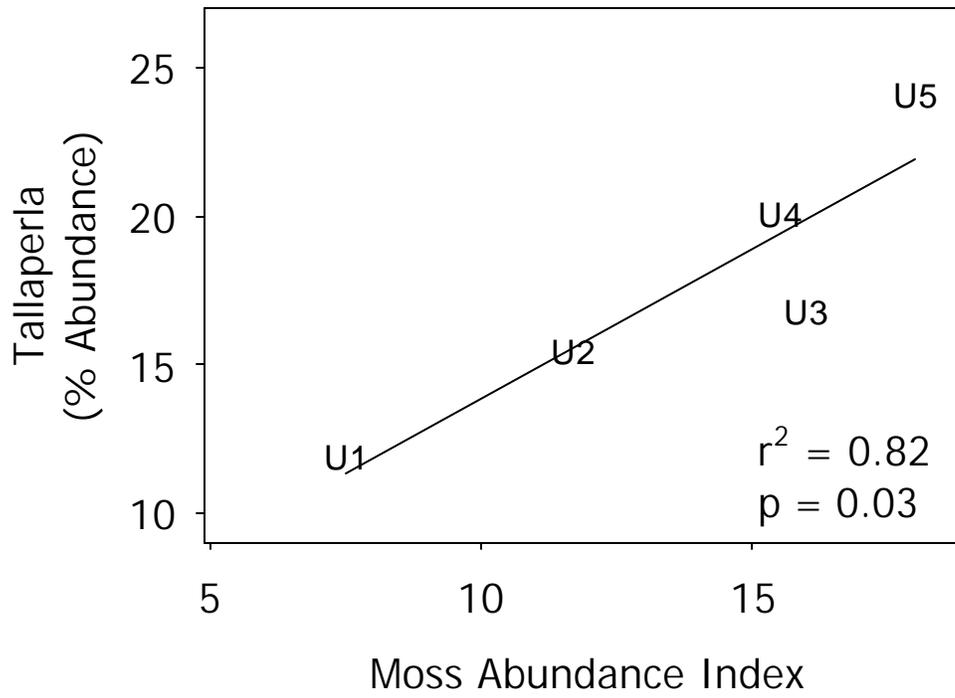


Figure 7. Pycnopsyche abundance (% of total taxa collected) versus % medium gravel and in unlogged (U1-U5) and versus % fine gravel in logged (L1-L5) streams in JKSRW.

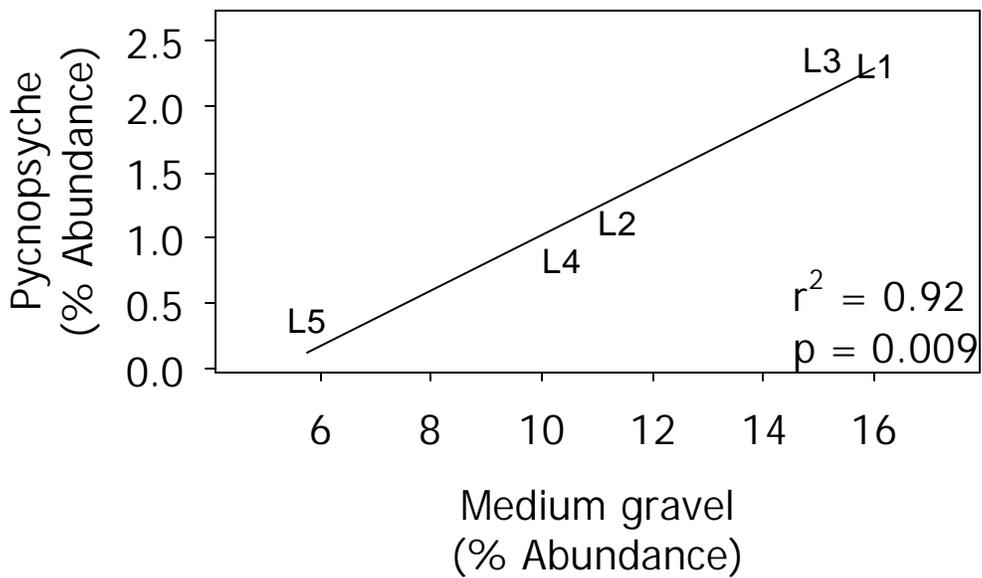
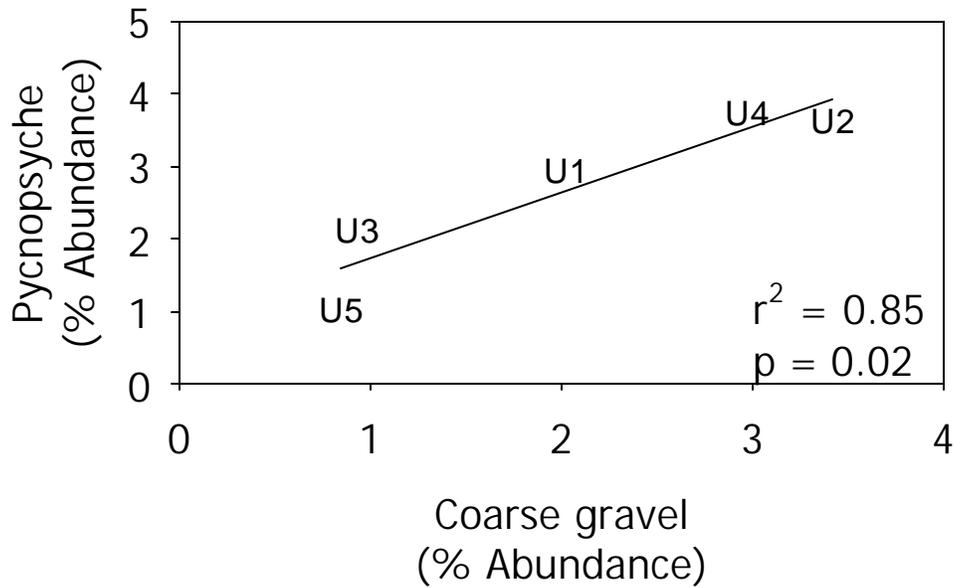


Figure 8. Fattigia abundance (% of total taxa collected) versus % abundance of fines in unlogged (U1-U5) and logged (L1) JKSRW streams.

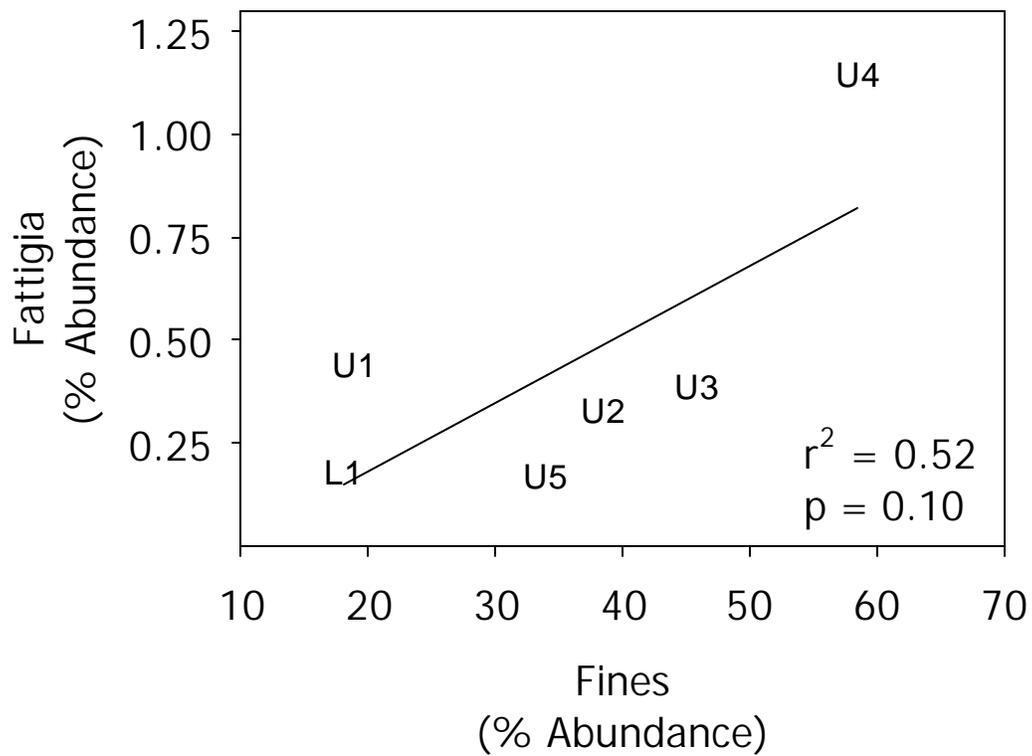


Figure 9. P/R index versus moss abundance in unlogged (U1-U5) and logged (L1-L5) JKSRW streams.

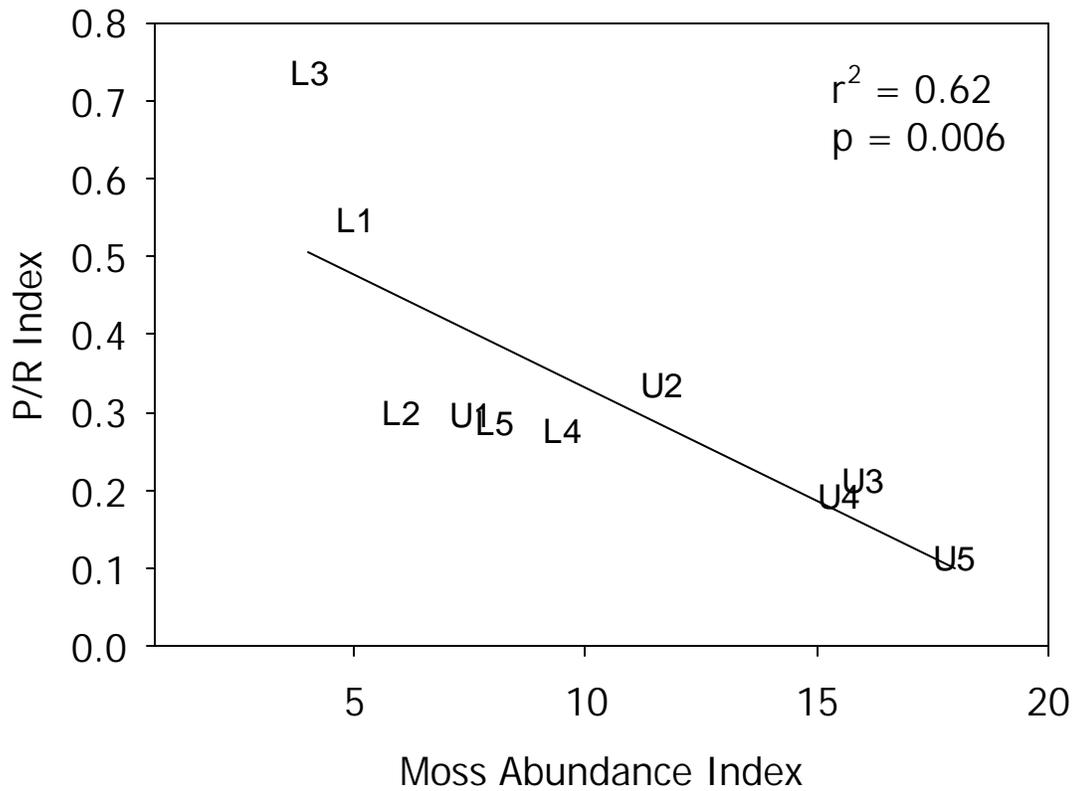
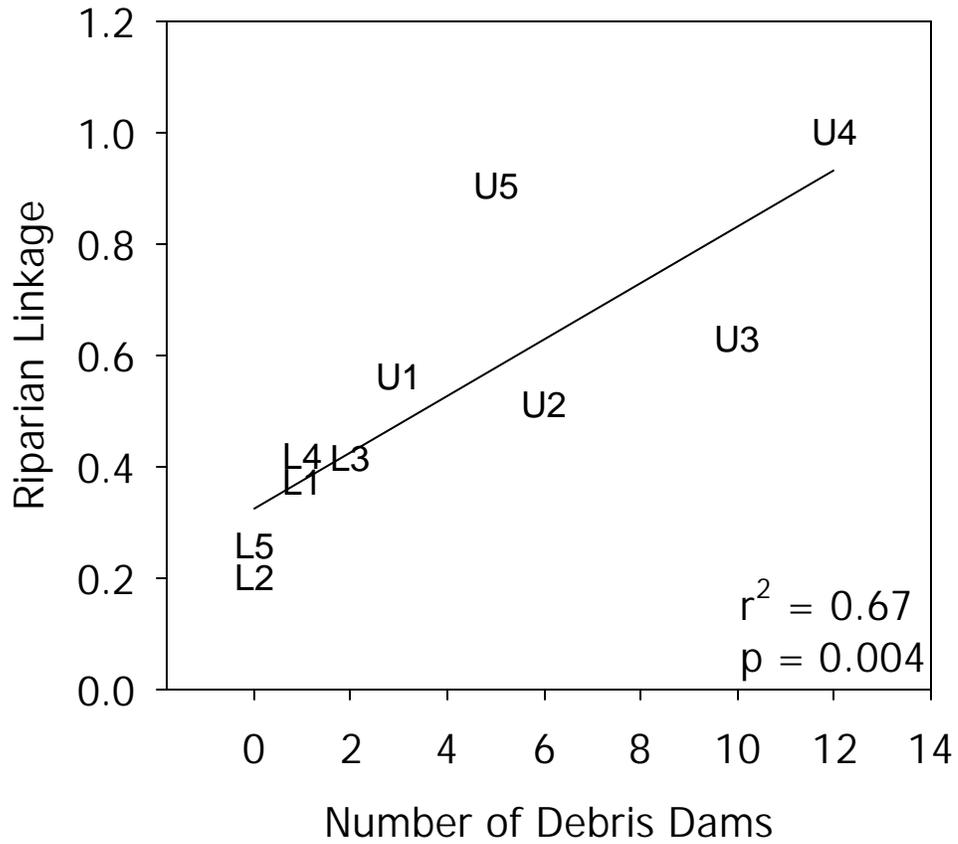


Figure 10. Riparian linkage scores versus the number of debris dams/100 m in unlogged (U1-U5) and logged (L1, L3, L4) JKSRW streams.



Chapter III

Nutrient retention and transient storage in unlogged and logged forests

Abstract

Transient storage and phosphorus (P) retention was studied in streams draining unlogged and logged catchments to determine if disturbance to nutrient and solute dynamics persists after 75+ y of recovery. Wood volume in streams draining unlogged catchments was several orders of magnitude greater than in logged catchments and streams in logged catchments had few or no debris dams in study reaches. Contrary to predictions, normalized transient storage was significantly greater in logged catchments rather than unlogged catchments and was negatively related to debris dam abundance that decreased streambed permeability. Additionally, P retention was not enhanced by transient storage and retention was negatively related to normalized transient storage. Uptake velocities were significantly greater in unlogged than logged streams and were high compared to published values for southern Appalachian streams. Nutrient retention was significantly related to debris dam abundance.

Introduction

Undisturbed southern Appalachian streams typically drain densely forested catchments and are heavily shaded. Most southern Appalachian forests are second or third growth reflecting the extensive regional logging that occurred following settlement by Europeans. Catchments without at least some logging history are very uncommon (Davis 1996). Wood is typically abundant in undisturbed low-order southern Appalachian streams, but streams in logged catchments often contain much less wood (Silsbee and Larson 1983, Fleebe and Dolloff 1995, Chapter 1) and removal of mature trees eliminates the primary input source of large wood capable of forming debris dams (Likens and Bilby 1982). Consequently, logging can decrease wood input rates for centuries.

Wood is important in stream geomorphology and ecosystem function (Bormann and Likens 1974, Sedell et al. 1978, Bilby and Likens 1980, Cummins et al. 1983, Silsbee and Larson 1983, Speaker et al. 1984, Harmon et al 1986, Fleebe and Dolloff 1995, Wallace et al. 1995, Wallace et al. 1997, Chapter II) and wood also influences nutrient dynamics (Munn and Meyer 1990, Wallace et al. 1995). Local geomorphology is important in nutrient retention and reaches containing debris dams can be the most retentive of some nutrients (Munn and Meyer 1990). Nutrient retention

should be highest in streams draining undisturbed forests and lowest in streams draining successional forests (Gorham et al. 1979, Webster and Swank 1985). Disturbances such as logging can increase nutrient export from forests to stream's and the absence of debris dams can reduce a streams ability to retain elevated nutrient loss and minimize downstream nutrient export (Odum 1969, Likens et al. 1970, Fisher and Likens 1973, Bormann et al. 1974, Vitousek and Reiners 1975). Consequently, nutrient retention in headwater streams has strong implications for downstream lakes, rivers, and estuaries (Meyer 1979). Because streams draining logged catchments in the Joyce Kilmer-Slickrock wilderness have significantly fewer debris dams than streams in unlogged catchments (Chapter I), I hypothesized logged streams in the Joyce Kilmer-Slickrock wilderness were less retentive of nutrients.

Nutrient dynamics in terrestrial and lotic habitats are inherently different due to the unidirectional flow of streams. Nutrients in terrestrial ecosystems may essentially cycle in place being absorbed, assimilated, and mineralized in approximately the same location. Nutrients in streams are continuously displaced downstream and therefore, spiral rather than cycle in place (Newbold et al. 1982). Spiraling length is the distance that a nutrient molecule travels before it is removed from solution (uptake length) plus the length that the same molecule travels until it is re-

mineralized (turnover length) (Newbold et al. 1982). Uptake length is the longest component of nutrient spiraling (Newbold et al. 1981). Measures derived from nutrient uptake used as indexes of nutrient retention length include uptake velocity (V_f) and areal uptake rates (U). Tracer (Cl^-) data from nutrient releases are used to determine if differences existed in solute storage (solute stored in the hyporheic and in backwater areas) in logged and unlogged streams. The cross-sectional area of the storage zone (A_s) relative to channel area (A) is commonly used as a measure of the size of the transient storage zone (Bencala et al. 1984, D' Angelo et al. 1993, Mulholland et al. 1997). The transient storage capacity of the hyporheic varies with channel morphology, bed roughness and permeability, and a permeable unconsolidated bed can have a significant transient storage zone (Triska et al. 1989). Because distinct differences exist in substrate composition and wood volume between unlogged and logged Joyce Kilmer-Slickrock wilderness streams, I predicted transient storage would also differ between unlogged and logged streams.

Study Site

This study was conducted in the Joyce Kilmer-Slickrock wilderness (Figure 1), which lies southwest of the Great Smoky Mountains National Park in the Nantahala National Forest. The Joyce Kilmer-Slickrock wilderness consists of two adjacent wilderness areas. Joyce Kilmer is in Graham Co. North Carolina and is one of the few remaining southern Appalachian forests that was never logged. The Slickrock wilderness was logged once and then allowed to recover. Slickrock wilderness borders the northwest boundary of Joyce Kilmer with portions of the forest residing in Graham Co., North Carolina and Monroe Co., Tennessee. Joyce Kilmer Memorial Forest is approximately 1540 ha and the Slickrock wilderness is approximately 4500 ha. Elevation ranges are from 670 m to 1585 m in Joyce Kilmer and from 330 m to 1585 m in Slickrock. Annual precipitation is normally > 200 cm per year (Daniels 1985). Joyce Kilmer is underlain primarily by arkosic metasandstone, muscovite phyllite and mica schist. Geology in Slickrock is similar and underlain by arkosic metasandstone, graphitic metagreywacke, and slate.

Vegetation types in the Joyce Kilmer-Slickrock wilderness include mixed mesophytic cove hardwood associations in moist lowlands and north facing slopes, mixed oak-hickory (Quercus spp.-Carya spp.) stands on steep side slopes, oak-pine (Quercus spp.-Pinus spp.) stands on

southern slopes, and rhododendron-laurel-azalea slicks on exposed ridges (Daniels et al. 1987). Eastern hemlock (Tsuga canadensis) is common throughout the Joyce Kilmer-Slickrock wilderness and is particularly abundant along streamsides, often with thick Rhododendron maximum understory. South facing slopes generally have thinner understory than north facing slopes.

Joyce Kilmer and Slickrock are similar geologically but differ in land use history. Joyce Kilmer was never logged and Slickrock was logged from 1917 until 1922. The area now designated as the Joyce Kilmer wilderness was examined for potential timber production at least as early as 1910 (Anon. 1910). The Joyce Kilmer wilderness was never logged due to several changes in ownership that repeatedly delayed logging and a flood around 1930 resulting from construction of Calderwood Lake Dam, which destroyed the only railroad access to the area. (personal communication, Cheoa Ranger Station, Graham Co., North Carolina).

The Babcock Land and Timber Company purchased the Slickrock portion of the Joyce Kilmer-Slickrock wilderness in the 1915. Babcock Land and Timber began logging in 1917 and logging ended in 1922 with the construction of Calderwood Dam. The area that presently composes the Joyce Kilmer-Slickrock wilderness was purchased by the U.S. Forest

Service in 1936 and designated wilderness in 1975 (personal communication, Cheoa Ranger Station, Graham Co., North Carolina).

Although forest composition is similar between Joyce Kilmer and Slickrock, evidence of past land-use in streams is present. Railroads were often constructed in streambeds because stream channels made the best roadbeds (Dolloff 1993) and logs were carried out of the forests on rail carts. Such railroads were constructed in many Slickrock streams (Homan 1990). In other instances, logs were simply pulled by Oxen or other animals downstream with out assistance of railroads. Although Babcock Land and Timber Company removed most of the rails, many streams still contain sections of track, pieces of cable, and other debris that was used in logging and later abandoned. Long sections of rail remain in stream L5 and long lengths of cable remain along the banks of L4. Old railroad grades are evident through other parts of the Slickrock wilderness and pieces of metal refuse are not uncommon.

Methods

Nutrient uptake length (S_w) and transient storage (A_s and A_s/A) in logged and unlogged catchments was examined by conducting nutrient (PO_4 -P) and conservative tracer (Cl^-) releases in six streams in the Joyce Kilmer-Slickrock wilderness (3 logged and 3 unlogged streams). Nutrient

uptake length and derived measures were used as a comparative measure of nutrient retention. Stream geomorphology was characterized and epilthon and chlorophyll-*a* standing crops and % organic matter of sediment were quantified. These data with substrate composition and wood data from Chapter I, were used to determine how differences in unlogged and logged streams affected nutrient uptake and transient storage.

Channel geomorphology and light

Wetted channel, active channel, and valley floor widths (sensu Gregory et al. 1991) were measured on transects perpendicular to the stream at intervals of five to ten meters along the length of each study reach (n = 7 – 13 transects/stream). Active channel (AC) dimensions were measured as the width of stream channel estimated to be occupied by annual high flow. Valley floor width (VFW) extended from hill-slope to hill-slope as indicated by gradient breaks between the hill-slope and stream channel. Mean values for each stream were used to characterize the study reaches as constrained or unconstrained based on the ratio of valley floor width to active channel (VFW:AC), where a ratio value greater than two is unconstrained and values less than two are constrained (sensu Gregory et al. 1991). Incident light was measured at mid-day at 7-13

evenly spaced locations along each study reach. Light was quantified as photon flux density ($\text{mol/m}^2/\text{s}$) with a Li-Cor LI-1000 Photometer set to integrate for a 1-minute interval at each station.

Epilithic organic matter and chlorophyll-*a* standing stocks were expressed as the mean of three samples taken from random locations along the stream reach. Each sample consisted of a composite scraping of a known area of three rocks of ca. 10 cm diameter collected randomly within a 10 m radius of a chosen sample site. Rocks were scrapped in the field and the composite slurry was filtered through an ashed and weighed glass fiber filter (Gelman Type AE) and then placed on ice for transport back to the laboratory. In the laboratory, filters were bisected and half used to quantify epilithic organic matter and half used to quantify chlorophyll. Epilithic organic matter was quantified as ash-free dry mass (AFDM) by drying filter halves for 24 hrs at 60° C, combusting them for 4 hours at 550° C, rewetting after cooling and subsequent drying for an additional 24 hrs. The second half of the filter was used to determine chlorophyll *a* content using buffered acetone extraction followed by monochromatic spectrophotometry (sensu Wetzel and Likens 1991).

Water chemistry

Water samples taken in the field were filtered within six hours of sampling using Gelman AE glass fiber filters and frozen until analyzed. Temperature, dissolved oxygen (DO), DO saturation (%), and temperature-compensated conductivity were recorded at 15-second intervals during the release using automated sondes (Hydrolab Minisonde 4A, Hydrolab Corporation, Austin, TX). Temperature, DO, and conductivity values recorded immediately before the releases were used to characterize background stream conditions. Background water samples were analyzed for chloride (Cl^-), $\text{NH}_4\text{-N}$, $\text{NO}_3\text{-N}$, ortho-phosphorus ($\text{PO}_4\text{-P}$), and dissolved organic carbon (DOC). Concentrations of Cl^- , $\text{NH}_4\text{-N}$, and $\text{NO}_3\text{-N}$ were determined on a Technicon Autoanalyzer II. Chloride was analyzed by the mercuric thiocyanate/ferric nitrate method (Zall et al. 1956). The phenolhypochlorite method (Solorzano 1969) and colorimetric analysis following cadmium reduction (Wood et al. 1967) was used to determine $\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$ concentrations, respectively. $\text{NO}_3\text{-N}$ in this study is the sum of $\text{NO}_3\text{-N}$ and nitrite-nitrogen. Ortho-phosphate was analyzed as SRP using the molybdate-antimony method (Murphy and Riley 1962) in a 10 cm flow path using a Shimadzu UV-1601 spectrophotometer (detection limit = 0.5 $\mu\text{g/L}$). Dissolved organic carbon was determined via persulfate digestion (Menzel and Vaccaro 1964) on an Oceanographic

International Model 700 Total Organic Carbon Analyzer. Total inorganic nitrogen (TIN) is presented as the sum of $\text{NO}_3\text{-N}$ and $\text{NH}_4\text{-N}$ and atomic N:P ratios calculated as $(\text{TIN}/ \text{PO}_4\text{-P}) \times 2.211$ (Shanz and Juon 1983).

Nutrient releases and transport modeling

Releases of a biologically active nutrient solute ($\text{PO}_4\text{-P}$) and a hydrologically conservative tracer (Cl^-) (Bencala et al. 1987) were conducted in each study stream during summer base flow and results were used to assess nutrient retention and transient storage. A concentrated solution of Cl^- (as NaCl) and $\text{PO}_4\text{-P}$ (as K_2HPO_4) was added at a constant rate to the head of each experimental reach using a fluid-metering pump (FMI, Inc.). The release solution was added at a natural constriction point and a reach of approximately 10-15 m was designated to ensure mixing of the release solution and stream water before the first sampling transect (sensu Triska et al. 1989a). Reach lengths for releases ranged from 50 – 80 m among study streams and 6 - 8 sampling transects were established at approximately equal intervals along each study reach. Background water samples were collected at each sampling transect before nutrient releases and samples were analyzed for chemical variables described above. All water samples were taken from mid-stream using acid-washed 125 ml HDPE bottles. After bottles were rinsed with stream

water, samples were collected and placed on ice within 2-4 hours of collection. Samples were filtered using glass-fiber filters (Whatman GFF, 0.45 μ m pore size), usually within 12 hours of collection and frozen for chemical analyses. At the sampling transect furthest downstream from the release, automated sondes (Hydrolab Minisonde Model 4A, Austin, Texas) were placed in the water at midstream to record conductivity, temperature, and dissolved oxygen every 15 seconds for the duration of the releases. Nutrient releases lasted an average of 3 hours reflecting the time required to reach plateau (steady state) conditions. Duplicate water samples were collected at each of the sampling transects and treated as described for background samples and analyzed for Cl^- and $\text{PO}_4\text{-P}$ to quantify nutrient retention (see below) once plateau conditions were reached. The release pump was stopped after collecting plateau samples and the sonde was monitored until conductivity returned to background values.

Solute Transport Modeling

A one-dimensional model of transport including inflow and transient storage (Bencala and Walters 1983, Runkel and Broshears 1991, D'Angelo et al. 1993, Hart 1995) was used to characterize hydrologic conditions in each study reach. Conductivity data from sondes were converted to Cl^-

concentrations using a regression derived in the laboratory. Chloride concentrations were used to analyze solute transport and to obtain predicted values of Cl^- concentration at the downstream transect using the model of Hart et al. (1995). Model output was compared visually with data collected by the sondes (sensu Harvey and Bencala 1993, Harvey et al. 1996, Harvey and Wagner 2000). A visual best-fit solution was derived and an optimization subroutine was used to statistically determine the best-fit parameters (see Hart et al. 1995, Harvey and Wagner 2000). Variables obtained from the model characterized features of both the surface channel and storage zone. Parameters included water velocity (v , m/s), stream channel cross sectional area (A , m^2), and storage zone cross sectional (A_S , m^2). The ratio A_S/A was used to estimate the storage zone size relative to the channel cross sectional area.

Analysis of plateau tracer concentrations: dilution and nutrient uptake

Stream depth (z , m) was determined from average width measures taken in the field and discharge and water velocity were derived from model output. Background and dilution corrected plateau $\text{PO}_4\text{-P}$ concentrations were natural-log transformed and regressed against distance downstream. Uptake lengths (S_W , m) were calculated as the negative inverse of the regression coefficient (Stream Solute Workshop

1990, Webster and Erhman 1996) and were normalized to stream depth and water velocity as the uptake velocity (V_f , mm/s) by equation (1):

$$V_f = ((vz)/(S_w)) 1000$$

where:

S_w = uptake length for PO_4 -P (m)

z = average stream depth (m)

v = average water velocity (m/s)

Uptake rates for PO_4 -P (U , mg P/m²/d) were calculated by equation (2) as the product of the uptake velocity and average background PO_4 -P concentration (Stream Solute Workshop 1990).

$$(2): U = (V_f [PO_4-P]) 8.64 \times 10^4$$

where:

U = areal PO_4 -P uptake rate (mg P/m²/d)

V_f = PO_4 -P uptake velocity (mm/s)

$[PO_4-P]$ = average background PO_4 -P concentration (mg/L)

This represents uptake rates under ambient nutrient conditions (Stream Solute Workshop 1990, Davis and Minshall 1999, Wolheim et al. 2000).

Statistical Analysis

Because of small sample size ($n = 3$ streams/forest type) and associated problems with tests of normality and equivalence of variance, non-parametric statistical analyses were primarily used to compare structure and function between streams in unlogged and logged catchments. Non-parametric t-tests (Wilcoxon Signed Rank test) were used to compare physical and chemical measures (e.g., stream geomorphology, solute transport parameters) and variables representing ecosystem structure (e.g., organic matter standing stocks, chl-*a*) and function (uptake length, uptake velocity). Spearman Rank Correlations were calculated for pairs of variables ($n = 6$) to assess relationships among streams. An alpha level of 0.05 was used for all statistical tests. Regressions were used to relate uptake parameters to independent variables predicted responsible for the observed differences. All regression models were run on natural log transformed variables except for variables that were arcsine square root transformed (DO % saturation, % sediment OM, relative abundance (%) of fine sediments) and those square-root transformed (atomic N:P ratio, ratio of valley floor width to width of active channel, normalized storage zone size, A_s/A). All variables were natural log transformed for parametric analysis in

regression models. Data are presented as mean \pm SD. All statistical analyses were performed on SAS Version 7.1 (SAS Institute, Carey, NC).

Results

Physical and chemical characteristics of streams

Background conductivity was relatively low in all study streams ranging from 7.2 to 11.9 μ S/cm and mean conductivity was significantly higher in logged (mean = 11.3 μ S \pm 0.21) than unlogged streams (mean = 8.3 μ S \pm 0.85) (p = 0.049, Table 1). All streams were well oxygenated and dissolved oxygen concentrations were not significantly different between stream types, but % saturation was significantly greater (p = 0.046) in logged than unlogged streams (88.7% \pm 0.67 versus 84.3 % \pm 1.76, respectively). Mean temperatures at the time of nutrient releases were significantly different (p = 0.046) and logged streams averaged 2.3 C° warmer than unlogged streams. Stream chemistry was not significantly different for any measures analyzed (Table 1) including concentrations of NH₄-N, NO₃-N, PO₄-P, DOC, and atomic N:P. Concentrations of NH₄-N and PO₄-P were low and similar throughout the study. Average TIN concentration was never greater than 180 μ g/L and NO₃-N was the major constituent (83 - 97%) due to low concentrations of

NH₄-N. Atomic N:P ratios corresponded to variation in NO₃-N concentration and ranged from 16.6 to 83. Average dissolved organic carbon concentrations were low in unlogged and logged streams (0.55 ±0.052 and 0.47 ±0.041 mg/L, respectively) and showed little variability.

Stream morphology

Values of stream channel morphology did not differ significantly between stream groups (Table 2) indicating similar valley floor and active channel widths. Valley floor widths were small (ca. 6-8 m) and active channels were approximately 2 - 3 m wide. Valley floor width was more variable among logged streams (CV = 37%) than in unlogged streams where VFW was relatively constant (CV = 6%). Ratios of VFW:AC averaged 3.42 and 2.15 for unlogged and logged streams, respectively, and were not significantly different. Light (photon flux density) beneath the canopy was low (12.2 - 14.2 mol/ m² /s) and not significantly different between stream types.

Average epilithic organic matter standing crop (AFDM) in unlogged streams was significantly greater than in logged streams (p = 0.049, Figure 2B). Epilithon standing crops in unlogged streams (10.2 ± 1.2 g AFDM/m²) were more than twice those in logged streams (4.1 ± 0.9 g AFDM/m²) resulting primarily from significantly greater organic matter

content per unit mass of epilithon ($p = 0.05$, Figure 2C). Average percent organic matter was $8.4\% \pm 1.0\%$ in unlogged streams, more than twice the average found for logged streams ($3.6\% \pm 0.7\%$).

Hydrology and transient storage

Base flow discharge ranged from a low 4.2 L/s in L4 to a high of 9.9 L/s in U3 and average discharge in unlogged and logged streams did not differ significantly (mean = 8.2 and 5.5 L/s, respectively) (Table 3). Stream cross-sectional area (A , m^2) and storage zone cross sectional-area (A_s) did not differ significantly with stream type, but the cross-sectional area of the storage zone normalized to stream cross-sectional area to channel area (A_s/A) was significantly different ($p = 0.05$). Streams draining logged catchments contained larger normalized transient storage zones than streams in unlogged catchments ($p = 0.05$). A_s/A was negatively correlated with the number of debris dams/100 m of stream ($r = -0.93$, $p = 0.01$, Figure 3).

Phosphorus uptake and retention

Stream water PO_4 -P concentrations were increased 3 times above ambient concentration during nutrient releases to an average of 0.008 ppm and 0.011 ppm in logged and unlogged streams, respectively.

Average uptake lengths (S_w) (Table 3) differed by a factor of almost two (45.7 m in unlogged streams and 87.6 m in logged streams) but did not differ significantly due high variability ($SE = \pm 10.7$ and 17.1 m, respectively) (Figure 4). Uptake lengths were significantly correlated with debris dam frequency ($r = -0.87$, $p = 0.02$). Uptake velocities (V_r) were significantly greater in unlogged streams (mean = 0.18 mm/s) than in logged streams (mean = 0.04 mm/s) ($p = 0.046$) and were correlated with debris dam frequency ($r = 0.99$, $p < 0.01$, Figure 5A) and sand abundance ($r = 0.83$, $p = 0.05$, Figure 5B). Correcting for ambient nutrient concentrations and expressed as uptake rate (U , $\mu\text{g}/\text{m}^2/\text{s}$), uptake velocities resulted in significantly ($p = 0.046$) greater rates of nutrient uptake (U) per area of stream bottom and uptake rates were related to debris dams ($r = 0.94$, $p = 0.01$, Figure 5C) and sand abundance ($r = 0.84$, $p = 0.025$, Figure 5D).

Discussion

Most southern Appalachian forests were commercially logged and virgin forest is uncommon in the region. A common long-term disturbance from logging to streams is a reduction of wood standing stocks (Silsbee and Larson 1983, Fleebe and Dolloff 1995, Chapter 1).

Logged streams in Slickrock had much less wood and fewer debris dams and differences in substrate composition were related to wood (Chapter 1). Because wood and inorganic substrate can influence nutrient demand and hydrologic characteristics, transient storage and nutrient retention were expected to differ between logged and unlogged Joyce Kilmer-Slickrock wilderness streams.

Contrary to my prediction, normalized transient storage size (A_s/A) was larger in logged than unlogged streams. My prediction was based on the assumption that debris dams (more abundant in unlogged streams) would result in aboveground slack-water areas that increase transient storage. Although unlogged streambeds had more debris dams, A_s/A was greater in logged streams and negatively related to debris dam frequency rather than positively as predicted. Recently, studies have cautioned against attributing storage to aboveground slack water areas (Harvey et al. 1996, Harvey and Wagner 2000) and accumulation of sand associated with debris dams can reduce water infiltration into the streambed (Munn and Meyer 1990). Hydraulic conductivity is related to particle size (Freeze and Cherry 1979, Fetter 1994) and unlogged streambeds had more sand (Chapter 1). The abundance of sand in unlogged streams probably decreased hydraulic conductivity and resulted in less hyporheic transient storage. Because of the absence of above ground storage potential (e.g.

debris dams) in logged streams versus the abundance of storage potential in unlogged streams, it is likely that much of the transient storage in Joyce Kilmer-Slickrock wilderness streams is hyporheic. Consequently, transient storage in these streams is strongly, but indirectly, influenced by debris dams that retain sand and influence substrate composition.

The transient storage capacity of the hyporheic varies with channel morphology, bed roughness and permeability and a permeable unconsolidated bed can have a significant transient storage zone (Triska et al. 1989). Solute storage can enhance nutrient uptake and storage can be greater in the hyporheic than in the stream channel at low flow (Triska et al. 1989). The interactive surface area between water and the hyporheic zone was likely greater in logged streams as indicated by A_s/A . Despite this, uptake velocities and rates were greater in unlogged streams, underscoring the importance of debris dams in nutrient retention. Munn and Meyer (1990) noted that uptake rates across debris dams might be lower than otherwise expected because of the accumulation of fines that reduces water infiltration and the total area of solute-streambed contact. I expected uptake length, velocity, and rate to be positively correlated with A_s/A , but uptake length and rate were not significantly related to A_s/A and uptake velocity was negatively related to A_s/A . These data suggest that differences in nutrient retention in Joyce

Kilmer-Slickrock wilderness streams result primarily from water-column demand rather than hyporheic uptake.

Uptake length did not differ between unlogged and logged streams, but uptake length is not necessarily the best index of nutrient retention. Nutrient retention decreases and uptake length increases as water velocity and depth increase because contact between the water column and streambed is decreased (D'Angelo and Webster 1991, Valett et al. 1996). Uptake velocity calculated from uptake parameters published streams in the region range from 0.007 to 0.07 (Newbold et al. 1983, Mulholland et al. 1990, 1997, Munn and Meyer 1990, Webster et al. 1991) and uptake rates in unlogged Joyce Kilmer streams are comparatively high. Uptake rate in unlogged Joyce Kilmer streams was most similar to an Idaho wilderness stream (range = 0.113-0.121mm/s) (Davis and Minshall 1999). My study was conducted in July when leaf input is minimal and the previous autumnal input had undergone many months of processing. Consequently, leaf accumulations were probably at or near annual lows and uptake velocity might be even greater at other times of the year when leaves are plentiful in streams (D'Angelo and Webster 1991, Webster et al. 1991).

I believe that differences in uptake are probably primarily due to biotic uptake rather than abiotic uptake. Benthic organic matter can

strongly influence P uptake rates in forested headwater streams (Newbold et al. 1983, Mulholland et al. 1985, D'Angelo 1990) and standing stocks of wood were much greater in unlogged Joyce Kilmer streams. Wood can increase nutrient demand by acting as a biologically active substrate (Tank et al. 1998, Tank and Webster 1999) and demand from wood can be greater than that by FPOM and sediment (Aumen et al. 1990). Sand abundance is related to wood probably because debris dams increase retention of fine particles and decrease scour (Bilby 1981). Small substrate can have higher P demand because of greater surface area to volume ratio, but it is unlikely that the greater abundance of small substrate in unlogged streams is responsible for differences in V_f . Sand was more abundant in unlogged streams, but streambeds were probably less permeable (as indicated by A_s/A). Consequently, the total interactive surface area between streambed substrates and the nutrient supply is probably less in unlogged streams (sensu Munn and Meyer 1990). Also, Munn and Meyer (1990) found that essentially all phosphorus uptake in nearby Hugh White Creek was the result of biotic uptake rather than abiotic sorption. Biological demand for phosphate in unlogged catchments is probably also greater due in part to uptake by epilithon that was greater in unlogged streams. Thus, nutrient retention in unlogged streams is greater than in logged streams due to the presence of more

wood that provides more biologically active substrate and perhaps because of greater standing crops of epilithon.

Disturbed ecosystems are often less retentive of nutrients than undisturbed ecosystems (Odum 1969, Fisher and Likens 1973, Bormann et al. 1974). Although logging can disturb stream ecosystems in numerous ways (see review by Campbell and Doeg 1989), the loss of large wood and debris dams can be the most persistent disturbance to streams and can last for centuries (Likens and Bilby 1979, Golladay et al. 1987). Differences in wood volume and debris dam frequency can cause successional streams to be less retentive of nutrients than undisturbed streams (Webster and Swank 1985). Unlogged and logged Joyce Kilmer-Slickrock wilderness streams drain mature forests and had similar geomorphology and Chl-*a* standing crops. Despite differences in land-use history, there was no significant difference in stream morphology, discharge, water velocity, and Chl-*a* standing crops. The most notable evidence of disturbance from historic land-use was that streams in unlogged Joyce Kilmer catchments contained more wood and more debris dams. Consistent with successional theory, logged streams were less retentive of nutrients and differences in retention were strongly related to debris dam frequency. Decreased wood standing stocks following logging are well documented (Bryant 1980, Silsbee and Larson 1983, Hedin et al.

1988, Flebbe and Dolloff 1995, Chapter 1) and there is little or no accumulation of large wood in Slickrock. Consequently, it is likely that nutrient retention will be dissimilar between unlogged and logged streams for centuries and will not recover until forest senesce and wood input rates return to pre-disturbance levels.

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Table 1. Chemical properties and temperatures of stream water in unlogged (U1, U3, U5) and logged (L2, L4, L5) JKSRW catchments.

| | Cond (μS/cm) | DO (mg/L) | DO (% sat.) | Temp. ($^{\circ}$C) | NO₃-N (mg/L) | NH₄-N (mg/L) | PO₄-P (mg/L) | DOC (mg/L) |
|---------------|--|----------------------|------------------------|---|------------------------------------|------------------------------------|------------------------------------|-----------------------|
| U1 | 7.6 | 7.7 | 81 | 17.6 | 0.054 | 0.004 | 0.005 | 0.65 |
| U3 | 7.3 | 8.1 | 85 | 17.3 | 0.020 | 0.004 | 0.003 | 0.54 |
| U5 | 10.0 | 8.5 | 87 | 16.5 | 0.124 | 0.005 | 0.005 | 0.47 |
| Mean \pm SD | 8.3 \pm 1.5 | 8.1 \pm 0.4 | 84.2 \pm 3.1 | 17.1 \pm 0.6 | 0.66 \pm 0.53 | 0.004 \pm 0.001 | 0.004 \pm 0.001 | 0.55 \pm 0.09 |
| L2 | 11.4 | 7.8 | 88 | 19.9 | 0.041 | 0.004 | 0.006 | 0.56 |
| L4 | 11.6 | 7.6 | 90 | 19.2 | 0.140 | 0.004 | 0.005 | 0.44 |
| L5 | 10.9 | 7.2 | 88 | 19.2 | 0.183 | 0.006 | 0.005 | 0.43 |
| Mean \pm SD | 11.3 \pm 0.36 | 7.5 \pm 0.3 | 88 \pm 1.2 | 19.4 \pm 0.4 | 0.121 \pm 0.073 | 0.005 \pm 0.001 | 0.005 \pm 0.001 | 0.48 \pm 0.07 |
| t-test | 0.049 | NS | 0.046 | 0.046 | NS | NS | NS | NS |

Table 2. Channel geomorphology, light (PAR), and epilithon in unlogged (U1, U3, U5) and logged (L2, L4, L5) JKSRW catchments.

| | Debris dams #/100m | Valley Floor Width (m) | Active Channel (m) | VFW/AC | PAR ($\mu\text{m}^2/\text{s}$) | Chl a (mg/m^2) | Epilithon (g/m^2) | Epilithon OM (%) |
|---------------|-----------------------------------|---------------------------------------|-----------------------------------|-----------------|--|--|---|---------------------------------|
| U1 | 2.25 | 7.46 | 4.03 | 1.85 | 8.0 | 38.5 | 11.43 | 8.1 |
| U3 | 10 | 7.90 | 2.25 | 3.51 | 19.9 | 33.1 | 11.45 | 10.2 |
| U5 | 5 | 8.44 | 1.72 | 4.91 | 14.7 | 27.6 | 7.76 | 6.8 |
| Mean \pm SD | 5.75 \pm 3.93 | 7.93 \pm 0.49 | 2.67 \pm 1.21 | 3.42 \pm 1.53 | 14.2 \pm 6.0 | 33.1 \pm 5.5 | 10.21 \pm 2.12 | 8.4 \pm 1.7 |
| L2 | 0 | 4.12 | 2.26 | 1.82 | 14.4 | 38.7 | 3.76 | 4.5 |
| L4 | 1 | 5.80 | 2.73 | 2.12 | 11.5 | 42.3 | 2.65 | 2.2 |
| L5 | 0 | 8.70 | 3.46 | 2.51 | 10.7 | 18.5 | 5.83 | 3.9 |
| Mean \pm SD | 0.33 \pm 0.58 | 6.21 \pm 2.32 | 2.82 \pm 0.60 | 2.15 \pm 0.35 | 12.2 \pm 1.9 | 33.2 \pm 12.8 | 4.08 \pm 1.61 | 3.6 \pm 1.2 |
| t-test | 0.02 | NS | NS | NS | NS | NS | 0.049 | 0.05 |

Table 3. Width (w), depth (z), discharge (Q), transient storage (A, A_s, A_s/A), and uptake parameters (S_w, V_f, U) for JKSRW streams.

| | W (m) | z (m) | Q (L) | A (m²) | A_s (m²) | A_s/A | S_w (m) | V_f (mm/s) | U (mg- P/m²/d) |
|------------|------------------|------------------|------------------|------------------------------|--|------------------------|------------------------------|---------------------------------|--------------------------------------|
| U1 | 1.81 | 0.061 | 6.5 | 0.11 | 0.060 | 0.545 | 58 | 0.076 | 33 |
| U3 | 1.22 | 0.147 | 8.2 | 0.18 | 0.064 | 0.356 | 54 | 0.269 | 70 |
| U5 | 1.72 | 0.064 | 9.9 | 0.11 | 0.065 | 0.591 | 24 | 0.204 | 88 |
| Mean | 1.58 | 0.091 | 8.2 | 0.13 | 0.063 | 0.497 | 45 | 0.183 | 64 |
| <u>±SD</u> | <u>±0.32</u> | <u>±0.049</u> | <u>±0.98</u> | <u>±0.04</u> | <u>±0.003</u> | <u>±0.125</u> | <u>±19</u> | <u>±0.098</u> | <u>±28</u> |
| L2 | 2.20 | 0.031 | 8.0 | 0.07 | 0.068 | 0.971 | 113 | 0.021 | 11 |
| L4 | 1.43 | 0.111 | 4.2 | 0.16 | 0.129 | 0.811 | 55 | 0.073 | 32 |
| L5 | 3.46 | 0.031 | 4.3 | 0.11 | 0.094 | 0.856 | 95 | 0.025 | 11 |
| Mean | 2.36 | 0.058 | 5.5 | 0.11 | 0.097 | 0.880 | 88 | 0.039 | 18 |
| <u>±SD</u> | <u>±1.02</u> | <u>±0.046</u> | <u>±1.25</u> | <u>±0.04</u> | <u>±0.031</u> | <u>±0.083</u> | <u>±30</u> | <u>±0.029</u> | <u>±12</u> |
| t-test | NS | NS | NS | NS | NS | 0.05 | NS | 0.046 | 0.046 |

Figure 1. Map of Southeastern United States showing location of the Joyce Kilmer-Slickrock Wilderness (JKSRW). Detailed map shows study sections of unlogged (U1-U5) and logged (L1-L5) streams.

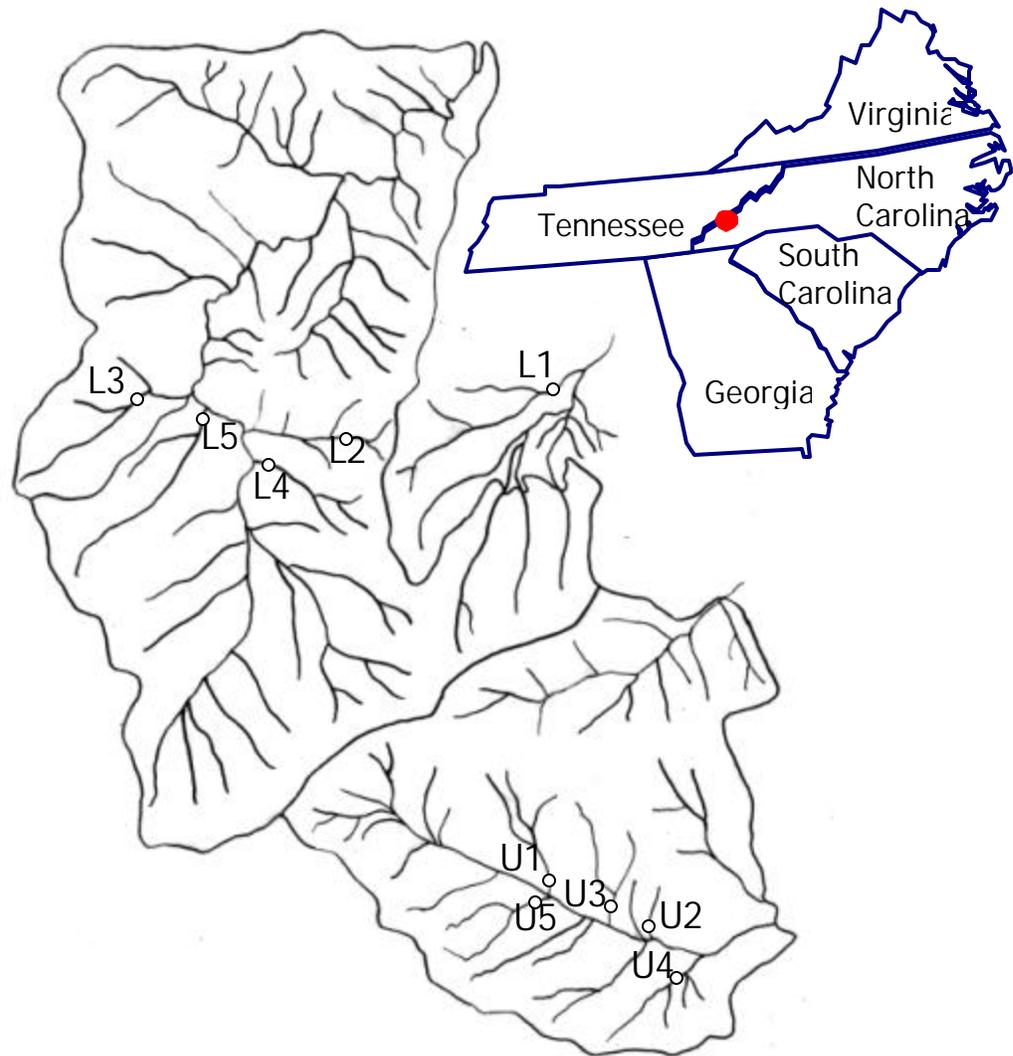


Figure 2. Mean Chl-a biomass (A), % organic matter of epilithon (B), and epilithon organic matter mass (C) in unlogged and logged JKSRW streams. Bars represent standard error.

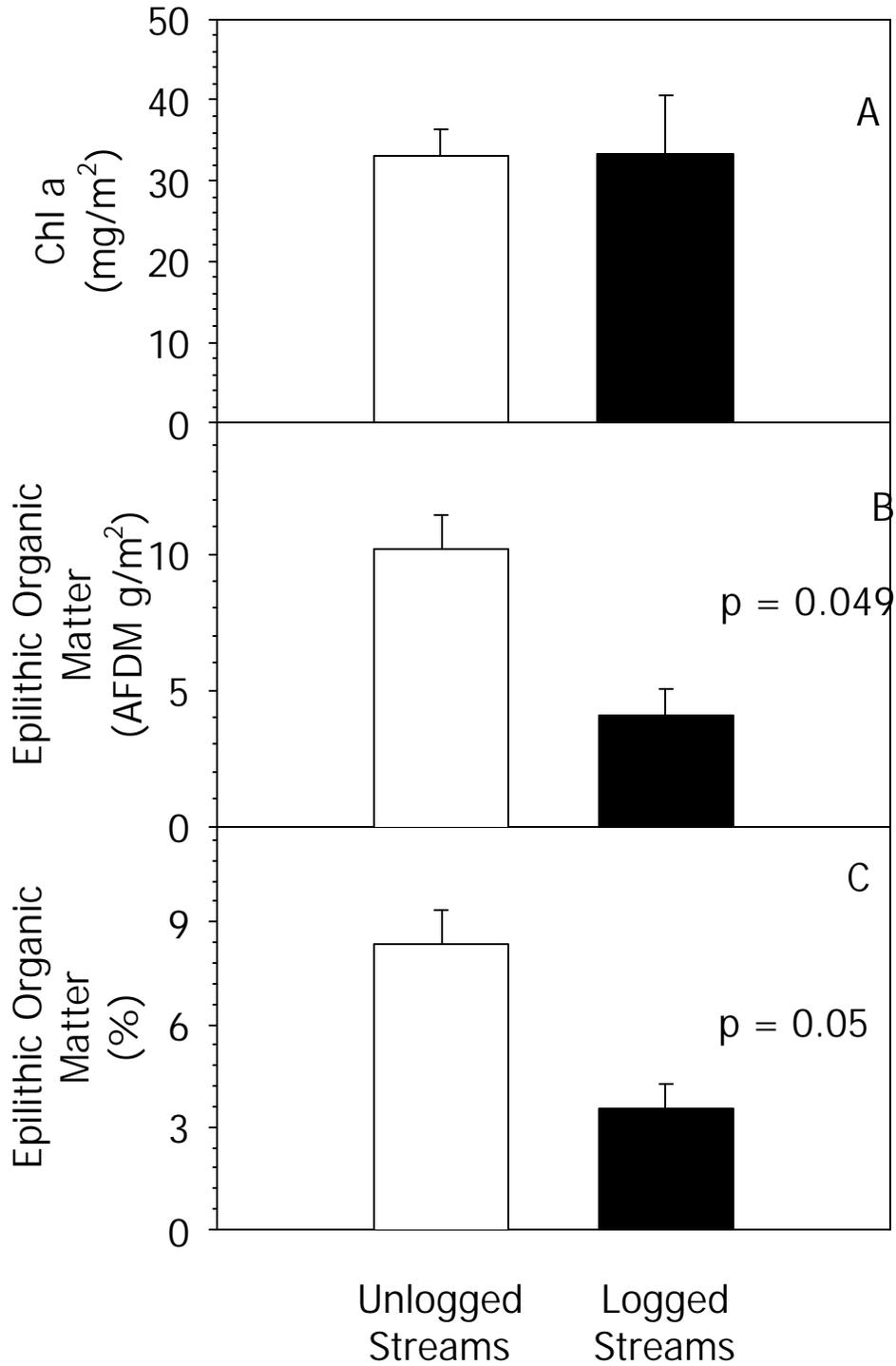


Figure 3. Transient storage versus debris dam frequency in unlogged (U) and logged (L) streams.

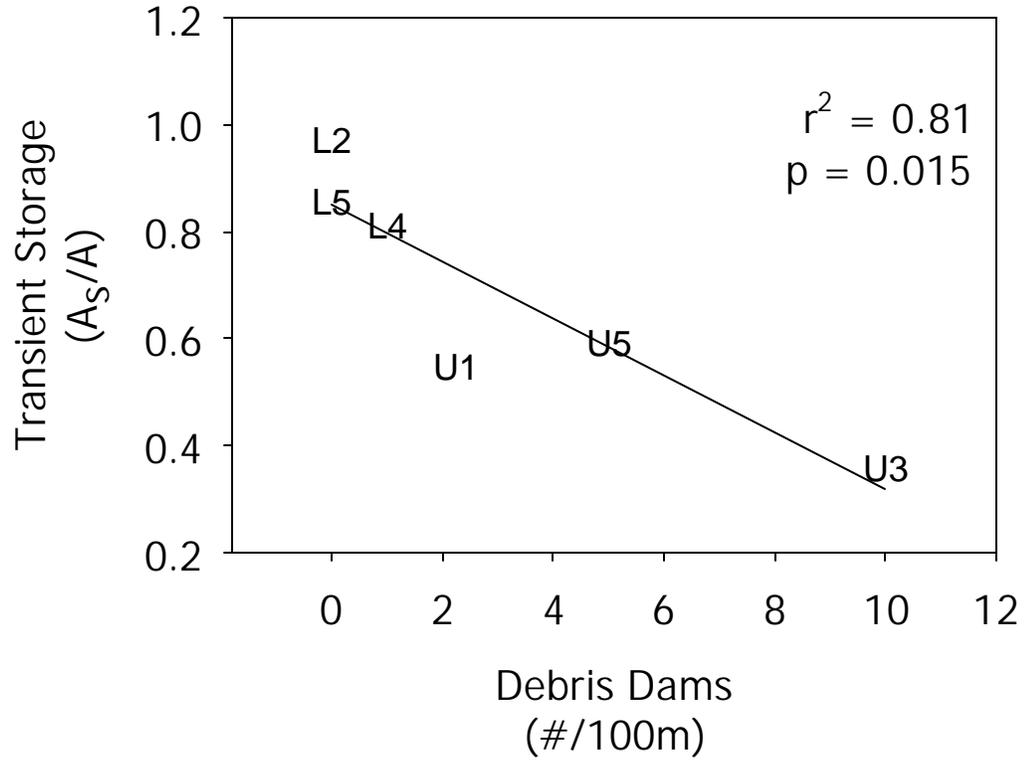


Figure 4. Mean uptake length (A), uptake velocity (B), and uptake rate (C). Bars represent standard error.

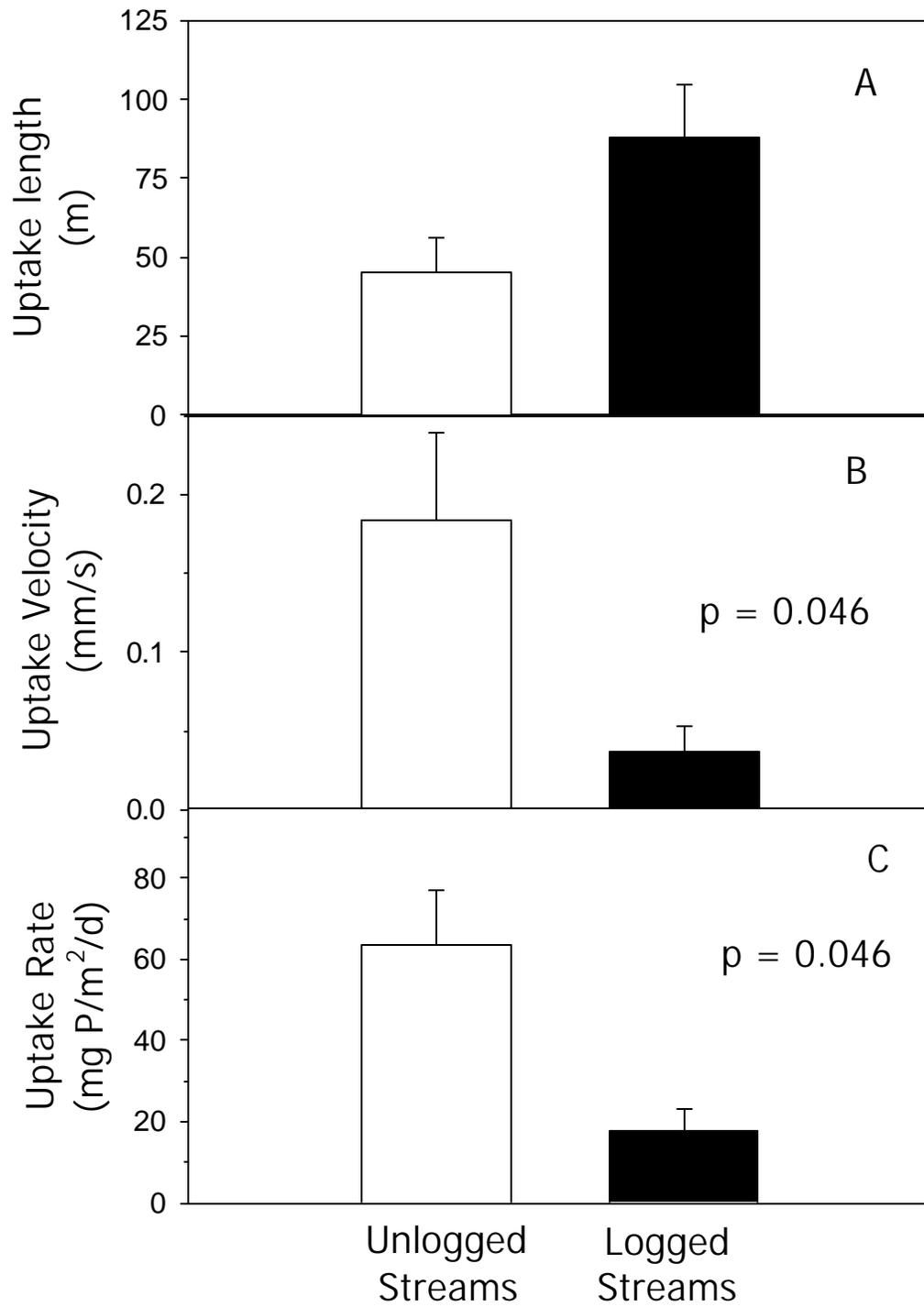
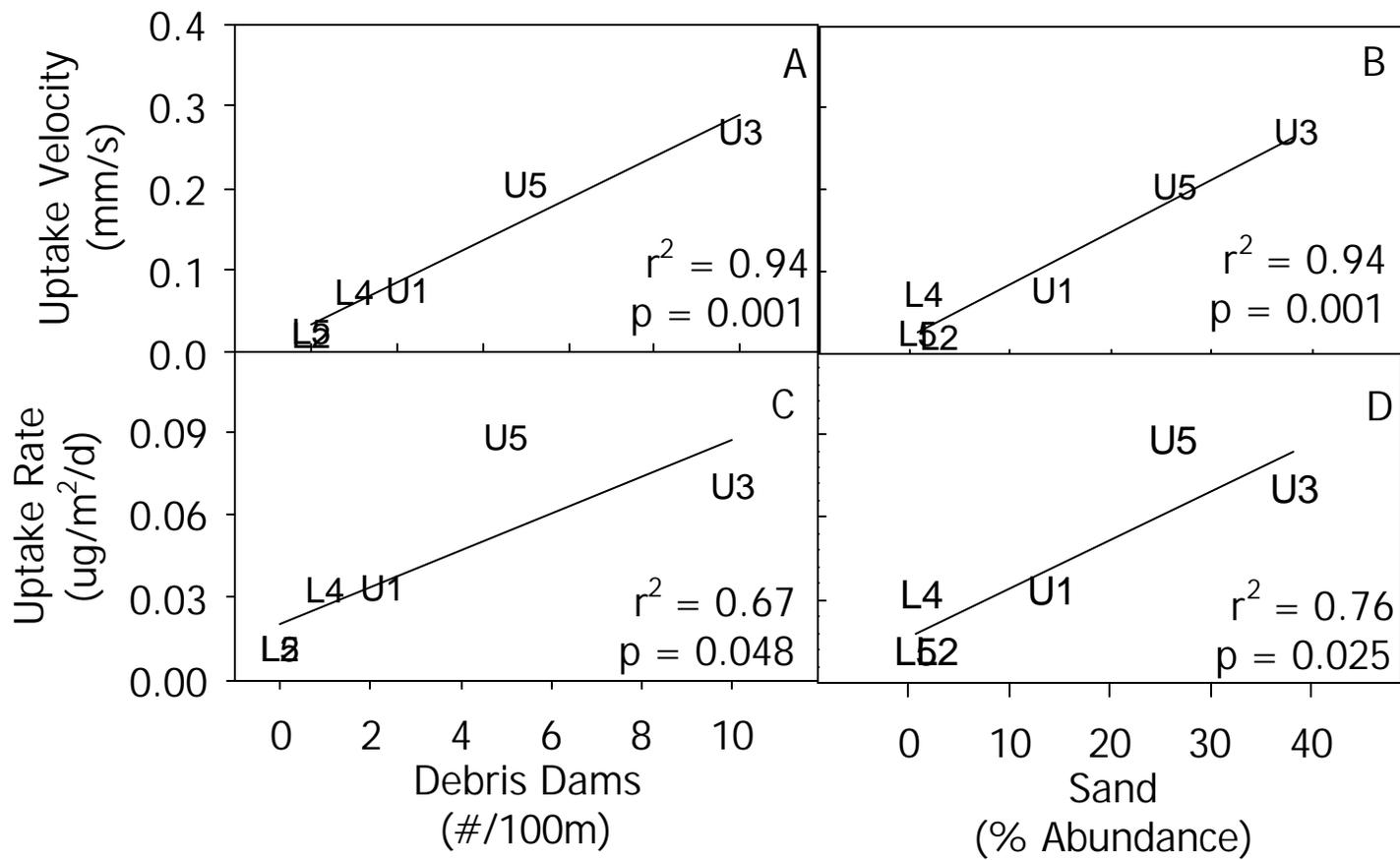


Figure 5. Uptake velocity of PO₄-P versus debris dam frequency (A) and sand abundance (B) and uptake rate of PO₄-P versus debris dam frequency (C) and sand abundance (D).



Chapter IV

The long-term effects of early 20th century logging on leaf and wood breakdown rates in streams.

Abstract

Wood and leaf breakdown were studied in unlogged and logged streams to determine if past land-use affects organic matter breakdown rates after 75 y of recovery. Mean breakdown rate of experimental leaf packs and wood veneers (sticks) was highly similar between unlogged and logged streams. Leaf breakdown was fast compared to other studies and strongly related to shredder colonization, while wood breakdown was unrelated to variables measured including nutrient concentration, debris dam frequency, and streambed substrate composition. Tallaperla sp. was the most abundant shredder in packs from unlogged streams and Amphinemura sp. was the most abundant shredder in leaf packs in logged streams. Data suggest that breakdown rates are restored to pre-disturbance levels following less than 75 y of catchment recovery.

Introduction

Headwater streams in undisturbed forests typically have well-developed riparian vegetation with dense overhanging canopies and are heavily shaded, resulting in little autochthonous primary production (Vannote et al. 1980, Minshall 1983). Energy in forested streams comes primarily from terrestrially fixed carbon and enters largely as autumnally shed leaves and year-round inputs of wood. Thus, forested headwater streams are tightly linked to the forests they drain by the processing of allochthonous inputs (Fisher and Likens 1972) and depend energetically on the processing of leaves, and to a lesser extent, wood.

Because forested streams are tightly linked to the catchments they drain, disturbances to forests can alter stream ecosystem structure and function. Most southern Appalachian forests were logged (Davis 1996) and disturbance from logging can persist in streams long after vegetation returns (Silsbee and Larson 1983, Harding et al. 1998). Disturbance from logging to streams can include elevated nutrient concentrations (Likens et al. 1970, Silsbee and Larson 1983, Campbell and Doeg 1989), increased sedimentation (Tebo 1955, Crickmay 1974, Lemly 1982), decreased organic matter retention, changes in macroinvertebrate functional feeding group abundances (Haefner and Wallace 1981, Hawkins et al 1982,

Silsbee and Larson 1983, Chapter II) and increased water temperatures (Webster and Waide 1982, Culp and Davies 1983). Changes in the aforementioned can alter organic matter processing rates (Sedell et al. 1975, Short et al. 1980, Webster and Waide 1982, Benfield and Webster 1985, Webster and Benfield 1986, Golladay and Webster 1988, Campbell and Doeg 1989, Griffith and Perry 1991, D'Angelo and Webster 1992, Tank and Webster 1998). Streams in the Joyce Kilmer-Slickrock wilderness continue to show response to past logging disturbance (Chapters I-III), and I investigated leaf and wood breakdown and invertebrate colonization of experimental leaf packs to determine if organic matter (OM) breakdown also responds to logging following 75 y of recovery.

Study Site

This study was conducted in the Joyce Kilmer-Slickrock wilderness (Figure 1), which lies southwest of the Great Smoky Mountains National Park in the Nantahala National Forest. The Joyce Kilmer-Slickrock wilderness consists of two adjacent wilderness areas. Joyce Kilmer is in Graham Co. North Carolina and is one of the few remaining southern Appalachian forests that was never logged. The Slickrock wilderness was logged once and then allowed to recover. Slickrock wilderness borders

the northwest boundary of Joyce Kilmer with portions of the forest residing in Graham Co., North Carolina and Monroe Co., Tennessee. Joyce Kilmer Memorial Forest is approximately 1540 ha and the Slickrock wilderness is approximately 4500 ha. Elevation ranges are from 670 m to 1585 m in Joyce Kilmer and from 330 m to 1585 m in Slickrock. Annual precipitation is normally > 200 cm per year (Daniels 1985). Joyce Kilmer is underlain primarily by arkosic metasandstone, muscovite phyllite and mica schist. Geology in Slickrock is similar and underlain by arkosic metasandstone, graphitic metagreywacke, and slate.

Vegetation types in the Joyce Kilmer-Slickrock wilderness include mixed mesophytic cove hardwood associations in moist lowlands and north facing slopes, mixed oak-hickory (Quercus spp.-Carya spp.) stands on steep side slopes, oak-pine (Quercus spp.-Pinus spp.) stands on southern slopes, and rhododendron-laurel-azalea slicks on exposed ridges (Daniels et al. 1987). Eastern hemlock (Tsuga canadensis) is common throughout the Joyce Kilmer-Slickrock wilderness and is particularly abundant along streamsides, often with thick Rhododendron maximum understory. South facing slopes generally have thinner understory than north facing slopes.

Joyce Kilmer and Slickrock are similar geologically but differ in land use history. Joyce Kilmer was never logged and Slickrock was logged

from 1917 until 1922. The area now designated as the Joyce Kilmer wilderness was examined for potential timber production at least as early as 1910 (Anon. 1910). The Joyce Kilmer wilderness was never logged due to several changes in ownership that repeatedly delayed logging and a flood around 1930 resulting from construction of Calderwood Lake Dam, which destroyed the only railroad access to the area. (personal communication, Cheoa Ranger Station, Graham Co., North Carolina).

The Babcock Land and Timber Company purchased the Slickrock portion of the Joyce Kilmer-Slickrock wilderness in the 1915. Babcock Land and Timber began logging in 1917 and logging ended in 1922 with the construction of Calderwood Dam. The area that presently composes the Joyce Kilmer-Slickrock wilderness was purchased by the U.S. Forest Service in 1936 and designated wilderness in 1975 (personal communication, Cheoa Ranger Station, Graham Co., North Carolina).

Study streams in the Joyce Kilmer-Slickrock wilderness (Figure 1) were selected based on land use history (streams in unlogged Joyce Kilmer catchments versus logged Slickrock catchments), similarity in size range between treatments, and similarity in slope. Five replicate unlogged catchments in Joyce Kilmer (U1-U5) and five replicate catchments logged ca. 75 y ago (L1-L5) were studied for comparison. Catchment area is the total area within each watershed upstream of each

sampling site and slope was estimated from USGS topographical maps. Streams in unlogged forests drained catchments ranging from 47 to 151 ha and stream gradients ranged from 8.8 to 21.8%. Logged catchments ranged from 35 to 227 ha and stream slopes ranging from 9.1 to 23.6 %, respectively.

Although forest composition is similar between Joyce Kilmer and Slickrock, evidence of past land-use in streams is present. Railroads were often constructed in streambeds because stream channels made the best roadbeds (Dolloff 1993) and logs were carried out of the forests on rail carts. Such railroads were constructed in many Slickrock streams (Homan 1990). In other instances, logs were simply pulled by Oxen or other animals downstream with out assistance of railroads. Although Babcock Land and Timber Company removed most of the rails, many streams still contain sections of track, pieces of cable, and other debris that was used in logging and later abandoned. Long sections of rail remain in stream L5 and long lengths of cable remain along the banks of L4. Old railroad grades are evident through other parts of the Slickrock wilderness and pieces of metal refuse are not uncommon.

Methods

I investigated leaf and wood breakdown determine if disturbance to OM breakdown from logging persists in forested streams following 75 Y of recovery. We used artificial leaf packs (White Oak: Quercus alba) and wood veneers (White Oak) to measure leaf and wood breakdown and invertebrate colonization of leaf packs.

White oak leaves were collected shortly (< 1 day) after abscission and dried to a constant weight at room temperature. Artificial leaf packs were made from approximately 10 g of leaves (weighed to the nearest 0.01 g) placed in 5 mm mesh nylon bags. 10 leaf packs were attached to a 5 m nylon cord at 0.5 m intervals and 3 sets of 10 leaf packs were placed in each stream. Three leaf packs were transported to each stream, returned to the lab, and reweighed to determine weight loss due to handling (see Benfield 1996). Untreated wood veneer strips (15 cm x 2.5 cm x 1 mm) were attached to flexible nylon mesh and affixed to cords in between leaf packs. Leaf packs and wood veneers were placed in riffles and anchored to the substratum using gutter nails. Three replicates of each were collected from each stream (3 each in unlogged and logged catchments) after 14, 68, and 87 days. Collections were scheduled for 30

and 120 days, but an extended problem of site access around day 30 and vandalism sometime after day 87 prevented collections.

After incubation in streams, leaf packs and wood veneers were placed in plastic bags containing a small amount of stream water, transported back to the laboratory in a cooler filled with ice and processed to determine weight loss and invertebrate colonization. Invertebrates were washed from leaf packs into a 250 μ m mesh sieve, preserved in 70% ethanol, and identified to genus according to Merritt and Cummins (1996). Shredders (sensu Merritt and Cummins 1996) were dried at 50° C for 48 hours and weighed. Once free of invertebrates, leaf packs were dried at 50° C for 48 hours, weighed, and then homogenized using a Wiley mill. Sub-samples were dried, weighed, combusted in an ashing oven at 550° C for 1 hour, weighed, wetted to restore water of hydration, dried, and weighed to determine ash-free dry mass (AFDM). Veneers were dried at 60°C for three days and weighed. A 2.5 x 3 cm sub-sample was removed from each veneer strip and ashed to determine AFDM. Leaf and wood breakdown rates (k) were calculated by regressing the natural log of mean % AFDM (g) remaining versus incubation time (days) (Benfield and Webster 1986). Triplicate water samples were collected with each collection of leaf packs and wood. Stream water was filtered in the field using Gelman AE glass fiber filters, transported to Coweeta

Hydrologic Laboratory (Macon Co., North Carolina), and frozen until analyzed. Samples were analyzed for NO₃-N and PO₄-P.

Data were analyzed using Minitab 12.1 and an alpha level of 0.05 was used for all comparisons. T-tests were used to test for significant differences between variables measured in unlogged and logged catchments. Shredder abundance and streambed substrate are expressed as percent of total (relative abundance). Data were transformed as necessary to meet assumptions of normality. Regression analysis (alpha = 0.05 for inclusion) was used to explain relationships between variables.

Results

Wood breakdown ($k\ d^{-1}$) ranged from 0.0021 to 0.0052 d^{-1} in unlogged streams and from 0.0027 to 0.0050 d^{-1} in logged streams and means did not differ significantly (Table 1-2). Wood breakdown was not significantly related to variables measured including nutrient concentration (Table 1), total suspended solids (Chapter I) or wood volume (Chapter II). Leaf breakdown rates ranged from 0.0113 to 0.0237 d^{-1} in unlogged and from 0.0133 to 0.0209 d^{-1} in logged streams and treatment means were not significantly different (Figure 2). Leaf breakdown rates were significantly related to mean shredder biomass (Figure 3). Across all

streams, mean leaf breakdown was four times faster than wood and means were significantly different ($p < 0.001$).

Taxonomic composition of leaf pack shredders differed between leaf packs in unlogged and logged streams (Table 2). *Tallaperla* sp. was the most abundant shredder in leaf packs in unlogged streams and was significantly more abundant in leaf packs ($p = 0.016$) and benthic samples from unlogged than logged streams ($p < 0.001$). *Amphinemura* sp. was the most abundant shredder in leaf packs in logged streams and was more abundant in logged than unlogged streams ($p=0.028$), however benthic proportions were not significantly different. No other species differed in abundance in leaf packs from unlogged and logged streams.

Discussion

All Joyce Kilmer-Slickrock wilderness study streams drained thickly forested catchments with well-developed riparian vegetation. Despite reforestation, the Slickrock wilderness continues to show response to land-use history (Chapters I-III). Consequently, I predicted that there would be significant differences between both wood and leaf breakdown rates in unlogged versus logged streams. Differences in OM breakdown rates can result from differences nutrient concentration (Likens et al. 1970, Silsbee and Larson 1983, Campbell and Doeg 1989, Tank and

Webster 1998), sedimentation (Tebo 1955, Crickmay 1974, Lemly 1982), organic matter retention time, changes in macroinvertebrate functional feeding group abundance (Haefner and Wallace 1981, Hawkins et al 1982, Silsbee and Larson 1983, Chapter II), and water temperature (Webster and Waide 1982, Culp and Davies 1983). Shredders are important in leaf breakdown (Sedell et al. 1975, Short et al. 1980, Benfield and Webster 1985) and different macroinvertebrate community structure between unlogged and logged streams was expected to affect leaf breakdown rates.

Although leaf breakdown rate per g of shredder biomass did not differ, shredder assemblages in leaf packs were different. Tallaperla sp. was the most abundant shredder in unlogged streams (Chapter II) and in leaf packs in unlogged streams. Tallaperla sp. was also the most abundant shredder in logged streams (Chapter II), but in leaf packs in logged streams Amphinemura sp. was most abundant shredder and Tallaperla sp. the second most abundant. It is not clear why the taxonomic composition of shredders in leaf packs differed between stream types, but despite taxonomic differences the breakdown rates were similar between stream types.

The range and means of wood breakdown rates in unlogged and logged streams in this study were similar. Rates were similar to

published values for white oak veneers but were closest to values for white oak veneers in cave streams (Table 2). Values in JKSRW were 1.4 to 3.46 times greater than nearby WS 55 (Coweeta Hydrologic Laboratory, Macon, NC, USA). Breakdown rates can be influenced by nutrient concentrations that stimulate decomposer activity (Meyer and Johnson 1983, Suberkropp 1995, Suberkropp and Chauvet 1995, Tank and Webster 1998, Simon 2000). Thus, it is not surprising that wood breakdown rates did not differ significantly between unlogged and logged streams because nutrient concentrations were also similar. Although some macroinvertebrates use wood, there was little evidence of feeding on veneers perhaps because of relatively short incubation time.

Leaf breakdown rates were generally faster than those reported for Q. alba from other southern Appalachian streams (Table 3). Some researchers have speculated that shredders are partly responsible for accelerated breakdown rates following logging (Webster and Waide 1982) and that experimental leaf packs act as islands of food that are otherwise a limiting resource (Benfield et al. 2001). Seasonal leaf standing stocks are not available for streams studied, but leaf fall is quite substantial in Joyce Kilmer-Slickrock forests. By mid to late autumn, leaf fall almost completely obscured the streambed in most study streams and leaves do not appear to be a limiting resource. It is therefore surprising that

breakdown rates of white oak leaves in Joyce Kilmer-Slickrock wilderness streams are comparatively fast because leaf inputs should be comparatively large (and not limiting). Joyce Kilmer-Slickrock streams had very well developed shredder assemblages (Chapter I, sensu Cummins et al. 1989). Such a relative large shredder assemblage might be particularly efficient at processing autumnal inputs. This is supported by the strong relationship between shredder biomass and leaf breakdown rate in both unlogged and logged streams. Shredders are clearly important in organic matter processing in Joyce Kilmer-Slickrock wilderness streams, but despite greater proportions of shredders in the benthos of unlogged streams (Chapter II), average shredder biomass in leaf packs did not differ significantly. If leaf pack breakdown was accelerated because leaves were a limiting resource, I would expect Slickrock streams to have higher leaf breakdown rates because of the absence of retentive debris dams (Chapter I). I did not quantify leaf export, but natural leaf accumulations on snags above base flow were estimated to be much greater in logged than unlogged streams. This suggests logged streams are less retentive than unlogged streams, which is not uncommon. Consequently, leaves should be most limiting in logged streams and breakdown should be faster in logged than unlogged streams if artificial leaf packs act as islands of a limiting resource. Because there were no

differences in leaf breakdown rates in unlogged and logged streams and breakdown rates are comparatively fast, I conclude that leaves are not limiting and that shredder assemblages in streams draining mature forests are better developed than in younger or more disturbed forests.

Furthermore, these comparatively well developed shredder communities increase the retention of riparian inputs by more efficiently processing leaves as evidenced by the high leaf breakdown rates in Joyce Kilmer-Slickrock wilderness streams.

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Table 1. Leaf and wood breakdown rates, NO₃-N and PO₄-P concentrations, and shredder abundance on leaf packs in unlogged (U1-U5) and logged (L1-L5) streams.

| | <i>k</i> (d ⁻¹) | | NO ₃ -N (mg/L) | PO ₄ -P (mg/L) | Shredder colonization (mg/g AFDM leaf) |
|------|-----------------------------|----------|------------------------------|------------------------------|--|
| | Leaf | Wood | | | |
| U1 | 0.0137 | 0.00519 | 0.0317 | < 0.002 | 12.61 |
| U2 | 0.0237 | 0.0038 | 0.0246 | < 0.002 | 21.20 |
| U3 | 0.0201 | 0.00212 | 0.0404 | < 0.002 | 23.10 |
| U4 | 0.0113 | 0.00466 | 0.0176 | < 0.002 | 9.18 |
| U5 | 0.0150 | 0.00353 | 0.1474 | < 0.002 | 12.28 |
| Mean | 0.0168 | 0.00386 | 0.0523 | | 15.67 |
| ± SD | ± 0.0050 | ± 0.0012 | ± 0.0538 | | ± 6.10 |
| L1 | 0.0209 | 0.00391 | 0.1389 | < 0.002 | 22.98 |
| L2 | 0.0161 | 0.00271 | 0.0563 | < 0.002 | 9.06 |
| L3 | 0.0146 | 0.00503 | 0.0703 | < 0.002 | 12.58 |
| L4 | 0.0133 | 0.0041 | 0.0771 | < 0.002 | 7.57 |
| L5 | 0.0205 | 0.00441 | 0.1453 | < 0.002 | 12.78 |
| Mean | 0.0171 | 0.00403 | 0.097572 | | 12.99 |
| ± SD | ± 0.0035 | ± 0.0009 | ± 0.0414 | | ± 6.01 |

Table 2. Taxonomic composition of shredders colonizing experimental leaf packs in unlogged (U1-U5) and logged (L1-L5) streams in JKSRW. Abundance is expressed as percent of total.

| | Unlogged | | | | | | Logged | | | | | | t-test (p) |
|-----------------------------|----------|------|------|------|------|------|--------|------|------|------|------|------|---------------|
| | U1 | U2 | U3 | U4 | U5 | Mean | L1 | L2 | L3 | L4 | L5 | Mean | |
| <u>Tallaperla</u> sp. | 41.1 | 49.2 | 42.0 | 20.9 | 29.5 | 36.5 | 20.9 | 20.9 | 17.3 | 18.2 | 25.5 | 20.5 | 0.016 |
| <u>Amphinemura</u> sp. | 17.9 | 13.8 | 18.0 | 30.2 | - | 15.9 | 17.6 | 30.2 | 48.0 | 40.0 | 39.2 | 35.0 | 0.028 |
| <u>Pycnopsyche</u> spp. | 33.9 | 24.6 | 24.0 | - | 18.0 | 20.1 | 22.0 | - | 1.0 | 1.8 | 19.6 | 8.9 | NS |
| <u>Lepidostoma</u> sp. | 7.1 | 4.6 | 10.0 | 16.3 | 23.0 | 12.2 | 13.2 | 16.3 | 11.2 | 27.3 | 5.9 | 14.8 | NS |
| Tipulidae | - | 6.2 | - | 4.7 | 11.5 | 4.5 | 5.5 | 4.7 | 7.1 | 10.9 | 5.9 | 6.8 | NS |
| <u>Fattigia</u> <u>pele</u> | - | - | 2.0 | - | 11.5 | 2.7 | - | - | - | 1.8 | - | 0.4 | NS |
| Leuctridae | - | 1.5 | - | 11.6 | 3.3 | 3.3 | 8.8 | 11.6 | 13.3 | - | - | 6.7 | NS |
| <u>Paraleptophlebia</u> sp. | - | - | 4.0 | 16.3 | - | 4.1 | 2.2 | 16.3 | - | - | - | 3.7 | NS |
| <u>Pteronarcys</u> sp. | - | - | - | - | - | - | 8.8 | - | - | - | - | 1.8 | NS |
| Brachycentridae | - | - | - | - | 3.3 | 0.6 | - | - | 2 | - | 2 | 0.8 | NS |
| Taniopterygidae | - | - | - | - | - | - | 1.1 | - | - | - | 2 | 0.6 | NS |

Table 3. Breakdown rates for leaves and wood veneers (*Quercus alba*) from unlogged (U1-U5) and logged (L1-L5) JKSRW streams and other study streams.

| Reference | k (d^{-1}) | | Site |
|---------------------------|------------------|------|-----------------------|
| | Leaves | Wood | |
| Griffith et al. 1995 | 0.002 | | 2 nd order |
| Benfield and Webster 1985 | 0.0021 | | 1 st order |
| Simon 2000 (D1) | 0.0033 | | Cave stream |
| Simon 2000 (D2) | 0.0033 | | Cave stream |
| Webster and Waide 1982 | 0.0038 | | 2 nd order |
| Griffith et al. 1995 | 0.0038 | | 2 nd order |
| Benfield and Webster 1985 | 0.0039 | | 1 st order |
| Wallace et al. 1982 | 0.0040 | | 1 st order |
| Petersen and Cummins 1974 | 0.0045 | | 2 nd order |
| Stout 1982 | 0.0045 | | |
| Hanson et al. 1984 | 0.0047 | | 3 rd order |
| Suberkropp et al. 1975 | 0.0047 | | 3 rd order |
| Golladay and Webster 1988 | 0.0056 | | 2 nd order |
| Griffith et al. 1995 | 0.0059 | | 3 rd order |
| Petersen and Cummins 1974 | 0.0059 | | 1 st order |
| Stout 1982 | 0.0062 | | |
| Webster and Waide 1982 | 0.0064 | | 2 nd order |
| Stout 1982 | 0.0072 | | |
| Suberkropp et al. 1976 | 0.0074 | | 3 rd order |
| Brussock et al. 1988 | 0.0075 | | Cave stream |
| Brussock et al. 1988 | 0.0085 | | Cave stream |
| Simon 2000 (C1) | 0.0085 | | Cave stream |
| Webster and Waide 1982 | 0.009 | | 2 nd order |
| Benfield and Webster 1985 | 0.0094 | | 2 nd order |
| Simon 2000 (C2) | 0.0102 | | Cave stream |
| Wallace et al. 1982 | 0.0108 | | 1 st order |
| U4 | 0.0113 | | |
| Golladay and Webster 1988 | 0.0116 | | 2 nd order |
| Witkamp and Frank 1969 | 0.0121 | | 2 nd order |

Table 3 continued.

| Reference | k (d^{-1}) | | Site |
|-------------------------------|------------------|---------|-----------------------|
| | Leaves | Wood | |
| L4 | 0.0133 | | |
| U1 | 0.0137 | | |
| L3 | 0.0146 | | |
| U5 | 0.0150 | | |
| Simon 2000 (D3) | 0.0158 | | Cave stream |
| L2 | 0.0161 | | |
| Bott et al. 1977 | 0.0169 | | 3 rd order |
| Benfield and Webster 1985 | 0.0182 | | 2 nd order |
| Simon 2000 (C3) | 0.0191 | | Cave stream |
| U3 | 0.0201 | | |
| L5 | 0.0205 | | |
| L1 | 0.0209 | | |
| U2 | 0.0237 | | |
| Simon 2000 (SO) | 0.0259 | | Cave stream |
| Tank and Webster 1998 (WS 55) | | 0.00146 | 1 st order |
| U3 | | 0.00212 | |
| L2 | | 0.00271 | |
| U5 | | 0.00353 | |
| U2 | | 0.0038 | |
| L1 | | 0.00391 | |
| Simon 2000 (D1) | | 0.004 | Cave streams |
| L4 | | 0.0041 | |
| Simon 2000 (C2) | | 0.0041 | Cave streams |
| Simon 2000 (D2) | | 0.0042 | Cave streams |
| L5 | | 0.00441 | |
| U4 | | 0.00466 | |
| Simon 2000 (C1) | | 0.0048 | Cave streams |
| Simon 2000 (D3) | | 0.0049 | Cave streams |
| L3 | | 0.00503 | |
| U1 | | 0.00519 | |
| Simon 2000 (SO) | | 0.0053 | Cave streams |
| Simon 2000 (C3) | | 0.0065 | Cave streams |

Figure 1. Map of Southeastern United States showing location of the Joyce Kilmer-Slickrock wilderness (JKSRW). Detailed map shows study sections of unlogged (U1-U5) and logged (L1-L5) streams.

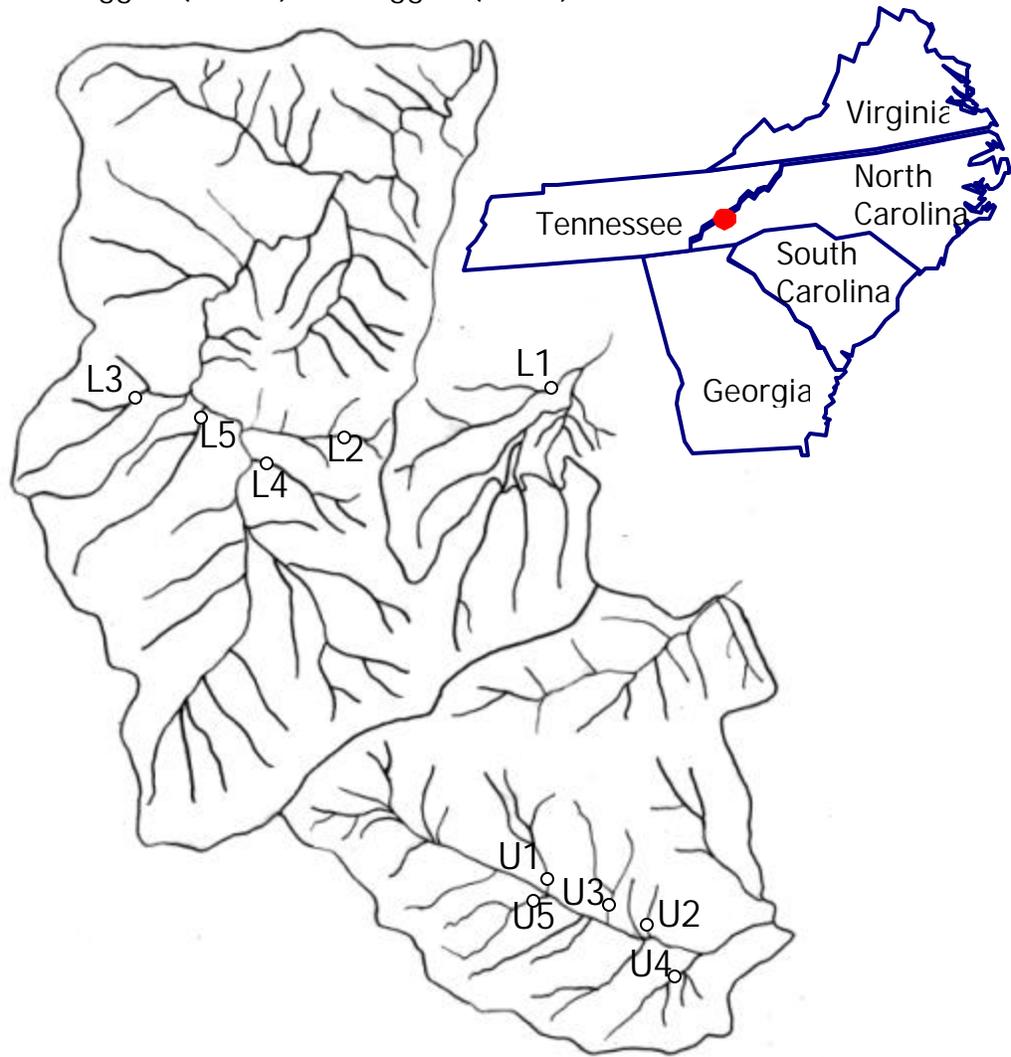


Figure 2. Mean breakdown rates of leaves and wood in unlogged and logged JKSRW streams. Bars represent the standard error of the mean.

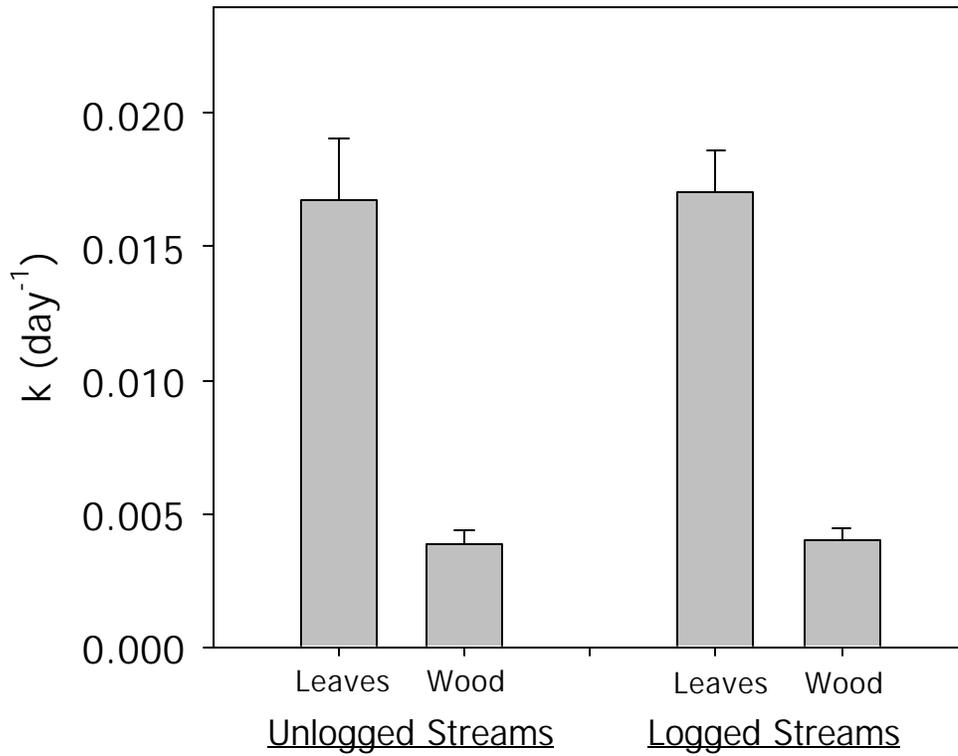
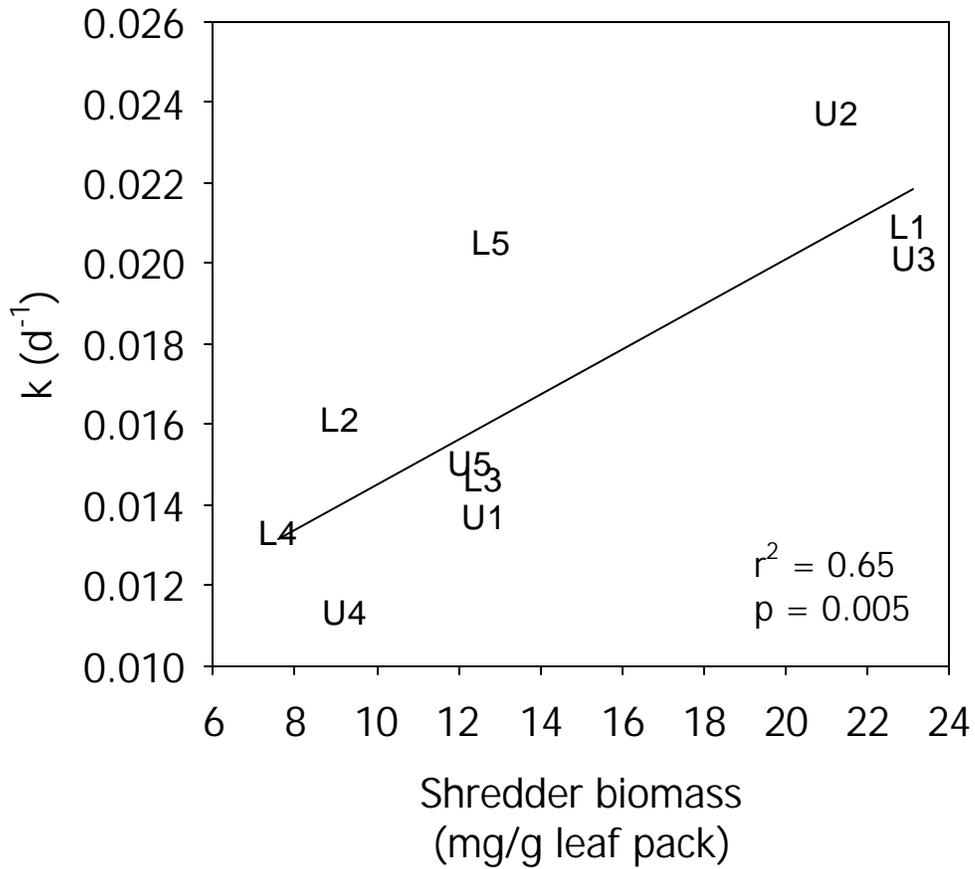


Figure 3. Shredder biomass (mg) versus breakdown rates in unlogged (U1-U5) and logged (L1-L5) JKSRW streams.



General Summary

Virgin forest is uncommon in the southern Appalachian Mountains (Davis 1996) and the most significant anthropogenic disturbance to the southern Appalachians following the arrival of Europeans was industrial logging (Davis 2000). Few, if any, environmental regulations existed governing logging during the early 20th century and timber harvesting was particularly destructive to streams (Davis 2000). The effects of logging on streams are well established, but how long logging disturbance persists in streams is less well known. I examined streams in forests that were never logged and streams in forest logged in the early 20th century to determine if disturbance persists.

This study was conducted in the Joyce Kilmer-Slickrock wilderness (Figure 1), which lies southwest of the Great Smoky Mountains National Park in the Nantahala National Forest. The Joyce Kilmer-Slickrock wilderness consists of two adjacent wilderness areas. Joyce Kilmer is in Graham Co., North Carolina and is one of the few remaining southern Appalachian forests that was never logged. The Slickrock wilderness was logged once and then allowed to recover. Slickrock wilderness borders the northwest boundary of Joyce Kilmer with portions of the forest residing in Graham Co., North Carolina and Monroe Co., Tennessee.

Joyce Kilmer Memorial Forest is approximately 1540 ha and the Slickrock wilderness is approximately 4500 ha. Elevation ranges are from 670 m to 1585 m in Joyce Kilmer and from 330 m to 1585 m in Slickrock. Annual precipitation is normally > 200 cm per year (Daniels 1985). Joyce Kilmer is underlain primarily by arkosic metasandstone, muscovite phyllite and mica schist. Geology in Slickrock is similar and underlain by arkosic metasandstone, graphitic metagreywacke, and slate.

Vegetation types in the Joyce Kilmer-Slickrock wilderness include mixed mesophytic cove hardwood associations in moist lowlands and north facing slopes, mixed oak-hickory (Quercus spp.-Carya spp.) stands on steep side slopes, oak-pine (Quercus spp.-Pinus spp.) stands on southern slopes, and rhododendron-laurel-azalea slicks on exposed ridges (Daniels et al. 1987). Eastern hemlock (Tsuga canadensis) is common throughout the Joyce Kilmer-Slickrock wilderness and is particularly abundant along streamsides, often with thick Rhododendron maximum understory. South facing slopes generally have thinner understory than north facing slopes.

Joyce Kilmer and Slickrock are similar geologically but differ in land use history. Joyce Kilmer was never logged and Slickrock was logged from 1917 until 1922. The area now designated as the Joyce Kilmer wilderness was examined for potential timber production at least as early

as 1910 (Anon. 1910). The Joyce Kilmer wilderness was never logged due to several changes in ownership that repeatedly delayed logging and a flood around 1930 resulting from construction of Calderwood Lake Dam, which destroyed the only railroad access to the area. (personal communication, Cheoa Ranger Station, Graham Co., North Carolina).

The Babcock Land and Timber Company purchased the Slickrock portion of the Joyce Kilmer-Slickrock wilderness in the 1915. Babcock Land and Timber began logging in 1917 and logging ended in 1922 with the construction of Calderwood Dam. The area that presently composes the Joyce Kilmer-Slickrock wilderness was purchased by the U.S. Forest Service in 1936 and designated wilderness in 1975 (personal communication, Cheoa Ranger Station, Graham Co., North Carolina).

Study streams in the Joyce Kilmer-Slickrock wilderness (Figure 1) were selected based on land use history (streams in unlogged Joyce Kilmer catchments versus logged Slickrock catchments), similarity in size range between treatments, and similarity in slope. Five replicate unlogged catchments in Joyce Kilmer (U1-U5) and five replicate catchments logged ca. 75 y ago (L1-L5) were studied for comparison. Catchment area is the total area within each watershed upstream of each sampling site and slope was estimated from USGS topographical maps. Streams in unlogged forests drained catchments ranging from 47 to 151

ha and stream gradients ranged from 8.8 to 21.8%. Logged catchments ranged from 35 to 227 ha and stream slopes ranging from 9.1 to 23.6 %, respectively.

Although forest composition is similar between Joyce Kilmer and Slickrock, evidence of past land-use in streams is present. Railroads were often constructed in streambeds because stream channels made the best roadbeds (Dolloff 1993) and logs were carried out of the forests on rail carts. Such railroads were constructed in many Slickrock streams (Homan 1990). In other instances, logs were simply pulled by Oxen or other animals downstream with out assistance of railroads. Although Babcock Land and Timber Company removed most of the rails, many streams still contain sections of track, pieces of cable, and other debris that was used in logging and later abandoned. Long sections of rail remain in stream L5 and long lengths of cable remain along the banks of L4. Old railroad grades are evident through other parts of the Slickrock wilderness and pieces of metal refuse are not uncommon.

The construction of railroads in streambeds would likely require the removal of most sizable obstacles, including debris dams. Initial investigations showed unlogged streams had an average of 417 m³ of wood/ha of stream versus 1.1 m³ of wood/ha of stream in logged catchments and there were significantly more debris dams in unlogged

catchments. Logged streams often have less wood in streambeds following logging (Silsbee and Larson 1983, Bilby and Ward 1991, Fleebe and Dolloff 1995) including some streams in the Great Smoky Mountains (Silsbee and Larson 1983). Differences in wood volume between unlogged and logged Great Smoky Mountain streams were, however, much smaller than differences found in unlogged and logged Joyce Kilmer-Slickrock streams. Many of the streams examined by Silsbee and Larson had railroad grades along the stream bank rather than in the streambed (personal observation), while most Slickrock streams had evidence of railroads or cable used to haul logs in the streambeds. I hypothesize that the relative absence of wood in Slickrock (logged) streams is due to the use of streams as conduits for timber removal. This is of particular ecologic and historic significance because most of the disturbance that persists in Slickrock streams relates to the absence of wood that is a result of the specific techniques (i.e., use of streams as railroad grades) used in early 20th century logging (Figure 2).

Wood is important in the retention of small substrate particles (Bilby 1981, Smith et al. 1993, Wallace et al 1995) and the loss of wood in streams can increase bed load transport (Smith et al. 1993) and scouring of stored sediment (Beschta 1979). Unlogged Joyce Kilmer wilderness streams had an average of 22 times more sand than logged Slickrock

wilderness streams (26.4 vs. 1.2%, respectively) and the abundance of fine substrates was related to the presence of wood (Chapter I, Figure 6).

Following logging, lower standing stocks of wood in logged catchments can result in less OM retention (Bormann and Likens 1974, Sedell et al. 1978, Bilby and Likens 1980, Cummins et al. 1983, Speaker et al. 1984, Harmon et al 1986,) that can disturb both benthic community structure and stream ecosystem function in logged catchments (Silsbee and Larson 1983, Wallace et al. 1988, Wallace et al. 1995, Wallace et al. 1997). Macroinvertebrate functional feeding group abundance can be strongly linked to the abundance of food such as leaves and other coarse particulate organic matter and periphyton and other in-stream primary production (Minshall et al. 1982). Shifts in a stream's energy base from or to allochthonous or autochthonous sources are reflected in shifts in functional feeding group (FFGs) proportions (Vannote et al. 1980, Merritt and Cummins 1996). Logging often results in functional shifts that change a forested streams energy base from allochthonous to autochthonous (Lyford and Gregory 1975, Murphy et al. 1981, Wallace et al. 1988, Stone and Wallace 1998).

Streams in unlogged catchments had significantly greater proportions of shredders while streams in logged catchments had significantly greater proportions of scrapers. Differences in scrapers and

shredders were related to moss, which was more abundant in unlogged catchments. Unlogged catchments were more heterotrophic (dependent on riparian inputs for energy) because of greater moss abundance that probably enhance CPOM retention and displace periphyton. Differences in moss abundance most likely relate to land-use history. Debris dams decrease water velocity (Trotter 1990) and frequent debris dams in Joyce Kilmer probably reduce storm flow velocity, providing more stable substrates for relatively slow growing moss. Other disturbance to ecosystem function was more directly related to the absence of wood in logged catchments. Ecosystem parameters derived from functional feed group analysis showed that linkages between streams and riparian vegetation were weaker in logged catchments and that linkage strength increased as debris dam frequency increased.

Nutrient retention should be highest in streams draining undisturbed forests and lowest in streams draining successional forests (Gorham et al. 1979, Webster and Swank 1985). Disturbances such as logging can increase nutrient export from forests to streams and the absence of debris dams can reduce a streams ability to retain elevated nutrient loss and minimize downstream nutrient export (Odum 1969, Likens et al. 1970, Fisher and Likens 1973, Bormann et al. 1974, Vitousek and Reiners 1975). Consequently, nutrient retention in headwater

streams has strong implications for downstream lakes, rivers, and estuaries (Meyer and Likens 1979). Because streams draining logged catchments in the Joyce Kilmer-Slickrock wilderness had significantly fewer debris dams than streams in unlogged catchments resulting from past logging (Chapter I), I hypothesized that nutrient retention differed between unlogged and logged streams in the Joyce Kilmer-Slickrock wilderness.

Benthic organic matter in streams can strongly influence nutrient uptake (Newbold et al. 1983, Mulholland et al. 1985) and standing stocks of wood were much greater in unlogged Joyce Kilmer streams. Wood increases nutrient demand by acting as a biologically active substrate (Tank et al. 1998, Tank and Webster 1999) and demand from wood can be greater than that by FPOM and sediment (Aumen et al. 1990). Uptake velocity was significantly greater in unlogged than logged streams and were high compared to published values for southern Appalachian streams (Chapter III). Furthermore, uptake rates were strongly related to the frequency of debris dams. Thus, the loss of wood in streams following logging decreases nutrient retention and further weakens the linkage between streams and the catchments they drain.

Legacies of early 20th century logging are clearly present in Joyce Kilmer-Slickrock wilderness streams. Evidence of past logging methods

that require removal of wood in streams suggests that the absence of wood in logged streams results from logging. Much of the persisting disturbance to streams by past logging was directly or indirectly related to differences in wood volume, debris dam frequency, and streambed substrate composition (Figure 2). Streams with less wood were less retentive of small substrates and had more permeable streambeds that stored more solute. Macroinvertebrate assemblages in logged streams had greater proportions of scrapers and fewer shredders than unlogged streams. Furthermore, logged streams derived less energy from riparian inputs than did unlogged streams. Unlogged streams had stronger stream-forest linkages and were also more retentive of nutrients. Both stream-forest linkages and nutrient retention were positively related to debris dams. Results support the hypothesis that logging results in a downstream shift from the headwaters in ecosystem function. Furthermore, logged streams are shifted downstream on a river size continuum and this downstream shift will likely persist for centuries because wood input rates do not return to natural levels for several centuries following logging.

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Figure 1. Map of Southeastern United States showing location of the Joyce Kilmer-Slickrock wilderness (JKSRW). Detailed map shows study sections of unlogged (U1-U5) and logged (L1-L5) streams.

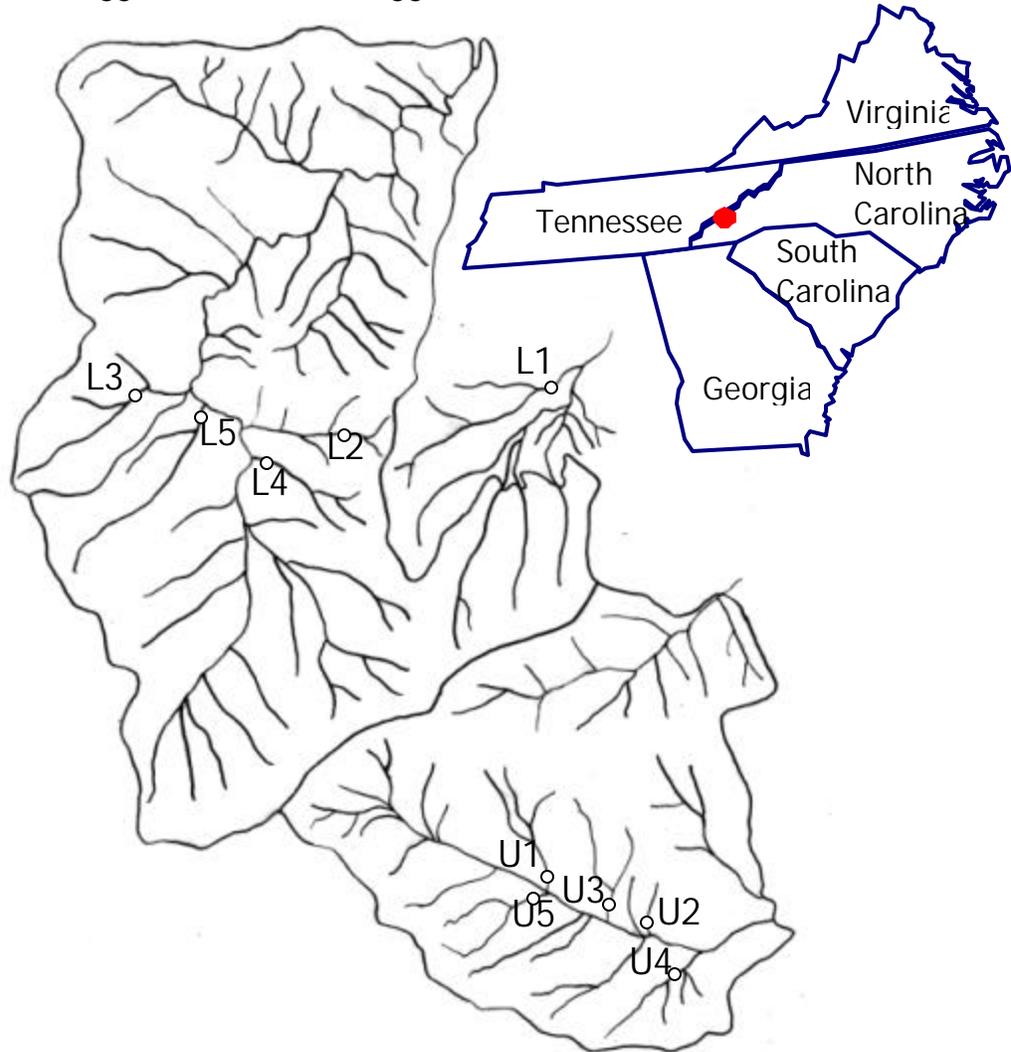
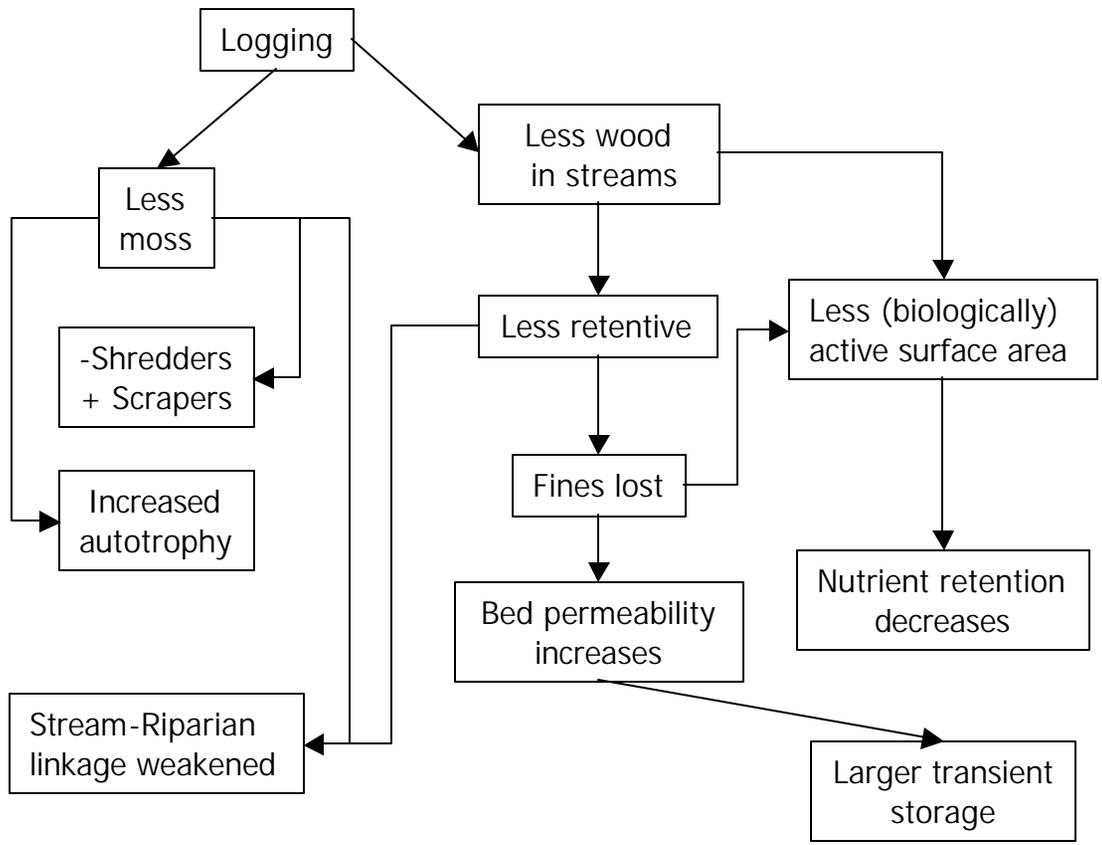


Figure 2. Conceptual model summarizing the effects of logging in streams studied in the Joyce Kilmer-Slickrock wilderness.

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CURRICULUM VITAE

Paul F. Wagner

Correspondence Address

125 Villa Park Drive
Lewisville, TX 75077
(972) 317-6046

Work Address

The Nature Conservancy
711 Navarro
San Antonio, TX, 78205-1721, USA
(540) 951-2234 w
email: pwagner@tnc.org

BIRTH 26 March 1969, Dayton, Ohio, USA

EDUCATION

Bachelor of Science in Biology, 1992

Minor in Chemistry
The University of North Texas

Masters of Science in Biology, 1995

The University of North Texas
Advisor Dr. James H. Kennedy
Thesis: The Life History of *Camelobaetidius mexicanus*
(Ephemeroptera: Baetidae) from Honey Creek, Oklahoma,
USA.

Doctor of Philosophy in Biology

Virginia Tech
Advisor Dr. E. F. Benfield
Dissertation: Legacies of early 20th century logging in southern
Appalachian streams.

EXPERIENCE

The Nature Conservancy

Regional Aquatic Conservation Ecologist, January 2000-present.

Graduate Teaching Assistantships

Teaching Assistant, Department of Biology, The University of
North Texas, Denton, TX. 1992-1995.

Laboratory courses taught

Animal and Human Biology, Biology for Education Majors, Invertebrate Zoology, Animal Ecology, Alpine Limnology.

Teaching Assistant, Department of Biology, Virginia Polytechnic and State University, Blacksburg, VA. 1995-1996, 1999.

Laboratory courses taught

General biology, Field and Laboratory Ecology.

Research Assistantships

Summer Research Assistantship, The University of North Texas Research Field Station.

Research Assistant for Dr. J. R. Webster and Dr. E. F. Benfield, Department of Biology, Virginia Tech, Blacksburg, VA.

Research Experience

Masters: Conducted macroinvertebrate sampling in karst streams. Studied aquatic insect taxonomy, life histories, and secondary production estimation.

Ph.D.: Conducted macroinvertebrate sampling. Characterized effects of disturbance on biota and habitat quality in streams. Used remotely sensed data and GIS software to characterize catchment features. Studied leaf breakdown and biofilm development in streams draining logged and unlogged catchments. Modeled transient storage of disturbed and undisturbed streams and estimated nutrient uptake lengths.

SOFTWARE EXPERIENCE

Operating systems: DOS 6.X, Windows 3.X, Windows 9X, Windows NT.

Web Authoring: MS FrontPage

Statistics: SAS, Sysstat, Sigma Stat, ToxStat, PC Ord, MiniTab, Statistica.

Hydrologic Modeling: OTIS, Solmod, Hartmod, FORTRAN.

Data presentation and Graphics: Microsoft Office (Word, Power Point, Excel), Corel Word Perfect Suite (WordPerfect, Quattro Pro), Harvard Graphics, Sigma Plot, Delta Graph, Adobe Acrobat, Adobe PhotoShop.

Geographic Information Systems and Spatial Analysis:

ArcView, ARC/INFO, ERDAS Imagine, ERDAS ORTHOMAX, Atlas GIS, Sigma Scan.

CONSULTING

Tom's Creek Rare Insect Survey. Conducted for Anderson & Associates (Blacksburg, VA) and the City of Blacksburg.

AFFILIATIONS

North American Benthological Society
Entomological Society of America
The Society of Conservation Biology
Sigma Xi

HONORS

Teaching Assistant of the Year Finalist (1995).
Discover Program Honoree, The University of North Texas Student Support Services Program (1994-1995).
Summer Research Scholarship, The University of North Texas (1994).
Phi Kappa Phi Honor Society.
Kosztarab Fellow (Virginia Tech)

GRANTS RECEIVED

Hydrolab of Austin Texas (2000). Negotiated \$135,000 equipment grant to The Nature Conservancy of Texas.
Freshwater Initiative (2000). Understanding the hydrology of Cuatro Cienegas, Mexico.
Freshwater Initiative (2000). Developing an Index of biotic integrity for the Cache River/Bayou DeView.
Freshwater Initiative (2000). Developing a long-term monitoring program for Love Creek, Texas.
Canon Corporation (2000). Equipment grant.
Virginia Museum of Natural History (1997)
Sigma Xi (1997, 1998)
Graduate Research Development Project of Virginia Tech (1997, 1998)
Virginia Tech Travel Fund Project Grant (1998).
Kosztarab Fellowship (1997)

SERVICE

- 1997 – 1999 Chair: Graduate Research Development Project of Virginia Tech
- 1997 – 1998 Commission on Research, Virginia Tech.
- 1997 – 1998 Graduate Student Appointee to the Executive Committee of the North American Benthological Society.
- 1997 - 1998 Organized first Graduate Student Resource Committee of the North American Benthological Society.
- 1997 Judge: Poster session of the North American Benthological Society Annual Meeting.
- 1998 Judge: Poster session of the North American Benthological Society Annual Meeting.
- 1997 - 1999 Department of Biology Delegate to the Graduate Student Assembly of Virginia Tech.
- 1998 – 1999 President, Graduate Student Assembly, Virginia Tech.
- 1998 – 1999 University Council, Virginia Tech.
- 1998 – 1999 Student Legal Services, Virginia Tech.
- 1998 & 1999 Judge: Poster session of the North American Benthological Society Annual Meeting.
- 1998-1999 Graduate Educational Review Taskforce, Office of the Provost of Virginia Tech.
- 1998-1999 Undergraduate Student Mentor for the Virginia Tech Student Mentorship Program.

RECENT MEETINGS & CONFERENCES

- 1997 Annual meeting of the North American Benthological Society. San Marcos, TX.
- 1997 Research and Graduate Studies Annual Fall Retreat. Donaldson Brown Hotel and Conference Center. Blacksburg VA.
- 1998 Annual meeting of the North American Benthological Society. PEI, Canada.
- 1998 Societas Internationalis Limnologiae (SIL). Dublin, Ireland.
- 1999 Annual meeting of the North American Benthological Society. Duluth Minnesota.
- 1999 Annual Meeting of the Entomological Society of America. Atlanta GA.
- 2000 Annual Meeting of the Freshwater Initiative, Ryde CA.

PRESENTATIONS

Wagner, P. F. and J. H. Kennedy. 1993. Contributions to the Life History of *Camelobaetidius mexicanus* (Ephemeroptera: Baetidae) from Honey Creek, Oklahoma. Texas Academy of Sciences Annual Meeting.

Wagner, P. F. and J. H. Kennedy. 1994. The Life History and Productivity of *Camelobaetidius mexicanus* (Ephemeroptera: Baetidae) from Honey Creek, Oklahoma. Entomological Society of America Annual Meeting.

Wagner, P. F. and J. H. Kennedy. 1995. The Life History of *Camelobaetidius mexicanus* (Ephemeroptera: Baetidae) from Honey Creek, Oklahoma. North American Benthological Society Annual Meeting.

Wagner, P. F., and J. H. Kennedy. 1996. Development and variation in claw morphology in the spatulate-clawed mayfly *Camelobaetidius mexicanus* (Ephemeroptera: Baetidae) (Traver and Edmunds). Annual meeting of the North American Benthological Society. Kalispell, Montana.

Wagner, P. F. and E. F. Benfield. 1997. Aquatic insect diversity in old growth and regrowth forests. Annual meeting of the Entomological Society of America. Nashville, TN.

Wagner, P. F. and E. F. Benfield. 1998. The long-term effects of logging on Southern Appalachian streams. Annual meeting of the North American Benthological Society. PEI Canada.

Wagner, P. F. and E. F. Benfield. 1999. The Long-term effects of deforestation on Southern Appalachian aquatic insects. Annual meeting of the Entomological Society of America. Atlanta, GA.

PUBLICATIONS

Bennett, W. A., R. J. Currie, P. F. Wagner, and T. L. Beiting. Cold tolerance and potential over-wintering of the red-bellied piranha *Pygocentrus nattereri* in the United States. Transactions of the American Fisheries Society, vol. 126, no. 5, pp. 841-849, Sep. 1997.

BOOK REVIEWS

Aquatic Fauna in Peril: The Southeastern Perspective. Book review for the Journal of the North American Benthological Society 18:146.