

STREAM-RIPARIAN CORRIDORS: DISTURBANCE, LINKAGES, AND RESISTANCE

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Riparian forests are known to restrict light and primary production in streams while providing organic matter import that fuels lotic food webs. Lateral interactions of this type generate intimate links between terrestrial and aquatic systems. There are equally strong upstream and downstream linkages within streams. By altering the linkages between terrestrial and aquatic elements, forest harvest is a disturbance that influences both hillslope and stream subsystems of watershed landscapes. Riparian processes may dictate how hillslope disturbance influences streams.

In this proposal, the PIs address how interactions between riparian vegetation and streams influence stream responses to forest clear-cutting. They focus on the **role of riparian vegetation through comparative studies among watersheds where clear-cutting will remove upslope vegetation but leave riparian zones of differing widths.**

Despite recognition of the importance of riparian vegetation in buffering terrestrial disturbance and the evident influence of upstream-downstream connections, little effort has been made toward quantitatively understanding how these co-occurring linkages interact to control lotic ecosystem responses to disturbance. The proposed research addresses the following questions: **1) How does the presence and extent of riparian vegetation buffer streams from the lateral effects of terrestrial disturbance? and, 2) How does riparian buffering within disturbed forest patches influence longitudinal recovery in downstream reaches flowing through intact forest?**

Two proposed research elements are designed to, 1) address how riparian vegetation buffers disturbance to the stream and organizes lateral linkages between terrestrial and lotic ecosystems, and 2) quantify in-stream gradients or recovery distances when different widths of riparian vegetation remain after forest harvest. **Research Element I** addresses how key measures of stream structure and function change following disturbance and how riparian zone width alters the direction and magnitude of response to upslope harvest. **Research Element II** addresses the spatial aspects of recovery within the stream by quantifying longitudinal gradients in stream structure and function as a means of determining recovery distances for various ecosystem components. Response variables include aspects of the stream's physical template (sediment, light, heat), organic matter dynamics (leaf breakdown, metabolism, and organic matter turnover), biogeochemistry (nutrient composition and concentration, N spiraling), and biotic composition (invertebrate community structure, algal biomass).

The PIs will pursue these questions with USDA Forest Service Southern Research Station scientists from the Coweeta Hydrologic Laboratory, NC. The team will direct forest harvest in 8 catchments to remove ca. 5-10 ha of upslope forest while leaving riparian vegetation buffers of different width. The proposal's broader impacts include providing information for policy formation through collaboration with research and management personnel from the Forest Service. Further, a team of post-Doctoral, graduate, and undergraduate students will be trained and directly involved in the research. The project will interact directly with members of the NSF Coweeta LTER program and further development of the research and education infrastructure. Finally, results will advance our understanding of disturbance and its influences, link research and policy formation, and address manager's concerns for southern Appalachian watersheds.

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Preface: The proposal presented herein addresses the ecological and managerial implications of varying riparian buffer width by assessing how it influences resistance and recovery of headwater streams following upslope forest harvest. In this resubmission, we have modified the sampling regime to allow for a time-series approach to assess buffer efficacy and incorporate responses to storms. We also address the applied literature where conceptual models predict how varying riparian width should influence different response variables. Finally, we call attention to participation by USDA Forest Service scientists from the Coweeta Hydrologic Laboratory who will study terrestrial soils and riparian vegetation employing a collaborative team approach.

1) RESULTS FROM PRIOR NSF SUPPORT

Collaborative Research: NO₃-N Retention in Headwater Streams: Influences of Riparian Vegetation, Metabolism and Subsurface Processes; NSF DEB-9815868; 06/01/99 ñ 03/31/04; Amount: \$800,000; PIs: H.M. Valett; J. Webster, P. Mulholland.

This research program has focused on the hydrologic and biogeochemical processes that influence the retention and transformation of nitrate in headwater streams. These features were addressed in 3 watersheds representing either mesic forests, with or without extensive understory, and semi-arid coniferous settings. Paired streams contrasting in the extent of surface-aquifer exchange were selected at each site to address the importance of subsurface process. We quantified N retention and transport using 12-hr additions of ¹⁵NO₃ and Cl and quantifying the distribution of these tracers in surface, subsurface and biotic compartments. During the second year, we conducted day-night injections to address autotrophic and heterotrophic uptake. We also employed a rising-limb analysis to determine the influence of sub-surface processes. During the third year of the program, we introduced labile carbon and NO₃-N to assess denitrification rates. Results have been presented at a number of national meetings (AGU 2000, NABS 2000-2004, International N Conference 2001) and in recent publications (see References Cited).

2) INTRODUCTION AND RESEARCH OVERVIEW

Aquatic ecosystems reflect their terrestrial settings and this is particularly true for streams in temperate forest biomes (Minshall et al. 1983). While restricting light and autochthonous (i.e., internal) primary production, streamside forests supply allochthonous (i.e., external) organic matter (OM) that fuels lotic food webs. Benthic macroinvertebrates within streams breakdown and process this OM and transform coarse particulate organic matter (CPOM, > 1 mm) to fine POM (FPOM, < 1mm). Riparian vegetation may also retain and transform nutrients entering from upslope flowpaths (Hill 1996). While upslope terrestrial environments influence basin-wide characteristics of streams, many studies show that conditions within the riparian zone control local variation in stream structure and function (e.g., Johnson and Covich 1997).

Lateral interactions like those described above generate intimate links between terrestrial and aquatic systems, but there are equally strong upstream and downstream (i.e., longitudinal) linkages within streams. Downstream reaches are replenished by water and materials delivered from upstream and the resulting longitudinal linkage has been investigated over short (i.e., reach, 100s of meters, Newbold et al. 1981) and long (basin scale, e.g., Vannote et al. 1980) distances. The fact that the flow of water organizes stream structure and function is formally recognized in the "nutrient spiraling concept", which describes the movement and processing of nutrients and OM in a longitudinally explicit manner (Webster 1975, Newbold et al. 1981). In streams, traditional nutrient cycles are elongated by downstream transport to form spirals, the spatial and temporal dimensions of which describe the propensity for a stream to retain and process material.

Terrestrial and aquatic ecosystems are most intimately linked in the headwaters where the vast majority of a catchment's stream length occurs (Dunne and Leopold 1978). Our past work has shown that these streams are critical points of retention that help determine the abundance, form, and timing of material transported to rivers and estuaries (Peterson et al. 2000, Webster et al. 2003). Because headwater streams are closely associated with land, they are influenced by natural (Resh et al. 1988) and anthropogenic (Webster et al. 1983) terrestrial disturbance.

Forest harvest (i.e., clear-cutting) is a form of terrestrial disturbance that disturbs lotic ecosystems by changing light availability, sediment composition, nutrient abundance, and OM dynamics (Likens et al. 1977, Webster et al. 1983). By altering the intimate links between terrestrial and aquatic elements, forest harvest is a disturbance that influences both hillslope and stream subsystems of watershed landscapes. The influence that terrestrial disturbance has on streams is mediated by the riparian zone (Likens and Bormann 1974, Peterjohn and Correll 1984, Pinay and Decamps 1989, Hill 1996) because it plays a critical role as a 3-dimensional ecotone between terrestrial and aquatic systems (Gregory et al. 1991). Thus, the riparian ecotone may buffer the extent to which disturbance alters the terrestrial-aquatic interactions that organize stream ecosystem structure and function. In this proposal, we use the term "buffer" much as it is used for chemical solutions whereby buffers minimize deviation from a given condition.

Given the association between riparian vegetation and streams, many have argued that the stream-riparian corridor (sensu Dahm et al. 1998) should be addressed as an integrated unit that together responds to terrestrial disturbance. With this perspective, riparian zones provide stability to stream-riparian corridors as resistant elements that maintain structure and function in the face of upslope disturbance (Webster et al. 1983, Herbert et al. 1999). Streams, on the other hand, contribute to stream-riparian corridor stability through resilience (i.e., recover quickly following disturbance, Fisher et al. 1982, Webster et al. 1983, Valett et al. 1994).

In this proposal, we ask how interactions between streams and riparian vegetation influence stream responses to small-scale forest clear-cutting. Further, we focus on the role of riparian vegetation by proposing comparative studies among watersheds where clear-cutting will remove upslope vegetation but leave riparian zones of differing widths.

For a number of years following clear-cutting, structure and function of the forest are severely altered as the ecosystem experiences a "reorganization" phase (sensu Bormann and Likens 1979). Reorganization is expected to act as a press disturbance (sensu Bender et al. 1984) to the stream-riparian corridor and continue to alter terrestrial-aquatic interactions over a number of years as the forest undergoes reorganization (Webster et al. 1983, Valett et al. 2002). Down gradient of the disturbed forest, however, streams undergo longitudinal succession (sensu Margalef 1968, Fisher 1983) where intact terrestrial-aquatic interactions combine with in-stream processes to return the stream to an undisturbed state. This "self-purification" has long been touted as a critical aspect of streams (McColl 1974) enabling them to recover from point source disturbance (Hynes 1960). Thus, streams are not only resilient systems, but also provide resistance to stream-riparian corridors by regulating the distance an upstream disturbance extends downstream.

Despite wide recognition of the importance of the riparian zone as a buffer from terrestrial disturbance and the evident influence of upstream-downstream connections, little effort has been made toward quantitatively understanding how these co-occurring, but perpendicular, linkages interact to control how lotic ecosystems respond to disturbance. In a theoretical context, we seek to understand how lateral linkages between aquatic and terrestrial ecosystems (e.g., OM inputs) interact with longitudinal processing to organize aquatic structure (e.g., benthic community composition) and function (e.g., N spiraling). We will address these issues by tracking the

influences of terrestrial disturbance through the terrestrial-aquatic ecotone (i.e., riparian zone) and through the aquatic ecotone established between stream reaches flowing through disturbed forest patches and adjacent downstream reaches flowing through intact forest.

Thus, our proposed research addresses the following questions: **1) How does the presence and extent of riparian vegetation buffer streams from the lateral effects of terrestrial disturbance? and, 2) How does riparian buffering within disturbed forest patches influence longitudinal recovery in downstream reaches flowing through intact forest?**

In cooperation with the USDA Forest Service Southern Research Station at the Coweeta Hydrologic Laboratory in western North Carolina, we propose to investigate these questions in 8 headwater catchments where forest harvest will remove ca. 8-10 ha of upslope forest while leaving riparian zones of differing widths. Replicate catchments in which no trees are removed will serve as reference systems. Upslope trees will be harvested in the remaining 6 catchments (i.e., two catchments per treatment). The three riparian treatments will retain riparian vegetation in widths of 30, 10 or 0 m along 200-300m lengths of first-order streams. These manipulations will provide the treatments required to assess how riparian vegetation buffers terrestrial disturbance and how this buffering is translated laterally and longitudinally to streams.

Our approach relies upon the ecological concepts of stability, ecotone permeability, and material spiraling. For each watershed, we will characterize terrestrial-aquatic interactions by quantifying the inputs of critical resources known to organize stream structure and function. Pre-disturbance data from each site will be combined with data from the reference systems (i.e., watersheds without manipulation), to explore how riparian vegetation buffers the influence of terrestrial disturbance (i.e., assess riparian contributions to stream-riparian corridor stability). Because the flow of water links upstream environments to downstream reaches, altered terrestrial-aquatic interactions in the disturbed reach should generate longitudinal ecotones in downstream reaches that will be characterized by gradients in stream structure and function. Ecotones of this type will extend characteristic distances into downstream reaches until conditions no longer reflect the influence of disturbance (i.e., stream contributions to stream-riparian corridor stability). These distances will reflect the nature of the longitudinal ecotone that exists between these paired stream reaches (i.e., upstream disturbed - downstream recovery) and is expected to vary for specific measures of stream structure and function. Thus, **we propose that lateral and longitudinal influences will combine to form instream ecotones that extend downstream of the interface between disturbed and undisturbed terrestrial systems.** Further, we propose that the 'recovery distance' will vary with the extent of riparian buffering as riparian zones maintain critical terrestrial-aquatic interactions.

We propose two related research elements (Figure 1) designed to 1) address how riparian vegetation buffers disturbance to the stream and organizes lateral linkages between terrestrial and lotic ecosystems, and 2) quantify in-stream gradients or 'recovery distances' when different widths of riparian vegetation are maintained during forest harvest. In **Research Element I**, we will quantify inputs of light, organic matter, and nutrients among the 8 catchments 1-2 years before harvest and for 2-3 years following the clear-cuttings. We will address how key measures of stream structure and function change following disturbance and how riparian zone width alters the direction and magnitude of response. Our response variables will include measures of the physical template (sediment, light, heat), OM dynamics (standing stocks, leaf breakdown, metabolism, and OM turnover length), biogeochemistry (nutrient composition and concentration, N spiraling), and biotic composition (invertebrate community structure, algal biomass). In **Research Element II**, we will address the spatial aspects of recovery within the stream by

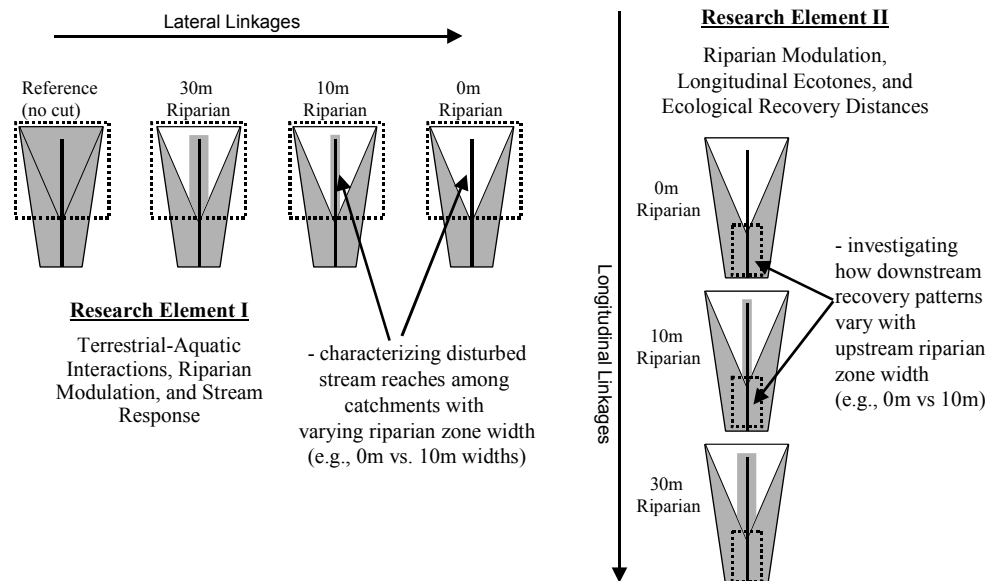


Figure 1. Schematic of Research Elements I & II. Trapezoids represent study catchments with thick vertical lines as streams. White triangular insets are up-gradient portions of the catchment that will be clear-cut. Shaded rectangles depict riparian zones of differing width that will not be harvested.

quantifying longitudinal gradients in stream structure and function as a means of determining recovery distances for various ecosystem components. Similar to Element I, we will focus on physical features, OM, nutrient dynamics, and biotic composition.

Besides determining the distance required for recovery, it is also our goal to characterize the shape of the response curves within the longitudinal ecotones created by upstream disturbance. We anticipate that longitudinal responses may be non-linear and variables may change rapidly at different points within the ecotone. Accordingly, we will address a reduced number of variables in a spatially-explicit design intended to quantify the longitudinal form of recovery curves.

Though research elements are presented independently, activities and products of each element are closely associated (Figure 1). For instance, Research Element I will quantify the mean state within upstream (i.e., disturbed and reference) reaches across catchments (i.e., along a gradient of riparian extent). In turn, these measurements establish the upstream condition from which longitudinal recovery will be assessed in Research Element II (i.e., assessing ecotone structure).

The proposal combines our experience working on headwater streams in the southern Appalachian Mountains with a valuable opportunity to collaborate with both research and management personnel in the USDA Forest Service. Clear-cutting will provide large-scale treatments allowing us to address responses at the ecosystem level. Results from this research will advance our understanding of how land-use practices alter aquatic resources while addressing managers' concerns for southern Appalachian watersheds. The research will be among the first to quantify the distance over which streams recover from forest cutting and how this distance changes for different levels of riparian disturbance. In addition, the research will address fundamental ecological concepts including ecological stability, terrestrial-aquatic interactions, and the development and maintenance of non-linear ecotones in open ecosystems.

3) ECOLOGICAL SIGNIFICANCE AND BROADER IMPLICATIONS

Terrestrial-Aquatic Interaction and Stream Ecosystem Stability: Expanding the concepts introduced by Holling (1973), Webster (1975) suggested that ecological stability in streams is related to their resilience (i.e., capacity to respond quickly following disturbance) rather than their resistance (i.e., capacity to minimize effects of a disturbance). The resilient nature of

streams has been well documented by studies of large-scale disturbances like flash-floods (Fisher et al. 1982), and whole-catchment clear-cutting (Webster et al. 1992). Disturbances that occur at smaller scales (e.g., blow downs, pest outbreaks) create patches of more localized terrestrial disturbance. Under these conditions, stream and riparian processes may provide resistance stability. Downstream processes that retain materials from upstream limit the spatial extent of disturbance and provide resistance within the stream-riparian corridor. Mechanisms occurring at the stream-reach scale lead to incorporation of these smaller scale disturbances when viewed at a larger scale. Considerable work in stream ecology has addressed the influence of large-scale disturbances to which streams respond quickly (Resh et al. 1988, Yount and Nemi 1990, Poff et al. 1997). Far fewer studies have addressed how lateral and longitudinal mechanisms result in spatial patterns of response to more localized disturbance.

Materials move in all ecosystems and spatially-arranged ecological organization is receiving increased attention outside of aquatic ecology (e.g., Reiners and Driese 2001). However, the importance of material movement is amplified in open, advection-dominated, aquatic ecosystems like groundwater flow paths (Vroblesky et al. 1994), lakes (Kling et al. 1999), rivers (Alexander et al. 2000), and streams. Coupling lateral and longitudinal linkages is critical to understanding terrestrial-aquatic interactions and how these linkages influence response to disturbance.

Stream ecotones as non-linear systems: Lateral processes (e.g., material supply) and longitudinal mixing created by flowing water (transport, deposition, and resuspension) are expected to generate identifiable in-stream transitions (i.e., ecotones) within the stream as it flows from a disturbed to an undisturbed terrestrial setting. A central task of the proposed research is to determine the length and characteristics of these longitudinal ecotones. Further, it remains to be seen whether non-linear or linear models best represent spatial patterns within stream ecotones. While a good deal of literature has addressed the longitudinal behavior of point-sources and the nature of lateral inputs, we know relatively little about the within-stream gradients that arise from large-scale terrestrial manipulations. Literature addressing material transport in streams suggests that many ecotone patterns are likely to be non-linear. For example, it has been consistently demonstrated that nutrient and OM transport conforms to a negative exponential model (Webster et al. 1999, Thomas et al. 2001). By extension, resources critical to many invertebrate functional feeding groups may be distributed in a non-linear fashion resulting in complex changes in density and composition at the boundaries between disturbed and undisturbed patches (Naiman et al. 1988, Cummins et al. 1989). Our proposal will generate numerical representations of in-stream ecotones and may provide novel, non-linear measures of stream responses to changing terrestrial-aquatic interaction in a spatially-explicit manner.

Broader impacts - managing forest harvests and catchment resources: Recently, Gosz (1999) emphasized the need for ecologists to combine studies of ecological theory with efforts to resolve sustainable and responsible stewardship of natural and managed ecosystems. In this proposal, we seek to understand stream ecosystem structure and function within the context of terrestrial land use. The impetus for the proposed research (i.e., upslope and riparian vegetation manipulation) originates from forest manager's need for more information regarding the spatial structuring of resource management. Throughout the USDA Forest Service's Southern Region (a 13 state area), maximum spatial extent of clear-cutting is now limited to ca. 10 ha, a patch size comparable to those that we will experimentally generate. Results from this work will help answer questions like: How wide do riparian buffers have to be to protect streams in these southeastern forests? How much stream length is needed to recover from upstream clear-cuts? Forest Service scientists from Coweeta will be detailing how soils and riparian vegetation

composition respond to these catchment manipulations. Coordinating our work with them throughout the project (see Appendix A) will enhance the scope of the work and help translate results to a better understanding of land use impacts on water resources and habitat quality.

4) BACKGROUND INFORMATION: CLEAR-CUTTING INFLUENCES ON HEADWATER STREAMS ñ LESSONS FROM STUDIES AT COWEETA HYDROLOGIC LABORATORY, NC

Our past work at the Coweeta Hydrologic Laboratory focused on Watershed 7 (WS7), a 59 ha catchment that was clear-cut and cable-yarded in 1977 and allowed to recover without further manipulation. Big Hurricane Branch (BHB) which drains WS7 received large amounts of sediment and elevated sediment transport was evident for decades following logging (Golladay et al. 1987). Removal of the streamside canopy resulted in temporary increases in temperature and light, and long term increases in N. These changes altered algal abundance and composition and generated a peak in primary production that lasted several years (Webster et al. 1992). Stream macroinvertebrates changed from functional feeding groups dominated by those that use CPOM (i.e., shredders) and FPOM (i.e., collectors) to those that use algae (i.e., scrapers) as a food source (Wallace and Gurtz 1986).

After logging, litterfall was reduced by ca. 98% (Webster and Waide 1982). Forest composition differed during regrowth resulting in a drastic increase in litter quality. Prior to logging, leaf species low in food represented 55% of litter input, but were virtually lacking following clear-cutting (Webster and Waide 1982). Over 3-5 years, the reversion in energy base from algae back to allochthonous OM returned dominance from scrapers to shredders and collectors (Stone and Wallace 1998).

Leaf breakdown rates have been consistently faster in BHB than before the clear-cutting (Benfield et al. 2001). Microbial activity and invertebrate feeding appear to be central causes. For the past 20 years, NO₃-N in BHB has been elevated from 3-10 fold over pre-logging values (Swank and Vose 1997). This nutrient supplement and higher detrital food quality may enhance microbial conditioning and make leaves more suitable for shredders (Gessner et al. 1999).

Stream research at Coweeta before and after clear-cuts has clearly shown that removing vegetation from entire catchments results in a number of rather significant changes in stream properties. We will base a number of our research approaches on what has been learned previously from these catchment manipulations. The current proposal is more temporally restricted (i.e., 2-3 yr. post-logging) emphasizing responses to forest reorganization rather than successional regrowth. The forest harvest treatments in this proposal will be restricted to ca. 8 ha at the top of catchments leaving substantial intact downstream reaches. This approach allows us to address how streams will respond to various levels of riparian vegetation disturbance not only within reaches proximate to the disturbances as well as downstream.

5) RESEARCH ELEMENT I: TERRESTRIAL-AQUATIC INTERACTIONS, RIPARIAN BUFFERING, AND STREAM RESPONSES

Upslope disturbance and changing riparian-stream interaction may be manifested as altered physical-chemical conditions, differing aquatic community composition, and altered rates and types of ecosystem-level processes. To date, most studies of streams have compared how they respond to the presence or absence of riparian vegetation. For instance, pasture streams contain a greater proportion of smaller sediments (Storey and Cowley 1997, Quinn et al. 1997) compared

to forested streams. Streamside vegetation reduces light and buffers thermal regimes (Rutherford et al. 1997) critical to resident macroinvertebrates and fish (Ward and Stanford 1982).

Loss of riparian forest during pasture production also reduces benthic OM by drastically lowering allochthonous inputs (Campbell et al. 1992). Scarcity of allochthonous POM in pasture streams results in invertebrate communities depleted in shredders (Benfield et al. 1977). Instead, increased algal abundance (Quinn et al. 1997) and higher rates of primary production may promote an abundance of grazing taxa. Rates of primary production, community respiration, and indices of organic carbon spiraling respond to the loss of riparian vegetation (Young and Hury 1997, 1999). Similarly, N and P spiraling were strongly altered by riparian forest removal along a headwater stream in Spain (Sabater et al. 2000).

While most studies have shown that removal of riparian vegetation is detrimental to streams, how diminishing riparian corridor widths affect stream responses is largely unknown. One major goal of the proposed research is to provide quantitative assessment of how the stream-riparian corridor responds to disturbance given decreasing abundance of riparian vegetation.

Question I: How does the presence and extent of riparian vegetation buffer streams from the lateral effects of terrestrial disturbance?

Hypothesis I: Riparian vegetation imparts resistance to the stream-riparian corridor because it maintains critical terrestrial-aquatic interactions that determine stream structure and function.

Prediction I-1: Intact riparian vegetation will maintain terrestrial influences (i.e., inputs of light, nutrients, and organic matter) and will provide treatment streams with inputs that are of similar type and magnitude to those documented in pre-disturbance or reference conditions.

Thus, stream-riparian corridors that include riparian vegetation will retain the basic links with adjacent terrestrial systems that organize them. This should be evident in stream structure and function.

Prediction I-2: Stream structure (e.g., OM standing stock, benthic community composition) and function (e.g., N spiraling) will be less altered in streams with intact riparian vegetation compared to catchments where upslope disturbance is not buffered by riparian processes.

We predict evident differences in streams with or without riparian vegetation, but the influence of variable riparian width is less clear.

Prediction I-3: Riparian resistance will vary for different response variables and may decline with decreasing riparian zone width.

Results from our past studies (e.g., Sponseller et al. 2001) suggest that 10m of riparian vegetation along headwater streams provides substantial inputs and promotes biotic diversity. Research in the applied sciences suggests that riparian buffer efficacy differs with response variable (NRC 2002). USDA guidelines (Dosskey et al. 1997) suggest that required buffer widths are shorter (ca. 10m) for sediment retention and OM input than for retention of soluble nutrients (ca. 30m). However, relatively little empirical work exists on how buffer widths change in-stream function and even less research has addressed downstream implications. The research proposed here has

the potential to provide valuable information on these applied issues while also addressing fundamental ecological principles. Integrating our results with the concerns of forest managers is a central goal of our collaboration with the Southern Research Station personnel.

Tests: To characterize ecosystem responses to terrestrial disturbance and altered riparian influence **we will explore how select terrestrial-aquatic interactions and in-stream characteristics change following forest harvest treatments to assess resistance and riparian buffering** (Table 1). Terrestrial-aquatic interaction will be addressed by quantifying inputs of

Table 1. Structural and functional measures proposed for studies of stream-riparian corridor responses to upslope and riparian harvest. Measures will characterize terrestrial-aquatic interactions and stream responses for biogeochemical, organic matter, and community components (see Methods section for details).

Variable	General Method
1) Terrestrial-aquatic interactions	
i) light and heat	i) light and temperature data loggers
ii) OM inputs	ii) litter traps
iii) sediment	iii) stream bed granulometry
iv) nutrient inputs	iv) groundwater nutrients and tracer injections
2) Biogeochemistry	
i) dissolved nutrients (inorganic N&P, organic C)	i) surface and groundwater nutrient sampling
ii) NO ₃ -N spiraling	ii) stable isotope (i.e., ¹⁵ NO ₃ -N) injections
3) Organic matter:	
i) standing crops of LWD, CPOM, FPOM, DOC	i) line-transect, benthic and suspended samplers
ii) decomposition rates (k)	ii) leaf pack breakdown assays
iii) metabolism (P, R)	iii) upstream-downstream O ₂ budgets
iv) C turnover length (S _T)	iv) respiration and OM standing stocks
4) Benthic Community Composition	
i) algal community	i) chlorophyll <i>a</i> ii) ash free-dry mass (AFDM)
ii) invertebrate community	iii) benthic multi-habitat sampling

light, heat, OM, and groundwater N using methods fully described later. Briefly, we will use litter traps distributed along the study reaches and automated meters to quantify OM inputs and light/heat regimes, respectively. Automated samplers (e.g., ISCO, Inc) will be used to measure export of nutrients and suspended OM on a relatively frequent (i.e. biweekly) basis. We will also use conservative tracer additions and install near-stream wells to quantify the location and magnitude of N inputs. On a seasonal basis, streams will be analyzed for i) biogeochemical, ii) organic matter, and iii) benthic community responses within the cut forests or reference catchments. Chosen variables (Table 1) represent widely used measures of stream structure and function and also provide integrative measures of stream conditions (i.e., benthic community structure). Finally, we have included measures of carbon and N spiraling that may be quantified over relatively short stream lengths to integrate measures of material transport and processing.

Additionally, the extent of riparian vegetation should influence stream hydrographs by influencing lateral interaction between storm water and the stream-riparian corridor. We will employ automated samplers (e.g., ISCO, Inc.) equipped with air-velocity flow meters to monitor nutrient and suspended material export during storms while also providing a time series of data on transport that may be used to statistically assess buffer influences (see section 7 below). Though we do not propose to focus on storms in this study, automated sampling should be sufficient to address how variable buffer width alters storm influence on stream structure.

6) RESEARCH ELEMENT II: RIPARIAN BUFFERING, LONGITUDINAL ECOTONES, AND ECOLOGICAL RECOVERY DISTANCES

Following the clear-cutting of terrestrial vegetation there will be discrete and evident boundaries delineating terrestrial patches of disturbed and undisturbed forest. The flow of water within streams is expected to propagate the influence of upstream conditions into adjacent downstream reaches. Thus, differences within streams are likely to be neither instantaneous nor as spatially distinct as those observed in the terrestrial system. **A fundamental goal of the proposed research is to provide an empirical understanding of how terrestrial alterations form longitudinal gradients in streams, how the gradients may vary under different alteration scenarios, and how they differ for numerous variables of interest.**

Research has demonstrated that streams respond longitudinally to altered terrestrial-aquatic interactions. At the basin scale, this forms the basis for the River Continuum Concept (Vannote et al. 1980) which predicts changes in community and ecosystem attributes as streams progress from headwaters to large lowland rivers. At smaller scales, conditions are documented to change as streams traverse forest-pasture boundaries. Storey and Cowley (1997) investigated these changes in 6 stream characteristics as water flowed from pasture-dominated headlands into forest remnants. Similarly, Swift and Baker (1973) observed thermal patterns with increasing distance in a stream draining a mosaic of forestry practices (e.g., clear-cutting, thinning, riparian forest buffers). In each study, nonlinear changes with distance were observed. These studies used a relatively small number of sites to describe downstream change. Characterizing the recovery profile will require more spatially-explicit resolution. Focused efforts designed to define longitudinal patterns in specific stream variables are generally lacking in the literature.

The influence of an upstream disturbed reach will penetrate into downstream reaches to varying degrees depending on the nature of the stream-riparian corridor existing upstream, local hydrological conditions, and the response variable of interest. After some characteristic ‘recovery distance’, the influence of the disturbed reach is no longer evident. Thus, downstream reaches minimize the spatial extent of disturbance and provide stability to the larger system. The longitudinal interface that exists between disturbed and undisturbed reaches reflects the combined effects of lateral and longitudinal linkages and provides the conceptual and empirical framework for pursuing the following question and hypotheses.

Question II: How does riparian buffering within disturbed forest patches influence longitudinal recovery in downstream reaches flowing through intact forest?

Hypothesis II: Upstream riparian vegetation organizes longitudinal recovery within the stream-riparian corridor because it controls disturbance effects (i.e., imparts resistance) within disturbed reaches and determines conditions for in-stream recovery processes in downstream reaches.

Prediction II-1: Recovery distances should be correlated with upstream resistance.

Recovery distances should increase with decreasing riparian width and be longest in catchments where riparian buffering is entirely lacking (i.e., 0 m riparian width). Alternatively, if riparian resistance remains similar despite decreasing width (see Prediction I-3), recovery distances may be longer only in catchments lacking riparian vegetation. Recovery distances for different responses may vary across treatments.

Prediction II-2: Longitudinal patterns in downstream recovery and their mathematical expressions will vary among response variables

Upstream disturbance and reestablished terrestrial-aquatic interactions downstream will differentially influence response variables and result in different recovery curves and distances.

Prediction II-3: Expressions used to describe recovery for a specific variable will be retained across riparian treatments while the values for best-fit will vary.

For a given variable, the fundamental relationships between disturbance, terrestrial-aquatic interactions, and recovery will remain the same across all treatments, but treatments may alter upstream buffering and generate different downstream recovery distances (see Prediction II-1).

Tests: Similar to Research Element I, we will focus on variables representing biogeochemical, energetic, and biotic components, but have chosen a reduced number of variables to assess in a spatially-explicit manner (Table 2). Methods and design are detailed in the Methods section.

Table 2. Response variables proposed for studies of longitudinal ecotones and recovery distances. See Methods section for details on response variables, methods, and experimental design.

Dependent Variable Type	Response Variable	Components
1) Biogeochemistry	i) nutrient composition ii) ^{15}N - NO_3 spiraling	i) dissolved N, P and C ii) ^{15}N vs. distance downstream
2) OM dynamics	i) particulate and dissolved OM ii) OM processing assays	i) LWD, CPOM, FPOM, DOM ii) leaf litter breakdown assays
3) Benthic community structure	i) periphyton abundance ii) benthic invertebrate structure	i) Chl <i>a</i> , ash-free dry mass ii) density, richness, functional groups

For each variable, we will quantify change with distance downstream from disturbed reaches to characterize the influence of longitudinal processing. We will quantify the longitudinal patterns along downstream reaches for each of the dependent variables in each of the experimental catchments. Because riparian influence is expected to vary with season, we will repeat many measures during the spring, fall, and summer. Macroinvertebrate sampling, however, will be restricted to early spring when larval stages are best suited for identification.

While detailed methods for measuring recovery curves and quantifying recovery distances are provided later (see Methods section), the general approach for each longitudinal ecotone will be similar and result in a mathematical expression representing the longitudinal gradient for a given response variable (Figure 2). We will initially measure longitudinal gradients in sediment size, nutrient concentration, OM standing stocks, and chlorophyll *a* abundance and use them to guide the placement of transects to be used for litter breakdown, macroinvertebrate, metabolism, and spiraling measures. Once longitudinal patterns of response variables have been established, they will be fit to mathematical expressions designed to relate parameter values to distance downstream of the disturbed reach.

Because recovery distances will be fundamentally related to transport, stream discharge (Q , $\text{m}^3 \text{s}^{-1}$) should exert strong but differing control over the longitudinal dimension of recovery profiles. We will standardize our recovery metrics to account for hydrologic conditions. The influence of flow on the transport of reactive solutes (Wollheim et al. 2001) and fine particles (Young and

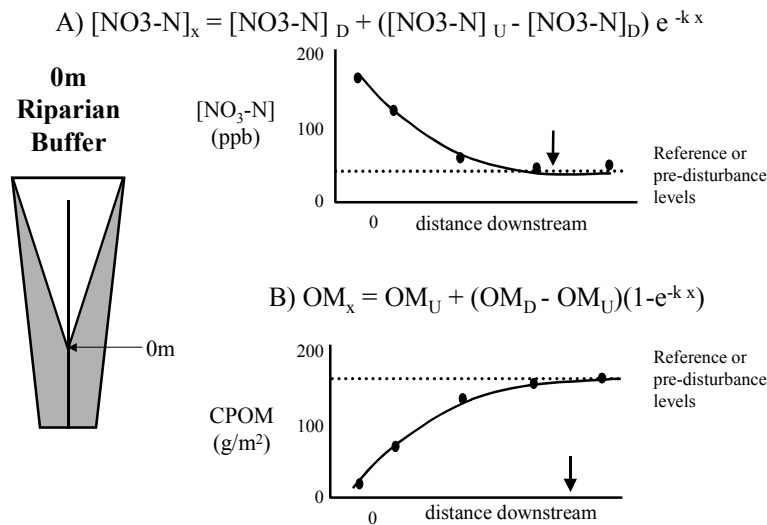


Figure 2. Schematic representation of longitudinal ecotones illustrated by changes with distance downstream (x) of a treatment reach where riparian vegetation is removed (i.e., 0m Riparian Buffer). In-stream processes causing retention of nutrients may result in an exponential decline to a minimum (A). Similarly, allochthonous inputs from riparian and upslope vegetation may cause CPOM standing stocks to increase as an exponential rise to a maximum (B). Subscripts U and R refer to upstream and reference conditions. Arrows on the x-axis illustrate the “recovery distances” at which in-stream conditions are similar to undisturbed values (i.e., reference or pre-disturbance conditions).

Different forms of recovery curves are expected for differing response variables. Figure 2 illustrates two potential forms, but others will undoubtedly exist. If in-stream boundaries are abrupt, the distance/strength of disturbance influence may be non-existent and variables within the downstream patch may recover immediately (i.e., represented by a step function). In other cases, multiple variables sensitive to changing riparian conditions (e.g., light availability, OM inputs) may interact to generate non-linear patterns of various complexities. Many studies have illustrated exponential responses down gradient from point sources in streams (Stream Solute Workshop 1990, Minshall et al. 2000). More complex scenarios (e.g., a sigmoid function) may be anticipated for community responses if benthic resource availability changes with distance.

For each longitudinal ecotone, alternative quantitative models for recovery pattern and distance will be developed by eye and by curve-fitting algorithms available in commercial graphics packages (e.g., SigmaPlot, Jandel Sci.). Alternative forms of recovery models will be compared via likelihood analysis (*sensu* Hilborn and Mangel 1997) to assess the aptness of linear and non-linear forms. Further, we intend to interact with Dr. Eric Smith, Director, Statistics Consulting Laboratory, Virginia Tech to continue development of appropriate “recovery” models.

7) STUDY SITES, RESEARCH TIMING, EXPERIMENTAL DESIGN, AND STATISTICAL ANALYSES

Study sites and preliminary results: Scientists from the USDA Forest Service Southern Research Station have identified two sets of sites that will receive the forest harvest treatments.

Huryn 1999, Thomas et al. 2001) is widely recognized. Because water depth and velocity are most intimately related to transport, it is their product, unit width discharge (Q_s , $\text{m}^2 \text{s}^{-1}$) that is most frequently used to standardize transport metrics (Stream Solute Workshop 1990, Cushing et al. 1993). Many studies of material spiraling in streams have used negative exponential models ($C_x = C_0 e^{-kx}$) to characterize solute and particle transport. In these analyses, discharge standardization is achieved by multiplying the longitudinal loss rate (k , m^{-1}) by Q_s . The resulting metric (m s^{-1}) is referred to as the uptake or deposition velocity (v_f ; reactive solutes and v_{dep} , particles). We will standardize for discharge by converting longitudinal change coefficients (k , Figure 2) to specific recovery velocities (ρ , m s^{-1} ; analogous to v_f).

Each set of sites includes 4 catchments of ca. 8 ha in the Nantahala National Forest (USGS Wayah Bald and Burningtown quadrangles) ca. 15 miles from the Coweeta Laboratory. The first set of sites (Burningtown) are now scheduled to be cut in Fall 2005 with the second sites slated for Fall 2006 or 2007. During Fall 2003, we initiated studies in the Burningtown sites including assays of litter fall, leaf breakdown, nutrient composition, and $\text{NO}_3\text{-N}$ spiraling. Each stream was instrumented with an array of 20 litter-fall traps and leaf breakdown assays carried out over 500-700m reaches situated within as well as beyond the patch of up-slope/riparian harvest. Results show that the streams are perennial and include active shredding macroinvertebrates and a diverse array of leaf species entering as allochthonous CPOM. Inorganic nutrients exist in low concentrations (e.g., $\text{NO}_3\text{-N}$, 50-150 ppb) and $\text{NO}_3\text{-N}$ is rapidly retained during leaf fall.

We will distribute the assessment of riparian buffering and longitudinal recovery differently over space and time depending on the variables of interest. For studies of OM and N spiraling, we will focus on summer and fall assays since our past work has shown that these are the most metabolically and biogeochemically active times of the year. Additionally, they are contrasting seasons in terms of riparian canopy conditions. For similar reasons, metabolism and OM spiraling assays will be conducted during the same seasons. Leaf litter breakdown assays will be initiated in fall and continued through spring. Benthic macroinvertebrate samples will be collected during early spring (e.g., March) when late instars will allow for greater taxonomic resolution. We will use pre-disturbance years to assess whether it is necessary to modify our methods (see below) and to assess natural variation in response variables.

Statistical analyses: As is generally the case for ecosystem-level manipulations (Carpenter 1989), we will have little power (i.e., $n=2$) for a classic ANOVA approach to statistical assessment. Instead, we will use regression and correlation analyses to assess experimental results. For upstream reaches, we will determine the mean state for response variables within the 3 disturbed reaches and calculate resistance as the % change in a state variable when compared to the reference stream (Grimm and Fisher 1989). Mean values for response variables and resistance calculations will be compared among treatments and with other stream characteristics using regression and correlation analyses (SAS Inc., 1991). A similar approach will be taken for the recovery distances and velocities derived from the second research element. In addition, we will employ times-series approaches that take advantage of the paired watershed design proposed here, but require a large number of observations to be collected before and after disturbance (e.g., BACI; sensu Stewart-Oaten et al. 1986, RIA sensu Carpenter et al. 1989). We will use these to assess how more frequently monitored variables (i.e., discharge, light, heat, nutrient and suspended particulate concentration) respond to variable buffer width and upslope harvest.

8) METHODS

Quantifying terrestrial-aquatic interactions:

Allochthonous Inputs: We will measure litter quantity and quality in the forest and mixed sites monthly in the experimental sites and downstream using a network of litterfall traps standard for our lab (e.g., Benfield et al. 2000). Collected litter will be sorted by leaves, twigs, and other (seeds, flowers, bark, etc.), and leaves will be identified to species and classified into quality categories according to known breakdown rates (Webster and Benfield 1986). Samples will be dried, weighed, and converted to AFDM by standard procedures.

Solar radiation and stream temperature. Total solar radiation will be continually measured above the channel at each transect using OnsetTM light intensity recorders. Light availability as photosynthetically active radiation will be measured periodically to calibrate total irradiance data obtained from the onset recorders. Stream temperature also will be continually recorded using Ibutton Thermochron Sensors^{AE} temperature loggers at each transect used in Research Element II.

Groundwater Nutrient Flux. In upstream disturbed and reference reaches, we will use techniques employed in our past studies of groundwater-stream interaction to quantify how groundwater inflow of N responds to upslope and riparian manipulation. Near-stream PVC wells will be installed by hand to depths of ca. 25 cm along the length of the reach. Locations and rates of groundwater inflow will be determined using conservative tracer injections (i.e., Cl⁻ or Br⁻ additions) and standard techniques to quantify groundwater input via tracer dilution (Stream Solute Workshop 1990). Nutrient fluxes to the stream will be calculated following the method of Chestnut and McDowell (2000) by coupling lateral inflow and groundwater concentrations. Well placement will be coordinated with Coweeta scientists involved in soil lysimetry and hillslope groundwater studies (see Appendix A). Resolving riparian processing along groundwater flowpaths is considered beyond the scope of our project and methods described here are designed to provide comparative indices of nutrient inputs.

Measures of Stream Ecosystem Structure:

Sampling plan: Our goal for stream reaches proximate to the forest manipulation is to estimate average values for each variable of interest. Hence, we will concentrate our sampling at the downstream end of the reach. Our goal for reaches downstream from the forest manipulation is to describe longitudinal patterns of response to the upstream manipulation. Thus, we will sample variables at multiple reaches on log scale of distance, e.g., 40m, 80m, 160m, 320m. Stream length below the experimental reaches range from 750-1000m.

Channel morphology and hydrology: Channel gradient, active channel depth and width, bankfull channel depth and width, and sediment characterization will be quantified throughout the study reaches using standard methods (Gordon et al. 1992). Stream discharge will be measured continuously at two sites (bottom of cut reach and downstream in the recovery reach) in each catchment by means of pressure transducers and automated samplers (see above) to monitor water elevation. We will develop rating curves by correlating stream elevation with discharge determined by dilution gauging (Webster et al. 1992). These measures will be compared to historical records from nearby Coweeta streams (Coweeta Hydrologic Laboratory) to assess current flows in the context of drought and wet years.

Dissolved nutrients: We will use ISCO samplers to provide bi-weekly replicate samples from the base of each experimental or reference reach. In addition, more extensive sampling will occur during seasonal ecosystem assessments. We will quantify concentrations of inorganic N as NO₃-N (Wood et al. 1967) or ammonium-N (Zhang et al. 1997), soluble reactive phosphorus (Murphy and Riley 1962), and dissolved organic carbon (DOC, Menzel and Vaccaro 1964) using standard analytical procedures established in our laboratory. These analytical methods generally involve colorimetric spectroscopy or ion chromatography. Recent QA/QC assessment showed that method-detection limits ranged from 1-5 ppb for N and P species and 250 ppb for DOC.

Benthic and suspended particulate organic matter (POM): Benthic POM will be collected using methods standard for our lab (Benfield et al. 2000). Collected material will be separated into fine and coarse fraction using a 1 mm sieve and dried to a constant weight. Sub-samples will be combusted at 550 °C for 2 hours and re-weighed for determination of ash-free dry mass (AFDM) and OM percentage (%OM). Suspended POM will be collected by ISCO and grab samples filtered onto a pre-weighed, pre-combusted, 0.45 mm glass fiber filter in the field. POM AFDM and %OM will be determined by combustion as described above. Filtered water samples will also be collected for determining of DOC using the protocol indicated in Table 2.

Algal biomass: Benthic biofilm biomass will be quantified monthly following Moulton et al. (2002) by collecting randomly selected rocks in each study reach that will be returned to the lab on ice in darkened containers. Rocks will be scraped into a beaker containing stream water and transferred to a graduated cylinder to measure total volume. Sample will then be vigorously mixed, and two sub-samples of known volume will be removed and analyzed for AFDM and chlorophyll a content using standard methods (Table 2).

Benthic invertebrates: Benthic invertebrates will be sampled using a multihabitat sampling scheme developed by the USEPA (Barbour et al. 1999). Sampling will be done in early spring when most aquatic insect larvae are at maximum size and most easily identified. Insects and other invertebrates will be identified to the lowest practical taxonomic level. Individuals of each taxon will be counted, measured to determine mass using length/mass ratios developed at Coweeta (Benke et al. 1999), and assigned to Functional Feeding Groups (FFG) after Merritt and Cummins (1996).

Measures of Stream Ecosystem Function

Leaf Breakdown: Leaf-packs will be constructed by standard methods (Benfield 1996) and placed at experimental sites in late autumn. Two leaf species, one fast-processor and one slow processor (Webster and Benfield 1986), will be employed to examine a range in breakdown responses. Leaf breakdown rates (k) will be determined by the standard method for our laboratory (Benfield et al. 2000). Benthic invertebrates will be sorted, identified, measured for mass determination, and assigned to functional feeding groups.

Gross Primary Production (GPP) and Community Respiration (R): Whole-system metabolism will be quantified using an upstream - downstream dissolved oxygen mass balance approach (Odum 1956) in the disturbed and downstream sections of each stream. The coefficient air-water exchange (reaeration), necessary for these calculations, will be quantified using field additions of propane or sulfur hexafluoride (SF₆) (Marzolf et al. 1994) or through the use of standard equations when this approach is inhibited by stream size (Young and Huryn 1997, 1999).

Nitrate Spiraling Indices: Our research program has a long history of applying solute addition techniques to study N spiraling in headwater streams (Valett et al. 1996, 1997, 2002, Webster et al. 2003). The approach relies on modeling downstream decline of the biologically-active solute using expressions developed as part of the nutrient spiraling concept (Newbold 1992, Stream Solute Workshop 1990). Analysis of downstream changes in tracer concentration yield uptake

lengths (S_w , averaged distance of travel for a dissolved nutrient), uptake velocities (v_f , described earlier as a uptake length normalized for discharge), and uptake rate (U , an areal measure of nutrient flux). Recently, our program has combined the use of stable isotope tracers in conjunction with the spiraling approach (Peterson et al. 2000, Webster et al. 2003). This allows for very small scale (i.e., on the order of meters of stream length) resolution of N spiraling. We will use $^{15}\text{NO}_3\text{-N}$ addition protocols established in our laboratory to assess N spiraling in upstream disturbed reaches. In addition, we will distribute sampling transects throughout the downstream reach to obtain longitudinal resolution of $\text{NO}_3\text{-N}$ spiraling to assess biogeochemical recovery distances.

Carbon Turnover Length (S_T): We will quantify OM processing rates and retention in the upstream reaches using the organic carbon turnover length equations originally developed by Newbold et al. (1982). Organic carbon spiraling length (S_T) estimates the average distance an atom of organic carbon will travel before biological oxidation. Calculation of S_T involves determining the net longitudinal velocity of the OM pool (V , m d^{-1}) using: (1) $V = (Q * \text{TOM}) / (w * \text{BOM})$; where: Q = discharge (m^3/d), w = width (m), TOM = transported OM (g/m^3) and BOM = benthic OM (g/m^2). OM cycling rate (K' , d^{-1}), a measure that relates biological processing to OM standing stocks, is determined by: (2) $K' = R / (\text{TOM} + \text{BOM})$ where: R = respiration ($\text{g OM m}^{-2} \text{d}^{-1}$). K' represents the percent of OM standing stocks respired per unit time. Finally, turnover length is calculated as: (3) $S_T = V / K'$.

Table 3. Methods and literature references for response variables proposed in Research Elements I and II.

Variable	Method/Reference
1) Physical and hydrologic structure	
i) stream width, depth, and gradient	i) morphometric measures (Gordon et al. 1992)
ii) discharge and water velocity	ii) conservative tracer additions (Gordon et al. 1992)
iii) sediment composition	iii) Wentworth granulometry (Wolman 1954)
2) Biogeochemistry	
i) nitrate-N	i) Cd-reduction-spectroscopy (Wood et al. 1967)
ii) ammonium-N	ii) phenolhypochlorite-spectroscopy (Zhang et al. 1997)
iii) soluble reactive phosphorus	iii) molybdate-spectroscopy (Murphy and Riley 1962)
iv) dissolved organic carbon	iv) persulfate digestion (Menzel and Vaccaro 1964)
3) Organic matter	
i) large woody debris	i) line-transect method (Wallace and Benke 1984)
ii) coarse particulate OM	ii) pot sampler (Webster et al. 1997)
iii) leaf breakdown	iii) leaf pack assays (Benfield 1996)
iv) fine particulate OM	iv) pot sampler (Webster et al. 1997)
v) whole-system metabolism	v) diel O curves (Odum 1956, Marzolf et al. 1994)
vi) OM turnover lengths	vi) OM spiraling techniques (Minshall et al. 2000)
4) Benthic Community Composition	
i) chlorophyll a	i) spectrophotometric analysis (Tett et al. 1975),
ii) epilithic biomass	ii) ash free-dry mass (AFDM), (APHA 1999)
iii) benthic macroinvertebrates	iii) multi-habitat sampling (Barbour et al. 1999)

REFERENCES CITED (* indicates products from previous NSF support)

- Alexander R.B., Smith, R.A., and G.E. Schwarz. 2000. Effect of stream channel size on the delivery of nitrogen to the Gulf of Mexico. *Nature* 403:758-761.
- American Public Health Association. 1999. Standard methods for the examination of water and wastewater. 20th edition. American Public Health Association, Washington, D.C., USA.
- Barbour, M.T., Gerritsen, J., Snyder, B.D., and J.B. Stribling. 1999. Rapid bioassessment protocols for use in wadeable streams and rivers: Pheryphyton, Benthic Macroinvertebrates, and Fish. 2nd edition. EPA841-B-99-002. USEPA; Office of Water, Washington, D.C.
- Bender, E.A., Case, T.J., and M.E. Gilpin. 1984. Perturbation experiments in community ecology: theory and practice. *Ecology* 65:1-13.
- Benfield, E.F. 1996. Leaf breakdown in stream ecosystems. Pages 579-590 *in* F.R.Hauer and G.A. Lamberti, editors. *Methods in Stream Ecology*. Academic Press, New York.
- Benfield, E. F., Jones, D.R., and M. F. Patterson. 1977. Leaf pack processing in a pastureland stream. *Oikos* 29:99-103.
- Benfield, E.F., Webster, J.R. Hutchens, J.J. Tank, J.L., and P.A. Turner. 2000. Organic matter dynamics along a stream-order and elevational gradient in a southern Appalachian stream. *Verhandlungen der Internationalen Vereinigung fur theoretische und angewandte Limnologie* 27:1341-1345.
- Benfield, E. F., Webster, J. R. Tank, J.L., and J. J. Hutchens. 2001. Long-Term patterns in leaf breakdown in streams in response to watershed logging. *International Review of Hydrobiology* 86:467-474.
- Benke, A.C., Huryn, A.D., Smock, L.A., and J.B. Wallace. 1999. Length-mass relationships for freshwater macroinvertebrates in North America with particular references to the southeastern United States. *Journal of the North American Benthological Society* 18:308-343.
- Bormann, F. H., and G. E. Likens. 1979. Catastrophic disturbance and the steady state in northern hardwood forests. *American Scientist* 67:660-669.
- Campbell, I. C., James, K.R., Hart, B.T., and A. Devereaux. 1992. Allochthonous coarse particulate organic material in forest and pasture reaches of two south-eastern Australian streams II. Litter processing. *Freshwater Biology* 27:353-365.
- Carpenter, S. R. 1989. Replication and treatment strength in whole-lake experiments. *Ecology* 70:453-463.
- Carpenter, S. R., T. M. Frost, D. Heisey, and T. K. Kratz. 1989. Randomized intervention analysis and the interpretation of whole-ecosystem experiments. *Ecology* 70:1142-1152.
- Chestnut, T. J., and W. H. McDowell. 2000. C and N dynamics in the riparian and hyporheic zones of a tropical stream, Luquillo Mountains, Puerto Rico. *Journal of the North American Benthological Society* 19:199-214.
- *Crenshaw, C.L., H.M. Valett, and J.R. Webster. 2002. The effects of augmentation of coarse particulate organic matter on metabolism and nutrient retention of hyporheic sediments. *Freshwater Biology* 47:1820-1831.

- *Crenshaw, C.L., H.M. Valett and J.L. Tank. 2002. Effects of coarse particulate organic matter on fungal biomass and invertebrate density in the subsurface of a headwater stream. *Journal of the North American Benthological Society* 21:28-42.
- Cummins, K. W., Wilzbach, M.A., Gates, D.M., Perry, J.B. and W. B. Taliaferro. 1989. Shredders and riparian vegetation. *BioScience*. 39:24-30.
- Cushing, C. E., Minshall, G.W., and J. D. Newbold. 1993. Transport dynamics of fine particulate organic matter in two Idaho streams. *Limnology and Oceanography* 38:1101-1115.
- Dahm, C. N., Grimm, N.B., Marmonier, P., Valett, H.M., and P. Vervier. 1998. Nutrient dynamics at the interface between surface waters and groundwaters. *Freshwater Biology* 40:427-451.
- Dosskey, M., D. Schultz, and T. Isenhardt. 1997. How to design a riparian buffer for agricultural land. *Agroforestry Notes*, USDA Forest Service, <http://www.unl.edu/nac/riparian.html>.
- Dunne, T., and L.B. Leopold. 1978. *Water in Environmental Planning*. W.H. Freeman and Company, New York. 818 pp.
- *Fellows, C.S., H.M. Valett and C.N. Dahm. 2001. Whole-stream metabolism in two montane streams: contribution of the hyporheic zone. *Limnology and Oceanography* 46:523-531.
- Fisher, S. G., Gray, L.G., Grimm, N.B., and D. E. Busch. 1982. Temporal succession in a desert stream ecosystem following flash flooding. *Ecological Monographs* 43:421-439.
- Fisher, S. G. 1983. Succession in streams. Pages 7-27 in J. R. Barnes and G. W. Minshall, editors. *Stream Ecology: Application and Testing of General Ecological Theory*. Plenum Press, New York, New York.
- Gessner, M.O., Chauvet, E., and M. Dobson. 1999: A perspective on leaf litter breakdown in streams. *Oikos* 85: 337-384.
- Golladay, S.W., Webster, J.R., and E.F. Benfield. 1987. Changes in stream morphology and storm transport of organic matter following watershed disturbance. *Journal of the North American Benthological Society* 6:1-11.
- Gordon, H.D., McMahon, T.A., and B.L. Finlayson. 1992. *Stream Hydrology: An introduction for ecologists*. John Wiley and Sons, New York.
- Gosz, J.R. 1999. Ecology challenged? Who? Why? Where is it headed? *Ecosystems* 2:475-481.
- Gregory, S. V., Swanson, F.J., McKee, W.A., and K. W. Cummins. 1991. An ecosystem perspective of riparian zones. *Bioscience* 41:540-551.
- Grimm, N. B., and S. G. Fisher. 1989. Stability of periphyton and macroinvertebrates to disturbance by flash flooding in a desert stream. *Journal of the North American Benthological Society* 8:293-307.
- Herbert, D. A., Fownes, J.H., and P. M. Vitousek. 1999. Hurricane Damage to a Hawaiian Forest: Nutrient Supply Rate Affects Resistance and Resilience. *Ecology* 80:908-920.
- Hilborn, R., and M. Mangel. 1997. *The ecological detective: confronting models with data*. Princeton University Press, Princeton, NJ.
- Hill, A. R. 1996. Nitrate removal in stream riparian zones. *Journal of Environmental Quality* 25:743-755.
- Holling, C. S. 1973. Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics* 4:1-24.

- Hynes, H.B.N. 1960. *The Biology of Polluted Waters*. Liverpool University Press, Liverpool, 202 pp.
- Johnson, S. L., and A. P. Covich. 1997. Scales of observation of riparian forests and distributions of suspended detritus in a prairie river. *Freshwater Biology* 37:163-175.
- Kling, G. W., Kipphut, G.W., Miller, M.M., and W. J. O'Brien. 1999. Integration of lakes and streams in a landscape perspective: the importance of material processing on spatial patterns and temporal coherence. *Freshwater Biology* 41:1-21.
- Likens, G. E., and F. H. Bormann. 1974. Linkages between terrestrial and aquatic ecosystems. *Bioscience* 24:447-456.
- Likens, G.E., Bormann, F.H., Pierce, R.S., Eaton, J.S., and N.M. Johnson. 1977. *Biogeochemistry of a forested ecosystem*. Springer-Verlag, New York, USA.
- Margalef, R. 1968. *Perspectives in ecological theory*. University of Chicago Press, Chicago.
- Marzolf, E. R., Mulholland, P.J., and A. D. Steinman. 1994. Improvements to the diurnal upstream-downstream dissolved oxygen change technique for determining whole-stream metabolism in small streams. *Canadian Journal of Fisheries and Aquatic Sciences* 51:1591-1599.
- McCull, R.H. 1974. Self-purification of small freshwater streams: phosphate, nitrate, and ammonia removal. *New Zealand Journal of Marine and Freshwater Research* 8:375-388.
- Menzel, D.W., and R.F. Vaccaro. 1964. The measurement of dissolved organic carbon and particulate organic carbon in seawater. *Limnology and Oceanography* 9:138-142.
- Merritt, R.W. and K.W. Cummins. (editors). 1996. *An introduction to the aquatic insects of North America*. Kendall/Hunt, Dubuque, IA.
- Minshall, G. W., Petersen, R.C., Cummins, K.W., Bott, T.L., Sedell, J.R., Cushing, C.E., and R. L. Vannote. 1983. Interbiome comparison of stream ecosystem dynamics. *Ecological Monographs* 53:1-25.
- Minshall, G.W., Thomas, S.A., Newbold, J.D., Monaghan, M.T., and C.E. Cushing. 2000. Physical factors influencing fine particle transport and deposition in streams. *Journal of the North American Benthological Society* 19:1-16.
- Moulton II, S.R., Kennen, J.G., Goldstein, R.M., and J.A. Hambrook. 2002. Revised protocols for sampling algal, invertebrate, and fish communities as part of the National Water-Quality Assessment Program. U.S. Geological Survey Open-File Report 02-150. U.S. Geological Survey. Reston, Va.
- *Mulholland, P.J., H.M. Valett, J.R. Webster, L.W. Cooper, S.K. Hamilton, and B.J. Peterson. 2004. Stream denitrification and total nitrate uptake rates measured using a field ¹⁵N tracer addition approach. *Limnology and Oceanography* 49:809-820.
- Murphy, J., and J. P. Riley. 1962. Determination of phosphate in natural waters. *Analytica Chimica Acta* 27:31-36.
- Naiman, R. J., Decamps, H., Pastor J., and C. A. Johnston. 1988. The potential importance of boundaries to fluvial ecosystems. *Journal of the North American Benthological Society* 7:289-306.
- Newbold, J. D., Elwood, J. W., O'Neill, R. V., and W. VanWinkle. 1981. Measuring nutrient spiralling in streams. *Canadian Journal of Fisheries and Aquatic Sciences* 38:860-863.
- Newbold, J. D., P. J. Mulholland, J. W. Elwood, and R. V. O'Neill. 1982. Organic carbon spiralling in stream ecosystems. *Oikos* 38:266-272.

- Newbold, J. D. 1992. Cycles and Spirals of Nutrients. Pages 379-399 in P. Calow and G. E. Petts, editors. *The Rivers Handbook*. Blackwell Scientific Publications, Oxford.
- National Research Council. 2002. *Riparian areas: functions and strategies for management*. National Academy Press, Washington, D.C.
- Odum, H. T. 1956. Primary production in flowing waters. *Limnology and Oceanography* 1:102-117.
- Peterjohn, W. T., and D. L. Correll. 1984. Nutrient dynamics in an agricultural watershed: Observations on the role of a riparian forest. *Ecology* 65:1466-1475.
- Peterson, B. J., W. M. Wollheim, P. J. Mulholland, J. R. Webster, J. L. Meyer, J. L. Tank, E. Marti, W. B. Bowden, H. M. Valett, A. E. Hershey, W. H. McDowell, W. K. Dodds, S. K. Hamilton, S. Gregory, and D. D. Morrall. 2001. Control of nitrogen export from watersheds by headwater streams. *Science* 292:86-90.
- Pinay, G., Decamps, H., Arles, C., and M. Lacassin-Seres. 1989. Topographic influence on carbon and nitrogen dynamics in riverine woods. *Archives fur Hydrobiologia* 114:401-414.
- Poff, N., Allan, D., Bain, M.B., Karr, J.R., Prestegard, K.L., Richter, B.D., Sparks, R.E., and J. C. Stromberg. 1997. The natural flow regime. *BioScience* 47:769-784.
- Quinn, J.M., Cooper, A.B., Davies-Colley, R.J., Rutherford, J.C., and B.R. Williamson. 1997. Land use effects on habitat, water quality, periphyton, and benthic invertebrates in Waikato, New Zealand, hill-country streams. *New Zealand Journal of Marine and Freshwater Research* 31:579-597.
- Reiners, W.A. and K.L. Driese. 2001. The propagation of ecological influences across heterogeneous environmental space. *BioScience* 51:939-950.
- Resh, V. H., Brown, A. V., Covich, A.C., Gurtz, M.E., Li, H.W., Minshall, G.W., Reice, S.R., Sheldon, A.L., Wallace, J.B., and R. Wissmar. 1988. The role of disturbance in stream ecology. *Journal of the North American Benthological Society* 7:433-455.
- Rutherford, J.C., Blackett, S., Blackett, C., Saito, L., and R.J. Davies-Colley. 1997. Predicting the effects of shade on water temperature in small streams. *New Zealand Journal of Marine and Freshwater Research* 31:707-721.
- Sabater, F., Buturini, A., Marti, E., Munoz, I., Romani, A., Wray, J., and S. Sabater. 2000. Effects of riparian vegetation removal on nutrient retention in a Mediterranean stream. *Journal of the North American Benthological Society* 19:609-620.
- SAS. 1991. *SAS User's Guide: Statistics*. SAS Institute, Inc. Cary, North Carolina.
- Sponseller, R. S., Benfield, E.F., and H. M. Valett. 2001. Relationships between land use, spatial scale, and stream macroinvertebrate communities. *Freshwater Biology* 46:1409-1424.
- Stone, M.K. and J.B. Wallace. 1998. Long-term recovery of a mountain stream from clear-cut logging: the effects of forest succession on benthic invertebrate community structure. *Freshwater Biology* 39:151-169.
- Storey, R.G., and D.R. Cowley. 1997. Recovery of three New Zealand streams as they pass through native forest remnants. *Hydrobiologia* 353:63-76.
- Stream Solute Workshop. 1990. Concepts and methods for assessing solute dynamics in stream ecosystems. *Journal of the North American Benthological Society* 9:95-119.

- Stewart-Oaten, A., W. W. Murdoch, and K. R. Parker. 1986. Environmental impact assessment: 'pseudoreplication' in time? *Ecology* 67:929-940.
- Swank, W.T., and J.M. Vose. 1997. Long-term nitrogen dynamics of coveeeta forested watersheds in the southeastern United States of America. *Global Biogeochemical Cycles* 11:657-671.
- Swift, L.W.J., and S.E. Baker. 1973. Lower water temperatures within a streamside buffer strip. USDA Forest Service Research Note SE-193.
- Tett, P., Kelly, M.G., and G.M. Hornberger. 1975. A method for the spectrophotometric measurement of chlorophyll *a* and phaeophytin *a* in benthic microalgae. *Limnology and Oceanography* 20:887-896.
- *Thomas, S.A., H.M. Valett, P.J. Mulholland, C.S. Fellows, J.R. Webster, C.N. Dahm and C.G. Peterson. In review. A regression approach to estimating reactive solute uptake in advective and transient storage sub-compartments of stream ecosystems. *Advances in Water Resources* 26:95-976.
- Thomas, S.A., J.D. Newbold, G.W. Minshall, T. Georgian, M.T. Monaghan, and C.E. Cushing. 2001. Transport and deposition of fine and very-fine organic particles in streams: implications for deposition mechanisms in turbulent environments. *Limnology and Oceanography* 46:1415-1424.
- *Thomas, S.A., H.M. Valett, J.R. Webster, P.J. Mulholland, C.S. Fellows, C.N. Dahm, and C.G. Peterson. 2001. Nitrogen retention in headwater streams: the influence of groundwater ñ surface water interaction. In *Optimizing Nitrogen Management in Food and Energy Production and Environmental Protection: Proceedings of the 2nd International Nitrogen Conference on Science and Policy*. TheScientificWorld 1:623-631.
- *Valett, H.M., Crenshaw, C.L., and P.F. Wagner. 2002. Stream nutrient uptake, forest succession and biogeochemical theory. *Ecology* 83:2888-2901.
- Valett, H.M., Fisher, S.G., Grimm, N.B., and P. Camill. 1994. Vertical hydrologic exchange and ecological stability of a desert stream ecosystem. *Ecology* 75:548-560.
- Valett, H. M., Morrice, J.A., Dahm, C.N., and M. E. Campana. 1996. Parent lithology, groundwater-surface water exchange and nitrate retention in headwater streams. *Limnology and Oceanography* 41:333-345.
- Valett, H. M., Dahm, C.N., Campana, M.E., Morrice, J.A., Baker, M.A., and C. S. Fellows. 1997. Hydrologic influences on groundwater-surface water ecotones: heterogeneity in nutrient composition and retention. *Journal of the North American Benthological Society* 16:239-247.
- Vannote, R. L., Minshall, G.W., Cummins, K.W., Sedell, J.R., and C. E. Cushing. 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* 37:130-137.
- Vrobesky, D. A., and F. H. Chapelle. 1994. Temporal and spatial changes of terminal electron accepting processes in a petroleum hydrocarbon contaminated aquifer and the significance for contaminant biodegradation. *Water Resources Research* 30:1561-1570.
- Wallace, J.B., and A.C. Benke. 1984. Quantification of Wood Habitat in Subtropical Coastal Plain Streams. *Canadian Journal of Fisheries and Aquatic Sciences* 41:1643-1652.
- Wallace, J.B. and M.E. Gurtz. 1986. Response of *Baetis* mayflies (ephemeroptera) to catchment logging. *Amer. Midl. Nat.* 115:25-41.

- Ward, J. V., and J. A. Stanford. 1982. Thermal responses in the evolutionary ecology of aquatic insects. *Annual Review of Entomology* 27:97-117.
- Webster, J.R. 1975. Analysis of potassium and calcium dynamics in stream ecosystem on three southern Appalachian watersheds of contrasting vegetation. Ph.D. dissertation. University of Georgia, Athens.
- *Webster, J.R. 2000. An example to follow: intersite research among ecologists at LTER sites. *The Network Newsletter* 13, 8.
- Webster, J.R. and J.B. Waide. 1982. Effects of clearcutting on leaf breakdown in an appalachian mountain stream. *Freshwater Biol.* 12:331-344.
- Webster, J.R., Gurtz, M.E., Hains, J.J., Meyer, J.L., Swank, W.T., Waide, J.B., and J.B. Wallace. 1983. Stability of stream ecosystems. Pages 355-395 in J.R. Barnes and G.W. Minshall, editors. *Stream Ecology*. Plenum Press, NY.
- Webster, J. R. and E. F. Benfield. 1986. Vascular plant breakdown in freshwater ecosystems. *Annual Review of Ecology and Systematics* 17:567-594.
- Webster, J.R., Golladay, S.W., Benfield, E.F., Meyer, J.L., Swank W.T., and J.B. Wallace. 1992. Catchment disturbance and stream response: An overview of stream research at Coweeta Hydrologic laboratory. Pages 231-253 in P.J. Boon, P. Calow, and G.E. Petts, editors. *River Conservation and Management*. John Wiley & Sons Ltd, London.
- Webster, J. R., Meyer, J.L., Wallace, J.B., and E. F. Benfield. 1997. Organic matter dynamics in Hugh White Creek, Coweeta Hydrologic Laboratory, North Carolina, USA. *Journal of the North American Benthological Society* 16:4-77.
- Webster, J.R., Benfield, E.F., Ehrman, T.P., Schaeffer, M.A., Tank, J.L., Hutchens, J.J., and D.J. DiAngelo. 1999. What happens to allochthonous material that falls into streams: synthesis of new and published information from Coweeta. *Freshwater Biology* 41:687-705.
- Webster, J.R., Mulholland, P.J., Tank, J.L., Peterson, B.J., Dodds, W.R., Valett, H.M., Bowden, W.B., Dahm, C.N., Findlay, S., Gregory, S.V., Grimm, N.B., Hamilton, S.K., Johnson, S.L., Marti, E., McDowell, W.H., Merriam, J.L., Morrall, D.D., Meyer, J.L., Thomas, S.A., and W.M. Wollheim. 2003. Factors affecting ammonium uptake in streams an inter-biome perspective. *Freshwater Biology* 48:1329-1352.
- Wollheim, W. M., Peterson, B.J., Deegan, L.A., Hobbie, J.E., Hooker, B., Bowden, W.B., Edwardson, K.J., Arscott, D.B., Hershey, A.E., and J. Findlay. 2001. Influence of stream size on ammonium and suspended particulate nitrogen processing. *Limnology and Oceanography* 46:1-13.
- Wolman, M.G. 1954. A new method of sampling coarse river-bed. *Transactions of the American Geophysical Union* 35:951-956.
- Wood, E. D., Armstrong, A.J., and F. A. Richards. 1967. Determination of nitrate in seawater by cadmium-copper reduction to nitrite. *Journal of the Marine Biological Association of the United Kingdom* 47:23-31.
- Young, R., and A.D. Huryn. 1997. Longitudinal patterns of organic matter transport and turnover along a New Zealand grassland river. *Freshwater Biology* 38:93-107.
- Young, R.G., and A.D. Huryn. 1999. Effects of Land Use on Stream Metabolism and Organic Matter Turnover. *Ecological Applications* 9:1359-1376.

- Yount, J., and G. Niemi. 1990. Recovery of lotic communities and ecosystems from disturbance-A review of case studies. *Environmental Management* 14:547-569.
- Zhang, J.A., Ortner, P.B., Fisher, C.J., and L.D. Moore. 1997. Determination of ammonia in estuarine and coastal waters by gas segmented continuous flow colorimetric analysis. Method 349.0. In *Methods of the determination of chemical substances in marine and estuarine environmental matrices* ñ 2nd edition. EPA/600/R-97/072. National Exposure Research Laboratory, Cincinnati, OH.